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Integrated management of diseases and insect pests of tree fruit

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NIAB EMR, UK

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Introduction

This volume reviews advances in understanding key diseases and insect pests of tree fruit. The chapters summarise current research on what causes key fungal diseases (apple scab, powdery mildew, apple replant diseases, apple canker and brown rot), and viral diseases (apple mosaic virus and plum pox). The volume discusses integrated fruit disease management techniques such as surveillance, breeding disease-resistant varieties, improved fungicide application including the use of biocontrol agents. Other chapters review the ecology of major insect pests (aphids, tortricid moths, mites and fruit flies). Chapters also address a wider range of tree fruit pest and ways of improving integrated pest management (IPM) techniques for tree fruit, from monitoring and forecasting to agronomic practices and methods of biological control.

Part 1 Fruit diseases

The first part of the book focuses on fruit diseases, starting with fungal diseases. Chapter 1 deals with apple scab (*Venturia inaequalis*) which is the most important disease on apple (*Malus* × *domestica*) worldwide. This fungus can infect both leaves and fruit. Although there are major resistance genes identified against *V. inaequalis*, nearly all commercial dessert cultivars are susceptible, thus requiring stringent control measures to minimise crop losses. The chapter introduces apple scab, explains the epidemiology of the disease, briefly describes management strategies.

Moving onto another fungal disease of fruit, Chapter 2 looks at powdery mildew. Tree fruits such as apple, cherry, apricot and peach, are amongst the most susceptible crops to powdery mildews. The fungus mostly affects vegetative tissues but can also infect the reproductive organs (flowers and fruits) of the tree. In the absence of appropriate management, multiple cycles of infections may significantly reduce tree vigour, fruit set and yield. The chapter summarises current knowledge on the biology, epidemiology, host resistance and control of powdery mildew species of apple (*Podosphaera leucotricha*) and cherry (*P. clandestina*).

The subject of Chapter 3 is apple replant disease (ARD) which significantly affects the worldwide apple industry. There are many factors that may contribute to ARD, including several plant pathogens; as a result, ARD is difficult to manage in the absence of broad-spectrum soil fumigants. This chapter summarises the main causes of ARD and the main methods to control ARD with specific reference to China (since ARD management for other regions has been reviewed recently), based on recent developments in knowledge of the physical and chemical properties of soil deterioration, allelopathic effects (phenolic acids),

and microbial community structure in apple orchards. The chapter discusses methods to manage ARD, including cultural practices such as soil disinfection, resistance breeding and biological control.

Chapter 4 considers the challenge presented by the apple canker disease in Europe, with a particular focus on European apple canker caused by *Neonectria ditissima*. The chapter discusses *N. ditissima* in the context of the tree production cycle, introducing the aetiology and epidemiology of the pathogen, reviewing the key control measures (covering cultural, chemical and biological control), and identifying a number of future research areas (including detection and diagnostics, and the use of endophytes). The chapter describes changes in the plant protection products available and in the methods of tree production and varietal susceptibility.

Chapter 5 considers the case of apple valsa canker in Asia. Apple valsa canker, caused by *Valsa Mali*, is mainly distributed in China, Japan, South Korea and North Korea. Apple valsa canker mainly damages the cortex of apple branches, causing the cortex to rot. The chapter describes the distribution and damage associated with valsa apple canker before going on to introduce the the pathogen in terms of its biology, epidemiology, infection process and pathogenesis. The chapter concludes with the recent research progresses in China on the management of apple valsa canker.

The final chapter on fungal diseases of fruit, Chapter 6, deals with brown rot. *Monilinia* spp. cause economically important diseases of pome and stone fruits. The chapter focuses on the four main *Monilinia/Monilia* species i.e. *Monilinia fructicola, M. laxa*, *M. fructigena*, and *M. polystroma*. The chapter concentrates on the general and specific features of the four brown rot fungi in relation to their impact on fruit hosts and to the integrated disease management. The chapter covers brown rot-related yield loss and its impact on fruit crops, the characteristics of causal organisms, and the disease's major fruit hosts and host resistance. The chapter goes on to describe brown rot symptoms on specific plant parts, methods for rapid and reliable identification and detection, epidemiology, disease prediction and disease management options.

