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WEST PALAEARCTIC REGIONAL SECTION

Integrated control of pome fruit diseases, Vol. II

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Scientific Editors: C. Gessler, D. J. Butt
Technical Editor: B. Koller

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Introduction

At the VIIth symposium of the IOBC (WPRS)[1] Working Group "Integrated Plant Protection in Orchards", held in 1985 (1), a meeting was proposed to discuss orchard diseases and their control. The need for such a meeting grew from the realisation that to attain the goal of fully integrated crop protection the Working Group would have to address pathogens as well as pests.

The meeting was held in 1987 at Lana, South Tyrol, Italy, where orchard pathologists met with a few entomologists to discuss the integrated control of pome fruit fungal diseases (2). This workshop provided the first opportunity for orchard pathologists from western Europe to meet as a group. The participants at Lana recommended that the parent Working Group should form a Sub-Group "Orchard Diseases" and stated the objectives of the proposed Sub-Group (2).

The present book contains papers presented at the 2nd workshop on integrated control of pome fruit diseases, held when the newly-constituted Sub-Group met at Brissago, Ticino, Switzerland, in 1988. Following the precedent set at Lana, this residential meeting was located in a region of outstanding natural beauty. The agenda was again limited to apple and pear but broadened to include bacterial pathogens.

The workshop opened with a period of silence in respectful memory of the late Dr. H. Steiner, the "founding father" of the Sub-Group. The programme concentrated on techniques for the better timing of interventions by growers, and on the production and testing of cultivars with stable resistance to pathogens. Papers were also included on side effects of fungicides and on the integration of pest and pathogen control. As at Lana, a session was allocated to storage diseases. Throughout, emphasis was given to techniques, problems and principles. By the end of the penultimate working session the complexity of the orchard system had been exposed, the participants were more aware of the interactions and reactions in orchard crop protection and we were all more conscious of the dangers of new problems replacing solved ones. The conclusions and recommendations of the 2nd workshop were considered in the last session and are included in this book.

Participants were encouraged to present personal views and judgements, as well as scientific findings: this subjective element is evident in this book, for which we make no apology in an attempt to present the 'state of the art'. Objectives of the Sub-Group include facilitating information exchange, fostering collaborative studies and standardising methods as necessary, all in order to reduce the usage of fungicides in orchards: the Brissago workshop built upon the foundations laid at Lana and successfully attained these objective.

1 International Organisation for Biological and Integrated Control of Noxious Animals and Plants (West Palaearctic Regional Section)

On the final day, a memorable excursion to the fascinating Maggia Valley was followed by a visit to the research station Cadenazzo, where apples of numerous cultivars were displayed for tasting.

We are pleased to acknowledge financial support from the IOBC (WPRS). Also, we are grateful to the following local organisations who generously contributed to the success of this meeting: Federazione Orto-frutticola Ticinese (F.O.F.T.); Associazione caricatori, Cadenazzo; Associazione Frutticoltori Professionisti Ticinesi; Associazione Cantonale Tecnici Agricoli (A.C.T.A.); Banca Popolare Svizzera; Migros Schweiz, Ciba-Geigy.

The locally-raised funds enabled us to invite to Brissago three colleagues from the U.S.A., to publish this book, and to enjoy excellent social occasions during our meeting. Our sincere thanks.

We thank B. Koller for producing this book, and also U. Rosenberger, P. Blaise, U. Merz, C. Valsangiacomo, P. Gessler and A. Mathis for assistance in organising and running the meeting and compiling this record of the proceedings.

Sound and vision recording of the workshop are available from U. Merz, Institut für Pflanzenwissenschaften/Gruppe Pathologie, ETH, Zürich,

C. Gessler, M. Jermini	Local Organiser, Brissago Workshop
D. J. Butt	Scientific Co-ordinator, Brissago Workshop
E. Dickler	Convenor, Working Group "Integrated Plant Protection In Orchards"

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Disease warning systems

Chairperson: W. E. MacHardy

Research Needs for Improving Apple Scab Warning Systems

W. E. MacHardy

Department of Botany and Plant Pathology, University of New Hampshire, Durham 03824, USA

Abstract

There is one main distinction between conventional spray schedules and spray schedules generated by warning systems: warning systems schedule fungicides based on predictions of scab development whereas conventional programs schedule fungicides based on tree growth stage, a specified time interval, or other criteria that have little or no regard for how favorable or unfavorable weather conditions are for scab development. When conditions are favorable for scab development, particularly during the primary scab season, the warning system and conventional spray schedules may be very similar. It is during seasons with extended intervals unfavorable for scab development, particularly during the spring, that notable differences in the spray schedules occur, with warning systems generating fewer sprays.

A predictive system will have limited influence on fungicide dose if it is coupled to a warning system with limited flexibility for scheduling fungicides once scab is predicted. Thus, a "rigid" warning system would reduce the fungicide dose only during extended dry intervals when scab was not predicted, whereas a "flexible" warning system may not recommend a fungicide application even though infection had been predicted and susceptible tissue is not protected. The potential ascospore dose (PAD) study in New Hampshire and related studies (1, 2) have demonstrated that inoculum levels do exist in commercial orchards that are below a density that require a fungicide treatment for early-season infection periods. Continued research is needed to explore the feasibility of action thresholds that identify when a scab fungicide schedule should be initiated and when subsequent sprays are needed.

A major reason warning systems do not provide greater flexibility in scheduling sprays is that the amount of scab permissible at each growth stages in not known. Consequently, the decision is often made that no scab should be allowed, i.e. **if apple scab has been predicted and susceptible tissue is not adequately protected, a fungicide should be applied.** Also it is generally assumed that the closer to bud burst the infection period occurs, the greater the need to protect the susceptible tissue. This is generally true not only with susceptible cultivars but also with cultivars that are more resistant to scab. Thus, the reasoning that provides the basis for applying sprays, with either the warning system or conventional approach, has changed very little since the 1930's and 1940's when the conventional schedules used today were being defined. In 1988, however, orchards are very different horticulturally, and disease control has improved considerably. The most

significant effect of these changes with respect to apple scab is the *sizable reduction in primary inoculum density* due to (i) smaller tree size and improved spray equipment that have combined to provide better coverage of susceptible tissue, (ii) more effective fungicides, and (iii) increased number and improved timing of fungicide sprays.

Fifty years ago, well-managed orchards had inoculum levels that demanded numerous applications of fungicide from green tip through terminal bud set (5). It is generally assumed that this demand exists in well-managed orchards today, but recent studies (1, 2, 4) have shown that this assumption is not always warranted. Today, the primary inoculum is often below a level that requires fungicide treatment of susceptible tissue beginning at green tip. Furthermore, the inoculum level may even allow us to disregard treating unprotected susceptible tissue with fungicide even though infection has been predicted. Thus, it appears that our current warning systems have incorporated only one of several strategies to improve our efficiency in scheduling fungicides. The extent to which warning systems will take advantage of low inoculum levels will depend upon research. Research programs must be initiated with an objective to couple assessments of ascosporic inoculum density (PAD or other indicator of inoculum density) with strategies to reduce the fungicide dose. The strategy may be simply to manipulate the fungicide schedule according to the level of ascosporic inoculum. A second approach is to develop strategies that incorporate sanitation practices to lower the inoculum density and complement the fungicide dose. The latter approach is more complicated and may involve more labour and equipment, but it also has a greater potential to lower seasonal fungicide doses. To be accepted by growers and advisory personnel, the research must provide convincing evidence that the new strategies can be employed *without increased risk* of an unacceptable build-up of scabbed fruit. It is critical that the research be conducted in commercial orchards or in research orchards with similar low levels of inoculum rather than in high inoculum research orchards with inoculum levels representative of the 1930's and 1940's. Since orchards and the disease situation have changed drastically in the approximately 50 years since the conventional spray schedules were developed, researchers should also challenge the evidence that underlies the reasoning that defines current fungicide schedules. Empirical evidence and unsubstantiated inferences derived from research should be supported by experimental data.

In 1936, Keitt (5) noted that the most important problem confronting plant pathologists in their search for improving methods of disease control was...."the need for a much sounder foundation of knowledge of the detailed phenomena and basic principles of disease development and control than that on which most of our current programs rest. Only in the light of such knowledge can we either clearly define our control problems or reliably evaluate the results of the measures used." A conclusion he drew from published studies was that "the ascosporic inoculum and *its quantitative level* are of primary importance in relation to the epidemiology and control of apple scab" (italics added for emphasis). It is an unsettling commentary on apple scab research programs that fifty-two years after Keitt made these statements we can arrive at identical sentiments regarding research needs and note that we have only recently begun to quantify the ascosporic inoculum and recognize that without this value we may misinterpret the data we collect or not fully appreciate and understand the significance of the data in relation to epidemiology or control. Research has greatly enhanced our knowledge of apple scab epidemiology and control in the past fifty years, but it clearly has not adequately addressed Keitt's concerns and conclusions. Can we realistically expect to significantly improve our current scab control programs without a substantial research effort that addresses his concerns and conclusions? Considering that our control programs have remained basically unchanged since the 1940's (they still rely entirely on the repeated application of fungicides), the answer is no. It appears that apple scab control programs have reached a plateau, and only with new, innovative research thrusts can we expect significant advances toward our goal of an integrated, environmentally- safe, scab management program. The need to validate a modified Mills' table is also proposed.

Key words: *Venturia inaequalis*, prediction, Mills' curves, forecasting, inoculum, infection criteria, fungicide schedules, control strategies.

Introduction

An apple scab warning system consists of (i) instruments to monitor weather variables, (ii) criteria to determine if environmental conditions necessary for infection have been satisfied, (iii) a strategy for scheduling fungicides, and (iv) a delivery system to inform the grower of infection conditions and control recommendations. Most warning systems schedule fungicide sprays according to predictions of scab development based on the infection criteria of Mills (9, 10) that identify the approximate number of hours of leaf wetting required for light infection in an orchard containing an abundance of inoculum. This strategy provides an alternative to the conventional strategy that schedules protectant fungicides on a calendar basis or according to tree phenological stages. An important feature of warning systems is their potential to eliminate unnecessary sprays during intervals unfavourable for infection.

The development of electronic, computer-programmed weather monitoring instruments, of criteria that allow greater flexibility for scheduling fungicide sprays based on predictions of infection, and of more effective delivery systems have increased efficiency in scheduling fungicides, and scab warning systems often recommend fewer fungicide applications than the conventional schedules. However, efficiency in scheduling fungicides with current warning systems has nearly reached its limit. Continued improvements in weather monitoring instruments, predictive criteria and delivery systems will help to "fine tune" current scab warning systems, but no significant reduction in current fungicide dosages is expected in orchards planted with susceptible cultivars unless new strategies and approaches are employed. Several areas of research that appear likely to either refine our current warning systems or introduce new strategies and approaches are discussed below.

The need to validate proposed revision of Mills' "infection curve" and criteria for predicting primary infection periods.

Mills' criteria for predicting infection periods have sometimes failed, and several warning systems have modified these criteria. A recent critical review of studies that investigated the relationship between temperature, length of leaf wetness and infection concluded that infection by ascospores requires three hours less than Mills reported. The discrepancy was explained by the daily periodicity of ascospore discharge in which nearly all ascospores are released during the daytime. A proposed revision of Mills' system computes primary infection periods from 0700 h when rain begins at night and utilizes a new curve (Mills/a-3) for predicting infection by ascospores. The proposed revision and its potential for improving our efficiency in scheduling fungicide applications has been published (6, 7).

Because scab warning systems are based on Mills' "infection curve" and there is considerable evidence that the curve is inaccurate, it is critical that a study be conducted to validate the proposed "Mills/a-3" curve (6, 7). Scab is the major apple disease world-wide because the predominant cultivars in each country are highly susceptible to. It is hypothesized that the "Mills/a-3" curve will predict the minimum hours for infection in orchards planted with these cultivars. To prove this hypothesis, it must be shown with each cultivar and in the various regions where apple scab occurs that the development of scab lesions is associated only with such infection periods.

A preliminary seedling study designed to validate the "Mills/a-3" curve was conducted in New Hampshire, U.S.A., in 1988. During each rainy period in the early spring, sets of cv. McIntosh seedlings were placed in a high-inoculum orchard. When the rain began at night (between 1800 and 0700 h), the seedlings were placed in the orchard at 0700 h. When the rain began during the day (between 0700 and 1600 h) the seedlings were placed in the orchard within 30 minutes after the rain began. The seedlings remained in the orchard the minimum hours for infection identified by the "Mills/a-3" curve (Fig. 1). The seedlings were then transferred to a greenhouse nearby, dried quickly and observed weekly for scab lesions. In four instances, the "Mills/a-3" curve correctly predicted that infection occurred in three hours less the minimum hours for infection indicated by Mills' curve. Additional data are needed to validate the curve at other tem-

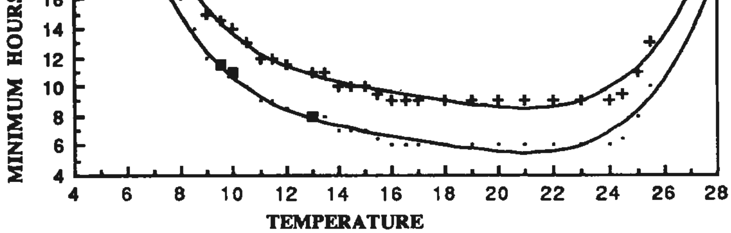

Fig. 1. The relationship between the hours of leaf wetting, temperature, and leaf infection by ascospores of *Venturia inaequalis*. The "Mills/a" curve was derived from Mills (9, 10). The "Mills/a-3" curve lowers the "Mills/a" curve 3 hrs to compensate for the daily periodicity of ascospore discharge (7, 8). Seedling/88 (solid blocks) refers to four instances in 1988 when foliar scab lesions occurred on potted McIntosh seedlings placed in an orchard during a rainy period and kept wet for the number of hours indicated.

peratures. It is also necessary to validate the curve with cultivars that are important in other regions and with the populations of *V. inaequalis* that exist in those regions. An international research project that includes fruit research stations in Belgium, France, India, Italy, the Netherlands, Norway, Switzerland, West Germany and the United States has been established with the initial objective of validating the "Mills/a-3" curve. Cultivars McIntosh, Golden Delicious and Jonagold are included in the study. If the "Mills/a-3" curve is validated a new objective will be to validate the "revised Mills warning system" that is based on the "Mills/a-3" curve.

The need to quantify the prediction of scab development.

Until now, the major contribution of research has been to establish criteria that predict infection **qualitatively,** i.e. predict that infection has, or has not, occurred. Current warning systems should not be expected to dramatically reduce fungicide recommendations without research that will establish criteria that predict infection **quantitatively** i.e. predict the amount of scab expected from an infection period. Further research would then be needed to relate the quantitative prediction of scab to a forecast of scab increase and to develop criteria that identify when an infection period warrants a fungicide treatment.

Mills (10) published curves that identified three risk levels of infection (light, moderate and heavy). Apparently, the "light" curve identified the minimum hours for infection and the "moderate" and "heavy" curves identified additional hours the leaves must remain wet for noticeable increases in scab incidence. The "moderate" and "heavy" curves are usually not incorporated into warning systems because the amount of scab associated with each level of infection was not reported. Also, variables other than the length of the wetting period significantly influence the amount of infection: the amount of inoculum available, the level of cultivar resistance and the tree growth stage. Research is needed to develop a system for assessing risk that integrates an infection curve with values for these variables, as suggested by MacHardy and Jeger (8), Oberhofer (11), and Olivier (12).

The most important of these variables is the amount of ascosporic primary inoculum, i.e. the potential ascospore dose (PAD), defined as the total seasonal production of ascospores per m^2 orchard floor (3). The PAD can vary greatly from orchard to orchard. The PAD in 18 commercial orchards in New Hampshire, for example, varied from 15 to 1,505,027 ascospores/m^2 orchard floor (3). Another study (unpublished) showed that the PAD within an orchard may be fairly consistent or vary greatly from year-to-year: during a 3-year period, the PAD in one orchard varied only slightly (510, 212, and 229), whereas the PAD in another orchard varied approximately 100-fold (3,142, 412, and 38). The PAD in well-managed orchards was usually less than 1,000.

With respect to warning systems, a calculation of PAD may help explain the results of studies that investigate integrated control measures. Consider a study to investigate the potential of sanitation measures to reduce the primary inoculum and, consequently, to reduce the fungicide dose. If a reduction in fungicide dose resulted in an unacceptable increase of scab, would that mean the sanitation treatment has no utility in scab management? The answer could be "yes" if the study had been conducted in a well-managed commercial orchard with a low PAD value, i.e. <2000. However, if the study had been conducted in a high-inoculum research orchard with a PAD >50,000, the question could not be answered with certainty. The reason is that such a high PAD (50- to 100- fold greater than in most modern commercial orchards) may have exceeded a level that would allow the sanitation practice to be coupled with a reduced fungicide dose. Thus, the sanitation treatment could have reduced the PAD by 90%, yet the resultant

Table 1. Potential Ascospore dose study; three-year summary, 1986-1988.

		Delayed first spray*			Grower's schedule**		
orchard/ year	first spray	unprotected infection periods	%scab leaves	%scab fruit	%scab leaves	%scab fruit	PAD
B-1986	Fr. Set	4	0.0	0.8	0.0	0.6	75
B-1987	Pink	3	0.0	0.7	0.0	1.3	410
B-1988	PF	3	0.0	0.7	0.0	0.0	10
G-1986	PF	2	0.0	0.7	0.3	0.6	20
G-1987	FS	3	2.4	0.0	0.1	0.0	119
G-1988	PF	4	0.5	0.4	0.1	0.2	19
C-1987	1/2"Fr.	5	0.0	0.0	0.0	0.2	300
C-1988	Fr.Set	4	-	0.2	-	0.0	12
M-1986	Pink	2	3.7	0.9	1.3	0.8	545
M-1987	TC	1	0.4	10.7	0.0	0.0	19700
M-1988	Pink	3	0.5	0.4	0.3	0.2	91

*The greatest delay in applying the 1st fungicide spray that still allowed an acceptable incidence of fruit scab (<1.0%) and control comparable to the grower's schedule.

**The conventional schedule recommends that the 1st spray for apple scab be applied at green tip. However, growers in this study applied their 1st spray at the 1/2 inch and tight cluster tree growth stage.

PAD may still have remained above the action threshold for safely reducing the fungicide dose. Knowledge of PAD values, or some other measure of primary inoculum, would be necessary to determine if a savinge in fungicide is possible with this strategy. Unfortunately, nearly all studies that have investigated the effectiveness of sanitation practices to reduce the primary inoculum and/or the amount of scab have been conducted in orchards with inoculum levels that were high and not typical of commercial orchards with adequate control of scab.

The need to include PAD values in scab control studies is clearly shown in a recent 3-year study (unpublished) conducted in four well-managed commercial orchards in New Hampshire (Table 1). The main cultivar was McIntosh (highly susceptible to scab), and environmental conditions each year were very favourable for scab. In nine instances, the season's first fungicide application was de-

Table 2. Comparison of apple orchard characteristics and apple disease control: 1938 and 1988.

Considerations	1938	1988
1. Orchard characteristics	Large "standard" trees; wide spacing; dense foliage	Smaller trees; semi-dwarfing rootstock; denser planting; more open canopy
2. Spray equipment/spraying	Poor coverage; time-consuming; dilute spray [3742 l/ha]	Improved coverage; shorter spraying time; concentrate spray [94-468l/ha]
3. Fungicides	Protectants; often phytotoxic	Protectants, curatives, eradicants; limited or no phytotoxicity
4. Fungicide efficacy	Mediocre	Excellent
5. Spray schedule	Tight cluster through primary scab season.	Green tip through terminal bud set
6. Control of fruit scab	Poor: ~10% scabbed fruit	Excellent: <1% scabbed fruit
7. Ascospore density [PAD][a]	50,000 to 100,000[b]	10-500[c]

[a] Potential ascospore dose [PAD]: the estimated seasonal production of ascospores/m^2 orchard floor calculated according to Gadoury and MacHardy (3).

[b] Estimated general range of PAD for well-managed commercial orchards in 1938 based on published reports of disease incidence

[c] The range of PAD estimates for most well-managed commercial orchards in New Hampshire, U.S.A., assessed for PAD in 1985-1988.

layed until the pink bud stage or later *without loss of acceptable control of fruit scab* , i.e. <1% scabbed fruit at harvest, even though two to five infection periods had been left unprotected with fungicide prior to the first fungicide application. These results indicated that fungicide sprays applied earlier than pink were unnecessary. However, in another instance nearly 11% fruit scab occurred when the first fungicide was applied at tight cluster and only one infection period had been left unprotected, suggesting it would be too risky to recommend that the first spray in a well-managed orchard be delayed beyond the first infection period. The level of PAD in the nine orchards was <600 compared to 26,500 in the one orchard where the delay strategy failed. This indicates that an **"action threshold"** for applying the first fungicide, based on a calculation of PAD, may be feasible because it appears that an action threshold was not reached until the pink bud stage or later in nine instances with <600 PAD and that it was exceeded prior to tight cluster in another instance with >26,500 PAD.

Warning systems sometimes predict that infection has occurred but a later disease assessment fails to detect scab associated with this prediction, indicating that the prediction was wrong. A calculation of PAD may help to determine whether or not the prediction was correct. The predictive criteria that comprise scab warning systems do not consider the amount of inoculum in an orchard. Nearly all warning systems utilize the "light" infection curve of Mills (9) that identifies the minimum hours of leaf wetting required for infection in a **very high PAD orchard;** this curve may not be appropriate for a low PAD orchard. In a **low PAD orchard**, lesions may develop from a rainy period that satisfied the minimum hours for infection, but there could be too few lesions to be detected or too few to cause any appreciable increase of scab if susceptible tissue had been left unprotected during the rainy period. Thus, scab infections may have occurred, as predicted, but not have been detected by the disease assessment method. This example also points out that a prediction of infection does not mean that a significant amount of scab will develop. Research is needed to develop criteria that adjust a "standard infection curve" to values of PAD. Adjusting the "standard infection curve" in low-inoculum orchards so that longer wetting periods are required for infection could avoid recommending fungicide applications for infection periods in which the amount of infection is insignificant.

The need to validate empirical evidence and "inferences" from research that influence decision-making for scheduling fungicide sprays

It was stated above that warning systems have often reduced fungicide usage (compared with conventional schedules) because they correctly identified long periods that were unfavourable for scab. However, it is possible that additional reductions could have been made, because the scheduling of scab fungicides throughout the season, even in orchards employing a warning system, is strongly influenced by the conventional practices in a region.

It is understandable that growers have confidence in conventional schedules. These schedules have generally provided acceptable control of scab since they were established in the 1940's and 1950's. It is also understandable that growers may be reluctant to accept a new strategy that requires fewer fungicide applications, because most growers have experienced at least one occasion when their conventional schedule resulted in too much scab, particularly if a spray had been missed. Because of the continued use of conventional schedules and the influence of conventional schedules on warning system spray recommendations, it is appropriate that we critically examine the scientific basis of the reasoning that defines the timing of conventional schedules.

The quantitative epidemiology of apple scab is poorly understood, particularly the build-up of scab on leaves and fruit with respect to inoculum potential and the relationship between early-season infections and the subsequent build-up of scab on the fruit. Consequently, a widely accepted practice is to apply the first scab spray when the first green tissue is exposed. Another common practice is to continue the fungicide schedule through the growing season if scab lesions appear during the primary season. Are these practices supported by research?

Research has increased our knowledge of many important, specific events that comprise the disease cycle. Strategies for scheduling fungicides are based on the research data, on inferences derived from these data, and on orchard observations and impressions developed from field experiences. The inferences and empirical evidence provide the most compelling reasons for recommending fungicide applications (i) as soon as green tissue appears in the spring and (ii) at repeated intervals until terminal bud set. As scientists, we must examine thoroughly and critically the decision-making criteria that drive our warning systems and conventional control programmes, and we must determine the extent and soundness of the scientific evidence upon which these criteria are based. Four examples are presented to illustrate the need to investigate some of the inferences that have significantly influenced conventional spray schedules and warning systems. Until these inferences are addressed, it will be difficult to convince growers, advisory service personnel and private consultants to adopt new approaches and criteria that will lower the fungicide dose, even though there is strong supportive evidence from research. The inferences *may be correct*, but is there published research to substantiate them? A first step is to identify what is substantiated fact and what is unsubstantiated inference. The unsubstantiated inferences can then serve as hypotheses for research.

Example 1. Numerous studies have shown that viable conidia are present on infected shoots at the time of bud break. When this occurs, these conidia comprise part of the primary inoculum and are available and strategically positioned to infect the earliest exposed susceptible tissue. Research has not established a relationship between conidia produced on overwintered shoots and scab epidemics. Nevertheless, in geographical regions where shoot infections have been reported, two inferences, unsubstantiated by research, are that (i) the first green tissue to emerge must *always* be protected or fruit scab at harvest will be above an acceptable level, and (ii) practices aimed at reducing the leaf litter density or pseudothecial density *will not be effective* because conidia from shoot infections will cause an unacceptable amount of early-season infection. Research conducted *in commercial orchards with reasonable scab control* is needed to investigate the hypothesis that conidia from infected shoots cause primary infections that result in the subsequent development of unacceptable levels of scabbed fruit. The research must establish a relationship between shoot infection density and scab build-up in orchards with very low ascosporic inoculum, e.g. <100 PAD. The occurrence of shoot infections appears to be a "local phenomenon" , commonly found *at high levels* only in a few geographical areas and often only in neglected, high inoculum orchards in these areas. Until research establishes that shoot infections are a source of inoculum that will likely cause economic loss, is their sufficient evidence to justify recommending fungicide sprays on the basis that shoot infections are present or may be present?

Example 2. Sepals are the first susceptible structures to appear when flower buds open, and numerous studies have shown that ascospores can infect the sepals when they emerge. An inference, unsubstantiated by research, is that sepals must *always* be protected with fungicide as soon as they emerge or the subsequent build-up of fruit scab will *always* be commercially unacceptable. Research is needed to investigate the hypothesis that, *in commercial orchards with reasonable scab control*, sepal infections will *always* result in an unacceptable level of fruit scab at harvest. The research should determine the relationship between the level of PAD, the severity of sepal scab, and the contribution of sepal scab to subsequent foliar and fruit scab. The research should also determine if there is a threshold of primary inoculum below which sepal infections will not subsequently cause an unacceptable level of fruit scab.

Example 3. Research long ago established that conidia produced on scab lesions cause secondary infections during the growing season. Two inferences, unsubstantiated by research, are that (i) scab lesions, regardless of when they occur, will produce conidia for the *remainder* of the growing season, and (ii) whenever *any* lesions are observed, fungicides must be applied for the *remainder* of the growing season or the level of fruit scab at harvest will be commercially unacceptable. Research is needed to show how long lesions remain infectious (i.e. produce conidia) and to establish a relationship between the lesion density at identifiable tree growth stages and the subsequent development of scab caused by conidia.

Example 4. Numerous studies have shown that discharged ascospores are airborne. An unsubstantiated inference is that ascospores released near an orchard will disperse to the orchard and cause an *unacceptable* build-up of scab. Research is needed to establish a relationship between amount of «outside» inoculum, distance of inoculum to an orchard, and build-up of scab in an orchard caused by the «outside» inoculum The influence of wind current patterns, air speed and local topography on spore dispersal gradients must also be considered. This information is particularly necessary for warning systems that are orchard-oriented rather than region-oriented, i.e. warning systems that operate within an orchard and base spray decisions on values determined from conditions in that particular orchard, such as PAD. With these systems, it will be critical to know how much an orchard's PAD must be increased to account for an outside source of ascospores.

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High-resolution weather forecasts to predict local apple scab infection

R. C. Seem[1], J. M. Russo[2], and J. G. W. Kelley[2]

[1]Department of Plant Pathology, New York State Agric. Expt. Sta., Geneva, NY, U.S.A. and [2]ZedX Inc, Boalsburg, PA, U.S.A.

Abstract

A new mesoscale weather forecasting technique has been applied to a local apple scab (*Venturia inaequalis*) infection model to give daily predictions of leaf wetness and scab severity for areas of 1 km^2. The weather forecasting technique, called Model Output Enhancement (MOE), generates high resolution, screen- level forecasts from upper-air output of a national numerical weather prediction model. The generated mesoscale forecasts were coupled with an apple scab algorithm based on the Mills' table to give local prediction of disease occurrence and intensity. The application of the technique to apple scab prediction was evaluated for a 3-day period in late spring 1987 at six locations in New York State.

Key words: Model Output Enhancement, Mills' table, Smith Periods, *Venturia inaequalis*, disease prediction, leaf surface wetness, warnings.

Introduction

Plant pathologists often have a peculiar concept of the term "forecast." To them it usually involves the *a posteriori* analysis of weather conditions in order to determine if disease has or has not occurred. In this sense "forecast" is a misnomer because there is no attempt to portend events unless one considers the future appearance of disease symptoms after an incubation period. Why do plant pathologists have this different concept? It turns out to be a matter of spatial scale.

Spatial scale refers to the size of area to which forecasts are applied. In general, plant pathologists work on a local scale (less than a kilometer), and even on a microscale (less than 100 meters) (8). Because the environment that affects disease development is usually unique to the field or orchard in which data are collected, the forecast area is very small in comparison to the local, regional and global scales used by metereorologists. As a result, plant pathologists find that traditional weather forecasts are of little help when attempting to determine precisely the likelihood of disease. Exceptions to this statement exist: (apple scab forecasting in FRG, British and Irish potato late blight forecasting and recently, onion blight forecasting in the USA (11).

In order to use weather forecasts plant pathologists need the specific weather parameters of interest (usually temperature, relative humidity, rainfall and duration of leaf surface wetting) over a short time frame (such as hourly) and at a very high resolution (such as an area of several hectares). This is a very challenging need when presented to meteorologists. The only way to even remotely achieve this degree of definition is to have customized weather forecasts prepared by a meteorologist who is familiar with the locale of the forecast. However, a recent development has changed approaches to weather forecasting for predicting plant diseases.

The intent of this paper is to present this new recent development and describe attempts to apply this technology to the forecasting of apple scab (*Venturia inaequalis*) in the northeastern United States.

The current status of weather forecasting

In order to explain how the new disease forecasting system works, it is necessary to first review how current weather forecasting is accomplished. A more detailed explanation of current forecasting techniques can be found in Kelley *et al.* (4).

Weather forecasts are generated from large, hemispheric computer models. These models have a voracious appetite for initial data consisting of current weather observations recorded around the world. Because of the time necessary to collect the initial data and the time it takes to process those data, the forecasts are generated once every 12 h. In spite of this sophisticated technology, the forecasts apply only to intersecting points on a global grid and represent conditions at specific levels ranging from the upper atmosphere to near the surface. In the United States, the principal model used by the National Weather Service is called the Nested Grid Model (NGM) and this forecasts at a resolution of approximately 100 km (i.e. the grid points are 100 km apart). The model used by the British Meteorological Office has a forecasting resolution of about 90 km while the European Center for Medium Range Forecasts has a resolution of about 200 km. In order to produce the public forecasts received from these centres, the computerized numerical output must be refined and enhanced for local conditions, either by meteorologists interpreting forecast data or by point-specific statistical methods.

High resolution weather forecasts

Kelley *et al.* (4) have revised the typical forecasting process by developing what they call Model Output Enhancement (MOE), an automated process that performs additional analysis of the numerical model output and produces a high resolution forecast at the surface. The approach is based on the knowledge that topography and other surface features exert a strong influence on regional weather systems and hence, can be used to predict smaller-scale, short-term conditions at the local level. Elevation data are taken from a digital terrain model. In the Unites States, one such terrain model, the "30-Second Point Topography," has a resolution of approximately 1 km (6). Thus, every square km of ground surface in the US can be associated with a mean elevation value. The MOE technique uses this information in a three-step process (Fig. 1). First, numerical model outputs are interpolated to the same resolution as the digital elevation data base using the Simple Multiquadratic Equation algorithm developed by Eyton (2).

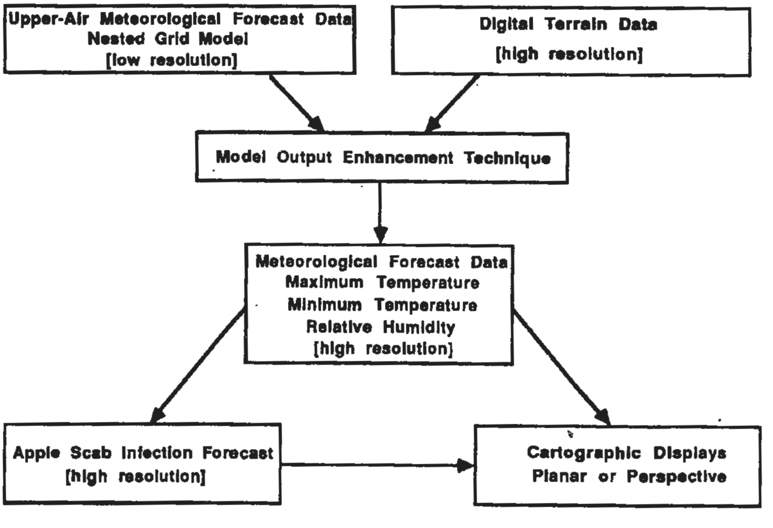

Fig. 1. Operational diagram of Model Output Enhancement (MOE) weather forecasts and their integration into the high resolution apple scab disease forecast.

Second, the high-resolution upper air forecasts are extrapolated to the ground surface. The extrapolation method depends on the type of weather variable. Temperature is brought to surface conditions using environmental lapse rates (ELRs), i.e. the rates at which temperature changes with elevation. Depending on the type of weather condition and the time of day, the ELR may range from inversion (temperature increases with elevation), to adiabatic (normal temperature decrease with height), to super adiabatic (much faster decrease with height), or anything between. Relative humidity is extrapolated by first converting to a dew point temperature, bringing that temperature to the surface using the appropriate ELR and then converting the dew point back to a relative humidity at the surface. Currently, rainfall is not extrapolated to the surface. The third step in the MOE process is the integration of the forecast data with the digital elevation data into a forecast for a specific location.

Although the numeric forecasts are generated every 12 h for up to 48 h in advance, the MOE data are presented in 6 2-h intervals. This is accomplished by estimating 2-h temperatures from sine curves based on the 12-h maximum and minimum temperatures. Relative humidity is computed similarly.

MOE forecasts represent a considerable amount of data. A region the size of northeastern Unites States (Pennsylvania, New Jersey, New York and the New England states) is nearly 800,000 km^2, and the MOE technique provides forecasts for each square km, or over one million predictions in this forecast domain. The shear size of the data set requires special methods of presentation. Cartographic displays are used either as two-dimensional maps or three-dimensional perspective displays and provide an easily interpretable image of the weather conditions over the region. Numeric forecasts can be given, however, for specific locations within the region.

Table 1. Locations of the biological and meteorological monitoring sites used to validate the MOE apple scab forecasts.

Site	Latitude (deg	min)	Longitude (deg	min)	Elevation (m)
Hudson Valley	41	44	73	57	122
Geneva	42	52	77	01	219
Lafayette	42	54	76	11	189
Williamson	43	15	77	12	106
Sodus	43	16	77	05	84
Peru	44	13	73	32	140

Apple scab forecasting

One of the diseases that has been typically forecast by plant pathologists is apple scab, caused by *Venturia inaequalis*. In the United States, apple scab is forecast by use of Mills' periods, an infection severity index based on average temperature and duration of leaf wetting (5). The MOE forecast for apple scab was demonstrated and verified using the original, unaltered Mills' table. The MOE technique was previously demonstrated for the forecast of potato late blight in Pennsylvania (7).

The original MOE forecast provided temperature data but did not include duration of leaf wetting. This latter parameter was estimated from two other MOE forecast parameters, rainfall and relative humidity. The wetting period duration, as defined by Smith (9), was computed as the number of hours relative humidity remained above 90% after rainfall. Based on the energy balance work of Thompson (10), it was assumed that wetting period estimation for an orchard could be reasonably based on Smith periods.

One enhancement was made to the Mills' forecast to handle split (consecutive) wetting periods. Wet periods were combined if they were separated by a dry period of less than 8 h duration (3). The dry period was not added to the time of wet period duration; it was assumed that the germination and infection processes of the pathogen were stopped but not damaged by the intervening event and that the processes resumed after suitable wetting conditions resumed.

Each MOE apple scab forecast was generated for two 24-h forecast periods. The first forecast period extended from the current local time to 24 h in advance of that time. The second period extended from 24 h to 48 h in advance. The apple scab forecasts utilized the 12 2-h weather estimates for the first period or 24 2-h weather parameters (48 h total) for the second forecast period.

Testing the MOE apple scab forecast

The apple scab forecast generated by the MOE technique was evaluated by comparing forecasts for the period 29 May to 3 June, 1987, to field observations. The numeric forecasts for the period 29 May to 1 June, issued by the National Weather Service's National Meteorological Centre were stored on computer tape and thus could be used repeatedly to produce MOE forecasts for that period of time.

The set of verification data consisted of observations from six weather and pest monitoring sites in the Biological Monitoring Network of the New York State Integrated Pest Management Program (Table 1). These six sites represent the geographic diversity of apple production areas in the State. Locational differences between sights ranged from several km (Sodus to Williamson) to several hundred km (Geneva to Peru, Williamson to Hudson Valley). The data collected at each site included maximum and minimum temperature, rainfall, and leaf wetting duration for the 24-h period preceding the 0800 h observation. Apple scab infection periods were calculated by personnel at each site.

Verification results

The verification results will be presented in a series of tables showing forecast and observed weather and apple scab infection conditions for the period of time 30 May to 2 June. As is typical with meteorological forecasts, the time of issue of a forecast is given in Universal Time Coordinate (UTC) or Greenwich Mean Time (GMT). Based on the time of year and the location of the forecast, the actual time of issue was 4 hless than the stated UTC time. For example, a forecast issued at 1200 UTC was actually issued at 0800 h local time. Differences between forecast and observed values were expressed as average absolute difference for temperature, duration of leaf wetting and apple scab forecast, and proportion of correct predictions for rainfall.

An example of the graphical output of the MOE model is demonstrated using a maximum temperature forecast for the area including Pennsylvania, New York, and all the New England states except Maine (Fig. 2). The forecast was issued at

Table 2. Comparison of today's MOE forecast (F), issued 1200 UTC 30 May 1987, to observed (O) conditions. Temperature (°C), precipitation (no=0/yes=1), wetness duration (h), and scab severity index data are for the 24-h period beginning 1200 UTC 30 May and ending 1200 UTC 31 May 1987.

	Av. Temp.			Precipitation			Wetness duration			Scab Sev.Index[1]		
Site	F	O	Dif.	F	O	Dif.	F	O	Dif.	F	O	Dif.
Hudson Valley	26.9	26.9	0.0	1	-	-	6	11	-5	0	1	-1
Geneva	27.2	25.5	1.7	1	0	1	6	0	6	0	0	0
Lafayette	27.0	23.9	3.1	1	1	0	6	3	3	0	0	0
Williamson	28.0	23.9	4.1	1	0	1	6	0	6	0	0	0
Sodus	28.0	22.5	5.5	1	0	1	6	0	6	0	0	0
Peru	25.0	25.0	0.0	1	0	1	8	4	4	0	0	0
	Average ±2.4			Correct ±0.20			Av. ±5.0			Av. ±0.2		

[1]Scab severity index: Not likely (0); Light (1); Moderate (2); and Heavy (3).

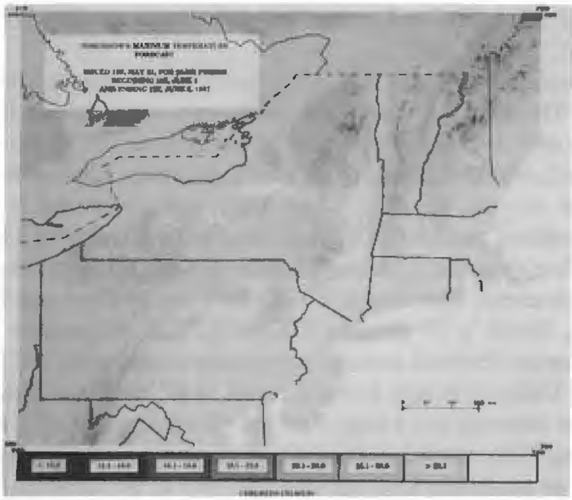

Fig. 2. Planar display of the Model Output Enhancement maximum temperature forecast for the northeastern United States, issued at 1200 UTC on 31 May and covering the 24-hr period starting 1200 UTC 1 June and ending 1200 UTC 2 June 1987.

Table 3. Comparison of tomorrow's MOE forecast (F), issued 1200 UTC 30 May 1987, to observed (O) conditions. Temperature (°C) and precipitation (no=0/yes=1) data are for the 24-hr period beginning 1200 UTC 31 May and ending 1200 UTC 1 June; wetness duration (h) and scab severity index are for the 48- h period beginning 1200 UTC 30 May and ending 1200 UTC 1 June 1987.

	Av. Temp.			Precipitation			Wetness duration			Scab Sev. Index[1]		
Site	F	O	Dif.	F	O	Dif.	F	O	Dif.	F	O	Dif.
Hudson Valley	25.8	25.2	0.6	1	1	0	14	34	-20	1	3	-2
Geneva	23.6	22.2	1.4	1	0	1	14	9	5	2	0	2
Lafayette	23.8	25.0	-1.2	1	0	1	14	3	11	2	0	2
Williamson	23.8	24.7	-0.9	1	0	1	14	6	8	2	0	2
Sodus	23.8	22.8	1.0	1	0	1	14	6	8	2	0	2
Peru	22.1	23.3	-1.2	1	0	1	14	6	8	2	0	2
	Average ±1.0			Correct ±0.17			Av. ±10.0			Av. ±2.0		

[1]Scab severity index: Not likely (0); Light (1); Moderate (2); and Heavy (3).

1200 UTC on 31 May 1987 and covers the period starting 1200 UTC 1 June and ending 1200 UTC 2 June 1987.

The first forecast was for the 24 h forecast commencing at 1200 UTC on 30 May (Table 2). The average temperature difference ranged from 0°C at Hudson Valley and Peru to 5.5°C in Sodus. Rainfall was forecast for all locations but was recorded only at Lafayette, resulting in a 20% accuracy. Closely associated with rainfall was leaf wetting duration; while 6-8 h were predicted, it was recorded only at three locations and ranged from 11 h at Hudson Valley to 3 h at Lafayette. However, at all locations no apple scab infection was forecast or observed.

The second forecast, also issued at 1200 UTC on 30 May, was for the second forecast period, 24-48 h in advance (Table 3). The temperature forecasts are much more accurate (overall average temperature difference 1°C), but rain fell only at Hudson Valley although it was forecast at all locations. Similarly, 14 h of leaf wetting was forecast but a long duration of wetting occurred at only two of the six locations. The extended duration of forecast wetting was sufficient to forecast a light to moderate scab infection periods at all locations; however, the only infection period occurred at Hudson Valley.

The next forecast was issued on 31 May for the first 24-h period (Table 4; this is the same period as the second 24-h forecast issued on 30 May, Table 3, but 24 h later). Temperature forecasts are still quite good, although slightly less accurate than the same forecast made on 30 May. Rainfall was still predicted but only observed at Hudson Valley. The leaf wetting observed at Geneva, Williamson, Sodus, and Peru was the result of dew formation and not rainfall. The MOE

Table 4. Comparison of today's MOE forecast (F), issued 1200 UTC 31 May 1987, to observed (O) conditions. Temperature (°C), precipitation (no=0/yes=1), wetness duration (h), and scab severity index data are for the 24-h period beginning 1200 UTC 31 May and ending 1200 UTC 1 June 1987.

	Av. Temp.			Precipitation			Wetness duration			Scab Sev. Index[1]		
Site	F	O	Dif.	F	O	Dif.	F	O	Dif.	F	O	Dif.
Hudson Valley	27.4	25.2	2.2	1	1	0	8	24	-16	0	3	-3
Geneva	23.6	22.2	1.4	1	0	1	8	9	-1	0	0	0
Lafayette	24.4	25.0	-0.6	1	0	1	8	0	8	0	0	0
Williamson	24.1	24.7	-0.6	1	0	1	8	6	2	0	0	0
Sodus	24.2	22.8	1.5	1	0	1	8	6	2	0	0	0
Peru	25.5	23.3	2.2	1	0	1	8	2	6	0	0	0
	Average ±1.4			Correct ±0.17			Av. ±5.8			Av. ±0.5		

[1]Scab severity index: Not likely (0); Light (1); Moderate (2); and Heavy (3).

system corrected itself (compared to the scab forecasts in Table 3) and predicted no scab infection periods. A major forecast error was the heavy infection period that occurred at Hudson Valley.

The 24-48 h forecast issued on 31 May maintained very acceptable accuracy on temperature forecasts and predicted correctly rainfall at all six locations (Table 5). Five of the six locations experienced significant leaf wetting that resulted in observed infection periods classed as moderate or heavy. Moderate-to-heavy apple scab infection forecasts were issued to all locations.

MOE forecasts issued on 1 June remained accurate for temperature and rainfall prediction (Tables 6 and 7). Eight to ten hours of wetting were predicted in both forecast periods. Although no scab infection was predicted and 4 of the 6 sites recorded infection periods during the first forecast period, infection was predicted and observed in the 48-h period after the issuance of the forecast.

Discussion

These results represent the initial attempts to link the MOE weather forecasting technique to plant disease forecasts. The comparisons, based on only six locations, serve as a preliminary verification of the technique, but represent only a

Table 5. Comparison of tomorrow's MOE forecast (F), issued 1200 UTC 31 May 1987, to observed (O) conditions. Temperature (°C) and precipitation (no=0/yes=1) data are for the 24-h period beginning 1200 UTC 1 June and ending 1200 UTC 2 June; wetness duration (h) and scab severity index are for the 48-h period beginning 1200 UTC 31 May and ending 1200 UTC 2 June 1987.

	Av. Temp.			Precipitation			Wetting Hours			Scab Sev. Index[1]		
Site	F	O	Dif.	F	O	Dif.	F	O	Dif.	F	O	Dif
Hudson Valley	25.8	24.7	1.1	1	1	1	8	24	-16	2	3	-1
Geneva	23.6	23.3	0.3	1	1	1	8	17	-9	2	2	0
Lafayette	23.8	22.5	1.3	1	1	1	8	8	0	2	0	2
Williamson	23.8	24.2	-0.4	1	1	1	10	16	-6	3	2	1
Sodus	23.8	21.9	1.9	1	1	1	10	15	-5	3	2	1
Peru	22.1	21.1	-1.0	1	1	1	8	23	-15	2	3	-1
	Average ±1.0			Correct ±1.00			Av. ±8.5			Av. ±1.0		

[1]Scab severity index: Not likely (0); Light (1); Moderate (2); and Heavy (3).

very small portion of the total data set (a potential of about 320,000 points in New York State).

Temperature forecasts are more accurate than any of the other forecast parameters. In fact, the accuracy of the predictions are considerably better than the 3-degree uncertainty range that is commonly expected in weather forecasts. The other weather parameters tested in this study are linked directly to upper air moisture. Although not tested directly, relative humidity forecasts (hours above 90% RH) were acceptable. We expected relative humidity to be accurate because it is based on upper air dew point, a very predictable parameter, and is extrapolated to the ground using the appropriate ELR, as in the case of temperature. Related studies using the MOE technique to predict potato late blight (Russo, Kelley, and Royer, unpublished) have shown that duration of relative humidity above 90% can be predicted accurately.

Precipitation and duration of leaf wetting initiated by precipitation do not have the desirable level of prediction accuracy. There are several reasons. First, precipitation is predicted directly from upper air moisture with no consideration for surface conditions. The association with surface conditions is more complex than using ELRs for temperature forecast. Second, the NGM precipitation algorithm is a major weakness in the numerical model. Third, synoptic analysis of satellite photographs for the period 29 May to 2 June show the great variability in moisture that can be encountered when a storm system moves through a region such as the northeastern US.

What was the accuracy of the plant disease forecast? Of the 36 forecasts shown in Tables 2-7, 24 (67%) correctly indicated no infection period when none

Table 6. Comparison of today's MOE forecast (F), issued 1200 UTC 1 June 1987, to observed (O) conditions. Temperature (°C), precipitation (no=0/yes=1), wetness duration (h), and scab severity index data are for the 24-h period beginning 1200 UTC 1 June and ending 1200 UTC 2 June 1987.

	Av. Temp.			Precipitation			Wetting Hours			Scab Sev.Index[1]		
Site	**F**	**O**	**Dif.**	**F**	**O**	**Dif.**	**F**	**O**	**Dif.**	**F**	**O**	**Dif.**
Hudson Valley	24.2	24.7	-0.5	1	1	0	8	0	8	0	0	0
Geneva	23.0	23.3	-0.3	1	1	0	8	8	0	0	2	-2
Lafayette	23.0	22.5	0.5	1	1	0	8	8	0	0	0	0
Williamson	23.6	24.2	-0.6	1	1	0	8	10	-2	0	2	-2
Sodus	23.8	21.9	1.9	1	1	0	8	9	-1	0	2	-2
Peru	22.5	21.1	1.4	1	1	0	8	21	-13	0	3	-3
	Average ±0.9			Correct ±1.00			Av. ±4.0			Av. ±1.5		

[1]Scab severity index: Not likely (0); Light (1); Moderate (2); and Heavy (3).

occurred (12) or indicated some level of infection when it did occur (12). Of the 12 misses, six erred conservatively by forecasting an infection period when none occurred and six were serious misses where no infection period was forecast but did occur. The most serious error occurred in the 24-h forecast on 31 May, when a heavy infection period was recorded at Hudson Valley but none was forecast (Table 4).

Implications of MOE disease forecasting

An accuracy of 67% for plant disease forecasting is not good enough for a disease such as apple scab. Knowing the likelihood of disease development 24 to 48-h in advance provides an extra margin of management flexibility for the control of apple scab. A grower may choose to apply a protectant fungicide before the start of the infection period, particularly if scab severity was forecast at moderate or heavy. The grower may also choose to "weather" through a predicted infection period but would have some advance indication about chemical and machinery demands if it is necessary to apply after-infection fungicides.

The MOE apple scab forecast will never replace local monitoring of disease and weather conditions. The MOE forecast is only a guidance tool; it is still necessary to determine whether or not an infection period actually occurred and what is the likelihood of disease. True plant disease forecasting and traditional plant disease forecasting are seen as complimentary activities.

Table 7. Comparison of tomorrow's MOE forecast (F), issued 1200 UTC 1 June 1987, to observed (O) conditions. Temperature (°C) and precipitation (no=0/yes=1) data are for the 24-h period beginning 1200 UTC 2 June and ending 1200 UTC 3 June; wetness duration (h) and scab severity index are for the 48-h period beginning 1200 UTC 1 June and ending 1200 UTC 3 June 1987.

	Avg. Temp.			Precipitation			Wetting Hours			Scab Sev.Index[1]		
Site	F	O	Dif.	F	O	Dif.	F	O	Dif.	F	O	Dif.
Hudson Valley	22.0	16.5	5.5	1	1	0	8	16	-8	2	1	1
Geneva	21.0	21.9	-0.9	1	1	0	8	22	-14	2	2	0
Lafayette	21.0	21.1	-0.1	1	1	0	8	12	-4	2	1	1
Williamson	21.6	23.6	-2.0	1	1	0	8	18	-10	3	2	0
Sodus	21.6	21.1	0.5	1	1	0	8	13	-5	3	2	0
Peru	20.6	20.8	-0.2	1	1	0	10	25	-15	2	3	-1
	Average ±1.5			Correct ±1.0			Av. ±9.3			Av. ±0.5		

[1]Scab severity index: Not likely (0); Light (1); Moderate (2); and Heavy (3).

Future directions of MOE disease forecasting

Testing and verification of the MOE technique indicate significant progress towards true forecasting of plant disease. However, there are some short-range and long-range accomplishments that must be achieved before the MOE technique can be accepted as a valid forecasting tool.

Foremost, the precipitation algorithm must be improved. A new algorithm is currently under test and some improvement is expected. However, the whole forecast system has limitations that may never be overcome by the MOE technique. The numerical models which provide input to MOE have a certain amount of error. The NGM precipitation forecast is crude and until it is improved the MOE prediction will carry that same limitation. Numerical weather models are constantly being improved and it is only a matter of time before these limitations will be overcome.

Delivery of the information produced by the MOE forecast to advisory personnel or growers can be slow or cumbersome. The information can be compressed into maps, permitting conditions in a whole regions to be interpreted easily, and maps can be transmitted electronically, either as graphic files or as facimile images. In both cases the technology is available and costs would permit transmission directly to growers. Forecasts can also be tailored to specific locations and simple text forecasts can be transmitted electronically or by voice. The delivery possibilities are broad. Consider the possibility of an early morning television weather program that displays regional maps of forecasts of disease on the major crops grown in that region!

The MOE technique is not only applicable to plant diseases. Temperature forecasts can be utilized to predict insect or crop phenology, heat stress in farm animals, and water use needs of crops. Because agriculture is so weather dependent, the general need for accurate weather forecasts will drive researchers to continually improve the forecasting techniques.

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Fireblight warning systems: problems and progress

C.M.E. Garrett

A.F.R.C. Institute of Horticultural Research, East Malling, Maidstone, Kent, England

Abstract

Fireblight, caused by *Erwinia amylovora*, has spread through much of Europe since 1957. Overwintering cankers produce bacterial ooze which is transmitted by pollinating insects and rain to primary (spring) blossom and later to secondary (summer) blossom or damaged shoots. Cultural methods are still important for disease control because there is a lack of effective bactericides. Of the risk-warning systems, the Billing system seems most appropriate to European conditions. Billing's original system was complex and some workers found its use difficult; her recently revised system is simpler. In some countries, computer programmes (based on the Billing system) issue regional warnings. Some microprocessor-based orchard environment monitors incorporate a fireblight risk model. The need for accurate and properly-maintained sensors is emphasised if orchard monitors are to give the expected precision.

Introduction

Fireblight, the destructive and complex disease caused by *Erwinia amylovora*, occurs on apples and pears, and also other *Rosaceae* of the subfamily *Pomoideae*; of these, *Crataegus* is probably the most important epidemiologically (8,24). Fireblight, known in the U.S.A. for about 200 years, reached English pear orchards in 1957 from where it has spread to many European countries and, more recently, to the Middle East (Table 1) (1,17,24).

Symptoms and spread

A brief summary of fireblight symptoms and spread is necessary in order to understand problems with the development of warning systems. For more detail see van der Zwet and Keil (25).

The bacteria overwinter in "holdover" cankers; these usually result from late-season infections the previous year and have indeterminate margins. When the bacteria resume activity in spring, a sticky ooze (bacteria in a polysaccharide matrix) may exude from the surfaces of the cankers. To infect, bacteria need entry sites, either natural e.g. nectaries, leaf scars, stomata, or artificial e.g. storm damage, pruning wounds. Bacterial ooze is transported to flower nectaries by insects or is spread by rain into open flowers. As a result of bacterial multiplication, the calyx cup may become filled with bacterial ooze which can be spread by pollinating insects or rain to other flowers or to soft shoots damaged by feeding insects, strong winds, hail etc. Under certain environmental conditions, hair-like "strands" (threads of bacteria in a polysaccharide matrix) may be extruded from infected tissue and disseminated by wind (13). Infected flowers and shoots wilt and turn dark brown or black. When host factors and environmental conditions are favourable. The disease progresses from spurs and soft shoots into branches.

On pear, a generally susceptible host, infection can progress in the plant rapidly: cultivars that regularly produce abundant secondary (summer) blossom

Table 1. First reports of fireblight.

Country	Year of first report
U.S.A.	1780
New Zealand	1919
England (S.E.)	1957
Netherlands, Poland	1966
Denmark	1968
England (S.W.), F.R.G.	1971
Belgium, France (N.)	1972
France (S.W.)	1978
Luxemburgh, Egypt	1983
Cyprus	1984
Israel	1985
Crete	1986
Greece, Eire, N. Ireland	1987
Norway, Sweden	
Czechoslovakia, Lebanon	1988

are particularly vulnerable. Symptoms on apple are similar to those on pear but the discolouration is more orange-brown and the disease progresses more slowly. Hawthorn (*Crataegus*) is very susceptible; hedges surrounding or in the vicinity of orchards are often the inoculum source (8). Because *E. amylovora* is not a true epiphyte the inoculum level in an orchard is dependent on the amount of disease present in or near the orchard. Because of the lack of effective bactericides, cultural methods are an important aspect of fireblight management: the planting of cultivars of low susceptibility; avoidance of excessive growth; the removal of secondary blossom; the removal of nearby hawthorn. If the latter is not possible, hawthorn hedges should be trimmed to prevent flowering (8). The few chemicals available for fireblight control are contact bactericides with no curative and little or no systemic action. Copper sprays, though reasonably effective, are often phytotoxic while streptomycin, usually reliable, is not permitted in the U.K. or many other European countries. Once the bacteria have entered plant tissues they are beyond the reach of contact sprays. Therefore preventive action must be taken to avoid infection, especially on pear. These considerations have prompted researchers to devise fireblight risk warning systems with two main aims:

1.To advise on the optimum time to inspect orchards for symptoms in order to ensure early removal of infected tissues. This will minimise the amount of tree that needs to be destroyed, restrict disease spread and avoid unnecessary inspections.

2.To advise on the optimum time to spray. This will normally be when conditions favour infection or at the time when fresh inoculum (ooze) may be expected to be produced from "holdover" cankers or new infections. Correct timing will avoid unnecessary expense in labour and materials and be cost-effective.

Table 2. Fire-blight warning systems

Author	ref	year	location
Mills	(16)	1955	New York, U.S.A.
Leupschen *et al*	(15)	1961	Illinois, U.S.A.
Powell	(19)	1965	Illinois, U.S.A.
Thomson *et al*	(22)	1975	California, U.S.A.
Zoller and Sisevich	(23)	1979	California, U.S.A.
Billing	(6)	1980	England
Beer *et al*	(3)	1984	New York, U.S.A.
Zutra	(24)	1987	Israel
Jacquart-Romon *et al*	(14)	1988	France
Billing (Revised)	(10)	1988	England

Fireblight risk warnings

It has long been realised that fireblight is favoured by warm (18 °C) wet weather (25). How are standard climatic data best used in a warning system that is simple to use yet precise enough to be of practical value to growers? It is advantageous if the system indicates not only when there is risk of infection but also the rate of subsequent tissue invasion and the times when symptom expression and ooze production may be expected. It must be emphasised that climatic factors alone are of limited value; knowledge of the host cultivar and growth stage, amount of blossom, bee activity and presence of hawthorn are all important in determining disease incidence and spread (3,14).

The first warning systems were devised in the U.S.A., where researchers concentrated on the primary blossom period of pome fruits because in America fireblight attacks on primary blossom are frequent (10,15,16,19,22,23,24). Many of the warning systems developed in the last 25 years (Table 2) have been discussed (9); all are based upon temperature and either rainfall or relative humidity, and some include orchard factors.

In England, the American systems are not satisfactory for three main reasons. Firstly, in contrast to the Eastern States, primary-blossom infection is rare, due to cool springs. Secondly, although fireblight is favoured by temperatures over 18^{o} C there is good field evidence for disease spread below this "threshold" temperature, as observed in the Western States (25). Thirdly, the importance of hawthorn in particular and other ornamental trees and plants as alternative hosts cannot be underestimated in England (and other North European countries).

Billing (9) developed a system complimentary to, but more comprehensive than, the early ones by the innovative idea of measuring the *in vitro* growth rate of the pathogen at various temperatures and using these data to estimate the daily number of potential doublings (PD) of the pathogen when moisture is not limiting (5). Theoretically, under optimal conditions thirty doublings of one infecting cell of *E. amylovora* will result in 10^9 cells: this is the number at which the population pressure results in the extrusion of ooze (4). When daily PD values are high, plant host development and bee activity are also stimulated. Rain spreads the inoculum (ooze) over the surfaces of infected plants and from one plant to another and also provides moisture at the site of multiplication of the pathogen. Billing (6) found a relation between the number of days D (development period) from infection to symptom appearance, and the accumulated daily PD and accumulated daily rainfall R (when "traces" and up to 2.4 mm were scored 0.5 and 2.5 mm or more was scored as 1.0. This relation is expressed as

$$\frac{D = R\ (PD - 6)}{36}$$

A high rain score may indirectly indicate low irradiation, high relative humidity or low evaporation rate. Development (D) periods are deemed to start on any wet day (>2.5 mm rain) or warm day (PD >9) up to early June and thereafter on days of PD of 7 or more plus any rainfall. In warm wet weather, D periods tend to be short while in cool dry weather several weeks may elapse from infection to symptom expression and ooze production. Two assumptions made in this model are (a) a constant inoculum dose and (b) an infection leads to symptoms appearing on a single day. Nevertheless, the system has worked well when backed by experience of disease behaviour.

The graphical "year at a glance" presentation of the Billing system, sometimes divided into system 1 (D-period analysis) and system 2 (infection risk, insect risk estimations and orchard factors) displays the daily risks of inoculum spread by insects (estimated from sunshine hours and temperature), infection, damaging storms and blossom periods of susceptible hosts, as well as PD, rainfall and D periods. Such displays have proved valuable for explaining the initial occurrences of fireblight in England, The Netherlands, Denmark, France and other countries (2,12,18,21). The graphical displays also facilitate comparisons of locations and of years at the same location. The Billing system has been widely used in Northern Europe to predict and monitor progress of the disease. It has also been used in countries free of the disease to predict the risk of fireblight becoming established. A disadvantage of the original Billing system was its complexity: skill and experience were required to interpret the information. Also, some users over-emphasised the climatic data to the virtual exclusion of the important infection and insect-activity factors.

Opinions differ as to whether the most useful fireblight warning systems are those that are specific to individual orchards or those that broadly indicate relative risks. For warnings to be specific to an individual orchard, many climatic and orchard factors must be fed into the model using data collected from instruments sited within the orchard (see below).

General warnings can be issued from a central or regional office to alert growers to possible fireblight risks, leaving individual growers to utilise the information, each taking account of orchard factors, local rainfall and storms. A computer programme based on the Billing system has been in use by the Ministry of Agriculture, Fisheries and Food in England for several years to issue warnings of relative fireblight risks in six regions. This has proved valuable in alerting growers and advisers to the appropriate times to search for the disease. These alerts are especially important in England where sprays cannot be used, because antibiotics are not permitted for this purpose. Similar warning programmes are in use in France, Germany, The Netherlands and Denmark. The Billing system has been revised in the light of more field data, revised PD values (20), experience from other climatic zones and in order to eliminate some of the operational difficulties. The revised version (10) is more precise and the graphical presentation is simpler. A full version of the revised system is not yet published but the new system gives better estimates of fireblight activity than the original (Billing, pers. comm.).

Microprocessor-based orchard environment monitors

There is increasing interest in orchard environment monitors capable of "driving" pest and disease models: some incorporate a fireblight risk model. The model in the RSS- 412 "Predictor" (Reuter-Stokes, U.S.A.) is based on accumulated degree hours over 18 °C and hours of humidity 80% RH. Daily data is summarised at midnight as nil-, low-, medium- or high- risk fireblight conditions the previous day. In 1987, the RSS-412 was operated on the agro- meteorological site at East Malling from mid-July to the end of September. The model performance of the monitor was compared with fireblight risk assessed by the Billing system (climatic data only), using, for the Billing system, temperature and rainfall values as recorded by the RSS-412. The monitor registered more fireblight risk days than the Billing system. A comparison, over this period of daily temperature and rainfall recorded by standard meteorological instruments on the agro- meteorological site (data collection period 09 h to 09 h) with the values recorded by the RSS-412 (00 h to 00 h) showed that the monitor generally recorded a slightly higher maximum temperature (on 71 out of 77 days) and frequently a higher minimum temperature (on 65 days). This was partly due to the difference in the time of the start of the daily recording period, but also to the fact that the RSS-412 sensor is a thermister housed inside a gauze-walled box, while the standard instrument is a mercury thermometer in a Stevenson screen. The reason why the rainfall recorded by the standard rain gauge (automatic siphon) and the RSS-412 (tipping bucket) did not always correspond was partly because the latter did not register trace amounts and partly due to the difference in the start of the daily recording period. It must be emphasised that the RSS-412 fireblight model is not based upon the PD values that are an integral part of the Billing system. If PD values were used, however, the higher temperatures recorded by the monitor would result in higher PD values than those calculated from the standard agro-meteorological site sensors (Table 3). Thus, between July 16th and August 31st, there were six occasions only (July 17,30; August 6,7,12,14) when PD values were common to both systems.

PD values and rainfall are used to calculate D periods in the Billing system. The effect of the type of instrumentation on D periods is shown in Table 4. Two D periods, beginning on July 16th and 17th, 1987, were each shorter by 1 day when calculated from the RSS-412 environment data rather than the agro-meteorological site data. In contrast, D periods beginning on July 22nd, August 1st and 8th were longer when calculated from the RSS-412 data by 2,4, and 2 days, respectively, than when calculated from the agro- meteorological site data. These differences can be explained by the fact that the first two D periods occurred during warm wet conditions favouring fireblight activity whereas the last three D periods coincided with drier conditions less favourable to fireblight activity, and when some trace amounts of rain were recorded by the standard rain gauge on the agro- meteorological site (scoring 0.5 in the Billing system) but not by the RSS- 412, thus lengthening the D period calculated from the monitors data.

In September 1988 the RSS-412 and another microprocessor-based orchard monitor, the KMS-P (Parr, Austria), were compared with standard meteorological instruments. The standard instruments were on the agro- meteorological site at East Malling and the two monitors were located on the edge of an adjoining orchard. The daily information given by the KMS-P is in the form of either "no risk" or "risk" of fireblight; there is a "risk" when that has day either a) a PD

Table 3. Potential Doubling (PD) values from mid July to mid August 1987 calculated from temperatures recorded by a mercury thermometer in a Stevenson screen and a thermistor attached to the RSS-412 orchard monitor

	July			August	
	East Malling agro-meteorological site	**RSS-412 "Predictor"**		**East Malling agro-meteorological site**	**RSS-412 "Predictor"**
16th	8.7	9.8	1 st	10.7	11.9
	6.3	6.3		9.5	10.9
	6.3	7.0		10.2	10.5
	7.0	7.6		6.5	7.1
	8.7	9.5		6.1	7.1
	6.3	7.0		5.8	5.8
	7.0	8.0		5.9	5.9
	7.4	6.3		6.2	6.8
	8.6	9.8		9.0	8.6
	6.1	6.6		7.5	8.2
	6.2	7.1		6.8	7.8
	9.5	9.8		9.8	9.8
	8.9	10.8		10.9	11.7
	9.9	10.7		12.4	12.4
	8.7	8.7		12.3	13.3
31st	13.6	12.3	16th	12.9	13.0

value (calculated from temperatures recorded 08 h to 20 h) were greater than 9, or b) a rainfall over 2 mm, or c) a minimum humidity was over 75% RH. The particular KMS-P instrument used has a rain gauge with a resolution of 1 mm and was therefore unable to detect the 2.5 mm threshold needed by the Billing system: other versions of the KMS-P have a resolution of 0.1 mm rainfall. It must be stated that the orchard monitors are designed for use in the spring blossom period, not September, and assessments of warnings at this time are not strictly valid. There was only one day when the calculation of risk by the Billing system agreed with both the orchard environment monitors; this was on a warm (PD 9) day with a trace of rain. Several other fire- blight risk days were identified by the Billing system; three corresponded with the KMS-P and one with the RSS-412.

Beer *et al* (3) in the U.S.A. have developed a computer model which incorporates a score of 1 to 11 for many of the orchard factors known to affect fireblight in the Eastern States. Some features of the climatic approach of Billing are used to indicate low, medium or high risk. The aim is to arrive at an overall assessment of risk of fireblight in a given orchard in a given season. The risk scores are interpreted as control action is needed (score 1-3), spraying is possibly worthwhile (score 4), spraying is worthwhile (score 6) and spraying is crucial (score 9).

In France, a computerised programme for fireblight spray warnings based upon the Billing system is under evaluation (14). It consists of daily computerisation of climatic data for an estimation of the risk of fireblight (scored as 1-6) and,as another component, an estimation of the local inoculum level according to the past history of the disease (scored 1-5). Combined scores of climatic and orchard/inoculum factors in three phases of the host growth early in the season result in warnings to growers to either take no action (total score 5), to search for

Table 4. Development (D) periods in July and August 1987 calculated from weather data recorded by standard agro- meteorological site (East Malling) instruments and the RSS- 412 orchard monitor

	Agro-meteorological site, East Malling		RSS-412 "Predictor"	
Date D period started	**Date ended**	**No. of days**	**Date ended**	**No. of days**
16 July	20 July	4	19 July	3
17 July	21 July	4	20 July	3
22 July	26 July	4	28 July	6
1 August	9 August	8	13 August	12
4 August	14 August	10	16 August	12

and cut out infections (total scores 6 or 7), or to spray (total score 8, or 7 if either component risk has been maximal).

Conclusions

Much progress has been made towards devising practical warning systems for apple and pear growers. With any system much depends on the incorporation of knowledge of local orchard factors. None of the present systems incorporate wind, other than as damaging storms: wind-borne dispersal of bacterial strands is difficult to quantify and its role in disease spread uncertain. Similarly, it is difficult to quantify bee activity.

Instruments used to monitor weather are of basic importance. The reliability of any warning system will depend on the sensors. Unless the sensors are accurate and record all the data needed to operate the fireblight model, the accuracy expected from microprocessor-based monitors sited in orchards will not be achieved. Butt (11) has demonstrated differences in the perfomances of three commercial orchard monitors in measuring the physical environment. Where instruments are to be used by growers rather than meteorologists or electronic engineers, failure to regularly check and calibrate sensors could lead to inaccurate warnings.

The simpler the system the greater will be its limitations. Whatever system is used, the information it produces must be supported by personal experience of the disease and daily alertness to fireblight.

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Electronic monitoring and interpretation of microclimates

K. Germann

Anton PAAR KG, Graz, Austria

Abstract

The KMS-P is a robust and reliable electronic weather-recording system with a built-in microprocessor, allowing direct evaluation of the environmental data. It is an easy-to-use device and its models provide warnings of apple scab (*Venturia inqequalis*), fireblight (*Erwinia amylovora*) and leaf roller (*Adoxophyes orana*). Other crop protection information for use in apple growing includes cumulative heat sums. Extra options offer good research facilities for scientists. The system can be adapted for other crops.

Key words: apple scab, electronic device, fireblight, leaf roller, lightning, microprocessor, monitoring, sensors, warnings, disease control.

Introduction

The monitoring of meteorological conditions is a basic requirement in supervised crop protection. The conventional ways of recording and interpreting temperature, leaf wetness and air humidity are time-consuming. Modern electronics, however, allow the use of inexpensive but automatic weather stations which, in addition, operate models built to give warnings and forecasts of pests and diseases.

Such an electronic warning system has to satisfy the following criteria:
- maintenance-free operation over a complete season.
- adequate accuracy and resolution of the sensors.
- approved predictive models.
- enable growers to take rational crop protection decisions.

For scientists, further requirements have to be met:
- data transmission to other computers.
- safe storage of data.

- extra sensors for either new or improved biometeorological models.

These requirements are discussed in the context of the instrument KMS-P (Anton Paar KG) (8) (Fig. 1).

Description of the KMS-P

The KMS-P is an instrument to which various environmental sensors can be connected. The basic assembly comes with two leaf-wetness sensors, one combined temperature and air humidity sensor (T/H Combi-Sensor) and one precipitation meter. The device must be located at a representative site on the fruit farm. The instrument and the T/H Combi-Sensor are housed in a standard meteorological screen or the T/H Combi-Sensor, equipped with a heat-radiation shield, is exposed in the field. The instrument must be protected from water. Eventually, the T/H Combi-Sensor, precipitation meter and one leaf-wetness sensor will be mounted on a mast.

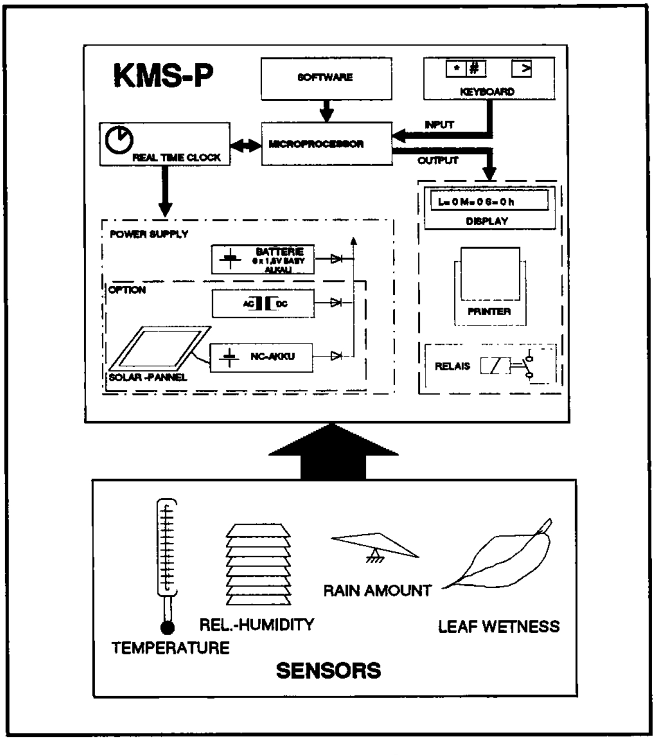

Fig. 1. Functional diagram of the KMS-P.

