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Fungicide Resistance

Since the appearance of the feature article on fungicide resistance by Delp in one of the first issues of PLANT DISEASE (6), fungal plant pathogens have taught us again and again that they are able to develop resistance against most modern single-site fungicides sooner or later if these are not used judiciously (5,16). For the farmer, attractive fungicides represent unrenewable resources that should be used in an intelligent way if their benefits are not to be lost to resistance too rapidly.

In some cases, eg, *Pseudoperonospora cubensis* and metalaxyl on plastic-house cucumbers, resistance development was very rapid (Fig. 1). In other cases, eg, *Botrytis cinerea* and dicarboximides on grapes, resistance problems developed more slowly. Even in situations where resistance was thought to be unlikely to occur for epidemiological or biochemical reasons, the target fungi eventually found a way to overcome the barriers put up against them by single-site fungicides. Multisite fungicides, on the other hand, continue to pose only minor resistance problems, even though resistance caused by decreased uptake or increased detoxification through metabolism is also possible against these compounds.

From these experiences a rather consistent pattern can be recognized by which fungicide resistance tends to appear. Single-site mode of action, exclusive use on highly susceptible cultivars, climatic conditions, and cultural practices favoring disease all appear to be key factors for resistance development. Unfortunately, describing conditions and measures that would prevent resistance against a given resistance-prone fungicide is more difficult. To improve the scientific base for decisions relating to resistance risk and antiresistance strategies, resistance research has become an integral part of research and development in several companies with promising fungicides in their hands. In addition, the possibility of cross-resistance between fungicides with the same mode of action has stimulated first attempts at coordination between the respective manufacturers in the area of resistance research. For instance, in 1981 industry established FRAC, the Fungicide Resistance Action Committee (1,7), with the goal of bringing producers of related fungicides together to help define research and use strategies that prolong the useful life of fungicides at risk. The major aim is to offer the farmer more durable solutions for disease control and better protection against crop losses that can arise through the unpredictable emergence of resistant forms of pathogens.

The need for increased research on fungicide resistance has also been recognized by researchers and advisers at universities and experimental stations. They, too, respond to the farmer's need for sounder advice on this relatively new topic that complicates disease control decisions. All parties involved have an interest in preserving the arsenal of fungicides, which in many cases has become frighteningly small.

We wish to highlight some of the recent lessons from practical experience and research that may help improve understanding of the development of resistance and help find ways to prevent it. Areas considered are factors leading to fungicide resistance, early assessment of resistance risks for new fungicides, development and implementation of strategies to delay or prevent resistance, monitoring for resistance in the field, and options for the future. Depending on the stage of development, market introduction, and relationship to existing products, these areas are pursued with changing emphasis.

Factors Leading to Resistance

When assessing the resistance risk and the development of countermeasures, the factors that influence the resistance risk in a given practical situation must be considered. It is useful to distinguish between the inherent risk factors relating to fungus biology and fungicide chemistry and the management risk factors relating to fungicide usage and, in a wider sense, to crop management (Table 1). The inherent factors serve to assess the basic resistance risk for a fungicide/fungus combination in a given area; they are largely fixed and beyond our control. The management factors are under the control of farmers, officials, and distributors of a fungicide, and it is from this group of risk factors that antiresistance strategies have to be derived, eg, use of resistant cultivars and cultural practices that reduce the disease pressure.

The theoretical relationship between the two groups of risk factors is shown in Figure 2. The higher the risks from inherent factors, the more stringently fungicide usage should be defined to limit the total risk to an acceptable level. Although this representation is an oversimplification, it shows that only where the inherent risk is very low (eg, multisite inhibitors) can the control over the management risk factors be relaxed and that, conversely, management risk factors have to be reduced substantially where inherent risk factors are present.

Basic Resistance Risks

The first and perhaps most difficult task in developing a new fungicide is estimating the inherent resistance risk against a given disease. This can be based on in vitro or in vivo laboratory studies or on early monitoring results and consideration of epidemiological parameters for a given disease situation. Prediction of resistance problems with these methods with any degree of precision has proved to be extremely difficult, and in several cases resistance has developed contrary to predictions. Multisite fungicides with broad spectra of activity, for instance, are generally considered low-risk compounds, but, still, Hg and Sn compounds have field resistance problems.