Moving on from fungal to viral diseases of fruit, Chapter 7 looks at apple mosaic virus. Apple mosaic virus (ApMV) has been detected in apple as well as in a number of other plant taxa including other members of the Rosaceae family. The chapter provides a comprehensive review of how the virus is spread and describes the symptoms displayed by affected host plants. The chapter goes on to discuss the geographical distribution of the virus, its epidemiology and the economic impact of infection on the fruit and nut industry. The chapter reviews ways to obtain virus-free material with meristem culture in combination with thermo- or cryo-therapy used to eradicate ApMV from propagation material. The chapter concludes with a discussion of the most reliable molecular detection methods for ApMV.

The section's final chapter, Chapter 8, considers a further viral disease of fruit: plum pox. Sharka disease, caused by *Plum pox virus* (PPV), is the most important virus causing significant yield losses in plums, with reduced fruit quality and premature fruit drop. The chapter summarises status of this disease around the world, with emphasis on strains, detection methods, orchard management and breeding for resistance. The chapter examines the challenge of PPV control for sustainable cultivation of plums and looks at the genetic and molecular basis of PPV resistance in *Prunus*.

Part 2 Integrated fruit disease management

The second part of the book examines the challenge of integrated management of diseases on fruit crops. Chapter 9 starts with a review of disease monitoring and forecasting in integrated fruit disease management. Regular inspection of fruit crops for diseases is a vital part of integrated disease management. Combining this information with that disease forecast models (usually based on weather information only) can play a significant role in producing perfect fruit with minimal use of fungicides. The chapter assesses fruit disease monitoring, disease warning systems and decision making; it then uses examples of specific diseases in apple and pear to illustrate the role of both orchard monitoring and disease warning systems in integrated disease management. The chapter covers apple scab, apple powdery mildew, European apple canker, sooty blotch, fly speck, fire blight and storage rots. The examples given demonstrate current 'best practice' in orchard monitoring and how disease warning systems can be integrated into integrated disease management programmes. The chapter also discusses the use of future technologies such as smart spore traps, drones and orchard scanners.

Moving on from disease monitoring to preventative breeding strategies, Chapter 10 considers the challenge of breeding fruit varieties with durable resistance to pests and diseases. Resistance breeding can make a lasting contribution to pest and disease control in an integrated management strategy provided that the resistance is durable. The chapter discusses strategies for achieving the breeding objective of durable resistance based on genes that target pathogen fitness, gene pyramiding and non-host resistance. The chapter also examines the application of a range of breeding tools.

The subject of Chapter 11 is on how plant propagation methods may improve disease control in fruit crops. The movement of plant propagation material across countries and continents allows for the exchange of high-quality planting material providing producers with superior germplasm, and enhancing farm sustainability and profits. However, this practice has hidden dangers, including the potential of moving infectious agents to new areas. The chapter

takes a systems-based approach on the detection, elimination and safeguarding against systemic pathogens that affect clonally propagated fruit crops. The chapter comprehensively discusses the steps taken to improve propagation material and presents a number of case studies including blackberry yellow vein disease and raspberry crumbly fruit and decline. The chapter discusses new technologies that allow for the rapid and accurate characterization of plant pathogens, including new tools such as high throughput sequencing which has proved invaluable in assessing the health status of high value plants and for the rapid identification and characterisation of unknown viruses.

Moving from plant propagation to a more direct method of disease control, Chapter 12 looks at improving fungicide use in integrated fruit disease management. With the rapid emergence of resistance to the limited number of fungicide classes in many pathogenic fungi, improving stewardship of extant fungicides is a priority. The chapter describes the evolution of fungicide resistance and examines ways of monitoring the development of resistance to fungicides. The chapter focuses on the importance of strain identification in monitoring resistance, and examines the adoption of informed decision-support tools to improve fungicide efficacy.