Six standard 1.5-volt alkaline batteries are used as the power supply for the instrument and sensors. For the basic assembly, one set of batteries is sufficient for six months.

The KMS-P is portable and can be used for after-season control of fruit stores. By replacing the batteries with a power supply unit, the software automatically changes to the fruit-store control mode. In this mode, a lower and upper limit for both temperature and relative humidity can be specified. A relay closes when a limit is exceeded, thereby setting off an alarm. In the case of stores with air-conditioning (which means constant a air humidity), the relative humidity can be controlled by means of the relay.

If more sensors are used - which can be achieved by "channel expansion" - there is an increase in power consumption: six Ni-Cd batteries, which can be recharged via a solar panel with a controller, are then needed. In addition, this solar panel permits light/dark recognition - the threshold value of which is adjustable.

Measured and calculated data are printed hourly. Furthermore, details for the 24-h day are printed at midnight. Current sensor readings are shown on the built-in LC display. The instrument is easy to operate with only three keys/buttons to push.

For research applications the KMS-P can be modified to accept a RAM-Card (same dimensions as a bank-card but 4 mm thick), allowing data storage for approximately 2 months. These data can be transmitted to another computer by means of a RAM-Card Interface via the RS 232 C serial interface (Fig. 2).

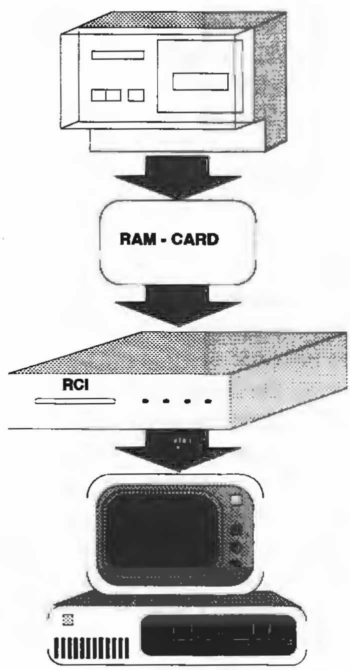

Fig. 2. Data transmission from the KMS-P

Sensors

The sensors which are used to record meteorological variables have to fulfil the following requirements:

- easy handling and operation with minimal problems.
- known performance details.
- known systematic errors thereby allowing the use of correction factors.

The measurement of temperature, relative humidity, leaf wetness and precipitation are essential for forecasting

Venturia inaequalis, Plasmopara viticola, Phytophthora infestans and *Pseudoperonospora cubensis*. Wind velocity and wind direction may also be of value.

Temperature

The T/H Combi-Sensor uses a thermistor, which is a semiconductor element on a metal-oxide base. The electrical resistance varies with temperature according to an exponential function with a negative coefficient of temperature.

The maximum measuring error of this thermistor is 0.2 °C in the range -10 to +60 °C. The total error (sensor plus electronics) is 0.3 °C, with a resolution of 0.1 °C. Calibration of the sensor results in a total measuring error of less than 0.3 °C (between -10 and +60 °C). To maintain accuracy over long periods, checking and readjustment of the thermistor must be done according to the German Standard VDI 3786 (9). Experience with thermistors indicates that checking every 6 months should be sufficient.

Incorrect installation of the KMS-P could cause errors due to heat radiation, heat conduction, precipitation, wind or air pollution. Even with correct installation in a meteorological screen and using a thermometer according to the German Standard 58656, the recorded temperatures may deviate from the actual values up to 2 °C higher in the day and up to 1 °C lower at night, assuming slight air movement and some clouds.

The T/H Combi-Sensor has an adequate radiation shield which allows excellent ventilation and minimizes the response time. The temperature sensor should be placed 2 m above ground, according to VDI 3786 (2). For a distance of 3 m from the sensor the ground should be fairly flat, free of obstacles and consist of short grass. Nearby obstacles should be at least as far away as their height.

Relative humidity

Air is a gas mixture consisting of a definite amount of water in solid, liquid or gaseous phases. This water generates a vapor pressure. The maximum water vapor pressure achievable at a specified temperature is called the saturated steam pressure: the relative air humidity is the ratio of the actual water vapor pressure to the saturated steam pressure at the given temperature (Fig. 3).

Various physical phenomena are used for measuring the relative humidity of air. Capacitive sensors are ideally suited for electronic measuring instruments: a hygroscopic dielectric placed between the two electrodes of a capacitor is in equilibrium with its surroundings, and the equilibrium is dependent on temperature and air humidity.

The humidity sensor used with the KMS-P is manufactured by the Finnish company VAISALA, which has much experience of measuring air humidity. The total measuring error of both the sensor and the electronics is less than 2% over the range 0.2 to 90% RH, and less than 3% over the range 90 to 100% RH, at an ambient temperature of 20°C. The temperature dependence of the sensor is less than 0.04%/°C. To achieve higher accuracies, single- and two-point calibrations are available. Errors of less than 1% are possible. Checks at least every 6 months are recommended to ensure the reliability of the sensor. Calibration can either be performed with special calibration boxes or with an Asmann psychrometer.

As with temperature, the measurement of relative humidity is affected by heat radiation, heat conduction, precipitation, wind and air pollution. The total measuring error depends on sensor installation. To minimize the total measuring error the sensor requires a radiation shield or must be housed in a meteorological screen.

Leaf wetness

Meteorologists do not measure leaf wetness. The drying behavior of plant leaves must be imitated by special sensors. The drying time of a leaf depends on its size, shape and position. It is only possible, therefore, with an electronic sensor, to produce an average value for the length of a wet period.

Anton PAAR KG wanted to develop a leaf wetness sensor for the KMS-P which satisfied the following needs:

- close imitation of the drying behavior of leaves
- variable drying times in specified ranges
- resistant to weathering
- maintenance-free.

These requirements led to a capacitive sensor, the drying time of which can be varied in the range 0.5 hours by using plastic string windings. Correct and horizontal mounting gives good drying characteristics. The threshold values for states of "WET" and "DRY" can easily be set in the software, thus allowing adaptation to the drying behavior of various crops under different conditions (eg. leaf canopy stages).

Two leaf-wetness sensors are used with the KMS-P. The first has to be positioned outside the tree canopy and is used to imitate the drying of the outer leaves. The second is placed within the canopy.

$$\text{RELATIVE HUMIDITY} = \frac{\text{VAPOUR PRESSURE}}{\text{SATURATION PRESSURE}} \bullet 100 \quad [\%]$$

Fig. 3. Calculation of the relative humidity.

Precipitation meters

Two rainfall meters with different resolutions are available for the KMS-P. Both models are based on the "drop sensor" method. The drop sensor is situated between a collecting funnel and a tipping bucket. Drops run into the tipping bucket until it tilts thus actuating an electronic switch (Fig. 4).

The smaller (standard) model has a resolution of 1 mm. Tests yielded deviations up to 15%. Incorrect installation and insufficient maintenance of the funnel are sources of error. Also, insects can tilt the bucket. For greater accuracy a precipitation meter with a surface area of 500 cm^2 and a 0.1 mm resolution is available. This model has an optional heater.

The accuracy of rainfall data is mainly influenced by evaporation, installation, debris in the funnel, insects and wind.

Wind direction and wind velocity

In the context of practical pest and disease forecasting, wind is of secondary importance. For scientists, however, this factor may be significant. According to VDI 3786 (10), ground wind should be determined at a height of 10 m. Wind direction and wind velocity have to be measured by two instruments which do not interfere with each other.

Incorrect values may be due to instrument wear, contamination, corrosion and mechanical interferences. Periodical maintenance is necessary.

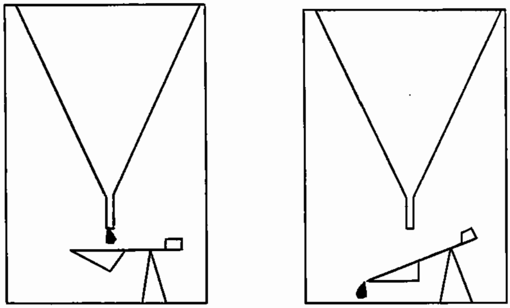

Fig. 4. Rainfall meter.

Lightning protection

Electronic instruments located outdoors are liable to damage from lightning strikes. The striking frequency of lightning per square-kilometer is 0.3 to 3 in Northern Germany and Scandinavia, 3 to 7 in the Lower Alps and 30 to 70 in subtropical and tropical areas (5).

No protection measure can economically or effectively prevent a direct lightning strike. Protection against indirect lightning strikes is, however, very important. Lightning damage is rare, especially if the leads do not exceed a few meters in length because then their impedance is too high. Long leads always cause problems, as shown in the two following examples (Fig. 5).

1. An electronic device in a building is connected to the ground. The sensor outside the building is connected to the device by a long signal line. In the case of a direct lightning strike to the ground the voltage potential of both the device and sensor will be increased. A voltage difference of more than 100 kV may occur at the site of the sensor causing a flashover due to voltage drag.

2. Device and sensor are both situated outdoors, are earthed and inter-connected by a long signal line. When lightning strikes, the lightning current flows to earth, causing a voltage funnel and a difference in voltage potential between device and sensor. A small part of the lightning current flows to the sensor over the signal line. The device is destroyed due to a high-stepping voltage.

To avoid interference due to indirect lightning strikes or resistance coupling, the KMS-P is installed in an orchard using short lines. All sensors and inputs to the basic instrument are protected from excess voltage. There has been no failure of the KMS-P due to lightning.

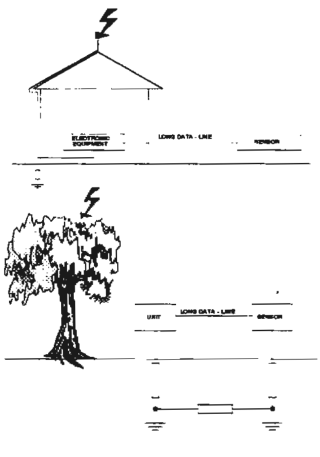

Fig. 5. Source of lightning damage.

Apple pest and disease warnings

Every hour, the risk of apple scab (*Venturia inaequalis*) infection is calculated according to a modified Mills' Table and printed. At midnight, information is printed, giving two Degree-Day sums (the base of which is selectable between 0 to 29 °C), the percentage development of leaf roller (*Adoxophyes orana*) eggs and of the fireblight (*Erwinia amylovora*) risk that day.

The calculations leading to these items of information can be discussed in the example printouts of 9th and 10th July, 1987 (Table 1).

On July 9th, leaves were wetted between 8 and 9 a.m.; column "N" shows the symbol "#" for wetness. A rain precipitation of 1 mm was recorded until 11 a.m., but during the next hour the rainfall was 7 mm. At an average temperature of 18.4 °C during the wet period the condition for slight infection by apple scab was fulfilled after 9 hours. This is indicated on the printout by the symbol "*". At the

Table 1. Printout of the KMS-P from the 9th and 10th July, 1987.

* 1987-07-09 *
Start : 1987-06-25
13:24 Uhr

Zt h	T C	RF %	NS mm	N	LMS	Std h
1	19.4	89				
2	19.9	87				
3	19.5	87				
4	18.5	85				
5	19.2	88				
6	19.0	90				
7	19.4	91				
8	20.3	84				
9	19.5	90		#		
10	19.5	93		#		
11	18.4	98	1	#		
12	17.5	99	.7	#		
13	18.3	99	4	#		
14	18.2	97	1	#		
15	18.2	98	1	#		
16	18.0	95	1	#		
17	17.7	99	1	#	* -	
18	17.6	99	1	#	* -	1
19	17.8	99		#	* -	2
20	17.2	99		#	** -	
21	17.0	99		#	** -	1
22	16.1	99		#	** -	2
23	15.2	99		#	** -	3
24	14.7	99		#	** -	4

GT - 0	: 678
GT - 10	: 309
NS - Start	: 22mm
NS - Tag	: 17mm
FSW-Ei	: 10.5%
! F B - T A G !	

* 1987-07-10 *
Start : 1987-06-25
13:34 Uhr

Zt h	T C	RF %	NS mm	N	LMS	Std h
1	13.9	88		#	** -	5
2	13.8	99		#	***-	
3	13.6	99		#	***-	1
4	13.6	99		#	***-	2
5	12.8	99		#	***-	3
6	12.8	99		#	***-	4
7	12.9	99		#	***-	5
8	13.0	99		#	***-	6
9	14.8	99		#	***-	7
10	16.8	94			...-	8
11	18.9	78			...-	9
12	20.1	75			...-	10
13	21.7	61			...-	11
14	23.2	58			...-	12
15	23.1	50			...-	13
16	23.9	48			...-	14
17	23.8	48			...-	15
18	23.3	47			...-	16
19	23.3	51			...-	17
20	22.2	58			...-	18
21	19.5	69			...-	19
22	17.2	77			...-	20
23	16.3	85			...-	21
24	15.4	88			...-	22

GT - 0	: 696
GT - 10	: 317
NS - Start	: 22mm
NS - Tag	: 0mm
FSW-Ei	: 8.1 %

same time, a counter started within the KMS-P which indicated the number of hours following the infection period. Rainfall continued and conditions for a medium risk of infection were satisfied at 8 p.m. and for a severe risk at 2 a.m. the following day. The printout showed by "...-8" that 8 hours had elapsed since the severe risk of infection was registered. Prior to starting a new recording period the counters are set to zero.

For 10th July, a value of 18 was calculated for the Degree-Days (DD) above 0 °C, and added to the accumulated sum obtained the previous day (678 + 18 = 696 DD). Likewise, a value of 8 DD was calculated above 10 °C and added to the cumulative value of the previous day (309 + 8 = 317 DD).

Table 2. Printout of the KMS-P.

```
*      1985-08-07       *
Start        : 1985-07-27
               10:09 Uhr

Zt  T   RF  NS N -Std SI
 h  C   %   mm         %

 1 13.4 81             59
 2 12.9 87             60
 3 12.5 92             60
 4 12.7 96             60
 5 13.3 89             61
 6 13.3 97     # - 13 61
 7 12.9 99   1 # - 26 62
 8 12.7 99     # - 39 62
 9 13.3 99   1 # - 52*62
10 13.4 99     # - 66*63

==========================
      NEUE PERIODE
*  1985- 08-07  10:30  *

Zt  T   RF  NS N -Std SI
 h  C   %   mm         %
--------------------------
11 14.0 99     # - 79*
12 14.2 97     # - 93*
13 15.5 94     # -108*
14 17.1 81     # -125*
15 18.5 75     # -143*
16 17.9 72
17 18.0 80
18 17.9 79
19 17.8 80
20 17.3 89
21 16.8 88
22 16.6 92
23 16.4 97
24 16.4 96
--------------------------
GT - 0             : 1424
GT - 8             :  844
NS - Start         :   0mm
NS - Tag           :   2mm
```

```
*      1985-08-08       *
Start        : 1985-08-07
               10:30 Uhr

Zt  T   RF  NS N -Std SI
 h  C   %   mm         %

 1 16.4 97
 2 16.0 99
 3 15.8 99
 4 15.6 99   1 # - 16 SP
 5 15.2 99     # - 31 99
 6 15.1 99     # - 46 99
 7 15.2 99     # - 61*IK
 8 16.2 99     # - 77* 1
 9 16.8 99     # - 94* 1
10 17.5 97     # -111* 2
11 18.2 90     # -129* 2
12 19.3 75     # -147* 3
13 20.7 70     # -167* 4
14 22.6 54              5
15 23.5 58              6
16 23.2 53              7
17 22.5 58              8
18 23.2 50              9
19 22.8 50             10
20 20.9 65             11
21 18.0 81             12
22 16.9 90             13
23 15.7 99             13
24 15.7 99             14
--------------------------
GT - 0             : 1442
GT - 8             :  854
NS - Start         :   1mm
NS - Tag           :   1mm
```

For determining the stage of development of leaf roller eggs, the average temperatures between 8 p.m. and 7 a.m. and between 8 a.m. and 7 p.m. are used. A percentage development value is given by these average temperatures. The daily percentage values are accumulated after frequent flights of the moth; at 100% the eggs have latched. This calculation is based on the temperature-sum rule by DeJong and Beeke (4).

On 9th July, the conditions for a possible fireblight attack were satisfied. The warning "FB-TAG" (fireblight day) is based on the fireblight forecasting model by Zeller (7), which is referred to by B (1,2,3). Another fireblight model is currently under preparation, based on the work by Schouten (6).

Disease warnings in other crops

Although not relevant to the topic of apple and pear diseases, it should be mentioned that the KMS-P can be provided with models for forecasting *Plasmopara viticola, Phytophthora* and *Peronospora cubensis*.

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Tests of temperature and humidity sensors supplied with microprocessor-based orchard environment monitors

D.J. Butt and C.V. McGlinn

AFRC Institute of Horticultural Research East Malling, Maidstone, Kent ME19 6BJ England

Abstract

Temperature and humidity sensors supplied with the Metos D,KMS-P & RSS-412 orchard environment monitors were tested under controlled conditions. Readings of standard instruments were synchronised with the scanning of the test sensors by the monitors. The overall performance of the temperature sensors was good, with the three semiconductor sensors used with the Metos D giving average deviations from the standard reading of 0.45-0.56 °C; the deviations with the thermistors of the other two monitors was slightly greater, and this difference was associated with their non-linear response curves. The average deviation from the standard readings of humidity read by the test sensors was 4.0-7.4% RH. With the capacitive-type sensors of the Metos D & KMS-P, only 33% of values were outside the limits of +/- 6%RH. The performance of the wet and dry-bulb thermistor system of the RSS-412 was greatly improved by ventilating its probes.

Keywords: disease control, apple, temperature, humidity, microprocessors, sensors, environment monitoring.

Introduction

Frost, drought and hail are examples of meteorological phenomena damaging to outdoor crops. Weather also threatens crops indirectly through affects on pathogens and pests. By monitoring the physical environment on fruit farms and knowing the effect of meteorological factors on key events in the life cycles of pathogens and pests, it is possible for growers to time control treatments according to local conditions. This decision-based (supervised) crop protection strategy enables a judicious use of chemicals which for environment, economic and scientific reasons is better than "calender" or routine spraying and the consequent intensive use of fungicides, so common in orchards. At the first meeting of this IOBC/WPRS subgroup, Galli (1) described instruments for monitoring orchard environments. He noted increased interest among growers in electronic devices giving automatic warnings when conditions have favoured certain pests and diseases. Galli stressed the need for adequate testing of the sensors and predictive models used with these instruments. It seemed to the authors that sensor tests must precede the evaluation of the predictive models. This paper reports the performance of the temperature and relative humidity sensors supplied with three orchard monitors.

Materials and methods

Microprocessor-based instruments under test

The three orchard monitors are named in Table 1. All are battery powered and each displays information on both an LCD and a printer. All three indicate when the minimal environmental conditions for infection of apple by scab (*Venturia inaequalis*) have occurred: the KMS-P and RSS-412 ("Predictor") give warnings of fire blight (*Erwinia amylovora*) and the KMS-P also calculates the daily egg hatch of the leaf roller (*Adoxophyes orana*). All three instruments display current and summarized values of temperature, relative humidity (RH), rainfall and the state and duration of surface wetness, and also calculate degree-days. Table 1 describes the sensors tested in this study in 1988. Table 2 shows the manufac-

Table 1. Types and positions of sensors tested on three orchard environment monitors

		screened sensors	Non-screened sensors	
Model	**Manufacturer**	**Temperature**	**RH**	**Temperature**
Metos D	Gottfried Pessl Wiez, Austria	semiconductor A	capacitive (Philips)	semiconductors (B,C)*
KMS-P	Anton Paar Graz, Austria	thermistor	capacitive (Philips)	-
RSS-412	GE Reuter-Stokes Twinsburg, Ohio, USA	thermistor A	thermistor (dry bulb A wet bulb B)	- -

* Integrated with the two surface wetness sensors

turers' performance specifications of the sensors supplied in 1988. The Austrian monitors have since been modified and improved.

Standard recorders

Temperature

A calibrated digital thermocouple with an accuracy of +/-0.1°C: an air-temperature probe was used except when recording the inner surface of the wick of the RSS-412 "wet-bulb" thermistor when a surface probe was used.

Relative humidity

1. A dew-point meter (Michell Instruments, Cambridge Series 3000) reading to +/-0.3-0.6% RH (at 21°C), using the above thermocouple for temperature readings. The dew-point meter was innaccurate above 26°C.

2. An aspirated thermistor-type digital psychrometer, reading to +/-1%RH.

3. An Assmann psychrometer. Both 2 and 3 were compared with the dew-point meter and found more accurate than other RH recorders tested. The average readings of 2 and 3 were used when a dew-point reading was not available (i.e. when the temperature was over 26°C).

Table 2. Manufacturers' specifications of sensors as supplied for each of three orchard environment monitors

Model	Resolution		System accuracy		Sensor scanning interval
	Temp	RH	Temp	RH	
Metos D	0.1°C	1%		+/-3%	12 min
KMS-P	0.1°C	1%	+/-0.5°C	+/-4%	15 min
RSS-412	0.1°C	1%	+/-0.5°C	+/-8-9%	1 min

Table 3. Room humidity recorded by the three monitors and the dew-point meter after re-calibration but before the series of RH sensor tests (Temp. 21.6°C).

Monitor	Relative humidity (%) Comparison 1	Comparison 2
Metos D	54	54
KMS-P	53	53
RSS-412	53	52
Dew-point meter	52	53

Test conditions

Temperature

Tests were in an insulated room giving temperature control in the range 2-30°C, each test being done only when a thermograph showed a steady temperature. Three replicate tests were done at each of five temperature levels.

Relative humidity

Before testing, the Metos D was recalibrated against the dew-point meter in the laboratory (21°C, 55%RH); the KMS-P was then calibrated against the Metos D (Table 3). Tests were conducted in two different glasshouse compartments, one polytunnel (with fogging equipment) and at one outdoor site, giving values in the range 40-100% RH. The highest RH was obtained in the fogging tunnel. All humidity tests were done with and without moving air: this was obtained with an electric axial fan 10 cm from the sensor, blowing air at 4.3 m/sec across the sensor.

Table 4. Performance of the three Metos D temperature sensors relative to the standard instrument (Ambient range 2-29°C)

Performance	Position and identity of monitor sensors		
	Screen A	Wetness detector 1 B	wetness detector 2 C
Average error (°C)	0.45	0.56	0.42
Maximum error (°C)	1.0	1.7	1.0
+/- 0.6°C (%)	47	40	20

Table 5. Performance of the single KMS-P temperature sensor relative to the standard instrument (Ambient range 2-29°C)

Peformance	Position of monitor sensor Screen
Average error (°C)	0.65
Maximum error (°C)	1.1
+/- 0.6°C (%)	53

Synchronisation of readings

The monitor values were read from the LCD displays. Each monitor, however, functions differently with respect to displaying the "current" values. The KMS-P can display the instantaneous current sensor reading. The value displayed by the Metos D (sensors scanned at 12 min intervals) is the stored value of the previous reading. The RSS-412 (sensors scanned at 1 min intervals) displays a 10-min average, updated every 5 min. Probes of the standard recorders were placed close to the test sensors: the shield around the KMS-P humidity sensor was kept in place. The standard-instrument probe was used to record temperature at both the top and middle of the RSS-412 dry-bulb thermistor probe. Also, with this monitor the dry-bulb data were collected at each controlled temperature before changing the probe of the standard to the surface-reading type for the wet-bulb reading. Standard instrument readings with the thermocouple (temperature) and dew-point meter (RH) were taken at the time each test sensor was scanned. In the case of the RSS-412, ten 1-min standard observations were taken and their average compared with the monitor value at the end of the same period. The digital and Assmann psychrometer (alternative RH-recording standards) were read at the start and end of the 10-min sampling periods with the RSS-412.

Data presentation

Each data point on the temperature graphs (Figs. 1-3) is the average of three replicate tests. The graphs show the relation of the temperature and RH recorded

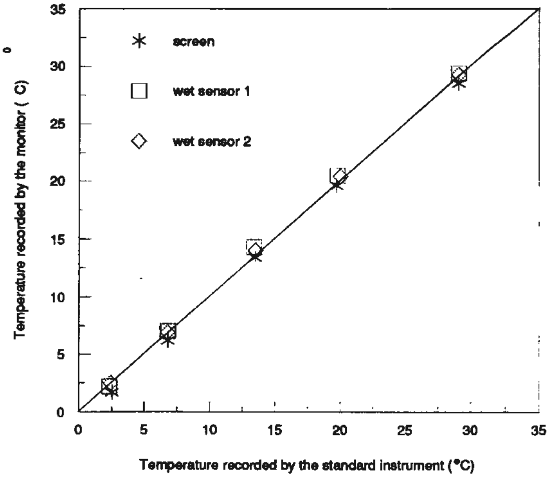

Fig. 1. Relation of temperature recorded by the Metos monitor to the standard reading.

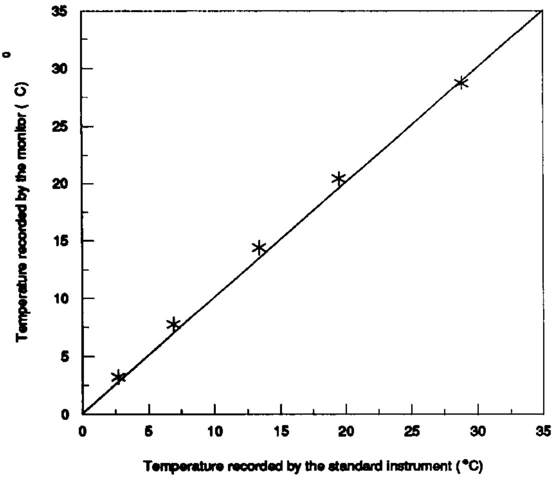

Fig. 2. Relation of temperature recorded by the KMS-P monitor to the standard reading.

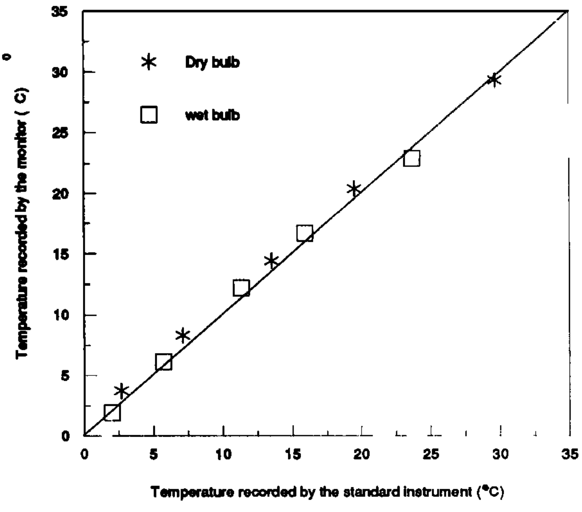

Fig. 3. Relation of temperature recorded by the RSS-412 monitor to the standard reading.

by the monitors to the values recorded by the standard instruments: perfect agreement is drawn as a straight line at 45° through the origin. In the Tables the performance of each test sensor is expressed as the average and maximum deviation (error) from the simultaneous standard reading, and the percentage of readings outside +/-0.6 °C and +/-3s and 6% RH of the standard instrument readings. The tolerance of 0.6°C is the sum of the tolerances of both monitors and standard instruments. (The vector sum is 0.55°C).

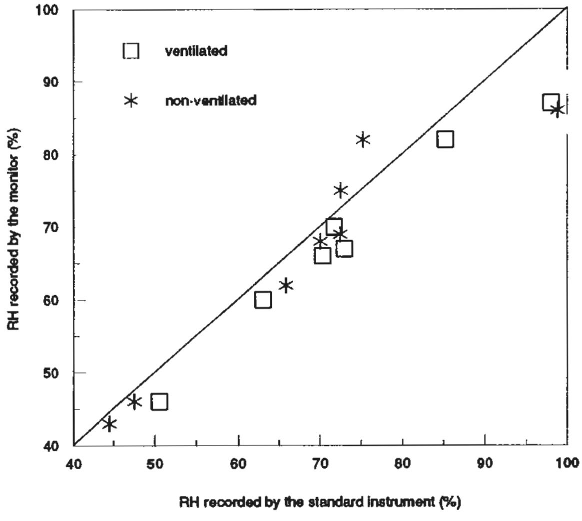

Fig. 4. Comparison of relative humidity recorded by the Metos monitor and standard instruments.

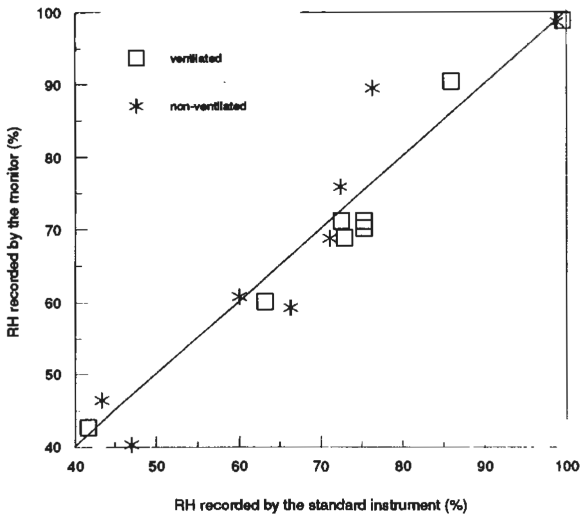

Fig. 5. Comparison of relative humidity recorded by the KMS-P monitor and standard instruments.

Results

Temperature

The RSS-412 results are for standard readings recorded at the mid-point along the monitor's probe; these were marginally nearer the monitor's values than readings at the top of the probe. Tables 4-6 show the performances of the

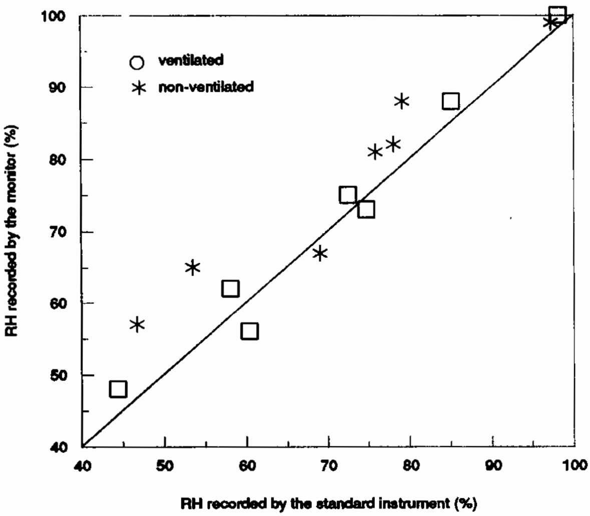

Fig. 6. Comparison of relative humidity recorded by the RSS-412 monitor and standard instruments.

tempèrature sensors on the three monitors. Figures 1-3 show the relation between test sensor and standard instrument over the range of controlled temperatures.

Relative humidity

Tables 7-9 show the performances of the RH sensors on the three monitors. Figures 4-6 show the relation between humidities recorded by the three monitors and by the standard instruments, in still and moving air.

Table 6. Performance of the two RSS-412 temperature sensors relative to the standard instrument (Ambient range 2-30°C)

Performance	Position and identity of monitor sensors	
	Screen - dry bulb	Screen - wet bulb
	A	B
Average error (°C)	0.87	0.59
Maximum error (°C)	1.3	0.9
+/- 0.6°C (%)	73	60

Table 7. Performance of the Metos D humidity sensor relative to the standard instruments (Ambient range 19-33°C)

Performance	Test sensor	
	Non-ventilated	Ventilated*
Average error (%RH)	5.5	7.4
Maximum error (%RH)	15.0	19.5
+/- 3% RH (%)	56	78
+/- 6% RH (%)	33	33

* Air blown over sensor from a fan

Table 8. Performance of the KMS-P humidity sensor relative to standard instruments (Ambient range 19-33°C)

Performance	Test sensor	
	Non-ventilated	Ventilated
Average error (%RH)	6.0	4.4
Maximum error (%RH)	21.0	12.0
+/- 3% RH (%)	56	56
+/- 6% RH (%)	33	33

Table 9. Performance of the RSS-412 humidity recorder relative to standard instruments (Ambient range 19-33°C)

Performance	Test sensor	
	Non-ventilated	Ventilated
Average error (%RH)	6.8	4.0
Maximum error (%RH)	11.5	9.5
+/- 3% RH (%)	78	56
+/- 6% RH (%)	56	11

Discussion

Overall, the performance of the temperature sensors was satisfactory. The semiconductors of the Metos D gave the most accurate readings (Table 4 c.f. 5 and 6), and their response curves over the range of test temperatures were linear (Fig.1). The performance of the thermistors of the other two monitors was less good, with a non-linear trend in their response curves (Figs. 2 and 3): these curves were slight but expected, and led to relatively low readings at the upper temperatures. The performance of the thermistors would be improved by suitable calibration. The performance of the humidity sensors was better than expected, given the well-known difficulties of recording this variable. The capacitive sensors of the Metos D and KMS-P resulted in only 33% of values lying outside the limit of +/- 6% RH (of the standard reading), in both still and moving air (Tables 7 and 8). The effect of ventilation on the wet- and dry-bulb thermistor system of the RSS-412 was marked (Table 9). In fact, the best humidity results were obtained when the RSS-412 was ventilated, with only 11% of readings lying outside the limit of +/- 6% RH. For many plant diseases, high humidity favours processes like sporulation and infection. It is clear from Figs 4 and 5 that although the Metos D and KMS-P use the same type of sensor, their measurement of RH above 90% RH differed, with the Metos D giving low readings. This can be corrected by better calibration at the upper humidities. Plant pathologists must make sure that manufacturers of crop environment monitors maximise the accuracy of recording over the range of humidities important to the disease models being 'driven' by the data.

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Tests of surface wetness sensors used with electronic disease-warning instruments

D.J. Butt and C.V. McGlinn

AFRC Institute of Horticultural Research East Malling, Maidstone, Kent ME19 6BJ England

Abstract

The electrical surface wetness sensors supplied with three commercial, microprocessor - based orchard environment monitors, were tested by applying distilled water in four different quantities and patterns, and comparing the duration of surface wetness with that of similarly-treated apple leaves. Tests were done in still and moving air. All sensors behaved more like leaves when drying in moving air; discrepancies were larger in still air and sometimes very large. The performance of the sensors, relative to leaves, depended on the method of wetting. Features of these results are discussed.

Keywords: disease control, apple, dew, rain, wet periods, surface wetness, environment monitoring, sensors, evaporation, drying time.

Introduction

Most airborne fungal pathogens of crops are "moisture loving", epidemics being most serious in wet conditions. The production, discharge and dispersal of spores of these fungi are often favoured by moisture in the form of vapour or free water, but the process most readily identified with the need for a minimal duration of wetness on plant surfaces is infection.

Surface wetness due to rain and dew is not a phenomenon included in standard meteorological observations, and so special sensors have been produced for use in crop protection (3,4). Representing the plant surface, these sensors indicate the dry/wet state of the crop and measure the duration of wet periods. Three commercial microprocessor-based environment monitors designed for use in orchards, all give warnings when the moisture and temperature conditions have satisfied the requirements for infection by apple scab (*Venturia inaequalis*). Tests of their temperature and humidity sensors have been reported (1). This paper describes tests of their electrical surface wetness sensors.

Materials and methods

Sensors under test

Table 1 shows the surface wetness sensors supplied with three orchard environmental monitors tested in 1988. Tests were conducted separately on each of the five sensors. The Metos D sensors consisted of a grid of gold-leaf foil on the surface of a plastic base measuring 50x25x5 mm. The KMS-P sensors consisted of a grid embedded in glass-reinforced plastic with an active surface 120x75x2 mm: these sensors are wrapped in perlon strings to disperse surface water. The RSS-412 sensor has a 15 mm -long coil of two alternate wires, wrapped around a 12 mm diameter plastic cylindrical former. Moisture on the Metos D and RSS-412 sensors changes their conductivity; with the KMS-P the capacitance changes.

Surface wetness measurements on apple leaves

A young apple leaf of cv. Cox's Orange Pippin was used as follows, as a standard for measuring surface wetness duration. The youngest unrolled leaf near the tip of a detached shoot collected from an orchard was supported on a glass slide by two rubber bands, whilst still attached to the shoot (standing in water). A

Table 1. Microprocessor-based orchard environment sensors and their surface wetness sensors

Model	Manufacturer	Sensor Number	Sensor Shape	Sensor Type
Metos D	Gottfried Pessl Wiez, Austria	2	flat	conductive
KMS-P	Anton Paar Graz, Austria	2	flat	capacitive
RSS-412	GE Reuter-Stokes Twinsburg, Ohio,USA	1	coil	conductive

grid of parallel tinned-copper wires spaced 2.5 mm apart was held against the exposed (adaxial) surface of the leaf. Alternate wires on the grid were connected to electrical terminals Conductance across the grid through water was indicated on a chart recorder.

Test conditions

In a laboratory at 19-22°C and 55-65%RH, the sensors and the apple leaf were wetted with distilled water by applying a single droplet (10μl) using a pipette, by spraying using an airbrush held 7.5 cm from the target, spraying for 1 or 2 seconds to give two levels of deposition resembling dew, and by immersing the sensors in water and then allowing a brief dripping. After wetting, the sensors and the apple leaf were fixed horizontally, except the RSS-412 coil which was held slightly inclined as recommended for use in the field. All wetness duration tests were done in still and moving air: air movement was obtained with an electric axial fan 10 cm from the sensor, blowing air at 4.3 m/sec across the sensor. The wet/dry state of the sensors and duration of wetness of the RSS-412, Metos D and apple leaf was indicated on a chart recorder; for this purpose the sensors of the RSS-412 and Metos D were detached from the monitors. A 7 volt electrical supply was connected to the sensors through a 1M ohm resistor. The potential difference across each sensor was monitored by the chart recorder, set for a full-scale deflection of 5 volt and a paper speed of 2 cm/min. It was not possible to record the state of the KMS-P sensors by this means because of the lack of an exposed conductive surface, and so their wet/dry state was judged by eye.

Data presentation

Surface wetness duration was measured as the number of minutes the pen was deflected above the chart's baseline. At least two replicate tests were done at each combination of sensor, wetting method and air state. For each treatment combination, the difference is duration of the wet period between the apple leaf and each sensor was calculated. The signs "+" and "-" indicate that the sensor dries slower or faster than the apple leaf, respectively.

Results

Table 2 shows the average drying times, in minutes, of the test sensors and apple leaf. Under the "dew" and single droplet conditions, the sensor of the RSS-412 dried the fastest. Drying of all surfaces was consistently faster in moving air. The longest wet periods on the artificial sensors followed drenching, but on the

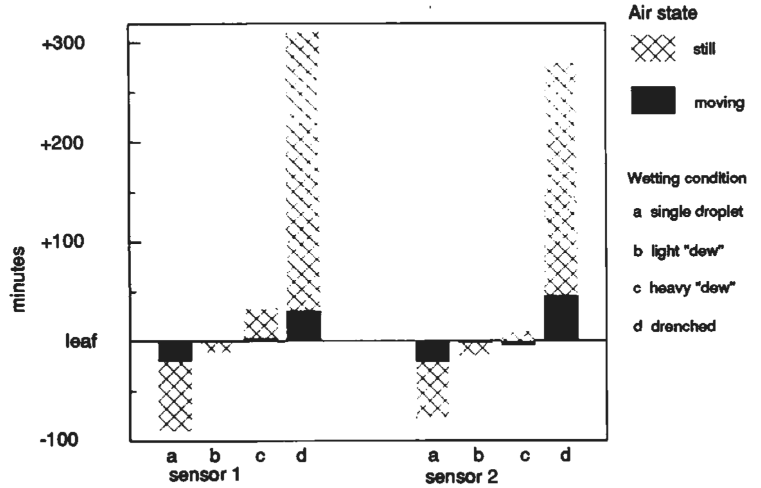

Fig. 1. Difference in wetness duration between an apple leaf and the Metos D sensors under four wetting conditions in still and moving air.

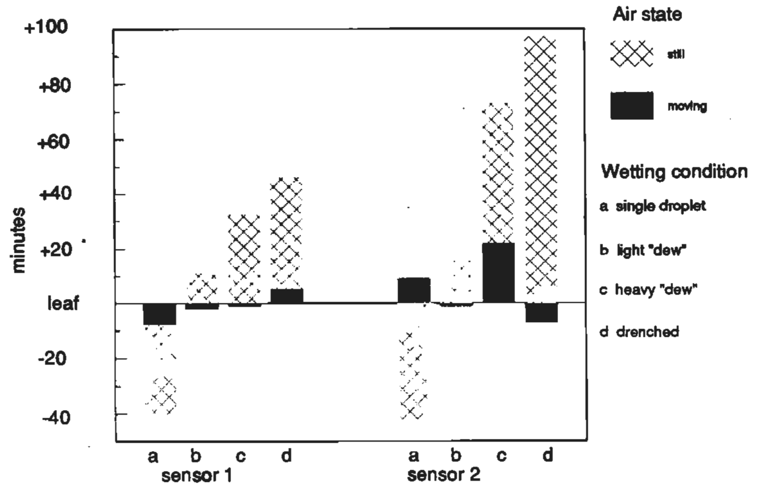

Fig 2. Difference in wetness duration between an apple leaf and the KMS-P sensors under four wetting conditions in still and moving air.

apple leaf the single droplet took nearly twice as long to dry as the water remaining after drenching.

There was an effect of air movement on the difference in drying rates between the apple leaf and the sensors: averaged for all five sensors under all four wetting conditions, the difference in the length of the wet period was 0.8 min and 27.3 min in moving and still air, respectively. The method of wetting also influenced the drying behavior of the sensors relative to the apple leaf (Table 3).

In moving air, the drying rates of the sensors were close to the drying rate of the apple leaf under all wetting conditions. Table 3 shows a trend under both air states: the larger the quantity of applied water the slower the drying of the sensors relative to the apple leaf. This was especially marked in still air, with single droplets on the sensors drying 73 min earlier than on the apple leaf, but drenched sensors taking 160 min longer to dry than the leaf. The performance of the individual sensors is shown in Figs. 1-3. The trend of slower sensor drying (relative to the leaf) with increased water is consistent. Likewise, all the sensors perform

Table 2. Average drying times (minutes) of sensors and apple leaf in still and moving air under four wetting conditions.

Wetting condition	Cylindrical RSS-412 Still air	Moving air	Flat KMS-P* Still air	Moving air	Flat Metos D* Still air	Moving air	Apple leaf Still air	Moving air
Light "dew"	4	1	46	5	20	4	32	6
Heavy "dew"	19	2	81	21	49	10	28	10
Single droplet	12	8	87	33	45	11	128	32
Drenched	131	23	138	23	337	57	66	17

Table 3. Effect of wetting method on the difference in wetness duration (minutes) between an apple leaf and the average of five artificial sensors in still and moving air

Air state	Wetting method: Single droplet	Light "dew"	Heavy "dew"	Drenched
Still	-73	-5	+21	+160
Moving	-13	-3	+2	+17

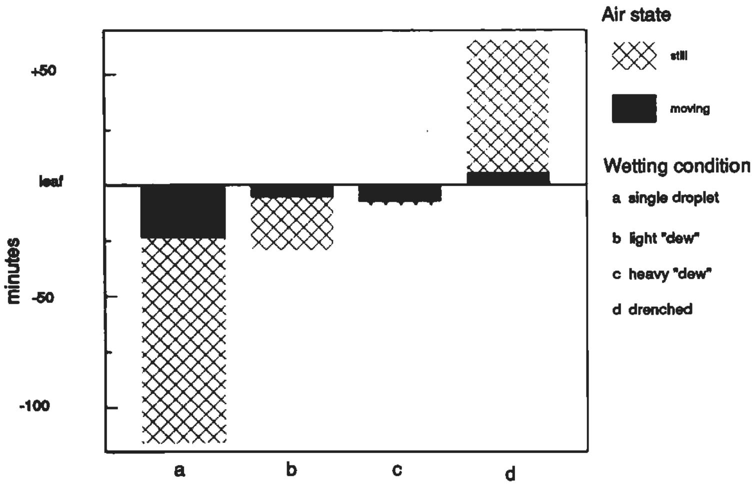

Fig. 3. Difference in wetness duration between an apple leaf and the RSS-412 sensors under four wetting conditions in still and moving air.

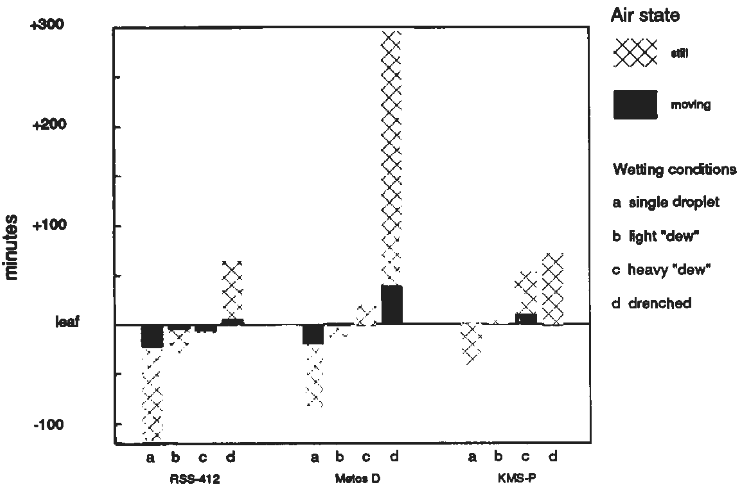

Fig. 4. Difference in wetness duration between an apple leaf and the sensors on three monitors under four wetting conditions in still and moving air.

best when in moving air. For convenience, the sensors of each monitor are shown against a common time scale in Fig. 4.

Discussion

Gillespie and Duan (2) found that droplets of equal size evaporated faster on cylindrical sensors than predicted for flat leaves. In the present study, "dew" and single droplets evaporated faster from the cylindrical RSS-412 than from the flat sensors and the apple leaf (Table 2). The reason may be the spreading of the water droplets between the parallel wires of the coil and hence thinner water films, rather than differences in heat conductance by the various bodies. Single droplets on leaves dried slower than those of equal volume on artificial sensors: this may be due to surface tension differences; drops on the natural leaf were more hemispherical and deeper and hence took longer to evaporate. After drenching, the apple leaf dried faster than the artificial sensors (Table 2). With this method of wetting there was no control over the volume or distribution of water retained on the various bodies. It had been expected that the larger heat capacity of the artificial sensors would have led to the opposite behaviour. It must be stressed, however, that these tests were conducted indoors where low exposure to radiation would have reduced differences in heat conductance. It seems likely that the waxy nature of the leaf retained smaller accumulations of water than on the artificial sensors and so dried faster. The electric current passing through the grid attached to the apple leaf would have had a negligible heating effect, but the grid itself might have dispersed the water retained after drenching, thereby favouring fast drying. The effect of such a grid on the drying behaviour of leaves needs to be studied. Of the four wetting conditions, light "dew" evaporated fastest (Table 2). The light "dew" appeared to consist of smaller deposited droplets than the heavy "dew" or single-droplet treatment. Drop size is a major determinant of evaporation rate (5). Gillespie and Duan (2) found that as air speed increased the evaporation rate of droplets on cylinders and flat surfaces increased, and the difference in evaporation rate between these two types of surface decreased, the drying time of flat surfaces approaching that of cylinders. In the present study all surfaces dried faster in moving air and, as observed by Gillespie and Duan (2), the difference in drying time between the cylindrical and flat sensors was least at the higher speed. Furthermore, all the artificial sensors, of whatever shape, behaved like the apple leaf when drying in moving air. A possible explanation for this effect of air movement is a differential decrease of the boundary-layer thickness around artificial sensors and leaves: the layer around the smooth sensors may be more responsive to increased air speed than the layer around the leaf. The relatively poor performance of sensors in still air would be serious in the field when calm weather followed rain or dew. If the relation of wind speed to sensor performance is quantified, it would be feasible to correct for the variable effect of wind speed on the discrepancy between wet periods on the crop and on the sensors. The KMS-P and RSS-412 performed well in comparison to the leaf (Fig. 4). It must be stressed that the recording of the KMS-P sensors was by eye, in contrast to the electrical measurement of the other sensors. Nevertheless, it was easy to recognise the moment when water disappeared from the KMS-P sensors. The performances of both Metos D sensors was very poor when allowed to dry in still air after drenching: it was noticed that this type of wetting produced large puddles of water held against the sharp edges of the horizontal surface. The resulting large difference in drying time between the Metos D sensors and the apple leaf would possibly be reduced by inclining the sensor to encourage dripping, and by rounding the sharp edges to reduce surface tension.

Acknowledgement

We would like to thank Miss Margo Fox and Mrs Joyce Robinson for their assistance

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Session 2

Disease assessment and simulation

Chairperson: R. C. Seem

Simulation and Optimization of Apple Scab Management

R. C. Seem[1], C. A. Shoemaker[2],
K. L. Reynolds[1], and E. A. Eschenbach[2]

[1]Department of Plant Pathology, New York State Agric. Expt. Sta., Geneva, NY and
[2]Department of Environmental Engineering, Cornell University, Ithaca, NY, U.S.A.

Abstract

Simulation and stochastic dynamic programing techniques are being used to determine better management strategies for the control of apple scab, with the goal of developing better management strategies for the use of fungicides. The disease simulator is linked to simulators for tree growth, weather, fungicide residue degradation and economics. Using available knowledge to estimate and adjust starting values, transfer rates and mortalities in the simulator, the computed level of disease was within 5% of actual orchard measurements made in 1987. Sensitivity analysis of the simulator has identified some important deficiencies in our knowledge of *Venturia inaequalis*, the most important being inoculum level, both ascosporic and conidial. The mathematical optimization of apple scab management, although not completed, is discussed in general terms.

Key words: *Venturia inaequalis*, modelling, disease models, epidemiology

Introduction

Apple scab, caused by the fungus *Venturia inaequalis*, is one of the most intensively managed plant diseases. Yet, in spite of extensive research on this pathogen and disease for the past five decades, current management is simply based on the recognition of weather periods that favour infection by the pathogen. Management actions based on other types of information such as amount of inoculum, tree growth stage and fungicide residue, are considered by decision makers but no formal attempt has been made to use this information in formulating optimal management strategies.

Stochastic optimization methods have been used to establish management policies, principally in the fields of engineering and operations research. Recently these techniques have been used in agriculture and more specifically, in the management of insect pests (e.g. 35), and to a very limited extent, plant diseases (23).

A wealth of new knowledge of apple scab has been incorporated into a refined simulation model for use in developing optimum apple scab management policies based on stochastic optimization techniques. This permits the estalishment of a methodology utilizing stochastic optimization methods as well as simulation models, which might be eventually used to develop effective management strategies for foliar plant pathogens. This research serves as an improved extension of the current strategy of spraying fungicides in accomodance with the occurrence of scab infection periods. Management decisions resulting from this study will be based on not only infection periods, but also available inoculum, tree growth, fungicide residue and the economic potential of the crop.

Background

Mathematical models have been used widely in the development of integrated pest management programs for disease and insect control. Most of the models are simulation models. Ruesink (25) and Conway (6) have reviewed a large number of such models used in the study of insect pests. Simulation models have also been developed for plant pathogens. Waggoner and Horsfall (41) developed one of the first disease simulators. Zadoks (43) has constructed a disease model which is a fundamental part of a supervised control program in the Netherlands. Bruhn (4) developed a detailed model of potato late blight; Fry and Fohner (10) have used this model in comparing conventional fixed-schedule fungicide programs with those based on the disease forecasting system BLITECAST. Teng (39), Teng *et al.* (40) and MacKenzie and King (19) have discussed the use of simulation models in the management of plant disease epidemics.

Apple scab simulation models and supporting experimental studies

Apple scab, caused by the fungus *Venturia inaequalis*, has been the subject of a number of simulation models, including those built by Kranz (15), Analytis (1), Minogue (22), and Arneson *et al.* (2). These models cover a wide range of simulation approaches from the traditional mechanistic model of Kranz's EPIVEN to the gaming methods of Arneson's APPLESCAB; from the regression equations of Analytis's model to the analytical approach taken by Minogue. All have varying strengths and weaknesses resulting from the modelling approaches and the amount of information available about the pathosystem at the time they were built (30).

Within the ten years since the development of the most recent apple scab simulators, considerable additional information on the biology and epidemiology of apple scab has been obtained. Much of this new information is quantitative and suitable for incorporation into simulation models. No one has developed a management model that includes a quantitative description of the impact of weather and management decisions on disease progress and economic damage and that utilises the data generated since 1978.

MacHardy and Jeger (18) analyzed the integration of resistant cultivars and sanitation with fungicide usage by mathematically relating the components that contribute to scab development; but this is a conceptual model that does not attempt to describe quantitatively the pathogen's life cycle or to make specific management recommendations. Several new component models for the maturation and release of *Venturia* ascospores have been published (14, 11) and are improvements over the original maturity model (20). More information is also now available on the infection process and on how genetic and age-mediated resistance is expressed in leaves (12, 24, 26) and fruit (28, 29).

In addition to new data on the biology of the pathogen, more is now known about the host in terms of its phenological development (3, 7, 33; Cullinan and Szkolnik, unpublished). A model uses key environmental data to determine the mean and associated variance of each phenological stage for the vegetative and reproductive apple phenology tracks. The physiological development of the apple tree has also received greater scrutiny (16). A whole-tree apple growth simulator has been described by Elfving *et al.* (8) and Seem *et al.* (34) that follows seasonal development. This simulator has been used to evaluate the effects of pests that affect tree physiology.

Other components of the apple scab system have similarly undergone significant improvement in quantitative information. A detailed dose response curve for the effect of the fungicide captan on infection of *V. inaequalis* on apple leaves has been completed (Seem *et al.* unpublished). This new dose response curve equates the amount of infection to micrograms of fungicide on the leaf surface. Thus the model can be directly linked to fungicide deposition and degradation models. Environmental degradation of captan in the orchard environment has been studied (36) and modelled (37; Seem, unpublished). This model predicts the amount and associated variation (in micrograms/cm^2) of either captan or azinphosmethyl on a fruit, shoot leaf or spur leaf based on the time since application and the accumulated rainfall.

Finally, quantification and estimation of fruit quality loss due to apple scab has been made by Seem and Gilpatrick (31). In their model, economic loss was calculated as the reduction in fruit value due to scab-caused downgrading of fruit according to the standard USDA grading system. Utilizing this method, losses due to apple scab can be isolated from losses caused by other pests or poor quality, thus assuring a true assessment of disease loss. Yield loss was not included since under most commercial situations, apple scab only causes blemish or quality loss. Model validation is currently being conducted.

In spite of all these research developments in apple scab and crop production, disease management still relies almost entirely on one simple decision aid, the Mills infection period (21). Although intuitively considered in many integrated pest management programs, the new information needs to be quantitatively and formally linked in order to utilize modern procedures for optimizing management decisions.

Use of optimization models in pest management

As explained below, there are major advantages associated with the use of stochastic optimization models, especially for management problems like disease control where random events, such as weather, can have a major impact on economic damage and on efforts aimed at limiting it. Optimization models have been applied in disease management to a very limited extent (23), but they have been applied to a number of insect pests. Wickwire (42) and Feldman and Curry (9) have written reviews which include a description of some of the applications of optimization models to insect pest management.

In order to use a simulation model to evaluate the economic impact of different management strategies, the simulation model must be computed for each strategy. This is not a difficult task if fungicide is only applied once per season because there are probably only a few schedules one would need to compare. For example, if there were eight different dates to choose between, then one would only need to compute the simulation model eight times. One might also want to consider several different weather patterns. With fifteen weather patterns only 15x8 = 120 simulations would be needed. Including several cultivars and sanitation options would still require less than one thousand simulations. Given the low cost of computing, this number of simulations would be feasible, although it would probably not be possible to perform such an analysis for each local area. The problem of using a model to compare management alternatives becomes much more difficult when there are a large number of control decisions made every year. For example, consider the situation in which a decision is neede on whether or not to apply a fungicide each week over a 12-week period. The possible number of spray schedules is $2^{12} = 4096$. Comparing these spray schedules over 15 different weather patterns would require 4096x15 = 61,440 simulations. This amount of computing might be feasible for a single cultivar in one location, although expensive and time-consuming. However, it would be impossible to repeat for several cultivars, cultural practices and regions.

Hence, it is not possible to use simulation models to compare all possible spray schedules if there are a large number of possile sprays and time periods. There are two ways to circumvent this problem. First, one can select for examination by trial and error simulation a few of the spray schedules thought most likely to be effective, and not consider the others. This is a reasonable approach but there is the possibility of not selecting in this initial screening the schedules which are most desirable. This is especially true if including a range of weather conditions, because the best policy would be expected to depend on temperature and rainfall. It would be difficult, without extensive trial and error simulations, to guess which policies would be best over a wide range of weather conditions.

A second approach is to use numerical optimization methods. Given a specified objective (like maximizing profit), optimization algorithms will select the management strategy which maximizes the objective without exhaustive trial and error simulation of every alternative. These procedures operate by analyzing the mathematical structure of the economic and population equations. As outlined above, optimization methods are most useful in situations where there are a large number of management alternatives, as is the case when fungicide spray applications need to be made many times each year, and when a large number of weather patterns can occur.

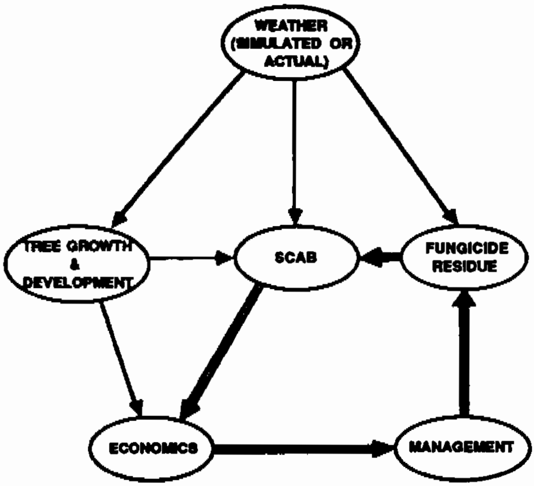

Fig. 1. General design of the simulation program for apple scab optimization.

Methods

Overview of the apple system

The apple scab system, as we have designed it, consists of six major components (Fig. 1). The components are Management, Fungicide Residue, Weather, Tree Growth, Economics and Scab. Four of the components (Management, Fungicide Residue, Economics, Scab) constitute the optimization portion of the system because disease control decisions (fungicide application) made in the Management component first affects Fungicide Residue, which in turn affects Scab; the level of scab directly influences Economics (yield and fruit quality), and the expected returns from the crop influence Management decisions. The remaining components, Weather and Tree Growth, are considered to be external to the optimization because weather and tree growth and development are not affected directly by control decisions.

In the simulation program, the Management component is the main program which takes the simulator through its daily iterations and calls for the application of fungicide. Fungicide Residue tracks the fungicide residue on leaf and fruit surfaces. Weather influences the level of residue after application. In the Scab component, the pathogen is tracked through its growth and development, including the amount of disease on fruit and leaves. Pathogen development is influenced by fungicide residue, weather and the area of tissue. The Economics component considers the distribution of disease on fruit and computes the damage resulting from loss of fruit quality. The yield and size distribution of fruit (from Tree Growth) and the amount of disease (from Scab), influence Economics. The Weather component contains either a simulator adapted from Bruhn *et al.* (5) and parameterized for Geneva, NY, or, for validation purposes, the actual weather data from Geneva, NY. The Tree Growth component consists of a carbon balance tree growth simulator (8, 34). This component also computes the amount of susceptible apple tissue.

The entire apple system simulator is written in Fortran 77 and contains approximately 4,000 lines of code. Development of the program was done on a Prime 9950 minicomputer, but the program can run on a microcomputer. When combined with the optimization program the simulator will be executed using IBM 3090 super computers located at Cornell University's National Supercomputer Facility.

Validation of the simulator

The apple system simulator was validated in a small (0.35 ha) apple orchard located at the New York State Agricultural Experiment Station, Geneva, NY. It consisted of a mixed planting of 9-year-old trees of McIntosh, Empire, and Golden Delicious cultivars on MM111 rootstock and M9 interstem. The orchard was divided into two treatments, with three replications for each cultivar. The two treatments consisted of no fungicide sprays and reduced-frequency sprays of captan 50W.

Environmental data were collected at an adjacent site using a data logger and electronic sensors to record temperature, relative humidity, leaf wetness, rainfall, solar radiation, and wind speed and direction. In addition, a volumetric spore trap (Burkhard) recorded ascospore discharge from a bait plot containing infected, overwintered apple leaves. All data were recorded at a frequency of one hour.

Measurements of tree growth and disease development were taken at regular intervals throughout the growing season. Tree phenology for both vegetative and generative tissue was recorded ten times using the numeric code system of Seem and Szkolnik (33). Individual leaf area measurements for shoot and spur leaves were made seven and six times, respectively. Total leaf areas for shoot and spur leaves were estimated at the end of the growing season based on sub-sample estimates of leaf numbers regressed on major scaffold branch cross-sectional area. Disease was measured six times during the growing season by counting lesions on subsamples of shoot, spur and fruit. Lesion areas were also measured twice during the season on the same tissue types.

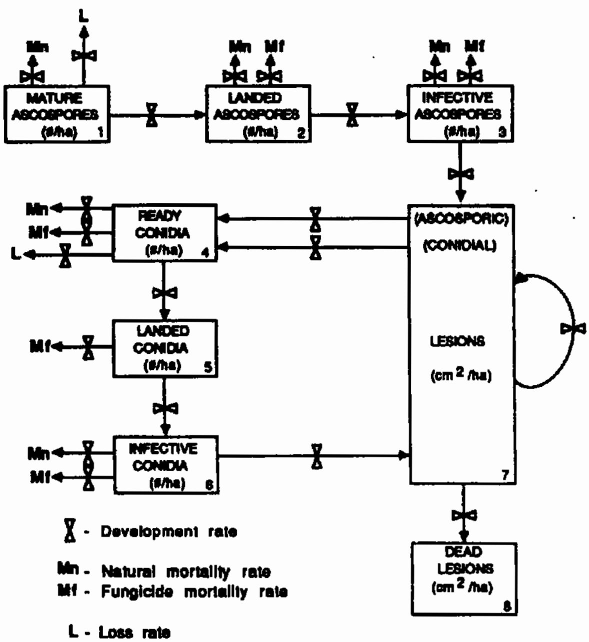

Fig. 2. Flow diagram of the apple scab component of the apple scab system simulation.

A limited sensitivity analysis of the simulator was conducted by varying some of the major variables, one at a time, while keeping all other variables unchanged. The variables used in sensitivity analysis were initial ascosporic inoculum, conidia production rate, the number of captan sprays, temperature, duration of leaf wetting and tree density.

Results

Apple system simulation

Because of the complexity of the apple scab system simulator, only the major components will be discussed here, including the disease simulator, the fungicide simulator and the economics component. Details of the tree growth simulator and weather simulator can be obtained from publications (4, 8, 34).

Apple scab component

The apple scab simulation module consists of eight state variables, Mature Ascospores, Landed Ascospores, Infective Ascospores, Ready Conidia, Landed Conidia, Infective Conidia, Lesions, and Dead Lesions (Fig. 2). Although the APPLESCAB game simulator served as the basis for this module, major revisions were made, particularly with the constants associated with mortalities and

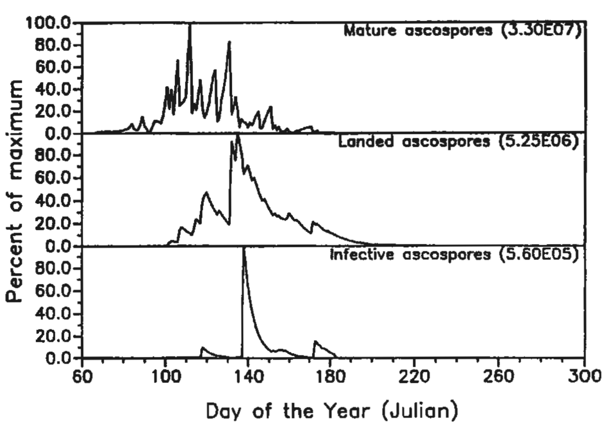

Fig. 3a. Seasonal dynamics of the state variables Mature Ascospores, Landed Ascospores, and Infective Ascospores during the simulation of the 1987 growing season. No fungicide was applied. Variables are expressed as percent of maximum, the number in parentheses (expressed in scientific notation).

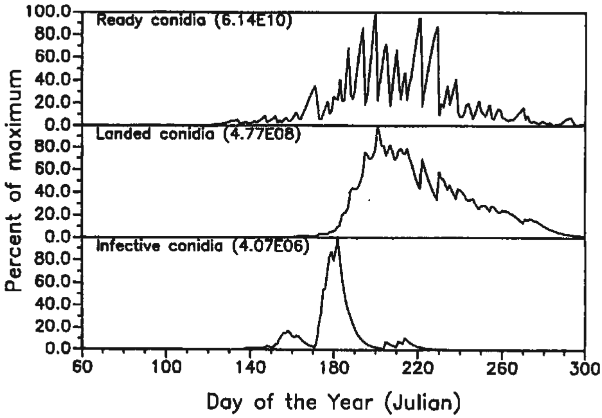

Fig. 3b. Seasonal dynamics of the state variables Ready Conidia, Landed Conidia, and Infective Conidia during the simulation of the 1987 growing season. No fungicide was applied. Variables are expressed as percent of maximum, the number in parentheses (expressed in scientific notation).

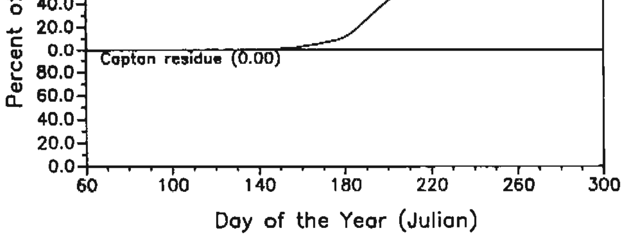

Fig. 3c. Seasonal dynamics of the state variables Active Lesions, Dead Lesions, and Fungicide Residue during the simulation of the 1987 growing season. No fungicide was applied. Variables are expressed as percent of maximum, the number in parentheses (expressed in scientific notation).

development rates. If the constant used in the APPLESCAB game could not be verified in the literature, it was removed or replaced with a constant that could be attributed to a literature source or to unpublished work.

Mature Ascospores are computed as the proportion of ascospores matured, based on accumulated degree days and rainfall from the previous 1 November (20). The total number of ascospores available for the entire season is one of the initial inputs into the simulator. There is a natural mortality (Mn) of 1-(0.9996**8) and mature spores can be lost (L) due to leaf wetting of the over-wintered leaves as a result of dew, and because all spores that are released due to rain do not land on apple tissue. The development rate from Mature Ascospores to Landed Ascospores is based on the ratio of total apple tissue surface area to the total tissue area plus orchard surface area, given rainfall is greater than 0.0 mm.

Landed Ascospores are subject to two natural mortalities (Mn). The first is due to exposure on the tissue surface before becoming an infective ascospore and is set at 90% per day. The second mortality is due to the loss of susceptible sites as a result of tissue aging after the spore has landed. This mortality is set at 50% per day. No fungicide mortality (Mf) affects the landed ascospores as Fig. 2 erroneously indicates. The development rate to Infective Ascospores is governed by favorability of environmental conditions for infection (as indicated by the Mills table), the residue of protectant fungicide, the ratio of susceptible tissue to total tissue area, the germination rate of ascospores and the ratio of uninfected sites to total infection sites.

Infective Ascospores are spores which have successfully undergone germination, penetration, and the resulting lesions are in their latent period. Ascospores in this stage are affected by natural mortalities (Mn) during the infection and penetration process. In addition, if the fungicide has some "after infection" activity, it is expressed as a mortality (Mf). Passage from this stage to the next, Lesions, constitutes the incubation or latent period. The development rate to lesions is determined by temperature and host resistance. It is at this point that the state variable changes from number of spores per hectare (Infective Ascospores) tolesions area as cm^2/ha (Lesions) based on the final component of the development rate, initial lesion size.

Lesions are the major reservoir for the disease simulator. It is from lesions that the secondary disease cycle originates by producing conidia which can form new lesions. In addition, there is an internal cycle that permits lesions to expand. The expansion is based on the average lesion area, the average lesion life and the availability of uninfected host tissue. The conidia are located in the state variable Ready Conidia. The rate of conidial production is a function of temperature, a predefined conidia production rate (#/cm^2 of lesion/day) and a feedback loop which slows conidia production if the existing conidia are not removed.

Ready Conidia have a natural mortality rate that is a function of temperature, particularly high temperature. Some mortality due to fungicide can occur if the fungicide has systemic activity. Removal of conidia is accomplished by rainfall and, to a much lesser extent, by wind. Most of the conidia removed by these methods are lost from the system because they land on something other than apple tissue. The conidia that do land on apple tissue, as determined by a special routine to determine deposition, pass through the developmental rate to the state variable Landed Conidia.

The Landed Conidia stage is short-lived and a high daily mortality occurs if conidia do not move immediately to the next stage. The developmental rate to Infective Conidia is a function of favorable weather for infection, the germination rate of conidia, the residue of protectant fungicide, the ratio of susceptible tissue to total tissue area, and the ratio of uninfected sites to total infection sites.

Infective Conidia are subject to a natural mortality (Mn) during the germination process as well as a fungicide mortality (Mf) if the fungicide has "after infection" activity. Passage to the Lesions stage is based on the developmental rate which is a function of temperature and host resistance. The conversion factor used for ascospores is also used to change conidia numbers to lesion area.

As lesions age and no longer expand or produce conidia, they move to the eighth state variable, Dead Lesions. This is the last developmental stage of the pathogen.

The ninth and final state variable is fungicide residue, expressed as micrograms per cm^2 of plant tissue. The calculation of fungicide residue is described below.

Fungicide residue

The fungicide residue model has been developed for the protectant fungicide captan. It is based on studies involving residue measurements on apple leaves and fruit after laboratory and field applications of the chemical (Seem, unpublished). The model is a dose response curve,

$$PL = 100/(1 + C/C50)k)$$

where PL is the percent of the number of lesions on a treated apple leaf or fruit, C is the fungicide residue (micrograms/cm^2) on the leaf or fruit, C_{50} is the fungicide residue required to reduce the lesion number by 50%, and k is a scaling factor which controls the spread of the dose response curve. This model has been parameterized for captan on the four most susceptible leaves on the growing apple shoot. A residue decline model, proposed by Stanley (34), is used to estimate the amount of captan available on a leaf or fruit surface,

$$C_t = C_0 e^{-A(CR,CC,t)R} + E$$

where C_t is the residue concentration at time t, C_0 is the initial concentration and is a random variable, A(CR,CC,t) is $a_1CR + a_2HDD + a_3T$ (where CR is cumulative rainfall and HDD is cumulative degree days over the time period t), R is a random variable reflecting the variation of loss intensity within a plant, and E is measurement error.

Economics component

The economics model is based on the assumption that all fruit are produced for fresh market. Harvested fruit are sized and graded into five discrete quality classes: U.S. Extra Fancy; U.S. Fancy; U.S. #1; U.S. Utility; culls. It was assumed that the probability of an apple falling into one of these 5 classes follows a multinomial distribution where the parameters of the density function are a function of disease incidence or severity. The quantitative relationship between the parameter estimates and incidence or severity of scab can be determined in two ways: (1) as a function of the incidence and/or severity of scab at harvest; and (2) as a linear combination of the amount of disease (incidence or severity) in each successive week during the growing season. The loss equation is a modification of the one proposed by Heaton *et al.* (13) which calculated the relative profit as a sum of the yield times price per unit for each grade, minus the production costs. The price per unit grade is estimated from actual market prices for packed fresh market fruit in Western NY. The total yield is generated from the tree growth simulation model. The harvested fruit is then distributed into quality classes based on the relationship between the incidence and severity of scab and the multinomial distribution mentioned above. The variable costs of production ($/ha) include the cost of fungicide spray materials and the application costs (equipment, labour, etc.).

Table 1. Effect of amount of initial inoculum (ascospores) on simulated final disease without fungicide or with four applications of captan.

Ascospores (#/ha/season)	Final disease (cm^2/ha) Not sprayed	Sprayed
$3.0x10^6$	120	35
$3.0x10^7$	1,425	340
$3.0x10^8$	153,800	3,474
$3.0x10^9$	48,490,000	43,840
$3.0x10^{10}$	48,490,000	5,274,000

Table 2. Effect of conidia production rate (number of conidia produced per cm^2 of lesion area per day) on simulated final disease without fungicide or with four applications of captan.

Conidia (#/cm2/day)	Final disease (cm^2/ha) Not sprayed	sprayed
$1.96x10^3$	11,220	3,377
$1.96x10^4$	13,970	3,386
$1.96x10^5$	153,800	3,474
$1.96x10^6$	48,490,000	4,172
$1.96x10^7$	48,490,000	7,222

Simulation results

The simulation has been run with many different combinations of starting values and seasonal variations, such as weather or number and timing of fungicide applications. Results of two runs of the simulator, using weather data from the 1987 growing season, are presented. The only difference between the two runs is that the first had no simulated fungicide applications while the second had four applications timed to coincide with the sprays applied in the validation orchard.