Resistance to benzimidazoles, which had occurred in many plant pathogens, was judged to be unlikely in *Pseudocercosporella herpotrichoides* on cereals because of monitoring results and epidemiological considerations (8). But now field resistance problems have

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A Continuing Challenge

Fig. 1. Plastic-house cucumbers treated with metalaxyl under heavy downy mildew pressure: (A) sensitive strains, (B) resistant strains.

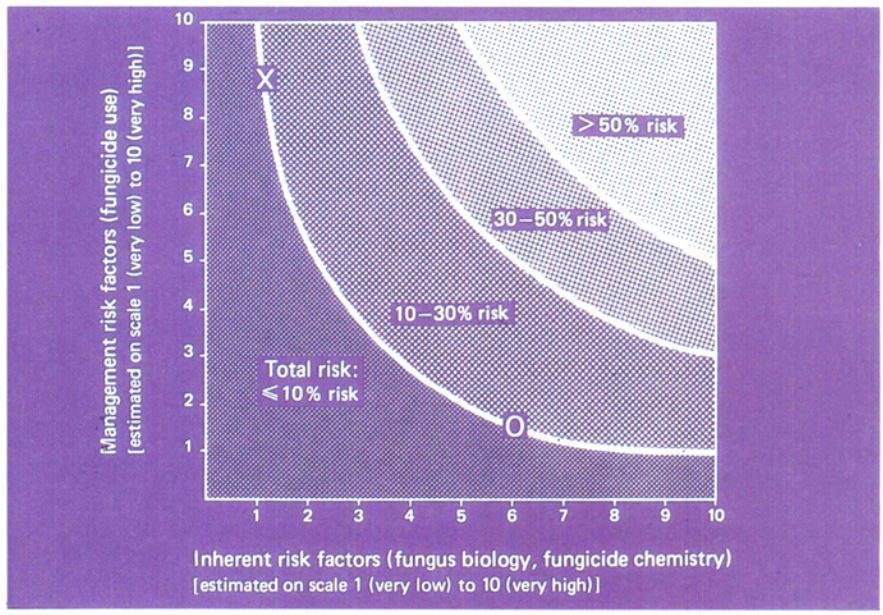

Fig. 2. Total resistance risk as derived from estimated inherent and management risk factors for resistance. X = multisite inhibitor with low inherent risk; exclusive use (high management risk factors) possible without running to much overall risk. O = single-site inhibitor with sizable inherent risk; severe use limitations necessary, eg, use mixture with multisite inhibitor for part of season.

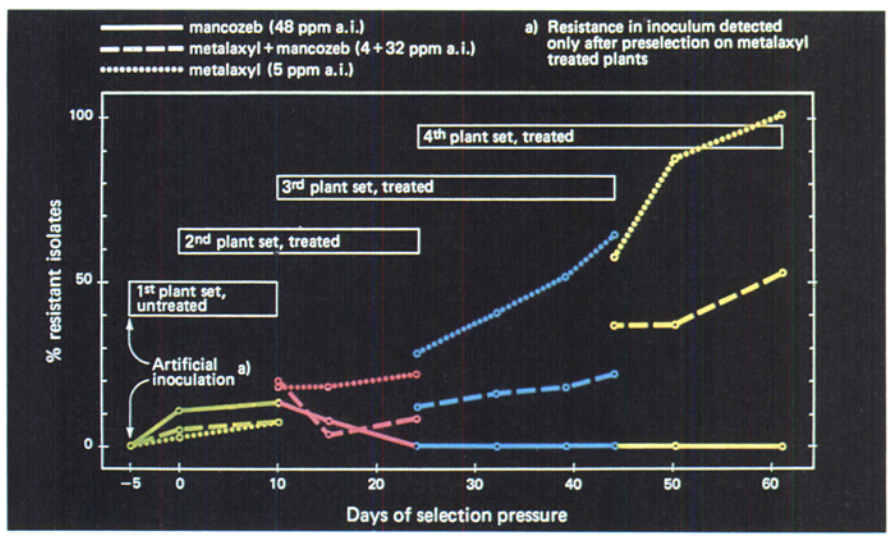

Fig. 3. Growth-room simulation of resistance buildup from a mixed population of metalaxyl-sensitive and metalaxyl-resistant sporangia (10,000:1) of *Phytophthora infestans* on potato plants (cv. Bintje) under different spray schedules.