The subject of Chapter 13 is the use of biocontrol agents and biostimulants in fruit tree disease management. Increasing demand for residue-free fruits, changes in regulation and a decreasing number of available synthetic fungicides favour growth of the market for alternative products. These products include naturally-occurring beneficial microorganisms which are used to control plant diseases. The chapter assesses the current status of biocontrol techniques and their practical application. This chapter reviews main biocontrol mechanisms, including competition, induced resistance, hyperparasitism and antibiosis. The chapter reviews the use of biocontrol agents for control of major fruit tree diseases such as fireblight, post-harvest fruit rots, brown rot, apple scab, European canker and pear brown spot. Commercial biocontrol products are registered mainly for control of fireblight in pome fruit and of post-harvest fruit rots in pome fruit and stone fruit.

The final chapter of the section, Chapter 14, looks at new techniques for managing post-harvest diseases of fruit. Chemical fungicides are traditionally used to preserve the quality of fruit and vegetables during storage or transportation. However, global concern about pesticide use and the reduced efficacy of chemicals due to pathogen-resistant strains have gradually led producers to evaluate safer alternatives for controlling postharvest diseases. Several means, such as natural compounds of animal and plant origin, organic and inorganic salts, antagonistic microorganisms, and physical means, are among the approaches that have been recently evaluated to manage fruit rots. The chapter reviews these new alternative means, and the latest solutions for controlling postharvest diseases in order to provide effective yet eco-friendly

solutions for disease management. The chapter deals with physical agents (UV light treatment, heat treatment, electrolyzed water), chemical agents (organic/inorganic salts, chitosan) and biological agents (biocontrol, botanicals).

Part 3 Insect pests of fruit

The third part of the volume is dedicated to insect pests of tree fruit. Chapter 15 looks at the threat posed by aphids (Homoptera, Sternorrhyncha, Aphididae), which currently include 5575 valid species. Aphids are characterized by some peculiar morphological and biological characteristics that make these insects unique. Although often under-reported, it is estimated that aphids cause very high economic losses each year worldwide. The chapter describes what we know about the biology of citrus aphids, apple and pear aphids and stone fruit aphids and describes their management.

Chapter 16 moves on to consider the major pests of tree fruit, tortricid moths. Members of this group are commonly the most destructive insect pests of deciduous tree fruits throughout the world. The chapter summarises recent research on tortricid biology and management. After an introduction to tortricid systematics and general biology, the chapter examines key species, distribution and dispersal mechanisms of tortricids. The chapter describes insecticide use in organic tree fruit production, as well as techniques of physical crop protection and biological control, including mating disruption and precision pest management. Finally, the chapter examines area-wide Integrated Pest Management (IPM) and postharvest management techniques.

Phytophagous (plant feeding) mites are considered in Chapter 17. Mites are a perennial pest of tree fruit crops worldwide. Foliar feeding by mites can lead to decreased photosynthetic activity, reducing plant vigor and yield. For some mite pests, fruit deformation or russeting can occur. Two main families of mites are found on tree fruits: tetranychids (spider mites) and eriophyids (rust, bud, and blister mites). The chapter reviews cultural and biological control tactics for controlling spider mites, which include choosing tolerant varieties and weed management, releasing predators into orchards to increase their numbers, and/or using management practices that conserve existing predator populations. The chapter considers the thresholds to determine when a spray application should be made and argues for biological control as the cornerstone of integrated mite management.