The unsprayed simulation run is presented in Figs. 3a-c, where the daily value of the state variables is plotted against time. Mature ascospores were present from approximately 10 March (day 70) to 28 June (180), with peak maturation on 20 April (110) (Fig. 3a). These dates corresponded closely to the observed ascospore maturation in the validation orchard. The peak discharge

Table 3. Effect of varying the number of captan sprays on the simulated final disease for 1987.

Spray dates	Final disease (cm^2/ha)
No spray	153,800
13 May, 19 May, 29 May	3,597
4 May, 13 May, 19 May, 29 May	3,474
27 April, 4 May, 19 May, 29 May	147

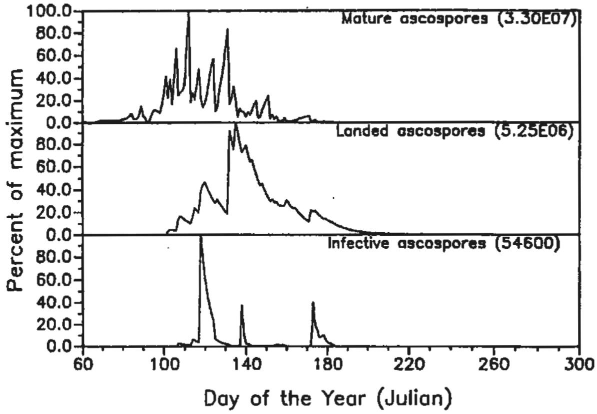

Fig. 4a. Seasonal dynamics of the state variables Mature Ascospores, Landed Ascospores and Infective Ascospores during the simulation of the 1987 growing season. Four captan sprays were applied. Variables are expressed as percent of maximum, the number in parentheses (expressed in scientific notation).

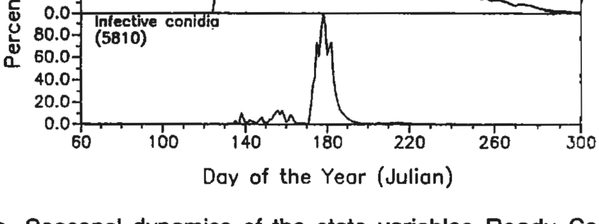

Fig. 4b. Seasonal dynamics of the state variables Ready Conidia, Landed Conidia, and Infective Conidia during the simulation of the 1987 growing season. Four captan sprays were applied. Variables are expressed as percent of maximum, the number in parentheses (expressed in scientific notation).

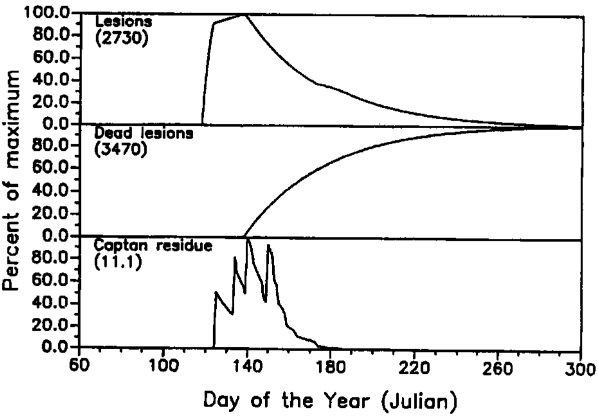

Fig. 4c. Seasonal dynamics of the state variables Active Lesions, Dead Lesions and Fungicide Residue during the simulation of the 1987 growing season. Four captan sprays were applied. Variables are expressed as percent of maximum, the number in parentheses (expressed in scientific notation).

periods of ascospores occurred around 1 May (120) and 20 May (140). The largest number of infective ascospores was available on 20 May (140), at a concentration of 560,000 spores/ha. Smaller peaks occurred on 1 May (120) and 23 June (175). Conidia production was cyclical due to the frequent removal of spores from the lesions by rain (Fig. 3b). Significant numbers of conidia were released and landed on apple tissue from the beginning of July (182) until leaf fall,

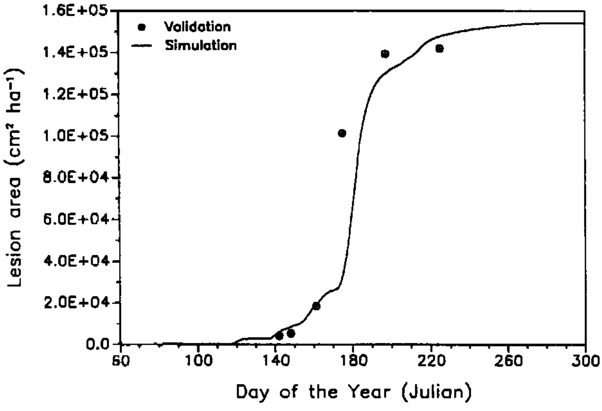

Fig. 5. Comparison of actual and simulated apple scab disease development for the 1987 growing season.

Table 4. Effect of decreasing or increasing temperature on the simulated final disease for 1987.

Temperature change (°C)	Final disease (cm^2/ha)
-4	3,261
-2	5,660
No change	3,474
+2	1,230
+4	3,478

Table 5. Effect of altering the length of wetting duration on the simulated final disease for 1987.

Change in wetness duration	Final disease (cm^2/ha)
20 % shorter	395
10% shorter	490
No change	3,474
10% longer	3,551
20% longer	3,680

Table 6. Effect of tree density on the simulated final disease for 1987.

Trees (#/ha)	Final disease (cm^2/ha)
52	907
103	3,426
206	3,426
412	6,599
824	6,599

with the largest deposition around 24 July (200). However, by that date there were very few infective conidia because the amount of susceptible tissue was so small that very few new infections occurred. The largest number of conidia infected tissue around 28 June, when a maximum of 4,070,000 conidia/ha produced infections. The upper two graphs in Fig. 3c show the seasonal progress of active and dead lesions, respectively. The total lesion area was approximately 158,000 cm^2/ha. Because no captan was applied in this simulation run, the captan residue in Fig. 3c remained at 0.

The second simulation run was identical to the previous except that four simulated applications of captan were made to the orchard. Because captan has no effect on ascospore maturation or deposition, the first two graphs in Fig. 4a are identical to the unsprayed simulation in Fig. 3a. The captan did have a significant effect on ascospore infection. Although some infection did occur, the maximum infection which occurred was only 54,600 infections/ha around 1 May (120). Two much smaller ascosporic infection periods occurred on 20 May (140) and 23 June (175). The maximum production of conidia (ready conidia) was almost 30 time smaller when compared to the ready conidia of the unsprayed simulation. In addition, the maximum occurred earlier in the season (10 May or day 130) because the captan effectively reduced the number of lesions and thus the number of conidia. Although conidia were being released for most of the season after 10 May, the total numbers were between 100 and 1000 times smaller than in the unsprayed simulation. The peak occurrence of infective conidia produced only 5810 lesions/ha around 28 June (175), after the captan residue had weathered to an ineffective level. The captan residue is shown as a series of four peaks in the bottom graph of Fig. 4c. After each application, some weathering did occur, but there was a slight buildup of residue over the first three sprays to a maximum level of 1.11 micrograms/cm^2. After the final spray the residue weathered quickly to zero. Total lesion area amounted to only 3470 cm^2/ha.

Validation and sensitivity analysis

The comparison of simulated disease development to actual disease development is presented in Fig. 5. The validation data fall very close to the simulation line and it is important to note that the graph represents the total area of disease per ha, not a proportion of total area diseased. However, two variables in the simulator were adjusted to provide the best fit to the observed data. Initial ascosporic inoculum (3.0 x 108 spores/ha) and conidia production rate (1.96 x 105 spores/cm^2 lesion/day) were estimated based on literature and previous work, but the estimates were crude and it was decided to calibrate the simulator to the 1987 validation data. This compromised the 1987 data and the comparison cannot therefore be considered a true validation.

Sensitivity analysis of the six simulator variables (Tables 1-6) showed considerable variation in sensitivity by the simulator. Adjusting the initial inoculum (3.0×10^8 ascospores/ha) to 10 and 100 times smaller or larger resulted in similar changes in final disease area only when the inoculum was reduced (Table 1). When the inoculum was increased, non-linear increases occurred in both the unsprayed and sprayed simulations. For example, a ten-fold increase in inoculum from 3.0×10^8 to 3.0×10^9 resulted in over a 300-fold increase in final disease area in the unsprayed simulation. In this case, final disease reached its maximum level of 48,490,000, the total amount of apple tissue/ha. Ten- and 100-fold changes in conidia production rate produced different results compared to the initial inoculum changes (Table 2). When no fungicide was applied in the simulation, the final disease area increase was not linear with the change in production rate. In the case of the sprayed simulation, the final disease was unaffected by conidia production rate. Fungicide use had an effect on final disease area, ranging from 153,800 cm^2 lesions/ha when no spray was applied to 147 cm^2 lesions/ha when four applications were made (Table 3).

Changing the environment had limited effect on the final disease produced by the simulator. Decreasing or increasing the daily temperature by as much as a constant 4 °C had a slight effect on final disease (Table 4). The effect of temperature was non-linear in the sense that greatest final disease was simulated when the temperature was 2 °C lower and the smallest final disease was simulated when the temperature was 2 °C higher. Changing the duration of wetting periods caused the simulated final disease to respond linearly to the change (Table 5). However, significant changes occurred only when the wetting periods were shortened, not lengthened. Finally, the tree density in the orchard did not have a large effect on final disease, and what effect occurred was not linear (Table 6). Halving tree density from the original 206 trees/ha had no effect on final disease, but quartering the original density resulted in a similar reduction in final disease. Doubling tree density from 206 to 412 trees/ha resulted in twice the final disease, while quadrupling the density to 824 trees/ha still resulted in only a doubling of final disease.

Discussion

The apple scab simulation presented here represents a significantly better understanding of scab development and management, as well as an advancement of the use of simulation methods to describe a disease and a perennial crop. Although the simulation is not complete at this point, the validation to date has shown the program to reflect accurately the pathosystem.

The need for a small number of state variables for optimization has been a major constraint on building the simulator. It would have been biologically more desirable to separate all stages of pathogen development and to incorporate distributed delays into components. Distributed delays provide a means of mimicking processes such as incubation and latency. These enhancements may eventually be added to a research simulator.

The components of the simulator are not fully linked. Leaf tissue area loss due to disease is not accounted for in the tree growth simulator. While this may appear to be a serious flaw, it has been assumed that typical levels of disease simulated for management optimization will be low and have little influence on photosynthesis capacity. Correction of this problem is not trivial because the disease simulator does not describe where lesions are located, i.e. spur leaves or different terminal leaves or fruits. As a result, the area of diseased tissue cannot be removed from the appropriate tissue type.

Sensitivity analysis

At this point in the simulator development, the sensitivity analysis provides some of the most useful information about the simulator operation. Of the six factors considered (Tables 1-6), analysis of the two inoculum variables, ascospores and conidia, reveals that the simulator is not functioning properly. As the factor being examined increases, the simulator should respond in a quantitatively similar manner. For example, a ten-fold increases in ascospore numbers should result in a ten-fold increase in final disease (Table 1). This does occur at the lower levels of inoculum tested, but at the higher levels, the rate of increase is considerably higher than expected. The simulator is currently being reviewed to discover why this problem is occurring.

Sensitivity analysis has also revealed interesting variation in the simulator. Altering temperature (Table 4) from an average of 4 °C below the validation temperature to 4 °C above the temperature caused erratic results in final disease. An increase of 2 °C resulted in the lowest final disease, while a decrease of 2 °C resulted in the highest final disease. Changes of 4 °C resulted in final disease intermediate to the two extremes. The reason is not yet known.

There is much work remaining before we can test optimal strategies for apple scab control. Yet we feel this work represents a new and useful approach to solving a complex problem such as scab control. As in other optimization studies (23), this work should also lead to the identification of disease thresholds which can be utilized in simplified control strategies.

Acknowledgement

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Session 3

Breeding for stable resistance to disease

Chairperson: F. H. Alston

Breeding pome fruits with stable resistance to diseases

2. Selection techniques and breeding strategy

F. H. Alston

AFRC Institute of Horticultural Research,
East Malling, Maidstone, Kent ME19 6BJ,
United Kingdom

Abstract

Efficient early screening techniques are available for resistance to the principle apple and pear diseases, mildew (*Podosphaera leucotricha*), scab (*Venturia inaequalis*), crown rot (*Phytophthora cactorum*), canker (*Nectria galligena*), fireblight (*Erwinia amylovora*) and storage diseases.

There are good prospects of locating genetic markers for the important resistance genes.

While some compromises can be made on relative levels of resistance during breeding and selection, there is little opportunity for compromise over the major components of fruit quality. The breeder must be prepared to moderate selection for disease resistance in order to retain high fruit quality.

Key words: screening, storage tests, major genes, polygenes, resistance genes, apple breeding, pear breeding

Introduction

Disease resistance is an important component of most pome fruit breeding programmes. Priorities vary but apple scab (*Venturia inaequalis*) mildew (*Podosphaera leucotricha*) and fireblight (*Erwinia amylovora*) have received the most attention. Initially disease resistance was introduced into breeding programmes as part of a long term aim to eliminate all pesticides from orchards. Later the economic benefits which could accrue from mildew and scab resistance in apples were emphasised. The control of those diseases can amount to 40% of the annual growing costs in some regions. Today, these developments are recognised as important components in environmental and food quality improvement, leading to the elimination of all pesticides from agriculture and horticulture (10).

Several apple cultivars are available with very high resistance to scab and moderate resistance to mildew, sufficient to be grown without sprays in some areas. None has yet been widely accepted in commerce in Europe because they lack some of the important quality components favoured in the markets. In recent years, further crosses have been made between these resistant cultivars and highly flavoured European cultivars, which promise to produce better quality disease resistant cultivars. Although these are important steps, the widespread concern over chemical residues in food has led to an important change in breeding priorities. The development of new cultivars which can be stored and marketed to a high standard without post-harvest dips is now of the highest priority. New cultivars will be developed from crosses combining important storage and shelf-life features with scab and mildew resistance.

Breeding policy

The selection and testing of new pome fruits can be delayed by the inherently long juvenile phase. In addition, the area of land required for selection plots can put severe restrictions on breeding programmes, because trees must remain in place for 4 to 8 years. To alleviate such constraints early selection techniques have been developed, which are applied in the first 2 years of growth and during the first two cropping seasons. Seedlings are screened for resistance to foliage and shoot diseases in the glasshouse, shortly after germination, and in the nursery, along with important primary sieves for precocity, yield and fruit size during the second growing season. Susceptible seedlings are eliminated at the earliest stage to ensure selection for quality is made amongst disease resistant trees only. This is most often achieved by rapid mass selection techniques, followed by verification after quality and yield selection.

Although there is strong interest in new cultivars that can be grown successfully without sprays, it is clear that few consumers are prepared to compromise on their desire for high fruit quality and flavour.

Storage diseases

The principle diseases include *Phytophthora, Nectria* and *Gloeosporium*, normally controlled by orchard sprays prior to harvest and by post-harvest fungicidal dips before long-term storage. Effective early selection for resistance is made as soon as sufficient fruit is available, 4 or 5 years after germination (8). Fruit samples are stored in sealed plastic bins ventilated with moist air at 1 liter/hr, creating a humid environment similar to that in commercial stores. For these tests, fruit is normally stored at 3.5 °C in air for 4 months. A simulated shelf-life period of 14 days at 10 °C follows before the incidence of fruit rots is recorded. Tests are based on fruit harvested from selection plots which do not receive pre-harvest sprays, and post-harvest dips are not used. Plots are established for a relatively short time, so that often the natural inoculum potential is low. This stage serves as a useful initial screen only, although results from a recent survey indicate that *Nectria galligena* can establish quickly in such situations. Where sufficient fruit is available samples should be inoculated; the variety collection of the National Fruit Trials was effectively screened for *Gloeosporium perennans* resistance in that way (1).

When physiological disorders are also taken into account, surveys of cultivars and progenies show a relatively low proportion of plants with fruit which can store without damage under the experimental conditions (8). Thus large progenies are required in apple breeding to ensure adequate opportunities to select for yield, precocity, resistance to foliar diseases, fruit size, flavour, colour and skin finish in addition to storage quality (7).

There is a good prospect of new apple cultivars which can store well in controlled atmospheres (CA), without needing orchard sprays or post-harvest dips, for marketing between May and August. A large number of possible parents has been surveyed, including many old cultivars with good reputations for long storage, but very few survived the simulated commercial storage test (8). The most useful material appears to be modern cultivars which combine high quality with good storage potential. Outstanding cultivars include Malling Kent, Malling Fiesta, Tydeman's Late Orange, Malling Falstaff, Summerland and Jonamac. Some 30,000 seedlings were produced at East Malling from crosses aimed at the production of new red and Cox-type apples which will store beyond April, without post-harvest dips. Eight very promising selections, chosen after fruit quality and storage testing, are now on trial at the National Fruit Trials.

Mildew and scab

Scab and mildew are the most serious foliar diseases of apple, their relative importance varying according to environmental conditions. In regions of high summer rainfall scab is most prevalent and in drier regions mildew is the predominant disease. In England 17 spray applications may be needed each year to control mildew adequately. Recent apple cultivars carry a higher level of mildew resistance than the widely established commercial cultivars Cox's Orange Pippin and Golden Delicious. This improvement by breeders was achieved through stringent field selection during the second or third season after germination. Such resistance only rarely provides complete protection, but it can keep the disease to a sufficiently low level to achieve economic cropping without sprays, in some cases (16).

The elimination of mildew by the use of intensive spray programmes can produce a large increase in the yield of high-quality fruit from some cultivars (12). Breeders are aiming to achieve the same effect by transferring very high levels of resistance from *Malus* species to the cultivated apple. Resistance transferred from *M. zumi* and *M. robusta* has remained stable in unsprayed plots for over 20 years. Derivatives from the second backcross to commercial apples, which have commercial sized fruit of good eating quality, were used in a third backcross to red commercial varieties to improve colour. Well coloured mildew-resistant selections, with good fruit quality, were produced.

Most screening is based on natural infection amongst seedlings in the nursery, 18 months after germination. Under these conditions resistant derivatives of *M. zumi* show no sign of the disease, while those from *M. robusta* show a necrotic reaction on the undersurface of leaves. Resistant plants from resistant commercial varieties usually show a low level of sporulation on leaves but rarely on stems.

The high level of resistance carried by *M. zumi* and *M. robusta* is determined in each case by two genes (4), giving 30-40% of seedlings without sporing colonies in the field. In contrast, resistance in commercial cultivars is under polygenic control (11), and less than 1% of seedlings show no sporing colonies. Often, no more than 10% show a low enough incidence of mildew to be graded as resistant. The two types of resistance can be combined in crosses to achieve stable resistance. The polygenic component can be estimated in *M. robusta* derivatives from the amount of necrosis on the leaves. Seedlings with a low incidence of necrosis carry a high degree of polygenic resistance in addition to the major genes (5). Progeny tests are necessary to assess the polygenic component of *M. zumi* derivatives, since no specific leaf symptoms are produced.

Alternative sources of high resistance which appear to be under simple genetic control include the ornamental crab apple White Angel, and the D series of selections which were derived from wild apples in the South Tyrol. Glasshouse screening, under optimum conditions of high temperatures and low humidity, is possible with these genes. A mist of conidia, dispersed in water with a wetting agent, is sprayed onto seedlings at the two-leaf stage in seed trays. Leaves are allowed to dry rapidly to facilitate good spore germination. Susceptible seedlings can be recognised and discarded after 4 weeks. Similar glasshouse screening can be effective with *M. robusta* and *M. zumi* derivatives but older plants, at the eight-leaf stage, must be used. In these cases, most seedlings show some sporulation, including some that will later show no sporulation in the field. Therefore careful grading is necessary. Conveniently, resistant seedlings from both sources can be recognised from the slight chlorosis or necrosis which accompanies the low level of sporulation. Under glasshouse conditions it is almost impossible to distinguish resistant and susceptible seedlings derived from commercial cultivars. At East Malling, where there is a high inoculum potential and favourable environmental conditions, it is often most convenient to screen all sources of resistance in the field at 18 months.

Glasshouse screening procedures have been widely adopted for scab resistance. Seedlings are inoculated at the two-leaf stage using a suspension of conidia. High humidity (70% RH) must be maintained during the incubation period of 2-3 weeks, when the temperature should be maintained at about 22 °C. For 18 h immediately following inoculation the humidity must be maintained at a minimum of 90% RH to obtain maximum spore germination. It is important to maintain active plant growth after inoculation to ensure maximum disease expression. Slow-growing and senescent susceptible plants can appear to be resistant (14). It is most important that ideal inoculation conditions should be maintained in order to avoid the rentention of a high proportion of scab-susceptible selections for fruit assessment. This is very important in areas with dry conditions where natural infections, while severe, might only occur spasmodically and be slow to build up in breeding plots. The effectiveness of good glasshouse screening was demonstrated after planting uninfected seedlings identified in glasshouse tests into an orchard with a high inoculum potential in a high rainfall region: over 90% remained free from scab. Widespread pathogenic variation is known in *Venturia inaequalis* (31). In addition to five major genes, each providing universal resistance, polygenic resistance appears to provide resistance to some but not all biotypes. There is evidence that the most resistant selections carrying the gene *Vf* owe their resistance to a combination of the single gene and polygenes (25). It is also possible that some resistant selections are not universally resistant to the pathogen, but only to the biotypes represented in the inoculum, since *Vf* may be absent. Consequently, it is important to test progenies in order to establish whether or not selections carry one of the 'key' genes. Fuller information on biotypes and their virulence is required. Trial plantings in different regions, together with test inoculations using a range of local isolates, help to assess the stability of resistance in new selections (19).

Other diseases

Important apple diseases are caused by *Nectria galligena* (apple canker) and *Phytophthora* sp. (crown rot). Both also cause serious fruit diseases in storage. Resistance to crown rot, caused by *P. cactorum*, a serious cause of tree loss, is a major objective in most rootstock breeding programmes. Mass screening techniques, based on flooding trays of seedlings at the two-four leaf stage with a zoospore suspension, have been investigated (27) and adopted as routine (13). So far, however, there is no direct evidence that such seedling tests are an efficient means of pre-selection (15). Although not suitable for large progenies, another method of crown rot resistance testing is a cut shoot test (2) based on inoculating 1-year shoots with agar discs of mycelium. There appears to be a good correlation between this test and the reported performance of rootstocks and parents. Although the results cannot be used as precise predictions of field performance, this technique appears to provide a good initial screen. Long and laborious field testing is necessary to determine precisely the resistance status of advanced selections, for although the effect of crown rot can be devastating in orchards its incidence is spasmodic.

In recent years apple canker has become a serious threat to the establishment of intensive orchards. Surveys (3, 9) have revealed sources of strong resistance and progeny surveys have indicated suitable parents amongst cultivated cultivars (17). Two types of inoculation technique have been used; wounds on 2-year wood and leaf scars on 1-year wood, using spore suspensions in both cases. Recent experiments on 2-month-old seedlings indicate that resistance screening may be possible shortly after germination (28, 29).

Fireblight is the most serious pear disease, causing serious losses in some parts of North America and threatening important production areas in Europe. Although needle inoculation of the growing points of seedlings at the 6-8 leaf stage in the glasshouse has proved an effective way of screening large populations, the method cannot reliable identify individual field resistant selections (32), and the risk of transferring infected material to disease-free orchard sites is too great in Europe. Tests can, however, be made on detached shoots in isolated orchards in areas where the disease is prevalent, or in glasshouse isolation compartments using specially propagated trees which are destroyed after testing. Detached shoot tests have only been moderately promising as a mass selection sieve (6). At East Malling, the testing of promising selections as maiden trees in an isolation compartment after yield, habit and fruit quality selection appears to be the most efficient method for this disease. These tests establish whether or not selections carry tissue resistance. The isolation glasshouse is cooled to 22 °C and sealed to prevent the spread of bacterial ooze and strands, the plants being maintained by a remotely controlled watering system. Resistance is assessed on the basis of the number of infected internodes after 14 days. These conditions have given results very close to the known field performance of key standard cultivars. Secondary blossom are the main infection sites in many regions and cultivars prone to producing many such blossom are seriously at risk, especially if they also have high tissue susceptibility. Laxton's Superb in England and Passe Crassane in southwest France are examples of good commercial cultivars taken out of production because of this risk.

In many ways, selection for the absence of secondary blossom might be the best way of dealing with fireblight during the breeding of new cultivars. However, direct selection for the absence of secondary blossom is likely to prolong breeding programmes. Secondary blossom appear rarely amongst fruiting plants in the first 7 years from germination, even amongst progenies derived from cultivars prone to producing secondary blossom (26). Fortunately it appears that selection for a low incidence of secondary blossom is achieved concurrently with selection for precocity, high yield and regular cropping (6). In some regions, tissue-susceptible cultivars present greater promise than current cultivars bred and selected for tissue resistance if, like Malling Concorde, they are precocious, regular cropping, produce few if any secondary blossoms and carry a range of other cultural and quality advantages.

Discussion

The prospect of producing new cultivars which can be grown to a high commercial standard without fungicide sprays are good. Indeed, in the case of scab and to a limited extent mildew, this has already been demonstrated by the apple variety Florina. However, the cultivars available today lack important quality components, particularly flavour, texture and storage life, and in some cases not all the necessary resistance components have been included. While it is possible to envisage some compromise being reached during breeding and selection on relative levels of resistance to various diseases, there is no room for compromise over quality components in these programmes. Therefore fruit colour, flavour, texture and skin finish must remain the final selection criteria and the breeder must be prepared to moderate selection for disease resistance to achieve the necessarily high quality standards required by commerce.

Although very high levels of resistance to scab and mildew are available, and these resistances determined by major genes have been combined with polygenic resistance, no commercial types have so far been produced which include more than one major resistance gene. However, mildew resistance from *M. zumi* (Pl_2) has been combined in crosses at East Malling with scab resistance from *M. floribunda* (*Vf*), the resulting selections having good fruit size, colour, skin finish and flavour. These have been crossed with established cultivars, like Malling Fiesta, with fine texture and a good storage life. A recent selection combines mildew resistance from *M. robusta* (Pl_1) with *Vf* and Cox-type aroma. Progress towards including more than one group of genes for resistance to each disease is hampered by problems of gene recognition, at present only possible through a series of time-consuming progeny tests. Fortunately, there are prospects of locating genetic markers for some of these resistance genes (20). Preliminary studies indicate that the genes for glutamate oxaloacetate transaminase (21, 22) may be useful markers.

In addition to extending the genetic base through the exchange of breeding material, international collaboration can provide an invaluable diversity of screening facilities, providing information on the response of resistant selections to a wider range of fungal isolates in differing environments. Recent tests in Switzerland (Kellerhals, personal communication), Yugoslavia (23) and West Germany (18) on progenies and selections supplied from East Malling have verified the resistance to mildew transferred from *M. zumi* and *M. robusta*, and to scab from all the universal scab resistance sources described by Williams *et al.* (30). These have all been combined with high fruit quality, including aromatic flavour.

Interdisciplinary collaboration is also essential for the rapid exploitation of genetic resistance. The early inclusion of resistant selections with high fruit quality in integrated control experiments is essential. It is important to define effective resistance levels, since it is likely that economical performance without fungicide sprays may be achieved without complete resistance, which might be diluted during selection for other characters. While it seems important to combine resistance genes from a range of sources as a long term insurance against resistance breakdown, it is important to realise that this is likely to hinder genetic progress in other economically important directions. The most widely used sources of resistance, *Vf* against scab and *Pl2* against mildew, have a good record of stability, being reinforced in many selections apparently by accumulations of polygenes for resistance. The trend towards relatively short replanting cycles gives more opportunities for changing cultivars and should allow the gradual introduction of genes for resistance over a long period. In certain cases breeders may decide not to incorporate resistance to a particular disease but prefer to develop a cultivar which can avoid the disease by other means. In some situations this approach is preferable, particularly where such features can be selected concurrently with tree habit, precocity and regularity of cropping, and has been achieved for fireblight through the new pear Malling Concorde.

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Breeding pome fruits with stable resistance to diseases

3 Genes, resistance mechanisms, present work and prospects

Yves Lespinasse

INRA, Station d'Amélioration des Espèces Fruitières et Ornementales, Beaucouzé, 49000 Angers France

ABSTRACT

The first part of this paper concerns the genes available to the plant breeder, and the resistance mechanisms involved in apple scab, mildew and fireblight resistance; pear breeding for disease resistance is briefly reviewed. The second part is devoted to the release of resistant cultivars; 30 scab-resistant apple cultivars have been released in the last 18 years but none are widely grown; the french scab resistant 'Florina' is well accepted in regions where it can produce bright red fruit. Recommendations are made to improve information on the cultivation of these new cultivars and cooperative work is proposed to face the host-parasite interaction on a world-wide scale; more research is needed on pathogenicity. Breeders are close to combining scab, mildew and fireblight resistance in new apple cultivars; a further step will be the combination of disease and pest resistance.

Key words: major genes, polygenic resistance, *Venturia inaequalis, Podosphaera leucotricha*, durable resistance, *Erwinia amylovora*, Vf scab resistance, cultivar Florina.

RESUME

Chez les arbres fruitiers à pépins, les programmes de sélection créatrice privilégient la résistance aux champignons parasites, aux bactéries et aux arthropodes nuisibles. La résistance à la tavelure du pommier présente de nombreux atouts : 5 gènes majeurs indépendants ainsi que plusieurs sources de résistance à contrôle polygénique. A l'INRA d'ANGERS, ce sont le gène Vf et dans une moindre mesure les gènes Va et Vr qui sont les

plus utilisés dans les plans de croisements; ils codent pour une résistance complète à l'égard de toutes les races connues du champignon parasite. Le système génique Vf apparait complexe et de ce fait offre une garantie certaine pour la durabilité de la résistance; l'hypothèse avancée est celle d'un groupe de gènes liés au locus Vf dont l'expression peut être renforcée par des gènes mineurs présents à d'autres loci et pouvant exister chez les parents sensibles. Les stratégies génétiques à mettre en oeuvre pour éviter le développement de races virulentes sont exposées. Plusieurs sources de résistance à l'oïdium du pommier ont été identifiées et des programmes d'hybridation sont en cours; malheureusement ils se heurtent à la méconnaissance du pouvoir pathogène de ce champignon parasite obligatoire. Quelques travaux ont été aussi engagés à l'égard du feu bactérien du pommier et la meilleure voie parait être la résistance à contrôle polygénique portée par quelques variétés ou hybrides déjà résistants à la tavelure. Chez le poirier, les études sont nettement moins avancées et concernent principalement la résistance au feu bactérien; la résistance au psylle est certainement un autre objectif prioritaire.

La mise sur le marché des premières variétés de pommier résistantes à la tavelure n'a pas eu beaucoup d'échos auprès des arboriculteurs . La variété INRA Florina Quérina® parait être aujourd'hui le meilleur compromis; des progrès restent à faire et les prochaines variétés devraient retenir l'attention de tous les acteurs économiques, producteurs, négociants et consommateurs. Une coopération internationale doit être mise en place pour mieux connaitre ces nouveautés et évaluer rapidement leurs chances de succès. Les chercheurs doivent en outre contrôler la stabilité de la résistance et considérer avec beaucoup d'attention toute souche de tavelure pouvant croître sur hôtes résistants. L'étude des composantes du pouvoir pathogène doit être prioritaire dans le cas de l'oïdium et de la bactérie responsable du feu bactérien. L'addition de résistances aux arthopodes nuisibles constitue une seconde étape mais essentielle pour réduire d'une façon sensible le nombre d'interventions phytosanitaires en verger.

Genes available to the plant breeder; Resistance mechanisms and durability

Apple scab (*Venturia inaequalis*)

Apple species and cultivars used as sources of resistance

Five different major genes (Vf, Va, Vr, Vb, Vbj) coding for scab resistance are available (Table 1). These genes are independent, dominant and code for complete resistance to all known races. The results of tests of allelism indicate that resistance in 11 different accessions is determined by the same locus, Vf, but most breeding works involve *M. floribunda* 821. The other four major genes are also used in a number of apple breeding programmes throughout the world. At INRA, Vf from *M. floribunda* 821 is most used and to a limited extent, Va and Vr; in addition, one progeny derived from 'Jonsib' has been tested. This is another monogenic source of resistance which shows very high hypersensitivity in the greenhouse; the gene from 'Jonsib' has not been named and is not included in Table 1. Va was identified from P.I.172623 but the parents available at Angers originate from P.I.172633; the two P.I accessions give the same reactions to scab in greenhouse tests and the same ratio of resistant seedlings; therefore, the gene Va is attributed to our parents CCR1T8 and CCR3T11 obtained from Ed. Wil-

Table 1. Apple species and varieties used as sources of resistance to scab

MONOGENIC		POLYGENIC
A. Resistant to all known races		**Field resistant to all known races**
Vf.	M. floribunda 821	M. baccata (selected seedlings)
	M. atrosanguinea 804 (3 type)	M. sargenti 843
	M. micromalus 245-38 (3 type)	M. sieboldii 2982-22
	M. prunifolia 19 651	M. toringo 852
	M. prunifolia microcarpa 782-26	M. zumi colocarpa
	M. prunifolia xanthocarpa 691-25	
	M. species MA. 4	
	M. species MA. 8	
	M. species MA. 16	Old european varieties
	M. species MA. 1255	
	Hansen's baccata n° 1	
Va.	Antonovka selection PI 172 623	
Vb.	Hansen's baccata n° 2	
Vbj.	M. baccata jackii	
Vr.	M. pumila R 127 40-7A	
B. Susceptible to race 5 only		
Vm.	M. micromalus 245.38 (pit type)	
	M. atrosanguinea 804 (pit type)	

liams at Purdue University, U.S.A (see Table 9). The gene Vm from *M. micromalus* 245-38 and *M. atrosanguinea* 804 coding for the pit type reaction to scab, is attacked by race 5 of the fungus (35) and is no longer included in the breeding lines. More details are in the review by Williams and Kuc (36).

Polygenic resistance is also found in *Malus* species and in some old European cultivars such as 'Rouchetaude', an old french variety, and 'Antonovka'. Our experience with derivatives from these latter two is disappointing: resistance is always partial, the correlation between leaf and fruit resistance is not good, and in some years trees have to be sprayed to keep the fruits free of scab.

Nevertheless, apple breeders have a large choice of genes in their breeding programmes and different strategies can be used to develop durable resistance.

Host-pathogen interactions

To date (Table 2), four physiological races of the fungus have been distinguished that can infect certain of the breeding lines developed from *Malus* sources resistant to the common race (race 1); h_2, h_3, h_4 and h_5 are the differential hosts for races 2, 3, 4 and 5. Golden Delicious is susceptible to all five races and pathodeme Vf is resistant to all these pathotypes or races.

Vf: a complex but promising mechanism for durable resistance

In a progeny containing the Vf gene, four classes of resistance can be recognized in the early seedling stage (17):

class 1 - pin point pits with no sporulation.
class 2 - irregular chlorotic or necrotic lesions with no sporulation.
class 3 - few restricted sporulating lesions.
class M - may be considered as intermediate between class 2 and class 3. It is recognized as a mixture of necrotic, non sporulating lesions and of sparsely sporulating lesions.
class 4 (= susceptible) - extensive, abundantly-sporulating lesions.

M. floribunda 821 and selected scab-resistant seedlings from five successive generations of a modified backcross programme were used in crosses with Lobo and McIntosh, both cultivars being highly susceptible to scab (31). After inoculation, seedlings were classified according to their reaction (Table 3). A reduction in the proportion of highly resistant seedlings occurred over the six generations. The original *M. floribunda* 821 gave a class 1 reaction, while F_2 26829-2-2 gave a class 2 reaction (32). This suggests that the original level of resistance is not due to a single qualitative gene, but either to a group of rather closely linked quantitative genes, or to a class 3 reaction qualitative gene closely linked with one or more quantitative genes (36). Moreover, by using different susceptible parents with the same resistant tester, slight differences in the distribution suggest that the susceptible parent also contributes to resistance; therefore it is assumed that modifiers support scab resistance coded by Vf. Effective

TABLE 2. Host-pathogen interaction for scab

	PATHODEME						
	DOLGO	GENEVA	R127-40-7A Si	R127-40-7A S'i	M. micromalus Vm	FLORINA Vf	GOLDEN
PATHOTYPE	h_2	h_3	h_2	h_4	h_5		
1	r	r	r	r	r	r	S
2	S	S*	S	r	r	r	S
3	r	S	r	r	r	r	S
4	r	r	r	S	r	r	S
5	r	r	r	r	S	r	S

r = Resistant
S = Susceptible
S* = Necrotic lesions in which fungus sporulates abundantly in moist atmosphere

Si = certain segregates of R127-40-7A
S'i = other segregates of R127-40-7A

combinations of the genes involved can be recovered by intercrossing two Vf selections (eg. 'Prima' and 'Coop11', Table 3); a 3:1 distribution occurred, as expected, because both parents carry a single dominant allele of Vf.

This genetic situation is not easy to explain and various schemes can account for the results. It is likely that Vf represents a genetic system and is a group of closely linked genes. This set of genes would be more or less eroded through recombination; the different stages of erosion might explain the different classes of reaction. The susceptible parent can also contribute minor genes for resistance, which are independent of the Vf locus.

The "gene" Vf has proved to be strong, because after more than 40 years it is still effective against all the known races. Its genetic structure is still in doubt but it appears complex. In a review of structure of disease resistance genes in annual crops, Pryor (29), suggested that such loci are complex, having either several closely-linked functional units or a more complicated arrangement.

Strategy for breeding durable resistance

Whatever the structure of Vf, experience in many crops indicates that resistance breakdown is always possible. Such an eventuality has to be faced by the apple breeder who must develop a breeding strategy for durable resistance. The first point of this breeding strategy is to work with various independent resistance mechanisms because it could be a mistake to depend on one source of resistance, such as Vf. At INRA, progenies from 'Nova Easygro' (Vr), from CCR1T8 and CCR1T11 (assumed to be Va) and from polygenic sources (Antonovka and Rouchetaude) are being screened. The independent sources of resist-

TABLE 3. Percentage of seedlings in each class of reaction following inoculation with Venturia inaequalis (adapted from ROUSSELLE et al., 1974)

PROGENY AND GENERATION		CLASS OF REACTION 1	2	M	3	4
		RESISTANT				SUSCEP.
• LOBO x						
M. floribunda 821	F_1	29	20	13	5	33
26 829.2.2.	BX_2	13	14	18	6	49
PR7 T41	BX_3	4	16	26	9	45
HAR 10T 190	BX_5	5	12	28	8	47
• Prima x Coop 11	BX_3 x BX_5	25	23	17	11	24

ance can be combined to reinforce the mechanism of resistance. Crosses Vf x Vf, Vf x polygenes, polygenes x polygenes have been made at INRA and it is intended to combine other genes in the crosses Vf x Vr and Vf x Va. It is necessary to do a progeny test to identify seedlings with the various genes.

Apple powdery mildew (*Podosphaera leucotricha*)

Apple species and cultivars used as sources of resistance

In comparison with scab a lower level of resistance to powdery mildew can be tolerated before fungicide sprays are necessary. Low susceptibility from some old cultivars (7) can be sufficient to avoid fungicides. Unfortunately, this low susceptibility is under polygenic control and difficult to detect. Resistance from wild species appears more useful (Table 4).

Malus robusta and *Malus zumi* carry strong resistances, in each species under oligogenic control (2). At INRA, Angers, mildew resistance derived from *Malus zumi* is studied (Table 5). Two different samples of the same progenies were compared after inoculation in the glasshouse (2 month-old seedlings) and in the nursery (2 year-old seedlings). The results show that most of the seedlings are susceptible in the glasshouse; in the nursery a clear-cut segregation between resistant and susceptible seedlings is found. Some of the so-called nursery-resistant seedlings appeared to be slightly susceptible in the field after 8 years, where 26 to 28% of the seedlings were found resistant. Although greenhouse screening is not possible, the proportion of resistant seedlings and the supposed complex structure of the mechanism of resistance favour the development of this breeding

TABLE 4. Apple species and varieties used as sources of resistance to powdery mildew

Malus robusta	Pl_1 + ...	KNIGHT and ALSTON, 1968
Malus zumi	Pl_2 + ...	ALSTON, 1977
'Mis'		DAYTON, 1977
'White Angel' 'David' M. x robusta 5 'R5' M. x robusta 'Korea' M. x robusta '24-7-7, 8'		GALLOT, LAMB, ALDWINCKLE, 1985
MA-8 M. sargenti (4x) M. zumi calocarpa M. baccata jackii		KORBAN and DAYTON, 1983

line. Progenies bred in 1987 combine Vf scab resistance and mildew resistance from *M. zumi*.

Of the other sources of resistance presented in Table 4, only 'MIS', 'White Angel' and 'Robusta 5' were studied at INRA, Angers. Progenies from these sources, when screened in the glasshouse, show a sharp 1:1 segregation after crossing with a susceptible parent. However, after successive inoculations while testing for stability in the glasshouse differences occur, and results obtained with 'Robusta 5' and 'White Angel' at Angers, France, and Geneva N.Y., U.S.A., were not the same (Table 6). At Angers, seedlings from 'Robusta 5' were free from infection all season, with chlorotic flecks on the leaves; in 1988, the 'Robusta 5' progeny tested at Geneva N.Y. showed no resistance (Aldwinckle, personal communication). In contrast, at Angers resistant derivatives of 'White Angel' become susceptible after repeated inoculations; the 'White Angel' progeny tested at Geneva N.Y. in 1988 maintained its resistance throughout the season. These different results suggest that pathogenicity of the pathogen populations differs at these sites. The sharp 1:1 segregation obtained with 'MIS', 'White Angel' and 'Robusta 5' suggests a single gene coding for resistance in each case. No allelism tests have been carried out to determine relationships between these genes. This situation with 'White Angel' and 'Robusta 5' might be comparable with the Vm scab resistance gene from *M. micromalus* and scab race 5. Breeders need to be aware of the situation to avoid the release of selections with resistance that is liable to breakdown. Nevertheless, other progenies from 'MIS' and 'White Angel', screened at Angers in 1981 and showing a 1:1 segregation after one ino-

TABLE 5. Mildew resistance from M. zumi - Pl_2 + ... ; results obtained at INRA Angers

	SUS	RES	% RES
• in the greenhouse (20°C - 2 month-old)			
Golden x TNR 17-72	67	4	6
Golden x TNR 17-39	59	6	9
• in the nursery (2 year-old)			
Golden x TNR 17-72	100	95	49
Golden x TNR 17-39	121	93	43
• in the field (8 year-old)			
Golden x TNR 17-72		55	28
Golden x TNR 17-39		55	26

TNR 17-39, TNR 17-72 } Sunset x A 143-14 (Jonathan x M. zumi o.p.)

culation in the glasshouse, produced seedlings which maintained their resistance in the field.

Fire blight (*Erwinia amylovora*) on apple

Apple species and cultivars used as sources of resistance

Gardner *et al.* (11) demonstrated dominant genes in certain highly resistant *Malus* species, *M. robusta* 5 and a selection of *M.*x *sublobata*, now called 'Novole', which were studied at Geneva, N.Y., for rootstock breeding. These clones are not completely resistant and a differential genotype x strain interaction was found (25, 28).

More promising for scion breeding are certain scab resistant cultivares and selections (1, 24, 20). Cultivars such as 'Priscilla' carry almost complete resistance under polygenic control with additive gene effects; however, there is no evidence of a close linkage between Vf and genes for fire blight resistance. This material has the advantage of producing fruits with a good size and flavour, as well as scab and fire blight resistance.

Pear diseases

Resistance appears to be polygenically inherited in all the available sources (Table 7). Therefore the situation is difficult for the breeder. Most breeders use fire blight resistance derived from *Pyrus communis*. In addition to fire blight re-

TABLE 6. Mildew resistance from M. robusta 5 (Rob 5) and White Angel (W.A.) ; results obtained in the greenhouse at INRA Angers and Geneva, N.Y.

	SUS		RES		
* Rob 5					
Rob 5 x Empire	1	:	1	stable all season	ANGERS,1987
Freedom x Rob 5	1	:	0		GENEVA, 1988
* W.A.	SUS		RES		
P22 (W.A.) x 3174	1	:	1	becoming ~1 : 0 at the end of the year	ANGERS,1987
Freedom x W.A.	1	:	1	stable all season	GENEVA, 1988

P22 (W.A.) = Liberty x W.A.

3174 = Winesap x CBR 9T28 (Vf selection) sistance, some progenies are also screened for scab (*Venturia pirina*) resistance at INRA, Angers.

Release of resistant cultivars and possibilities for cooperation

Apple scab resistance

Thirty scab-resistant cultivars have been released (Table 8) of which 26 originate from *M. floribunda* 821 (Vf); 'Nova Easygro' has the Vr gene; 'Murray' and 'Rouville' have the gene from *M.micromalus* and are susceptible to race 5. 'Generos' from Rumania has a polygenic resistance from *Malus kaïdo*. 'Freedom' from Geneva, N.Y., combines Vf and polygenes from Antonoka. None of these cultivars are widely grown, except possibly in Rumania where they have recently propagated a lot of trees. Information is urgently needed on the performance of these cultivars in commercial orchards. In particular, it is important to study the effect of the absence of sprays against scab on minor pathogens such as *Gloeodes pomigena* (sooty blotch disease) and *Leptothyrium pomi* (fly speck disease). In certain years with a wet summer and in experimental orchards, these two diseases become severe on the fruits. Sooty blotch can be brushed off the fruit but sprays may be necessary to control fly speck. A light spray programme

TABLE 7. Sources of polygenic resistance for pear breeding

Venturia pirina	P. calleryana P. serotina P. communis THIBAULT, 1983 review
Fabraea maculata	P. calleryana BELL and VAN DER ZWET, 1989
Erwinia amylovora	P. calleryana P. betulaefolia P. ussuriensis P. serotina P. communis VAN DER ZWET and KEIL, 1979 review
Psylla piri	P. ussuriensis HARRIS and LAMB, 1973
	P. communis QUARTA and PUGGIONI, 1984 BELL, 1984

may be needed to avoid damage from both these fungi on scab-resistant cultivars.

An important development is the establishment of an orchard for determining pathotypes and pathodemes, including differential hosts representing the main genes for resistance. In France, replicates of such an orchard are located in Angers (Loire valley), Bordeaux (Garonne valley) and Valence (Rhone valley). These high-density orchards have several blocks, each with 16 trees of a pathodeme (Vf, Vr, Va, polygenes and the differential hosts (Table 9)); the susceptible cultivar Golden Delicious surrounds each block to maintain a high inoculum pressure. In this way, at the end of each year, plant breeders and pathologists can evaluate the behaviour of each pathodeme and can study inoculum development on differential hosts. In this type of orchard, hybrids containing polygenes from 'Rouchetaude' and 'Antonovka'; were disappointing in some years supporting the idea that polygenic resistance should be associated with a major gene such as Vf. With such an orchard in each country it would be possible to exchange precise information and inoculum. The inocula from susceptible and resistant material could be compared in one laboratory to assess pathogenicity in terms of aggressiveness and virulence. With scab, signs of sporulation on a resistant cultivar have to be noted with concern. Breeders and pathologists should then be warned and inoculum collected for study. Cultivars like 'Prima', which give a class 3 reaction to scab, should be checked carefully each year. In France, no scab has been noticed on 'Prima' but in West Germany, J. Krüger (22) has found some spots on leaves in recent years but has not been able to cultivate isolates from these infections. Differential hosts have been recorded each year

TABLE 8. The thirty scab resistant varieties released throughout the world.

U.S.A.	Prima	VF	1970
	Priscilla	Vf	1972
	Sir Prize	Vf	1975
	Liberty	Vf	1978
	Jonafree	Vf	1979
	Redfree	Vf	1981
	Mac Shay	Vf	1981
	Freedom	VF + Poly.	1983
	Dayton	Vf	1988
	William's Pride	Vf	1988
CANADA	Mac Free	Vf	1974
	Nova Easygro	Vr	1975
	Novamac	Vf	1978
	Moira	Vf	1978
	Trent	Vf	1979
	Britegold	Vf	1980
	Murray	Vm	1980
	Rouville	Vm	1983
	Richelieu	Vf	1983
RUMANIA	Generos	Poly.	1972
	Pionier	Vf	1983
	Romus 1	Vf	1984
	Romus 2	Vf	1984
	Voinea	Vf	1985
ENGLAND	Gavin	Vf	1977
BRAZIL	Primicia	Vf	1988
FRANCE	Priam	Vf	1974
	Florina-Querina (R)	Vf	1977
	Judeline (R)	Vf for juice	1986
	Judaine (R)	Vf for juice	1986

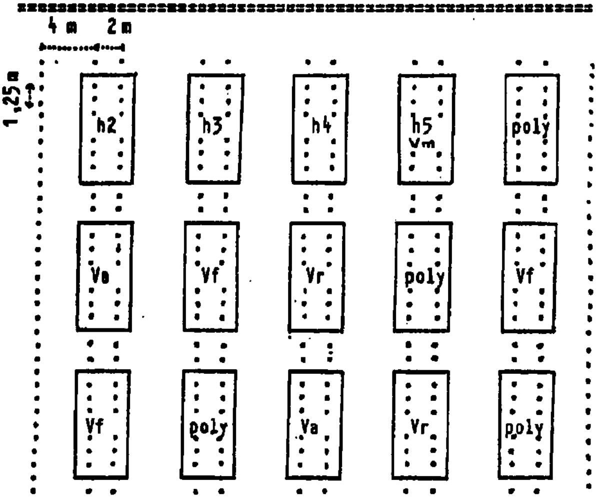
at Angers since 1980; race 2 is common, race 5 occurs occasionally; a few spots of race 4 were observed one year and race 3 is not present.

Another possibility for cooperation is the study of resistance and susceptibility using electron microscopy, as recently done at Geneva, N.Y. (Yepes), Zürich (Gessler, Valsangiacomo) and Angers (Chevalier). A precise description of resistance from each source could help towards understanding the mechanisms involved.

Mildew and fire blight resistance

Study of the pathogenicity of these diseases is important. For mildew a "mildewtron" was built at INRA ANGERS to evaluate and compare different inocula. The "mildewtron" has six separate compartments, each with filtered air under a slight positive pressure to avoid contaminations. The system was developed from

TABLE 9. High density orchard to control pathotypes and pathodemes



• Golden Delicious
Vf = Florina - Prima
Vr = Nova Easygro
Va = CCR1 T8 - CCR3 T11 (P.I. 172 633)
Polygenes = TNA 48-9 = Rouchetaude x Melrose
P7R4-4 = Z 185 o.p. (Antonovka)
h2 = TSR 34 T15, Dolgo : differential race 2
h3 = St R8 T24 : differencial race 3
h4 = TSR 33 T239 : differencial race 4
h5 = Vm = 9AR 2T196, 9AR 2T128, OR 45T 132 : differencial race 5

a "mildewtron" built to study mildew of *Cucurbitaceae* (9). Watering and feeding are automatic to avoid opening of the doors. Each compartment is supplied with the same resistant genotypes (MIS, White Angel ...) and a control; these budded trees are put in place before bud burst. After leafing out, inocula from different countries can be introduced, one in each compartment, and the genotype reactions observed.

In vitro culture should also be very useful for the study of this obligate parasite. Promising results were obtained by Korban and Trier (21) and Parisi at Angers (personal communication).

For fire blight, the main results obtained in recent years involve differential genotype x strain interactions (25, 26, 27). These *Erwinia amylovora* strains have to be studied very carefully and their occurrence understood in all countries. Breeding material has to be evaluated using these strains. A cooperative programme is working on this topic at Angers and Geneva N.Y.

Introduction of disease resistant cultivars into commercial production: Florina Quérina®

'Florina' was released in 1977. The first orchards were planted in 1979-1980. The total area grown today is less than 100 ha. Growers were asked their opinion of this cultivar (23). By checking all the orchards this cultivar's stable scab resistance, low susceptibility to fire blight and tolerance to rosy apple aphid have been verified; it is an outstanding genetical advance. The growers reported a marked decrease (more than half) in the total number of spray applications, good yield, easy harvesting, good fruit size, resistance to bruising and good taste. 'Florina' should be grafted on to a dwarfing rootstock like M9, pollinated by a scab resistant selection such as the ornamental crab 'Golden Gem', and the crob sold between November and February. Fruit colour is irregular i.e. not fully red (half red on a yellow ground colour); therefore 'Florina' is not chosen by growers selling through large cooperatives which are devoted to standard cultivars like Golden Delicious, Red Delicious and Granny Smith. Despite this drawback, 'Florina' is suitable for growers who have their own distribution network. Conditions giving an early bright red fruit colour are fulfilled at altitudes such as at Limousin or Haute-Savoie. Fruit harvested at the right time stores well and maintains a good quality.

Two INRA scab-resistant cultivars were released in 1986 for juice production (Table 8):

JUDELINE (Vf): Golden Delicious x Priam; 88,000 trees have been propagated in the past 2 years.

JUDAINE (Vf): Reinette du Mans x Priam; 132,000 trees have been propagated in the past 2 years.

Orchards of these letter cultivars will be maintained only by lowering production costs. In this context, resistance is very welcome. Moreover, fruit shape and skin finish are not important! This makes the release of such cultivars easier. In 1987, special crosses to produce cider apples resistant to scab and with a low susceptibility to mildew and fire blight were made in Angers.

Fruit shape and skin finish can hampered release of good-tasting apple for the fresh market. This is one of our problems. Selection with a nice green skin finish is likely to be the next scab-resistant apple released from INRA; the susceptible parent is Granny Smith.

Future trends in conventional breeding for complete disease and pest resistance

As a priority, breeders need to combine genes coding for resistance to scab, mildew, fire blight and storage diseases. Combining scab, mildew and fire blight resistance is well advanced; more work is needed to add storage disease resistance but this programme is progressing well at the Institute of Horticultural Research, East Malling (3).

Pest resistance is also being considered. Some material is already available and germplasm has been released by Goonewardene (12, 13, 14, 15). Each of his selections is scab-resistant and possesses good resistance to one or more of the following pests: European spider red mite (*Panonychus ulmi*); codling moth (*Cydia pomonella*); plum cucurlio (*Conotrachelus nenuphar*); apple maggot (*Rhagoletis pomonella*); red banded leafroller (*Argyrotaenia velutinana*). It will be important to evaluate this American material in European conditions, especially for European red mite and codling moth resistance.

Pest resistance work in INRA first involved rosy apple aphid (*Dysaphis plantaginea*). At present, hypersensitivity coded by Smh (4) is being compared to tolerance believed to be polygenically inherited from 'Florina' and its derivatives. In some years, Smh hypersensitivity is so severe that growing points are severely damaged, making its value doubtful. The tolerance observed in 'Florina' and also in some other scab-resistant selections looks promising although nothing is known about the resistance mechanism and its durability. Under an INRA research project, entomologists will begin in 1989 to study the response of breeding stocks and advanced selections to European red mite, codling moth, rosy apple aphid and also two summer fruit tortrix moths (*Adoxophyes orana* and *Pandemis heparana*). Electron microscopy will be used to study the host-insect interaction of rosy apple aphid.

In the future, molecular genetics offers the promise of improving our understanding of the nature of plant resistance genes. However, standard methods for cloning genes based on a knowledge of gene products are not available for plant resistance genes. Alternative approaches are available and are being actively pursued by a number of research groups throughout the world (29). Meanwhile, breeders will have to use conventional breeding methods to produce new cultivars suitable for growers, dealers and consumers and with durable resistance to the principal diseases.

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Breeding of pome fruits with stable resistance to diseases

Development of disease resistant pome fruit varieties

M. Kellerhals

Swiss Federal Research Station,
CH-8820 Wädenswil, Switzerland

Apple scab (*Venturia inaequalis*)

Search for resistant apple cultivars

The earliest tests, using artificial inoculation of apple scab (*Venturia inaequalis*) over a five year period (1897-1901) on 160 apple cultivars, showed considerable differences in susceptibility but no cultivar was immune (1). Wiltshire (52) suggested that toxic substances were the reason for the inhibition of scab development in cultivars with low susceptibility. He produced extracts from the leaves of resistant and susceptible cultivars in which he observed the germination of conidia. Germination was slower in the extracts from resistant cultivars. Wiesmann (50) isolated ascospores from five apple cultivars. He then reinfected field trees of the same cultivars. Scab pathotypes were most aggressive on the leaves of the cultivar from which they were isolated and less so on the other cultivars.

First breeding attempts

The first attempts to breed scab resistant apple cultivars were undertaken in Germany. The aim was to combine resistance with good fruit size and quality. It was suggested that a mass screening method for the selection of resistant seedlings should be developed and that resistant selections should be tested a second

Fig. 1: Massinoculation of apple seedlings in the 1930s.

time with different races or sources of the fungus. Schmidt (41) described a mass infection method for one-year-old apple seedlings in outdoor frames (Fig.1). The floor of the frames was covered with infected leaves which were watered several times to release ascospores. During the growing season seedlings were inoculated every 2 weeks with a water suspension of conidia. By these means an intensive infection pressure was created.

Rudloff und Schmidt (37) developed an inoculation method for single plants. A spore suspension was sprayed onto the young leaves, afterwards enclosed by a pergament bag filled with a filter paper in contact with water in an Erlenmeyer-flask. The bag was kept around the leaves for 3-4 days. This method was used in the field. Only 3 % of the seedlings were resistant in progenies from susceptible cultivars, whereas in crosses with *Malus* species an average of 27 % seedlings were resistant. However, the prospects of combining the high scab resistance found in several *Malus* species with good fruit size and quality did not appear promising. Therefore the work was continued with large-fruiting material carrying polygenic scab resistance, such as 'Antonovka' and 'Ernst Bosch' (41). After 1945, Zwintzscher (56) based his pro-

Symbol	Original source
Vf	*Malus floribunda*
Vm	*Malus micromalus*
Vr	a Russian apple
Vbj	*Malus baccata jackii*
Vb	Hansen's baccata # 2
Va	Antonovka (pit)

gramme on these sources and some of the material was used in other programmes round the world. No commercially interesting cultivar has been produced from these programmes. It seems that 'Antonovka' is not a useful parent.

The Coop-Programme

After World War II the Coop-Programme was started in the USA involving the following Universities:

- Purdue University (E.B. Williams, F.H. Emerson and J.R. Shay)
- Rutgers University (L.F. Hough, Catherine Bailey)
- University of Illinois (D.F. Dayton and J.B. Mowry)

It was also called PRI-programme (*P*urdue, *R*utgers and *I*llinois). The gene for scab resistance used in this programme was first identified by L.F. Hough from a collection of Malus species and hybrids assembled by Prof. C.S. Crandall at the University of Illinois in the early 1900s. Crandall made studies on the inheritance of fruit size in apple and used the small-fruited *Malus* species for that purpose (14). In 1914 he made a famous cross between 'Rome Beauty' and '*Malus floribunda* 821' and in 1926 a full sib cross between two F1 selections (*Malus floribunda* 821 x Rome Beauty) x (*Malus floribunda* 821 x Rome Beauty).

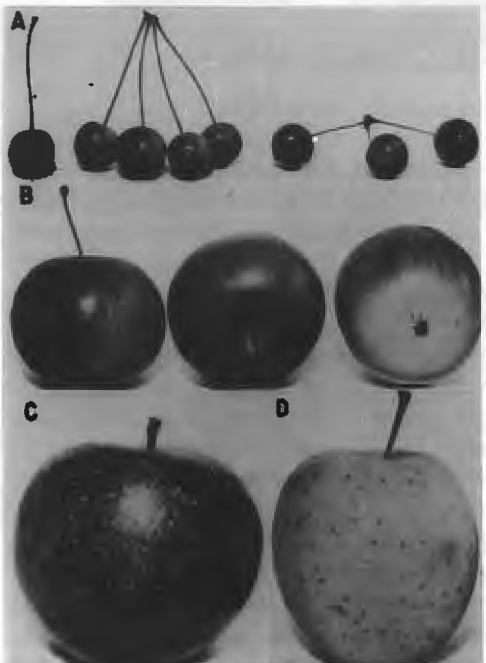

FIG. 2. *A* — Fruits of *M. floribunda* 821. *B* — Fruits of 26829-2-2 = (Rome Beauty x 821) x (Rome Beauty x 821). *C* — Fruit of 47-77 = Jonathan x 26829-2-2. *D* — Fruit of 14-145 = Golden Delicious x 26829-2-2. All fruits ca. ¾ nat. size.

Fig.2: The development of scab resistant cultivars in the Coop- Programme

As a result of a severe epidemic of apple scab which defoliated all susceptible unsprayed apple trees, Hough noticed in 1942 that one progeny from Crandall's F1 cross showed an almost 1:1 segregation for scab resistance. Further crosses with two resistant selections from this cross (F2 26829-2-2 and F2 26830-2) indicated that resistance was determined by a single dominant gene subsequently named Vf (*Venturia* resistant from *floribunda*). Selections F2 26829-2-2 and F2 26830-2 are the source of the resistance in all the apple cultivars carrying Vf.

Later studies showed that over 20 *Malus* species and hybrids carry genetic resistance to scab

(49). Eventually, through a series of intercrosses (tests of allelism), it was established that resistance in many of these sources was determined by the same gene. Six distinct genes (defined gene pools) were isolated as follows:

However, the development of races of *Venturia* has resulted in the elimination of some of these genes from breeding programmes. In particular, race 5 was found to overcome Vm. The Vf resistance has not, however, been overcome by fungal mutation and is the mainstay of present programmes.

The transfer of Vf to the cultivated apple was achieved through a series of backcrosses of selections heterozygous for the Vf gene, to high quality but scab-susceptible commercial cultivars. Seedlings were screened for scab resistance in the greenhouse during the winter.

Resistant plants were then planted in the field or nursery. Thus, only scab resistant plants were grown to fruiting in the field. Selections were then made to provide the best parents for the next generation.

After three or four generations Vf was introduced into a mainly cultivated apple genetic background. To avoid inbreeding, the high quality susceptible cultivars were different in each generation.

The success of the Coop-programme has been achieved through the coordination of apple breeding projects. The Apple Breeders Cooperative was formed in 1963 to coordinate research among a wider circle of apple breeders, with special attention to disease resistance. As a consequence of this effort a number of disease resistance programmes have been organized throughout the world. Important work is going on at the New York State Agriculture Experiment Station, Geneva, USA, in Ottawa, Canada and at various stations in Europe.

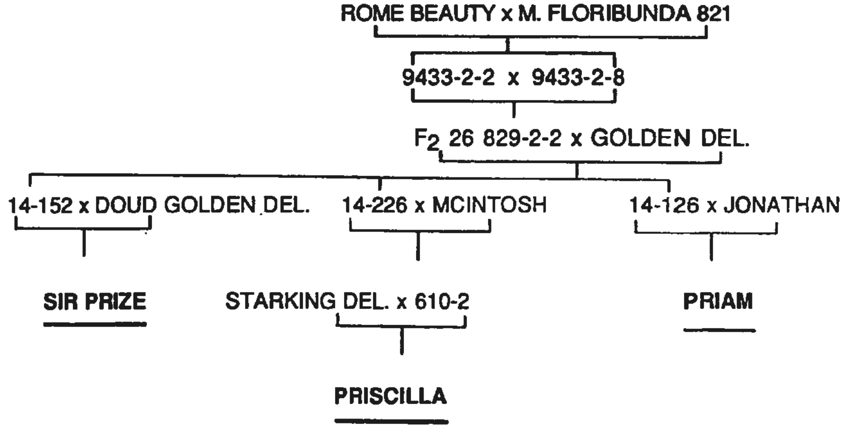

Fig.3: Pedigree of the cultivars 'Priscilla', 'Sir Prize' and 'Priam'.

Apple mildew (*Podosphaera leucotricha*)

Many workers have recorded different levels of powdery mildew resistance in apple cultivars. Extensive surveys of cultivar responses have been made (9,18,27,35,39,40,42,46,22), from which it is evident that the cultivated apple provides a complete range of reaction from full susceptibility to what is often described as immunity. Few genetic sources of high resistance or immunity to apple mildew are known (15). Examination of some 2000 cultivars at East Malling and the National Fruit Trials near Faversham, England, suggests that it is improbable that true immunity exists in the cultivated apple (3). Brown (11), working with crosses involving some 23 named cultivars and various unnamed seedlings, suggested that mildew resistance in the cultivated apple is invariably under polygenic control. Data by Sarasola (39) and other breeders (24) support this view, which is also the experience at the Institute of Horticultural Research, East Malling. In a search for sources providing immunity or near immunity a survey of wild *Malus* species was undertaken by Knight and Alston (25). In selecting plants for use as parents, preference was given to parents of progenies showing clear segregation of some 50% or more of 'immunes' or in which no 'susceptible' occurred. The first of the selected seedlings started flowering in 1962 and in the two succeeding years crosses were made of seedlings from *M. robusta* (MAL 59) and *M. zumi* (MAL 68) with mildew-susceptible cultivars. The resulting progenies were repeatedly dusted with heavy loads of mildew spores during two successive seasons and their response was assessed using a 0-6 grading system. Genetic studies showed that the high resistance found in an

Fig. 4. The apple cultivar «Priam» - a result of the Coop-Programme.

open-pollinated seedling of *M. robusta* (MAL 59/9) and an open-pollinated seedling of *M. zumi* (MAL 68/8), is determined by single dominant genes, Pl1 and Pl2, respectively (25). Later, this hypothesis was revised to account for two different genes plus modifiers (24,7). Gallott *et al.* (16) also examined progenies of 48 small-fruited *Malus* species and cultivars for heritable, high-level resistance to mildew.

A valuable bonus arising out of the transfer of mildew immunity from *M. zumi* and *M. robusta* to the cultivated apple is a short juvenile phase (3-4 years) derived from these species; concurrent transference of this character has been achieved (7). Two types of resistance have been observed: seedlings with resistance from *M. zumi* have remained totally free from mildew in the field while resistant derivatives of *M. robusta* often show a necrotic or hypersensitive response to the disease without apparent sporulation.

In greenhouse tests for mildew resistance, Dayton (15) identified a single plant grown from open-pollinated seeds of 'Starking Delicious' as highly resistant. One parent appears to have been a *Malus* species. It was named 'Mildew immune selection' (MIS). Progeny tests indicated a single gene from MIS conferring immunity to *P. leucotricha* in both the greenhouse and the field and therefore distinct from those reported by Knight and Alston (25). Lespinasse (32) reported a virulent biotype of mildew which seemed to overcome the resistance of MIS in Dayton's plantation. The stability of MIS resistance is therefore not certain.

While screening fungicides on young apple seedlings during the 1960s in the greenhouse, Philips Duphar Laboratories in The Netherlands found a number of seedlings with high mildew resistance. From 1972 onward they were used as parents in a crossing programme in Wageningen (45) and were named the D-series. The origin of these selections is uncertain but possibly northern Italy. They also showed some scab resistance. Visser and Verhaegh (45) supposed that both the mildew and scab resistance of the D-series might be based on a number of genes.

Besides *M. robusta, M. zumi* and MIS, Lespinasse (32) has also used *Malus hupehensis* and the ornamental cultivar 'White Angel'. 'White Angel', 'David', *Malus robusta* 'Robusta 5', *Malus robusta* 'Korea' and *Malus robusta* '24-7-7,8' may also hold promise as sources of high mildew resistance (16).

Fireblight (*Erwinia amylovora*)

Origin of the disease and sources of resistance

Fire blight, caused by the bacterium *Erwinia amylovora*, is the most serious bacterial disease of pomaceous fruit trees and apparently indigenous to North America. It was first noticed in the late 18th century in New York and was not reported from any other country until over a century later (54). The disease probably occurred on native American plants, such as crab apple, hawthorn and mountain ash. From these native hosts the bacterium probably spread to the susceptible cultivated pears and apples planted by the early American settlers.

In Europe, fire blight first occurred in 1957 in England and spread from there to The Netherlands (1966), Poland (1966), Denmark (1968), West Germany (1971) and Belgium and France (1972).

The bacterium was probably brought to England on infected plant material or on contaminated fruit boxes from overseas.

Waite (47,48,49) was the first to undertake research on fire blight. He found that the blight organism could enter blossom nectaries without punctures and that bees spread the bacterium from infected to healthy pear flowers.

Breeding of fireblight resistant pear cultivars

With the introduction of a wide range of pear and apple cultivars from Europe to the USA, large differences in fire blight resistance were observed. Blight-resistant pear material was introduced from China and Japan. Breeding for fireblight resistance in pear began in the nineteenth century after introduction of the Chinese sand pear (*P. pyrifolia*) to the USA (19).

The cultivars 'Le Conte', 'Kieffer', and 'Garber' were derived from interspecific hybridization and were grown because they were substantially more resistant to fire blight than the European cultivars (*P. communis*), but they were inferior in terms of fruit quality. It was not long after their introduction that work was initiated in the USA to breed high-quality pears resistant to fire blight (34). Sources of resistance identified by Reimer (36) and by others (20,13,29,43) led to a rational approach to blight resistance breeding with a good choice of parental material and effective screening methods. Major fire blight resistance breeding programmes in the USA included those at the USDA (10), New Brunswick, New Jersey (21); Geneva, New York (29); West Lafayette, Indiana (23). In Canada, the major programme was at Harrow, Ontario (30,31). In Europe, breeding programmes for fire blight resistance in pear exist at IHR, East Malling, England, at INRA, Angers, France and at ISF, Rome, Italy.

The extent of blight penetration in plants is strongly affected by the age, vigour and nutrition of the host, by environmental factors, particularly temperature and humidity, by soil type and moisture content and by cultural practices, and a combination of one or all of these factors with the time of bloom. Therefore, the most realistic measure of the degree of blight resistance for any cultivar, seedling or clonal selection can best be determined when the plant material is grown and tested under optimum conditions for blight development. The five most important *Pyrus* species, ranked in descending order of blight resistance are *ussuriensis, calleryana, betulaefolia, pyrifolia*, and *communis*. In each species, however, there is a range of resistance which makes it difficult to assign specific resistance categories to each species. *P. ussuriensis* 76 provides a source of very high resistance to fireblight and has been used in a number of breeding programmes. A series of backcrosses to cultivated pears will be necessary before commercial cultivars combining high resistance and high fruit quality are available. Although high levels of resistance have been transferred from *P. ussuriensis* and *P. serotina* the most promising commercial selections available are derived from *P. communis* (54). Genes for resistance have been postulated in wild species (6) and genes for susceptibility in cultivated varieties (44). In apple, a series of crab apple cultivars and selections have consistently been found to be resistant to fire blight and other diseases such as apple scab (*V. inaequalis*) and mildew (*P. leucotricha*). As with pears, there are marked differences among species and cultivars of apples in their response to attack by fire blight.

Breeding fire blight resistant rootstocks

Efforts have also been undertaken to select fire blight resistant apple and pear rootstocks.

In an extensive apple rootstock breeding project at Geneva, N.Y., USA, resistance to fire blight is a major objective (17). Large numbers of seedlings from controlled crosses are screened during their first year for susceptibility to crown rot, woolly apple aphid and fire blight.

Inoculation techniques

Many techniques have been tested and employed for the artificial inoculation of plant material to determine the degree of fire blight resistance in pears, apples, *Pyracantha, Cotoneaster* and other rosaceous hosts. The method most used is needle inoculation of the succulent shoot tip. With orchard trees inoculation is often performed with a hypodermic syringe (33). Thibault at Angers (1988, oral communication) uses scissors, dipped in a suspension of the bacterium, to cut leaves of young seedlings in the glasshouse. At Beltsville several techniques of tissue injury in combination with spray inoculations were tested (54). Several investigators have successfully inoculated pear blossoms by spraying them with a bacterial suspension. Early greenhouse selection techniques cannot successfully identify field resistant selections (55). Tests on maiden trees, however, give results which are closely correlated with the field performance of mature trees (53). This method is used at East Malling in an isolation glasshouse.

The main infection sites for fire blight are often the secondary blossoms produced in July, August or September. Emphasis is placed on selection for fire blight avoidance by using parents with little tendency to produce secondary blossom (8).

Recently, Lespinasse and Paulin (33) described an *in vitro* method to find fire blight resistant mutants among well-known cultivars.

Fire blight resistant cultivars

High quality fire blight resistant pear cultivars, 'Harrow Delight' and 'Harvest Queen', resulted from the Canada Agriculture programme at Harrow. Other fire blight resistant cultivars are 'Magness' and 'Moonglow', originating from the USDA at Beltsville. A large number of unnamed advanced selections are under evaluation in programmes round the world. However, no fire blight resistant selections with late maturity and good storage potential have yet been produced.

Apple canker (*Nectria galligena*)

Nectria galligena Bres., the cause of perennial branch or stem encircling cankers, is becoming more widespread and creating considerable concern among growers (12). Trees on heavy soil seem prone to attack. Few investigations have been carried out on this disease. Resistance has been reported in a number of cultivars (28). Alston (4) tested 18 apple cultivars with a reputation for resistance by putting a droplet of a spore suspension on leaf scar following defoliation. Only four cultivars seemed resistant and were used as parents in breeding programmes. Other tests by Alston have shown that several *Malus* species carry resistance, but genetic studies are not complete.

Crown rot (*Phytophthora cactorum*)

P. cactorum is a soil-borne fungus which invades and rots the bark tissues of apple, killing the tree if the trunk becomes girdled. This disease is primarily of importance in rootstocks. Mass selection of apple seedlings resistant to *P. cactorum* may be carried out effectively following inoculation of detatched twigs in the laboratory (5). A survey of 43 cultivars at East Malling revealed possible sources of resistance among those more widely grown in Europe. The resistance of Northern Spy appears to be under simple genetic control (Pc). High levels of resistance are present in James Grieve, Laxtons Superb and Melba. Crosses with Northern Spy resulted in a series of resistant rootstocks, such as MM 109 and 111.