Table 1. Factors influencing resistance risks

Inherent factors (fungus biology, fungicide chemistry)	Management factors (fungicide usage)
Biochemical mode of action	Duration of exposure (in generations)
Fitness of resistant strains	Presence of other controlling factors (effective mixture partners, host resistance)
Reproduction rate of target fungus	Size of target population, escape, overkill (protective vs. curative use)
Spore mobility	Proportion of crop area treated
Duration of high disease pressure (climate)	

occurred in England, France, and Germany.

With the dicarboximides, resistant mutants of *B. cinerea* were easily produced in vitro, and soon resistant strains were found in the field, without, however, being correlated with reduced disease control (2). The reason apparently was reduced fitness of the resistant strains. With prolonged use of dicarboximides under high infection pressure, however, clearly reduced performance was in some cases associated with the resistant strains (13). This indicated that even where resistant mutants and isolates show reduced fitness, resistance problems can occur if prolonged and exclusive use of a fungicide group under high disease pressure is permitted.

The sterol inhibitors are another important group of fungicides for which, despite laboratory indications for low risk, intensive use may lead to problems in practice. For one subgroup, the inhibitors of C-14 demethylation (DMI) in sterol biosynthesis, this possibility is indicated by the appearance of resistant strains of *Sphaerotheca fuliginea* leading to reduced efficacy of DMIs on cucurbits (12). In cereal powdery mildew, shifts in sensitivity to DMIs have also been reported, although in this case the correlation with poor control is not established (9; Ciba-Geigy, *unpublished*). A vital and still unresolved question for this group of fungicides is whether cross-resistance can occur between the inhibitors of C-14 demethylation and the morpholines, which interfere at a neighboring metabolic site in sterol biosynthesis.

With acylalanines, first studies indicated that in vitro resistance was not expressed in vivo, and in vivo selection experiments with various pathogens did not yield resistant strains (3,14). The use of mutagens in combination with in vitro selection of *Phytophthora* spp. led to the first demonstration that target fungi can develop in vivo resistance to acylalanines (3,4). The indications from these studies were nearly simultaneously confirmed by the appearance of resistance problems in cucumber downy mildew in Israel and later in other crops (15,16).

These examples show that the resistance risk of a new fungicide group can at best be determined in a very general way by laboratory studies and theoretical considerations. For each new group, the extrapolations made from laboratory studies to field conditions can be subject to a new set of uncertainties. In practice, stepwise selection for resistance and fitness, yet undiscovered rare mutants, or hidden epidemiological constraints may lead the development of resistance in unexpected directions. Assessment of the resistance risk therefore is also a matter of subjective judgment and thus is influenced by past experiences with resistance. Farmers, officials, and manufacturers who lose money or credibility because of cases of fungicide resistance are more cautious the next time around.

Antiresistance Strategies

General design. When the inherent resistance risk is assessed and the extent of its uncertainty realized, one faces the difficult question of countermeasures. Ideally, the extent of countermeasures necessary can be determined from the inherent risk factors and the quality of the countermeasures can be deduced from the management factors that may contribute to the overall resistance risk (Table 1, Fig. 2). On the basis of uncertain predictions, however, it is hard to justify the implementation of strategies that are often costly in short-term profits for the manufacturers and users of fungicides and are difficult to get compliance for in practice.

This uncertainty aside, for some management factors the rationale of how to lower the resistance risk is clear: reduce selection pressure by decreasing disease pressure through cultural practices and resistant cultivars and reduce selection time through shorter exposure to the fungicide at risk. How the size of the treated population, overkill, partial kill, and escape influence the appearance of resistance is less clear. Partial kill and escape, favored by mathematical models (6,10), seem risky elements with explosive diseases such as late blight of potatoes. A farmer would be ill-advised to let such diseases get a head start in the field. Experience with metalaxyl suggests that treatments after substantial levels of disease are established should be avoided, since it was usually under such conditions that resistance first emerged (15). Also, in mixtures with contact fungicides, curative products act as if used alone on established infections.

Mixtures vs. alternations. There is general agreement that where the inherent resistance risk factors are high, a fungicide should not be used exclusively. In some high-risk situations, as in glasshouses or plastic houses, it may even be advisable not to use such fungicides at all. Apart from this most stringent use limitation, the two basic strategies for avoiding the exclusive use of a resistance-prone fungicide are the use of fungicide mixtures and the alternation of fungicides with differing modes of action (Table 2). For a chemical company, a more basic decision may be whether to market the single product or to sell prepack mixtures exclusively. Of course, where the basic mixture is still judged too risky to be used season long, it can be alternated with a low-risk chemical (Table 2, line 2).