The final chapter on insect pests, Chapter 18, looks at the problems posed by fruit flies. The vinegar fly *Drosophila suzukii* Matsumura (Diptera: Drosophilidae) commonly known as Spotted Winged Drosophila (SWD) is a highly polyphagous invasive pest, native to Asia, which causes significant damage to a wide variety of berry and stone fruit crops. The chapter reviews the significant progress that has since been made in understanding the biology of

the fly, providing key information required for the development of sustainable and integrated control methods. The chapter assesses the fly's impact on crops and describes its biology and ecology, host range and host susceptibility, detection methods, and management and control strategies.

Part 4 Integrated management of fruit insect pests

The volume's final section focuses on integrated pest management (IPM) of insect pests of tree fruit. Chapter 19 deals with cultural control and agronomic practices to prevent or manage fruit insect pests. Perennial systems, such as temperate tree fruit, present interesting challenges and opportunities for the practice of cultural pest management tactics. The chapter outlines key cultural tactics for managing arthropod pests in temperate tree fruit, including modification of trees, tree architecture, orchard floor management, cultivation practices, mowing and the cultivation of orchard cover crops. The chapter includes a detailed case study on integrating rotational hog grazing and apple production.

Moving from control to monitoring, Chapter 20 focuses on improving monitoring and forecasting in integrated management of fruit insect pests. The efficient and accurate monitoring of insects and mites is a cornerstone of IPM. Pheromone baited traps are probably the best known, most convenient, and specific method used for monitoring in orchards. However, mating disruption strategies have complicated the interpretation of monitoring via pheromone traps, leading to the development of alternative (bisexual/food based) baits. The chapter describes both manual and automated monitoring systems (sensor and camera-based), models for forecasting the phenological dynamics and spatial distribution of insects and the challenge of understanding the relationships between monitoring data, absolute pest densities and economic threshold values.

The subject of Chapter 21 is biological control in integrated management of fruit insect pests, with a particular focus on the use of semiochemicals. Over the past 25 years, semiochemical-based technologies have emerged as essential components of pest management programmes in deciduous fruit production systems. Pheromone-based mating disruption is by far the most widely adopted behavioral control, with nearly 800 000 hectares of fruit crops treated worldwide. The chapter reviews both the progress that researchers and practitioners have made, along with the hurdles encountered as they conceptualized, developed and implemented behavioral controls. The chapter focuses on the uses of behaviour-modifying chemicals for direct control of insect pests of deciduous tree fruits and berry crops. The chapter pays particular attention to the development and future prospects of mating disruption. The chapter covers pheromone-mediated mating disruption, mass

deployment of attractant-baited traps, and the application of attract-and-kill formulations/devices. The chapter concludes with a detailed case study on codling moth (*Cydia pomonella*) mating disruption (CMMD) covering pheromone Identification, early research and adoption, demonstration and areawide programmes, companion insecticides and dispenser development.

The final chapter of the volume, Chapter 22, looks at optimising insecticide use in integrated management of fruit insect pests. The integrated pest management approach was conceived to reduce grower reliance on pesticides by combining and optimising pesticide use with biological, physical and agronomical control tools. Natural enemies are an essential component of the agroecosystem and play a valuable role in controlling insect pests in fruit orchards. Growers need to understand how to protect them from harmful agronomic practices and how these natural allies could be integrated with other control tools. The chapter describes old and new monitoring tools, robust monitoring protocols available for estimating abundance of pest and beneficial insects, use of available phenology models to predict crucial future events important for pest management (e.g. the use of precise timing for surveillance) and pest control. The chapter includes three detailed case studies of common fruit pests as examples of how optimisation of insecticide applications could be implemented within a framework of an integrated management of fruit insect pests.