Other diseases and outlook

There are other diseases of some importance in pome fruit production, such as storage diseases, apple rust (*Gymnosporangium juniperi-virginianae*) in the United States, pear scab, leaf blight (*Fabraea maculata*) and pear rust (*Gymnosporangium sabinae*). Disease resistance cannot be isolated from pest resistance. The choice of which diseases and pests can be included in a breeding programme depends on their economic importance and the availability of genetic sources of resistance. This review has shown how laborious and time consuming breeding for disease resistance can be. However, some important steps have been made. In the future, the experience from the past together with new breeding techniques could allow for more efficient procedures. Almost ten years ago, Aldwinckle and Lamb (2) were very optimistic with respect to the introduction of disease resistant cultivars: "we expect that new resistant varieties will gain acceptance in coming years to the extent that by the 1990's they will form a substantial proportion of new plantings in the eastern United States. By the year 2000 most new plantings may be of disease-resistant varieties".

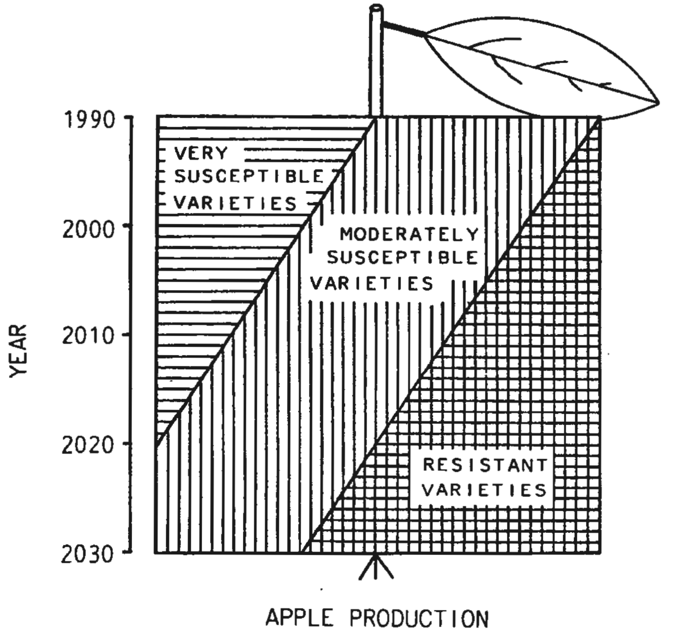

Fig. 5: Model of possible future trends in apple growing

In Europe it will be important to develop and grow resistant cultivars adapted to the wishes and taste of the consumer. Excellent fruit quality and storage capacity will be essential for the success of such cultivars. The success of resistant cultivars will also be promoted through further restrictions in pesticide use. However, it will be some time before all established commercial cultivars are replaced by disease resistant cultivars.

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Breeding disease resistant apple cultivars in Switzerland

M. Kellerhals

**Swiss Federal Research Station,
CH-8820 Wädenswil, Switzerland**

Abstract

The apple breeding programme started in 1986. It is based on results from trials with disease resistant cultivars and on international collaboration with other breeding institutes. The main aims are stable disease resistance against scab, mildew and storage diseases, excellent fruit quality and high productivity. The seedlings are screened for scab resistance in the glasshouse and for mildew resistance in the nursery. The 18-month-old pre-selected seedlings are budded on to M27-rootstocks for the evaluation of fruit and tree characters under unsprayed conditions. Promising selections will be further tested on M 9 at various locations.

Key words: *Venturia inaequalis, Podosphaera leucotricha*, screening, durable resistance.

Introduction

In Switzerland, as in many other countries, there is increasing concern about the use of pesticides in agriculture. Consumers strongly desire minimal to zero treatment of agricultural products. 'Integrated fruit production' is promoted by the official advisory services, the Ministry of Agriculture (Research Stations), the Fruit-Union of Switzerland and some supermarkets.

The development of integrated pest management has contributed to a considerable reduction of pesticide use in fruit-growing. However, a further reduction seems only possible with the introduction of disease- and pest resistant cultivars. Scab (*Venturia inaequalis*) and powdery mildew (*Podosphaera leucotricha)* are economically the most serious diseases in our apple orchards.

In 1986, the Swiss Federal Research Station, Wädenswil, started a programme to breed for disease resistant apples. The main aim is to combine stable resistance to scab, mildew and storage diseases with excellent fruit quality and good productivity. In order to be accepted by the majority of growers, retailers and consumers, disease resistant cultivars need to be high yielding, with good storage capacity and a quality similar or better than present commercial cultivars. Besides the dessert (fresh fruit) market, there is also a strong interest in disease resistant cultivars grown as standard trees for the production of apple juice and cider.

The programme is being developed in close collaboration with the Institute of Horticultural Research, East Malling, England, other breeding stations and the Federal Institute of Technology (ETH) in Zürich.

It is based upon results from trials with disease resistant and disease tolerant cultivars (1) and on experience in breeding conventional cultivars (2). The breeding programme is considered complementary to the testing of new cultivars originating from abroad.

Breeding and selection scheme

The breeding and selection scheme is shown in Fig. 1.

Choice of parental material

To ensure the appropriate choice of parental material for the crosses, due attention is paid to the main breeding aims. The best new disease resistant cultivars such as Florina, Liberty and Jonafree are used as sources of stable resistance to diseases, particularly apple scab. In addition, through collaboration with IHR East Malling, advanced scab- and/or mildew-resistant selections carrying alternative resistance genes are available as parents in the breeding programme.

The main limitation of disease resistant cultivars already released arises from their relatively poor fruit quality and storage behaviour. It is hoped to overcome these disadvantages by crossing disease resistant cultivars and selections with high-quality cultivars such as Elstar, Rubinette, Fiesta, Gala and the Swiss selections 'FAW-2706 (Kidds Orange x Idared)' and 'Maigold'.

The programme follows two main lines:

a) short term: breeding new commercial cultivars for maximum disease resistance combined with high quality and productivity

b) long term: breeding selections incorporating durable resistance from a wide range of genetic sources (several resistance genes; polygenes)

High fruit quality is difficult to define, being a combination of characters including:

- balanced suger/acid ratio
- crisp texture
- juiciness
- medium and regular fruit size
- resistance to physiological disorders
- good skin finish without russet
- colour
- good storage life

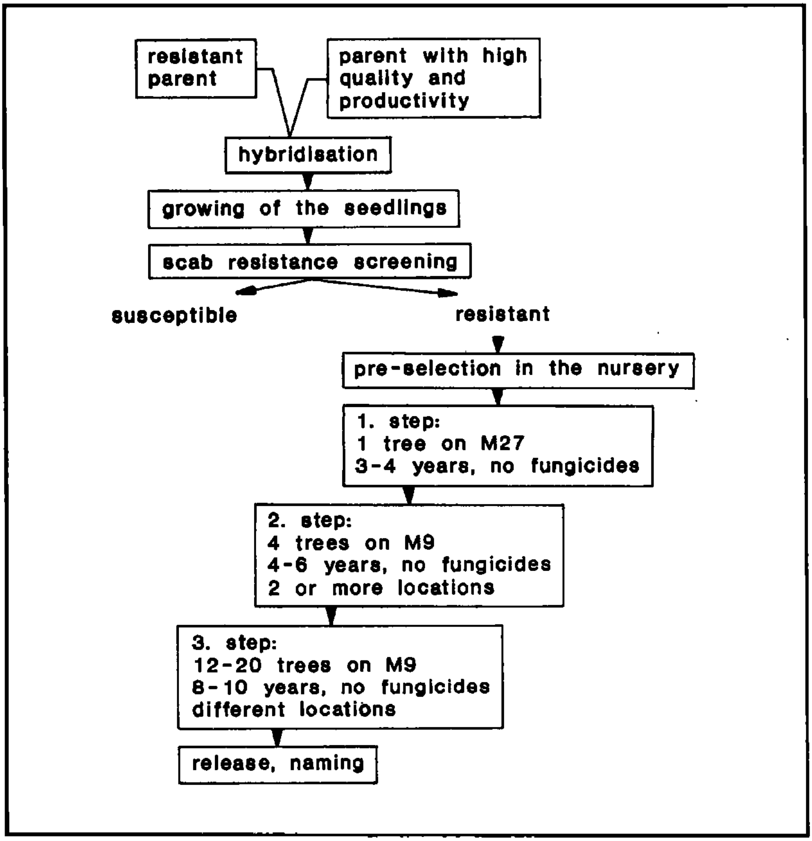
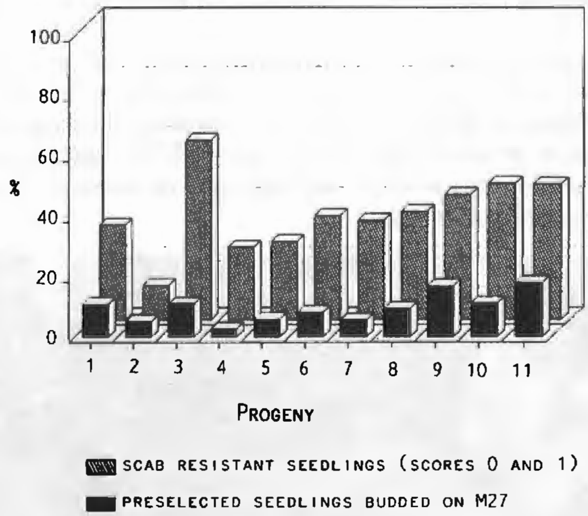


Fig. 1. Scheme for breeding and selecting disease resistant apple cultivars in Switzerland.

Most of these characters can only be observed at the fruiting stage. It is important to use only parents in which the desired characters are strongly expressed in order to achieve a high proportion of high quality advanced selections. Stable disease resistance is a challenge for the apple breeder. As an insurance against resistance breakdown it is advised to use a range of resistance sources. In the case of scab resistance it is aimed to combine different genes, including Vf, Va, Vb, Vbj, Vr and minor genes, in one genotype. Progeny tests and specific marker genes will aid the identification of such resistance complexes.



PROGENIES 1986	No OF SEEDS (=100%)	RESISTANCE GENES
1: ARLET x FREEDOM	329	V_F + POLY
2: GREENSLEEVES x LIBERTY	633	V_F
3: GALA x FLORINA	484	V_F
4: ELSTAR x JONAFREE	1034	V_F
5: RUBINETTE x FLORINA	732	V_F
6: FLORINA x RUBINETTE	572	V_F
7: FLORINA x ELSTAR	533	V_F
8: GOLDEN DEL. x A 849-5	500	V_F + PL_1
9: GLOSTER x A 849-8	400	V_F + PL_1
10: INGRID MARIE x A 849-6	350	V_F + PL_1
11: JONATHAN x A 849-7	350	V_F + PL_1

Fig. 2. Early selection of disease resistant apple progenies.

It seems important that the disease susceptible but high quality parent should not be very susceptible in order to avoid severely diluting the background resistance of the resistant parent. In the cultivar trials it is therefore necessary to identify cultivars with a high level of polygenic resistance. Old local cultivars with a high level of polygenic disease resistance might also be used in the crossing programme. However, they must also have an acceptable level of productivity and fruit quality. Most new commercial cultivars carry some mildew resistance under polygenic control. Today, highly mildew-resistant selections with good fruit size and quality are available for use in breeding programmes. Such resistance, transferred from *Malus zumi* and *Malus robusta*, has proved to be stable (4).

Early selection

Crosses in 1986 (Fig. 2) produced 5948 seeds. 1956 seedlings (=32.9%) were scab resistant (grades 0 and 1) in the glasshouse and 489 (8.2%) were preselected for habit and precosity, and propagated on the rootstock M27 for field evaluation.

Selection for scab resistance is on seedlings whilst in seed trays in the glasshouse, inoculated once or twice (second inoculation about 4 days after the first) with a spore suspension of a field isolate of *V. inaequalis*. Inoculation is done at the 2-4 leaf stage in the glasshouse at 20 °C and 95% RH, and the seedlings are graded after about 3 weeks at 18 °C and high relative humidity. The following scale is used to grade the seedlings:

Fig. 3. Young apple seedlings in the glasshouse showing different reactions to inoculation with a spore suspension of *V. inaequalis*.

0 = no symptoms of infection
1 = very small 'pin point' lesions
2 = necrotic flecks
3 = slight sporulation (less than 25% of the leaf surface)
4 = severe sporulation

Although the glasshouse facilities are poor (no automatic control of temperature and humidity) the success of the inoculations is good. However, it is important to check for the appearance of scab symptoms on selected seedlings planted in the nursery and later on in steps 2 and 3. In collaboration with the ETH Zürich we will retest advanced resistant selections in the glasshouse and verify their reaction to scab. The resistant seedlings are hardened and planted in the nursery at 90 x 30 cm. After 16 months, further selection for disease resistance (mainly powdery mildew), growth habit, foliage and precosity is done in the field in the budding season in August (3). Selected plants are budded on to M27 rootstocks (one for each field selection) to shorten the juvenile phase and to save space. These worked trees are planted 15 months later in the field at 3.5 x 0.8 m.

The first fruits on the most precocious selections can be expected the 4th year after crossing. No fungicide treatments are applied. Because postharvest fungicide dips are not allowed in Switzerland, selection for resistance to storage diseases is most important at fruiting . However, appropriate choice of parental cultivars with closed calyx tubes, and resistance to skin cracking and physiological disorders will contibute to a reduced susceptibility to storage diseases in the progeny. The main selection for yield, fruit quality, storage quality and growth habit occurs in the second and third growing season on M27. The best selections will then be budded onto M9 rootstocks for further testing at different locations.

Tests for suitability for processing into apple juice or cider will be carried out and promising selections will be grown as standard trees.

In orchards not receiving fungicide treatments the occurrence of diseases such as sooty blotch (*Gloeodes pomigena*) and fly speck (*Leptothyrium pomi*) has been seen. The side effects of growing disease resistant cultivars without the use of fungicides on the orchard ecosystem and on the storage capacity of fruits must be examined: the results will be essential for the development of the breeding programme as well as for the development of integrated fruit production strategies using resistant cultivars.

Conclusion

On the basis of international collaboration and efficient preselection techniques, the Swiss Federal Research Station of Wädenswil has established a breeding programme for disease resistant apple cultivars. This programme is adapted to the limited resources of a small country, with respect to labour and space. The programme follows two main lines:

- breeding new commercial cultivars with maximum disease resistance combined with high quality and productivity.
- breeding selections incorporating resistance from a wide range of sources (several resistance genes; polygenes)

Future development of the programme will aim to improve glasshouse conditions screening seedlings (control of temperature, humidity, light) and to define the identity and source of fungal inocula.

The breeding programme will be incorporated into research directed towards integrated fruit production strategies.

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Breeding for resistance to *Nectria galligena* in apple: differences in resistance between seedling populations

W.E. van de Weg

Institute for Horticultural Plant Breeding,
PO Box 16, 6700 AA Wageningen, The Netherlands

Abstract

Breeding for resistance to *Nectria galligena* (European canker) in apple is hampered by the absence of a suitable screening method and lack of knowledge of the inheritance of resistance. This study investigated whether differences in resistance between and within progenies can be detected in seedlings, and whether the ranking of these progenies with respect to resistance resembled that of their parents. For this purpose, five-month-old seedlings of six progenies were artificially inoculated with macroconidia of *N. galligena* applied to wounds. Resistance was evaluated by lesion lengths and the rate at which lesions girdled the stem.

Cox's Orange Pippin, James Grieve, IVT 74114 and IVT 6304-61 were used as highly susceptible parents and Golden Delicious and Jonathan as highly resistant parents.

The progeny of Cox's O.P. x James Grieve and of IVT 6304-61 x IVT 74114-17 proved to be more susceptible than that of IVT 74114-17 X Golden Delicious. IVT 74114-17 x Golden Delicious was more susceptible than the progenies of Jonathan x Cox's O.P., Jonathan x IVT 6304-61 and Jonathan x IVT 74114-17.

Thus, progenies differed in their level of resistance and their ranked order resembled that of their parents. These results suggest that this screening method is suitable for detecting differences in resistance and that a positive correlation exists between the relative levels of resistance of juvenile and mature plants.

Evaluation of the lesion lengths of the Jonathan x IVT 74114-17 progeny suggested that Jonathan has two major resistance genes.

Key words: *Malus* sp., *Nectria galligena*, resistance, seedlings, screening, inoculation technique, lesion size.

Introduction

Nectria galligena Bres. is the causal agent of European apple stem canker. This fungus causes considerable damage to apple orchards in north-western Europe. Chemical and mechanical control methods are laborious and do not prevent serious damage. Cultivars with a high level of resistance would be important for effective disease control.

Breeding for resistance to *N. galligena* is hampered by the absence of a suitable screening method and lack of knowledge of the inheritance of resistance. Therefore research has been started at the Institute for Horticultural Plant Breeding (IVT), The Netherlands, to overcome this problem.

Spinks (2) and Krüger (1) have evaluated the level of natural infection of mature trees in several seedling populations. Research on differences in resistance of artificially inoculated progenies has, however, not yet been reported. Recently, Van de Weg (4) showed that 16-week-old apple seedlings can be infected by *N. galligena*. In this report it is investigated whether differences in resistance between progenies can be detected at a young seedling stage. Further attention is given to the within- progeny variation. As no specific resistance to *N. galligena* is known to occur, attention is focussed on differences in partial resistance.

Material and methods

Plant material

Seedlings were derived from the crosses cv. Cox's Orange Pippin x James Grieve, IVT 6304-61 x IVT 74114-17, cv. Golden Delicious (clone Smoothee) x IVT 74114-17, cv. Jonathan x Cox 's Orange Pippin, Jonathan x IVT 6304-61 and Jonathan x IVT 74114-17. Artificial inoculations of detached shoots of mature trees of apple cultivars and experience of Dutch growers showed that Cox's Orange Pippin (COX) and James Grieve (JG) are highly susceptible (S) to *N. galligena* and that Golden Delicious (GD) and Jonathan (JO) are highly resistant (R) (Van de Weg (5)). Experience with mature trees of IVT 6304-61 (6304) and IVT 74114-17 (74114) at the IVT indicated that these selections are moderately to highly susceptible. The first two progenies may thus be considered as 'SxS' crosses and the others as 'RxS' crosses.

Selection 6304 originated from the cross Odin x (GD x Taunton Cross). Selection 74114 originated from the cross Septer x COX.

Forty seedlings of each progeny were used, except for 6304 x 74114 and JO x 74114 progenies. Of the former, only 23 seedlings were available. With JO x 74114, a larger progeny of 137 seedlings was used to investigate the within-progeny variation of an 'RxS' cross.

Seedlings were about 5 months old at the time of inoculation. They were planted in 4.5 litre plastic pots and kept in the field until inoculation.

Inoculation method

The fifth, seventh and ninth leaves from the top of the plant were removed by cutting just below their second (basal) abscission layer; the corresponding axillary bud was also removed. Within 1-5 minutes of cutting, 3 µl of a conidial suspension was placed on the wound with an automatic micropipette. Inoculated wounds were covered with vaseline within five minutes after the droplet was absorbed. Four days after inoculation the vaseline was wiped away with tissue paper. After inoculation the plants were moved to an unheated glasshouse.

To obtain macroconidia, potted infected trees of JG and COX were placed in a glasshouse at a relative air humidity of 100%. One day before inoculation sporodochia were removed from the cankers and collected in distilled water. A suspension of 3x105 macroconidia was made and stored at room temperature for use as inoculum. Seedlings were inoculated on 16-9-1987.

Observations

Lesion (canker) length was measured with a strip of paper having a scale in millimetres. Records were taken 27, 34, 41, 48, 55, 69, 84, 97, 111, 125, 153, 180, 196, 209, 223, 236, 259, 279, 301, 322, 357 and 376 days after inoculation. At the same time it was observed whether lesions had girdled the stem, causing death of the stem above the lesion. When a lesion had girdled the stem it was impossible to measure its length because the upper margin could not be distinguished from the shriveling and blackening stem. These lesions were given a constant value equal to the last true reading. The same was done with lesions located above the one that girdled the stem. Lesions receiving a constant value due to the girdling and death of the apical part of the stem will be referred to as 'stem-girdling lesions'.

Experimental design

A randomized complete block design was used with 40 blocks. Each block contained one seedling of each progeny except JO x IVT 7114-17 of which four seedlings were present in each block. There were three inoculated wounds on each seedling.

Results

Incidence of infected wounds

Percentages of infected wounds (%IW) for all progenies are presented in Table 1 which shows that %IW varied between 81% and 94%, with an average of 90%. Differences between progenies were very small, some being statistically significant at the 0.05 probability level and none being significant at the 0.01 level. (Only two seedlings did not show any symptoms of *N. galligena*.)

Absence of infection may be due to a high level of resistance, escape from infection due to experimental variation, or both. Hereafter, uninfected wounds will be regarded as escapes and therefore be treated as missing values in calculating percentage of lesions girdling the stems (%SGL) and mean lesion length (MLL). In this way the susceptibility of the most susceptible seedlings will not be underestimated. On the other hand, the susceptibility of highly-resistant seedlings will not be grossly overestimated in cases where absence of infection was due to resistance, because lesions will be small.

Stem-girdling lesions

Percentages of stem-girdling lesions (%SGL) are presented in Fig.1 for each progeny and for all dates of observation. It is seen that progenies differed greatly in %SGL. On the final date of observation, %SGL was higher in 6304 x 74114 and COX x JG than in 74114 x GD and JO x 77114. Further, the %SGL for each of these four progenies was higher than those of JO x 6304 and of JO x COX.

Table1. Percentages of infected wounds on six apple progenies.

Progeny	Percentage of inoculated wounds infected with *Nectria galligena*	
COX x JG	81	a[1]
6304 x 74114	84	ab
JO x COX	89	ab
JO x 6304	91	b
74114 x GD	93	b
JO x 74114	94	b
Mean	90	

[1] different letters indicate a significant difference according to a two-sided t-test (ã=0.05)

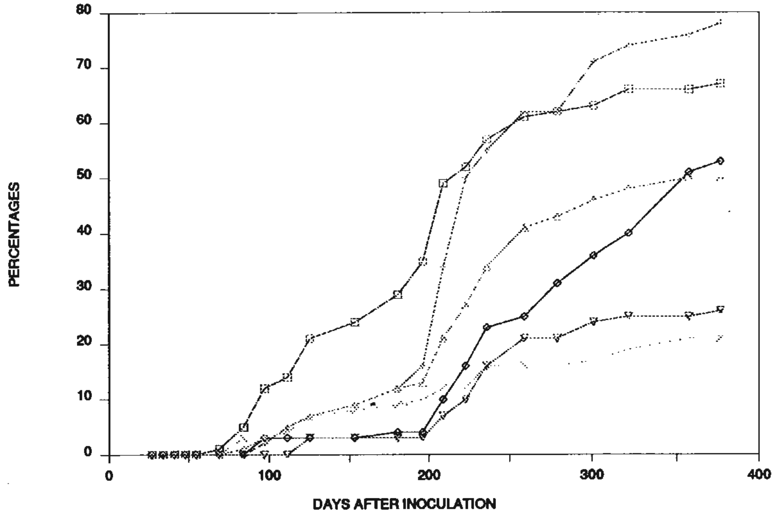

Fig. 1. Percentages of lesions of *Nectria galligena* girdling the stem of six apple progenies after inoculation. Legend: □ COX x JG, + 6304 x 74114, ◊ 74114 x GD, Δ JO x 74114, ∇ JO x COX, x JO x 6304

Lesion size

Mean lesion length (MLL) is presented in Fig.2 for each progeny and for each date of observation. Fig.2 shows that there were large differences between progenies in their 'final' MLL. On the last day of observation, COX x JG, 6304 x 74114 and 74114 x GD had a similar MLL which was larger than that of the JO progenies. Fig.2 further shows that the MLLs of COX x JG and 6304 x 74114 increased with time in a similar way and initially increased faster than the MLL of 74114 x GD.

In all progenies, except 74114 x GD, MLL increased only slightly after the 16th observation, 236 days after inoculation. This can probably be explained by two phenomena. Firstly, at that time many of the large lesions had girdled the stem (Fig.1). As lesion lengths could not be accurately measured after girdling, growth could no longer be determined. Secondly, from that time many small lesions were recovering, sloughing off diseased tissue while callus was growing over the surface of the wound. At the last date of observation several infections seemed to have recovered by being completely overgrown with callus. Thus after a while, lesion length of most large and most small lesions did not increase.

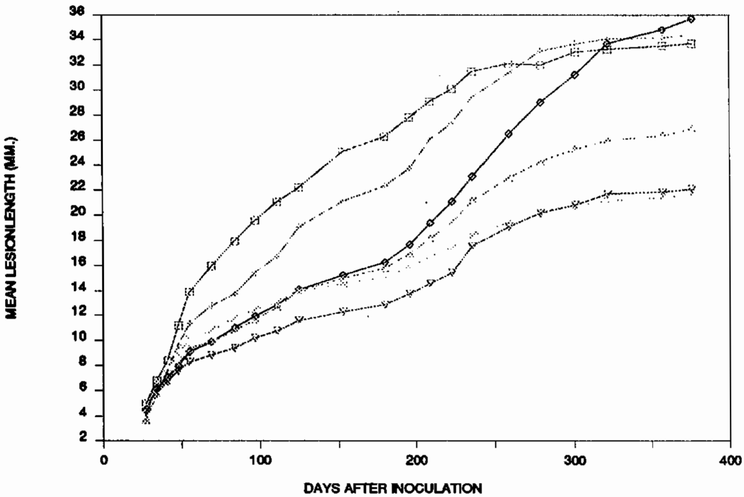

Fig. 2. Mean lesion lengths of *Nectria* cankers on progenies after inoculation. Legend: □ COX x JG, + 6304 x 74114, ◊ 74114 x GD, Δ JO x 74114, ∇ JO x COX, x JO x 6304

Frequency distribution of lesion length

The JO x 74114 progeny had most seedlings and was used to examine the distribution of average lesion length (ALL) of individual seedlings. The cumulative distributions of JO x 74114 and COX x JG differed maximally 180 days after inoculation. At that time, differences between relatively susceptible and relatively resistant seedlings will probably be largest.

Frequency distributions of JO x 74114 and COX x JG show that the variation in ALL is large in both progenies and that both distributions are continuous and have a similar range (Fig.3). The overlap of both distributions is large and the JO x 74114 distribution in considerably skewed. The JO x 74114 distribution proved to have more seedlings with small lesions than COX x JG (Kolmogorov-Smirnov two-sample test, $P<=0.001$). Frequency distributions of the other progenies of JO were not significantly different from that of JO x 74114 (Kolmogorov-Smirnov two-sample test, $P=0.05$). The distributions of COX x JG and 6304 x 74114 were also similar.

Analyses of the JO x 74114 distribution showed that it consisted of a mixture of two normally-distributed subpopulations (Table 2). The parameters which determine the mixture density were estimated by the method of maximum likelihood (3). A computer programme has been written for numerically approximating these estimates and assessing their accuracy. The more resistant subpopulation comprised about 75% of the total population, 78% when the ALL's of the JO x 74114, JO x 6304 and JO x COX progenies were joined. The mean and standard deviation of the more susceptible subpopulations were similar for those of COX x JG and those of the 'composite progeny' of COX x JG and 6304 x 74114.

Discussion

This investigation shows that progenies may differ in incidence of infection and rate of canker development when young seedlings are tested. The percentage of infected wounds (%IW) of the 'SxS' crosses tended to be lower than those of the 'RxS' crosses. This result is in contrast to what was expected, considering the level of resistance of the parents. However, differences in %IW were only small and never significant at the P=0.01 level. By contrast, large differences were found between progenies in percentage of lesions girdling the stem (%LGS) and in mean lesion length (MLL). The latter two parameters may therefore be more suitable for evaluating the level of resistance of progenies than %IW.

COX x JG and 6304 x 74114 had higher percentages of stem-girdling lesions (%SGL) and their relatively large mean lesion lengths (MLL) were reached sooner than with 74114 x GD and the progenies of JO. This result is in agreement with the level of resistance of the parents and suggests that this screening method can be used to detect differences in resistance based on a positive corre-

Table 2: Estimated mixing ratios (F), means and standard deviations (Sd) of subpopulations of several progenies and the standard deviation of these estimates. Parameters are estimated by the method of maximum likelihood.

Progeny	Subpopulation				
	I			II	
	F(%)	Mean (mm)	Sd	Mean (mm)	Sd
JO x 74114	75 ±5.5	12.1 ±0.4	3.4 ±0.4	27.3 ±3.8	11.0 ±1.2
JO x 'S'*1	78 ±3.7	11.7 ±0.3	3.2 ±0.3	27.7 ±2.9	11.3 ±1.0
COX x JG				26.3	16.1
'S' x 'S'*2				24.9	15.1

*1: composite of JO x 74114, JO x 6304 and JO x COX.
*2: composite of COX x JG and 6304 x 74114.

lation between the resistance of seedlings and mature trees. These indications have to be verified. If they prove to be true young seedlings can be used in screening for resistance to *Nectria*.

The MLL of 74114 x GD was higher than that of JO x 74114, showing that JO passed a higher level of resistance on to its progeny than GD. JO is considered more resistant than GD.

Frequency distributions of average lesion length (ALL) of seedlings of the COX x JG and JO x 74114 progenies were continuous. Numerical analyses of ALL for the JO x 74114 progeny and the composite population of the three JO progenies suggested that they consist of two subpopulations, the more resistant subpopulation consisting of about 75% of the total. The mean and standard deviation of the more susceptible subpopulation were similar to those of the 'SxS' progenies. Therefore the difference in resistance between the 'JOxS' and 'SxS' progenies may be caused by two major heterozygous resistance genes in JO. Further research is needed on this hypothesis.

Acknowledgements

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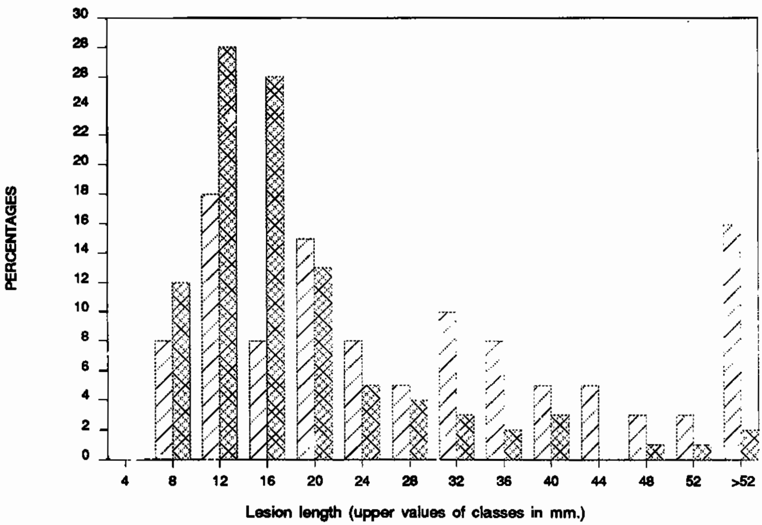

Fig. 3. Frequency distribution of lesion lengths of COX x JG (☐) and JO x 74114 (☐) 180 days after inoculation.

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Session 4

Disease-resistant apple cultivars

Chairperson: C. Gessler

Experiences at Bavendorf (FRG) with scab-resistant apple cultivars

R. Silbereisen

University Hohenheim, Research Station Bavendorf, D-7980 Ravensburg-Bavendorf, FRG

Abstract

An assessment is given of the scab-resistant cultivars Prima, Priam, Priscilla and Sir Prize grown at Bavendorf, near Lake Constance, FRG, 1979-87. Attention is drawn to their agronomic characteristics, to their acceptability by growers and consumers, and to the apparent lack of winter hardiness of Prima and Sir Prize at this site. Preliminary results with scab-resistant cultivars in a new trial are described.

Key words: apple scab, resistant cultivars, variety trials, *Venturia inaequalis*

The idea of breeding dessert-quality apple cultivars resistant to scab (*Venturia inaequalis*) began 80 years ago, and is made more necessary today by the pressures to cease spraying fungicides.

American and Canadian breeders led this work: Crandall (2), for example, discovered the character of scab resistance in six small-fruited *Malus* species. He

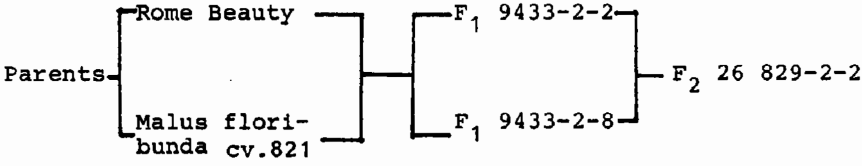

Fig. 1. Pedigree of the breeding-stock Nr. 26 829-2-2.

started a programme with a cross between *Malus floribunda*, carrying Vf resistance in dominant monogenic form, and cv. Rome Beauty. In 1926, two siblings were crossed to produce an F_2 population of 38 plants. These segregated into highly susceptible and highly resistant plants in the ratio 1:1. From this F_2 population a highly scab-resistant plant with good-sized fruit was selected and given the number 26 829-2-2. This one plant has been the most important source of scab resistance in apple breeding programmes. Figure 1 illustrates this history.

In the 1930s, similar programmes were undertaken by the Germans Rudloff and Schmidt (9, 10), and continued after 1945 by Zwintzscher (14). In the USA meanwhile, the Cooperative Apple Breeding Programme (ABC) started, with experts at the Universities of Purdue and Illinois, and later at Rutger University. The initial letters of these co-operating universities were used as a prefix in the names of the first cultivars released from this programme e.g. PRIma, PRIam, PRIscilla and Sir PRIze (3, 5, 13). Figure 2 shows the pedigree of the cultivar 'PRIam', which after two back-crossings to Jonathan and Golden Delicious and following selection at the INRA station at Angers (France), was released for cultivation.

Table 1 lists cultivars with scab-resistance, and clearly shows the importance of Vf-controlled resistance. Cultivar Freedom has polygenic resistance from Antonowka in addition to Vf resistance. The scab resistance of Nova Easygro is from the Russian seedling R 12740-7A, derived from *M. pumila*, and cv. Murray is dominant from *M. micromalus*. Seedlings which currently only have numbers could be added to this list.

Breeders today are working worldwide to produce apples with absolute resistance (or field immunity) or partial resistance to scab. Usually within these programmes attempts are made to incorporate resistance to other diseases, like powdery mildew, apple canker and collar rot. From these efforts there are hopeful expectations of an early increase in the number of disease-resistant apple cultivars, especially using the advantages of gene technology.

In Table 2 are grouped those cultivars being used for backcrossing, beginning with the F_3 generation, from which indications can be deduced about the ex-

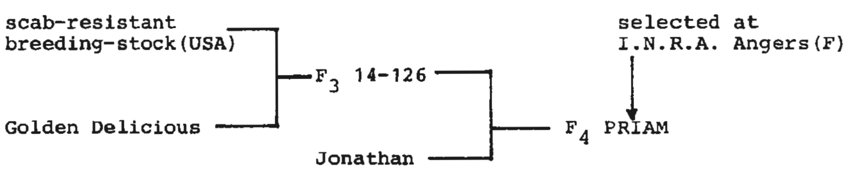

Fig. 2. Pedigree of the scab-resistant cultivar "Priam".

Table 1. Scab resistant apple varieties*.

Variety and country	Source of resistance	Printed
USA		
Prima	Vf	1970
Priscilla	Vf	1972
Sir Prize	Vf	1975
Liberty	Vf	1978
Jonafree	Vf	1979
Redfree	Vf	1981
Freedom	Vf + poly	1983
FRANCE		
Priam	Vf	1974
Querina (= Florina)	Vf	1977
CANADA		
Mac Free	Vf	1974
Nova Easygro	Vr	1975
Novamac	Vf	1978
Murray	Vm	1981
United Kingdom		
Gavin	Vf	1977
Redsleeves	Vf	1984

Additionally some seedlings, which are differentiated with numbers.

*) LESPINASSE, Y. et al.: Florina Querina, la Resistance du pommier á la tavelure. Arboric. fruit 378, 43-47, 1985, modified and completed.

pected fruit quality. Also in Table 2 are details of disease resistances noted by breeders. Priscilla is resistant to powdery mildew, whereas the remaining cultivars have a moderate (Sir Prize) or small resistance to this disease. An important purpose of cultivar trials is verification of such statements under various ecological conditions in various apple-growing regions. How are the cultivars Prima, Priam, Priscilla and Sir Prize performing in terms of cultivation, marketing and consumer acceptance?

Figure 3 shows the harvest date and storage information of four PRI-cultivars tested at Bavendorf since 1979; (Prima was planted earlier). The other information has been taken from published reports.

Redfree is an early ripening cultivar and Prima ripens a little later; Querina matures very late. First experiences are that most of the scab-resistant cultivars store satisfactorily in CA (controlled atmosphere) stores.

Bavendorf cultivar trial 03/4, 1979-1987

To interpret the results of this cultivar trial it is important to note certain environmental factors at Bavendorf (Table 3):

- the low annual mean temperature of 7.6 °C,
- the very low temperature in January 1985,
- the slightly clayey soil, fluctuating in water content.

Table 2. Characteristics of scab-resistant cultivars on the base of the source Nr. 26 829-2-2 (Vf).

	for back-crossing used cultivars, beginning with F_3	further resistances are existing against
Prima	Gold.Del., Melba, Red Rome Beauty, Starr, Wealthy	fireblight high mildew low
Priscilla	Gold.Del., McIntosh, Red.Del., Starking	fireblight high mildew high
Sir Prize	Gold.Del., Douds Gold.Del., tetraploid	fireblight low mildew moderate
Priam	Gold.Del., Jonathan	mildew low
Querina (Florina)	Gold.Del., Red Del., Starking	mildew low

Table 3. Geographical and ecological data of the research station Bavendorf, University Hohenheim, Germany.

Federal state	Baden - Württemberg
Region	Lake of Constance
Height above sea level resp. altitude	500 m
Temperature - annual mean	7.6°C
Minimum temperature at 4.1.85	- 23°C
Rainfall - annual mean	920 mm with maximum June to August
Soil - condition	heavy loam, changing in humidity
- quality	moderate
- pH-value	about 6.5
Indicator plants for humidity in soil	Deschampsia caespitosa Potentilla anserina Ranunculus acer

Table 4. Productivity of scab resistant and standard cultivars on rootstock M9 during the first six planting years (2x9 trees/cv).

	Mean crop/tree and year kg	%
Sir Prize	10,7	100
Priscilla	9,7	91
Priam	9,6	90
Prima	8,2	77
Red Boskoop, Schmitz-Hübsch	10,7	100
King of the pippin	6,4	60

Table 5.

FRUIT SIZE DISTRIBUTION (%) related to the WEIGHT
- **Records from 1983 to 1987, mean values**
- **M9; similar fruit-density at tree**

	Classes of fruit size in mm									Percentage
	< 55	55/60	60/65	65/70	70/75	75/80	80/85	85/90	> 90	70 mm and more
Priam	4	12	32	40	11	1				12
Priscilla	3	8	15	39	25	9	1			35
Prima		2	9	31	34	18	6			58
Sir Prize***		2	7	18	29	24	17	2	1	73

*** triploid cultivar

The ecological conditions at Bavendorf - representative of extensive areas in the region of Lake Constance - are not ideal for apple growing.

Crop yield is important in any apple cultivar. Table 4 shows that the scab-resistant cultivars are good bearers in comparison with the standards Red Boskoop, Schmitz-Hübsch and King of the Pippin.

Fruit size data are shown in Table 5. The four cultivars show a clear ranking: Priam fruits must be classified as small to medium, Priscilla and Prima as medium and the triploid Sir Prize as large.

Measurements of sugar content (refractometer values) and titratable acids and their ratio allow conclusions about taste quality: high sugar and acid levels are more favourable than low levels or an imbalance. Priscilla is rich in sugar but poor in acidity and has a high sugar-acid ratio of 25:1 (Table 6); with this ratio Priscilla is grouped with Red Delicious, well known for a flat, sweet-

Table 6. Content of sugar and acidity of fruits from scab-resistant cultivars. Mean values from 1982 to 1987, Rv=Refractrometer value, tA=titrable acidity.

	RV in %	tA in g/l	Relation Sugar/ Acidity
Prima	12,2	8,2	14:1
Priam	13,2	7,9	15:1
Priscilla	14,5	5,3	25:1!!
Sir Prize	14,6	8,9	15:1

Table 7. Characteristics of fruits of average size from scab-resistant cultivars. Mean values from 1983 to 1985.

	specific gravity	Index: Height to width	Firmness of fruit flesh kg/cm^2
Prima	0,80	0,84	4,2
Priam	0,76	1,02	3,9
Priscilla	0,85	0,80	6,2
Sir Prize	0,80	0,97	3,0

ish taste. The other three cultivars have sugar and acidity characteristics liked in Germany.

Table 7 shows the soft fruit flesh of Sir Prize, at only 3.0 kg/cm^2. Sir Prize is not, therefore, for the regional market and is even doubtful for the local market.

Storage data are given in Table 8. These results refer to long-term storage at 6 °C. There is little bitterpit, a moderate susceptibility for fruit rots in Priam, a

Table 8. Fruit deficiencies from scab-resistant cultivars after cool-storage at 6 °C. Observations from 1983 to 1987.

	bitter pit	fruit rots	internal breakdown	greasiness of the skin
Prima	low	low	low to moderate	low to moderate
Priscilla	not any	low	strong	not any
Priam	very low	moderate	low	low
Sir Prize	not any	low	low	very strong

Table 9. Frost-induced damages of scab-resistant apple trees.

	n	Severe damages or losses	Regeneratable Part-damages	Damages on buds
Priscilla	18	1	0	0
Priam	18	4	2	1
Prima	18	9	2	1
Sir Prize	14	9	0	0
Summerred	18	2	2	3
Red Boskoop, Schmitz-Hübsch	18	2	6	0

strong tendency for internal breakdown in Priscilla and a greasiness of the skin of Sir Prize.

Table 9 concerns the serious problem of the duration of tree life. As a consequence of the severe winter from January to March, 1985, Prima and Sir Prize suffered the loss of 50% of the trees. In contrast, Priscilla and Priam proved to be cold-hardy, with losses comparable with Red Boskoop and Schmitz-Hübsch.

Summary of trial 03/4

PRIMA
- resistant to scab
- moderate vigor; well suited for training as a slender spindle bush
- short life span
- precocious; good yield and regular bearing
- medium-sized fruits; medium specific gravity; a broad fruit, round-shaped like cv. Calville; partly blushed, partly patchy red colour
- low to medium acidity, depending of storage conditions; pleasant in autumn; high vitamin C content
- small-celled and very juicy, but good taste for only 4 to 5 weeks
- in suitable ecological conditions a useful apple for consumption in autumn, but marketing duration may be short

Table 10. Scab infections on scab-resistant cultivars.

- without any chemical treatment
- 2-years old/ rootstock M9
- completed with 20 local and new cvs.
- n = 10 to 18/cv.
- Bavendorf

	Classification+ in %	
	21.7.1987	22.7.1988
Priscilla	0	0
Sir Prize	0	0
Liberty	0	0
Redfree	0	0
Priam	0	0
Jonafree	4	0
Querina	5	0
Prima	8	0
Ribston Pepping	0	0
Rubinette	95	25

+5 leaves, selected by chance, at well-developed shoot were classified on each tree according to the statement: SCAB yes or no !

PRIAM
- resistant to scab
- low to moderate vigor; broad canopy
- precocious, good yield and regular bearing
- small to medium fruit size; fruit as high as wide; low in specific gravity
- prevailing red colour
- fruity in taste, moderately aromatic; fine-celled and juicy, refreshing taste

- because of the mostly small fruit size unsuitable as a commercial cultivar

PRISCILLA
- resistant to scab
- moderate vigor and plentiful spurs
- precocious, heavy cropper, bearing regularly
- medium fruit size; prevailing red colour with a pale blue hue; a broad-shaped fruit; high specific gravity
- flavour sweet but rather flat
- texture firm, coarse, moderately juicy, becoming crisp later
- good cultural features, but flavour and flesh not ideal for the FRG market

SIR PRIZE
- resistant to scab
- vigourous; shoots and spurs resemble Golden Delicious
- short life span
- precocious; eventually good yields, but not bearing regularly
- large fruit size; medium specific gravity; oblong to cylindrical shape
- russet-free but tendency to be greasy; ground colour greenish-yellow; fine fruity flavour, aromatic; soft and juicy flesh but very tender
- because of very tender flesh and skin, and also because of short life span, unsuited as a commercial cultivar

Table 11. Mildew infections on scab-resistant cultivars.

- without any chemical treatment
- Bavendorf 1988

	Classification+ in % primary infections	Classification+ in % secondary infections
Priam	0	0
Prima	0	0
Priscilla	10	0
Jonafree	11	6
Sir Prize	0	30
Querina	28	17
Liberty	11	56
Redfree	43	57
Roter Berlepsch	0	0
Idared	76	82

+ each tree was classified according to following steps: 0 - no infection
1 - small infections
2 - moderate infections
3 - strong infections

Bavendorf cultivar trial 01/2

Cultivar trial 01/2 started in 1987 with nine scab-resistant cultivars planted with twenty one old, local and new cultivars, like Malling Kent, Rubinette, Falstaff and Ingol. They are grown with and without chemical treatments. Preliminary results are as follows:

In 1987, with frequent scab infection periods in spring, Prima, Querina and Jonafree showed some foliar scab. Similar results for Prima are reported by Indenko (6) from the Moldavian region, by Grauslund (4) in Denmark and by other workers in the FRG. In 1988, however, all scab-resistant cultivars remained free of scab. Ribston Pepping had no scab in either year, whereas Rubinette was highly susceptible.

In 1988, primary and secondary mildew were noted on Jonafree, Querina, Liberty and Redfree; Priscilla, considered highly resistant to powdery mildew, had primary mildew only. Sir Prize only had secondary infections. Priam and Prima had no mildews. Idared confirmed its high susceptibility to mildew; Red Berlepsch remained free of attack. In Poland (1), Liberty, Priam and Priscilla are susceptible to apple mildew.

Red spider mites were observed on Sir Prize, Prima, Redfree and Priscilla, the attacks being relatively severe and similar to that on James Grieve. The infestation was much less on Priam, Querina and Falstaff.

In both years severe damage was caused by aphids, mainly on Sir Prize, Priscilla and Idared. Other scab-resistant cultivars were moderately attacked. Relatively good aphid resistance was shown by the new cultivar Rubinette.

Table 12. Red mite infestation on scab-resistant cultivars.

- without any treatment
- 2-years-old/rootstock M9
- Bavendorf 1988

	Classification+	
	30.May	20.June
Priam	0-1	0-2
Querina	0-1	1
Jonafree	1	0-2
Liberty	1-2	0-2
Sir Prize	1-2	1-2
Prima	1-2	1-3
Redfree	1-2	1-3
Priscilla	2	0-1
Falstaff (A 120/3)	0	1
James Grieve	2	2-3

+each resp.each 3.tree was classified according to following stepd:

0 - no attack
1 - small attacks
2 - moderate attacks
3 - strong attacks

Table 13. Aphids (*Aphis pomi*) infestations on scab-resistant cultivars.

- without any chemical treatment
- Bavendorf

	Classification+ in %			
	1987		1988	
	21.7.	13.8.	30.5.	13.6.
Jonafree	1-2	0-2	1	1-3
Redfree	1-2	0-1	1	2-3
Querina	2	1	1	1-3
Liberty	2	1-2	1	2-3
Priam	1-2	0-2	1-3	3
Prima	2-3	2-3	0-1	1-3
Sir Prize	3	1-2	2	3
Priscilla	3	1-3	1-2	3
Rubinette	1-2	0-1	0-1	1-2
Idared	3	2-3	1	2-3

+ each resp. each 3.tree was classified according to following steps:

0 - no attack
1 - small attacks
2 - moderate attacks
3 - strong attacks

Conclusions

1. Scab-resistant apple cultivars must have attributes satisfactory for growers, marketers and consumers.
2. New scab-resistant cultivars must also be resistant to powdery mildew, canker, red spider mite, aphid and perhaps other enemies.
3. Breeders must be encouraged to produce, in a short time, apple cultivars that will not require chemical treatments.

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Scab resistance of apple cultivars, selections and progenies with the Vf gene

Jutta Krüger

Bundesforschungsanstalt für gartenbauliche Pflanzenzüchtung, Ahrensburg, FRG

Abstract

This paper describes the stability of resistance to scab (*Venturia inaequalis*) in several crosses. Eight out of the selections with Vf resistance become infected with scab in plots with a high natural inoculum. No relation was found between the stability of resistant parents and the progeny: in particular, a high proportion of Prima progenies became attacked. The stability of progenies from Vf x Vf crosses was little better than that of progenies from scab-resistant x scab susceptible crosses. The influences of modifying genes is discussed.

Key words: apple scab, resistant cultivars, Vf gene, scab resistance, stability, progeny tests.

Introduction

Resistance to scab (*Venturia inaequalis*) in apples bred from *Malus floribunda* 821 is believed to be determined by a single dominant gene Vf (2), and has proved stable. Most new scab-resistant cultivars carry this resistance and are successfully grown world-wide without the need for scab fungicides. These cultivars can be traced back to a Rome Beauty x *M. floribunda* 821 cross made at the beginning of this century. Since 1945, scab-resistant parents derived from this initial cross have been used in breeding programs in the USA and many other countries, including the FRG at Ahrensburg.

Materials and methods

Since 1980, cultivars and selections with Vf resistance have been grown at Ahrensburg in orchards where fungicides are not applied and insecticides only occasionally. Progenies which remain free of scab in glasshouse tests are planted in these orchards. The first test for resistance takes place with the artificial inoculation of young seedlings at the 2- to 3-leaf stage. Scab-free seedlings are planted in the field under natural infection conditions. During the past 5 years the infection potential of *Venturia inaequalis* has increased rapidly in the experimental plots and therefore the trees are now exposed to a high inoculum potential. At the end of the first growing year the plants are re-evaluated and in the following years, prior to fruiting, scab incidence is recorded in July and September. The following cultivars and selections with Vf resistance were used in crosses: Prima, Coop2, 6, 7, 8, 9 and 10, Priscilla, A59/24, A163/42, 5002, 5053, HAR30T106 and TSR15T3. Beside being crossed with scab-susceptible parents, scab-resistant selections were inter-crossed.

Table 1: Stability of cultivars and clones with Vf resistance in the field at the BFA, Ahrensburg

clone/cultivar	Number of years in the field	Number of years without scab	year when slight scab present
Prima*	4	2	3+, 4+
Coop2*	8	6	7+
Priscilla	7	7	
Coop6	8	8	
Coop7#	5	2	3, 4, 5
Coop8	6	6	
Coop9	8	7	8
Coop10	9	7	8
A59/24	7	3	4, 5, 6, 7
A163/42	8	6	6, 7
5002	4	4	
5053	8	8	
HAR30T106	8	7	8
TSR155T3	3	3	

* the two clones may not be identical

it is not sure if this is the original clone Coop7

+ only single scab spots

Table 2. Percentage of scab incidence in progenies of crosses with Coop10 and TSR15T3 selected being healthy after the first year.

cross	2./3. year				4. year				5. year				6. year				7. year				8. year				9. year			
	h[1]	sl	m	s	h	sl	m	s	h	sl	m	s	h	sl	m	s	h	sl	m	s	h	sl	m	s	h	sl	m	s
Coop8 x	100	–	–	–	100	–	–	–	100	–	–	–	80	20	–	–	87	13	–	–	100	–	–	–**				
Coop10	100	–	–	–	100	–	–	–	100	–	–	–	92	8	–	–	73	27	–	–	93	7	–	–***				
Coop10 x	100	–	–	–	97	3	–	–	100	–	–	–	71	29	–	–	79	21	–	–	100	–	–	–				
Coop8	100	–	–	–	93	7	–	–	100	–	–	–	79	21	–	–	36	50	14	–	100	–	–	–				
Coop10 x	100	–	–	–	100	–	–	–	100	–	–	–	95	5	–	–	80	20	–	–	100	–	–	–				
Coop7	100	–	–	–	100	–	–	–	100	–	–	–	100	–	–	–	90	10	–	–	100	–	–	–				
Coop10 x	100	–	–	–	100	–	–	–	100	–	–	–																
Cox Orange	100	–	–	–	100	–	–	–	100	–	–	–																
Ingrid Marie x	100	–	–	–	100	–	–	–	100	–	–	–																
Coop 10	100	–	–	–	100	–	–	–	100	–	–	–																
TSR15T3 o.p. x	100	–	–	–	83	17	–	–	83	17	–	–	72	28	–	–	78	22	–	–								
Coop 10	100	–	–	–	94	6	–	–	100	–	–	–	94	6	–	–	96	4	–	–								
Coop10 x	100	–	–	–	47	29	24	–	18	76	6	–	35	65	–	–	82	12	6	–								
TSR15T3 o.p.	100	–	–	–	53	35	6	6	82	18	–	–	18	47	35	–	88	6	6	–								
TSR15T3 x	100	–	–	–	100	–	–	–	99	1	–	–	97	3	–	–	81	18	1	–	64	36	–	–	86	12	2	–
Astramel	100	–	–	–	100	–	–	–	98	1	1	–	100	–	–	–	88	12	–	–	54	39	6	–	88	12	–	–
Astramel x	100	–	–	–	100	–	–	–	100	–	–	–	100	–	–	–	93	7	–	–	79	21	–	–				
TSR15T3	100	–	–	–	100	–	–	–	100	–	–	–	100	–	–	–	71	29	–	–	50	50	–	–				
TSR15T3	100	–	–	–	100	–	–	–	100	–	–	–	98	2	–	–	82	18	–	–	70	30	–	–				
Elstar	100	–	–	–	100	–	–	–	100	–	–	–	98	2	–	–	96	4	–	–	44	46	10	–				
Elstar x	100	–	–	–	100	–	–	–	100	–	–	–	100	–	–	–	83	17	–	–	78	22	–	–				
TSR15T3	100	–	–	–	100	–	–	–	100	–	–	–	100	–	–	–	90	10	–	–	50	41	9	–				

[1]h: healthy
sl: slight scab infection
m: moderate
s: severe
** evaluation in July
*** evaluation in September

Table 3.

cross	4. year				5. year				6. year				7. year				8. year			
	h	sl	m	s[1]	h	sl	m	s	h	sl	m	s	h	sl	m	s	h	sl	m	s
Prima x	77	18	5	–	90	5	3	3	79	18	3	–	82	16	3	–	92	8	–	–**
A142/5	92	6	3	–	82	10	5	3	87	13	–	–	67	26	5	3	87	13	–	–***
Prima x	20	59	20	2	2	35	52	11	7	41	62	–	–	43	52	5	45	55	–	–
A143/24	17	54	28	–	–	33	59	9	21	79	–	–	–	7	45	48	21	62	17	–
Prima x	86	13	1	–	38	56	5	1	18	59	21	3	27	69	4	–	55	44	1	–
clone 40	77	21	–	1	39	48	9	5	43	43	14	–	37	39	23	1	63	36	1	–

[1]h: healthy
sl: slight scab infection
m: moderate
s: severe
** evaluation in July
*** evaluation in September

Table 4: Percentage of scab-free apple seedlings in progenies of Vf x Vf crosses: artificial inoculation in spring and natural inoculation in autumn of the first year

cross	% scab free apple seedlings after: glasshouse during inoculation	% scab free apple seedlings after: field infection in autumn
Coop7 x Coop2	53	27
Coop8 x Coop7	100	89
Coop8 x Coop10	70	64
Coop10 x Coop7	71	71
Coop10 x Coop8	88	88
Coop10 x TSR15T3	59	59
TSR15T3 x Coop10	61	61
5053 x HAR30T106	38	27

Results

Because of the high level of inoculum in the orchard plots in recent years not all selections and cultivars with Vf resistance remained free of scab. Although scab was usually absent from this material, the leaves and/or fruits of some selections developed single small, sporulating lesions or a few larger weakly sporing lesions (Table 1). Over an 8-year period, 8 of the 14 selections were infected by scab in one or more years. Some selections (Coop2, Coop9, Coop10, A163/42) had scab only in years when there was intense infection pressure; 1985, 1986, and 1987 were such years, while in 1988 there was a moderate to severe incidence of scab at Ahrensburg. The infected trees differed in the grade of scab intensity: Prima and Coop2 only developed single scab lesions while a few larger lesions were present on the other selections.

The stability of scab resistance in selections from progenies derived from different Vf-resistant sources varied in the field. No correlation was observed between the stability of the resistant parent and that of its progeny. Progenies of Priscilla, Coop6, 7, 8 and 9, A59/24, A163/42, 5002, 5053, and HAR30T106 exhibited a slight incidence of scab in a very few cases and a moderate incidence only occasionally. In contrast, a high proportion of progenies of Prima, TSR15T3 and Coop10 showed a slight and to a certain degree a moderate to severe scab incidence from the fourth year: they can divided into two groups, progenies of Prima (Table 3) being more susceptible than progenies of Coop10 and TSR15T3 (Table 2). The stability of the progenies from Vf x Vf crosses was little better than that of progenies from crosses between scab-resistant material and scab-susceptible cultivars. The number of attacked trees was small in years with a low infection pressure, such as 1988 (last column of each Table). In years with a high inoculum potential, trees with a severe scab attack could be found, especially in the cross between Prima and the very susceptible selection A143/24 (Jonathan x *M. zumi*). Although the scab susceptibility of clone 40 (an open-pollinated Goldparmäne) was less than that of A142/5 (Jonathan x *M. robusta*; medium susceptible), scab incidence in the progeny of Prima x clone 40 was higher than that in Prima x A142/5.

In autums the proportion of susceptible plants recorded in progenies selected as resistant in the glasshouse was not dependent on the source of Vf resistance (Table 4). It was notable that progenies of Vf x Vf crosses had a higher proportion of healthy plants (Table 5).

Discussion

As scab resistance from *M. floribunda* 821 is said to be under monogenic control (2), it might be expected that resistant derivatives would respond identically to the diseases. This is not the case, however, because plant reaction to the pathogen is also determined by varying numbers of modifying genes which intensify as the result of the effects of the major (Vf) gene. Rousselle (1) reported that in the absence of these modifier genes the Vf gene allows weak sporulation of the fungus. The above-mentioned scab resistant selections are derived from several backcrosses, to different commercial cultivars, of a progeny of the cross Rome Beauty x *M. floribunda* 821. The number of modifier genes may be reduced or augmented in each generation and in that way scab stability of clones may decrease or increase, explaining the varied scab response of selections with Vf resistance.

The development of a new race of *V. inaequalis* virulent against the Vf gene does not seem likely because Vf selections in the field were not equally susceptible; different grades of symptom-expression occurred.

Table 5: Percentage of scab-free apple seedlings in progenies of crosses with 1 parent with Vf resistance: artificial inoculation in spring and natural inoculation in autumn of the first year.

cross	% scab-free apple seedlings	
	glasshouse during inoculation	field inoculation in autumn
Prima x clone 40	71	55
Prima x A142/5	95	59
Prima x A143/24	78	42
Priscilla x Ingrid Marie	55	29
Ingrid Marie x Priscilla	24	18
Priscilla x Cox Orange	57	25
Ingrid Marie x Coop9	51	13
Cox Orange x Coop9	15	8
Ingrid Marie x Coop10	47	24
A59/24 x Golden Delicious	68	15
HAR13T57 x Golden Delicious	26	7
Coop7 x Ingrid Marie	74	31
Coop8 x Ingrid Marie	29	17

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Genetics of the interaction *Venturia inaequalis* - *Malus*: the conflict between theory and reality

C. Gessler

Institute of Plant Sciences/Phytomedicine, Universitätstr. 2, 8092 ETH-Zürich, Switzerland.

Abstract

Much information is available on the interaction between *Venturia inaequalis*, incitant of the apple scab disease, and the host *Malus*. This information is analyzed with regard to the genetic interaction. Special attention is paid to the resistance (Vf) bred into commercial apple cultivars from *M. floribunda* 821. The example of this resistance is related to general principles of host-pathogen interaction and is also discussed in relation to durability of resistance.

Key words: resistance, Vf, breeding, inheritance.

Introduction

In 1819 E. Fries described the fungus causing scab symptoms on apple as *Spilocea pomi* Fries. This asexual stage was independently named by Wallroth (1833 in *Flora Cryptogamica Germanica*) *Cladosporium dendriticum* Wallrot and changed later by L. Fuckel to *Fusicladium dendriticum* (Wallr.) Fckl..

In the following 60-70 years the main objective of scientists was the description and classification of the two scab fungi. Some rather curious affirmations were made: e. g. Sorauer in 1875 found spermogonia, pycnidia and perithecia on pear leaves and believed that all belonged to *Fusicladium pirinum*. Cooke (1866) described the sexual form of a newly discovered fungus, *Spaerella inaequalis*, Cooke renamed later by Winter as *Venturia inaequalis* (Cooke) Winter. The relationship of the perithecia and ascospores of *Venturia* to the asexual *F. pirinum* and *F. dendriticum* (*Spilocea pomi*) forms was probably first resolved in 1887 by Goethe (22). However, this work was published in a general journal (Gartenflora) and no names were given to the sexual forms. In 1896 the connection between the sexual and asexual phase was officially established by Aderhold (1) in the species *Venturia chlorospora* Ces. He renamed the fungus, after differentiating it from other *Venturia* species, *V. inaequalis* (Cooke) Aderh. (3). In Aderhold's work we find the first complete and correct description of the life-cycle as well as a long discussion with some experimental results on the variability of the fungi *in vitro*, extended later (3) with data on the relation between climate, scab epidemics and control measures. The number of works dealing with different aspects of the scab disease increased steadily, culminating in reviews (6, 61).

Understanding of the genetic interaction between pathogens and hosts increased, but became more confused as new theories were developed (50, 52, 55, 56). Definitions were often vague. This paper attempts to analyze published data on the interaction *V. inaequalis-Malus* in the light of these theories, adopting the definitions given in relevant textbooks (39, 51) and quoting them where appropriate. Older works often considered only the aspects of the host (13, 23, 38, 44); however in modern breeding it is essential to understand the genetics of the host, the pathogen and of the interaction.

Phenotypic variation of the interaction

In the chapter on "artificial infection and cultivar susceptibility (Sortendisposition) of apple", Aderhold (1) described how he successfully used ascospores and conidia collected in the field and conidia produced in cultures to infect leaves of apple and pear in the field; he recovered from the lesions the conidia of *V. chlorospora* (= *V.inaequalis*) and *V. pirinum*. He inoculated only young leaves, giving as reasons that the success probably would have been greater than with older leaves and because the latter were already contaminated by other fungi. A few years later in a remarkable lecture, Aderhold (2) illustrated, with photographic documentation, that different apple cultivars were defoliated to different extents by the scab fungus, being therefore differently susceptible. Noting that this property would have a practical meaning only if it was constant, he went on to demonstrate that this was not the case and that in different years the ranked order of susceptibility of the cultivars in the same orchard could change, and that it could also change between orchards and due to soil conditions. He gave a possible explanation: the growth of the cultivars changed from year to year due to variation in the climatic conditions but not in the same way for all cultivars, so that the potential susceptibility varied among them. But he noticed that susceptibility did not depend only on the cultivar and the influence of the environment but also on the interaction between a specific fungus (strain?) and a specific host (cultivar?). For example, infection of *F. pirinum* was most probably successful if the inoculum was taken from the cultivar on which the inoculation was subsequently made. He called this the accommodation of the fungus to a certain cultivar and recommended to the nurseries not to distribute material with scab because the fungus may not yet be accommodated to a new cultivar in the destination orchard. Disease severity would be low until the fungus accommodated to the cultivar newly planted in that orchard. He concluded that more resistant cultivars should be sought even if it may demand much time and that aspects such as climate, soil and fertilization have to be considered.

Similar observations on changes in the ranking of susceptibility were made by Wallace in 1913 (57). He thought that the fungus adapted itself to life on the "resistant" hosts. At the time, Wiltshire (63) pointed out that "the absence of adequately definite facts makes it at present unprofitable to formulate hypotheses to account for the phenomena". Wiltshire was more concerned by the reasons why young leaves of certain cultivars and old leaves of all cultivars were immune. After describing the different interactions in astonishing morphological detail and speculating on the role of chemotropism he concluded: "what the limiting factor in immunity is, we can only speculate - it may be simple starvation of the fungus, as suggested by the gradual reduction of growth" with the increasing age of the leaves. Moreover, in the same work he stated that immunity does not depend on protection by the cuticle, as was confirmed 70 years later (53), but "suggest the probability of the cell sap of the host being in all cases antagonistic to the fungus".

The possibility of adaptation of the fungus to a specific host was not considered again until 1931, when Wiesmann (58) undertook specific experiments. He found great variability *in vitro* among single spore isolates in relation to growth, colour, sporulation intensity and response to pH variation of the substrate (later confirmed by many others, 26, 35, 37, 40, 41, 45) for both scab fungi, and great variability in the morphology of the conidia of the apple scab fungus. He also confirmed that a relation exists between the origin of the inoculum and the success of artificial inoculation on leaves of different cultivars. The percentage of inoculations resulting in symptoms was always greatest in the combinations where the inoculum source was the same cultivar as that on which the artificial inoculation was subsequently made.

The protocol of his experiment was: scabbed leaves were collected in May and June in an orchard planted with different cultivars in a mixed stand. Detached leaves, or leaves on detached twigs or on trees in the orchard, were inoculated with conidia freshly washed off the diseased leaves. Wiesmann then counted the number of inoculation sites showing scab symptoms. The results of two to four assays per combination are summarized in Table 1. Unfortunately, he did not succeed in infecting leaves with the many monosporic isolates that he made.

We can assume from the biology of the fungus and from current knowledge, that the inoculum at the beginning of the season came predominantly from ascospores, in which a recombination of the genotypes had happened. Since ascospores cannot choose to land on the tree to which they are best fitted, we can also assume a random distribution of the ascospores leading to a random primary distribution of genotypes on all trees. During the subsequent asexual cycle, the pathogen is then more or less restricted to individual trees.

The genotype which best fits a particular tree reproduces more and becomes predominant so that, for example, the Boiken-type isolate on cultivar Boiken will have the best epidemiological characters, and, after a number of cycles of reproduction, it will displace other types on this particular cultivar.

Wiesmann observed not only qualitative differences in pathogenicity (virulence avirulence *sensu* yes\no, respectively) between conidia from different origins, but also quantitative differences in pathogenicity (degree of aggressiveness) because on "non-corresponding" hosts different strains could cause variations in symptoms such as flecks varying from yellow to brown, or a clearing of leaf colour.

Three interpretations can be formulated:

1. The conidia from a particular tree (Wiesmann called this cultivar "the main host") represent a race which is differentiated from the other races not only by its main host but also by its ability to attack other cultivars ("secondary hosts") to a different degree. (This was Wiesmann's interpretation). The following conditions have to be satisfied: all the inoculum from a particular host was genetically homogeneous; a high degree of pathogenicity to a particular host cultivar is linked with a low degree of pathogenicity toward the others.
2. The inoculum consisted of a mixture of pathotypes (races), each pathotype being strictly specific for a particular cultivar (single race). This seems improbable because the non-corresponding races would not be able to maintain themselves on the tree.
3. Strains with genetic information enabling them to attack more than one cultivar (complex races) were present together with simple races. So in the inoculum from Boiken, the gene for virulence on Boiken was always present, whereas the gene for virulence towards Wellington was present in 28.5 percent, the one for

Table 1. Infection success of a conidial suspension from *Venturia inaequalis* originating from leaves of different cultivars; the infection success was measured in % of inoculation sites developing symptoms (Data from Wiesmann, 55).

Cultivar	Origin of the conidial suspension			
infected	Boiken	Wellington	Gravensteiner	Virginia
Boiken	26.3	20.0	6.5	6.6
Wellington	7.5	26.0	16.6	9.0
Gravensteiner	9.3	14.0	30.4	13.6
Virginia	12.8	7.0	23.8	26.6

Gravensteiner in 35.4 and for that Virginia in 48.7 percent of the conidia (Table 2).

This leads to the question why a single strain able to attack all cultivars has not developed since recombination is obligatory during winter (see pages 18-19). From this data we are unable to calculate the real frequencies of complex strains, nor can we evaluate which hypothesis corresponds better to reality. These questions can be answered only by using completely described inoculum.

Similar observations on the variability of the pathogenic characteristics of *V. inaequalis* were made by others (35); e. g. the cultivars Ingram and Haralson were abundantly infected by some isolates and only sparsely by others, and cultivars such as Yellow transparent were not infected by some isolates.

From the phenotype to the genotype analysis

Genetics of pathogenicity

Schmidt (40, 41) tested 473 single spore isolates and was able to differentiate 448 morphological different types, with no association of those types to a specific origin of the isolates. If the morphological variation was great, the range of pathotypes was not much less. Schmidt (42, 43, 44) and co-workers analyzed the interaction between the scab fungus and apple cultivars in many experiments and classified the reaction into three types: no symptoms, clear scab symptoms and necrosis or chlorotic flecks. They classified single spore isolates into pathotypes using a test range of commercial cultivars. Isolates originating from a particular cultivar were always able to infect that cultivar (Goldparmäne/Goldparmäne; Boskoop/Boskoop), but not necessarily other cultivars (Table 3). The capacity of the isolates to infect other cultivars varied from isolate to isolate; for example,

Table 2. Theoretical relative frequency of pathotypes in conidial suspensions of *Venturia inaequalis* originating from leaves of different cultivars (Data recalculated from Table 1).

Genome pathogenic to	Pathotype Boiken	Wellington	Gravensteiner	Virginia
Boiken	100.0	76.9	21.4	24.8
Wellington	28.5	100.0	54.6	33.8
Gravensteiner	35.4	53.8	100.0	51.1
Virginia	48.7	26.9	78.3	100.0

the isolate from Goldparmäne in York seemed to be a complex race, able to infect all of the 15 differential cultivars which Schmidt tested. On the other hand none of the isolates was able to infect only one cultivar and therefore representing a simple race [detailed data in (42)]. Schmidt also showed that particular isolates could infect certain wild *Malus* species. Isolates from wild *Malus* species could also selectively infect commercial cultivars.

Keitt and Langford (25) tested the pathogenicity of 32 ascosporic isolates cultured from four asci on nine cultivars, obtaining differential results on six cultivars. In 12 cases, virulence versus avirulence segregated in a 1:1 ratio, from which it may be concluded that virulence to a certain cultivar is governed by a single gene or a linked group of genes. However, in two other cases the segregation was 2:6 between isolates that produced sporulating lesions and those that produced non-sporulating flecks (Table 4). The authors did not attempt to explain these observations, but they can be interpreted as indicating that at least two genes determine virulence on cultivars Ben Davis and Wealthy. These are loosely linked as they sometimes segregate [third ascus/Ben Davis, second ascus/Wealthy] and in other cases they do not [first, second and fourth ascus/Ben Davis, first ascus/Wealthy].

To further complicate the interpretation of data, epistasis (suppression of the effect of one virulence gene by another) has to be considered. As Boone (6, 7) reports, when two or more virulence genes control the virulence to a cultivar, there is often an epistatic effect between an avirulence allele at one locus and virulence allele(s) at other loci.

Further tests on the inheritance of "pathogenicity" (4, 6, 8, 26, 27, 28, 48, 59, 60, 62) led to the conclusion that virulence to apple cultivars is controlled by as

Table 3. Reaction of leaves from different apple cultivars to monosporic isolates of *Venturia inaequalis* taken from the apple cultivars Winter Goldparmäne and Schöne Boskoop at different sites (Wä.=Wädenswil, Switzerland; Mü.=München, Pilln.=Pillnitz, York, all in Germany) (Selected data from Schmidt, 42).

Cultivar inoculated	Origin of the isolate						
	Winter Goldparm.			Sch. Boskoop			
	Mü.	Wä	York	Mü.	Pilln.	Wä	York
Winter Goldparm.	+	+	+	+	–	–	+
Sch. Boskoop	–	–	+	+	+	+	+
Gravensteiner	+	+	+	–	–	–	(+)
Berner Ros.	+	–	+	–	+	+	–(+)

– = yellowish flecks; + = clear scab symptoms; (+) = necroses or chlorotic flecks.

many as 19 genes. These virulence genes are mostly independent (62) and are therefore redistributed randomly each year, and are probably widespread (at least in the U.S.A.) so that it is not worthwhile describing the great number [2^{16} to 2^{19}] possible races (6, 8). However, in breeding programmes for apple scab resistance it is advantageous to classify *V. inaequalis* into races (6, 33, 38, 49, 60) if the corresponding resistance genes are or were used in the programme. The races are not named strictly after the pathogenicity genes, but after the cultivars which they are able to attack. Race 1 has no particular virulence genes and can only attack susceptible cultivars or clones of other *Malus* species. Race 2 has a complex virulence genotype: it is virulent on the clone Dolgo (*M. baccata*), a particular clone of *M. pumila* nr. R12 740-7A (differential of race 2), and clone Geneva (*M. pumila* var. *niedzwetzkyana*), having therefore the virulence genes *p-8*$^+$,*p-9*$^+$and *p-11*$^+$. Race 3 has the virulence gene *p-10*$^+$, enabling it to attack Geneva (62). Race 4 is virulent to a particular clone of *M. pumila* nr. R12 740-7A, different from the differential of race 2. Race 5 attacks clones carrying only Vm resistance. The symptoms which developed in the different interactions varied from 3 to 4 for the *p*$^+$ genes. The virulence genes p- condition mostly the 2 reaction, but sometime the 1 reaction, depending on the combination with the host. Details can be found in overviews (6, 7, 33, 61,62) and elsewhere in this book (e.g. Lespinasse).