Several points speak in favor of using prepack mixtures wherever an effective mixing partner is available (Table 3). Enforceability, especially, is very crucial, and the use of prepack mixtures clearly gives greater assurance of user compliance. Users, concerned less with antiresistance strategies than with other priorities, tend to abuse popular products. The potential for abuse (in the sense of favoring resistance) is clearly higher if the at-risk product is available singly. Unfortunately, some registration agencies do not accept the prevention of fungicide resistance as sufficient grounds for registering a mixture. They require, in addition to resistance considerations, that a mixture have other performance advantages.

For unstable types of resistance, as with *Botrytis* and the dicarboximides, alternation should also be included in the strategy, since this allows the population to shift back toward normal sensitivity. The alternation can be done on a spray-by-spray basis or blockwise (Table 2, lines 2–5).

Validation. But just how sure are we that fungicide mixtures or alternations do delay resistance? The concept is largely based on rather crude theoretical models and circumstantial evidence from practical experience (6,10). For a company, this is rather unsatisfactory as a basis for costly decisions. Therefore, we have tried to validate the mixture concept on the basis of growth chamber experiments (16). In each of three growth rooms, epidemics of *Phytophthora infestans* were simulated on four successive sets of 152 potato plants. The plant sets were treated with metalaxyl,

metalaxyl + mancozeb, or mancozeb before introduction into the respective growth chambers. The initial *Phytophthora* population contained 0.01% metalaxyl-resistant sporangia. Estimation of the disease development showed comparable epidemics among the treatments. Resistance was monitored throughout the experiment with a potato leaf disk assay.

A considerable delay in the buildup of resistance could be shown for the fungicide mixture (Fig. 3). Whereas the pure metalaxyl schedule resulted in 100% of the leaf disks showing resistance, the metalaxyl + mancozeb mixture schedule had reached only 54% by the end of the experiment. Loss of resistance in the mancozeb treatment may indicate a competitive disadvantage of the resistant isolate used in the experiment. Results were similar in a repeat experiment.

These data represent a first experimental support for the mathematical models published (6,10) that indicate mixtures delay the buildup of resistance. These models, however, have severe limitations. For instance, they do not take into account possible epidemiological stress during overwintering that could eliminate rare resistant mutants. Blue mold of tobacco, for example, tends to start from very few foci each year in temperate zones. Further evidence for the effect of different fungicide schedules on resistance buildup is urgently needed. The uncertainty about this effect has led to some wild and often contradictory speculations and has often made it difficult for companies and registration and/or advisory agencies to reach agreements on use strategies.

Implementation. The implementation of antiresistance strategies has proved to be a most critical point in many cases. Growers seem to have unlimited imagination in adapting the use of a new attractive fungicide to their particular problems and likings. Some of their innovations can lead to fungicide abuse. They have been known to introduce more susceptible cultivars, creating excessive disease pressure and thus a higher resistance risk. In other cases, prepack mixtures containing a systemic and a residual fungicide were applied to the soil against foliar pathogens, making the nonsystemic mixing partner ineffective and useless for suppressing resistant strains.

The cooperation between producers of fungicides with cross-resistance is another weak link in the chain of elements constituting an antiresistance strategy. It is virtually useless for one producer to exercise caution (in the sense of reducing the resistance risk) with his fungicide when another with a related fungicide does not. The reluctance of registration agencies to consider prepack mixtures is another obstacle to be faced in some countries.

Thus, compliance with antiresistance strategies has to be a key element in their evaluation. Independent of the strategy selected, good coordination and cooperation with the official extension services are essential to successful implementation. The farmer is to be convinced to use a fungicide cautiously in the sense of preventing resistance only if all those who have a role in informing him speak the same language. The common interest, to prolong the useful life of a valuable fungicide and to prevent crop losses due to fungicide resistance, should facilitate cooperation among manufacturers, registration agencies, extension services, academia, and farmers in coping with the resistance threat. Promising steps in this direction were the 1980 and 1981 postgraduate courses in Wageningen, Netherlands, that dealt with all aspects of fungicide resistance and brought together researchers from industry with independent researchers and advisers (5).