Part 1

Fruit diseases

Chapter 1

Epidemiology and management of apple scab

Tom Passey and Xiangming Xu, NIAB EMR, UK

1 Introduction
2 Apple scab epidemiology
3 Host resistance
4 Managing scab
5 Future trends
6 Where to look for further information
7 References

1 Introduction

Apple scab, caused by *Venturia inaequalis*, also known as black spot in Australasia, is the most important disease of apples worldwide, especially so in temperate regions with wet and mild climates. This pathogen rarely kills its host, but can significantly reduce fruit yields and quality. This is especially true because of the market demand for blemish-free fruit. Mycelial growth on the fruit surface leads to an olive-brown coloured lesion, which generally forms a brown 'scabby' area (Fig. 1). Severe scabbing of the fruit can lead to cracking of the fruit skin and a potential route for secondary infection from other pathogens (often resulting in post-harvest fruit rot). Infection of young fruit can also lead to a reduction in fruit size and misshapen fruit.

Leaves are also infected (Fig. 2) and, though less frequent, infection of shoots is possible (leading to wood scab). A severe epidemic mid-season can lead to defoliation, potentially reducing wood growth and restricting fruit bud formation for the following year. The wealth of knowledge on the biology, epidemiology and management of apple scab has been captured in a published scab monograph (MacHardy, 1996). Therefore, only details of publications since 1996 are usually explicitly given.

V. inaequalis attacks only *Malus* spp. although *formae speciales* of *V. inaequalis* are known on other species of the Rosaceae family such as *Pyracantha* spp. and loquat (*Eriobotrya japonica)* (Le Cam et al., 2002; Gladieux

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Figure 1 Symptoms of apple scab on apple fruit by *Venturia inaequalis*.

Figure 2 Symptoms of apple scab on leaves by *Venturia inaequalis*.

et al., 2010). The pathogen is likely to have originated in Central Asia (Gladieux et al., 2008) alongside *Malus* spp. (Harris et al., 2002). *V. inaequalis* is a haploid organism, and conventional cytology suggests that it has seven chromosomes. One linkage map of *V. inaequalis* (Xu et al., 2009) has 11 linkage groups spanning 1106 cM in length, while another has 15 linkage groups spanning

972 cM (Broggini et al., 2011). Construction of a bacterial artificial chromosome library estimated the genome size to be 102 Mb (Broggini et al., 2007). Whole genome sequencing has estimated the genome size to be between 40 Mb and 72 Mb (Deng et al., 2017; Passey et al., 2018). It is estimated that 36 Mb of the genome is non-repeated DNA (Bowen et al., 2011), making assembly more complicated. The *de novo* assembly and annotation of the *V. inaequalis* transcriptome have been published (Thakur et al., 2013).

2 Apple scab epidemiology

Figure 3 shows a simplified diagram of the annual life cycle of *V. inaequalis* on apple. Annual epidemics of apple scab start with primary infections of leaves in the spring by overwintered inoculum in leaf litter, buds and wood scab on twigs. These primary infections lead to the first wave of visible lesions, with the length of incubation largely determined by ambient temperature. Conidia produced from these lesions are then rain-splash dispersed and can lead to further infections of leaves, fruit and shoots, namely secondary infection.

This cycle of secondary infections continues throughout the summer, until the leaves fall in the late autumn. The frequency of secondary infection and scab severity are largely determined by cultivar susceptibility, tissue susceptibility and weather conditions.

In most apple-growing regions, *V. inaequalis* survives in winter mainly as pseudothecia on dead, scabbed leaves on the ground (MacHardy, 1996). This pathogen is a heterothallic fungus and hence requires strains of opposite mating types to mate and produce ascospores. Predicting the dynamics of ascospore

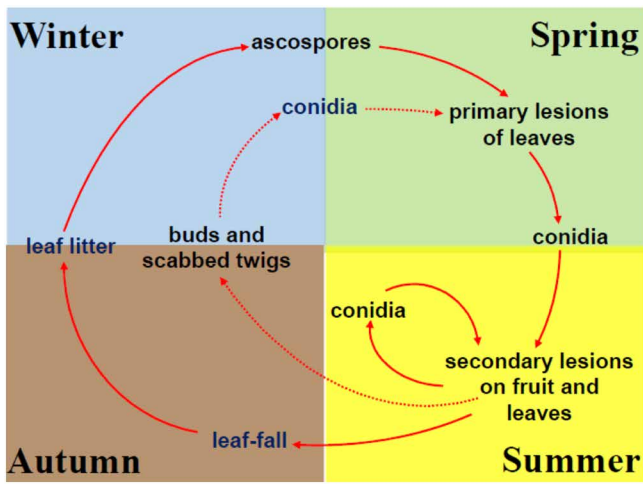

Figure 3 A simplified life cycle of the apple scab fungus *Venturia inaequalis*.