The important point is that there is evidently a large number of pathogenicity genes, some with different effects, conditioning different types of symptoms and probably influencing differently the dynamics of pathogenesis. In most cases no clear linkage groups can be determined, so it can be assumed that the genes are distributed widely over the seven chromosomes and mostly distant from the cen-

Table 4. Virulence of monoascosporic isolates of *Venturia inaequalis* originating from four asci towards four apple cultivars (Selected data from Keitt and Langford, 25).

Cultivar inoculated	isolate ascus and ascospore nr.			
	1	2	3	4
	1 2 3 4 5 6 7 8	1 2 3 4 5 6 7 8	1 2 3 4 5 6 7 8	1 2 3 4 5 6 7 8
Ben Davis	- - + + + - - +	+ + - - - - + +	- - - - - - + +	- - + + + + - -
Wealthy	- - - - + + + +	- - + + - - - -	- - - - - - - -	- - - - - - - -
Haralson	- - + + + - - +	+ + - - - - + +	+ + + + + + + +	- - + + - - + +
Yellow Transp.	+ + + + + + + +	+ + + + + + + +	- - + + + + - -	- - + + - - + +

– = yellowish flecks, + = clear scab symptoms tromeres; as cross-overs are exceptionally frequent, all combinations of pathogenicity genes can arise during sexual recombination (e.g. Table 5).

Being an ascomycete, the first four haploid ascospores in *V. inaequalis* usually descend from one of the nuclei of the first meiotic division, the second four from the other, so that the product of each meiotic event (ascospore pair) is positioned in such a way that the centromere-linked genes, which segregate in the first meiotic division, will be distributed between the first and the second four ascopores in one ascus (Fig.1). Tetrad analysis is therefore possible and facilitates genetic work, even if some errors may occur such as changes in position of ascospores in the ascus after they have been formed (e. g. Table 4; ascospore nr. 8 and 6 or 5 and 7 in ascus 1). Without crossing over, all genes on the same chromosome will be distributed together. Centromere-linked genes will then be distributed between the first and the second four ascospores. Because sister ascospores derive from a mitotic division it is only necessary to indicate one symbol for each set of sister ascospores. Centromere-linked genes are therefore positioned in the ascus as A,A,a,a or a,a,A,A (the position in the ascus being the centromere marker). Independent genes (on different chromosomes) will be randomly reshuffled, but again resulting in parental or nonparental ditypes with the first four ascospores containing a different genotype from the second four. An uneven number of cross overs between the analyzed gene and its centromere during the second meiotic division will lead to a tetratype [for example a,A,a,A or a,A,A,a]. Four different genotypes will be present after the meiosis in the ascus. *V. inaequalis* presents an unusually high number of second-division segregations of the virulence alleles, ranging from 26.1 % to 88.9 % (7, 8), evident also in Table 5 since the frequency of crossing over is proportional to the tetratype frequency.

Table 5. Genome analysis of monosporic isolates of *Venturia inaequalis* originating from four asci in serial order; capital letters = clear scab symptoms, small letters = no symptoms. A,a genes conditioning pathogenicity to the apple cultivar Ben Davis; B, b to Wealthy; C, c to Haralson and D, d to Yellow Transparent. X and Y designate the two groups for sexual compatibility (selected data from Keitt and Langford, 24).

Ascospore no.	ascus 1	2	3	4
1, 2	a b c D X	a B C D X	a b C d X	a b C d X
3, 4	a B C D X	A b c D X	a b C D Y	a B C D Y
5, 6	A B C(?) D Y	a b c D Y	a b C D Y	a B C d Y
7, 8	A b c(?) D Y	a B C D Y	a B C d X	a b C D X

Any exchange between the first tetrad (ascospores no. 1 to 4) and second tetrad (no. 5 to 8) is due to second-division segregation after crossing over. Sister ascospores should have equal genoms (excPeptions are noted with ?). Differential results not splitting in 4 : 4 but 3 : 1 may be due to epistatic effects.

Susceptibility and resistance of the host

In today's literature, a gene-for-gene interaction between *V. inaequalis* and apple is reported (15, 39). A relationship fulfilling the requirements for the gene for gene hypothesis can be accepted as proven for just a few of the many pathogenicity genes, though it may well exist in many other cases where some known or supposed single genes for resistance are present. Bagga and Boone (4, 5) studied the inheritance of resistance in 41 crabapple species and clones to a particular isolate of *V. inaequalis*. The scab resistance to this isolate was controlled by a single dominant gene in 25 clones, in 11 other clones by two major dominant genes and in the remaining 5 the data indicate that three major dominant genes controlled the resistance. In the field, 26 clones were resistant for at least 5 years. (Unfortunately, the author has no information on the current level of this resistance.) Fourteen of those 26 clones had just one dominant gene for resistance. To conclude that these resistances are durable may be too bold. It would be most interesting to follow the behavior of the clones mentioned (4, 5, 12, 13, 46, 47, [Table 6]) in the centre of origin and under natural conditions, since it is impossible to collect all possible variants of *V. inaequalis* to test the clones and this would be dangerous because new pathotypes could be spread accidentally. On the other hand, it could be interesting for breeding programmes to collect locally resistant individuals and test the new selections in other regions so as to widen the genetic base of resistance.

A generally accepted rule is that the gene centres (centres of origin) of cultivated plants are the best places to find durable resistance (31) because such resistance (possibly ephemeral but highly dissociating resistances, see page 16) can

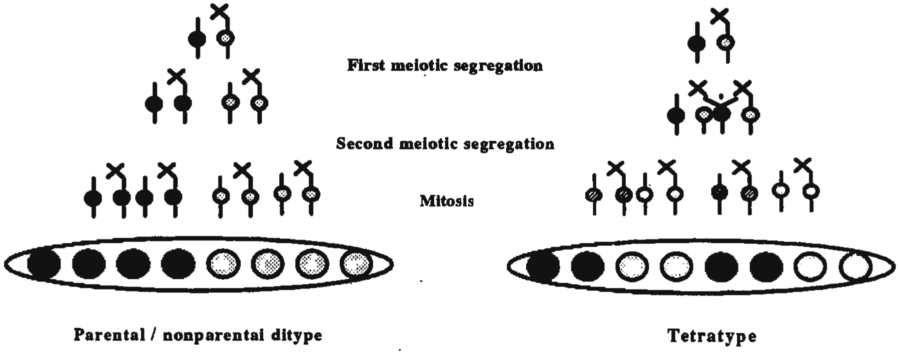

Fig. 1. Arrangement of the ascospores in an ascus: left, first division segregation, no crossing over; right, second division segregation due to one crossover between the centromere and the examined locus. Circles indicate by their shades a marker.

be recognized only in the field. The genus *Malus* evolved in five centres of origin. For many crabapples North America seems to be the centre. *M. angustifolia* Michx., *M coronaria* Mill. and *M. ioensis* Britt. originate from the north-east to the south-east USA. The East Asiatic centre, including China and Japan, and the eastern Siberia centre contain the species *M. baccata* Moench, *M. floribunda* Sieb., *M. halliana* Koehne, *M. hupehensis* Rehd., *M. kansuensis* Schneid., *M. spectabilis* Borkh., *M. toringo* Sieb., *M. toringoides* Hughes, *M. transitoria* Schneid., *M. trilobata* Schneid. *M. tschonoskii* Schneid. and M. *yunnanensis* Schneid. The Balkan region, Europe and the Mediterranean region are centres for

Table 6. Classification of clones from different *Malus* species on the basis of maximal symptom development and length of time until visible symptoms appear after inoculation with *Venturia inaequalis* under glasshouse conditions (Selected data from Shay and Hough, 46).

Clone	class	min incubation period in days
M. Honanensis (1582-35)	0	-
M. toringo (852)	0	-
M. atrosanguinea (804)	1	2.5
M. floribunda (821)	1	6
M. micromalus (245-38)	1	2.5
M. sieboldii (2972-22)	1	10
M. baccata var Alexis	2	6
M. pumila (R#12740-7A)	2	4
F_2Vf -26829-2-22	7	
F_2Vf -26830-2	2	11
M. baccata jackii	3	18
M. ? (M.A. #8)	3	26
M. ? (M.A. #16)	3	12
Jonathan	4	9
Golden Delicious	4	9

Reaction classes: 0 = no macroscopic evidence of infection, 1 = pin point pits and no sporulation, 2 = irregular chlorotic lesions, 3 = few restricted sporulating lesions, 4 = extensive abundantly sporulating lesions the species *M. florentina* Schneid., *M. silvestris* Mill. and *M. trilobata* Schneid (16).

Traditionally, the progeny of a cross between a scab-resistant and a scab-susceptible parent is classified into two groups, susceptible and resistant, even if several classes of reaction type are known (0, 1, 2, 3,and 4); the need for an additional class (M = non sporulating and sparsely sporulating lesions) was felt. The distinction between susceptible and resistant seems to vary from author to author but mostly is between classes 0, 2, M, 3 (= resistant) and 4 (= susceptible), with class 1 as a special case of resistance due to hypersensitivity. Data on segregation in the F_1 progeny of crosses between wild resistant *Malus* species and susceptible commercial apple cultivars fit mostly a 1 : 1 ratio with classification into two groups, sometimes 3 : 1, and, less frequently, 7 : 1. The conventional interpretation is that the tested wild resistant *Malus* species are heterozygous for resistance, and the resistance is dominant and controlled by one gene (or a group of closely linked genes), sometimes by two and rarely by three genes (6).

Vf-resistance

Progeny of crosses between susceptible commercial apple cultivars and clone 821 of *M. floribunda* carrying the Vf-resistance were first rated for scab with the scale 0 to 4 (including class M). Considerable shifts in rating of the same seedlings occurred during the various test stages between classes 1 and 2 and between M and 3. In later years, therefore, the seedlings were divided into only two classes, resistant (0, 1, 2, M and 3) and susceptible (4). Hough *et al.* (24) state that a dominant gene conditioning field immunity to apple scab is present in *Malus floribunda* 821 - and that there appears to be no important linkage of re-

Table 7. Expression of scab resistance (% scabbed seedlings) in the progeny of 8 apple crosses (heterozygote Vf-resistant x susceptible parent) evaluated under experimental conditions in Geneva N. Y., U.S.A., and in Purdue Illinois, U.S.A. (Data from 29).

Site	cross							
	1	2	3	4	5	6	7	8
Geneva	27	28	30	33	33	38	39	42
Purdue	60	60	51	50	56	56	54	54

sistance with small fruit size or other undesirable fruit or tree characters. Williams and Kuc (61) reviewing the resistance in *Malus* to *V. inaequalis* write that for *M. floribunda* 821 the progeny segregation ratio of approximately 1:1 indicates that the resistance in this selection is controlled by a single qualitative gene (present as a dominant allele) or by a block of closely linked quantitative genes. Genetic analysis of different resistance sources (13, 14) led to the conclusion that not only *M. floribunda* 821 carries the Vf-resistance gene (or genes) but that other *Malus* species (e.g. *M. atrosanguinea* 804, *M. prunifolia* sp. ecc.) also have the resistance gene located at the Vf locus. On the other hand, genes conditioning the pit-type reaction of rapidly developing pin-point necrotic pits (hypersensitivity) are independent from the Vf and present in *M. micromalus* (pit type) and *M. atrosanguinea* 804 (pit type) at the same locus, Vm. This gene is rendered ineffective by race 5. Segregation independent from the Vf and Vm resistance genes and also from each other was recorded for the resistance genes Vr (Russian seedling), Vb (Hansen's baccata # 2), Vbj (*M. baccata jackii*) and Va (Antonovka selection PI 172612); so far, these have not been matched by the pathogen, nor has their reaction been described as the rapid pit type (12).

Most interesting is the statement by Williams and Kuc (61) that "the original *M. floribunda* 821 resistance was expressed as a class 1 reaction", but the resistant progeny used in the breeding programmes showed reactions of class 2 to 3. We may conclude that the original *M. floribunda* 821 resistance was due to one pit type gene and one (or a group of closely linked genes) conditioning a class 2-3 reaction. The first gene was either lost in the segregation of the crosses or was readily overcome by *V. inaequalis*. From other data (30) the situation is less

Table 8. Classification of the progeny in % of crosses of scab-resistant and -susceptible parents after the symptoms following inoculation with *Venturia inaequalis* (Selected data from 36).

Parents	Reaction class					total
susc./resist.	1	2	M	3	4	pop.
Lobo/*M. flor.* 821	19	29	13	5	33	224
Lobo/26829-2-2	13	14	18	6	49	457
Lobo/Prima	8	7	26	8	51	287
Lobo/PR7T19	12	9	20	9	50	309
McIntosh/*M. flor.* 821	16	19	18	8	39	705
McIntosh/26829-2-2	1	7	29	14	49	445
McIntosh/Prima	2	7	32	12	47	311
McIntosh/PR7T19	1	5	23	13	58	691

clear. Instead of a 1:1 segregation of the progeny from Vf x susceptible, Lamb and Hamilton recorded a lower proportion of resistant progeny. Their classification was different in that they considered only seedlings without any sporulating lesions as resistant, so that class 3 was recorded as susceptible. By changing the environmental conditions (light intensity, day length and temperature), the percentage of resistant progeny changed: low light intensity, short day and low temperature gave fewer resistant progeny. Also, the percentage of seedlings from the same crosses classified as resistant was clearly lower in Geneva, U.S.A., than in Purdue, U.S.A. (Table 7), reflecting environmental and perhaps evaluation differences. The classification of the progeny into susceptible or resistant was also influenced by the parents (Tables 8 and 9).

The progeny of a cross between a heterozygote RS (Vfvf) and homozygote SS (vfvf) is expected to segregate 1:1 (50% Vfvf and 50 % vfvf) (Fig. 2, left side). Some of the deviation between the genotype and the observed phenotype frequencies may be attributed to the environment and evaluation criteria. The only explanation for the constant and directional difference between the genotype and the phenotype frequencies is that the genetic background modifying genes (= genes that have a modifying action on the expression of a major gene; the resistance gene may require the presence of another gene before it can be fully expressed), contributed by either parent, causes a phenotype shift; in other words, some of the Vf-carrying progeny will be of susceptible phenotype and classified as susceptible. Thus Vf interacts with the genetic background, leading to either a greater or lesser level of resistance expression.

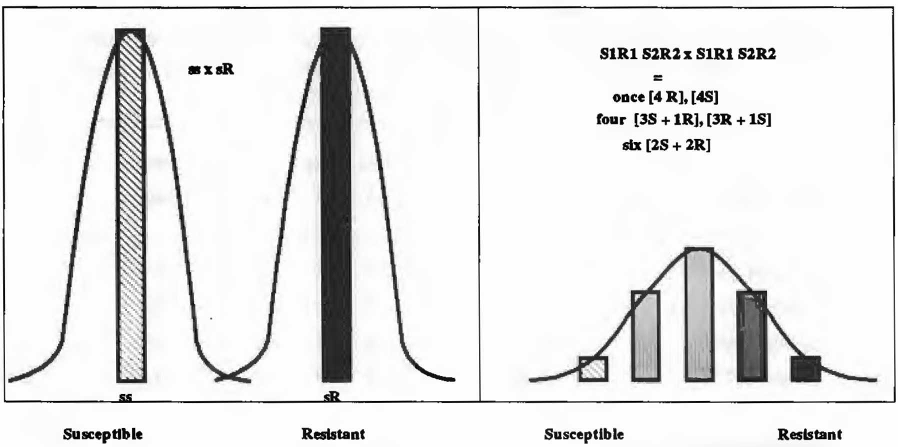

Fig. 2. Distribution of the progeny from crosses between: left, a heterozygote with a dominant resistance in one locus and a susceptible parent, the progeny splits in two classes in a 1:1 ratio; right, parents both heterozygote with two additive genes, all alleles have equal effect, the progeny splits in 5 classes with a ration 1:4:6:4:1.

To explain the shifting proportion of seedlings classified by the breeders as resistant (mostly less than 50%), the subpopulation carrying Vf-resistance (50 % of all seedlings) is assumed to be distributed continuously over a range of phenotype classes, therefore under equal conditions also representing a range of genotypes (Fig. 2, right side). In Fig. 3, the population of progeny carrying Vf-resistance is fitted to a continuous distribution over all classes (without the hypersensitive reaction type 1). The susceptible population is assumed to be in class 4, even if it may vary in susceptibility, albeit at a low level.

Rousselle *et al.* (36) first postulated the presence of cumulative minor genes whose action can increase the level of resistance to scab conferred by the Vf gene. These minor genes can originate either from the susceptible or the resistant parent. Rousselle showed that the distribution of the progeny within the resistant classes (1, 2, M and 3) fitted almost a normal distribution and about 50% of the progeny from many crosses still remained in the susceptible class 4 (Tab. 8). Moreover, the authors state that the modifiers of the major gene appear to be inherited independently from the major gene and in a quantitative manner, with mostly cumulative effects.

If it is postulated that minor additive genes change the effect of Vf, only two loci each with two alleles are needed to explain the continuous distribution of the Vf-carrying progeny from a cross between a susceptible and heterozygote Vf-resistant parent (Fig. 3). The Vf-modifying genes (*sensu* 11, 36, 51) have to be present naturally in the susceptible cultivars as well as in the scab resistant clones since different percentages of resistant progeny can be found by varying any parent in a cross (Tables 8 and 9).

The cultivars Delicious and Golden Delicious were considered less susceptible than Macoun and Cortland in New York, and in the crosses with a Vf-resistant clone the less susceptible Delicious and Golden Delicious clearly yielded a higher percentage of resistant progeny then the crosses with the more susceptible cultivars. At least in the mentioned cases there seem to be a correspondence between the degree of susceptibility of the susceptible parent and the final level of resistance of the Vf-carrying progeny. If these results are confirmed, it means that there is an additive effect of resistance genes of small effect to the Vf-resistance gene (or genes) showing a large effect.

The concept of durable and ephemeral resistance

As seen, every effort is usually made to fit the segregation of a progeny into two classes giving discontinuity in the response, so as to allow simple selection. Clear borders separating resistant and susceptible subpopulations are drawn. A 1:1 segregation of the progeny into resistant and susceptible groups from a cross heterozygote resistant x homozygote susceptible, such as in Vf-resistance, is classically interpreted as the presence in the resistant progeny of one dominant R-allele. Generally, and deduced from many known cases such as in *Phytophthora infestans* on potato or rust fungi and their hosts, it is assumed that monogenic resistance is ephemeral (unstable) because it may require, to overcome it, only a single mutation in the pathogen, which may occur frequently. The example of gene Vm seems to demonstrate this for apple scab.

> **Ephemeral is used as a synonym of unstable or transient. The effect of an ephemeral resistance gene lasts only for a short time because of the development and spread in the pathogen population of resistance-breaking variants of the pathogen. The term durable merely implies that the resistance has given effective control for some years and is still effective; strictly, the assumption that the pathogen had every possibility to adapt itself should be fulfilled.**

The Vf-resistance incorporated into commercial cultivars is assumed in almost all literature (33, 61) to be due to a single dominant allele and therefore to be unstable (34); a preliminary report even hints that a new "race" has already overcome the Vf-resistance in "Prima" in the Moldavia region (17), but the "Prima" reported may not be the cultivar Prima with Vf-resistance. On the other hand, numerous examples are known of major-gene resistances which are durable (39).

Vanderplank (55, 56) points out that generally in plant pathology continuous variation and polygenic inheritance are wrongly treated as synonymous. Other models with as few as two independently segregating loci each with two alleles of additive effect may well be sufficient to give a continuous distribution if the resolution of the evaluation system is not better than five classes (Fig. 1). If there

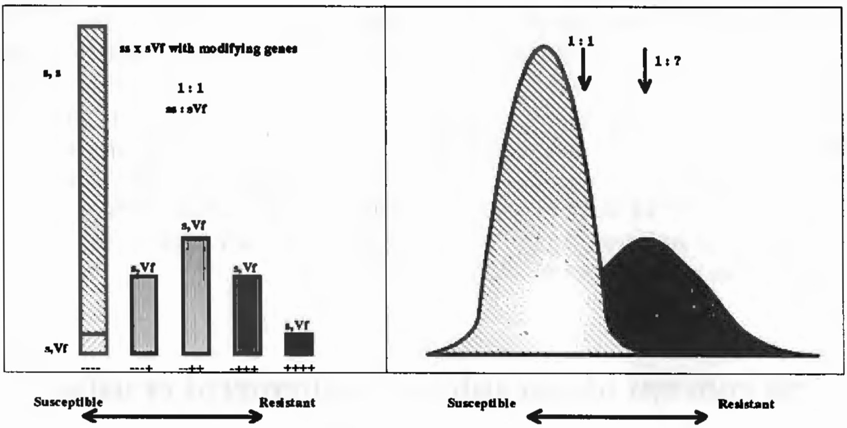

Fig. 3. Distribution of the progeny of a cross between a heterozygous parent having one major gene for resistance and a homozygous susceptible parent into 5 classes: left theoretical distribution assuming the effect of two modifier genes with additive effect of +alleles, with -alleles having no effect; right, as it appears from the available data (see text) with the arrows indication possible border used to distinguish resistant from susceptible progeny and % of the progeny classified as resistant.

are unequal effects, or linked groups of genes, any type of distribution may be possible. Another conflict lies in the argument that polygenic resistance is likely to be durable and that safety lies in numbers, because the more resistance genes the pathogen has to overcome the less likely will it be able to overcome the resistance as a whole. Again citing Vanderplank, "polygenic resistance" can be substituted by "genetic variance mostly additive" with reasonable confidence.

Polygenic inheritance (traits that result from the interaction of several gene effects) is not liked by breeders (9, 39), because it is often assumed that the genes are independent and will be lost during backcrossing. Moreover the progeny will show continuous variation which complicates the selection procedure. On the other hand, breeders can easily manipulate additive inheritance by mating the most resistant individuals among themselves. The resistance is passed to the progeny as the mean of the resistance of the parents. Success may be slow and particular qualities of one of the original parents may be lost. In maize breeding programmes many such successes (e. g. adult plant resistance against maize rust) can be found and demonstrate that, so far, the resistance is in all cases durable.

We have to consider Vf-resistance in the light of additivity (preceding chapter). Considering the 50 % of the progeny which carries Vf, then this population follows the pattern of additive inheritance. No statement can be made on durability but, as Vanderplank (55, 56) points out, additive resistance is durable in all known cases. Furthermore the effect of these modifier genes may result in resistance in the absence of the Vf gene (assuming that they are accumulated to a sufficient amount), a great advantage if a race which could nullify the effect of gene Vf should develop. The consequences of these points are: (a) the genetic background into which Vf is hybridized is of the utmost importance, (b) breeding programmes should follow techniques used for selecting additive inherited characteristics, (c) plants should be screened under conditions in which differences can be recognized within subpopulations of resistant progeny, (d) intense selection for modifier genes should be made. Care should be taken to maintain diversity in the different breeding lines so not to loose any efficient combinations (36).

From the work of Schmidt (42, 44) and others (38, 49), the presence of vertical partial resistance in commercial apple cultivars has to be assumed, but its effect is no longer apparent in current popular cultivars because the planting of large areas with one cultivar leads to selection of the corresponding pathotype. The pathogen population may still contain many other pathotypes and any combination may arise during the annual recombination of the genome of *V. inaequalis*. In mixed stands of apple trees with differing resistance genes, the frequencies of the pathotypes (simple and complex) of the ascospores should reflect the relative frequencies of those pathotypes at the end of the season. A low frequency of complex races after sexual recombination would be desirable, especially when the initial inoculum (ascospores) is low and therefore the probability of the correct virulence type landing on its preferred host is small.

The work of Wiesmann lacks data showing changes in frequency of the pathotypes from early spring to later in the season on the different cultivars. We can assume a similar frequency of all pathotypes on all tested trees early in the season. Wiesmann's data from May/June show different distributions of the pathotypes depending on the cultivar. Therefore, the unnecessary virulence genes decreased in frequencies from the beginning of the epidemic until May/June. In the absence of continuous selection pressure in favour of the complex pathotypes, the pathogen population seems to lose the unnecessary virulence genes. Two main explications can be given.

1) Combined virulence brings disadvantages. Under this concept there will be a tendency of the virulence toward the different cultivars to dissociate in *V. inaequalis*.

The tendency of the virulence genes to dissociate will lead to an equilibrium of the frequencies of those virulence genes in the pathogen population. In other words, the selection exerted on the pathogen population will lead to a stabilization of the relative frequencies. On this topic Vanderplank (55) writes, "This indicates an adverse genetic load due to virulence must be present, as we have to consider that if a virulence gene carried no adverse genetic load the advantage given by the virulence to the population of the pathogen would cause the gene to become fixed in the species and a fixed gene for virulence would be undetectable". The concept of stabilizing selection is still much discussed.

2) The differences between the pathogen populations on the four hosts analyzed by Wiesmann are due to selection of the correct pathotypes from a random population, immigrating from other trees. The low frequency of complex races often found in the absence of positive selection is attributed to random chance. Unnecessary virulence genes bring no disadvantage.

By this reasoning we assume an immigration of the initial inoculum from leaves not exerting any directional selection pressure and start from simple races. The virulences toward any of the four host genomes (Boiken, Willington, Gravensteiner and Virginia) were each present in 25 % of the pathogen population. Recombination during winter led to complex races toward any two hosts in 6.25 %, to three in 1.6 %, to all four in 0.4% of the pathogen population. Ascospores representing these races landed on Boiken, where only the simple race Boiken and the complex races having Boiken pathogenicity reproduced. After asexual reproduction the conidia population all had the Boiken virulence, 25% had also one virulence toward any other of the four hosts, 6.25 % to two and 1.2% to all three other hosts. Taking this conidia population, only about a third coul attack another host, reflecting the results of Wiesmann.

The controversy between the two interpretations cannot be resolved without additional data. Although the concept of stabilizing selection impresses, the data can also be explained by random selection. The main arguments (64) against stabilizing selection are the lack of recombination of the pathogen genotypes and the failure to define boundaries of the sample population, which leads to mixing data on virulence frequency obtained from various conditions and from subpopulations submitted to various selection pressures. Often, spores originating from hosts exerting a different selection pressure are assayed together with the required material. The concept of stabilizing selection may be false, as most data presented to support it contain major flaws (64). If the possibility of the immigration of inoculum is excluded then, under the conditions of Wiesmann, slowly and over many seasons, complex races of *V. inaequalis* should emerge. On the other hand, the concept of stabilizing selection seems to fit the data presented above, especially considering the absence or low frequency of complex races, together with the characteristics of a pathogen like *V. inaequalis*, with an obligatory sexual reproduction, long-range distribution through ascospores and, in the epidemic phase, a limited splash dispersal.

The concept of dissociation of virulence genes can be of great value. By incorporating into the host the resistance genes favouring this dissociation we may stabilize the resistance. The same effect can be achieved in an orchard by mixing apple cultivars with differing resistance genes, chosen so as to promote dissociation of the virulence genes of *V. inaequalis*.

Mechanisms of resistance

To gauge the potential durability of a particular type of host resistance, it may be helpful to understand the mechanism of that resistance and to compare this with other cases. If those mechanisms which confer durability of resistance are identified, they can be positively selected for in breeding for resistance. Resistance involving hypersensitivity has often proved to be race specific and to have the drawback that it masks the expression of other types of resistance, thereby precluding selection for such other types (39).

Unfortunately, very little is known. Vm-resistance is probably due to hypersensitivity and is ephemeral. On the other hand, the ontogenic resistance present in all apple cultivars is durable but the mechanism is only hypothesized (19). Vf-resistance is not due to hypersensitivity and has many features in common with ontogenic resistance (18, 19, 20, 21, 53, 54). Preliminary results indicate that Vb, Vbj and Vr resistances are also not of the hypersensitive type. In the interaction between field isolates of *V. inaequalis* from Switzerland and an apple clone carrying the Va resistance gene, the author (unpublished results) found reaction types ranging from 1 (hypersensitive) to 0, 2 and M. To which fact to attribute this result is not yet known, but it may be due to the use of field mixtures of inoculum leading to different interaction types, because the fungal inoculum is genetically not homogeneous.

To attribute a role to any differences and/or changes between susceptible and resistant tissue, the dynamics of pathogenesis has to be known: e.g. when does the fungus start to behave differently on the different tissues. Correct timing of the observed changes with the changes in pathogenesis is essential (20, 21, 32). Cell death and the appearance of necrosis 2-3 days after inoculation may well be due to hypersensitivity, but the same reaction after 6-10 days probably signifies that other defense mechanisms are present. Not only is the timing important but also the localization of the changes: e.g. where toxic substances are located. If these points are observed results will only be useful if they can be compared, but this seems to be an easy need to resolve.

Conclusion

The goal of the orchard protection specialists meeting at the 1988 IOBC workshop on integrated control of pome fruit diseases is the production of high quality fruit (29) but "in an ecologically acceptable system" (10) under economical constraints. For many the reduction of fungicide use is a major aspect. Disease resistant cultivars seem likely to offer the most elegant solution, but only if breeders can produce cultivars with durable resistance.

An understanding of the host-pathogen interaction from a genetic as well as a phenological viewpoint may help to avoid major failures, which are, in the case of apple, extremely costly in invested time and money. Careful choice of the susceptible parents may help to increase resistance and reduce the risk of the insurgence of pathotypes aggressive to new cultivars. As modern techniques will allow rapid advances in obtaining resistant cultivars, so gene deployment strategies will become possible and necessary, because the risk of ephemeral resistance will increase, through the incorporation of one specific resistance gene in cultivars and through the increased acreage planted with these cultivars.

Frequent exchanges of research technology and opinions as well as the coordination of research in this field are necessary, because the spread of information through scientific papers is too slow and imprecise. As noted recently, the terminology used in describing pathogenesis can vary. Therefore clear definitions should be agreed and standard terms used.

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Aspects of host resistance and pathogenesis in the interaction between *Venturia inaequalis* and apple leaves.

C. Valsangiacomo, K. Wagner, B. Stadler, M. Ruckstuhl, P. Manini-Gessler, M. Michel and C. Gessler.

Institute of Plant Sciences/Phytomedicine, Universitätstr. 2, 8092 ETH-Zürich, Switzerland.

Abstract

This paper summarizes our efforts to understand apple resistance against scab. The methods used ranged from anatomical studies (light and electron microscopy) to physiological approches (biochemical interaction). We were able to show that several mechanisms such as impenetrable cuticular membrane, hypersensitive reaction and papilla formation play no more than a limited role in host resistance (ontogenic and Vf-resistance were taken in consideration, see below) though they are known to play an important role in other host-pathogen interactions. We elucidated some aspects of the biochemical interaction, such as host cell wall degradation by the pathogen where we were not able to detect any resistance mechanism. Potential factors for resistance at the level of cell wall interaction are discussed.

Introduction

In biotrophic parasitism, where cells of the infected tissue remain alive and active over a long period of time, a precise and intimate relationship between the two organisms is required. *Venturia inaequalis* is characterized by a peculiar type of parasitism in which the relationship with apple leaves is established in the first stages of infection; epidermal cells begin to collapse only at the sporulation stage. After penetration of the cuticular membrane the fungus forms stromata between the cuticular membrane and the epidermal cells. In older leaves of susceptible varieties and in young leaves of scab resistant varieties (e.g. Vf-resistance from *Malus floribunda*, clone 821) the fungus is not able to establish a biotrophic relationship and thus the leaves are resistant.

In discussing aspects of host resistance and pathogenesis in the apple scab interaction, we distinguish between ontogenic and Vf-resistance. The former referring to the resistance acquired by any apple leaf by ageing, and the latter to a specific scab resistance bred into "genetic" resistant cultivars from wild *Malus* species. All the studies presented here utilized the susceptible variety Golden Delicious and the resistant variety Liberty. *M. floribunda* 821 was used in the microscopical studies of stroma formation and expansion in addition to Liberty.

Role of the cuticular membrane in resistance

Venturia inaequalis attacks its host by penetrating the cuticular membrane and invading the space between the cuticular membrane and epidermal cells (Fig. 1C).

Maeda (8) first reported enzymatic breakdown of the cuticular membrane, using transmission electron microscopy. She was able to show changes in the electron density of the cuticular membrane located below the appressorium shortly before penetration by the pathogen (this observation was later confirmed (12)).

Valsangiacomo and Gessler analyzed the role of the cuticular membrane in resistance using electron microscopical techniques (12). From these studies, the cuticular membrane could be excluded as a factor for resistance in both ontogenic and Vf-resistance. The cuticular membrane of leaves of the resistant variety and old leaves of Golden Delicious was always penetrated, but no further stroma expansion was observed in old leaves.

Pathogen behaviour on callus

Callus cultures are non-structured tissues without a cuticular membrane and therefore provide a useful system for studies in pathogenicity of *V. inaequalis*.

Beech *et al* (3) were able to infect intact apple callus with a conidial suspension of *Venturia inaequalis*, while Saad (11) was unsuccessful. Conidia applied to callus tissue germinated and developed long germ tubes (average thickness comparable to that on young leaves, 1.5-2 µm in diameter) and appressoria. Primary stromata developed, and broadened directly into a stolon-like hypha and secondary stromata with lateral branch initials. The secondary stromata were approximately 1.5 times thinner on callus tissue (3-5 µm in diameter) than on apple leaves (5-9 µm in diameter) but still clearly broader than germ tubes. The fungus sporulated on tissue cultures producing conidia from the anellidic conidiophores arising from the cells of intercellular secondary stromata, in a manner similar to that on leaves. The host plasmalemma in callus cells adjacent to stroma cells was invaginated and often highly vesiculated. TEM and SEM studies (2) showed that the structure of the cell wall was altered suggesting enzymatic degradation. In uninfected tissue and in regions where the host cell did not closely interact with fungal hyphae the plasmalemma adhered to the host cell wall. The zone between the host cell wall and invaginated host plasmalemma was electron translucent.

No differences were noted between calli from Vf-resistant (Mac Free) and those from susceptible varieties. Regardless of the degree of resistance, the pathogen was able to in infect the tissue. Based on these observation we concluded that tissue differentiation is a preliminary condition for the expression of resistance.

Pathogen behaviour on leaf tissue

In order to be able to compare results of studies on the process of penetration and subcuticular propagation of the fungus a suitable definition of the different fungal structures is necessary. Adopting the terminology used by Nusbaum and Keitt (10) we assume that the fungus penetrates the cuticular membrane with a penetration hypha. The fungus then produces a primary hypha, developing with time into a normal stroma structure. In figure 1, these three stages are illustrated on micrographs taken in the TEM and through the light microscope. Of these three structures the first (penetration hypha) is detectable only with the transmission electron microscope. Normal stroma is easily detectable with the light microscope but primary hyphae are barely visible, being thin and sometimes smaller than the overlaying appressorium.

Gessler and Stumm (5) demonstrated the expression of ontogenic and Vf-resistance as lack of sporulation on resistant leaves. Further they observed a dramatic reduction of the rate of stroma forming appressoria with increasing age of the infected leaves. The reduction of stroma formation in the Vf-resistant varieties, also detected by light microscopy, was even more dramatic when compared with data from susceptible varieties. However, in these studies, penetration and primary hyphae were not counted, only normal stroma were taken into consideration. Stadler (*unpublished*, PhD thesis) performed a more accurate count of subcuticular structures, taking into consideration all forms of subcuticular entities visible in the microscope , including barely visible primary hyphae (4). By taking in account such small structures in evaluating the rate of penetration, the reduction of the rate of the stroma forming appressoria observed by Gessler and

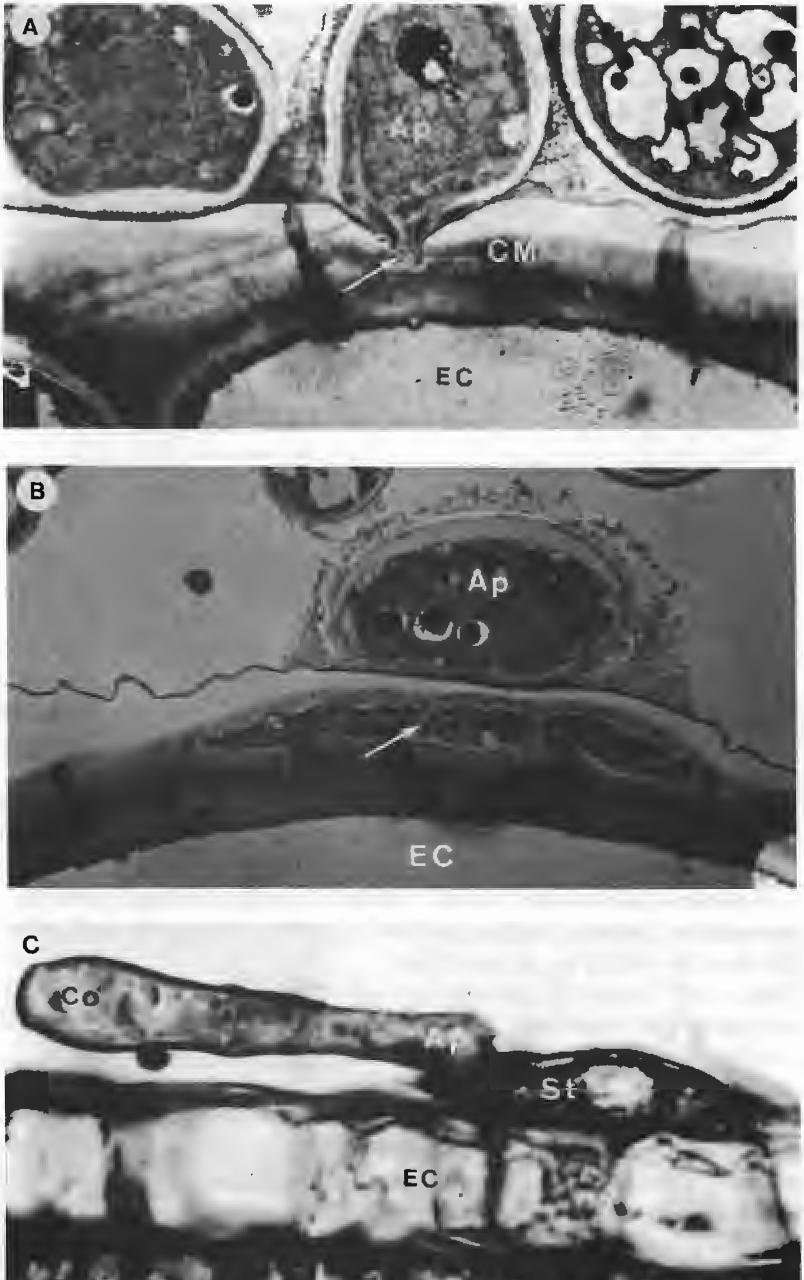
A
Ap
CM
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Fig. 1. A (previous page): TEM micrograph showing penetration of the cuticular membrane (CM). The penetration hypha (arrow) is visible in the low part of the appressorium (Ap). **B:** TEM micrograph showing the primary hypha (arrow) below the cuticular membrane. **C:** germinated conidium (Co) forming appressorium and subcuticular stroma (EC=epidermal cell).

Stumm was less dramatic but still evident. It was surprizing that this rate was higher in the case of Vf-resistant varieties if recorded 1 to 2 days after inoculation and significantly lower if recorded later (4). Using transmission electron microscopy, Valsangiacomo and Gessler (12) were able to visualize thin stroma formations smaller than the overlaying appressorium. It was shown that penetration occurred in all cases but that there was considerable stroma development only in compatible interactions.

Stadler further showed that varietal resistance is responsible for the reduction of stroma formation by slowing down the developing of stroma (Fig. 2).

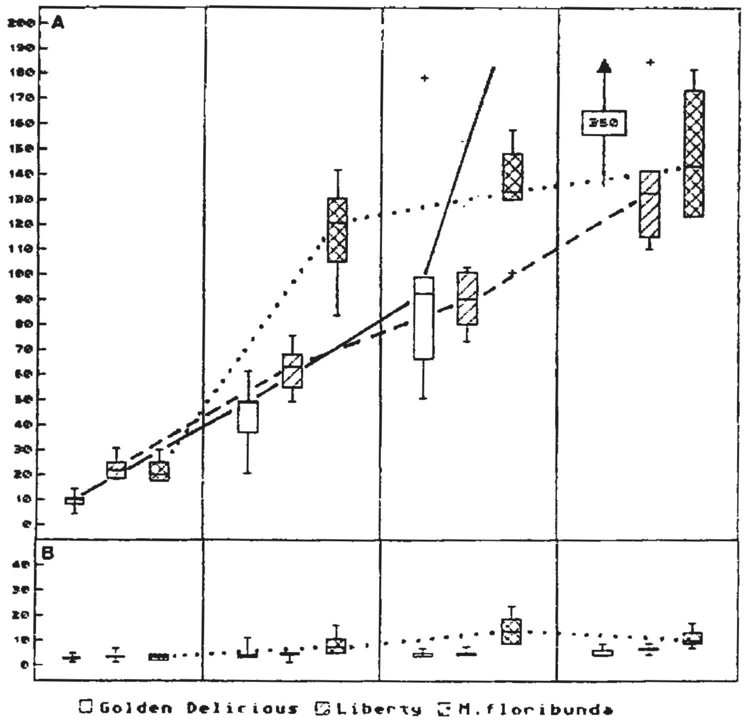

Fig. 2. Growth of stromata (area) on young (**A**) and old (**B**) apple leaves from the cultivars Golden Delicious, Liberty and *Malus floribunda* recorded at different times after inoculation (statistical analysis with the multiple wisker plot method).

Post-infectional resistance mechanisms such as cell collapse and papilla formation were observed and classified as mechanisms of secondary importance in age and Vf-resistance because their frequency increased mostly only after stopping of stroma expansion, and concerning only a small fraction of all observed penetration sites (4).

Further studies using transmission electron microscopy (partially performed using a new technique of high pressure freeze-drying) showed changes in the electron density of the epidermal cell walls. This phenomenon (already observed

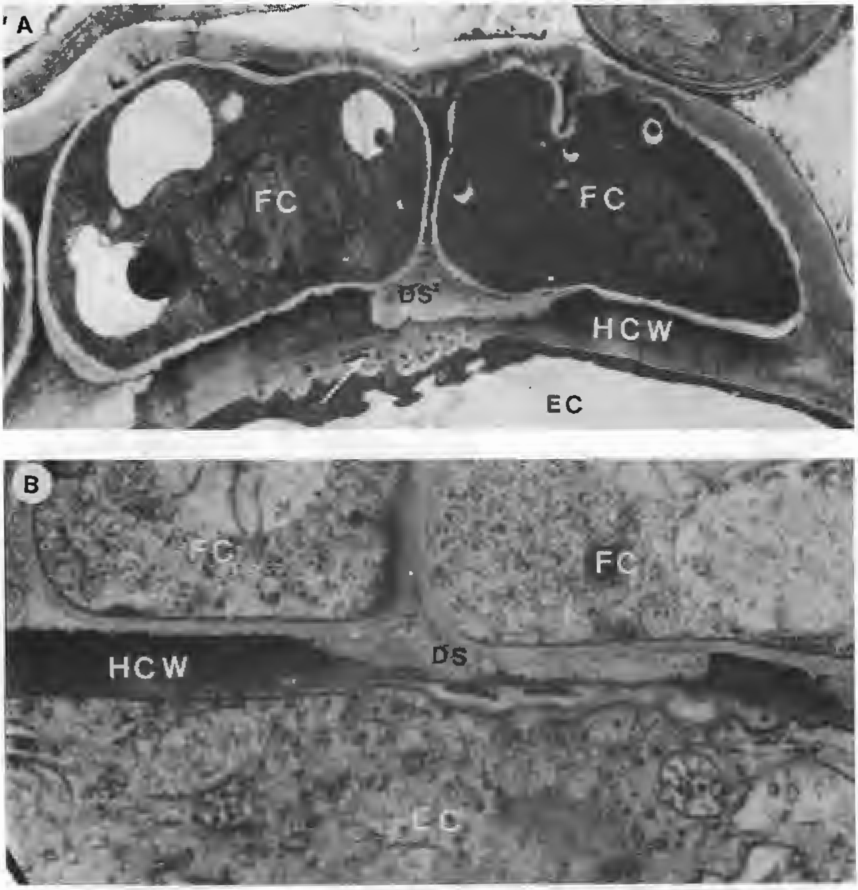

Fig. 3. A and **B** show the host-pathogen interface at the transmission electron microscope. Fungal stroma cells (FC) are in direct contact with host epidermal cells (EC). In both pictures degradation spots(DS) of the host cell wall (HCW) are visible as electron transparent zones. In **A** arrow shows an host reaction to cell wall degradation: cell wall appositions. In **B** tissues were prepared with high pressure freeze-drying techniques, in **A** tissues were traditionally prepared by chemical fixation .

by Maeda, 6) was interpreted as cell wall degradation (Fig 3). Enzymes potentially involved in this process were extracted (discussed below).

Two related reactions were observed in the epidermal cells in contact with fungal stroma cells: in one case cell wall appositions were noted below the degradation spot (Fig 3A) and in another they were noted in an area where the pathogen tried to invade the intercellular spaces between adjacent epidermal cells (Fig 4). The significance of both reactions is not known.

Sporadically hypersensitive reaction and papilla formation were also observed.

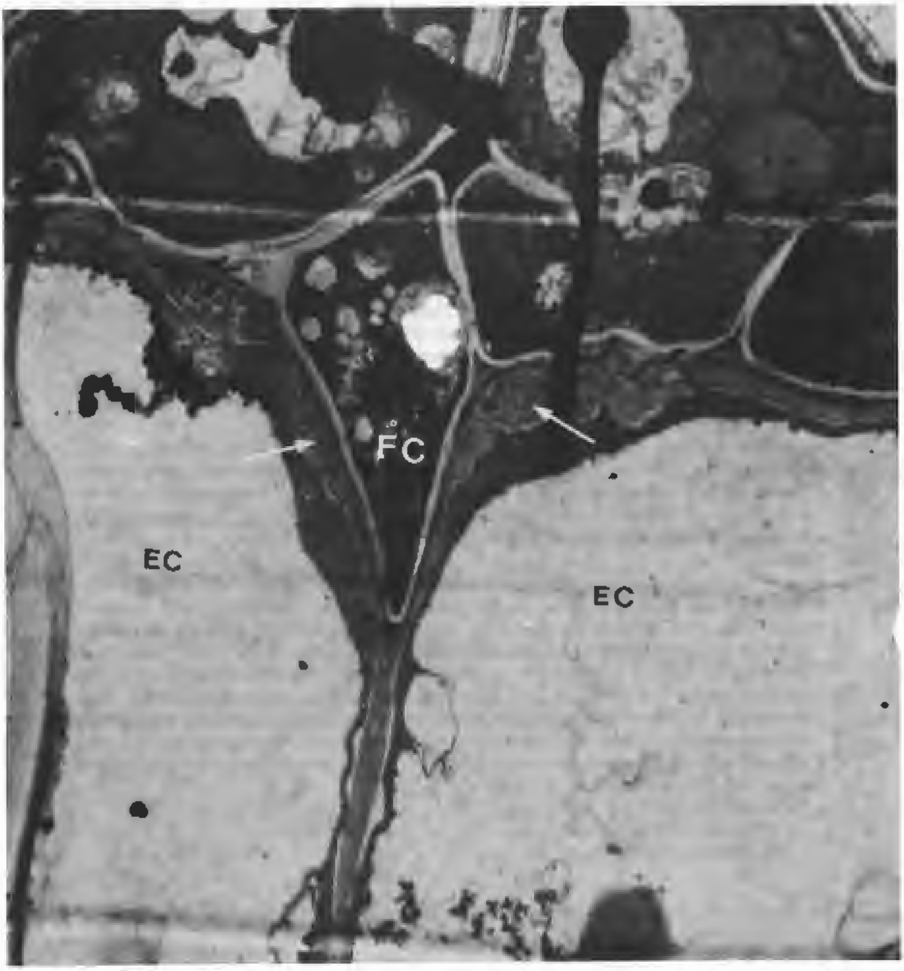

Fig. 4. Stromatic fungal cells (FC) invading the intecellular spaces between two epidermis cells (EC). As a reaction of the host a thickening of the cell wall is produced through cell wall appositions (arrow).

Enzymology

Different enzymes potentially involved in the phenomena observed in the TEM (cuticular membrane and cell wall degradation) were extracted from liquid culture of *V. inaequalis*. In 1988 Wagner (13) demonstrated cellulolytic activity and in 1989 Köller (6) demonstrated cutinolytic activity. More recently we found pectinolytic activity in liquid culture of *V. inaequalis* supplied with apple pectin as the sole source of carbon.

Pectinolytic enzymes are considered to have a major role in degradation of plant cell walls and in general are considered to be the most important enzymes produced by pathogens against plants.

Material and methods

Enzyme extraction and detection of PG activity. *V. inaequalis* has been grown in a common Czapek medium supplied with 1% apple pectin as sole source of carbon. A raw protein extract was prepared from the mycelial fraction. Mycelium, after filtering through several layers of cheesecloth, was rinsed several times in distilled water and further homogenized in acetate buffer 50 mM pH 5.5 using a glass beads (0,45 mm) homogenizer at 2 °C during 2 min. After separation from glass beads the mycelial suspension was centrifuged for 10 min. at 10 000 g. The supernatant was desalted in Sephadex G 25 and tested for pectinolytic activity by measuring the release of reducing sugars in an incubation mixture containing 0.2% polygalacfturonic acid in 50 mM acetate buffer pH 5.5. Reducing sugars were tested after the method of Nelson-Somogyi.

PG extraction using salt solutions. Filtered mycelium was rinsed several times in distilled water, split in 4 equal fractions and homogenized with a glass beads homogenizer (beads 0.45 mm in diameter) for 2 minutes. Each fraction was treated with salt solutions containing 0 to 500 mM NaCl in four steps (0, 100, 300 and 500 mM). The suspension was subsequently centrifuged and the supernatant desalted and tested for PG activity as described above.

***In vitro* cell wall degradation.** Cell walls with ^{14}C incorporated were extracted after Mankarios and Friend (9) from plants grown in $^{14}CO_2$ atmosphere (7) and incubated respectively with enzymes extracted from mycelium of the pathogen and with commercial enzymes from different sources. After a suitable incubation time the reaction mixtures were filtered with a special Sartorius device (Centrisart RI 20 000 D). Only the particles passing through a filter of 20 000 D remained in the supernatant, fractions larger than 20 000 D were sedimented in the pellet. CPM (counts per minute) in the supernatant fraction was taken to be a measure of cell wall degradation (as a control a reaction mixture containing denatured enzyme was used). Degradation in each tube where incubation was performed was expressed as per cent of the total CPM in the tubes:

% Degradation = (S/P + S) * 100

Where S= CPM in the supernatant

P= CPM in the pellet

The pectinolytic enzyme extracted from mycelial fraction of a liquid culture of *V. inaequalis* is an exo-polygalacturonase. Transeliminative nature of the degradation of pectin was been excluded by carrying out a specific test for detection of unsaturated monomers (Thiobarbituric acid test); the test always showed negative results. Further, 0,02 M Ca^{++} in the reaction mixture inhibited the enzyme activity and the optimum of activity was at slight acid pH (Fig. 5A); both these data are typical of polygalacturonases produced by other microorganisms. Temperature optimum of activity was around 50 °C (Fig. 5B); above this value the enzyme was rapidely inactivated. The *exo* nature of the enzyme activity was characterized by separating the degradation products using HPLC (Fig. 6).

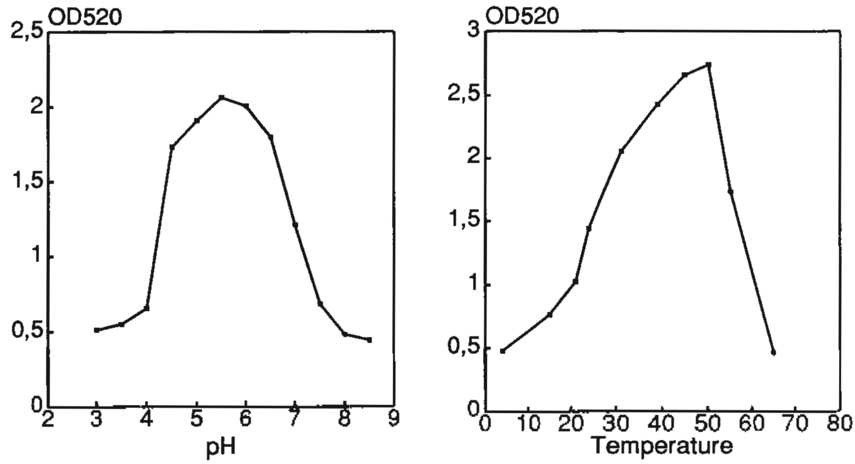

Fig. 5. pH (**A**) and temperature (**B**) optima of pectinolytic activity in mycelium raw protein extracts of V. inaequalis. In **A** a reaction mixture containing 50 mM phosphate buffer was incubated at 40 °C. In **B** the mixture was buffered at pH 6.0. After 2 h incubation aliquots of the reaction mixtures were colorimetrically tested for reducing sugars (OD_{520}). In reaction mixtures where enzyme was not added an optical density of 0.4 was recorded.

Most of pectinolytic activity could be detected in mycelial extracts. In contrast to most of the pectinase producing pathogens, *V. inaequalis* seems not to release the enzyme in culture filtrate. More recently, little acitivity could be found in culture filtrates, using acetone precipitation (in contrast to the usual ammonium-sulfate precipitation, this method shows a higher recovery of activity). The hypothesis that the pectinase is electrostatically bound to the cell wall of the fungus could be partially confirmed by homogenizing intact mycelium in salt solutions of different molarities.

The aim of the experiment was to exchange ionically the enzyme bound to the cell wall. The results (Fig. 7) showed that using solutions of increasing molarity an increasing amount of PG could be extracted. Cell wall bound PG are not known in pathogens, which invade tissues by macerating and penetrating cells.

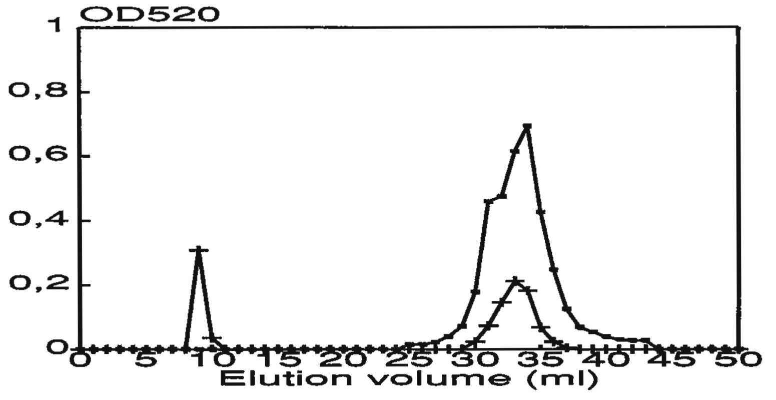

Fig.6. Reaction mixtures were separated using HPLC with an anion exchange column Synchropak WAX-300. Elution of uronic acids (substrate and degradation products) was performed with a gradient 0-1000mM ammonium carbonate buffer pH 8.2. Fractions of 1 ml were collected and tested for uronic acids (Meta Phenyl Phenol method). Crosses: incubation mixture at time 0, Points: incubation line after 3 h incubation. In a calibration run the pure monomer (galacturonic acid) was eluted in fraction 9, coincident with the elution of degradation products in the reaction mixture.

Fungal cell wall bound PG and more in general cell wall bound CWDE (plant cell wall degrading enzymes) could be a peculiar property of pathogens like *V. inaequalis* which grows without macerating or penetrating cells. To our knowledge only one other PG has been extracted from a mycelial fraction, from *Geotrichum candidum* by Barash and Klein (1), however the authors found PG activity in culture filtrates as well.

The fact that *V. inaequalis* does not release its CWDE into the surrounding medium could represent a valuable contribution to the explanation of the unusual type of parasitism exhibited by this pathogen. The *exo* nature of the PG activity may not allow the pathogen to colonize intercellular spaces in the epidermis and further parenchimatic tissues.

In vitro cell wall degradation

A new method was developed to study the process of cell wall degradation *in vitro*, in the experiment in wich ^{14}C-labelled cell walls were incubated with enzyme extracts (see material and methods). Both purchased enzymes and crude

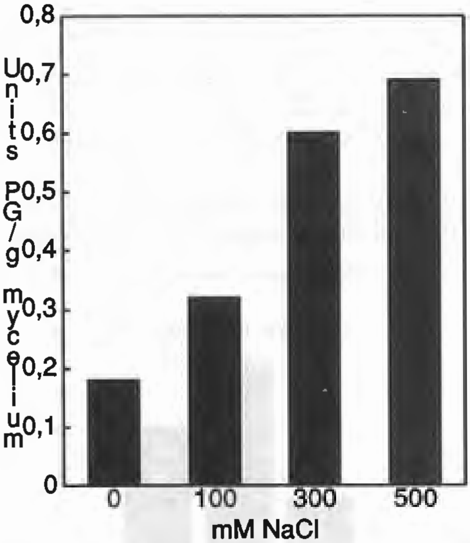

Fig. 7. Different mycelial fractions of 1 g (fresh weight) were homogenized with a glas beads homogenizer using NaCl solutions of different molarities. Solutions were buffered at pH 5.5 acetate 50 mM. The amount of enzyme recovered from each fraction is expressed in Units (1 U is the enzyme amount releasing 1 mmol galacturonic acid in 1 min).

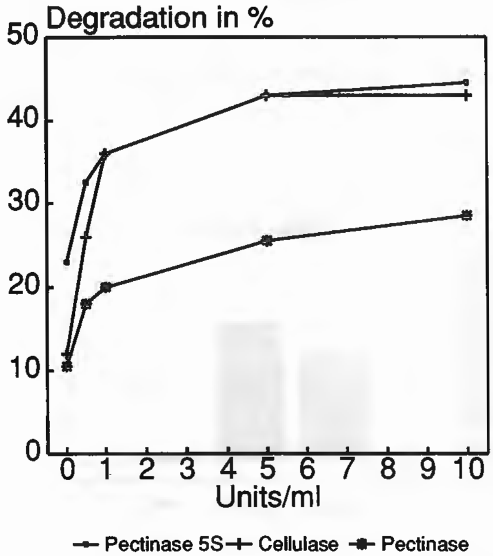

Fig. 8. *In vitro* degradation of ^{14}C-labelled cell walls using purchased enzymes (Serva). The reaction mixtures were incubated at 30 °C for 24 h.

extracts of *V. inaequalis* enzymes degraded ^{14}C-labelled cell walls *in vitro* (*unpublished results*). In experiments carried out with purchased enzymes up to 35% of cell wall material was degraded, measured as radioactivity in the supernatant (Fig. 8). In the experiment carried out with crude extracts of *V. inaequalis* enzymes, the amount of degradation was much lower, reaching a maximum of 8% after 24 h incubation.

The role of cell wall degradation in the fungus-plant interaction could not be elucidated up to now and no evidence of involvement of this process in resistance

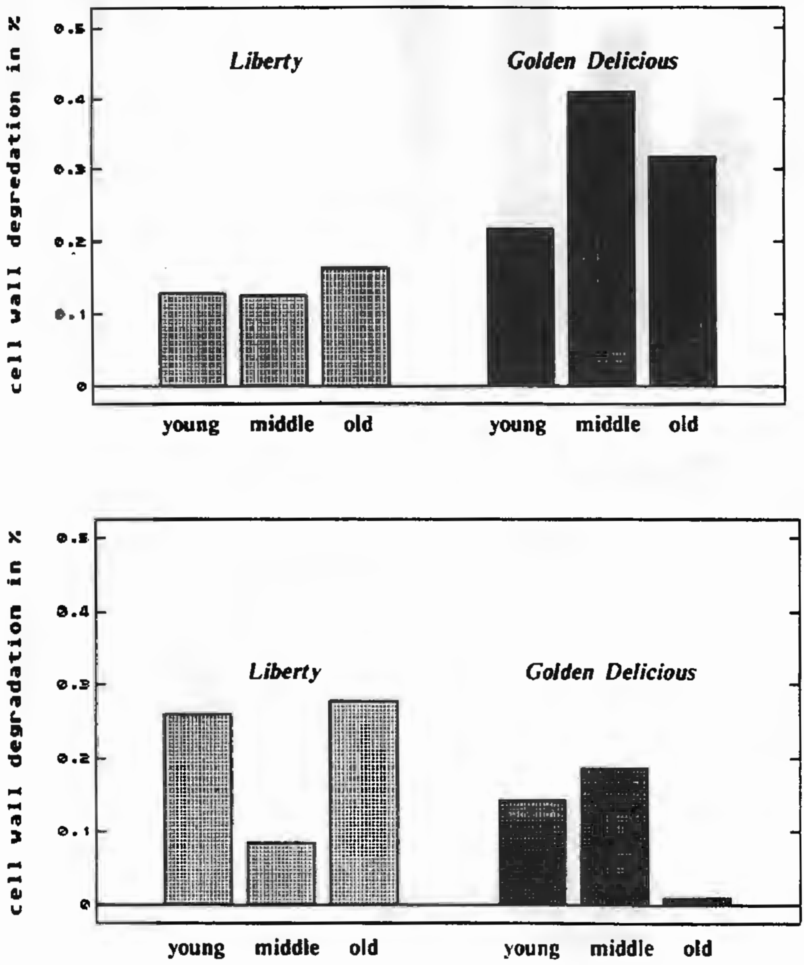

Fig. 9. *In vitro* degradation of ^{14}C-labelled cell walls using *V. inaequalis* raw protein extracts. Figures show results from two experiments carried out under identical conditions.

could be shown. Cell walls of both young and old leaves and of both susceptible and resistant varieties were incubated. We were never able to detect any difference in the degree of degradation of cell walls in extracts from leaves of different ages. A tendency for reduced degradation in cell walls extracted from the susceptible variety was observed but not confirmed in further experiments. The controversial results of several experiments are illustrated by two model examples in figure 9.

Our next step in the study of cell wall degradation will be the purification of the enzymes and the combination of different cell wall degrading enzymes in the incubation mixture. Even though the literature on cell wall degradation indicates pectinases are an obligatory first step in the process, we cannot exclude the likelyhood that other enzymes are needed to better simulate this process. Inhibitors potentially involved in the expression of resistance could play an important role. A better purification and characterization of the enzymes involved in cell wall degradation would be useful for further studies on this subject.

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Susceptibility of apple cultivars and selections to scab and powdery mildew in The Netherlands

H.A.Th. van der Scheer

Research Station for Fruit Growing, Wilhelminadorp, The Netherlands

Abstract

In the integrated control of apple scab (*Venturia inaequalis*) and powdery mildew (*Podosphaera leucotricha*), the level of resistance of cultivars under local conditions is an important factor with respect of the number of sprays needed for the control of both diseases. A study between 1984 and 1988 evaluated the susceptibility of apple cultivars currently grown in The Netherlands and also cultivars and selections which, according to the literature, are resistant to scab.

Key words: disease resistance, plant breeding, resistance tests, disease incidence.

Introduction

There is almost total reliance upon fungicides for the control of apple scab and powdery mildew. Decision-making schemes for the control of scab and powdery mildew in The Netherlands have been designed to minimize the number of sprays (6,7). These schemes are based on assessing both diseases on leaves of Golden Delicious, a highly susceptible and widely grown cultivar. Within a few years, however, this cultivar will loose its predominant position in The Netherlands and be overtaken in acreage by Elstar and Jonagold (2).

The level of resistance of cultivars is an important factor in reducing the number of sprays needed to control scab and powdery mildew. In this respect the most susceptible cultivar is limiting in mixed plantations. Information on the resistance of apple cultivars to these diseases under local conditions is indispensable.

Material and methods

In the spring of 1983, single trees of various cultivars were planted at 3.5x1.5 m in each of eight plots. Each block had 30 trees planted in three rows of ten trees. In addition to most of the cultivars currently grown in The Netherlands, some others which according to published reports are resistant to scab were also included. The latter group has been bred from *Malus floribunda* 821 (5,8,9). In 1983, captan (1.9 kg a.i. in 1500 l water per ha) and bupirimate (0.2 kg a.i. in 1500 l water per ha) were applied for the control of scab and powdery mildew, respectively, as a regular spray programme. Starting in 1984, one or both fungicides were omitted in some plots, giving two plots of oeach of 4 treatments. The plots were separated by trees of cultivar Golden Delicious to reduce the drifting of fungicide spray between plots.

The incidence (% diseased leaves) of scab and powdery mildew on long shoots was assessed each year in August by visual examination of shoots on the two sides of each tree next to the grassed alleys. These assessments were in 6 grades: 1 = 0%, 2 = 1-10%, 3 = 11-50%, 4 = 51-90%, 5 = 91-99%, 6 = 100% disease. At harvest, all fruits from each tree were examined for scab. The data on disease incidence in Tables 1-3 refer to assessments carried out in plots not sprayed for that particular disease. In only one year, 1988, the wood on 40 long shoots per cultivar was examined with a magnifying-glass to detect scab pustules (wood scab); these shoots were collected in September from trees that had not received captan.

Results and discussion

The incidence of scab (Tables 1, 2) and powdery mildew (Table 3) varied considerably between years in the 1984-88 period. Scab was consistently present but most abundant in 1987 due to the highly favourable weather conditions that year, whereas powdery mildew was important only in 1984 and to a lesser extent in 1985. The large reduction in the incidence of powdery mildew after 1984 was related to the occurrence of three successive cold winters; mycelium overwintering in buds cannot survive low temperatures (3).

Golden Delicious has been the cultivar used for the assessment of scab and powdery mildew in orchards where decision-making schemes for the control of

Table 1. Percentage scabbed leaves in August in plots not treated with scab fungicide.

Cultivar/ selection	1984	1985	1986	1987	1988	Average incidence
Alkmene	3	5	0	20	0	5.6
Cox's Orange P.	1	2	0	30	3	7.2
Coop 6	0	0	0	0	0	0
Coop 8	0	0	0	0	0	0
Coop 9	0	0	0	0	0	0
Coop 11	0	0	0	-	-	0
Discovery	0	2	0	3	0	1.0
Egri Piros	10	5	1	60	1	15.4
Elan	-	5	1	50	5	18.7
Elstar	15	25	2	75	15	26.4
Florina	0	0	0	0	0	0
Gavin	0	0	0	0	0	0
Gloster	20	60	5	-	-	28.3
Golden Delicious	20	50	15	100	30	43.0
IVT 5544-173	2	10	2	-	-	4.7
IVT 78039-8	-	-	-	0	0	0
IVT 78039-18	-	-	-	0	0	0
IVT 78039-20	-	-	-	0	0	0
IVT 78039-26	-	-	-	0	0	0
IVT 78039-27	-	-	-	0	0	0
James Grieve	1	10	1	40	10	12.4
Jonafree	0	0	0	-	-	0
Jonagold	40	20	5	95	30	38.0
Karmijn de S.	3	10	1	50	5	13.8
Liberty	0	0	0	0	0	0
Lombarts Calville	0	0	0	15	1	3.2
Macfree	0	0	0	0	0	0
Priam	0	0	0	0	0	0
Prima	1	0	0	0	0	0.2
Priols Delicious	2	5	0	10	5	4.4
Priscilla	0	0	0	0	0	0
Redfree	0	0	0	0	0	0
Sir Prize	0	0	0	3	0	0.6
Summerred	20	75	15	-	-	36.7
TSR 18T156	0	0	0	2	1	0.6

Table 2. Percentage scabbed fruits at harvest in plots not treated with scab fungicide.

Cultivar/ selection	1984	1985	1986	1987	1988	Average incidence
Alkmene	0	34	2	43	15	18.8
Cox's Orange P.	0	24	6	97	10	27.4
Coop 6	0	0	0	0	0	0
Coop 8	0	0	0	0	0	0
Coop 9	0	0	0	0	0	0
Coop 11	2	0	0	-	-	0.7
Discovery	0	19	0	83	4	21.2
Egri Piros	13	29	6	98	67	42.6
Elan	-	-	4	100	73	59.0
Elstar	0	11	4	100	87	40.4
Florina	0	0	0	0	0	0
Gavin	0	64	0	0	0	12.8
Gloster	22	54	15	-	-	30.3
Golden Delicious	2	66	13	100	96	55.4
IVT 5544-173	3	22	7	-	-	10.7
IVT 78039-8	-	-	-	0	0	0
IVT 78039-18	-	-	-	0	0	0
IVT 78039-20	-	-	-	0	0	0
IVT 78039-26	-	-	-	0	0	0
IVT 78039-27	-	-	-	0	0	0
James Grieve	0	17	5	89	22	26.6
Jonafree	0	0	0	-	-	0
Jonagold	23	15	16	88	69	42.2
Karmijn de S.	0	5	4	63	33	21.0
Liberty	1	0	0	0	0	0.2
Lombarts Calville	0	9	3	95	21	25.6
Macfree	0	0	0	0	0	0
Priam	0	0	0	0	0	0
Prima	0	1	0	0	0	0.2
Priols Delicious	0	0	2	3	3	1.6
Priscilla	0	0	0	0	0	0
Redfree	0	0	0	0	0	0
Sir Prize	0	0	0	0	0	0
Summerred	0	26	20	-	-	15.3
TSR 18T156	0	2	0	47	4	10.6

Table 3. Percentage mildewed leaves in August in plots not treated with mildew fungicide.

Cultivar/ selection	1984	1985	1986	1987	1988	Average incidence
Alkmene	5	2	0	0	0	1.4
Cox's Orange P.	30	10	2	0	2	8.8
Coop 6	10	3	0	0	0	2.6
Coop 8	20	3	1	0	0	4.8
Coop 9	15	5	1	0	0	4.2
Coop 11	30	10	1	-	-	13.7
Discovery	3	1	0	0	0	0.8
Egri Piros	5	5	0	0	0	2.0
Elan	-	2	0	0	0	0.5
Elstar	30	10	0	0	0	8.0
Florina	20	3	2	0	0	5.0
Gavin	20	3	0	0	0	4.6
Gloster	30	3	1	-	-	11.3
Golden Delicious	30	3	2	0	0	7.0
IVT 5544-173	10	3	2	-	-	5.0
IVT 78038-8	-	-	-	0	0	0
IVT 78039-18	-	-	-	0	0	0
IVT 78039-20	-	-	-	0	0	0
IVT 78039-26	-	-	-	0	0	0
IVT 78039-27	-	-	-	0	0	0
James Grieve	5	2	0	1	0	1.6
Jonafree	3	3	0	-	-	2.0
Jonagold	30	5	2	0	1	7.6
Karmijn de S.	20	15	1	0	2	7.6
Liberty	30	5	2	0	0	7.4
Lombarts Calville	5	2	0	0	0	1.4
Macfree	30	10	2	0	0	8.4
Priam	15	3	0	0	0	3.6
Prima	3	2	0	0	0	1.0
Priols Delicious	5	2	1	0	0	1.6
Priscilla	2	1	0	0	0	0.6
Redfree	3	2	0	0	0	1.0
Sir Prize	20	3	2	0	0	5.0
Summerred	15	2	0	-	-	5.7
TSR 18T156	20	2	2	0	0	4.8

both diseases are developed (7). From the data in Tables 1-3 it is evident that Jonagold will be an adequate replacement when its planted area exceeds that of Golden Delicious in the near future. Both cultivars have the same level of susceptibility to scab and powdery mildew but the leaf:fruit scab ratio is higher and thus more favourable with Jonagold.

Trees of the currently-grown cultivars Elstar, Gloster, Golden Delicious and Jonagold had visibly more scab on both leaves and fruits than trees of the other scab-susceptible cultivars. Summerred and Priols Delicious were the only cultivars characterized by the occurrence of distinctly more scab on leaves than on fruits (Tables 1 and 2).

Only Golden Delicious and Karmijn de Sonnaville had wood-scab pustules, on 22.5 and 42.5 %, respectively, of the long shoots in 1988, the number of pustules per affected shoot being 2.1 and 1.6, respectively. Sporulation of the pustules was confirmed microscopically. For this purpose the sticky surface of a piece of Scotch Tape was pressed against a pustule and the tape was mounted in a drop of lactophenol on a glass slide. Scab spores were sometimes also seen on Scotch Tape pressed against wood without visible pustules, which indicates that spores were widely dispersed in the trial orchard.

Cultivars and selections which according to the literature are resistant to scab nevertheless showed signs of the disease in some years (Tables 1 and 2). This phenomenon had previously been observed in The Netherlands (1) and was recently reported from Germany (4). It is conceivable that under extreme infection pressure the initial stroma which normally remain small can develop into visible scab lesions.

Discussions during the IOBC Workshop on Integrated Control of Pome Fruit Diseases at Lana, Italy, in 1987 (10) suggested that among the newer scab-resistant apple cultivars only Florina has been performing acceptably for both yield and fruit quality. Nevertheless, these properties are still inferior compared to Golden Delicious, Jonagold and Elstar. Florina appeared in this trial to be moderately susceptible to powdery mildew (Table 3). Scab-resistant cultivars with a better fruit quality are needed. In this respect it is hoped that crosses of Prima and Priscilla with Elstar, made at the Horticultural Institute for Plant Breeding at Wageningen, will be successful. In 1987, some of these were included in the experiment discussed above (Tables 1-3).