Monitoring for Resistance

Most efforts of agrochemical companies in the area of resistance research have been aimed at resistance monitoring in the field. Monitoring can be useful 1) during the development and introduction of a new fungicide (assessing resistance risk, establishing baseline sensitivity data), 2) in analyzing product failures and resistance rumors after market introduction, 3) in following up resistance under practical conditions (checking success of antiresistance strategies), and 4) in determining stability of resistance (from year to year or after withdrawal of the fungicide).

Choice of sensitivity test method. The technique used for sensitivity testing depends on the purpose of the monitoring and the fungus/fungicide combination. Simple, fast techniques, such as spore germination tests on agar, are ideal in many cases. Large numbers of spores (eg, *Venturia inaequalis* or *Monilinia* spp. against benomyl) can be analyzed for their sensitivity within a few days, allowing detection of low resistance levels in mainly sensitive populations. We are not always free to select these easy methods, however. Many fungi do not readily sporulate; for them, radial growth of mycelial mass transfers on fungicide-amended agar may be used to determine sensitivity levels (Fig. 4A). Some modern fungicides such as the acylalanines do not inhibit spore germination at all; in addition, in vitro inhibition of mycelial growth shows little correlation to their in vivo activity (14). In these cases, in vivo methods on leaf disks (Fig. 4B), detached leaves, or entire plants (Fig. 4C) have to be used for sensitivity testing. The major setbacks of these latter methods in comparison with a spore germination test are the low number of individuals that can be tested and that samples may react sensitive or resistant while in fact they are mixtures at various ratios of both. With in vivo methods we cannot be sure to detect resistance levels below 1% in a given population.

Interpretation of data. Thus, for correct interpretation of monitoring results, the resistance detection levels of the sensitivity tests used must be known. In addition, baseline sensitivity data of wild untreated populations are needed to detect shifts in the sensitivity of treated populations. To compare results of different methods and locations, known sensitive and, if available, resistant reference isolates must be included in every test as standard procedure.

Resistance rumors and product failures. A special and important case of sensitivity testing is involved in the analysis of product failures. Here, reliable

Table 2. Use concepts to cope with resistance[a]

With prepack mixtures										
(A+B)	—	(A+B)	—	(A+B)	—	(A+B)	—	(A+B)	—	(A+B)
(A+B)	—	B	—	(A+B)	—	B	—	(A+B)	—	B
With single products										
A	—	B	—	A	—	B	—	A	—	B
A	—	A	—	A	—	B	—	B	—	B
B	—	B	—	A	—	B	—	B	—	B

[a] A = high resistance-risk fungicide; B = low resistance-risk fungicide.

Table 3. Comparative merits of the two basic use strategies[a]

Merit	Mixtures vs. alternations
Reduction of resistance selection pressure	≅
Overall disease control (including secondary pathogens)	>
Reduction of crop loss potential in event of resistance	>
User compliance with antiresistance strategies	≫

[a] For decisions, strategies by competition are critical.