maturation and release has received much attention as these predictions can help growers to determine the timing of primary infections (Schwabe et al., 1989; Stensvand et al., 2005; MacHardy, 1996; Roubal and Nicot, 2016). Pseudothecium formation occurs under a wide range of temperatures with the light enhancing pseudothecial production. The pseudothecial maturation is primarily determined by temperature (i.e. thermal time). Rain is necessary for the growth of mycelium into the leaf lamina and for initiation of the ascigerous stage; however, continuous wetness can delay ascospore maturation. Mature ascospores are discharged during or following rain events and ascospores are more likely discharged in daylight (MacHardy, 1996). Thus discharging (the majority) of ascospores following a rainfall event during the night may be delayed until dawn. The actual level of ascospore inoculum in the spring (i.e. PAD – potential ascospore dose) can also be estimated with scab severity the previous season, winter conditions (temperature, rainfall and snow cover) and the extent of leaf litter degradation over the winter (MacHardy, 1996).

V. inaequalis can also survive in winter as conidia and thus these overwintered conidia can initiate primary infections. Conidia are shown to overwinter on the inside of bud tissues, leading to infections of young leaves in the spring (Holb et al., 2004; Becker et al., 1992). Conidia may have contributed 20–50% of the primary inoculum in one specific orchard under UK conditions (Passey et al., 2017). Thus, it may be prudent not to ignore conidia as a source of primary inoculum in scab management.

Primary infection by ascospores and conidia leads to olive-green/grey lesions on leaves. Hyphae grow between the cuticle and epidermal cell wall resulting in the development of stromata. Conidiophores and, thus, conidia form and rupture the cuticle. *V. inaequalis* is able to sporulate at temperatures from 5°C to 25°C. The latency period length (i.e. the time from infection until the occurrence of sporulating lesions) depends on temperature. For example, it is about 8 days at 18°C and 17 days at 9°C.

Ascospores can germinate between 0°C and 30°C, with the optimum at 15–25°C. The key requirement for ascospore germination and subsequent infection of host tissues is the availability of free or high-moisture conditions. Conidia are able to germinate at temperatures between 10°C and 30°C under high-moisture conditions, usually ≥ 95% RH. The exact duration of high-moisture conditions required for infection differs between conidia and ascospores (MacHardy, 1996). Under a given temperature, the longer the wet period, the severer the infection is. Germinating/infecting spores can survive for various lengths of dry periods, depending on their developmental stage, the temperature and the humidity in the dry periods. Much research has been directed to develop forecasting/warning systems for apple scab in order to assist growers in better timing intervention measures (MacHardy, 1996; Xu et al., 1995; Aćimović and Rosenberger, 2018). Most of these forecasting models are

based on the simple lookup table provided by Mills and La Plante (1954); this table gives the duration of surface wetness under a range of temperatures required for scab (light, moderate or severe) infection.

3 Host resistance

In total, 18 gene-for-gene relationships have been identified in the *Malus–V. inaequalis* pathosystem: 17 were described by Bus et al. (2011) and subsequently an additional one (*Rvi18*) added (Soriano et al., 2014). Research in identifying and using major R genes against *V. inaequalis* in commercial breeding has focused on genes from wild *Malus* species rather than domesticated apple. The only exception is *Rvi1* (formerly *Vg*) from 'Golden Delicious', but this gene can be overcome by ca. 87% of the scab population in Europe and is described as "an exception to the premise that narrow spectrum R genes should be excluded from the nomenclature" (Bus et al., 2011). A number of these R genes have now been cloned and characterised, including *Rvi1* (Cova et al., 2015), *Rvi6* (widely referred to as *Vf*) (Malnoy et al., 2008) and *Rvi15* (Schouten et al., 2014). Markers for R genes have been identified for their potential use in breeding programmes (e.g. Padmarasu et al., 2014; Soriano et al., 2014).