Acknowledgments

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New research in Trentino, Italy, on apple disease resistance and the assessment of scab-resistant cultivars

A. Scienza, D. Forti, L. Martinelli, A. Dalpiaz

Istituto Agrario Provinciale, 38010 S. Michele a/Adige (Trento), Italy

Abstract

At the Institute of S. Michele a/A, Trentino, Italy, research projects on apple resistance to fungal pathogens are being developed, and the use of biotechnical methods in this field is being considered. Aspects of this programme are discussed.

Key words: apple research, old cultivars, techniques, integrated control.

Introduction

The Institute of S. Michele a/A was founded in 1874 as an agricultural teaching and advisory centre, and today instruction is an important activity.

In 1985, research was started in the areas of viticulture and vine-making, biological and integrated pest control and the agricultural uses of compost, derived from urban wastes.

More recently, a genetic improvement unit was formed which will be fully functional in 1989 with the completion of genetic and bioengineering laboratories. Future programmes will strengthen S. Michele as a multi-disciplinary institution where research activities and teaching are directed at the needs of local agriculture.

In Trentino, apple growing, with its annual yeald of 350'000 tonne, is one of the main sources of income, particularly in the hilly areas and the Non Valley.

This calls for research directed towards disease resistance, using biotechnology for basic studies of resistance mechanisms and to improve plant disease resistance. By this means, it is intended to make practical advances appropriate to Trentino, where there are large differences in local agroclimate.

General aspects of the problem

As is the experience with many crops and regions, a few improved clones introduced into Trentino progressively replaced the original apple and grape populations. This phenomenon, understandable commercially, reduced the local genetic pool in a few decades. What steps can be taken to correct the 'genetic erosion' and re-introduce valuable genes, especially those for local adaption? First, it is necessary to make plant collections from Trentino and the whole alpine area. This task calls for patience, but finds great support at the Institute of S. Michele.

Secondly, research is based upon activities at several institutions. The principal aim is to select morpho-functionally improved plants resistant to the main diseases and also to environmental stress.

Within this framework, a distinction is made between laboratory and field studies because they present different although integrated aspects of the overall programme.

Laboratory research

Laboratory work is based on *in vitro* propagation studies and biotechnical research. The main research topics are:

- the induction of somaclonal variation by means of *in vitro* culture of cell suspensions.
- improvement of selection techniques for pathogen resistance by exposure to toxins or filtrated cultures of pathogens.
- use of transpositive mutagenic techniques (DNA transfer) through the engeneering of bacterial vectors.

It is hoped that in developing and evaluating these techniques, genes that code for resistance to specific pathogens can be introduced into apple (and grape).

- quantification, using protein characterization by electrophoresis of distinctive traits among apple (and grape) clones, particularly in collections of old cultivars.

– indexing of old and improved material using ELISA techniques in order to assess plant health with respect to viruses.

Field research

Field research will be coordinated with the laboratory research because it comprises the assessment of selected individual plants for productivity, precocity etc., and the testing of resistance for stability under field conditions.

Other related studies are:

– collecting and stuying old cultivars obtained locally and from the alpine area There is increasing interest in the preservation of these cultivars because of their intrinse value as genetic sources for environmental adaptation, fruit quality (taste) and disease resistance. So far, 100 cultivars from several northern Italian regions have been collected and grafted.
– genetic improvements by means of conventional breeding techniques (single and multiple crossing), with the assessment and selection of glass-houses and in the field
– clonal selection project for apple cultivar "Renetta Canada", aimed at clonal improvement. During the summer of 1988 about 100 clones from the Non Valley area were collected and grafted.
– field performance of improved cultivars resistant to scab, and development of integrated production methods and biological pest control.

This last aspect of the program represents the climax of the work towards chemical-free apple production; it is necessary to investigate the economics of this type of apple cultivation. The use of scab-resistant cultivars is a step towards chemically-free fruit-farming techniques, but economic uncertainties remain in the context of the Trentinian and Italian markets. The last project is also an economic comparison of at least four fruit-growing methods using common cultivars, e.g. Golden Delicious and the more resistant cultivars available today such as Querina and Florina, in a 4-ha-orchard.

Session 5

Storage rot diseases

Chairperson: C. Verheyden

Pome fruit storage disease control in Belgium: past, present and future

C. Verheyden and P. Creemers

Research Station of Gorsem (IWONL), 3800 Sint-Truiden, Belgium

Abstract

A general survey is given of the storage of apples and pears, including refrigeration and controlled atmospheres.

Emphasis is placed on mineral composition of the fruits and on their maturity in relation to physiological disorders. A distinct relationship between bitter pit and calcium content, or the K:Ca ratio in the fruit. Special attention is drawn to Blossom-end rot and Mouldy core.

The benzimidazole fungicides were especially effective for controlling storage disease fungi but resistance has occurred in *Botrytis*, *Penicillium* and even in *Gloeosporium* in neighbouring countries. Fungicides to control storage fungi are discussed: Storage disease management spray programs are targeted at *Botrytis* on pears and at *Gloeosporium* on apples. To avoid resistance, mixed-fungicide strategies are proposed.

Interesting postharvest treatments discussed are dipping, drenching and thermal fogging to apply fungicides, the use of natural aromatic components and prospects for biological control.

Key words: Storage rots, disease control, postharvest treatments, fungicides, orchard sprays, resistance, tolerance, aromatic compounds.

Introduction

Postharvest diseases of fruits (and vegetables) are major problems in food production. Losses are difficult to estimate but the authors' data and those of others (1, 11) indicate that losses can amount to 40%. Even an average 10% loss of a high-value commodity like apple has a large impact on the total cost of production. Disease-resistant cultivars must be regarded as important in contributing towards reducing spray residues in food and in the environment; cultivars which can be stored and marketed to a high standard without the need of orchard sprays or postharvest treatments deserve a high priority in breeding programmes. Selection of apple and pear breeding material for resistance to storage diseases and with good storage potential is increasingly important.

Meanwhile, storage diseases of apple and pear have to be controlled by cost-effective postharvest treatments, including refrigeration and controlled atmosphere (CA) storage. The different methods can be summarised as follows:

- Cold storage refrigeration in normal air conditions. Fruit, however, cannot be kept very long by this method.
- Controlled atmosphere (CA) storage in gas-tight rooms with 5 - 6% CO_2 and 16 - 15% O_2). The advantage of the method lays in the inhibition of respiration by a decrease of oxygen and an increase of carbon dioxide.
- Scrubbed gas storage with 1 - 5% CO_2 and 2 - 3% O_2. The low oxygen level results from respiration of the fruit; the carbon dioxide is regularly removed by a scrubber and replaced by fresh air. The ripening of many fruits can be dramatically hastened by ethylene and so ethylene scrubbing can be an additional feature.
- Ultra low oxygen (U.L.O.) storage with 1 - 5% CO_2 and 1,5% O_2. Oxygen concentration is analysed and adjusted with an electronic computerised controller. Otherwise anaerobic (or fermentative) respiration will be caused by an excessively low oxygen level (below 1%).

In addition to these storage systems to reduce losses, major methods which have been investigated to control postharvest diseases use chemicals, heat and irradiation. Only chemical treatments have found widespread application.

In addition to losses from diseases, mention must also be made of losses from modern fruit-handling practices.

Table 1 : Percentage apple fruits with an open calyx tube and the incidence of mouldy core according to the fungicide treatment.

Fungicide (*)	Fruit size (kg) >75 mm	% fruits with open calyx	% fruits with mouldy core
Control	23.5 a (**)	66.1 b	19.4 b
Iprodione	25.5 a	53.1 a	5.0 a
Triadimefon	11.5 b	80.3 c	46.6 c

(*) Four weekly treatments between full bloom and start of June drop.

(**) Means in the same column followed by the same letter are not significantly different (P = 0.05).

Postharvest diseases

Postharvest diseases are often extensions of phenomena occurring in the orchard, and can be physiological disorders or caused by pathogenic organisms.

Physiological disorders

The occurrence of physiological disorders during storage depends on the mineral composition of the fruits and on their maturity.

The date of picking is the main factor determining the behaviour of apples and pears during storage and their quality. If the fruit is picked early, loss of weight during storage will be greater and internal breakdown may occur. If the fruit is picked late, scald, core flush and senescence rot may occur. Picking late may be even more harmful for fruits from fairly charged trees and for pears cooled too slowly or in the presence of a too high CO_2 content in the storage room. All factors favouring maturity stimulate scald.

Bitter pit is usually regarded as a disorder occurring during storage. Susceptibility to the development of pitting depends, however, upon conditions during the time the fruit is on the tree. Calcium is a very important element in plant cells and a major factor preventing physiological disorders in fruit. Conditions influencing the calcium content of fruit are: soil, fruit size, pruning, transpiration rate (low rates result in high final calcium levels) and, of course, calcium sprays.

Trials at the Research Station of Gorsem using cv. Boskoop involved regular sprays of technical-grade calcium nitrate (1 %) starting 3-4 weeks after blossom. The effects on bitter pit were very favourable (Fig. 1).

Table 2. Activity (% control) of fungicide dip treatments on *Botrytis cinerea* on Conference pear. Dipping time: 30".

Fungicide	Conc. ppm	After 7 days at 20 °C and 100 % RH MBC-sensitive inoculum	MBC-resistant inoculum
Thiabendazole	1500	87.7 b*	0.0 b
Vinclozolin	500	98.5 a	97.3 a
Iprodione	500	99.5 a	99.8 a

* Values in the same column followed by the same letter are not significantly different (P = 0.05).

Table 3. Activity (% control) of postharvest fungicide dip treatments on *Penicillium expansum. Dipping time : 30".*

Fungicide	Conc. ppm	After 7 days at 20 °C and 100 % RH. Conference pear	Golden Delicious apple
Thiabendazole	1500	31.6 b*	43.4 b
Imazazil	375	92.7 a	98.4 a

* Values in the same column followed by the same letter are not significantly different (P = 0.05).

Such results have been obtained by many workers using calcium nitrate (O,65%) or calcium chloride (0,5%). These trials demonstrated that the effectiveness of the calcium spray programmes varied between orchards. In some, a potential bitter pit incidence of 5% was not effectively controlled, while in others a potential of more than 30% was completely controlled. In only half of the trials

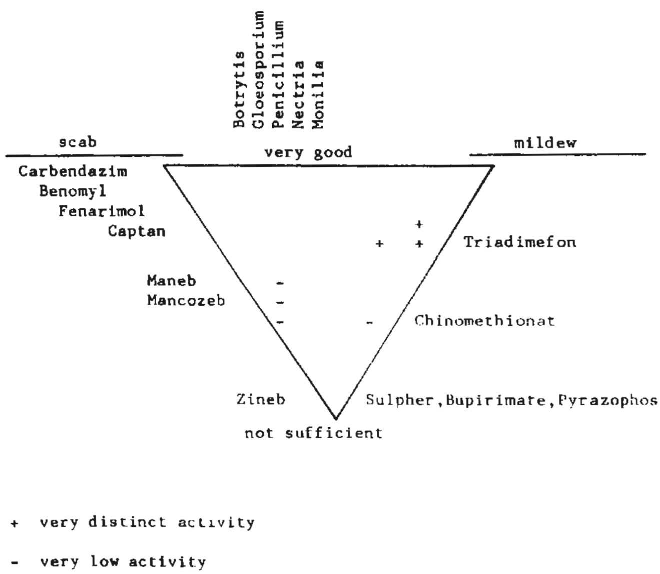

Fig. 1. Bitter-Pit (stip): scheme of treatments (12) 1% $Ca(NO_3)_2$.

was the fruit calcium content increased by more than 1 mg/100 g, stressing the need to improve the application method.

Fruit intended for storage should be harvested at optimal maturity, before the rise in respiration, and should be cooled promptly after picking. Internal resistance decreases as ripening advances.

It is well known that many physiological disorders are more likely to develop during storage in fruits deficient in calcium and/or rich in potassium and magnesium. Fruits with a high K:Ca ratio show a faster climacteric respiration increase, ripen quicker and loose their internal resistance earlier.

The mineral composition of fruit influences the occurrence of storage rots (Fig. 2).

Maintaining fruit at high "vitality" enhances natural disease resistance and the ability to heal wounds. As Sommer (14) mentioned, several measures for minimizing postharvest diseases are important and should be followed as much as possible:

- Harvest fruit at the time of optimum maturity.
- Avoid wounds: these provide an entrance for pathogens and also stimulate respiration and ethylene evolution (which may trigger ripening).
- Cool fruit promptly to ensure high "vitality" and natural

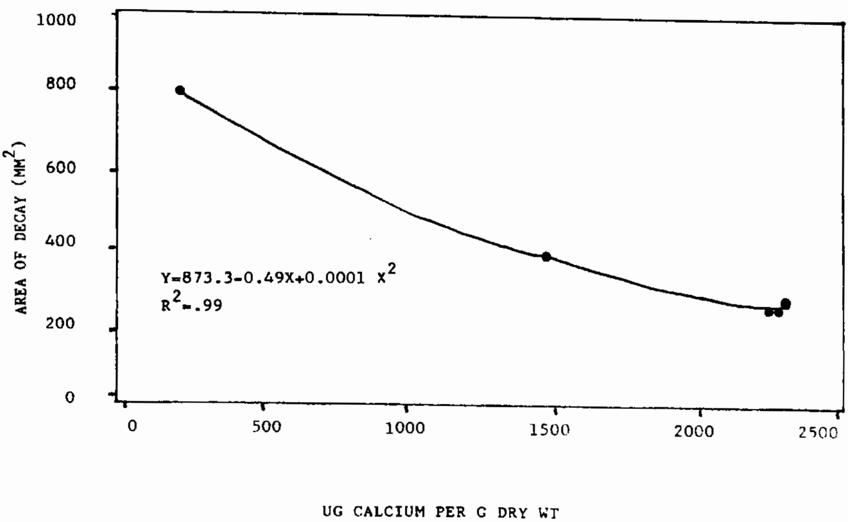

Fig. 2: Relationship between area of decay and calcium concentration of apple tissue in fruits pressure infiltrated with calcium chloride ($CaCl_2$). Data points from left to right are concentrations of 0, 2, 4, 6 or 8% $CaCl_2$ solutions, respectively (2).

disease resistance throughout the postharvest period.
- Store at the lowest temperature that will not damage the fruit.
- Use controlled or modified store atmospheres.

Pathogenic organisms

More than 40 fungi can be responsible for fruit rot. General surveys of the most important pome fruit storage diseases were given by Kennel (9) and Creemers (3). In this paper, attention is drawn to Blossom-end rot and Mouldy core.

Blossom-end rot

Blossom-end rot can be very damaging in some years on certain apple cultivars. In 1987, losses from blossom-end rot were very severe, especially on the cultivars Boscoop and Jonagold.

Infection occurs at petal fall, when the styles and stamens wilt. If this period is prolonged by cool and moist weather, the risk of infection is increased. After the blossom period, a dry brown spot appears around the remains of the sepals, with a surface area of only a few square millimetres at harvest. The flesh of the fruit around the lesion matures prematurely and sometimes affected fruits drop.

Isolations made shortly after the appearance of symptoms always reveal determined *Alternaria* spp., mostly in combination with *Botrytis cinerea* Pers. Fr. Isolations later in the season and during storage reveal *Nectria galligena* Bres. There is no certain explanation for this difference: there may be two infection periods, with *B. cinerea* infecting during the blossom period and *N. galligena* later. Alternatively, *N. galligena* may be secondary on fruits already infected with *B. cinerea*. In other countries, the same two fungi are described in the group of pathogens causing Blossom-end rot.

During storage, some of the latent infections resume activity and colonize the whole fruit. Vinclozolin is approved for the control of Blossom-end rot in Belgium.

Mouldy core

One of the new apples interesting fruitgrowers in recent years is the German cultivar Gloster. The incidence of mouldy core in this cultivar is very high in some years. The fungi isolated from the core region belong to several genera: *Alternaria* spp. are the most common (6, 8). The fruits have a grey- to black-coloured fungal growth over the seeds and carpel walls. Occasionally, the surrounding fruit flesh is also affected and from these fruits *Fusarium* spp. and sometimes also *Trichothecium roseum* (Pers.: Fr.) Link. are isolated.

The period of latency can be very short. If the development of the fungus takes place whilst the fruit is on the tree, the infected fruits ripen and colour prematurely. The elimination of these more-coloured fruits is not, however, guaranteed to eliminate mouldy core problems after harvest.

Gloster belongs to the group of cultivars which often have an open calyx tube. On these cultivars, the five flower styles which normally join at the base fail to unite under certain conditions.

In trials of fungicides applied during the postbloom period, good results were obtained at Gorsem with iprodione. The application of compounds with growth regulating effects can, however, increase the percentage of fruits with an open calyx and indirectly, therfore, the incidence of mouldy core (Table 1).

Preharvest treatments

The causes of the most important storage diseases in Belgium can be summarized as 95% *Botrytis* and 5% others (*Monilia, Penicillium*) on pear and 50% *Gloeosporium* and 50% others (*Botrytis, Penicillium, Cylindrocarpon, Alternaria* etc.) on apple.

For the control of storage fungi, the benzimidazoles are especially valuable. The following fungicides belong to this group: benomyl, thiophanate-methyl, carbendazim, thiabendazole. These systemic compounds can penetrate into fruit, reaching the latent mycelium of the pathogens. The fungicides have excellent activities against fruit-rot fungi such as *Gloeosporium, Botrytis, Penicillium* and *Monilia*. In Belgium it is recommended not to use these compounds in the orchard to control scab and powdery mildew, but to restrict them for the control of storage rots.

In recent years, and despite the restricted number of actual applications, some of these target fungi have developed resistance against all fungicides in the benzimidazole group. This was first noted *B. cinerea*, the most important storage fungus on pear. *Botrytis* is a polyphagous pathogen which is not restricted to apple and pear but attacks numerous other crops. On most of these crops the benzimidazoles are no longer used against *Botrytis* because of resistance problems.

A second widespread fungus that developed resistance to benzimidazoles was *Penicillium*. This resistance became general in stores. Recently, resistance in *Gloeosporium* (*Pezicula malicorticis*) was detected in the Federal Republic of Germany and also in the Netherlands (11, 17). In Belgium, resistance in this fungus is not yet proved and the results obtained with benzimidazoles against *Gloeosporium* remain excellent.

Apart from resistance problems, there is also a shift in the fungal spectrum as a result of the increasing importance of fungi which are naturally less sensitive or insensitive to benzimidazoles (18).

Also, changes in production methods shift the fungal spectrum. Thus,

- increased mechanisation in fruit handling has led to more injured and bruised fruit, which explains the increase of *Penicillium* and *Botrytis* fruit rots.

- general use of pneumatic pruning has increased cankers, resulting in an increased infection pressure, especially of *N. galligena*.
- increased application of zinc fungicides for scab control, although these compounds are not active against fruit rot fungi (Fig. 3).

The resistance level of fungi resistant to benzimidazoles is very high; moreover, it is a persistent resistance. In such cases, either fungicides with a different mode of action are needed or alternative control methods. Another problem can be negative cross resistance between two fungicides. Fortunately, a new fungicide, diethofencarb, has proved very effective against benzimidazole-resistant strains of various fungi (5). The possibility of using diethofencarb for the control of storage diseases is the subject of trials in 1988 and the first results are expected in 1988-89.

For the control of *B. cinerea* on pear, very good results were obtained with the dicarboximides (Table 2). Only vinclozolin is currently approved for use in Belgium; iprodione has been phytotoxic on the pear Doyenne du Comice. Apart from their excellent activity against *Botrytis*, dicarboximides are also very efficient against *Monilia*. These two fungi are responsible for almost all storage rots on pear, and so these compounds are especially suited for the control of fruit rot on pear.

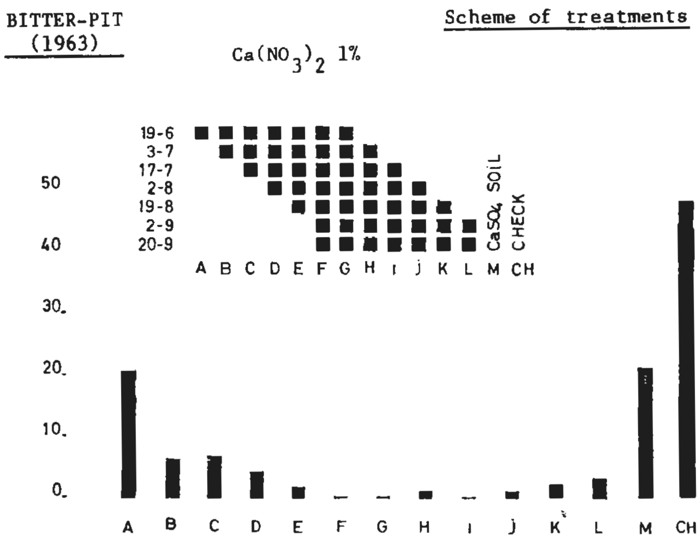

Fig. 3: General survey of the side-effect of fungicides applied against apple scab and mildew on the occurrence of the parasitic storage rots (10).

For *Penicillium*, the second fungus with widespread general resistance to benzimidazoles, imazalil has given very satisfactory control (Table 3). This fungicide has been cleared in Belgium for postharvest applications (see below).

In the past, the chemical control schedules applied to apple and pear were identical; nowadays, more specific schedules are followed for each commodity. On pear, the control schedule is directed at *Botrytis*; on apple, *Gloeosporium* is the main target. In order to prevent a selection of resistant strains or a shift in fungal spectrum, schedules with more than one fungicide, each having a different mode of action, are recommended. On pear, a specific *Botrytis* compound (vinclozolin, tolylfluanid) is the most important component, but is mixed or alternated with a benzimidazole, thiram or captan. On apple, benzimidazoles remain the most important component, alternated or mixed with contact fungicides such as captan, thiram, tolylfluanid or vinclozolin.

The number of applications depends on the weather. In normal circumstances three treatments are sufficient. The sequence of the various compounds in the schedule is determined by the need to minimize visible residues and the minimum "safe" interval allowed before picking the crop.

Postharvest treatments

The control of fungal storage pathogens of pome fruits by means of postharvest applications is very recent in Belgium. It is important to delay the chemical control of storage diseases until after harvest because selection pressure on the inoculum sources will then disappear and resistance problems will be avoided. Also, better chemical coverage of the fruit is obtained and wounds occurring during picking are protected. Another advantage of postharvest treatments is that the harmful effects of benzimidazoles on beneficial organisms such as earthworms and predator mites are avoided.

In some other European countries, postharvest treatments of fruit are applied not only to reduce parasitic attacks, but also to reduce physiological disorders during storage. As mentioned above, imazilil is approved in Belgium as a postharvest treatment for the control of *Penicillium*.

1. Dipping and drenching

Treating picked apples with the anti-oxidants diphenylamine (DPA) or ethoxyquin is approved in many countries to control superficial scald. These treatments are carried out soon after harvest, either by dipping or drenching fruit in water-dispersions of the chemical agents. The equipment for such postharvest treatments is not common in Belgium for two main reasons:

– good results are given by preharvest treatments

- only one third of the total production of pome fruit is stored at the cooperatives: the remainder is stored by the fruitgrowers.

Some factors limiting the success of dipping and drenching are contact time, temperature of the solution and fruit, the need to maintain the concentration of the solution, dirtiness of the solution and the need to renew the solution.

2. Thermal fogging

Imbroglini, Bompeix and Morgat (7) have tested a new method based on the thermal fogging of chemicals; this appears to be much simpler and easier than dipping or drenching. Thermal fogging is the production of a fog of tiny drops containing the chemical agents; the size of the drops has to be about one micron in order that the fog persists long enough to permit the drops to penetrate among the fruit in the bins.

The advantages are clear; the method is simple, fast and relatively cheap. Thermal fogging is possible in CA stores without any large change of atmosphere (approx. 1% increase of oxygen) or temperature (transitory increase of 0,5 °C).

Tests are being conducted for the extension of the method to active ingredients such as fungicides.

3. Aromatic components

Natural metabolites evolve in stores: hexyl acetate, butyl butyrate and butyl acetate are the major components, with other esters, alcohols and carbonyl compounds of lesser importance as components of fruit aroma.

Davis and Smoot (4) reported the inhibition of *Penicillium digitatum* spores by long-chain aliphatic aldehydes at concentrations of 1.0, 0.2, 0.1 and 0.06 mole/l. This inhibition was not observed with the alcohols, esters and terpenes.

The effect of some volatile components of fruit aroma on in vitro spore germination and development of *Colletotrichum gloeosporioides* has been investigated at the Research Station, Gorsem (11). Fungicidal and fungistatic activities of the components were evaluated by measuring mycelial growth during 7 days after treatment.

a. Fungicidal (lethal) activity

Complete inhibition of mycelial growth of *C. gloeosporioides* was observed for 1-hexanol and 1-heptanol after a fumigation exposure of 24 h. 1-butanol and 1-pentanol had no lethal activity at a fumigant concentration of 0.25% v/v, but at 5% v/v a fumigation of 3 h stopped the growth of the fungus. Acetaldehyde had a lethal effect after short exposures. Results obtained for acetaldehyde, 1-butanol and 1-pentanol indicated an inverse relation between concentration and fumigation time.

Methanol, ethanol, 1-octanal, methyl acetate, ethylacetate and 1-pentyl acetate had no lethal activity, while 1-propyl acetate, 1-butyl acetate and hexylacetate produced a lethal effect only at 5% v/v and an exposure of at least 3 h.

b. Fungistatic activity on mycelial growth

With a 24 h exposure to a low concentration (0.25% v/v) of the fumigant, most aromatic components such as methanol, ethanol, 2- propanol and all the mentioned acetate compounds, produced only a very slight inhibition of mycelial growth of *C. gloeosporioides*. 1-butanol and 1-pentanol partially reduced the development of the fungus, while 1-hexanol and 1-heptanol completely inhibited growth for at least 7 days. Treatment with acetaldehyde resulted in an inhibition for 2 days; then the mycelium started to grow again, at a rate equal to the untreated fungus.

When concentration was increased to 5% v/v, all the aromatic components inhibited mycelial growth for several days, but growth resumed after 2 to 6 days.

c. Influence of treatment on sporulation of *C. gloeosporioides*

The embedding of conidia in a pinkish mucous and the formation of acervuli depended on the aromatic component, its concentration and the duration of exposure to the fumigant.

d. Spore germination

Acetaldehyde inhibited the germination of spores of *C. gloeosporioides* more than the three alcohols tested. Methyl acetate and 1-propyl-acetate had no appreciable effect on spore germination, even with exposures of 24 h, while the aldehyde and the alcohols inhibited spore germination with a fumigation exposure of 24 h at concentrations of 0.5 and 1.0% v/v.

e. Conclusions on aromatic compounds

The conclusions of this experiment by Pittevils (12) are that natural volatile metabolites of fruits have a specific fungicidal and/or fungistatic activity on the development of *C. gloeosporioides*, a very important storage pathogen. Acetaldehyde and the tested alcohols had high inhibition activities on the growth of the fungus, while the acetate compounds had some effect but only at high concentration. Acetaldehyde had a considerably higher inhibition activity on spore germination than the other components.

4. Biological control

Although limited, work on the biological control of postharvest diseases is encouraging. The few studies have met with considerable success, like *Trichoderma sp.* against Decay Green mould, *Botrytis* rot, etc.

Wilson and Pusey (19) inoculated peaches, nectarines, apricots and plums with suspensions of antagonistic bacteria. One isolate of *Bacillus subtilis* (B-3) gave excellent control of Brown rot caused by *Monilinia fructicola* in storage.

Antagonistic microorganisms for epiphytic biocontrol are often effective in Petri dishes or in the glasshouse but fail in the field. Under storage conditions for fruit, antagonists avoid the uncertain environment faced in the field, but the cardinal temperatures for the growth and reproduction of antagonists need to correspond with those of the target pathogen.

Competition for nutrients in a biological niche provides for another form of biocontrol. Wounds are a special niche in which nutrients for microbial growth abound, but more information is needed on host defense responses to wounding and on microorganisms at the site of the wound.

Wilson and Pusey (19) mention three reasons why biological control may be appropriate to stored apple and pears:

1. One of the main reasons for the failure of biocontrol procedures has been the failure to control environmental conditions. Environmental conditions must, however, be controlled in the case of harvested food.

2. Targeting biocontrol agents to the effective site is often difficult. Harvested fruit does not present that problem because the target areas are much more limited than on whole plants.

3. Elaborate and often costly control procedures that may not be feasible under field conditions are cost-effective for harvested fruits.

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Storage rots of apple and pear in South-East England 1980-88: incidence and fungicide resistance

A. M. Berrie

Ministry of Agriculture, Fisheries and Food, Agricultural Development and Advisory Service, Wye, Ashford, Kent, England.

Abstract

To survey apple and pear storage rots in South-East England (particularly in Kent, a major fruit-growing county), fruit stores and packhouses were visited weekly or monthly from January to May in 1981 (pear only), 1983-85 and 1988, and the rotting of stored Cox's Orange Pippin and Bramley's Seedling apples and Conference pears, grown the previous year, was assessed. In the surveys of 1983-1985, losses of cv. Cox due to fungal rots were low (1-2%), with *Botrytis cinerea*, *Monilinia fructigena* and *Phytophthora syringae* the main fungi identified. In 1988, the loss of Cox was more than 6%, over half of which was due to *Nectria galligena*. With cv. Bramley's Seedling, *M. fructigena* was the main rot identified in most years, with losses of 1-2%; in 1985, however, the losses increased to 4%, mostly attributable to *P. syringae* and *Mucor pyriformis*. With cv. Conference pear, losses due to rotting were approximately 2%, with *B. cinerea* responsible for over half.

Over 70% of *B. cinerea* isolates and all those of *Penicillium expansum* were resistant to benzimidazole fungicides. Resistance to this group of fungicides was not detected in the other pathogens. A few isolates of *B. cinerea* were resistant to vinclozolin.

Introduction

The harvesting period for most British apples and pears is mid-September to mid-October. Long-term controlled atmosphere (CA) storage enables the industry to regulate its supply of fruit onto the UK market for most of the year, allowing competition with imports from EEC and other countries.

A knowledge of factors causing physiological storage disorders such as core flush and bitter pit is of obvious importance, but as important is the control of fungi causing fruit rots in stores. As technology will enable the storage period to be further lengthened, so fungal rots will become of greater importance. It is therefore essential that the fungi responsible for rotting are identified and new problems detected early. This is done by periodic surveys of rots present in fruit coming out of stores.

In a national survey of losses in stored Cox's Orange Pippin apples in the period 1961-65, stores in each region were visited on a number of occasions and fungal rots were counted and identified visually. Fungal rots were only responsible for about half the losses (1): of these, *Gloeosporium* spp. were responsible for up to 33% in some stores. *Monilinia fructigena* (brown rot) was also important, but other rots were insignificant (Table 1).

Post-harvest techniques have changed in the last 20 years and one major development which has affected the incidence of rots is the use of pre- storage fungicide dips or drenches. The purpose of this study was to identify the fungi responsible for rotting in stores in the 1980s. Benzimidazole compounds (e.g. benomyl (Benlate), carbendazim (Derosal Liquid, Stempor) and thiophanate methyl (Mildothane Liquid)) are used in most post-harvest dip/drench treatments. Isolates of *Botrytis cinerea* and *Penicillium expansum* resistant to these compounds are known to occur widely, but resistant isolates of *M. fructigena*, *Gloeosporium* spp. and *Nectria galligena* had not been detected in the UK. It was also essential, therefore, to monitor the sensitivity of the rot fungi to the fungicides used to treat them.

Table 1. Overall mean percentage losses of fruit due to fungal rots in apple cv. Cox's Orange Pippin, 1961-65 national survey.

Fungal rot	1961-62	1962-63	1963-64	1964-65
Monilia fructigena (brown rot)	1.5	0.3	0.2	0.5
Gloeosporium spp. (bitter rot)	1.3	2.0	3.8	1.8
Other rots (including *Nectria galligena*)	0.2	0.4	0.3	0.7
Secondary rots (*Botrytis, Penicillium, Rhizopus/Mucor*)	0.2	0.1	0.4	0.2
Total losses due to rots	3.2	2.8	4.7	3.2
No. farms/stores sampled	22	34	36	22

Surveys of storage rots in the 1980s

Methods

1980-81 storage season

In a survey of rots in pear (cv. Conference) undertaken in conjunction with the AFRC Institute of Horticultural Research, East Malling, ten commercial stores were visited on farms in Kent and Sussex and at co-operatives in Kent and Essex in 1981. These stores and packhouses were visited weekly when fruits were being graded. Rejected fruits with fungal rots were collected and the rots identified visually. Isolates of *M. fructigena* and *B. cinerea* were tested for resistance to benomyl and vinclozolin (Ronilan).

1982-85 storage seasons

A fruit co-operative serving about 100 farms, mostly in Kent, was visited weekly during the storage season and observations made on fungal rots of apple (cvs. Cox's Orange Pippin, Bramley's Seedling), and pear (cv. Conference) during grading. One hundred rejected rotted fruit of each cultivar were examined on each occasion and the rots identified visually. *M. fructigena*, *N. galligena* and *Gloeosporium* spp. were tested for resistance to benomyl and vinclozolin.

1987-88 storage season

Sixteen commercial stores and three fruit co-operatives in Kent were visited between January and April, 1988. Observations on fungal rots were made as in 1982-85. Isolates of *B. cinerea*, *M. fructigena*, *N. galligena*, *Gloeosporium* spp. and *P. expansum* were tested for resistance to benomyl and vinclozolin.

Table 2. Fruit storage conditions

Fruit	Cultivar	Storage conditions
Pear	Conference	Air storage at -1.0 to -0.5°C
Apple	Cox	Controlled atmosphere store with CO_2 scrubber (% CO_2, 2% O_2 at 3.5 to 4°C)
Apple	Bramley	Controlled atmosphere (CA) store (8-10% CO_2 at 4 to 4.5°C)

Tests for fungicide resistance

Agar was amended with benomyl (Benlate) or vinclozolin (Ronilan), both at 2 ppm and 20 ppm. Inoculated plates were assessed after 2 or 7 days, depending on the fungus. Isolates showing no colony growth after 2 or 7 days were regarded as sensitive, whereas those showing normal growth were considered resistant.

Pre-storage treatments

Most fruit in long-term storage (conditions in Table 2) had received a post-harvest fungicide treatment (Table 3). For apples this was usually a dip/drench in a benzimidazole compound; for pears in the early 1980s it was a benzimidazole fungicide, but by the mid to late 1980s most pears were dipped/drenched in vinclozolin. Bramley apples intended for long-term storage were also dipped/drenched in anti-scald chemicals, usually diphenylamine (DPA) or ethoxyquin: in the early 1980s fungicide was not included.

Results of the survey of fungal rots

Most fruit had received a post-harvest chemical treatment (Table 3) and so losses due to fungal rotting were low; only about 2% or less in most crops in most years.

Table 3. Post-harvest chemical treatments

Crop	Cultivar	Target Fungus	Chemical Treatment
Pear	Conference	*Botrytis cinerea*	benzimidazole fungicides
		Monilinia fructigena	(e.g. Benlate, Bavistan, Mildothane)
		or vinclozolin (Ronilan)	
Apple	Cox	*Monilinia fructigena*	
		Gloeosporium	benzimidazole fungicides
		Nectria galligena	(e.g. Benlate, Bavistan, Mildothane)
		Monilinia fructigena	
		Gloeosporium	metalaxyl + carbendazim
		Nectria galligena	(Ridomil MBC 60 wp)
		Phytophthora syringae	
Apple	Bramley	As for Cox but with the addition of DPA or ethoxyquin	

Table 4. Mean percentage losses of fruit numbers due to fungal rots in apple cv. Cox's Orange Pippin

Fungal Rot	1982-83	1983-84	1984-85	1987-88
Botrytis cinerea	0.1	0.5	1.1	0.6
Monilinia fructigena	0.2	0.4	0.1	0.6
Gloeosporium spp.	0.1			0.6
Nectria galligena	0.2	0.2	0.2	4.2
Phytophthora syringae	0.6	0.5	0.4	0.1
Mucor	0.1	0.1	0.4	0.0
Other rots - including *Penicillium, Fusarium, Diaporthe*	0.2	0.1	0.2	0.2
Total losses due to rots (%)	1.5	1.8	2.4	6.3
Farms sampled	14	15	18	21

(1) Apple cv. Cox's Orange Pippin

Brown rot (*M. fructigena*) caused a low incidence of rotting in most seasons (Table 4). *Phytophthora syringae* was responsible for nearly half the rotting in 1982-83. In 1987-88, *Nectria* was the main cause of rots, resulting in losses of 4% on average but 50% in one fruit store. The majority of *Nectria* rots on Cox were at the stalk end (Table 5). A small lesion at the stalk end is easily missed during grading although internally the rot may be extensive. Rots due to *B. cinerea*, *P. expansum* and *Mucor* also increased over the survey period with *B. cinerea* accounting for nearly half the losses in 1984-85. *Gloeosporium* spp. were present at trace levels in most years but increased in 1987-88.

(2) Apple cv. Bramley's Seedling

Bramley losses due to rotting were generally low except in 1984-85 (Table 6). In most years, brown rot (*M. fructigena*) was the main problem with *P. syringae* also causing losses, particularly in 1984-85. September 1984 was notably

Table 5. Sites of *Nectria galligena* rot on fruits of apple cv. Cox's Orange Pippin.

Number of fruit with *Nectria*	(% number of fruit) Stalk end	Cheek	Eye (calyx) end
896	55	28	16

Table 6. Mean percentage losses of fruit numbers due to fungal rots in apple cv. Bramley's Seedling

Fungal Rot	1982-83	1983-84	1984-85	1987-88
Botrytis cinerea	0.1	0.2	0.2	0.1
Monilinia fructigena	1.0	0.5	0.2	0.3
Nectria galligena	0.1	0.1	0.1	0.3
Phytophthora syringae	0.2	0.2	1.6	0.1
Mucor		0.1	1.4	0.1
Penicillium expansum	0.1	0.1	0.1	0.1
Other rots - *Fusarium, Diaporthe*	0.1	-	-	0.0
Total losses due to rots (%)	1.6	1.2	3.7	1.0
Farms sampled	3	5	11	11

Table 7. Mean percentage losses of fruit numbers due to fungal rots in pear cv. Conference

Fungal Rot	1980-81	1982-83	1983-84	1984-85	1987-88
Botrytis cinerea	1.0	2.5	1.1	1.8	0.8
Monilinia fructigena	0.4	0.4	0.3	0.2	0.5
Nectria galligena	-	<0.01	-	0.1	0.3
Phytophthora syringae	-	<0.01	-	0.1	0.1
Mucor	0.1	0.2	0.3	0.6	0.1
Other rots (including *Penicillium, Alternaria, Fusarium, Gloeosporium*)	0.1	0.1	0.1	0.3	0.0
Unidentified stalk-end rot	-	-	-	-	0.2
Total losses due to rots (%)	1.6	3.2	1.8	3.1	2.0
Farms sampled	60	12	29	31	12

Table 8. Fraction of isolates with fungicide resistance in storage-rot fungi of apple

Fungus	Cultivar	Fungicide	1982-83	1983-84	1984-85	1987-88
B. cinerea	Cox	benomyl	9/12	9/14	7/10	31/41
B. cinerea	Cox	vinclozolin	-	-	-	4/41
M. fructigena	Cox	benomyl	-	0/7	-	0/8
M. fructigena	Bramley	benomyl	-	0/3	0/12	0/10
P. expansum	Cox	benomyl	-	-	-	15/15
Gloeosporium	Cox	benomyl	-	-	-	0/8
N. galligena	Cox	benomyl	0/7	0/9	0/5	0/151
N. galligena	Bramley	benomyl	-	0/1	0/1	0/14

Table 9. Fraction of isolates with fungicide resistance in storage-rot fungi of pear cv. Conference

Fungus	Fungicide	1980/81	1982/83	1983/84	1984/85	1987/88
B. cinerea	benomyl	177/196	10/11	18/27	14/22	40/71
B. cinerea	benomyl (a)	4/29				
B. cinerea	vinclozolin	-	-	-	-	10/71
M. fructigena	benomyl	0/30	0/3	0/11	0/5	0/20
M. fructigena	vinclozolin	-	-	-	-	0/20
P. expansum	benomyl	-	-	-	-	15/15
N. galligena	benomyl	-	-	-	-	0/12

[(a) Drenched before storage with captan, *not* a benzimidazole.]

wet (Table 11) and in that storage season (1984-85) rotting due to *Mucor pyriformis* became a new problem. *Mucor* rots seemed to originate in the fruit core and were soft; the affected fruits disintegrated during grading, fouling the grader and contaminating other fruit. As with Cox, the incidence of *Nectria* rots was highest in 1987-88, but losses due to this rot were not insignificant.

(3) Pear cv. Conference

In all years the pattern of rotting was similar, with *B. cinerea* and *M. fructigena* accounting for most losses (Table 7). Losses from *Botrytis* were highest in 1982-83 and 1984-85. *Mucor*, although causing only a low incidence of rots in most seasons can be a nuisance when grading: affected pears disintegrate, foul the grader and the stone cells (scleroids) scratch
intact pears. Other rots, such as *P. syringae*, *P. expansum* and *Gloeosporium* spp. were also present at low levels. In 1987-88 a stalk-end rot was common: the causal fungus has not been identified.

Results of fungicide resistance tests

All tested isolates of *P. expansum* were resistant to benomyl. No resistance to benomyl was detected in *Gloeosporium* and no isolates of *M. fructigena* were resistant to either benomyl or vinclozolin (Tables 8 and 9).

Of the tested isolates of *B. cinerea* from apple, about 70% were resistant to benomyl and there was little change in this percentage over the period of the survey. In contrast, about 90% of tested *B. cinerea* isolates from pear were resistant to benomyl in pears in 1980-81 and 1982-83, whereas the level of resistance had declined to just over 50% in 1987-88.

In 1980-81, captan has been used as the post-harvest fungicide on pear; most isolates of *B. cinerea* tested that season were sensitive to benomyl (Table 9).

A few isolates of *B. cinerea* were resistant to vinclozolin.

In 1987-88, 177 isolates of *N. galligena* were tested. Variation in sensitivity was detected between sources (Table 10) with about 25 and 75% of isolates overall being sensitive to 2 and 20 ppm benomyl, respectively.

Table 10. Sensitivity of *Nectria galligena* isolates to benomyl.

Crop	Cultivar	Isolates tested (No.)	Sensitive to benomyl at: 2ppm (%)	20ppm (%)
Apple	Cox's Orange Pippin	151	35	65
Apple	Bramley's Seedling	14	7	93
Pear	Conference	12	33	67

Discussion

This survey of storage rots in Cox apples was geographically more limited than the 1960s survey (see Introduction), but is probably representative of most apple stores. *Gloeosporium* was the most important cause of rotting in Cox in the 1960s but changes in cultural practices and the introduction of benzimidazole fungicides have now reduced *Gloeosporium* to trace levels in most years: this rot is not often seen except where fruit nutrition is faulty. Brown rot (*M. fructigena*) is present in stored Cox in most seasons but is adequately controlled by post-harvest fungicide treatments. *P. syringae* is particularly serious when conditions during harvest (September) are wet. September 1982 was notably wet, particularly in central Kent (East Malling, Table 11), and in the 1982-83 storage season *P. syringae* caused nearly half the rotting in Cox. With the introduction of herbicide strips in orchards, *Phytophthora* emerged as a problem in stored fruit in the 1970s (2). The use of metaxyl-plus-carbendazim (as Ridomil MBC) as the post-harvest treatment when harvest conditions are wet adequately controls this rot.

Table 11. Rainfall (mm) in Kent, South-East England

Manston, East Kent						
Year	**July**		**August**		**September**	
	mm	**% ***	**mm**	**%**	**mm**	**%**
1982	29	(62)	33	(63)	29	(46)
1983	21	(45)	15	(28)	25	(40)
1984	11	(23)	32	(61)	62	(98)
1985	44	(86)	46	(88)	7	(11)
1987	109	(232)	91	(175)	15	(24)
East Malling, Central Kent						
Year	**July**		**August**		**September**	
1982	27	(50)	40	(70)	61	(101)
1983	11	(21)	15	(26)	35	(58)
1984	30	(56)	16	(29)	59	(98)
1985	46	(86)	77	(136)	9	(15)
1987	91	(170)	55	(97)	30	(49)

(* percentage of the long-term average 1951-1980)

In Cox, secondary rots caused by *B. cinerea*, *P. expansum* and *Mucor* have also increased in importance since the 1960s. This may be related to longer storage, although tests show that most *Botrytis* and all *Penicillium* isolates are resistant to the benzimidazole fungicides. The fungicides currently available do not control *Mucor*.

In all pome fruit cultivars, but particularly apple cv. Cox, *N. galligena* has increased as a storage problem. A survey was not conducted in 1985-86, but *Nectria* was a problem in stored Cox that season. In 1987-88, losses due to *Nectria* fruit rot were high. The increase in *Nectria* rots is associated with the increased incidence of *Nectria* canker in orchards. Reasons for the increase in canker include more intensive cultivation methods, susceptible cultivars, inadequate fungicides and possibly the general reduction in spray volume. Perhaps the most significant factor has been, however, a succession of wet seasons, particularly in autumn when heavy rainfall has coincided with leaf-fall and therefore favoured the infection of leaf scars.

Infection of fruit is favoured by wet summers, and *Nectria* eye rot can be seen in orchards from July onwards. Evidence indicates that August is the main month for *Nectria* infection of fruit in England (3). Heavy rainfall in August will, therefore, favour the disease. In 1985 and 1987, August rainfall was unusually high, especially in East Kent (Table 11). Fruit infections in August do not usually show in store until after December. Post-harvest dips or drenches with benzimidazole fungicides are ineffective: this is not due to resistance (Table 8), but may be because spores in the stalk cavity are not accessible to the fungicide, or because the fungus has become established (though not visible) at the time of treatment. Orchard trials (unpublished) have demonstrated that benzimidazole sprays in July and August reduce storage *Nectria* to negligible levels. Although a post-harvest treatment with a benzimidazole fungicide will not eradicate the fungus from infected fruit, secondary spread in stores is prevented.

Control of *Nectria* storage rot largely relies on controlling *Nectria* canker in the orchard, rather than on post-harvest treatments. Current recommendations for the control of *Nectria* fruit rot harvested from badly- cankered orchards are either to apply a programme of benzimidazole fungicide sprays in the orchard in August or to market the fruit early, preferably before Christmas.

In Bramley, storage rots were low except in 1984-85, when *P. syringae* and *M. pyriformis* caused significant losses. *Mucor* caused rotting in most seasons: the reasons for its sudden increase in 1984-85 were associated with the wet harvest in 1984, the tendency for Bramley fruits to have an open calyx, and the change of the DPA formulation which resulted in damage to the fruit core through the open calyx (4). No fungicides control *Mucor* but this problem can be solved by attention to hygiene: avoiding contamination of the drench tank with muddy bins, and frequently changing the drenching solution to prevent the accumulation of mud and debris.

The variation in sensitivity to benomyl (Table 10) of *N. galligena* isolates is interesting. There is also considerable variation in the morphology of cultures which does not appear to be related to the sources of the isolates. In practice, there is no evidence of failure of benzimidazole fungicides to control *Nectria*. In other studies (unpublished), where orchards have been sprayed intensively with carbendizim (Bavistin) over four seasons (a total of 48 sprays) to reduce canker, extensive testing of isolates of *N. galligena* has not revealed resistance.

The difference in sensitivity to benzimidazole fungicides of *B. cinerea* isolates from apple and pear may reflect the fungicide used as the post- harvest treatment in these crops. In pears, a benzimidazole fungicide was initially included in the post-harvest drench, but most pears now receive vinclozolin (Ronilan) for the control of *Botrytis* and *Monilinia*. In apples, a benzimidazole fungicide is generally included in the drench tank for the control of *Gloeosporium*,against which vinclozolin is ineffective. The use of benzimidazole fungicides in orchards is not generally advised in England and therefore the level of resistance of *B. cinerea* to benomyl suggests that most of the *Botrytis* infecting apple and pear originates in the packhouses and stores.

Tests for sensitivity of *P. syringae* to metalaxyl were not included in the studies described here, but should be included in future surveys.

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Control and monitoring of apple storage diseases in Switzerland

Elisabeth Bosshard, W. Siegfried, Maja Bodmer and Beatrix Buchmann

Eidg. Forschungsanstalt für Obst-, Wein- und Gartenbau, CH-8820 Wädenswil

Abstract

Captan is essential for the protection of apples from attack by fungi causing storage diseases under the climatic conditions prevailing in Switzerland. The best results were obtained when captan was mixed with SBI-fungicides, and used against scab (*Venturia inaequalis*) and powdery mildew (*Podosphaera leucotricha*) and as an orchard treatment to prevent storage rots. The dates and the number of captan treatments in August and September were important for the prevention of storage diseases. Storage conditions influenced the number of fungi inducing storage rot. Monitoring storage diseases at the latent stage proved impossible for predicting *Gloeosporium album*, the most important fungus causing storage rots in Switzerland.

Key words: Disease control, storage rots, chemical control, fungal rots.

Introduction

Apples produced in experimental orchards where the efficacy of new fungicides is tested are inspected after storage in order to evaluate the effect of the different spray schedules on fungi causing storage diseases.

In Switzerland, sterol biosynthesis inhibiting (SBI) fungicides are registered for use only in mixture with captan. Experiments were conducted to investigate if the number of captan treatments could be reduced, if treatments against scab (*Venturia inaequalis*) and powdery mildew (*Podosphaera leucotricha*) with SBI fungicides alone, or in mixture with captan could influence the development of storage diseases, and how storage diseases develop in controlled atmosphere (CA) storage.

An attempt was also made to detect fungi capable of causing storage rot disease by monitoring latent infections present at harvest.

Tables 1-5. Influence of different spraying schedules on scab and storage diseases.

Tab. 1: Experimental orchard Grüntal, Wädenswil; Variety: Golden Delicious planted 1970
Storage time: 16.10.1987 - 29. 2. 1988; storage conditions: + 2 ° C, 92 % ±2 r.h.

treatment	scab on leave Aug-87		scab on fruit Sep-87		water loss		marketable fruit		Gloeosporium spp.		storage scab		various rots	
	%	SD	%	SD	%	SD	%	SD	%	SD	%	SD	%	SD
untreated	84.8	±14.5	96.0	±2.	5.9	±0.1	1.0	±1.3	1.8	±2.3	95.3	±4.7	2.1	±1.9
7 x Flusilazol	0.6	± 1.1	0		3.9	±0.2	71.6	±16.7	18.1	±18.5	8.5	±2.7	1.8	±0.9
7 x Flusilazol 3 x Captan	0.6	± 1.1	0		3.9	±2.1	89.5	±5.3	7.0	±4.9	2.1	±1.6	1.2	±1.9
7 x Flusilazol+Captan	0.8	± 3.6	0		5.6	±0.9	90.0	±7.1	4.3	±2.3	5.0	±5.1	1.2	±1.5
7 x Flusilazol+Captan 3 x Captan	0.8	± 3.6	0		5.4	±0.8	95.8	±3.1	1.1	±0.9	1.8	±1.6	1.3	±1.2

Flusilazol (20 % A.I., WP), 0.0125 %; against scab and powdery mildew (April-July)
Flusilazol + Captan (20 % A.I.,WP), 0.0125 % and (83 % A.I.,WP), 0.075 %; against scab and powdery mildew (April-July)
Captan (83 % A.I.,WP), 0.15 %; against storage diseases (August + September)

Tab. 2: Experimental orchard Srickhof, Lindau; Variety: Golden Delicious planted 1974
Storage time: 16.10.1987 - 29. 2. 1988; storage conditions: + 2 ° C, 92 % ±2 r.h.

treatment	scab on leave Aug-87		scab on fruit Sep-87		water loss		marketable fruit		Gloeosporium spp.		storage scab		various rots	
	%	SD	%	SD	%	SD	%	SD	%	SD	%	SD	%	SD
untreated	94.0	±4.7	100				0		0		100		0	
9 x Flusilazol 2 x Captan	0		0		2.9	±0.2	81.5	±4.5	18.2	±4.2	0		0 2	±0 3
9 x Myclobutanil 2 x Captan	0.1	±0.4	0		2.6	±0.1	82.9	±3.9	15.8	±2.3	0.3	±0 5	0 7	±1 3
9 x Captan-Penconazol 2 x Captan	0.3	±0.9	0		2.9	±0.2	91.4	±4.3	6.1	±4.6	0.4	±0.6	0	
6 x Captan-Penconazol 3 x Zineb-Captan 2 x Captan	5.2	±8.9	0.3	±0.8	2.7	±0.5	92.3	±3.4	4.7	±1.4	2.5	±2.2	0	

Flusilazol (20 % A.I., WP), 0.0125 %; against scab and powdery mildew (April-July)
Myclobutanil (6 % A.I., WP), 0.1 %; against scab and powdery mildew (April-July)
Captan-Penconazol (47.5% +2.5% A.I.,WP), 0.1 %; against scab and powdery mildew (April - July)
Zineb-Captan (37% + 25 % A.I., WP), 0.2 %; against scab (3 treatments after bloom to prevent fruit russeting)
Captan (83 % A.I.,WP), 0.15 %; against storage diseases (August + September)

Tab. 3: Experimental orchard Strickhof, Lindau; Variety: Golden Delicious planted in 1974
Storage time: 21.10.1987 - 26. 2. 1988 ; Stoage conditions: +2 ° C, 92 % r.h.

treatment	scab on leave Aug-87		scab on fruit Sep-87		water loss		marketable fruit		Gloeosporium spp.		storage scab		various rots	
	%	SD	%	SD	%	SD	%	SD	%	SD	%	SD	%	SD
9 x Captan-Penconazol	6.4	±6.1	0		4.7	±0.3	10.0	±13.8	3.5	±3.1	85.5	±14.0	1.1	±0.4
9 x Captan-Penconazol 3 x Flutriafol 2)	6.4	±6.1	0		3.8	±0.5	84.9	±6.4	0.5	±0.6	7.1	±7.6	7.4	±9.2
9 x Captan-Penconazol 3 x Dichlofluanid 2)	6.4	±6.1	0		3.8	±0.5	91.4	±5.7	0.7	±0.5	7.8	±6.1	0	
9 x Captan-Penconazol 3 x Fenpropimorph 2)	6.4	±6.1	0		4.3	±0.5	93.4	±2.3	4.0	±0.6	0		2.7	±2.0
9 x Captan-Penconazol 3 x Folpet 2)	6.4	±6.1	0		3.2	±0.6	94.8	±5.9	0.9	±0.4	4.1	±5.8	0	

Captan-Penconazol (47.5 %+2.5 % WP), 0.1 %; against scab and powdery mildew (April - July)
2)= storage treatements (August and September)
Flutriafol (12.1 % A.i., SC), 0.006 %; Dichlofluanid (50 % A.I.,WP), 0.15 %
Fenpropimorph (79 % A.I., EC), 0.15 %; Folpet(80 % A.I., WP), 0.125 %

Tab. 4: Experimental orchard Qu 34, Wädenswil; Variety: Golden Delicious planted 1981

treatment	storage conditions	water loss		marketable fruit		Gloeosporium album		Gloeosporium fructigenum		storage scab		various rots	
		%	SD	%	SD	%	SD	%	SD	%	SD	%	SD
7 x Captan-Pyrifenox	natural cellar 4 - 12 ° C	7.9	±0.6	84.3	±5.4	4.1	±2.4	1.8	±1.8	5.4	±1.6	0	
7 x Captan-Pyrifenox 3 x Captan	75 - 85 % r.h. Okt.16. - Jan. 26.	7.0	±1.0	88.3	±2.1	0		8.5	±4.3	0			
7 x Captan-Pyrifenox	cold storage +2 ° C	3.2	±0.8	93.7	±4.5	0.4	±0.3	1.3	±0.9	1.0	±0.1	0	
7 x Captan-Pyrifenox 3 x Captan	92 % ±2 r.h. Okt.16.-Febr.29.	2.5	±1.8	94.4	±1.7	0.2	±0.1	1.6	±1.5	0.7	±1.3	0.1	
7 x Captan-Pyrifenox	CA-storage, +2°C 4%CO2, 2%O2	2.7	±2.7	91.1	±7.9	0.6	±0.6	1.0	±0.7	4.5	±2.7	2.8	±2.4
7 x Captan-Pyrifenox 3 x Captan	92 %±2 r.h. Okt.16.-July 4.	3.5	±2.3	92.7	±1.2	0.4	±0.5	3.4	±3.3	1.2	±1.2	2.3	±1.7

Captan-Pyrifenox (60% +5% A.I.,WP), 0.1 %; against scab and powdery mildew (April - July)
Captan (83 % A.I.,WP), 0.15 %; against storage diseases (August+September)

Tab. 5: Experimental orchard Qu 34, Wädenswil; Variety: Golden Delicious planted 1975
Storage time: 16.10.1987 - 29.2.1988; storage conditions: +2 ° C, 92 % ±2 r.h.

treatment	water loss		marketable fruit		Gloeosporium album		Gloeosporium fructigenum		storage scab		various rots	
	%	SD	%	SD	%	SD	%	SD	%	SD	%	SD
7 x Captan-Pyrifenox	4.3	±0.6	77.1	±18.8	8.4	±14.3	0		13.5	±6.5	0	
7 x Captan-Pyrifenox 1 x Captan 1.only	4.1	±0.4	86.2	±5.2	4.8	±2.0	0		8.4	±4.1	0.15	
7 x Captan-Pyrifenox 2 x Captan 1. and 2.	3.9	±0.3	92.3	±4.8	3.0	±4.5	0		3.5	±2.0	0.2	
7 x Captan-Pyrifenox 3 x Captan	3.9	±0.2	93.8	±5.2	3.8	±3.9	0		0.8	±1.6	0 3	

Captan-Pyrifenox (60% +5% A.I.,WP), 0.1 %; against scab and powdery mildew (April - July)
Captan (83 % A.I.,WP), 0.15 %; against storage diseases (August+September)

General information

SBI fungicides tested in 1987 as sprays in three experimental orchards gave excellent control of scab on leaves and fruit, but varied in their effects on storage diseases such as scab and *Gloeosporium* spp. (Tables 1-3). Records of the number of rotten fruit and the types of rot at the end of storage showed that captan significantly reduced the percentage of diseased apples when used in combination with SBI fungicides to enhance protection against scab from April until the end of July, and/or when used in August and September for storage disease control.

Flutriafol and fenpropimorph were also tested as protectants against storage diseases of apples: both were phytotoxic and caused severe damage to fruit. Compared with other European countries (5, 9), losses of apples due to storage rot are less in Switzerland in recent years. This is due to relatively dry weather in Autumn and to orchard treatments with captan, folpet or dichlofluanid. Benzimidazole compounds have not been used in Switzerland for storage rot control in the field nor as postharvest dips, and no shift in the spectrum of fungal pathogens has been observed (2, 4, 5, 9).

Experiments to show the influence of captan treatments and storage conditions on storage diseases were performed in Autumn 1987 in the experimental orchard Qu 34 on cv. Golden Delicious trees planted in 1975 and 1981. Seven treatments were applied from April until the end of July with the triazole fungicide pyrifenox in combination with captan, sprays being timed according to scab infection periods .

Plots were left untreated, or were sprayed between 1 and 3 times with captan in August and September (Fig.1). Apples were harvested on 15 October and were stored in a cellar, in a cold store or in a controlled atmosphere (CA) store.

As can be seen in Tables 4 and 5, the fruits were attacked by the same range of fungi, independent of fungicide treatments or storage conditions. Fruit not treated against storage diseases had more storage scab and *Gloeosporium* rot than captan-treated apples, the percentage of marketable fruit increasing with the number of spray treatments.

Apples grown on the older trees were more susceptible to *Gloeosporium album* whereas *G. fructigenum* developed only on fruit of the younger trees (2). Captan treatments did not prevent the development of rots caused by *G. fructigenum*.

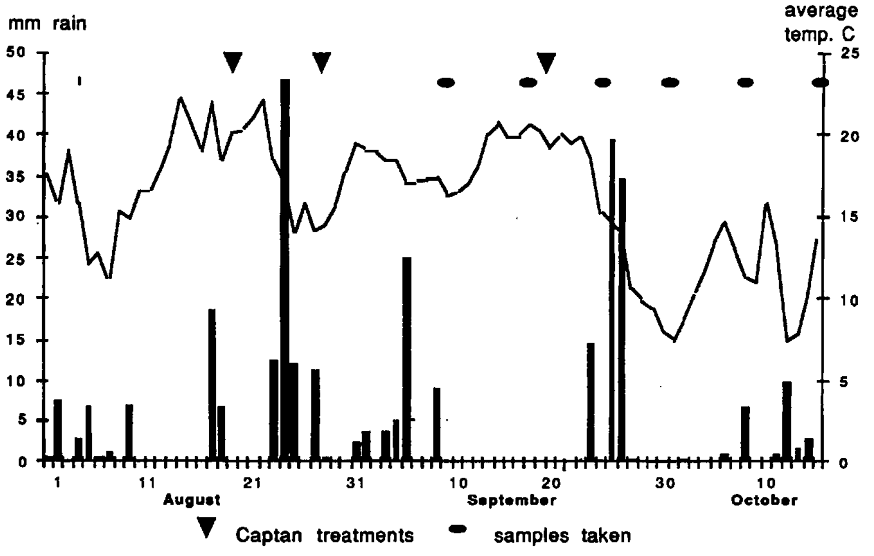


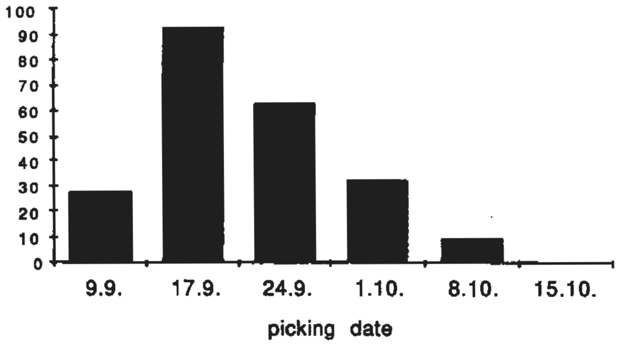
Fig. 1. Climatic conditions Wädenswil Qu 34 1987

Monitoring

Apples on the trees planted in 1981 which had not been sprayed with captan against storage diseases were picked at weekly intervals from the beginning of September until mid-October 1987 (Fig.1). The fruits were stored in perforated plastic-bags at room temperature to induce the early development of storage rots. The condition of the fruits was assessed each week from 26 October until the end of 1987, when only very few apples were still healthy.

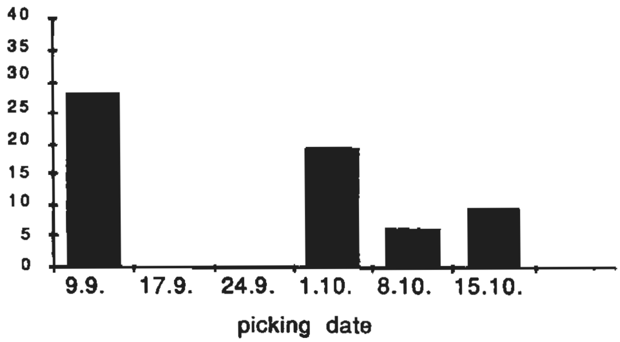
Apples picked in September were severely attacked by *Trichothecium roseum* (Fig.2), a fungus which had not previously been known to cause storage rot on apples in Switzerland. Apples picked in October were almost free of this disease in storage. Fruit picked soon after rainy periods developed sooty blotch caused by *Gloeodes pomigena* (Fig.3) With increased ripening the number of apples attacked by *Gloeosporium fructigenum* increased (Fig.4); rots caused by this fungus were also detected on fruits after storage (Table 4).

Attempts to isolate *Gloeosporium album*, a major cause of storage losses in Switzerland (7), from discoloured lenticels present in Autumn failed, in spite of the fact that the fungus was present on the fruits and developed in storage. A valid forecast of outbreaks of fungal diseases in storage is therefore not possible, as was by Urban in 1982 (8).



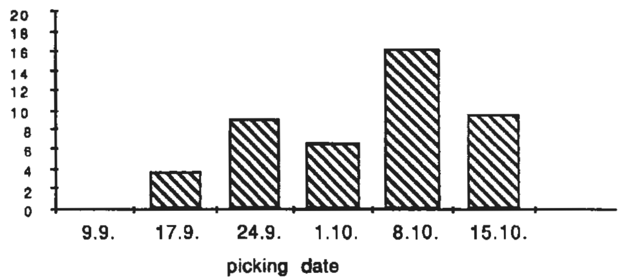
Waedenswil Qu 34: Golden Delicious planted 1981
Treatments: 7xcaptan-pyrifenox (April-July)

Fig. 2. Apples attacked (in %) by *Trichothecium roseum*, October 26, 1987.



Waedenswil Qu 34: Golden Delicious planted 1981
Treatments: 7xcaptan-pyrifenox (April-July)

Fig. 3. Apples attacked (in %) by sooty blotch (*Gloeodes pomigena*).



Wädenswil Qu 34: Golden Delicious planted 1981
Treatments: 7xcaptan-pyrifenox (April-July)

Fig. 4. Apples attacked (in %) by *Gloeosporium fructigenum*, December 3, 1987.

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The integrated use of benzimidazole fungicides to control *Gloeosporium* fruit rot of apple

W. Kennel

University Hohenheim, Research Station Bavendorf, D-7980 Ravensburg 1

Abstract

The advantages and disadvantages of benzimidazole fungicides (BZF) for the control of *Gloeosporium* (*Pezicula alba, P. malicorticis*) fruit rot of apple are described. The excellent effect of BZF against *Gloeosporium* fruit rot is demonstrated by means of experimental results. Even when BZF were applied outside the growing season these compounds still gave remarkably good results against fruit rot. This is explained by the fact that BZF reduce the sources of inoculum overwintering on woody parts of apple trees. BZF have a negative effect on the earthworm *Lumbricus terrestris*, predominant in apple orchards. Because of the low population of the earthworms, leaf litter remains on the ground for a long time and harmful organisms, such as *Venturia inaequalis*, living in the litter are encouraged in BZF-treated orchards.

Key words: disease control, fungicide programmes, orchards, chemical control, *Venturia inaequalis*, IPM.

Introduction

The chemical control of *Gloeosporium* fruit rot of apple has for many years been based on the benzimidazole fungicides (BZF). The use of these compounds in apple orchards provides considerable advantages as well as disadvantages which should be taken into consideration within the framework of the integrated control of apple diseases. In some European countries the use of BZF in orchards is discouraged in favour of their use as postharvest dip or drench treatments: but

Table 1. Number (out of 5 each) and spatial distribution of leaf- and fruit scars infected by *Pezicula alba* on the cultivar Golden Delicious in a 5-year-old orchard[1)]

Row no.	Type of scar[2)]	Tree no. 1	2	3	4	5	6	7	8	9	10
5	LS	4	3	5	4	3	3	1	4	5	2
	FS	5	5	4	3	1	3	3	4	4	1
17	LS	1	4	4	4	4	2	4	3	5	3
	FS	5	2	5	4	1	3	4	5	5	1
29	LS	4	4	4	3	4	4	5	4	4	5
	FS	4	4	4	1	3	5	0	4	5	5
41	LS	1	4	0	3	5	2	4	4	4	
	FS	5	3	2	5	5	0	5	2	5	3

1) Sprayed only with sulfur
2) LS = leaf scar; FS = fruit scar

such treatments are not permitted in certain countries, where orchard sprays of BFZ are therefore used.

Advantages of the orchard use of BZF against *Gloeosporium*

The advantages are:

1) Compared to conventional fungicides, only a few treatments with BZF are necessary to achieve commercial control.

2) Control can be achieved outside the growing season.

3) Fruit rots other than *Gloeosporium* are controlled by BZF.

A consequence of points 1 and 2 is a lower contamination of the environment with chemicals and fewer problems with fungicide residues on harvested fruit. The effect mentioned under point 3 is well known, as is the fact that BZF have led to resistance problems.

This paper will concentrate on observations concerning the first two points. It is well known that fewer treatments with BZF provide the same effect (or even a better one) as larger numbers of treatments with conventional compounds. According to personal experience, one treatment can, under certain conditions, adequately control *Gloeosporium*. This powerful action is due to:

- direct protection of the fruit
- reduction of sources of inoculum.

This "double action" can be seen in Fig. 1 (from 3, altered), which shows that with benomyl, treatment of the source of infection (shoots) alone was sufficient to reduce the incidence of *Gloeosporium* fruit rot to 5 %, even with a severe inoculum potential (see control plot). With captan this degree of control could not be reached even when both shoots and fruit were treated. Fig. 1 shows the effect on the attack of fruit of reducing the inoculum sources. On the other hand, the treatment of fruit (without treating the shoots) provided total control.

The direct effect on inoculum sources is best shown by means of experiments on leaf- and fruit scars, which are probably the most important sources of *Gloeosporium* inoculum (1). The incidence of *Pezicula. alba* on leaf- and fruit scars in an apple orchard is demonstrated in Table 1 (from 3, altered). Although the surface colonies are macroscopically invisible, their importance lies in their strength as sources of inoculum. The high proportion of leaf- and fruit scars colonised by *P. alba* and the wide distribution of colonised scars in the orchard can be seen in Table 1. Though the number of samples was low, the fungus was found on each of the trees examined. Similar results were obtained with cultivars Golden Delicious, Cox's Orange Pippin and James Grieve. It must be stressed that in the surveyed orchard only sulfur was sprayed and this has no effect on *Pezicula.*

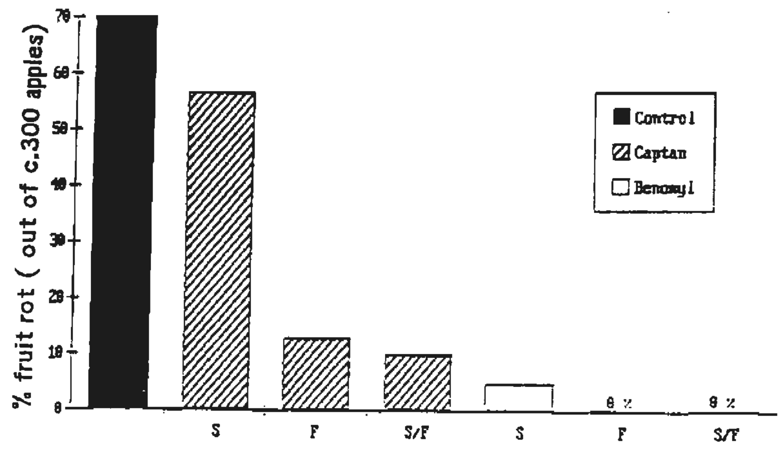

Fig. 1. Fruit rot on Golden Delicious apples following 5 sprays with captan (0.1 % a.i.) or benomyl (0.015 % a.i.) applied to shoots (S) - artificially inoculated with *Pezicula malicorticis* - fruit (F) or both shoots and fruit (SF).

Tables 2 and 3 show the outstanding effect of BZF on the colonisation of apple twig leaf scars artificially inoculated with *P. alba* and *P. malicorticis*. It can be seen that copper and captan failed to prevent infection, even though, among the protective fungicides, the latter chemical is the most effective against *Gloeosporium* rot.

The data in Tables 2 and 3 explain the success of 'winter sprays' with the BZF (Table 4). The reduction of the *Gloeosporium* attack could only have resulted from a reduction in the sources of inoculum overwintering on branches and shoots.

Table 2. Effect of fungicides on the colonisation of leaf scars by *P. alba* (cv Golden Delicious).

Treatment	Per cent a.i. in the spray	Infected leaf scars (%)[2]
No fungicides	None	100
Captan	0,175	82,5
Copper[1)]	0,225	97,5
Benomyl	0,015	7,5
Benomyl	0,025	2,5
Thiophanate-methyl	0,1	7,5

[1)] copper-oxychloride
[2)] 40 scars per treatment

Table 3. Effect of fungicides on the colonisation of leaf scars by *P. malicorticis* (cv Golden Delicious)

Treatment	Per cent a.i. in the spray	Infected leaf scars (%)[2)]
No fungicide	None	100
Captan	0,175	96
Copper[1)]	0,225	100
Benomyl	0,025	0

[1)] copper-oxychloride
[2)] 25 scars per treatment

Disadvantages of the orchard use of BZF against *Gloeosporium*

The disadvantages are:

1) Harmful effect on earthworms, especially *Lumbricus terrestris*.
2) Promotion of *Phytophthora sp.* and *Alternaria sp.*
3) Danger of resistant strains developing.
4) Because of the excellent control of *Gloeosporium*, research into alternative, nonpesticidal control methods is postponed.

With regard to these disadvantages this paper will be confined to one problem: the harm to earthworms. Fig. 2 shows this effect: the data are for 240 samples from apple orchards over the Federal Republic of Germany. After 1-2 treatments per year with BZF (within a regular spray schedule), the number of earthworms was considerably reduced. The species *L. terrestris* was affected most. This species is particularly interesting for fruit growing because it represents more than 60 % of the total earthworm population in orchards, and because it is the only species of those earthworms regularly occurring which can decompose litter on the surface of the soil (2, 4, 5).