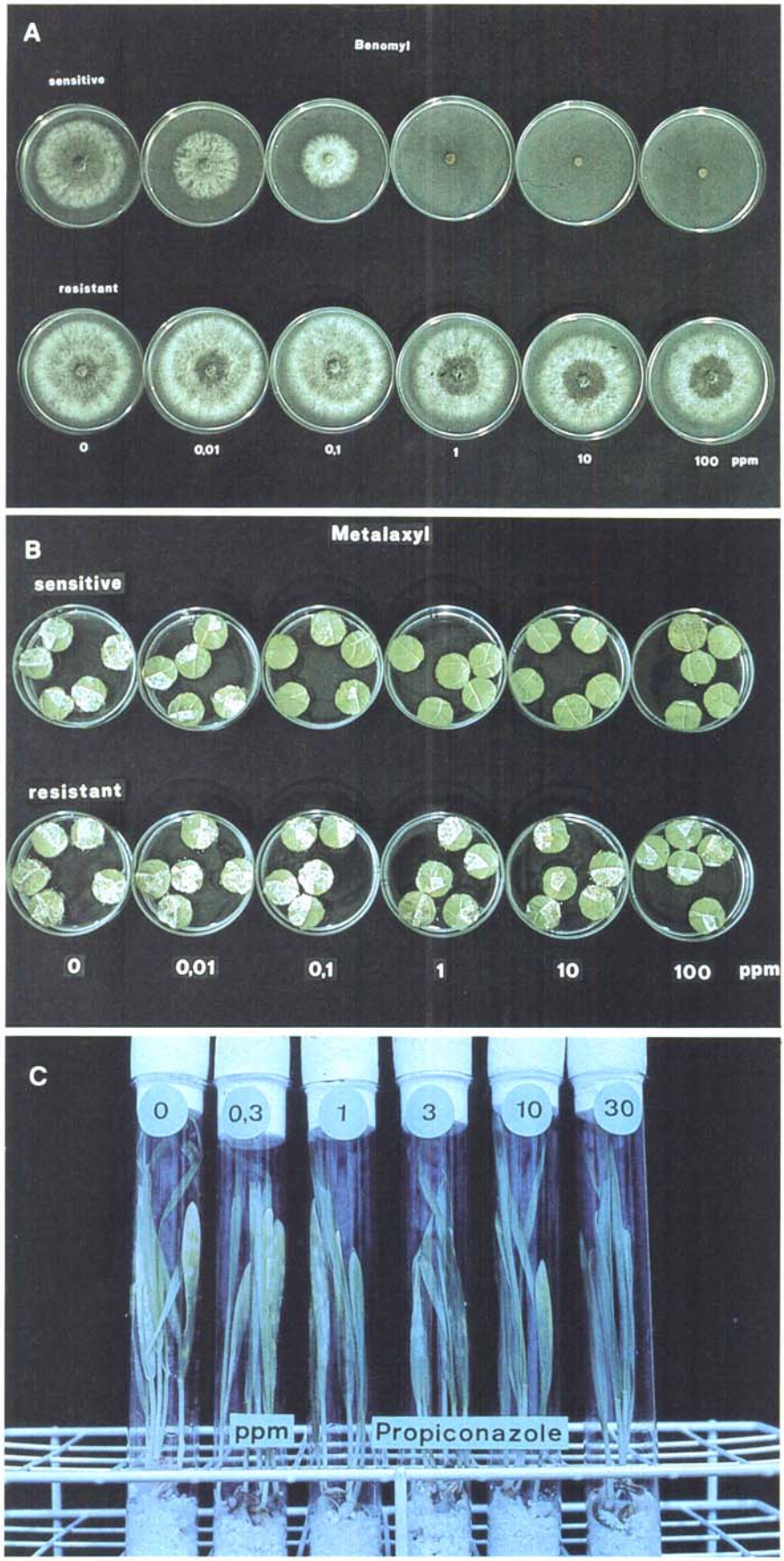

Fig. 4. Sensitivity test methods: (A) Radial growth of a sensitive and a resistant strain of *Botrytis cinerea* on benomyl-amended agar plates. (B) Grape-leaf disks floating on metalaxyl-containing water and inoculated with a sensitive and a resistant strain of *Plasmopara viticola*. (C) Tube test used for testing *Erysiphe graminis* f. sp. *hordei* on barley (cv. Golden Promise) against propiconazole added to the growth medium 7 days after seeding; a strain in the normal sensitivity range is shown.

sensitivity test methods and baseline sensitivity data are particularly useful. Fast availability of the results for a suspicious fungus sample is often crucial to making the right decision in time. The decision can range from withdrawing the product from the area if results show a high frequency of resistance to correcting use recommendations if results do not show resistance and the cause of product failure lies elsewhere.

A related problem arises when isolated reports of resistance are published without sufficient baseline sensitivity data or without critical evaluation of the test method. For example, in vitro data are not sufficient for acylalanines and *Phytophthora* spp. because of a low correlation between in vitro and in vivo resistance behavior in these disease control systems. Similarly, spore germination data are not very meaningful as indications for resistance to fungicides that primarily inhibit mycelial growth and are much less active on spore germination, eg, some DMI compounds. Despite all its inadequacies, field monitoring can be a valuable tool for assessing aspects of the development of resistance to fungicides. Monitoring does not prevent resistance, however, and because detection is often possible only in late phases of the overall selection process and close to or after product failures, the major efforts must be directed at strategies to prevent or delay the buildup of resistance and at implementing these strategies as early as possible.

Options for the Future

Once a fungicide group has lost effectiveness in the field, the level of resistance may remain so high that even increased rates are ineffective and it must be withdrawn from use in that area.