There is a range of susceptibility to *V. inaequalis* across domesticated apple cultivars, suggesting that seemingly susceptible cultivars contain potential resistance factors (Koch et al., 2000; Barbara et al., 2008; Papp et al., 2016). Partial resistance against *V. inaequalis* in cultivars, not conditioned by a (known) R gene, might come from multiple loci (including those old 'defeated' R genes) that have a quantitative effect. A number of quantitative trait loci (QTLs) associated with scab resistance have been identified in a cross between 'Discovery' and 'Fiesta' (Liebhard et al., 2003), as well as in a cross between 'Discovery' and the apple hybrid 'TN10-8' (Calenge et al., 2004). Partial resistance from QTLs may be more durable than that of the qualitative resistance offered by an R gene (Bastiaanse et al., 2016), but could still be subject to erosion, although this erosion might be slow (Caffier et al., 2016). Locally adapted, susceptible cultivars may possess effective resistance against *V. inaequalis* strains from other regions (Xu et al., 2008).

The only major R gene that has been incorporated into commercial apple cultivars is the *Rvi6* gene. Although the *Rvi6* resistance was durable for around 50 years, breakdown was first seen in Europe in the last decade of the twentieth century (Parisi et al., 1993; Roberts and Crute, 1994). Since then, breakdown in the *Rvi6* resistance has been reported in many European countries, predominantly in organic orchards; no confirmed breakdown has yet been reported in North American commercial orchards (Gessler and Pertot, 2012). Only a few cultivars with the *Rvi6* are grown commercially (e.g. 'Topaz', a relatively popular cultivar in Germany) as named varieties.

The breakdown of R-gene resistance, as seen with *Rvi6*, shows that the use of a single R gene to confer resistance against *V. inaequalis* is not likely to be a durable solution. Pyramiding scab resistance genes, i.e. incorporating a number of resistance genes within a single cultivar, has been proposed as a way of breeding cultivars with durable scab resistance (Gessler and Pertot, 2012). The erosion of a single broad-spectrum resistance factor in a genotype could allow a rapid epidemic resulting from the virulent pathogen race, whereas pyramiding these resistance factors would require an isolate to have all the necessary virulence factors to overcome the differing resistance factors. Pyramiding of three QTLs for resistance against apple scab increased the efficiency of resistance compared to any of the individual independent QTLs (Laloi et al., 2017). However, it should be noted that these three specific QTLs (Laloi et al., 2017) affected *V. inaequalis* development at different stages. It is, therefore, expected that pyramiding these QTLs should benefit from resistance targeted at different stages of pathogen development.

In addition to inherent genetic resistance against *V. inaequalis*, apple tissues also possess age-related resistance/susceptibility (MacHardy, 1996); this age-related resistance is often called 'ontogenic resistance'. Young leaves are much more susceptible to *V. inaequalis* than old leaves; this ontogenic resistance is mainly manifested in the reduced lesion density and lengthened incubation period on old leaves. Mycelia on old leaves grow so slowly that they may not lead to visual symptoms at the time of leaf-fall, even though some of these symptomless colonies have already produced conidia when viewed microscopically (Li and Xu, 2002). A considerable amount of symptomless infections may therefore be expected on old leaves in autumn, which may have considerable impact on the amount of primary inoculum in the following season. These symptomless colonies may be one of the reasons responsible for the difficulties in estimating PAD accurately. Similarly, apple fruits are highly susceptible in the early stages of development, but become increasingly resistant as they mature (Xu and Robinson, 2005).