Table 4. Incidence[1)] of *Gloeosporium* rot[2)] and Red lenticel disease (RLD) on fruit of Golden Delicious trees treated twice with benomyl (standard conc.) as "winter sprays"[3)]

Year	Treatment	*Gloeosporium* rot	Red lenticel disease
1976	benomyl	7,0	33,5
	Control	12,8	69,0
1977	benomyl	1,8	7,5
	Control	10,8	32,0
1978	benomyl	12,5	1,5
	Control	49,4	20,0

1) % out of 600 apples
2) Caused by *Pezicula alba*
3) In the growing season the trees (the control trees included) were sprayed with sulfur and metiram, non-effective against *Gloeosporium*.

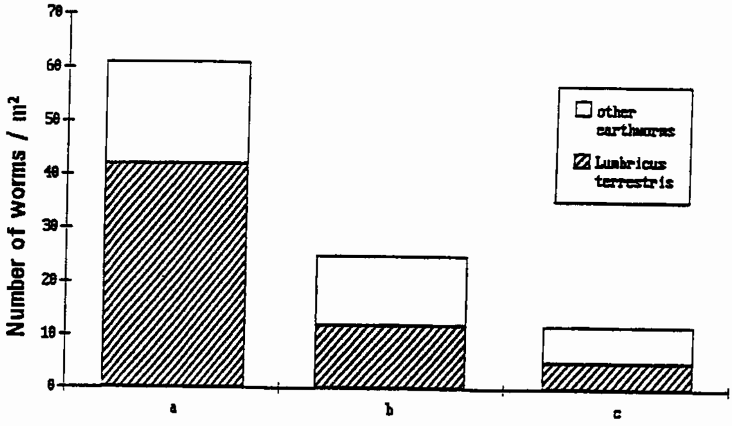

Fig. 2. Number of earthworms in apple orchards treated with BZF at different frequencies. a = orchards without BZF, b = orchards sprayed once or twice/year, c = orchards sprayed more than twice/year

Thus *L. terrestris* contributes to a considerable degree to the reduction of the pests and pathogenic fungi overwintering in the litter (leaves, prunings) of orchards. The activity of orchard worms when removing apple twigs and the damaging effect of BZF on this activity are represented in Fig. 3. The results in Fig. 3 were obtained in 10-litre plastic containers filled with garden compost, and

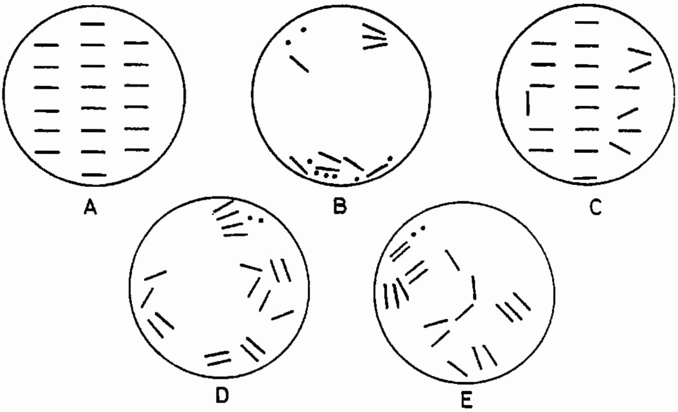

Fig. 3. The change in the original position of apple twig litter by the activity of earthworms following various fungicide treatments. The points indicate the sites where the twigs were completely or partly pulled into the soil.

with 10 adult earthworms in each. The containers were treated with fungicides as indicated.

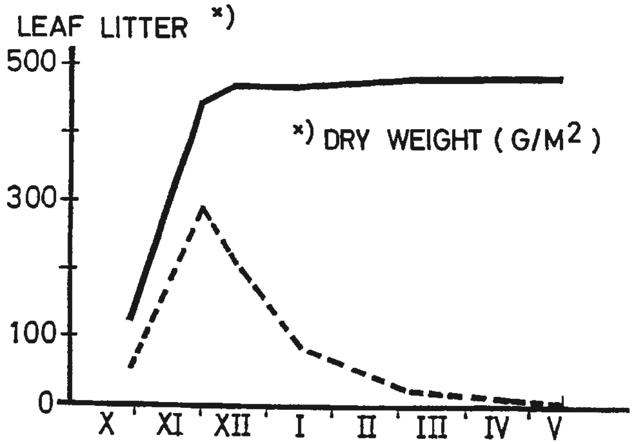

Fig. 4. The quantity of fallen apple leaves on plots with (---) and without (-) *Lumbricus terrestris.*

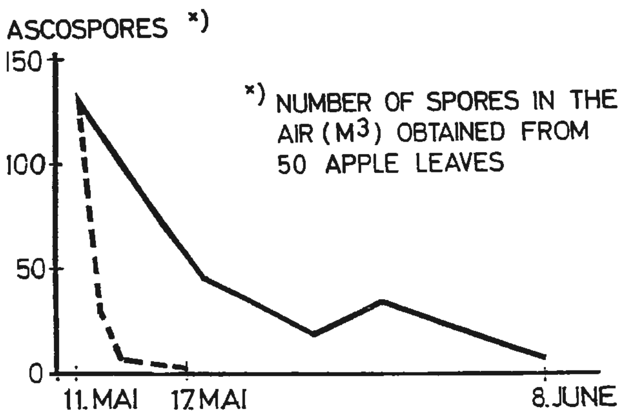

Fig. 5. Ascospore potential of *Venturia inaequalis* on plots with (---) and without (-) *L. terrestris.*

The effect of earthworm activity on leaf debris is shown in Fig. 4 from a study in an apple orchard which was partly treated with BZF (line "without *L. terrestris*") and partly with harmless compounds (broken line "with *L. terrestris*").

Fig. 5 shows the effect of the absence of orchard worms (because of sprays of BZF) on the inoculum potential of the scab fungus. This effect is not confined to *V. inaequalis*, but comprises all harmful organisms that live temporarily in fallen leaves and prunings.

Conclusions

The experiments reported here show that benzimidazole fungicides (BZF) are to be preferred for controlling *Gloeosporium* fruit rot of apple because of their outstanding effectiveness as orchard sprays as well as their unique effect on reducing sources of inoculum of both species of *Pezicula*. Because of the problems enumerated in the chapter on disadvantages, especially the harmful effect of BZF on the activity of earthworms, these fungicides should be used judiciously in orchards. They should only be applied when severe losses are expected. In such cases one or two treatments can be very effective. This recommendation assumes that the grower is prohibited from using postharvest BZF as dip or drench treatments before storing the crop.

Zusammenfassung

Es werden zunächst die verschiedenen Vor- und Nachteile aufgezählt, die mit dem Einsatz von Benzimidazol-Fungiziden (BZF) bei der Bekämpfung von *Gloeosporium*-Fruchtfäule (verursacht durch *Pezicula alba* und *P. malicorticis*) verbunden sind. Anschliessend wird aufgrund von Versuchsergebnissen die im Vergleich zu konventionellen Fungiziden ausserordentlich gute Wirkung der BZF gegen *Gloeosporium*-Fruchtfäule herausgestellt: Selbst bei Anwendung der BZF ausserhalb der Vegetationszeit (Winterspritzungen) zeigten diese Mittel noch eine bemerkenswert gute Wirkung gegen die genannte Fäule. Diese Wirkung ist darauf zurückzuführen, dass die BZF auch die auf den Zweigen von Apfelbäumen überwinternden Infektionsquellen der beiden *Pezicula*-Arten erheblich reduzieren. Bei den Nachteilen wird näher auf die negative Wirkung der BZF auf die in Apfelanlagen vorherrschende Regenwurmart *Lumbricus terrestris* und die damit verbundenen Folgen eingegangen. Infolge der Dezimierung der Regenwürmer bleibt die Bodenstreu unverhältnismässig lange liegen, und somit werden die darin lebenden Krankheitserreger und Schädlinge erhalten und gefördert. Im Rahmen von Massnahmen zur integrierten Bekämpfung sollten die angeführten Vor- und Nachteile der BZF sorgfältig erwogen werden.

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Session 6

Disease control

Chairperson: D.J. Butt

Did Swiss apple scab control strategies stand the extreme conditions of 1988?

W. Siegfried, E. Bosshard and H. Schüepp,

Eidg. Forschungsanstalt für Obst-, Wein-und Gartenbau, CH-8200 Wädenswil, Switzerland

Abstract

Intense scab (*Venturia inaequalis*) infection pressure in spring led to early primary infection when, on April 10, heavy rain washed conidia from wood-scab pustules on the twigs into the opening buds (stage C). The first fungicide treatment in the experimental orchard at Grüntal on April 15 did not prevent this attack and the disease slowly developed, despite a well-timed spray schedule using SBI fungicides.

By mid-June, up to 20% of the leaves were diseased; further spread of scab was prevented by applying two treatments of double-concentrated spray at an interval of 5 days.

Isolates of *Venturia inaequalis* were collected from treated and untreated plots and tested for their sensitivity to SBI-fungicides using three methods. In contrast to the results obtained in 1987 in an SBI-treated orchard with scab problems, all isolates tested in 1988 showed normal SBI sensitivity.

Key words apple disease, chemical control, fungicide tolerance, spray timing.

Introduction

Sterol biosynthesis inhibiting (SBI) fungicides have been applied in Swiss apple orchards in response to scab (*Venturia inaequalis*) infection periods since 1980. Climatic conditions in years 1986-1988 were dominated by long rainy periods which favoured scab epidemics and did not always allow post-infection treatment at the correct time. For some orchards where scab was not controlled sufficiently, climatic conditions and dates of treatments were analyzed and scab isolates were tested for SBI sensitivity in order to explain the reason for the poor efficacy.

Data are presented which were collected in an experimental orchard at Wädenswil Research Station, where the efficacy of SBI fungicides decreased from 95-100 % control in preceding years to only 60-70 % in 1988.

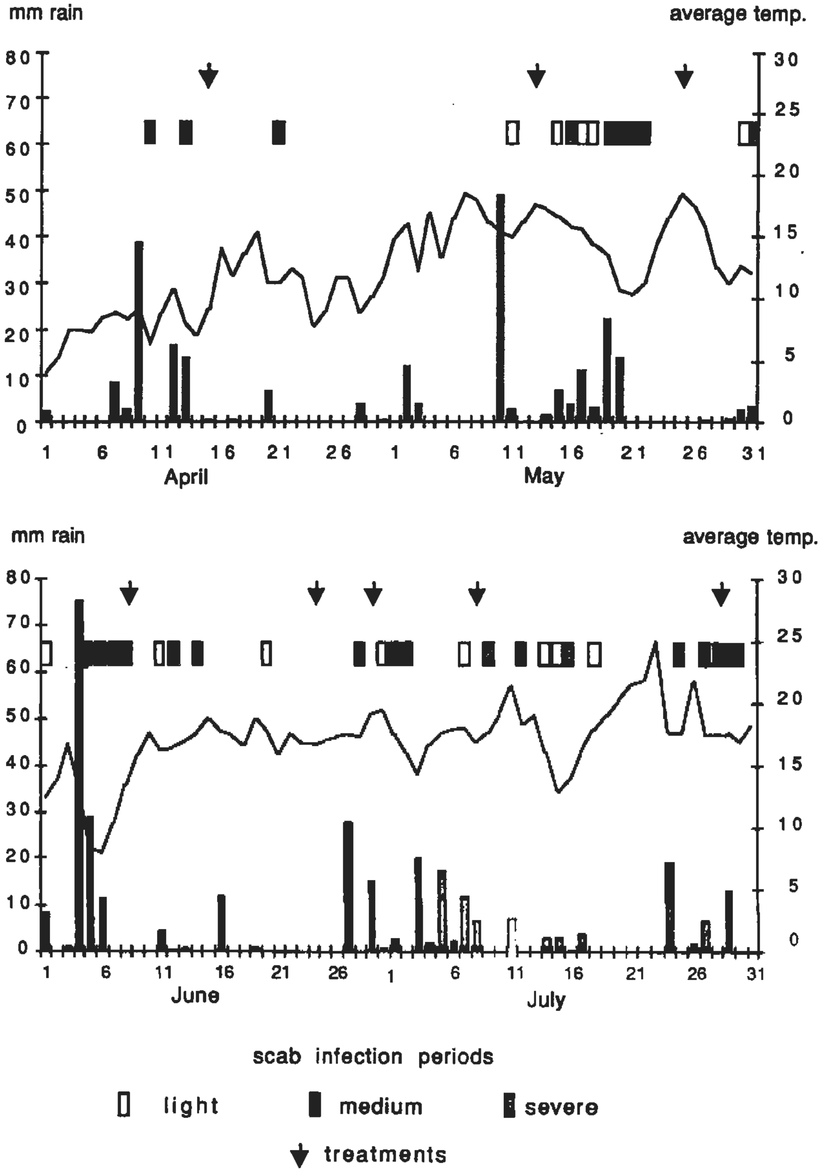

Fig. 1. Weather conditions at Wädenswil in 1988 and calculated scab infection periods. Fungicide application dates are indicated by the arrow.

Methods and results

The serious scab attack of 1987 and the extremely mild winter 1987/88 led to a high inoculation pressure in spring 1988. The first infection period was registered in Wädenswil on April 10 at growth stage C (Fig.1). In the experimental orchard Grüntal (cv Golden Delicious, 18 years old), where SBI fungicides were tested for their efficacy as sprays timed according to scab infection periods, the first treatment with a mixture of captan and penconazol (Topas C) was on April 15th. Despite the many rainy periods during May and June all treatments were applied curatively, after infection periods. After the detection of scab symptoms on treated leaves and fruit about June 20th it was attempted to prevent further spread of the disease using various fungicides. Double concentrated spray liquid was applied twice within 6 days (Fig.1) and again on July 8th and 28th. Assessment of leaf scab on July 22th showed that scab development had been stopped by most fungicides (Fig.2).

In order to understand the reason for the scab outbreak in the treated plots of the Grüntal orchard, weather data and spray application dates were analysed. Considering all known facts it must be assumed that the primary infection was induced by conidia formed on the twigs being washed into the opening buds by the heavy rainfall of April 9th. The fungicide applied on April 15th was too late for this first infection period.

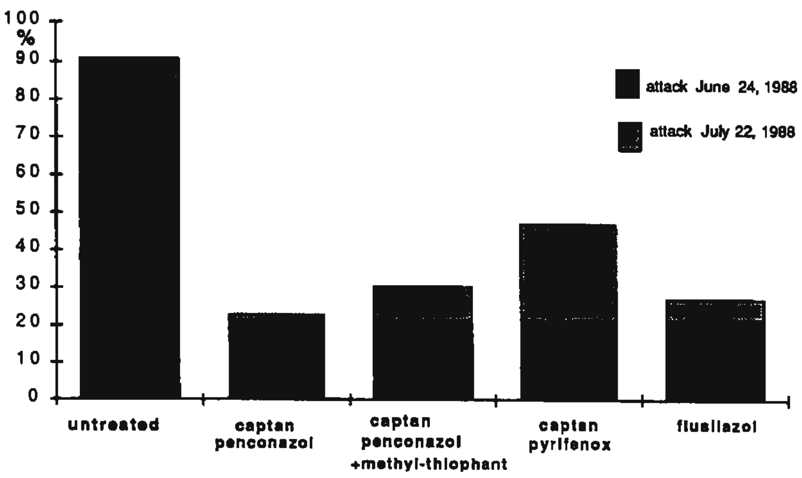

Fig. 2. Attacked leaves (%) before and after 3 treatments to stop scab development. Orchard Grüntal, Wädenswil; variety: Golden Delicious, planted 1970. Orchard treated according to scab infection period s. 4xcaptan-penconazol from April 15 -June 8.§

Table 1. Fitness and sensitivity of *Venturia inaequalis* isolated from treated and untreated plots. Grünthal Wädenswil 1988.

Nr.	Origin	Isol. date	%Germination on		Growth		Sens. test (Penconazol)	
			maltagar	H2O	on agar	on seedlings	on agar	on seedlings
111	Grüntal FAW Golden 4x Topas-C	June 22	95	87	normal	normal	growtn at 0.1mg/l	100% efficacy
112	Grüntal FAW Golden untreated	June 22	96	80	normal	normal	growth at 0.1mg/l	100% efficacy
113	as 111, 2 additional treatments with Topas-C + MBC	July 7	45	0	normal	normal	growth at 0.1mg/l	100% efficacy
114	as 111, 2 additional treatments with Topas-C	July 7	61	0		poor		
115	as 111, 2 additional treatments with Rondo	July 7	60	0		very poor		
116	as 111, 2 additional treatments with Nustar	July 7	64	0		poor		
117	as 112, untreated	July 7	85	80	normal	normal	growth at 0.1mg/l	100% efficacy

Topas C = Captan (47.5 % A.I.) + Penconazol (2.5 % A.I.), 0.1 %

MBC = Methyl-thiophanat (70 % A.I.), 0.1 %

Rondo = Captan (60 % A.I.) + Pyrifenox (5% A.I.), 0.1 %

Nustar = Flusilazol (20 % A.I.), 0.0125 %

Reduced SBI sensitivity of *Venturia inaequalis* has been reported from some European countries in the last 3 years (4,5,3,2); it therefore seemed to be reasonable to investigate *Venturia* isolated from leaves of treated and untreated plots in the Grüntal orchard. Fitness and SBI sensitivity of *Venturia* isolates were tested using the following methods :

Tests of **fitness**:

- germination rate of conidia in water and on malt agar
- colony growth in culture on PDA medium
- development on apple seedlings under controlled conditions

Tests of **SBI sensitivity**:

- development of germ tubes on fungicide-containing agar (assessment done by Ciba-Geigy)
- colony growth on fungicide agar (FAO recommendation)
- development on SBI-treated seedlings under controlled conditions (FAO recommendation)

Isolates collected in treated and untreated plots on June 22nd, immediately after the detection of scab symptoms on treated leaves and fruit (isolates 111 and 112; Table 1) were similar in fitness and SBI sensitivity. Conidia collected from leaves treated twice with double-concentrated spray liquid to stop further scab development showed normal germination (isolates 113-117), but growth on seedlings was poor in some cases (isolates 114-116). Isolate 113 (2x captan-penconazol plus thiophanate-methyl) was as fit as 117 (untreated plot), and it also showed the same range of SBI sensitivity.

The development of scab on treated apple trees was due to very early infection on the unprotected sepals and not to reduced SBI sensitivity of the scab population. The following recommendations are therefore given for scab control in 1989: to prevent early scab infections one treatment at stage B-C with a protective fungicide (i.e. copper, dithianon, folpet or captan) toxic to scab conidia overwintering on the twigs is recommended for scab-susceptible cultivars. Subsequently, treatments should be applied according to scab infection periods using SBI fungicides in mixture with captan.

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Eutypa canker on pome-fruit trees

A. Bolay

Federal Agricultural Research Station, Changins,
CH-1260 Nyon (Switzerland)

Abstract

The fungus *Eutypa lata* is the causal agent of cankers and/or dieback of grape, apple, pear and apricots. The biology and epidemiology on apple and pear are reviewed and control measures discussed.

Key words: eutypiosis, disease control, fungicides, orchard disease, fungicide application technique, *Libertella blepharis*, pruning cuts, wound infection.

Introduction

The ascomycete *Eutypa lata* (Pers.: Fr.) Tul. (syn. *Eutypa armeniacae* Hansf. and Carter.), the anamorph of which is *Libertella blepharis* A.L. Smith, is a fungus responsible for canker and dieback of branches of more than eighty species of fruit, forest and ornamental trees and shrubs. It causes severe losses to apricot, almond, grapevine, apple, pear and black currant (1, 15). *E. lata* occurs in most regions of the world with a temperate or Mediterranean climate (13, 4).

The symptoms of eutypiosis

The most common symptoms of eutypiosis are cankers and/or dieback of branches (color plates). On grapevine the symptoms are different: affected vines show a weakening and stunting of some or all shoots, with smaller leaves and shorter internodes. The leaves on the affected shoots show degrees of yellowing, speckling, distortion and necrosis but they do not wilt. Longitudinal or transverse sections of diseased branches several centimetres below the stunted shoots reveal extensive areas of dead or necrotic wood tissues (5).

The fungus

The fungus forms its anamorph on infected living branches. The teleomorph appears two or more years later on dead branches from which the conidial stage has more or less disappeared.

The ascogenous stroma a mixture of fungal and host tissues. The perithecia are immersed in the stroma and each has a polar ostiole protruding slightly above the surface. The asci are unitunicate, elongated, with an apical pore. The ascospores are allantoid and yellowish brown, 7-11 x 1.5-2 µm. The conidia are hyaline, bent to arcuate, ameroid, 18-35 x 1 µm and are extruded in a moist shining yellowish mass, or in yellowish tendrils. A description of the fungus was given by Carter and Talbot (20) and by Rappaz (36).

The fungus can be isolated easily from small pieces of infected wood or grown from ascospores. It grows well on malt agar or potato dextrose agar at temperatures in the range 20-25 °C. A white mycelium develops after 3-4 days of incubation. Perithecia are not produced in culture, but pycnidia containing pycnospores of *Libertella* usually form after 6 to 8 weeks.

Epidemiology

E.lata is dispersed entirely by airborne ascospores produced from subcortical stromata on dead wood of the host. The formation of perithecial stromata is rare in regions where the mean annual rainfall is less than 350 mm. Once formed, a stroma may continue to liberate ascospores for five years or more, following a regular cycle (27). Spores are discharged from perithecia only during and after rainfall : the eight ascospores are ejected simultaneously from each mature ascus and dispersed as octads. Ramos *et al.* (34) have now provided substantial evidence that in certain geographical situations viable ascospores may be carried for distances of more than 100 km to infect trees in drier regions, where inoculum is not produced locally. It is occasionally possible to find pycnidia (*Libertella*) of the pathogen on infected host tissue, but the asexual spores are not infectious and play no part in the disease cycle (6, 22). Ascospores infect wounds in which the vascular tissue is exposed, the most common point of entry being fresh pruning wounds. Arrival of the inoculum is usually a two-stage process, involving deposition of ascospores on branches and foliage and dispersal by rain-splash and rain-washing (8). Wounds usually lose their susceptibility within about two weeks after pruning, although Ramos *et al.* (35) showed that under Californian conditions, duration of susceptibility of pruning wounds depends on the time of the year. Loss of susceptibility of wounds has been attributed to colonization of the exposed sapwood by other microorganisms (14, 33).

Eutypiosis on pome-fruit trees

Apple

In southern Australia, Carter (7) isolated perithecia of *E. lata* from dead branches of apple trees in orchards near Adelaide. In the same region the author had the opportunity in 1983 to examine several apple trees with large cankers showing numerous tendrils of *Libertella* (Fig. 1). Isolates from dead apple wood were highly virulent when inoculated onto apricot branches (4).

In several provinces of Austria, apple trees of the cultivar McIntosh have cankers causing a dieback of large branches and sometimes the death of the whole tree. Messner and Jahnel (25) isolated from necrotic wood a fungus which developed conidia in culture; Messner and Sutton (26) attributed the isolates to *Libertella blepharis* A. L. Smith. In autumn 1981, the author received from Austrian colleagues two cultures of *Libertella* isolated from McIntosh apple trees. When inoculated to apricot and black currant they caused typical symptoms of eutypiosis.

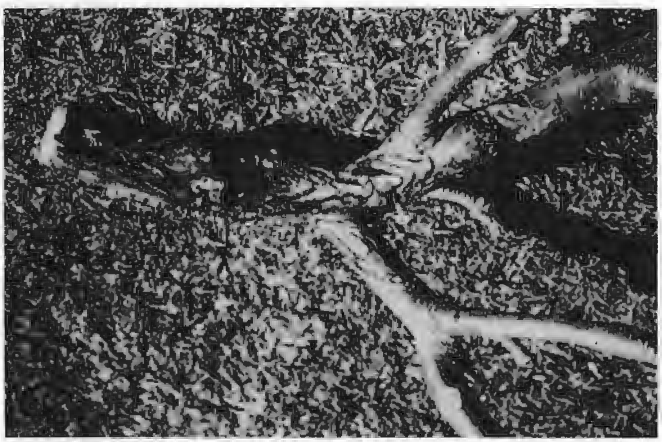

Fig. 1. Eutypa canker on Granny Smith apple tree. Lenwood, South Australia, Oct. 1983.

McIntosh apple trees cultivated in Hungary in the Balaton lake region are also affected by cankers attributed to *Libertella blepharis* by Vajna (37).

In Washington State, USA, Glawe *et al.* (24) isolated *E. lata* from dead wood of Golden Delicious apple trees in the Yakima region. The cultures from these isolates cause cankers when inoculated to apricot.

In 1984, the author found many cases of eutypiosis in the french-speaking part of Switzerland on several apple cultivars (Golden Delicious, Gravenstein, Jonathan, Kidd's Orange Red, McIntosh, Canada Reinette and Starking)(Fig. 2). Cankers of various size appeared on pruning wounds. Tendrils with *Libertella* or perithecia of *E. lata* were present on the surface of most cankers. In Valais, eutypiosis is frequently associated with damage caused by the apple clearwing moth (*Synanthedon myopaeformis* Borkh); the fungus *E. lata* is easily isolated from the bark and dead wood, and also from the sawdust left by the caterpillars of this insect in their tunnels.

Perithecia of *E. lata* frequently develop on pieces of wood left in the orchards after pruning. They can also be observed on cankers and dead branches of tall standard trees in old orchards.

Pear

In southern Australia (10), eutypiosis causes severe cankers on several pear cultivars (Josephine, Lemon Bergemot and Packham's Triumph) in the region of Adelaide.

In Switzerland, the cultivar Bon Chrétien William's, which is grown mainly in Valais, is often affected by cankers which develop from pruning cuts or other wounds and which then extend to larger branches. It was shown in 1976 (3) that these cankers are caused mostly by the joint action of the apple clearwing moth

Fig. 2. Eutypa canker on Golden Delicious apple tree, Ardon, Valais, Switzerland, Feb. 1984.

(*Synanthedon myopaeformis* Borkh.) and the fungi *Cytospora spp.* and *E. lata.* Tendrils of both *Libertella blepharis* and *Cytospora spp.* can be seen on some cankers.

In the eighties, the author and colleagues examined again cankers on pear in Central Valais and in the Lake Leman region. Isolates from dead wood revealed in most cases the simultaneous presence of *E. lata* with one or several of the following fungi: *Chondrostereum purpureum, Cytospora spp., Nectria galligena, N. cinnabarina* and *Phomopsis spp.* Cultures of *E. lata* isolated from pear, apple, apricot, black currant and grapevine were inoculated on twigs of Bon Chrétien William's pear trees. Typical cankers developed, but the progress of the fungus was slower than on apricot or black currant.

Control

The following measures are recommended to control *E. lata* :

- reduce inoculum.
- prune late, when pruning cuts are resistant.
- disinfect pruning cuts.

The burning of infected branches reduces the potential for infection, but it is not sufficient to totally avoid the contamination of pruning cuts because ascospores are disseminated by wind over long distances. Moreover, *E. lata* can develop and fructify on most forest and ornamental trees and bushes, except conifers. Hedgerows, groves and forest edges are therefore a constant source of inoculum that cannot be eliminated. When conditions are favourable, a single spore can initiate infection (34).

As mentioned above (see Epidemiology), the susceptibility of wounds diminishes with time because of the development of other microorganisms antagonistic to *E. lata.* On apricot, leaf scars remain susceptible for at least 42 days, but wounds made just before bud break become resistant to the fungus within 14 days (35).

In Valais, cultures of *E. lata* were inoculated to apple and pear trees at different periods of the year. Positive results were obtained only with inoculations made at the end of summer or in autumn (2). In orchards with a risk of eutypiosis it is therefore advisable to prune late, just before bud break.

Disinfection of pruning cuts was tested by Australian and American workers. The first useful results were obtained by Moller and Carter (28, 29) with a single benomyl spray just after pruning. Under experimental conditions, when each cut was sprayed individually a control of over 90 % was achieved. When the same fungicide was applied in the orchard using conventional sprayers, however, protection was poor because the quantity of fungicide reaching each cut surface was insufficient (21, 31). Carter and his co-workers combined pruning with the application of a protective fungicide by fitting pneumatic secateurs with a spray nozzle. This was developed as the pneumatic injection secateur "Felcomatic

WASP" (16, 12, 17), which is perfectly suited to the control of eutypiosis. The nozzle sprays the fungicide laterally as soon as the twig is cut, and the duration of spray can be altered to ensure that the whole surface is treated. Many fungicides were tested against eutypiosis, but only those of the benzimidazole group (MBC) were sufficiently effective: benomyl, carbendazim, thiophanate-methyl and thiabendazole (28, 29, 31, 30, 32, 23, 2).

Attempts were also made to prevent *E.* infections by spraying suspensions of spores of various antagonistic fungi. Such biological control was developed by Carter and Price (18, 19) and Carter (9,11) using cultures of *Fusarium lateritium*. However,for as long as the effectiveness of benzimidazoles is not reduced by the appearance of resistant strains of *E. lata* it is likely that biological control will not be commercialised, because of the difficulty of producing spores of the antagonist.

On fruit trees, the use of the pneumatic injection secateur to apply fungicides of the benzimidazole group at a concentration of 1 % of the formulated product is the only control method which is effective and practical.

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Diseases of pome-fruit orchards in India and research objectives

G.K. Gupta

Dr. Y.S. Parmar University of Horticulture and Forestry, Regional Horticultural Research Station, Bajaura, Distt. Kullu (HP)-175125, India.

Introduction

Although India is a tropical country, about 200,000 ha of apples and other temperate fruits are grown in the northern hills. Apples occupy nearly 160,000 ha, mostly with cultivars of the Delicious group (e.g. Starking Delicious, Red Delicious, Rich-a-Red Delicious). The economic importance of growing apples in India is considerable: cultivation and marketing problems led to the establishment of the University of Horticulture and Forestry at Solan, Himachal Pradesh in 1985. This University is the second of its type in the world and since opening, research has been a priority. Pears are grown over a wide range of climates, from sub-mountainous regions to high hills (700-2700 m.a.s.l.) but in a limited area. The largest area of pome- fruit production is on the slopes of the hills, with smaller areas in the valleys. Jammu & Kashmir is the only State where apples are grown mainly on flat land.

Major pome orchard diseases

Apple scab

History of apple scab outbreaks

Apple scab (*Venturia inaequalis*) is the most important disease in Indian orchards. Early introductions of apple by the British and French were free from scab. The first record of scab was in 1930 on a native cultivar, Ambri, in the Kashmir valley (Jammu & Kashmir State). For many years scab caused little damage and no efforts were made to control it. In 1973, however, an epidemic seriously damaged cv. Red Delicious, with a loss of US $540,000 in one season: Red Delicious is very susceptible to scab and occupied nearly 70% of the apple-growing area in Kashmir valley in 1973. Other cultivars grown in Kashmir include White Dotted Red (Versifield or "Mahaaji"), Cox's Orange Pippin, Ambri, Jonathan, Benoni (Hazrat Wali), and American Apirouge. These cultivars have a range of resistance to scab. In Himachal Pradesh, apple cultivation extended rapidly after 1960 and occupied 40,000 ha in 1977 when scab appeared in localized pockets of several districts. Within six years the disease spread to almost every orchard (Table 1): even isolated trees surrounded by dense forest were attacked.

This rapid spread raises questions of long-distance spore dispersal, an aspect of scab epidemiology needing examination. In 1982 and 1983, scab was so

Table 1. Status of apple scab in Himachal Pradesh during the six years 1978 to 1983.

District	Area of apple cultivation (ha)	Area (ha) affected with scab					
		1978	1979	1980	1981	1982	1983
Shimla	20,122	34	64	70	160	18.000	20,000
Kullu	11,199	96	696	5670	5872	11.000	11,000
Mandi	7,303	16	24	64	160	6,000	6,480
Chamba	2,180	4	4	53	65	1,300	1,300
Sirmur	3,126	-	-	-	-	-	150
Kinnaur	2,403	-	-	-	4	4	400
Solan	493	-	-	-	-	2	60
Kangra *	472	-	-	-	-	-	-
Lahaul & Spiti*	56	-	-	-	-	-	-

* Not surveyed

Table 2. Occurrence of apple scab infection periods in 1982.

Month	Infection period* (days) Followed by rain			Followed by dew			Total
	L	M	H	L	M	H	periods
March (from 20th)	0	0	6	0	6	0	12
April	0	1	8	7	0	2	18
May	0	0	8	0	9	0	17

* Based on hours of surface wetness (leaf) and temperature.
L - light, M - moderate, H - heavy infection risk

severe in Himachal Pradesh that the survival of apples as a commercial crop was endangered. The incidence of scabbed fruit ranged between 10 and 50%, and in 1983 nearly 10% of the total crop of 300,000 tonnes was rendered unfit for market and destroyed at a loss of US $1.5 million. Reasons for the severity this epidemic are the many infection periods in 1982 (Table 2) and 1983, and the predominance of very susceptible cultivars of the Delicious group. Today, scab is established in all apple-growing areas of the country, which include UP hills, Arunachal Pradesh, Sikkim and Nilgiri Hills of TamilNadu.

During the last 15 years, the epidemiology of the disease and the biology of the fungus have been examined, and these studies have led to a better understanding of the factors responsible for the outbreak of scab (3,5,7,8,10,13-16,18-20,31-33,35,38,42-44).

Table 3. Effect of post-harvest fungicide sprays on ascospore production

Treatment	Concentration (%)	Mean ascospore production	Reduction in ascospore discharge (%)
Untreated	-	76,500	-
Carbendazim (50WP)	0.05	0	10
Dodine (65WP)	0.10	0	100

Chemical control of apple scab

Chemical control studies have been aimed at (i) the elimination or reduction of pseudothecia, (ii) the prevention of ascospore release, and (iii) protection against primary and secondary infections. These objectives have been achieved by carrying out trials in the post-harvest period

(6,17), in the pre-leaf fall period (6,17,19,22,34) and in the growing season (6,11,12,28,30,34,39,40,48). Table 3 shows that two sprays of either carbendazim or dodine, applied one month apart after harvest, disrupted the life cycle of the pathogen and prevented the production of ascospores in spring.

In India, most apples are harvested from August to October and leaf-fall occurs 1.5-3 months later. During this interval, dew in the valleys permits foliar infection: many terminal leaves develop numerous scab lesions and produce many pseudothecia the following spring. To break the life cycle, single pre-leaf fall sprays of 5% urea or other chemicals, particularly sterol biosynthesis inhibitors like bitertanol (17) and triforine, have suppressive effects on the ascigerous stage of the fungus (Table 4) and consequently allow reduced numbers of sprays the next summer. The application of 5% urea has become standard practice (14,16,19), and besides controlling scab has been found to increase crop yield (17).

Growing-season fungicde trials have resulted in a protective spray schedule (Table 5) which comprises 7-8 sprays of contact or systemic fungicides and a single spray of urea before leaf-fall. The first spray is between silver- and green tip, followed after 10 days by the second spray at pink bud-early bloom: further sprays are at 14-day intervals until harvest. Fungicides are expensive and the market price of apples fluctuates. To make the schedule economical and encourage its use, the national and state governments provide for half the fungicides costs.

Table 4. Effect of pre-leaf-fall spray of chemicals on ascospore productivity of *Venturia inaequalis*

Treatment	Concentration (%)	Mean ascospore production	Reduction in ascospore discharge(%)
Untreated	-	12,000	-
Copper oxychloride (50WP)	0.5	6,800	52
Triforine (19EC)	0.2	0	100
Urea	5.0	0	100

To reduce the number of sprays, a curative programme is based on applications or bitertanol or myclobutanil 72 or 96 hr after infection period warnings. This strategy has been more effective in controlling primary and secondary scab than the protective spray schedule, and saved three sprays (48). It is not always possible to spray in response to infection periods within the necessary time. Fun-

Table 5. Protective spray schedule to control apple scab.

Spray no.	Development stage	Fungicide/100 l water
1	Silver tip - green tip	Dodine (100g), or captafol (300g), or mancozb (400g), or dithianon (75-100g)
2	Pink bud - early bloom (10 days after Ist spray)	If captafol has not been used in 1st spray, then spray dithianon (50g), or a mixture of mancozeb (300g) plus wettable sulphur (200g), or bitertanol (100g).
3	Petal-fall (14 days after 2nd spray and continuing at 14-d intervals	Carbendazim (50g), or thiophanate-methyl (50g).
4	Fruit set (Pea stage)	Dodine(100g), or captan (300g), or dithianon (50g), or mancozeb (300g).
5	Fruit development	Mixture of carbendazim/thiophanate methyl (25g) plus mancozeb (250g), or bitertanol (100g), or dithianon (50g), or mancozeb (300g), or captan (300g).
6	Fruit development	Repeat the fungicides of 5th spray
7	Pre-harvest (15-20 days before harvest)	Captafol (150g), or mancozeb (300 g).
8	Pre-leaf-fall (7-10 days prior to general leaf-fall)	Urea (5kg)

Use adjuvants like Selwet-99 (12.5g), Teepol (25ml) or Selwet- E/Tritone/Uphaar/Sandovit (50-75ml) in 100l spray liquid.

gicides can be sprayed late in the incubation period, however, 2-3 days before symptoms appear. Experiments show that carbendazim, thiophanate methyl, dodine, guzatine and sterol-inhibiting fungicides (bitertanol, etaconazole, myclobutanil, penconazole (plus captan), PP523, prochloraz, fenarimol and triforine) sprayed two days before the appearance of scab symptoms resulted in atypical, chlorotic or reddish-brown, lesions on the foliage; Myclobutanil results in necrosis of hyphae and is fungitoxic, whilst bitertanol is fungistatic (48). Another strategy when scab is severe is to spray weekly, using carbendazim, carbendazim plus mancozeb, dodine, or bitertanol on 2 or 3 occasions. (28,30,39,40,48). Once the disease is under control sprays of these or contact fungicides are applied every 14 days.

In all these experiments, inoculated potted plants are held in muslin- covered chambers for 24-36 h and then incubated, either outdoors under natural condi-

Table 6. Ascospore maturity and discharge and incubation period of *Venturia inaequalis*, during spring 1987, at two sites.

Site and development stage	Ascospore maturity category (% number of pseudothecia) 1	2	3	4	5	Ascospore discharge *	Incubation period ** (days)
Jhiri							
Green tip	0	4	32	28	36	4.1	18
20% petalfall	0	0	0	0	100 (most empty)	0.4	
100% petal fall	0	0	0	0	100 (most disintegrated)		
Kadauli							
Green tip	90	10	0	0	0		
Pink bud	8	32	32	20	8	1.2	21
100 % petal fall	0	0	0	12	88		
Fruit set	0	0	0	8	92 (many disintegrated)		
14 days later	-	-	-	-	100 (most disintegrated)	0.0	

* Mean per microscope field of view

** Days to the first appearance of symptoms after infection tions in months when the relative humidity is around 85%, or under an HDPE-laminated fabric cloth-covered net house.

Apple scab prediction

Ascospore maturity and productivity have been studied in relation to weather and tree phenology (10,13-15,18-20). Observations in 1981 showed that ascospores were mature at the silver-tip stage and there was a need to spray by this time (10). In most years the winter is wet, due to snow or rain, the spring receives frequent rainfall and ascospore maturity coincides with bud break. In 1984, however, ascospore maturity was delayed until the fruits were 2 cm in diameter. This was mainly due to dry weather in winter (35). Studies in 1987 showed that ascospore maturity does not coincide with the same phenological stage in all localities (Table 6). It is necessary, therefore, to properly time fungicide sprays in each locality.

In spring, duration of surface (leaf) wetness is measured with a DeWit 7- day recorder, a Belfort hygrothermograph or electronic orchard environment monitors, either the RSS-412 "Predictor", (Reuter-Stokes, USA) or the Biomat SWG (FRG). Ascospore discharge in orchards is monitored with Rotorod spore samplers which are more sensitive to low ascospore concentrations than the Burkhard volumetric trap.The rotorod sampler provides for rapid determination of spore catches after each rainfall: the rods are easy to handle and require less time to examine than the melinex tape from the Burkard trap. Also, heavy deposits of dust on the tape can interfer with the detection of ascospores when using the Burkard trap.

There are five scab-monitoring laboratories in Himachal Pradesh all equipped with these various predictive devices and giving warnings to growers for timely

Table 7. Susceptibility to scab of four local apple hybrids compared to cv. Starking Delicious

Apple hybrid	Lesions per leaf	Lesion type*	Conidia per lesion
Ambred	26	2-3	8,000
Ambstarking	34	2-3	3,000
Ambroyal	23	2-3	18,000
Ambrich	19	2-3	6,000
Starking Delicious	68	4	66,000

* 2 - chlorotic, 3 - light sporulation, 4 - heavy sporulation

spraying. It is not known how large an area a single predictive station can represent: efforts are being made to establish field stations every 5-10 km^2.

Scab-resistant cultivars

Eleven resistant cultivars (Prima, Priscilla, Sir Prize, Jonafree, Red Free, Macfree, Nova Easygro, Novamac, Co-op-12, Liberty and Freedom) bred in North America have been established at Mashobra and Bajaura (47). Co-op-12 and Red Free are promising in the low and mid-altitude hills of Himachal Pradesh, where cultivars of the Delicious group do not develop a good skin colour (46). The apples of these cultivars mature early, develop a scarlet- red colour within 84-96 days, are comparatively sweet and store well. Locally-bred hybrids (Ambstarking, Ambroyal, Ambrich and Ambred) (47) have a high tolerance (field resistance) to scab, and in comparison to the scab- susceptible cv. Starking Delicious they develop only few, sparsely-sporing lesions when under potentially severe scab conditions (Table 7). These hybrids mature late and are best suited to the upper altitudes (above 2400 m.a.s.l) in Himachal Pradesh.

White root rot

White root rot, caused by *Dematophora necatrix* Hartig (*Rosellinia necatrix* Prill.), is another important disease of pome-fruit nursery and orchard plants. The only treatment is the use of 20 ppm aureofungin (an antibiotic) or 0.1 % carbendazim (9,41) as a soil drench or a spray of 20ppm aureofungin. Aureofungin is not fungitoxic (21), but acts indirectly, possibly by altering the host's metabolism. Carbendazim is toxic to earthworms and leads to hardening of the soil structure. Moreover, the application of chemicals to soil is expensive and gives only partial control. None of the clonal rootstocks or seedling stocks are immune to *D. necatrix*. Efforts are being made to breed resistant root-stocks; also, a search is being made for biological agents, particularly among rhizosphere fungi, antagonist to *D. necatrix*.

Collar rot

Collar rot, caused by *Phytophthora cactorum* (Lebert-Cohn) Schroet, affects pome-fruit trees in heavy and poorly-drained soil. In recent years this fungus has caused, in addition to collar rot, severe fruit rot, particularly in cvs. Golden Delicious and Red Gold grown as dwarf trees (23). Among the clonal rootstocks MM 106 is especially prone to severe root rot in clay-loam soil (21). Besides chemical treatments, young plants usually escape from collar rot by having their graft union at least 30 cm above soil level. The fruit-rot phase is usually controlled by routine sprays of mancozeb: metalaxyl is not available.

Powdery mildew

Caused by *Podosphaera leucotricha* (Ell. and Everh.) Salm. and *Erysiphe heraceli* (D.C.) St. Am. (45), powdery mildew is most damaging to apple seedling stock and nursery plants, while in orchards it is severe on susceptible cultivars including Cox's Orange Pippin, Versifield or White Dotted Red, Benoni, Jonathan, Ambri, Granny Smith, Buckingham, Winter Delicious and Golden Delicious. About 60-80% of orchards in the major apple-growing areas comprise cultivars of the Delicious group; these are moderately resistant and do not require specific control measures. The usual control strategy against powdery mildew is based on reducing primary inoculum by pruning infected shoot tips in winter (37), and spraying every 7-14 days in the growing season (27,29,49).

Canker diseases

Thirteen kinds of canker disease attack pome-fruit trees in India (1,2,4,21,24-26). Of economic importance are black rot (*Botryosphaeria quercuum*(Schw.) Sacc. (with the conidial stage *Botryodiplodia iuglandicola* (Schw) Sacc. or *Sphaeropsis malorum* Berk.), pink disease (*Botryobasidium salmonicolor*(Berk. & Br.) Venkatarayan), nail-head canker (*Nummularia discreta* (Schw.) Tul.), and silver-leaf disease (*Chondrostereum purpureum* Pers.ex.Fr.) Pouz. All three phases of black rot occur, namely fruit rot, frog-eye leaf spot and canker (2,4). The severity of canker diseases is mainly the result of faulty framework training and pruning, depletion of soil micro- and macro-nutrient elements, and wounds and injuries caused by pests. Marginal apple-growing areas at altitudes of 900-1200 m.a.s.l., where chilling is insufficient and trees develop succulent vegetative growth, are congenial for canker diseases (1,2,21).

Sooty blotch and fly speck

Both diseases appear in most years with the onset of rains in late summer, and then increase in severity in the foggy weather and high humidity from July to September. None of the commercial cultivars is resistant and Golden Delicious, Winter Delicious, Granny Smith, Cox's Orange Pippin, Yellow Newton, Buckingham, Rymer, and Jonathan are highly susceptible. These two diseases are controlled by the regular sprays targeted against apple scab (14). Where scab sprays are omitted these diseases are controlled by two applications of captafol, mancozeb or carbendazim (36), the second application being 15-20 days before harvest. These late sprays also improve the storage quality of the fruits by controlling various fruit-rot fungi.

New disease problems

White rot

White rot, caused by *Botryosphaeria dothidea* (Moug. ex.Fr.)Ces & de Not., is a serious problem on apple cvs. Red Delicious, Winter Delicious, Golden Delicious, Black Ben Davis, Granny Smith, White Dotted Red and Cox's Orange Pipppin when the late summer months are very wet. The best control available is a schedule of 2-3 carbendazim sprays starting six weeks before harvest.

Brown rot

Monilinia fructigena was seen for the first time in apple orchards during the wet summer of 1988 (23). Orchard sanitation and timely sprays of carbendazim, as recommended in other countries, have been recommended. Work on this disease has been started.

Necrotic leaf blotch

Starkspur Golden Delicious apples usually show a necrotic leaf blotch in late summer, leading to premature defoliation. No pathogenic fungus or bacterium has been associated with this condition which is possibly a physiological disorder.

Bitter pit

This malady of the fruits, associated with calcium deficiency, is now appearing on the apple trees as well as in stores. Research in Himachal Pradesh has shown that two sprays of calcium chloride (0.5%), 15 days apart with the first six weeks before harvest, help to reduce this problem.

Other diseases of importance

Commonly occurring and damaging are crown gall, hairy root, apple mosaic virus, rubbery wood (MLO) and starcrack (Graft Transmissible Pathogen). Work on these diseases is still in its infancy and is based on producing healthy planting material through nursery inspection and certification schemes.

Conclusions

Major diseases are scab, white root rot (*Dematophora necatrix*), *Phytophthora* collar rot and fruit rot, cankers, sooty blotch and fly speck. Powdery mildew is mainly a problem of nursery plants. Newly emerging diseases are white rot, brown rot (*Monilinia fructigena*), necrotic leaf blotch (physiological) and bitter pit (calcium deficiency). New methods and chemicals are being tried for disease management: these must be adapted to various agro-climatic zones. Emphasis is on breeding resistant rootstocks and cultivars. Accuracy in apple scab management is obtained through the network of disease prediction stations.Work on bacterial and viral/MLO/GTP diseases is in its infancy.

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Apple tree decline in Geneva State, Switzerland: the relation between soil and plant

Ch. KEIMER

Station phytosanitaire cantonale de Genève, CH - 1254 Jussy, Switzerland

Abstract

The most serious phytosanitory problems in apple orchards in Geneva State, Switzerland, are associated with decline of the trees. Based on observations in orchards, attempts are made to determine the influence of soil type, ground water dynamics, apple cultivar and rootstock on the disease-pest complex ravaging the orchards, notably crown rot (*Phytophthora cactorum*), European canker (*Nectria galligena*), apple clearwing moth (*Synatnthedon myopaeformis*) and European shot-hole borer (*Anisandrus dispar*).

Key words: soil water, apple diseases, apple pests, drainage, dieback.

Introduction

Integrated pest management is widespread in apple orchards in Switzerland, and damage to fruits by the common pests and diseases is no longer serious; usually, less than 1 % of the fruits are affected by scab (*Venturia inaequalis*) or caterpillars. Tree decline, however, is important in half of the apple orchards in Geneva State. In a normal year, 1 to 3 % of the trees die due to decline (3); in rainy or humid years losses can reach 10 %.

A complex of diseases and pests attacking the wood are responsible for apple tree decline; roots, collar, trunk and branches may be injured. Fungi frequently found on affected trees are crown rot (*Phytophthora cactorum* L. and C. Schroet) and European canker (*Nectria galligena* Bres.). The most common pests associated with decline are the apple clearwing moth (*Synanthedon myopaeformis* Borkh.) and the European shot-hole borer (*Anisandrus dispar* F.) (1, 2, 3, 5).

This complex of diseases and pests occurs on apple trees grown in asphyxiating soils, where roots may lay under the upper level of ground water.

Annual reports of the Phytosanitary Station in Geneva over the last 20 years establish the importance of apple decline, as shown in Table 1. As a general rule, in years with a wet spring (irrespective of the mildness of the preceding winter),

Table 1. Review of the problems observed in apple orchards in Geneva state.

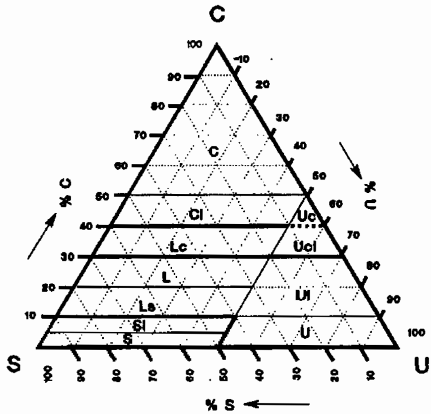
Year	Collar / Crown rot	European canker	European shot-hole borer	Apple clearwing moth	asphyxiating soil
1988	+ + +	+	+ +	+ + +	+ + +
1987	+	+	+ + +	+ + +	
1986	+	+	+ + +	+ + +	
1985	+	+	+ +	+ +	
1984	+ + +	+		+	+ + +
1983	+	+		+	
1982	+	+		+	
1981	+ + +	+	+ +	+	+ + +
1980	+ + +	+	+	+	+ + +
1979					
1978					+ + +
1977					
1976		+			
1975					+ + +
1974	+ + +		+ +		
1973			+ +		?
1972			+ +		
1971			+ +		?
1970					
1969		?			

trees show symptoms of asphyxiated roots and of attacks by the parasitic complex. Every 2-3 years the cases of decline are numerous and severe.

In order to better understand this phenomenon, the influence of the soil (type of soil and water dynamics) on the plant (cultivar and rootstock) is being studied.

The soil type

Soil analyses by the Agronomy Section of the Laboratory of Agricultural and Horticultural Technics, Geneva, are used to characterize all the soils in the region. Figure 1 shows the classification of soils based on texture. Texture is



SOIL TEXTURE GROUPS

HEAVY SOIL:	C	clay
	Cl	loamy clay
	Uc	clayey silt
MID-HEAVY SOIL:	Lc	clayey loam
	Ucl	clayey-loamy silt
MEDIUM SOIL:	L	loam
	Ls	sandy loam
	Ul	loamy silt
	U	silt
LIGHT SOIL:	Sl	loamy sand
	S	sand

Fig. 1. Soil texture: grain size distribution used in Switzerland.

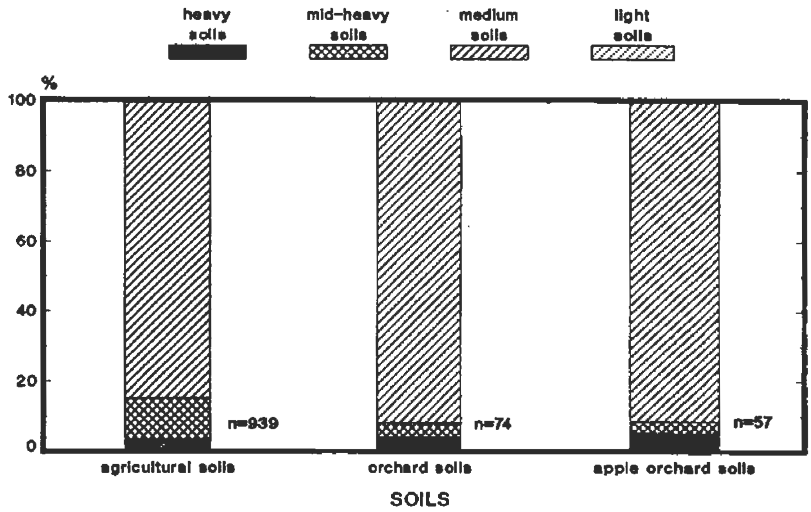


Fig. 2. Type of the agricultural soils and of the orchard soils in Geneva State.

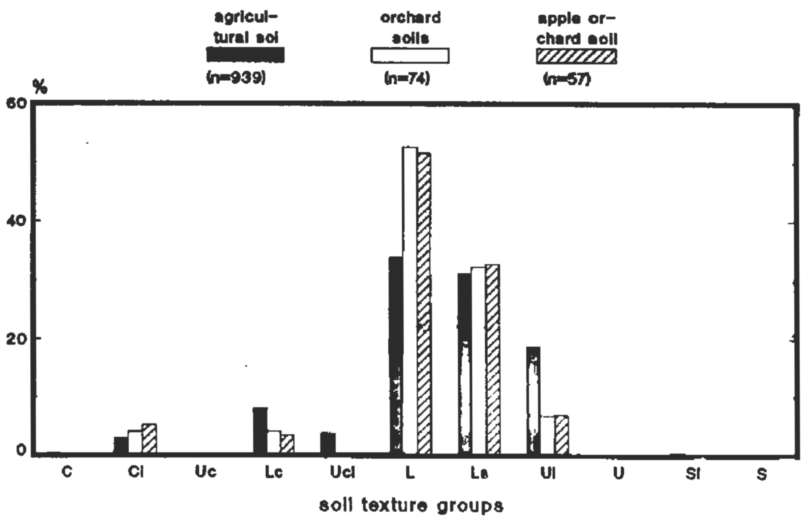


Fig. 3. Detailed classification of the agricultural soils and of the orchard soils in Geneva State (Legend: see Fig. 1).

shown as particle size distribution and the results are given in percentages of clay (C, 2 %), loam (U, 2-20 %) and sand (S, 50-2000 %). Figure 2 compares agricultural field-crop soils, the soils of all orchards and soils of the apple orchards in Geneva State. There are no major differences between the soils of these groups. Most soils in Geneva State belong to the loamy (medium) soil type. Four types of soil can be divided into eleven specific classes, as shown in the Figure 3: again there are no consistent differences between the agricultural and orchard soils.

The reason why the distribution of soils in Geneva appears to be so uniform resides in their extreme diversity. Within the same field many types or classes of soil can occur. The soil map of Geneva State is a richly diversified mosaic.

A comparison of soil texture in healthy apple orchards and apple orchards where tree decline occurs does not reveal any clear difference (Fig. 4). Soils in orchards with decline belong mostly to the loamy group i.e. the medium type of soil.

It is generally reported that soil type has an important influence on the presence of apple tree parasites: crown rot (*Phytophthora cactorum*) and European canker (*Nectria galligena*) are favoured by heavy soil. In Geneva State these fungi are found in orchards in all types of soil, however, so it is concluded that the nature of the soil is not of great importance for the presence of the complex of diseases and pests associated with apple tree decline. This agrees with the view of Bompeix (4).

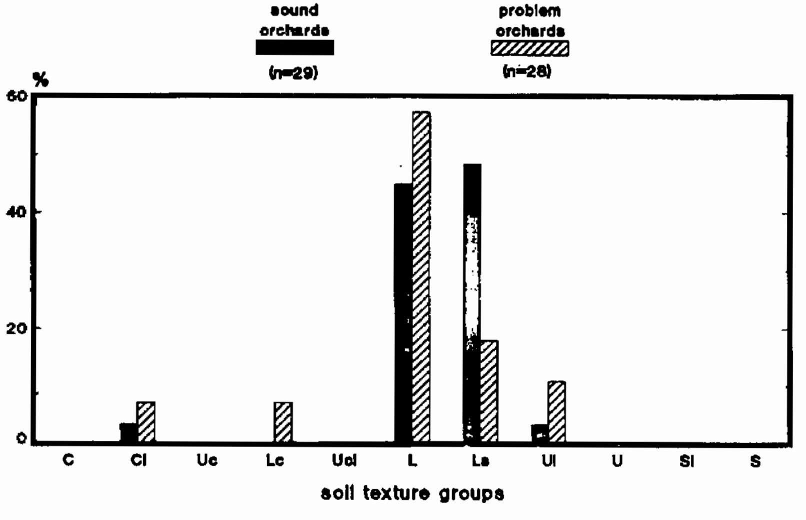
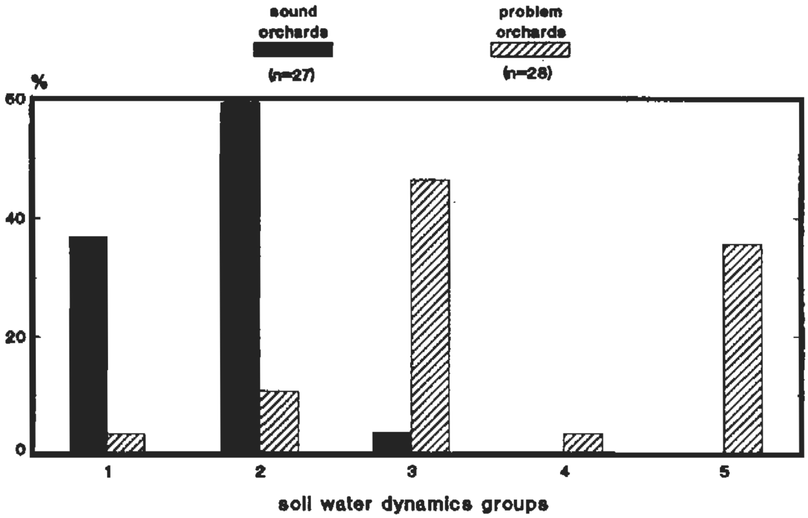


Fig. 4. Detailed classification of the soils in sound an problems orchards (Legends: see Fig. 1).



SOIL WATER DYNAMICS GROUPS

1 Soils drying out quickly

2 Soils drying out slowly in the depth

3 Soils drying out slowly, fewly blocking water (well structured soils)

4 Soils drying out slowly, localy blocking water at the surface

5 Soils drying out slowly, periodicaly strongly blocking water

Fig. 5. Ground water dynamics in the sound and in the problem orchards.

The soil ground water dynamics

The dynamics of the soil water in Geneva State have been studied by the Swiss Federal Institute of Technology in Lausanne. This project was ordered by the Service of Agriculture in Geneva State. The results are presented as a map.

The dynamics of the water are characterized by the drying capacity of soils. Figure 5 shows classes (1 to 5) of drying capacity in relation to healthy orchards

Table 2. Apple varieties and rootstocks grown in Geneva State.

Apple varieties	Sound orchards								Problem orchards								Sum
	Rootstocks							Sum	Rootstocks							Sum	
	27	9	26	106	7	111	104		27	9	26	106	7	111	104		
Golden Delicious		7	4	4	2	2	1	20		7	6	4	1			18	38
Idared		6	4	1				11			5	1	2			8	19
Jonathan ssp		2		3	2		1	8			5		2			7	15
Maigold		6						6	1	5	2		1			9	15
Prime Red		2	5					7		2	4					6	13
Jonagold		1	2	1				4		3	2					5	9
Gravenstein								0		7	1					8	8
Kidd's orange red			1					1		4	2					6	7
Boskoop			2					2		4	1					5	7
Red Delicious ssp					2			2			2	1	1			4+1*	7
Reinette ssp		2	2		1			5		2						2	7
Gala		1	1					2		2	2					4	6
Summerred		2						2		2						2	4
Yellow Transparente		1	1					2		1	1					2	4
Elstar		1	1					2								0	2
div. varieties		2	4				1	7		1	6		2			9	16
Sum	0	35	25	9	7	2	3	81	1	40	39	6	9	0	0	96	176

* free

and in orchards where the parasitic complex occurs. The soils of the healthy orchards possess a high drying capacity: they dry quickly, or slowly only at depth; the impermeable layer lies at least at a depth of 80 cm, below the level of most of the roots.

The soils of orchards in which the complex of diseases and pests occurs have a low drying capacity: they dry slowly over all the profile.

The water dynamics, namely the presence of ground water, is an important factor favouring the parasitic complex. This factor is often cited.

Apple cultivars

The principal apple cultivars grown in Geneva State are listed in the Table 2. The cultivars that are the most susceptible to root asphyxiation and to the complex of diseases and pests are, in decreasing order of importance, Gravenstein, Kidd's Orange Red, Boskoop, the Red Delicious group and Maigold.

Generally, Gravenstein has almost disappeared from commercial orchards in Geneva State, but Kidd's Orange Red, Boskoop and Red Delicious are still grown in a few orchards. Only Maigold is grown extensively.

Apple rootstocks

Examination of the phytosanitory reports of the early seventies (Table 1) shows that apple trees grown on rootstock M 104 were highly susceptible to decline. This statement is corroborated by Bompeix (4). Table 2 shows that the apple growers in Geneva State no longer use the most vigorous rootstocks (MM 104 and MM 111) in orchards where the parasitic complex occurs. The cultivars that are susceptible to decline are relatively vigorous cultivars grown on dwarfing rootstocks: M 9 for example and M 26 in a few cases.

According to Julis *et al.* (1977), cited by Bompeix (4), in the nursery the rootstock M 9 revealed itself as more resistant than M 26 to crown rot (*Phytophthora cactorum*).

The formation of an excrescence at the graft union favours attacks by the clearwing moth (*Synanthedon myopaeformis*). The rootstock M 9 appears to be particularly susceptible, although all the rootstocks can be attacked. (1, 2).

In orchards in Geneva State there are no obvious differences in susceptibility to decline between the most popular rootstocks, M 9 and M 26.

Conclusion

Our investigation of apple tree decline in Geneva State, Switzerland, shows that under the local soil and climatic conditions the most important factors are the dynamics of the ground water in the soil and the cultivar.

Direct control measures, whether preventive or curative, against the different pests and diseases involved in apple tree decline can be undertaken. It is difficult, however, to simultaneously control several pests and pathogens.

The most practical solution consists in taking preventive measures before planting: careful consideration must be given to the choice of soil and to improvements in drainage, etc., as necessary. Cultivars and rootstocks must not be chosen only for their commercial value and vigour, but also according to soil conditions and the risks of decline.

Acknowledgments

The data required for conducting this study were collected and examined by Roland Gysi, Ing. Agr. ETH, Zurich.

The data on soil analysis were provided by the Agronomy Section of the Laboratory for Agricultural and Horticultural Technics, and the data on the dynamics of the water by the Service of Agriculture, both in Geneva. I thank all who supported this project.

Résumé

Le dépérissement des arbres fruitiers pose le problème phyto sanitaire le plus grave dans les vergers de pommiers genevois (CH). Sur la base d'observations effectuées sur le terrain, nous examinons les relations existant entre les maladies (mildiou du collet et chancre commun) et les insectes (sésie et bostryche disparate), et d'une part le sol - type de sol et dynamique de l'eau - et d'autre part la plante - variété et porte-greffe de pommiers.

Zusammenfassung

Das wichtigste, in den Apfelkulturen des Kantons Genf (CH) auftretende Pflanzenschutzproblem stellt das Absterben der Bäume selbst dar. Aufgrund der im Feld gemachten Beobachtungen werden die Zusammenhänge zwischen Pflanzenkrankheiten (Kragenfäule des Apfels, Apfelbaumkrebs) und Schädlingsproblemen (Apfelglasflügler, Holzbohrer) mit den Bodeneigenschaften (Bodentyp, Dynamik des Bodenwassers) einerseits und der Pflanze (Sorte, Unterlage) anderseits untersucht.

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Session 7

Conflicts between pest and pathogen control

Chairperson: M.G. Solomon

The conflict between pest and disease control in orchards

M.G. Solomon

AFRC, Institute of Horticultural Research East Malling
Maidstone, Kent, ME19 6BJ, England

Introduction

The fungicides used in apple and pear pathogen management programmes can influence the phytophagous pests and predatory and parasitic insects and mites present on the trees. Whilst any toxicity of fungicides to pest species is usually welcomed, the same effect on natural enemies of pests is potentially damaging to integrated pest management (IPM) programmes. An understanding of these possible side effects of fungicides is necessary if an undesirable conflict between phytopathological and entomological requirements is to be avoided.

That the side effects of agrochemicals on orchard beneficials is regarded as important by entomologists, is demonstrated by the fact that there is a subgroup of the IOBC Working Group "Integrated Plant Protection in Orchards" titled "Influence of Pesticides on the Beneficial Fauna in Fruit Trees". [Proceedings reported in Bulletin IOBC/WPRS (1982) V (2); (1984) VII, (2); (1986) IX (3)]. Additionally, the IOBC Working Group " Pesticides and Beneficial Organisms", which coordinates the testing work of entomologists in West European countries, includes among its standard test species two predatory mites, four predatory insects and two parasitic insects that occur in fruit orchards. In a summary of the work of this Group from 1977 - 1985 (18), of the 42 orchard chemicals tested, 13 are fungicides.

In order to assess the seriousness of fungicide toxicity to natural enemies, a general perception of the relative importance of the various species of predator and parasite that occur in orchards should be established. As a preliminary to this, it is necessary to consider which are the pests that might be regulated at an acceptably low level by their natural enemies, within an IPM programme.

The pests suitable for regulation by natural enemies

The potential for a long-term stable relationship between a pest species and its natural enemies implies the continuing presence of at least low numbers of the pest species. Relationships resulting in local extinctions of the pest are usually characterised by extinctions of the natural enemy, followed by local reinvasion and outbreaks of the pest. It is necessary, therefore, to consider the relationship between population density and crop value for each pest; it is helpful to categorise pests on this basis.

1. Low economic injury level pests, causing economic damage even when present in only low numbers (Figure 1). Pests in this category usually attack the fruit itself. An example found almost everywhere in European top fruit culture is the codling moth, Cydia pomonella, of which every larva may cause severe damage to several fruits. Another example is the rosy apple aphid, *Dysaphis plantaginea*, which causes severe indirect damage. The feeding of the aphids on apple leaves causes the leaves to curl but also, and much more seriously, causes fruits developing close to the attacked leaves to remain small and become misshapen.

2. High economic injury level pests, generally feeding on parts of the plant other than the fruit. The Eurpean red mite, *Panonychus ulmi*, for example, feeds on the underside of leaves and, whilst defoliation can result from very high population densities, feeding by moderate populations of a few mites per leaf rarely results in a detectable effect on cropping. Pear psyllids, (*Psylla pyricola* and *P. pyri*) feed on leaves but also produce honeydew, a sugary liquid which may drip

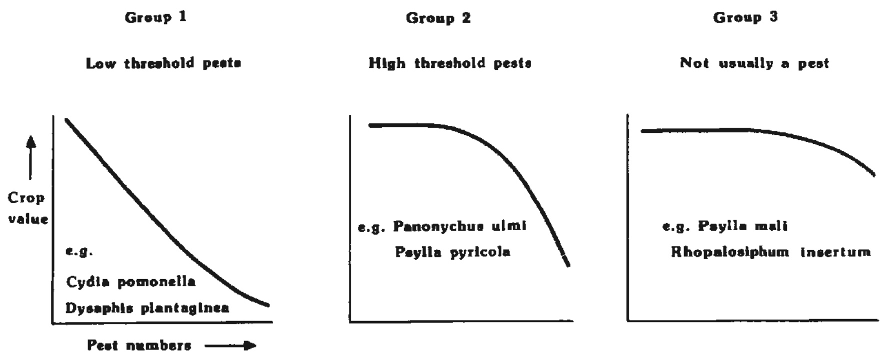

Fig. 1. A categorisation of fruit pests according to the relationship between population density and crop value.

onto fruits, causing sticky patches in which sooty moulds grow. The apple rust mite, *Aculus schlechtendali*, also feeds on leaves, but is so small that even population densities of several hundred per leaf may result in no detectable effect on cropping. Recent evidence (12), however, has shown that when very abundant early in the season this mite may also feed on developing fruits, leading to russeting or cracking of the skin.

3. Very high economic injury level pests, or, perhaps more properly, phytophagous species that are not usually damaging. The apple psylla, *Psylla mali*, the apple grass aphid, *Rhopalosiphum insertum*, and leafhoppers, *Typhlocyba* spp., are examples of phytophagous species that have been shown rarely to reduce cropping, even when present at very high population densities.

Group 1 ("low economic injury level") pests do not lend themselves to regulation by their natural enemies at an acceptably low population density, because they cause economic damage even at low population densities. Group 3 ("very high economic injury level") pests may be regulated at low population densities by natural enemies, but these relationships are not usually critically important from the pest management point of view; these pests are not important, even at high population densities. It is clearly among the group 2 ("high economic injury level") pests that the potential lies for effective biological control within IPM programmes. It is on the natural enemies of the pests in this group that attention should be focused when assessing the importance of the side effects of fungicides.

The predators important for IPM

In pear orchards, the most serious pests are psyllids (*Psylla pyricola* and *P. pyri*). Predatory anthocorids (mostly *Anthocoris nemoralis*) attack the psyllids and pest management programmes on pear are usually based on the need to avoid damaging these predators (e.g. 4, 19, 26). Anthocorids appear to be unaffected by the fungicides used in pear orchards, so this system is not usually threatened by fungicide applications.

In apple orchards, IPM programmes are usually based on the regulation of the European red mite, *Panonychus ulmi*, by predators (e.g. 2, 25). During the past 30 years this pest has become resistant to most of the acaricides that have been used against it (8) and it seems likely that the of acquisition of resistance will continue with new acaricides. There is thus a pressing requirement for the exploitation of non-chemical means of managing this pest.

Many species of predator attack *P. ulmi* and other pests of apple and contribute in a general way to their reduction (6). Coccinellids, chrysopid larvae, syrphid larvae and cecidomyid larvae may all be useful in some circumstances, but the groups of predators that are most often important are mirid and anthocorid bugs and phytoseiid mites (Figure 2). Many species of phytoseiid mites are found on unsprayed apple trees (5) but in selectively sprayed orchards in England it is *Typhlodromus pyri* that usually colonises and multiplies (13, 23). The same species occurs in most other apple-growing regions of the world where the climate is similar (2, 22). *T. pyri* has three or four generations each year in England, compared with the one or two generations of the predatory insects, and is therefore better able to increase in numbers rapidly if prey numbers increase.

Sufficient selective pesticides are available to allow the design of a pest management programme for treatment of those pests that require it, while allowing mirids, anthocorids and *T. pyri* to survive. Such programmes have usually been based on the selective aphicide pirimicarb, with diflubenzuron for the control of larvae of moth pests (13, 17) (Table 1).

During the 1970s, resistance to organophosphate (OP) insecticides was found in *T. pyri* in New Zealand (7, 20) and the USA (29), and then in England; these resistant mites are now widespread in the fruit-growing region of S.E. England (27), and in Western Europe are also reported in orchards in Austria, The Netherlands, Italy and Switzerland (2). The strains found in England are resistant to

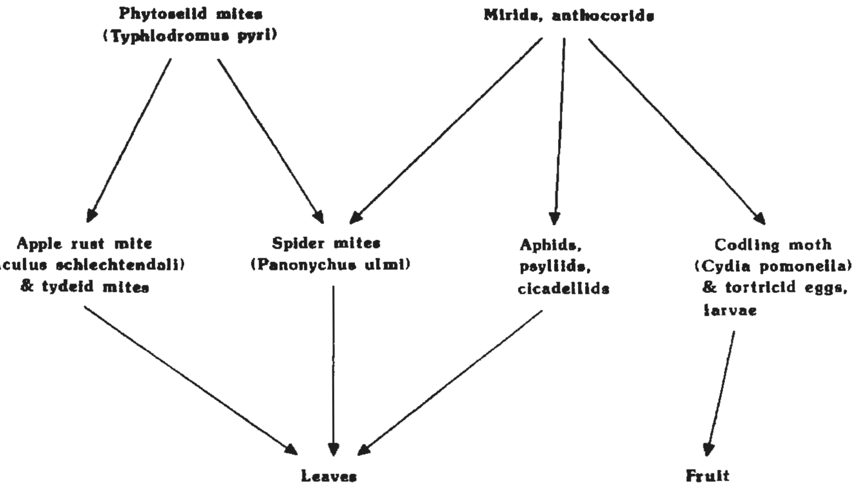

Fig. 2. The feeding relationships among some of the phytophagous species and their predators in apple orchards where the pesticide programme allows their survival.

most OPs and to carbaryl (9, 21). The presence of these resistant predators in orchards makes possible an approach to IPM in which OPs or carbaryl are used against aphid and moth pests, leaving resistant *T. pyri* to attack phytophagous mites (e.g. 24) (Table 1). The predatory mirids and anthocorids are killed by these insecticides, but *T. pyri* alone is capable of regulating *P. ulmi* and the rust mite, *A. schlechtendali*, at a low level in most years.