New modes of action. The simplest solution would appear to be a search for new types of fungicides when existing ones become ineffective. However, the development of fungicides with novel mechanisms of action has become increasingly difficult and costly and does not seem rapid enough to keep up with the pace of emergence of resistance to modern fungicides. In fact, there appears to be a tendency in the chemical industry to concentrate research efforts for new molecules on the few most active fungicide groups introduced during the last decade. This underlines the importance of use strategies that prevent or delay the buildup of resistance against these few fungicidal mechanisms.

Synergists, negative cross-resistance. Synergists, as they are known for some instances of insecticide resistance, do not commonly exist for fungicides. This may be due to the differing biochemical mechanisms of resistance. Whereas the severe cases of fungicide resistance appear, for the most part, to be based on a target-site resistance, most instances of

insecticide resistance are based on increased metabolic detoxification. A notable exception is resistance in *Pyricularia oryzae* against organophosphorus fungicides, which is based on increased metabolism and can be reversed by appropriate synergists (11). The search for fungicides with negatively correlated cross-resistance, although interesting from a theoretical viewpoint, seems to hold little promise for practice because such compounds generally do not work against all resistant mutants.

Integrated crop and disease management. It seems evident that an increased emphasis on integrated control programs that exploit genetic, biological, and cultural methods optimally in connection with fungicide programs offers good opportunities to reduce the selection pressure for fungicide resistance. This is especially true for crops where disease control relies heavily on fungicides and, consequently, the resistance risk is particularly high. Here the idea of considering fungicides as valuable unrenewable resources, just as we do resistant cultivars, becomes particularly appealing. By combining the different resources in an intelligent way we will be able to preserve both cultivars and fungicides for a longer time to come.

Conclusions

Present status. 1) Resistance monitoring has increased as a consequence of increased fungicide resistance problems. 2) Antiresistance strategies have been implemented, often only after resistance has become a problem and rarely as a preventive measure. 3) Predictions of resistance risk from laboratory studies have not always been accurate enough to be a reliable basis for the determination of use strategies. 4) In some countries, registration agencies do not consider the resistance argument as sufficient grounds for registering an antiresistance mixture.

Future needs. These are: 1) increased commitment to designing and implementing antiresistance strategies early enough; 2) closer cooperation within industry and with registration and advisory services; 3) basic research on genetics and population dynamics of resistance for sounder strategy decisions; 4) improved assessment of the inherent resistance risk, including judicious use of mutagens; 5) increased diversity of fungicides; 6) improved approaches to plant disease control (biological, cultural, genetic, and chemical); and 7) optimal integration of all these to provide effective plant health without a one-sided reliance on fungicides (which spells resistance risk) in intensive agriculture.

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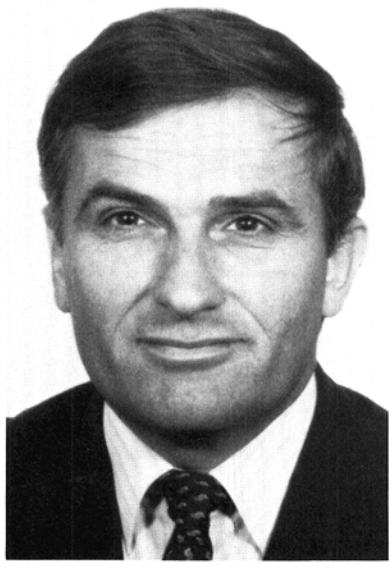

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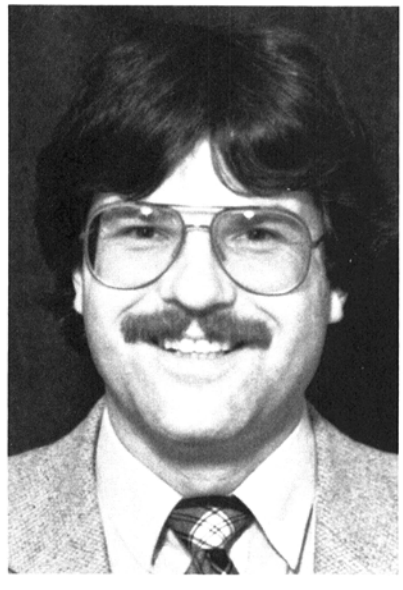

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