Effects of fungicides on *Typhlodromus pyri*

This relationship of *T. pyri* with the phytophagous mites on which it preys is the central theme of IPM in apple orchards, but it is rather sensitive to disruption by agrochemicals, including fungicides. When assessing the potential threat to the system posed by any particular chemical it is necessary to consider the relative toxicity to *T. pyri* and to the phytophagous mites, particularly *P. ulmi* (Table 2). Those chemicals with little or no toxicity to either species (a "neutral" effect), can be used without disturbing the balance between predator and prey. Fortunately, most of the fungicides used in apple orchards are in this category, as are the selective insecticides diflubenzuron and pirimicarb. Provided that the *T. pyri* in the orchard are OP-resistant, then most OP insecticides and carbaryl are also neutral. Chemicals with an approximately equal toxicity to both species ("suppressive") may lead to outbreaks of *P. ulmi*, because this species has a faster reproductive rate than *T. pyri* and can recover more quickly following treatment.

Table 1. Two pesticide programmes that exploit the action of predators against the mite, *Panonychus ulmi*, on apple.

	Selective programme	**Organophosphate (OP) based programme**
Panonychus ulmi	predatory insects (mirids, anthocorids)	OP-resistant *Typhlodromus pyri*
Aphids	pirimicarb	OP
Cydia pomonella + other *Lepidoptera*	diflubenzuron	OP or carbaryl
Diseases (mildew, scab)	non-acaricidal fungicides (see Table 2)	non-acaricidal fungicides

The fungicides dinocap, sulphur and binapacryl (the latter widely used until 1987) are all moderately toxic to both species; their use tends indirectly to increase *P. ulmi*. Also "suppressive" with a rather high toxicity to both *T. pyri* and *P. ulmi*, are the acaricide amitraz and the acaricidal pyrethroid insecticide fenpropathrin. "Disruptive" pesticides, such as most synthetic pyrethroids, are even more damaging because they are very toxic to *T. pyri* and hardly at all to *P. ulmi*; no fungicides are in this category. A few "corrective" acaricides, but no fungicides, have the very desirable combination of properties of high toxicity to *P. ulmi* and low toxicity to *T. pyri*.

Particular insecticides and acaricides may be applied only once or twice during a season, so a small "suppressive" effect, reducing *T. pyri* populations by perhaps 10 or 20%, may cause no serious perturbation of its relationship with *P. ulmi*. A similar level of activity in a fungicide that may be applied many times during a season would, of course, have a much greater cumulative effect on *T.*

Table 2. Some orchard pesticides categorised according to their relative toxicity to *Panonychus ulmi* and OP-resistant *Typhlodromus pyri* and [modified from (10)]

Category	Toxicity to		Pesticides	
	T. pyri	*P. ulmi*	Insecticides/acaricides	Fungicide
Disruptive	xxx	o-x	cypermethrin, deltamethrin (pyrethroids); pirimiphos-methyl, dimethoate (OPs)	
Suppressive	xx-xxx	xx-xxx	fenpropathrin(acaricidal pyrethroid); amitraz (acaricide)	dinocap, sulphur, benomyl, carbendazim
Neutral	o-x	o-x	diflubenzuron, pirimicarb, carbaryl; Most OP insecticides	bupirimate, fenarimol, triadimefon, captan, dodine, dithianon
Corrective	o-x	xxx	tetradifon, clofentezine (acaricides)	

o - no toxicity; x - low; xx - moderate; xxx - high toxicity *pyri*. Ten applications of a fungicide that kills 10% of a population with each application results in a total reduction of 65%; if a single application kills 20%, then the total reduction after ten applications is 89%. A mortality of 20% or less may well go undetected in a laboratory bioassay; it is only after a programme of repeated applications, more easily carried out in the field, that this level of activity would become clear.

Economic influence of multiple applications of fungicides

It is desirable that growers use a system of pest monitoring procedures and treatment thresholds (e.g. 1, 14, 28). Thresholds reflect the economic injury level of the particular pest species; the rosy apple aphid, *Dysaphis plantaginea*, for example, which causes severe damage to developing fruits, has a zero threshold (i.e. no aphids of this species can be tolerated), whereas for the apple grass aphid, *Rhopalosiphum insertum*, which does not damage fruit, the threshold is high (five or more aphids on 50% of sampled trusses) (1, 14).

Pest management decisions are not, however, made in isolation; they take place within a framework of seventeen or so fungicide applications. If an insecticide or acaricide can be tank-mixed with a fungicide, then the cost of the treatment is effectively reduced to the cost of the chemical itself; the labour and machinery costs can be written off against the fungicide treatment.

In these circumstances there is an increased likelihood of risk-averse growers, and growers with no strong commitment to IPM, avoiding the task of monitoring and applying the chemical regardless, or of applying the chemical as an "insurance" even when monitoring does not indicate the necessity. Thus the fungicide spray programme can indirectly undermine IPM.

There are, on the other hand, circumstances in which the removal of the application costs from the equation can have a beneficial influence on pest management strategy. The codling moth (*Cydia pomonella*) granulosis virus (CpGV) is a potent and specific means of killing codling moth; it can be applied in aqueous suspension by conventional orchard spraying equipment (16). CpGV has, however, very short persistence in the field, being rapidly inactivated by sunlight (15). It has been shown that the virus is more effective against codling moth if, instead of being applied as two high-dose treatments, the same total quantity of virus is applied as a series of between four and nine weekly treatments mixing with several of the commonly-used orchard fungicides does not reduce its efficacy (3, 11). Thus, the existence of the framework of frequent fungicide applications makes possible an optimum application strategy for CpGV at no extra cost. This may well prove to be a critical factor in the future exploitation of CpGV, which is on the brink of large-scale commercialisation after more than ten years of reseach and development in various European countries.

Conclusion

As might be expected of a programme involving as many as 15-20 chemical applications a year, there is a high possibility of fungicides having an impact on pests, beneficials, and on the strategy for managing them. Merely by providing this framework of treatment dates on which the application costs are already committed, the fungicide programme may indirectly influence pest management philosophy, increasing the likelihood of a decision to apply an insecticide or acaricide. More likely to cause problems for pest management, however, are the toxic side effects of fungicides on predators. Some of these effects are not acute, and are, therefore, difficult to detect or attribute. Nevertheless, they influence pest management; an understanding of these effects is necessary if conflicting requirements in the management of pathogens and pests in orchards are to be avoided.

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Side effects of apple fungicides on beneficial organisms: results in Switzerland and practical aspects

M. Jermini, M. Baillod, A. Stäubli

Federal Agricultural Research Station of Changins, 1260 Nyon, Switzerland

Abstract

Results of the side effects of fungicides on *Anthocoridae* and phytoseiid mites (*Typhlodromus pyri* and *Amblyseius andersoni*) are shown. Application strategies in apple orchards are discussed in relation to certain fungicides and their harmful action against populations of beneficial organisms.

Key words: integrated pest management, apple diseases, apple pests, toxicity tests, chemical control, orchards.

Introduction

Nowadays, orchard crop protection is increasingly based on the concept of integrated pest management (IPM). In this context, pest and disease management are two subsidiary systems. Knowledge of the toxicity towards beneficial organisms of the various pesticides used in fruit growing is basic in the achievement of IPM. The choice of active ingredients becomes critical because of the implications for IPM and possible ecological repercussions. The use of damage thresholds, the introduction of various forms of biological control and the discovery of active ingredients increasingly more specific and selective have determined a major change in the strategic use of insecticides. Today, apple growers do not aim for the elimination of pests populations but for their regulation. Although much progress has been made with warning systems and with active ingredients, the control of the principal diseases is still based on many fungicide treatments, mainly to prevent infections. Fungicides are important in planning an integrated approach to the protection of apples from pests and pathogens. This article describes how it is possible to determine side effects of pesticides. Results concerning the side effects of some fungicides are presented, as well as examples showing how a fungicide can harm a population phytoseiid mites.

Determining the toxicity of a pesticide towards beneficial organisms

The toxicity of a pesticide is measured in stages, beginning in the laboratory and ending in the field (Fig. 1). Each test is standardized in order to enable results to be exchanged and discussed within the IOBC working group "Pesticides and Beneficial Organisms".

The main purpose of this procedure is to rapidly determine the toxicity of pesticides to beneficial organisms. The controlled laboratory test is the first phase. If a certain pesticide shows no harmful action in the laboratory its safety will be confirmed in the field. Laboratory tests do not consider the possible cumulative effects of repeated applications. Additional to laboratory results, therefore further verification is done in the field with at least three applications of the fungicide.

The field test is important because it represents orchard conditions, even though there are experimental disadvantages such as lack of uniformity, the uncontrolled influence of external factors and the population complexity of the beneficial organisms.

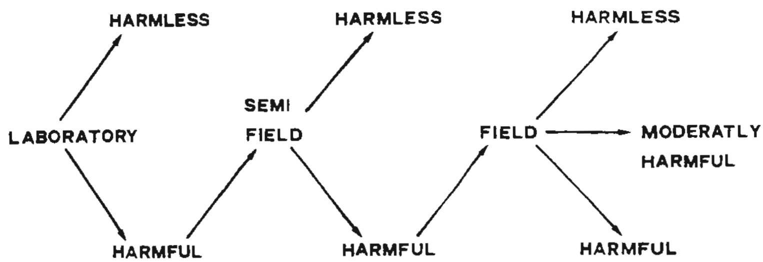

Fig. 1. Test procedures to measure the side effects of pesticides on beneficial organisms.

Toxicity results from Switzerland

In Switzerland, results of tests of the side effects of pesticides on beneficial organisms are collected by the Swiss Society for Phytiatry, and these include the results of laboratory, semi-field and field tests conducted in Swiss research institutes (3). These data show that most fungicides used in Switzerland range from harmless to slightly harmful to beneficial organisms. In fact, only the dithiocarbamate group and dinocap exert a harmful action against phytoseiid mites. Sulphur is harmful to the Coccinellidae, but for the phytoseiid mites its toxicity depends of the concentration of sulphur.

During recent years the research station at Changins has increased work on measuring the side effects of pesticides on beneficials used in orchards, giving particular attention to a species of *Anthocoridae* (*Anthocoris nemoralis*) and two species of phytoseiid mites, *Typhlodromus pyri* for the french part of Switzerland and *Amblyseius andersoni* for Ticino.

With the *Anthocoridae* (Table 1) fungicides so far tested in the field are rated harmless to slightly harmful. In laboratory trials on larvae of *Anthocoris nemoralis*, only maneb was moderately harmful.

Table 1. Toxicity of fungicides to *Anthocoridae* (7, 8, 9).

	Test in	
Active ingredient	**Laboratory**	**Field**
BITERTANOL	1	1
BUPIRIMATE		1
CAPTANE+PENCONAZOL	1	
DITHIANON	1	
FENARIMOL	1	
FENPROPIMORF	1	
FOLPET	1	
IPRODION	1	
MANEB	3	
METIRAM	1	
NUARIMOL	1	
OXYCHLORURE Cu	1	
PENCONAZOL	1	
PROPICONAZOL	1	
PROPINEB	1	
SULPHUR		2
TRIADIMEFON		2

1: harmless, 2: slightly harmful, 3: moderately harmful, 4: harmful

Table 2. Toxicity of fungicides to *Typhlodromus pyri* and *Amblyseius andersoni* (Baillod, 1987).

Active ingredient	Toxicity towards *T. pyri*	Toxicity towards *A. andersoni*
BITERTANOL	1	1
BUPIRIMATE	1	
CAPTAFOL	1	
COPPER	1	1
DICHLOFLUANID	2	2-3
DINOCAP	3-4	
DITHIANON	1	1
FENARIMOL	1	1
FOLPET	1	1
IPRODIONE	1	1
MANCOZEB	3	3
MANEB	3	
METIRAM	2-3	1-2
PENCONAZOL	1	1
PROCYMIDONE	1	1
PROPINEB	3	3
WETTABLE SULFUR 0.2%-0.5%	1-	3
SULFUR	2-3	
TRIADIMEFON	1	1
TRIADIMENOL	1	1
VINCLOZOLIN	1	1
ZINEB	3	3
CAPTANE+METIRAM	1-2	
CAPTANE+PENCONAZOL	1	1
DICHLOFLUANID+Cu	1	
FOLPET+Cu	1	
FOLPET+CYMOXANYL	1	
FOLPET+Cu+CYMOXANYL	1	
FOLPET+METALAXYL	1	1
FOLPET+OFURACE	1	
MANCOZEB+Cu	1-2	
METIRAM+CAPTANE+NITROTAL	2	
METIRAM+Cu	1-2	
NITROTAL+S	1-2	
PHOSETYL-AL+FOLPET	1	1
PROPINEB+Cu	1-2	
PYRIFENOX+CAPTANE	1	1
ZINEB+CAPTANE	2	
ZINEB+Cu	1-2	

1: harmless to slightly harmful, 2: moderately harmful, 3: harmful, 4: very harmful

With the phytoseiids, Table 2 confirms the toxicity of dithiocarbamates and dinocap and the harmless to moderately harmful action of sulphur and wettable sulphur, depending on concentration. These results also show differential toxicities to the two species: metiram is moderately harmful to harmful against *Typhlodromus pyri* but only harmless to moderately harmful against *Amblyseius andersoni*. A better example is that of methidathion and vamidothion. Both these organophosphorus insecticides are very harmful to *T. pyri* but harmless to *A. andersoni*. Such a difference between two species will change if a species (in this example *T. pyri*) develops a resistant strain.

Pest control using pesticides harmful to beneficial organisms: is it possible to use harmful fungicides?

In the management of pests the use of insecticides harmful to beneficial organisms is possible. For example, the product can be restricted to a part of the plant (localized treatment, Fig. 2,B), or to a sector of the field (mosaic treatment,

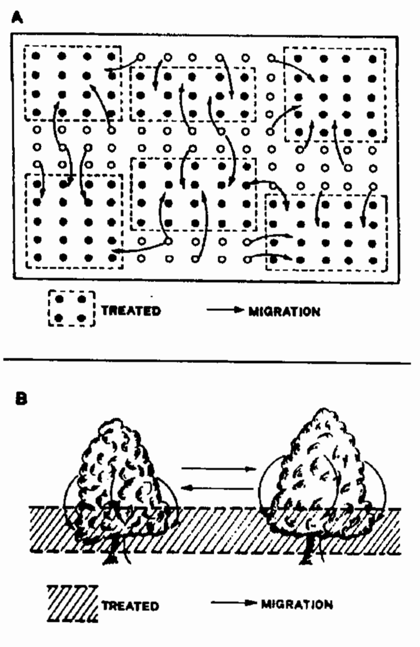

Fig. 2. Two techniques to avoid harming beneficial organisms with toxic pesticides: mosaic treatment (A) and localized treatment (B).

Fig. 2,A). These techniques allow the survival of beneficial organisms on the non-treated areas, from where they re-colonize the treated section of the orchard or tree.

These techniques are possible with some insecticides when relatively few interventions are needed and spaced in time. These techniques become impossible in the protection of orchards from disease, because pathogens exert a more continuous infection pressure over a long period of time and therefore compel the farmer to exert a continuous and overall protection of the plants. Fungicides are therefore potentially dangerous products for the maintenance of populations of beneficial organisms. Depending upon the active ingredient, fungicides may be considered limiting factors within integrated pest management strategies.

Factors other than intrinsic toxicity affecting effects of fungicides on beneficial organisms

Additional to the intrinsic toxicity of an active ingredient towards beneficial organisms, fungicide harmfulness can be influenced by other factors:

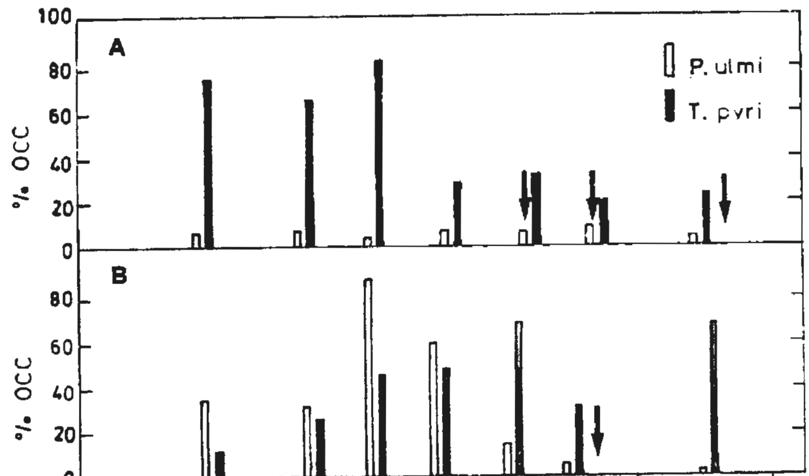

Fig 3. Side effects of dichlofluanid on *Typhlodromus pyri* in two apple orchards; (A) treated three times with dichlofluanid (8.8.86, 22.8.86 and 22.9.86) (B) treated only once (22.8.86) (4,5).

a) Number and timing of treatments

Experience in the field shows that in many cases a regular (routine) fungicide schedule may have a remarkable impact on the structure of populations of beneficial organisms. A typical example is mancozeb. If this fungicide is applied only once, at the time of appearance of the hibernating females of phytoseiid mites, its harmful action is limited because in their adult stage these predatory mites can fairly well resist this compound. If, however, mancozeb is applied repeatedly at regular intervals, it acts on other stages of development (larvae, nymphs), which are increasingly sensitive to it, and the consequence is the elimination of the beneficial populations. This illustrates another important point; the timing of applications in relation to the stage of development of the beneficial population. Another example is diclofluanid, for when applied three times in an orchard it can considerably slow the growth of populations of phytoseiid mites, so that they remain at a low density for the whole season (Fig. 3,A). One treatment with diclofluanid was harmless and the population of phytoseiid mites reached a normal density (Fig. 3,B).

An experience with diclofluanid in viticulture shows the same trend in viticulture as in apple culture (Table 3). In fact two treatments with diclofluanid may cause a mortality of 69% of the population 9 days after the last treatment. This harmful action was still evident 31 days after the last treatment. The other two fungicides tested in this experiment were harmless to *Amblyseius andersoni*. The number of applications is important because it can affect the toxicity of certain active ingredients. A fungicide that shows a slight or moderate harmful action in the laboratory may, for example, become toxic to beneficials in the field if it is applied regularly, often because it will exert continuously its action on some stages of the organism due to slowing down the development of the population.

Table 3. Evolution of populations and % mortality of *Amblyseius andersoni* on grape-vine 9 and 31 days after the last fungicide treatment [first treat. 17.6.87; second treat. 21.6.87 (6)].

	Phytoseiides/25 leaves		**% mortality**	
	Date		Date	
Active ingredient	30.6.87	22.7.87	30.6.87	22.7.87
FOLPET	33	38.67	27.13	10.76
THIRAM	34.33	36.67	24.27	15.37
CONTROL	45.33	43.30	--	--

b) application method

Any error in application or incorrect adjustment of the spray machine can affect, either positively or negatively, the populations of beneficial organisms. Also important is the choice of machine in relation to the type of orchard.

c) concentration

This factor is sometimes ignored, but in the context of side effects it is important because fungicide toxicity to beneficials may vary with concentration. A classic example, more frequent in viticulture than in fruit growing, is the influence of sulfur and wettable sulfur on phytoseiid mites. On *T. pyri*, a concentration of 0.2% wettable sulfur is harmless to slightly harmful, while concentrations over 0.5% are harmful. This effect interacts with other factors, in particular the volume of water applied per hectare.

Conclusion

In the context of integrated pest management, fungicides play a role as important as insecticides; their choice is very important. This has been brought into prominence in the spray programme for apple disease and insect control recommended by the Swiss Federal Agricultural Research Station of Changins (1), in which integrated pest management has been stressed. The guide shows how to maintain populations of beneficial organisms and also lists acceptable chemical agents for this purpose. The guide points to negative effects of these products. If in the past there were conflicts between the aims of pathologists and entomologists in Switzerland, nowadays the situation has changed because both groups of specialists are working for the same purpose: the achievement of integrated management. Therefore, in the development and, later, in the choice of an active ingredient, the pathologist considers its side effects on beneficial organisms as well as its efficacy against the target pathogens. In this way it is possible to rationally integrate pest and disease management programmes.

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Fungicide side effects on the dynamics of an acarine predator-prey system in apple orchards: an explorative study with simulation models

J. Baumgärtner, M. Bieri, A. Klay, M. Genini, and Ph. Zahner

Institute for Plant Sciences ETH,Division of Phytomedicine, CH-8092 Zurich, Switzerland

Abstract

The integrated pest management (IPM) concept requires the use of compatible pest control measures. Unfortunately, the application of many fungicides does not meet this requirement, because they negatively affect natural enemies of arthropod pests. The sensitivity of the phytoseiid predator *Typhlodromus pyri* Scheuten to fungicides, for example, has been studied experimentally because the mite is a useful control agent of spider mites in IPM programs. A demographic, tritrophic simulation model of the dynamics of apple tree growth and of interactions between the European red spider mite *Panonychus ulmi* (Koch) and the phytoseiid predator *T. pyri* has already been validated and subjected to sensitivity analyses, and is available for application work such as the investigation of temporal effects of fungicide applications. In this study, however, we use a simplified version of the model which reduces the tree growth module to a leaf growth function and considers half a growing season only. Furthermore, only a particular case is investigated: the initial predator-prey ratio is set to 2:250, and the temperature data recorded in 1980 at the meteorological station Sion (Valais, Switzerland) are used to drive the model. The fungicides are applied at 12-day intervals beginning 5 days after bud break, and they affect the daily survival of either all (study a) or only immature mobile (study b) life stages. The effect of different survival rates is expressed in mite-days accumulated during the period under study. The response surface obtained when plotting the final mite-days against predator and prey survival differs considerably between the two studies. Much higher values are obtained in study (a) where adult predators are affected. In addition, the results indicate that spider mite outbreaks occur if the survival of all predator life stages is reduced by ≥30%. These results demonstrate the potential of the model for evaluating the side effects of pesticides. However, they are specific to the particular case under study and more work is undoubtedly needed to draw general conclusions on the interference of fungicides with biological control of spider mites.

Key words: IPM, *Typhlodromus pyri, Panonychus ulmi,* beneficial organisms, pest control, population dynamics, tree growth.

Introduction

In 1980 a project entitled 'analysis of the apple tree ecosystem' was initiated at the division of Phytomedicine ETH, Zürich (6). In this work a demographic approach was used because other analyses had already shown the promises of applying population theory to agroecosystems analysis (7,16,18,19). Consequently, it was assumed that apple trees and their subunits (leaves, shoots, fruits and roots) had demographic qualities, and that their dynamics could be analyzed similar to the dynamics of associated arthropod or disease populations. Furthermore, populations were considered as integral elements of the apple tree system, whose yield formation is conditioned by population interactions (5). Empirical evidence suggests that the degree of interaction varies considerably between the different populations: some interact strongly with each other and form therefore a subsystem. Such a subsystem may have weak links to other subsystems with a similar internal organization. The age structure of each population is considered as an important demographic element. Because it often changes through time, simulation models were found necessary to analyze the temporal dynamics of the different populations (7,11,16,32).

This study addresses the apple tree-mite subsystem which is composed of apple trees and their subunits (components), the phytophagous mites *Panonychus ulmi* (Koch) and *Tetranychus urticae* Koch, and the phytoseiid predator *Typhlodromus pyri* Scheuten. The individuals of the acarine populations pass through distinct life stages in their development, which are considered important enough to divide the acarine populations into components of eggs, larvae and nymphs, and adults (phytophagous mites) or eggs, larvae, nymphs, adult females and adult males (*T. pyri*).

At the beginning of the analysis neither *T. pyri* nor other natural enemies of spider mites were present in the orchard under study, and the dynamics of *P. ulmi* and *T. urticae* were controlled by the influences of host plant characteristics and weather; chemical control was the only measure available to the decision maker to keep the mite populations below a critical density (1,34,35,36). However, a sensitivity analysis of the population model with respect to the timing of acaricide applications showed that threshold-based mite control was inefficient. The acaricides available at that time killed only postembryonal life stages, hence the age structure of the target population needed to be considered to time the applications. For the conditions under study the period at the end of the hatching of winter eggs and the beginning of summer egg hatching was most appropriate for the first chemical control operation (8). Today, the decision-maker can use acaricides with egg toxicity. Therefore, the age structure may be less important, but no study with the population model has been undertaken so far to verify this point. Instead, it was found more important to investigate the high colonization rate by *T. urticae* observed in the experimental orchard (35), and a subsequent study showed that this was dependent on the management of the orchard floor. If the ground was covered by graminaceous plants rather than subjected to herbicide treatments, the movement of *T. urticae* into the tree crown was greatly reduced (3). At the same time the phytoseiid predator *T. pyri* was established in the experimental orchards and population models were constructed to investigate the acarine predator-prey interactions (2,13,14,21). Although these studies will be the basis of the evaluation of fungicide side effects in this paper, a detailed presentation of the relevant work is avoided.

As in many other fruit-growing areas the control of spider mites by *T. pyri* was satisfactory but sensitive to pesticide disruption. For example, in one orchard under study an outbreak of San José scale *Quadraspidiotus perniciosus* (Comstock) required the use of an insecticide which disrupted the acarine predator-prey system. Likewise, some fungicides were found harmful to the predator population, and decision makers were recommended to avoid applying them in orchards subjected to biological mite control (9). The toxic effect of fungicides was mainly assessed in the laboratory, and the extrapolation of the results to field conditions is therefore difficult. However, field experimentation with multiple applications of a pesticide affecting tritrophic population interactions is difficult for many reasons. For example, great investments have to be made to follow the behaviour of the acarine systems in orchards subjected to different spraying programs. As an alternative to field experimentation population models are used here to explore the response of the acarine system to different levels of fungicide-induced toxicities.

From a theoretical standpoint the work addresses exclusively the application of a simulation model (12). This is possible because model validation and sensitivity analyses have already been carried out and can be referred to in the subsequent sections.

Material and methods

Description of the aging process

The index j is used throughout this work for state variables. An apple tree is composed of leaf (j=1), shoot (j=2), fruit (j=3) and root (j=4) components which develop on a perennial frame (j=5). To obtain the total weight of a tree reserves (j=6) have to be added. Because *T. urticae* was missing in the orchards with *T. pyri* presence, it is disregarded in this study. The *P. ulmi* population comprises four life stages (components): winter eggs (j=7), summer eggs (j=8), immature mobile stages (j=9) and adults (j=10). The *T. pyri* population is divided into the following components: egg and larval stages (j=11), nymphal stages (j=12), adult male (j=13), non-diapausing adult females (j=14) and diapausing adult female (j=15). The development of all components (j=1,15) is expressed in physiological units of daydegrees, implying a linear relation between temperature and aging rate above a lower component-specific threshold. In general, this linear model proved to be adequate under Swiss conditions (5). Consequently, developmental times of immature mite stages as well as longevities of tree components and adult mites can be conveniently represented by a thermal constant (15). However, the developmental rate or the aging of feeding predator life stages (j=12,13,14,15) also depends on food availability: the aging rate is slower under conditions of limited food (13,18,21).

The aging process differs between individuals, hence variance in developmental times for immature mites (j=7,8,9,11,12), life spans for tree organs (j=1,2,3,4) and longevities of adult mites (j=10,13,14,15) were taken into account. Time varying age structures and variabilities in aging processes are appropriately represented by distributed delay models (18). Because, in the system under study, developmental times and longevities are represented by thermal constants, time-invariant rather than time-varying distributed delays are used (7, 23, 30). A time-invariant distributed delay can be modelled with a set of cascaded delay substages, and the equations for storage in the delay are given by (30).

$$dQ_{j,1}(t)/dt = x_j(t) - r_{j,1}(t) - \mu_j(t) \cdot Q_{j,1}(t)$$

$$dQ_{j,2}(t)/dt = r_{j,1}(t) - r_{j,2}(t) - \mu_j(t) \cdot Q_{j,2}(t) \qquad [1]$$

$$\vdots$$

$$dQ_{j,k}(t)/dt = r_{j,k-1}(t) - y_j(t) - \mu_j(t) \cdot Q_{j,k}(t)$$

where i = index denoting the substage (i=1,k),

k = number of substages (order of the delay), specific to a component j and corresponding to the ratio of the estimated developmental time D_j to its variance s_j ($k=D_j^2/s_j^2$),

j = index denoting the components (see text),

$r_{j,i}(t)$ = transition rate from substage i into substage i+1,

$Q_{j,k}(t)$ = storage (mass for tree components or number of mite stages) in substage i,

$\mu_j(t)$ = growth or loss (death) rate due to population interactions (see below) or mortalities

$x_j(t)$ = input in substage 1 of component j (initial mass of tree organs j=1,4, initial winter egg densities of *P.ulmi*, initial number of overwintering females for *T. pyri* and egg numbers laid subsequently by adult females of *P. ulmi* and *T. pyri*),

$y_j(t)$ = output rates for component j (e.g. drop of leaves and fruits that were not harvested, mass of shoots and roots that becomes part of the frame, the passage of mites to the subsequent life stages, their intrinsic death rate at the end of the adult stage).

Initial numbers are assigned to the different components which change during the aging process according to mortality and fecundity schedules, but migration is disregarded in the model under study. For simulation purposes, it is more convenient to write eqn. 1 in terms of flow rates (30), so that the equation for substage i becomes:

$$dr_{j,i}(t)/dt = k/D_j \cdot \{r_{j,i-1}(t) - [1 - \mu_j(t) \cdot D_j/k] \cdot r_{j,i}(t)\} \qquad [2]$$

with $r_{j,0}(t) = x_j(t)$ and $r_{j,k}(t) = y_j(t)$

Eqn. 2 is used to simulate the development of all components j in the delay process with a time step of 1 daydegree. The reader is referred to (7,11,15) for a detailed discussion of temperature profiles and the computations of physiological time units. A discussion of the relevant parameters for eqn. 2 would undoubtedly go beyond the scope of this work and interested readers may consult the papers of (10,35) as well as the PhD theses (14,21), extracts of which are currently prepared for publication.

Nevertheless, a brief discussion of relevant population interactions is given here because it is a prerequisite for the understanding of the model. As opposed to the aging process presented above, they are simulated with a time step of 1 day to save computer time.

Population interactions

Competition for carbohydrates among tree components

The metabolic pool model (16,1,18,19) is used to model tree growth and development (10). Briefly, the arguments of (19) are followed and genetically controlled maximum demand rates for carbohydrates to leaves (j=1), shoots (j=2), fruits (j=3), roots (j=4), the frame (j=5) and the reserves (j=6) are assigned. In the currently-used tree model the demand of shoots and roots is assumed to decrease with decreasing daylength. Respiration processes (maintenance and conversion) also require carbohydrates and their demand has to be added to the above demand rates to obtain the total demand $B_1(d)$ rate per day (d):

$$B_1(d) = \{\sum_{j=1}^{6} b_j \cdot (1/z_1) + \sum_{j=1}^{6} M_j \cdot z_{2,j} \cdot (T)\} \cdot \Delta u \qquad [3]$$

where b_j = demand for organ j per daydegree (estimated from field observations or simulation studies),

M_j = mass per organ j,

z_1 = coefficient for converting assimilates S(d), eqn. 4, into plant material, 0.72 (see 31)

$z_{2,j}$ = maintenance respiration of organ j (see 27)

T = temperature,

Δu = number of daydegrees, above a common threshold for all tree components, accumulated per day.

$B_1(d)$ is embedded in the photosynthesis function to model the sink effect on the photosynthesis of the tree (18,19). With the following equation including the available reserves R(d), the amount of carbohydrates S(d) available per day can be calculated:

$$S(d) = \Omega \cdot E(d) \cdot \{1 - \exp[\{-B_1(d)/(\Omega \cdot E(d))\} \cdot \{1 - \exp(-(s \cdot \Omega \cdot E(d)/B_1(d)))\}]\} + 0.05 \cdot R(d)$$

where E(d) = global radiation in cal cm^{-2} day^{-1} per unit surface shadowed by an apple tree (20),

Ω = coefficient for converting radiation into CH_2O m^{-2} day^{-1} (22), i.e. 3.875 (19),

s = search rate of photosynthetically active organs [calculated from Beer's law for a single tree (after 20)]

$$s = \exp(-0.6 \cdot I/A) \qquad [5]$$

where I = surface of photosynthetically active organs,
A = area shadowed by a tree.

R(d) = reserves, i.e. 30% of the weight of a tree at the beginning of the growing season (see 28), but weight differs according to rootstock and cultivar (25),

A priority scheme is subsequently used to allocate the available carbohydrates to basic respiration and growth processes: Respiration costs are covered first, the demand of fruits is satisfied next, remaining carbohydrates are subsequently used by leaves and shoots which have priority over roots, and reserves are assumed to have the lowest priority in the allocation process. If the demand of fruits cannot be met a proportion of fruit mass and numbers (equal to the relative carbohydrate deficit) is tagged and shed 10 days later via ($\mu_3(t)<1.0$) in eqn. 2. However, if their demand can be satisfied they grow via ($\mu_3(t)>1.0$) in eqn. 2. Shedding occurs only at the beginning of fruit development; once the shedding window is closed the fruit number remains constant but the growth of the fruit mass is restricted. If the plant has no carbohydrates left that can be allocated to vegetative organs they stop growing (reserves may be decreasing, eqn. 5). However, if the demand of vegetative organs can be fully or partially satisfied, leaf, shoot and root growth is simulated via the input rates x_j in eqn. 1. This procedure enables us to simulate age structures of vegetative components throughout the growing season. Fruits are harvested 121 days after the T-stage (beginning of stem hollow formation) and leaves start dropping in fall once a frost has occurred.

Interactions between the tree and *P. ulmi*

As demonstrated in the cassava system (19), feeding stages of phytophagous mites can be easily added to the metabolic pool to study plant-mite interactions. In this work, however, we did not model the influence of *P. ulmi* on tree growth and development, because the mite numbers found under our growing conditions were considered too low to produce any significant effect on growth and development of tree organs. In northern Italy, no noticeable affect on tree productivity was produced by up to 42 mites feeding on an apple leaf (26), and this number is much higher than the density of two to four mobile stages tolerated in the experimental orchards under study (1,34). However, in the model there is an influence of host plant quality on mite fecundity. As mentioned above, the tree model permits the computation of an average age a(d) of the leaf mass present at any point in time. Thus, if leaf age is accepted as a surrogate for leaf quality and if one neglects aspects of spatial distributions, the fecundity rate $e_1(t)$ per daydegree of *P. ulmi* adults can be calculated after eqn. 6 and used as input into the egg stages $x_1(t)$ or $x_2(t)$ in eqn. 1:

$$e_1(t) = f_1\{\tilde{a}(d)\} \cdot \varnothing \cdot \sum_{i=1}^{k}(r_{10,i}(t) \cdot D_{10}/k \cdot m_i) \qquad [6]$$

where $f_1\{\tilde{a}(d)\}$ = reduction in fecundity due to average leaf age $\tilde{a}(d)$,

$\varnothing$ = sex ratio (assumed to be constant throughout the year),

$r_{10,i}(t)$ = transition rates between substages i and i+1

m_i = per capita fecundity per daydegree of females in substage i

D_{10} = adult longevity in daydegrees,

k = order of the process for the adult stage.

Photoperiod and temperature control the flow of eggs $e_1(t)$ in either the diapausing winter egg (x_1) or the summer egg (x_2) population component. The reader is referred to (35) for a more detailed description of the relevant processes.

Interactions between *P. ulmi* and *T. pyri*

The metabolic pool model is a conceptual framework for the formulation of the predator-prey interactions, i.e. for functional and numerical responses (7,17). In contrast to the plant model, emphasis was given to behavioural elements and preferences when the functional response model was constructed, while elements of nutritional physiology were embedded in the numerical response model (7,16,17,18). The global form of Ivlev's model (21,29) was considered the appropriate functional response model to calculate the number of attacked prey individuals, expressed in larval equivalents (21). Given the predator density P and the initial prey number N_0 (expressed in larval equivalents), eqn. 7 computes the number of prey individuals $N_a(.)$ (expressed also in larval equivalents) killed per day :

$$N_a(.)=(-1/a')\cdot\ln\{[1-\exp(a'\cdot B_2(d)\cdot p(.))]\cdot[\exp(a'.N_0)]+\exp[a'\cdot B_2(d)\cdot p(.)]\} \quad [7]$$

where a' = search rate which considers the nutritional value of the different prey components, and is obtained from a series of observations made in a complex searching environment (21).

N_0 = number of prey individuals expressed in larval equivalents per leaf (all immature stages of the predator *T. pyri* are included in N_0 to represent cannibalism).

$B_2(d)$ = the demand rate of all feeding predator life stages combined (i.e. excluding eggs and larvae) expressed in larval equivalents,

$p(.)$ = proportion of time the predators spent on leaves. The ratio of dry matter supply to demand (as a surrogate for hunger) controls the time spent searching on a leaf. The greater the relative food deficit, the more leaves are visited by the predators, and the more time is lost as transition time on prey-free shoots between leaves.

The number of larval equivalents acquired $N_a(.)$ per day inflicts a mortality among the prey components ($N_{a,j}$) and permits predator reproduction. A detailed presentation of the distribution of the mortality among the j-th prey component (*P. ulmi* nymphs and adults but not eggs, *T. pyri* eggs, larvae and nymphs) goes beyond the scope of this work and interested readers are referred to (21,24) for a detailed discussion. Although the food-related reproduction rate $e_2(d)$, as well as the mortality and aging rates of predators, is considered to be of more general interest it is mentioned only briefly. A more detailed explanation is given by (18,21). The input function $x_j(t)$ for the predator egg component (eqn. 1) is calculated by dividing the daily egg production by the number of daydegrees, accumulated per day.

$$e_2(t) = \{z_{1,14} \cdot N_{a,14} - z_{2,14}(M_{14},T)\} / \Delta u \qquad [8]$$

where $z_{1,14}$ = conversion coefficient specific to predator females with mass M (j=14),

$z_{2,14}$ = maintenance respiration of female predators (j=14)

$N_{a,14}$ = amount of food allocated to predator females.

The supply-demand ratio $\{N_a(d)/B_2(d)\}$ is also used to correct aging rates of feeding predator life stages, and affects the daily survival of the feeding predator life stages. This is accomplished in the model by multiplying daily the storage $Q_{j,i}$ of eqn. 1 (having an average age a_i) with

$$\{1-v_i \cdot [1-N_{a,j}(d)/B_2(d)] \cdot a_i/(a_i+1)\}^{\Delta u(d)}$$

where v_i represents the approximated intrinsic mortality rate per daydegree in substage i (14,21), and other symbols have been defined above.

Model simplifications

In this paper the tritrophic model comprising the tree, *P.ulmi* and *T. pyri* components is used to demonstrate the temporal behaviour of the subsystem. However, to explore the side effect of fungicides on the dynamics of the two predator populations a simplified version is used. Fig. 1 is taken from (1) and gives merely an overview of this model, but does not reflect accurately the model components as defined above. An obvious way to simplify the model is to shorten the period investigated. By starting at budbreak and restrict the period to 154 days, the influence of leaf age on mite fecundity can be neglected. Furthermore, the process of entering into diapause by predator females and *P. ulmi* eggs is avoided. By confining the interaction to a single shoot, a simple polynomial regression model to describe the number of leaves replaces the tree model (21). The number L(d) of leaves present on the shoot under study is expressed as a function of $Tsum_{>4.4^{\circ}C}$, i.e. the number of daydegrees above the 4.4°C developmental threshold

$$L(d) = c \cdot (-\,1.4871^{-5} \cdot (dd^4) + 1.8914^{-3} \cdot (dd^3) - 7.4712 \cdot (dd^2) + 1.3247 \cdot dd + 8.0143) \qquad [9]$$

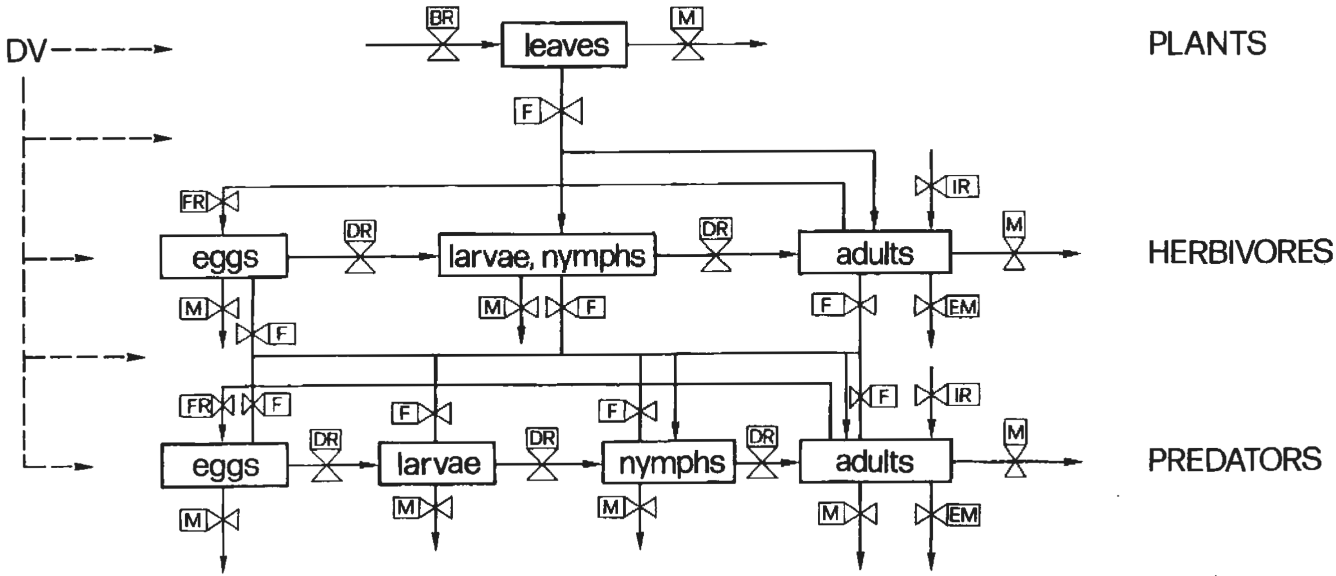

Fig. 1. Relational diagram for the simplified model operating under the influence of driving variables (DV): rectangles denote mass or densities and valves denote rates (BR=birth rates for leaves, F=feeding rates or functional responses, FR=fecundity rates related to numerical responses, DR=developmental rates, EM/IR= emigration or immigration rates, M=mortality rates due to other factors than trophic interactions). The state variables (rectangles) do not correspond exactly to the age groups defined in the text.

where dd = $(Tsum_{>4.4^{\circ}C})/15.6$

c = empirical constant used to adjust laboratory conditions to field conditions (c=0.5)

Model initialization

For the complete model, weather data from Sion (Valais, Switzerland) in 1980 was used because the apple tree system was intensively studied at this time (33). In the experimental orchard near Nyon (Vaud, Switzerland), 960 opening buds (initial shoots and leaves) and 2012 flower buds at the beginning of the growing season were counted, the estimated weight of an eight-year-old Golden Delicious tree was 32 kg dry matter, and 11.2 m^2 ground area was available for the tree, but only 40% was shadowed (14). 2270 winter eggs of *P. ulmi* and 400 adult females of *T. pyri* were estimated at the beginning of the growing season (14).

The simplified model starts at budbreak on day 82, while egg hatching and mite interactions start 50 days later, i.e. at the time maximum egg hatching of *P. ulmi* was observed in the field (33). 250 winter eggs of *P. ulmi* and 2.0 adult *T. pyri* females were estimated to be present around a bud which, during the growing season, produces leaves as described by eqn. 9.

Evaluation of fungicides

The effect of fungicides was built into the simplified model in two different ways. First, fungicides were assumed to kill all life stages of both the predator and the prey. Second, mobile immature life stages only were killed, because they are known to be most sensitive to fungicides among the mite life stages (4). Unlike in the study on acaricide effects on spider mites (8), the dynamics of the fungicide effect were not included. Only after maximum egg hatching a proportion of the sensitive life stages was killed on the day the chemical was applied. i.e. on every 12th day. The first fungicide treatment was carried out on the 5th day after bud break. The effect of mites feeding on the plant was expressed in mite-days, i.e. the number of feeding life stages present (immature life stages were assumed to have smaller consumption rates than adults). Each day the number of mite-days was computed and added to the sum of the previously accumulated mite-days. On the day of fungicide treatment, the proportion of mites killed varied by 0.1 between 0 and 1.0 for both the prey and the predator. Therefore, the evaluation study produced on eleven occasions eleven different numbers of mite-days, which are used to define a response surface.

Results and discussion

Fig. 2 summarizes the growth pattern of a tree and the dynamics of phytophagous and predatory mites as represented by the tritrophic population model. After bud break (BB), the number of leaves increases until reaching a plateau, which is because carbohydrate production (eqn. 4) is unable to meet the high demand of the growing fruits. Because the number of leaves varies through time, the spatial dimension for predator-prey interactions changes; at the beginning the predators have to search a greater area to find the same number of prey individuals. Spatial features have already been identified as important factors in acarine predator-prey systems (9), hence this aspect is not pursued here. The relative carbohydrate deficit decreases the number of fruits (JD= June drop) as long as the shedding window is open. Later, the number of fruits is not affected until harvest (H): if the carbohydrate supply is unable to meet the demand the growth rate of the fruits is reduced. Leaf drop (LD) begins as soon as the first frost has occurred in fall. This growth pattern has already been commented upon several times and interested readers are referred to (7,10,33) for more details. The *P. ulmi* density first increases and then drops to low numbers due to predation by *T. pyri*. The high initial predator-prey ratio is mainly responsible for

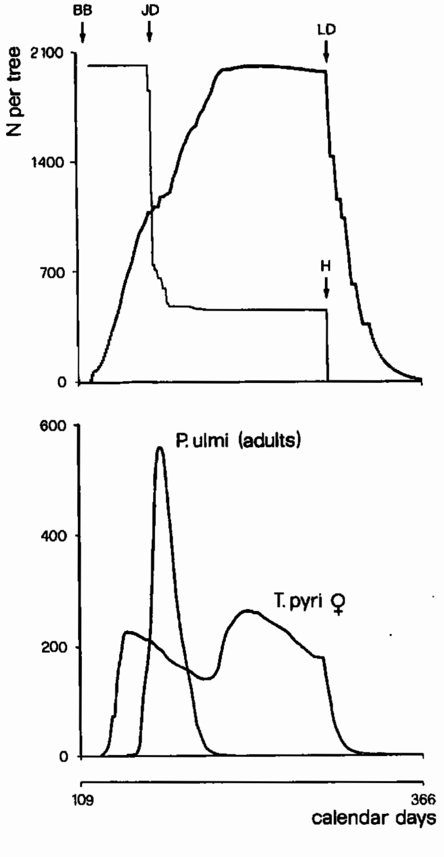

Fig. 2. Tree growth and mite dynamics simulated at Sion (Valais, Switzerland, in 1980) by the tritrophic population model. (The number of leaves with leaf drop = LD due to frost, the number of fruits affected by June drop = JD and harvest date = H, BB=bud break, mite numbers per tree).

quick control. It has typically been found in the first few years after successful predator introductions in Swiss apple orchards.

According to Fig. 3 a complicated pattern of predator-prey interactions is produced by the simplified model. The hatching larvae and the subsequent nymphal stages of *P. ulmi* are immediately attacked by predators, so that a relatively small percentage escape predation to reach the adult stage. Since the chance of survival is best for mites which develop fastest, noticeable egg numbers are laid only at the beginning of the appearance of prey adults. The predators, however, can find initially abundant food and reproduce quickly. Later, the prey available becomes scarce and the area to search increases because the prey is distributed on a larger number of leaves. This does not permit high predator numbers and the predator-prey system starts interacting at low mite densities. Therefore, the number of mite-days increases, first quickly but slowly at the end of the simulation period (Fig. 4). The difference between the two curves in Fig. 4 shows the effect of predation. If *T. pyri* is excluded from the system the number of mite-days reaches a much higher value.

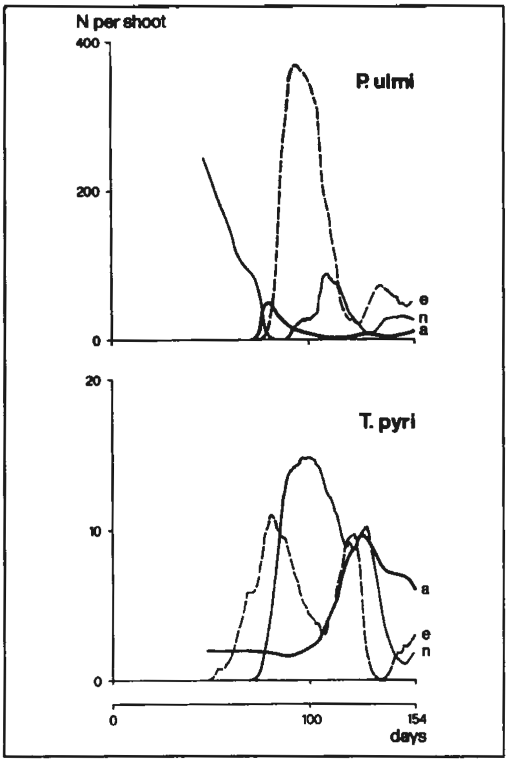

Fig. 3. The time-varying age structure of mite populations simulated by the simplified model. (Weather data recorded at Sion 1980, N = number, a= adults, n=nymphs, e=eggs).

Fig. 5 suggests that the number of mite-days increases quickly provided more than 30% of all predator life stages are killed, and *P. ulmi* outbreaks are prevented only if the prey suffers a similar amount of mortality. Fungicide side effects were only evaluated qualitatively (4), but the wide array of possible effects indicates that our response surface is realistic. If the fungicides kill immature mobile life stages but not adults, a lower number of mite-days is reached after the experimental period of 154 days (Fig. 6). This difference is due to the high prey consumption rate of adult predators which remain unaffected in the latter case. However, it is premature to conclude that fungicides affecting exclusively immature life stages are less disrupting to the acarine system: once adult predators have reached the end of their life span they need to be replaced by young adults to keep the system sustainable. In this temporally limited study this aspect cannot be addressed in a satisfactory way. Nevertheless, one can foresee that suppression of immature live stages can lead to low predator-prey ratios, both in the second half of the growing season and in the subsequent year, threatening the sustainability of the acarine system. In addition, the comparison between the shaded areas of the two simulation studies (Fig. 5, 6) suggests that a more complicated response surface is generated if the fungicide effect is age-dependent, and the outcome of predator-prey interactions is consequently more difficult to predict. Therefore, the susceptibility of different mite life stages to fungicides clearly deserves attention in any future study of fungicide side effects.

These results give insight into temporal effects of mortalities but do not permit the drawing of general conclusions. First, the effect of the fungicides was included in a simple way that did not take into account the persistence of the chemical. The models listed by (8) could permit the construction of a more realistic model on pesticide dynamics, which is likely to lower the critical number found in this study. Second, the model was evaluated under the weather condi-

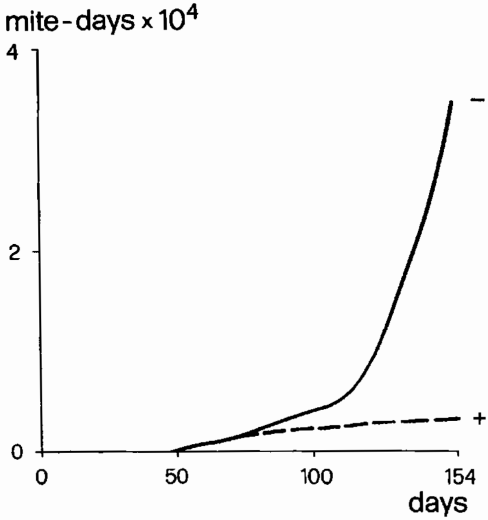

Fig. 4. The number of mite-days for *Panonychus ulmi* simulated with the simplified model in presence (+) and absence (-) of predators. (Weather data recorded at Sion 1980).

tions of one year only, and the outcome of the simulation studies is likely to be different if the weather patterns change. Third, the period investigated was restricted to 154 days to permit cost-efficient simulation studies. This restriction did not allow investigating of the temporal effect of diapause on prey and predatory mites in the current and at the beginning of the subsequent growing season. Fourth, it is difficult to draw general conclusions because predator-prey densities of a supposedly sustainable orchard system were used: there was no attempt to investigate the effect of initial mite numbers on the temporal behaviour of the acarine systems. This was a serious limitation because there is empirical evidence which stresses the importance of initial conditions.

Nevertheless, the results show the usefulness of dynamic population models with variable age structures to explore fungicide side effects. Among other results discussed above the study has enabled us to identify gaps in the current understanding of fungicide side effects on population interactions. The number of field studies required to obtain similar information clearly exceeds the practical capabilities of controlled experimentation. Even though the simulation studies yielded primarily qualitative information they appear, nevertheless, helpful for setting priorities for future research work and for designing relevant laboratory

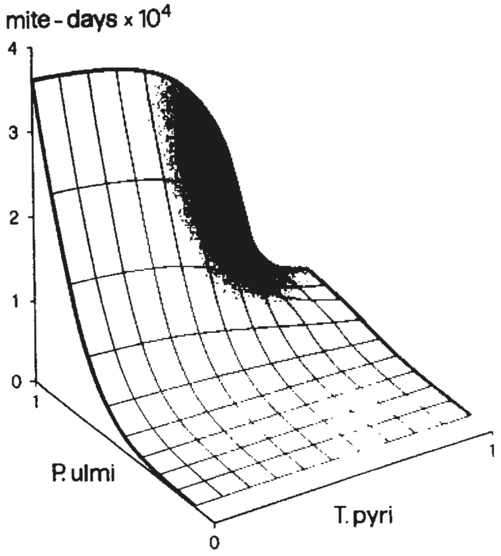

Fig. 5. The simulated number of mite-days for *Panonychus ulmi* accumulated 154 days after bud break: the survival of all life stages of both the prey (*P. ulmi*) and the predator (*Typhlodromus pyri*) is affected by fungicides. (Survival rates varying from 0 to 1.0).

and field experiments to obtain quantitative information. Thus the population model is concluded to be a complement and not a substitute for field experimentation. In the terminology of (12), the area of application is in directing further systems analysis and not in assisting the management and development of the real systems. Furthermore, the model has additional qualities not explored in this study. For example, it may become useful for the investigation of long-term effects of fungicide applications which are of particular interest in orchard crops. This is important because the mode of predator selection and introduction in this project has been directed towards sustainability of the acarine system; the ideal management policy should not rely on periodic predator releases or chemical control measures to correct predator-prey ratios.

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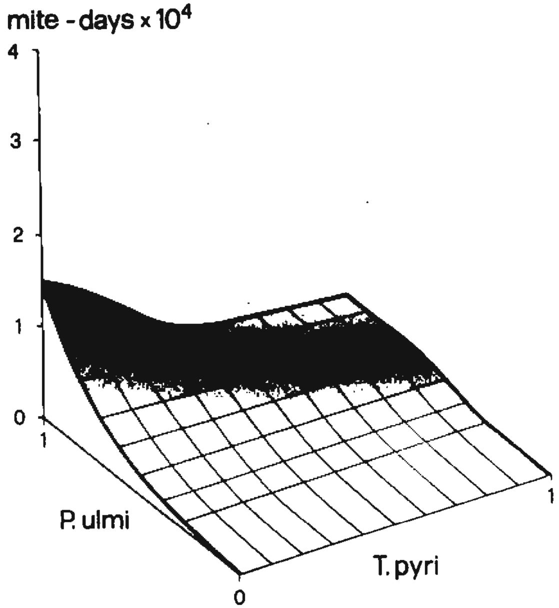

Fig. 6. The simulated number of mite-days for *Panonychus ulmi* accumulated 154 days after bud break: the survival of nymphs of both the prey (*P. ulmi*) and the predator (*Typhlodromus pyri*) is affected by fungicides. (Survival rates varying from 0 to 1.0).

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The choice of fungicide: a complex task for the apple grower

W. Waldner

South Tyrolean Advisory Service for Fruit and Winegrowing, Lana, Italy

Abstract

A glance at the spray schedule for any South Tyrolean apple orchard shows that fungicides dominate the chemical agents. Figure 1 illustrates this with two 1988 examples. In an orchard of cv. Golden Delicious (on M9) in the Vinschgau, the sprayed application/ha was 1-6 kg synthetic insecticide, 29,2 kg synthetic fungicide, and 60 kg mineral oil. In a cv. Rome Beauty orchard (seedling rootstock) in the Etsch Valley, the respective amounts were 9,2, 42,0 and 75 kg and also 18 kg sulphur. The complex basis for selecting a fungicide is discussed in the context of the spectrum of activity against the main pathogens, strategy to control scab (*Venturia inaequalis*), tenacity in rain, phytotoxicity, including effects on pollen, crop residues and toxicological factors. Fungicides are selected to minimise disturbance to the biological control of spider mite (*Panonychus ulmi*)

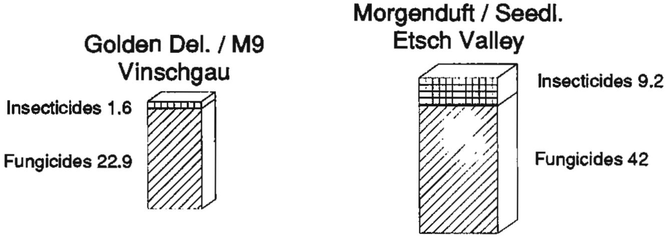

Fig. 1. Consumption (kg) of synthetic pesticides in two South Tyrolean apple orchards.

Key words: chemical control, phytotoxicity, curative treatments, residues, toxicology, pollen germination, *Venturia inaequalis*, side effects.

How do apple growers choose fungicides?

The South Tyrolean apple grower chooses a fungicide mainly because of its effect on a target fungus. In spring, from the green-tip stage to the end of ascospore release, effectiveness against apple scab (*Venturia inaequalis*) is a major consideration. In late summer, the grower chooses a product to control possible attacks of late scab and also pathogens causing post-harvest storage diseases.

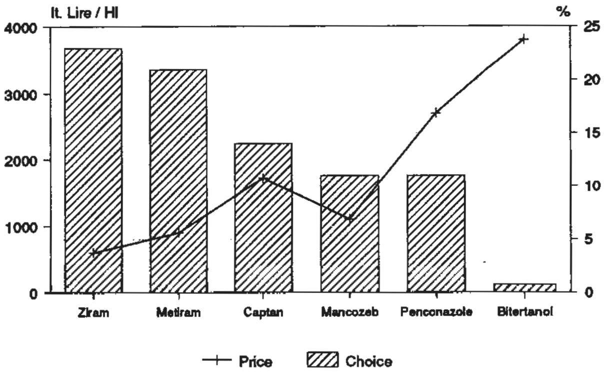

Fig. 2. Price (ital. lira/hl) and choice of some apple fungicides.

Table 1. Activity spectrum of some apple fungicides.

	Scab	Mildew	Gloeosp.	Botrytis	Phytophth.
Fosetyl-aluminium					O
Benzimidazoles	O	O	O	O	
Binapacryl		O			
Bitertanol	O	O			
Bupirimate		O			
Captan	O		O	O	
Oxythioquinox		O			
Dichlofluanid	O		O	O	
Dinocap		O			
Dithianon	O		O		
Dithiocarbamate	O				
Copper	O				O
Nitrothal-isopropyl		O			
ner sterol inhibitors	O	O			
Sulphur	O	O			
Triadimefon		O			
Dodine	O				
Pyrazophos		O			
TMTD	O			O	O

Table 2. Tenacity of fungicides to rainfall

zineb	15-20 mm
metiram, propineb, ziram	35-40 mm
captan, dithianon, dodine, mancozeb	50-60 mm

Table 1 shows a classification of fungicides and their effects on *Venturia, Podosphaera, Gloeosporium, Botrytis* and *Phytophthora*. Nevertheless, in spring, apple growers still have many products at their disposal. For later treatments they only have the choice of captan, dithianon; chlorothalonil and dichlofluanid. The latter is not registered in Italy for apples.

In the South Tyrol, apple growers still choose fungicides mainly according to price. As Fig. 2 shows, cheap scab fungicides are used much more than expensive ones. However, it is not only price that influences choice. Due to the extensive scab-warning system operated in the region, which is easily accessible to everybody, and to the small size of the farms, most South Tyrolean apple growers are able to respond to a scab warning within 5-6 hours, using the earliest oppor-

Table 3. Phytotoxicity and other harmful effects on apple cultivars of fungicides. o=not recommended, Golden=Golden Delicious, Red D=Red Delicious, Jonath=Jonathan, Granny=Granny Smith, Jonag=Jonagold, Morgend=Morgenduft

	Golden	Morgend.	Red D.	Jonath.	Gloster	Granny	Jonag.	Winesap	Idared	Elstar
Binapacryl	o									
Bupirimate	o	o							o	
Oxythioquinox	o									
Dinocap	o									
Nitrothal-Isopropyl										
Triadimefon	o									
Sulphur			o			o		o		
Sterol Inhibitors										
Captan			o					o		
Dichlofluanid	o									
Dodine	o			o			o			o
Dithianon										
Mancozeb	o						o			o
Metiram										
Propineb	o									
Ziram	o									
Zineb										
Copper	o			o			o		o	o

tunity to spray during or immediately after a Mills' period to control infection. The contact fungicides ziram, metiram and propineb have a curative effect if applied within 20-24 hours from the beginning of rainfall (1). If later than this, growers can apply mancozeb or captan to obtain a curative effect up to 30-36 hours, dithianon up to 36-48 hours, dodine up to 48-60 hours and finally sterol inhibitors up to 96 hours from the beginning of rainfall.

In the South Tyrol the proportion of sterol-inhibiting fungicides used is generally low. Pre-blossom, when there is little leaf surface available, the temperatures are too low for an optimal effect of this group of chemicals. Moreover, sterol inhibitors have practically no effect on pathogens causing storage diseases and are not well suited for the prevention of late scab on fruit. This reduces their usefulness against scab, but not against mildew (*Podosphaera leucotricha*). Where the danger of russeting is low, e.g. on the slopes in the Vinschgau, many growers use sterol inhibitors almost exclusively against scab and mildew in spring. These growers are advised to alternate groups of chemical agents so as not to induce resistant strains of scab: sterol inhibitors should be used only three or four times a season.

In general, growers are advised to use products that resist being washed off by rain (Table. 2).

Side effects on fruits and leaves

The first question a fruit grower asks about the possible side effects of a fungicide on his trees is "does the product cause russeting?". As Table 3 shows, the scab fungicides captan, dithianon, metiram and zineb can be used post-blossom on cultivars susceptible to russeting, especially Golden Delicious. On ideal Golden Delicious sites, sterol inhibitors can also be used during the critical period. In the valleys, wettable sulphur is mainly used to control mildew on Golden Deli-

Table 4. Effects of fungicides on pollen germination (%)

sulphur	85.1
fenarimol	76.0
triadimefon	74.5
bitertanol	70.2
ziram	67.3
dithianon	66.1
metiram	59.5
penconazole	36.2
mancozeb	8.0
captan	6.7

cious. The cultivars Red Delicious and Winesap do not tolerate captan until July; therefore metiram is preferred in mixed-cultivar orchards. There are also reservations on using mancozeb in unfavourable weather, because this material can cause leaf spots after repeated use in cool and wet conditions. Dithianon leaves an ugly brownish deposit on fruits, which cannot be prevented by the addition of a surfactant. Chlorothalonil-products have caused burnings of the fruit-skin on sites at high altitude and these products are rarely used as late-season sprays. Copper products are used only in the green tip stage, particularly to control *Pseudomonas* on Red Delicious. Bupirimate can be used only with reservations: Rome Beauty, Idared and Gravensteiner react to this product with leaf injuries, and fruits of Golden Delicious are liable to be russeted by post-blossom applications.

Side effects on apple pollen germination

The basic recommendation is to avoid any treatment during full blossom, if possible. Experiments (2) on pollen germination with fungicide-containing solutions have shown significant influences. More data are shown in Table 4. If scab control is necessary at full bloom it is advised to avoid captan and mancozeb, especially in years with poor bloom and unfavourable weather conditions. It is rare, however, to find a case where low yield can be ascribed with certainty to harmful effects on pollination.

Table 5. Toxicity of fungicides towards fish (carp).

chemical	LC 50 (ppm)	chemical	LC 50 (ppm)
ziram	0.075	sulphur	1.0
binapacril	0.1	dichlofluanid	1.0
chlorothalonil	0.11	dithianon	1.5
dinocap	0.16	metiram	1.7
dodine	0.17	nitrothal-Isopr.	3.1
folpet	0.20	mancozeb	4.0
captan	0.25	TMTD	4.0
copper sulphate	0.54	oxythioquinox	4.6
captafol	0.5	benomyl	7.5

Side effects on apple fruit size and yield

Three-year trials with sterol inhibitors at the local research station (3) have demonstrated that these products do not significantly diminish the average fruit weight (size) or the yield, even if applied frequently.

Side effects on the environment within apple orchards

Side effects of fungicides on phytoseiids and other predators of harmful spider mites are well explored and widely known. Test results (mainly those of the IOBC/WPRS subgroup "Side effects of pesticides on beneficial insects and mites") are adopted: binapacryl, oxythioquinox, dinocap, and pyrazophos have not been recommended since 1983. Unfortunately, some fungicides harmful to phytoseiids must be used because there are no alternatives. In these cases growers are advised to minimise their use. Growers who follow this advice can stop using acaricides after some years, thus cutting costs considerably.

The side effects of fungicides on earthworms are still ignored. Earthworms reduce the number of leaves on the ground and therefore the number of scab ascospores. The benzimidazole fungicides are highly noxious to earthworms and copper repels them (4), this being another reason why these products are recommended only in special cases.

None of the usual products is noxious to birds, except that ziram causes hens to lay eggs without shells. Progressive South Tyrolean apple growers have recently been trying to lure titmice and other singing birds into their orchards with the help of suitable breeding-cages, because these birds feed mainly on larvae.

Side effects on the environment outside apple orchards

When spraying near surface water fruit growers should keep in mind the toxicity of fungicides to aquatic animals, especially fish. According to Yoshida and Nishiuchi (5), ziram, binapacryl, chlorothalonil, dinocap, dodine, folpet, captan, copper sulphate and captafol are extremely poisonous to fish. The LC 50 for carp is, after 48 or more hours, less than 1 ppm of these products. Sulphur, dichlo-

Table 6. LD 50 of some pesticides

phosalone	120-170	dithianon	638
pirimicarb	147	dodine	1.000
ethiofencarb	411-499	ziram	1.400
diazinon	300-850	bitertanol	5.000
diflubenzuron	4640	captan	9.000

fluanid, mancozeb, TMTD, oxythioquinox and benomyl are also highly toxic to fish. (LC 50: 1-10 ppm, cf. Table 5).

The problem of pesticides, especially fungicides, contaminating drinking water is becoming more important since the EEC established a tolerance level for each pesticide at 0.1 ppb and a total for all pesticides at 0.5 ppb (6). In the Federal Republic of Germany (FRG) this will lead to the prohibition of 72 pesticides within water catchment areas: the list will include metalaxyl and nitrothal-isopropyl and is expected to also include sterol inhibitors.

Fungicide residues on marketed fruit.

When recommended harvest intervals and rates of use are observed and the various groups of fungicides are used alternately, the legally acceptable residue levels will not be exceeded. Some large Italian food chains, however, demand a higher standard. Italy's biggest chain, the COOP, offers consumers a range of products containing not more than 50 % of the residues allowed by law. If the residues exceed this limit, the suppliers are liable to pay a fine and make compensation for the financial loss. If fruit growers want to keep these markets they and their advisers must take these more demanding requirements into consideration. It is also necessary to be careful when selling to the producers of dietary products, including babyfoods. In this respect the legal maximum residue of pesticides in the FRG is, only 10 ppb.

Fungicides and human health

The most common measure of the acute toxicity of a pesticide is the LD 50. In this respect most fungicides are "safe" in comparison with insecticides (Table 6), but this "one-sided" view is outdated today. Public concern about the content of ETU in dithiocarbamates has caused the Italian Ministry of Health to limit the maximum content of this cancer-provoking compound in fungicides to 0.5 %. ETU can result when apples containing residues of most dithiocarbamates are cooked, and therefore most producers of babyfoods reject this group of agents. Some captanoids can cause mutations in bacteria and yeast. The Environment Protection Agency in the USA suspects captan to be mutagenic. Hayes (6) believes this agent to be toxic to human embryos. These reasons induced the Swedish authorities to prohibit captanoids, reducing the tolerance level to zero. Other Scandinavian countries will probably follow thicases example. The EEC has lowered the tolerance level for captan from 15 to 3 ppm, and captafol and folpet have been prohibited on apples. The FRG has withdrawn approval for the use of captan, and Austria is following in this regard the legislation of the FRG.

Babyfood producers refuse these agents, and also refuse to buy apples treated with copper products or sulphur. Copper is a heavy metal and sulphur interferes with the analysis of residues.

Conclusion

When apple growers take into consideration the harmful effects of certain fungicides on phytoseiid mites, the conflict between pest and disease control in orchards can largely be avoided. This has been proved in the South Tyrol in the last five years on about one thousand hectares of orchards.

It is necessary, however, to study the effects of fungicides on other, not so conspicuous and less economically interesting beneficial insects and species, inside and outside the orchard.

Problems arising from the application of fungicides such as the contamination of water and residues on fruits show the importance of breeding disease resistant cultivars and of less intensive use of fungicides through better disease management.

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Recommendations for future work

H. S. Aldwinckle

Cornell University, N.Y.S. Agr. Expt. Station,
Geneva, N.Y., 14456, USA

General: Use common terminology

Disease assessment: Critical to all aspects of integrated control, survey of current methods

General

1. Need better understanding of principles of disease measurement.
2. Assessment must be quantitative and qualitative.
3. Method must be adapted to particular disease and purpose.
4. Standardization must be strongly encouraged.
5. More use of damage, action, and economic thresholds.

Specific

1. Assessment of effective PAD of scab.
2. International project to determine incidence/severity relationship (for scab and mildew?).
3. Economically tolerable level of disease (e.g. scab) on fruit?

Epidemiology and forecasting

General

1. Need more knowledge of biology and epidemiology of pathogens and diseases.
2. Quantification of parameters of an epidemic (latent period length, sporulation quantity, infection period length, extension of lesions, etc.) on different cultivars (not only scab resistant cultivars).
3. Modeling of epidemics to evaluate the effect of changing the value of certain parameters through breeding and/or cultivation methods.

Specific

1. Quantification of infection periods.
2. Importance of conidia in primary inoculum.

3. Weather monitoring instrumentation:
   a) Good equipment available, b) Must be reprogrammable, c) Data storage desirable d) Interactive units desirable.
4. High resolution 48 hour weather forecast would be very useful.
5. Simplification of Billing's system for fire blight is welcomed. Orchard factors are critical.
6. Need information on degradation of chemicals.

Genetics of hosts and pathogens

General

- Stability of resistance.
- Need for international coordination.
- Terminology

Specific

- Genetics of host
  1. Genetics of resistance in apple to scab and mildew must be understood.
  2. "Minor genes" of additive effect in commercial cultivars must be considered as well as in resistance sources.
  3. Need to determine the mechanisms of resistance of different resistance genes at ultrastructural and biochemical levels.
  4. Need to study and use V genes other and Vf and new genes.
- Genetics of pathogens
  1. The genetic systems and life cycles of different pathogens must be considered.
  2. Must determine variation for virulence and fitness in populations of races of the pathogens.
  3. Must determine epidemiology of different races of pathogens.
  4. Must determine distribution of races (geographic and frequency in the population).

Cultivar development

1. Need for clear priorities for an expensive project with limited resources.
2. Establish relative priority of classical breeding and biotechnological methods.
3. Establish clear priority of quality requirements.
4. Establish relative priority among diseases and pests in relation to the country and prospective markets.
5. International coordination essential to avoid duplication as much as possible but essential work should be repeated independently.
6. Consideration of IPM methods available for control of certain pests.
7. Tolerance of advanced selections to selected foliar diseases may be productive.
8. Storage disorders are critical criteria.

9. Testing of disease/pest resistant cultivars is critical. Need for rapid submission of information and pathogen isolates to originating breeding team.

Integration of pest and disease Management

Effects of fungicides on predatory mites:

1) It is clear that small effects, or effects on only one stage in the life cycle are not serious if a fungicide is applied only once. Such effects may be difficult to detect in single-application tests. The problem is that fungicides are applied many times during a season. The model described by Marcus Bieri, while not offering a substitute for field experiments, does show clearly the importance of a small effect of a frequently-applied fungicide; it disrupts the predator/prey relationship, leading to an outbreak of spider mite.

2) In fungicide trials there may be a great deal of potential information on effects of fungicides on predatory mites. There is a valuable opportunity for collaboration between the pathologist and the entomologist. If we avoid the use of acaricides and acaricidal insecticides in those trials, then mites can be sampled so acaricidal effects of fungicides can be detected.

3) Effect of sulfur on phytoseiid mites.

Storage diseases

Objectives

- Reduce use of fungicides before and after harvest.
- Avoid harmful side effects of fungicides on beneficial organisms and the environment.

1. Breeding: must do effective early selection for resistance to fruit storage diseases to obtain new cultivars that combine high quality, disease resistance and good storage potential.
2. Cultural measures: a) Reduction of infection pressure by: (i) Proper picking time, (ii) Avoidance of bruises and other injuries, (iii) Elimination and control of cankers
   b) Increased natural resistance by influencing the mineral composition (Ca).
3. Technical measures: Cool fruit promptly at the lowest temperature in controlled atmospheres.
4. Chemical measures: a) How to avoid or to inhibit resistance? b) How to control fungal diseases already resistant?
   Possible solutions:
   1. New compounds
   2. Post harvest treatments: dipping, drenching, fogging