4 Managing scab

Although current scab management still relies on frequent applications of synthetic fungicides, there is a consensus now that we urgently need to develop and implement an integrated approach with far less reliance on synthetic fungicides to manage crop diseases. Crop management practices are applied to reduce disease pressure, including reducing inoculum levels, reducing the amount of susceptible tissues, and altering microclimates. Whenever possible, alternative products (particularly microbial products, e.g. biocontrol products) should be used instead of synthetic fungicides. Frequent disease monitoring

in conjunction with disease prediction/forecasting is necessary to better time intervention measures.

4.1 Fungicides

For very susceptible cultivars, the most effective control is still through a programme of chemical sprays. It is not unusual for 12–18 spray applications to be applied to an orchard every year. It was Mills who in the 1920s began research on the importance of timing of sprays against scab (MacHardy, 1996). More recently, scab forecasting models have been used to optimise fungicide sprays as well as selection of the type of fungicides (protectant, curative or eradicant) (Berrie and Xu, 2003; Aćimović and Rosenberger, 2018). Multi-year orchard trials showed that integrating scab and powdery mildew forecasting models in managing apple diseases resulted in similar or better control than a routine programme, but with reduced fungicide input (5% to 45%) and costs, even in seasons exceptionally favourable for these diseases (Berrie and Xu, 2003).

Fungicides account for around two-thirds of the total pesticides used in orchard crops in the UK. There is ever-increasing legislation around the use of pesticides and a decreasing number of products available. Demethylase inhibitors, or DMIs, are a group of fungicides including piperazines, pyridines, pyrimidines, imidazoles, triazoles and triazolinthiones. They target the protein 14-α demethylase, which is part of the ergosterol biosynthesis pathway. Its inhibition by DMIs renders isolates unable to make ergosterol, badly damaging the cell membrane (Joseph-Horne and Hollomon, 1997). The DMI family has a strong pre-symptom (curative) activity, preventing early infections from developing into lesions and significantly reducing conidium production (Schwabe et al., 1984; O'Leary and Sutton, 1986). Furthermore, both within-season and post-harvest applications of DMIs lead to reduced production of pseudothecia and therefore ascospores (MacHardy, 1996).

Over-reliance on a number of fungicides for scab control has led to emergence and subsequent spread of resistance against fungicides. For instance, fungicide resistance in *V. inaequalis* has been reported for dodine (Köller et al., 1999; Chapman et al., 2011) and DMIs (Errampalli, 2004; Xu et al., 2010). Some of the resistance mechanisms that are thought to be involved include mutations in the CYP51A1 gene, overexpression of the gene, and transporters that work in the efflux of the antifungal compounds (Jobin and Carisse, 2007; Pfeufer and Ngugi, 2012). The resistance against DMIs in *V. inaequalis* is likely to be under polygenic control (Jobin and Carisse, 2007; Schnabel and Jones, 2001; Xu et al., 2010) as field isolates showed a spectrum of sensitivity levels to myclobutanil (a DMI fungicide) rather than just a sensitive and an insensitive phenotype. Tebuconazole (another DMI fungicide) as a

substitute for myclobutanil to control scab may also face an uncertain future, as it has been shown to be losing efficacy in a number of countries (Jobin and Carisse, 2007; Chapman et al., 2011; Pfeufer and Ngugi, 2012).

Nevertheless, most of these products, against which resistance in *V. inaequalis* has been reported, are still recommended for use and will provide acceptable control of scab for commercial production in orchards where fungal resistance against these fungicides has not been observed. Furthermore, some of these products are also effective against other diseases, for example myclobutanil against apple powdery mildew, another important apple disease. The Fungicide Resistance Action Committee (FRAC) recommends mixing the use of fungicides with differing modes of action to improve disease control. Mixed use of fungicides combines the characteristics of the components in the mixture, minimises crop losses due to fungicide resistance, and reduces resistance build-up against individual fungicides.

4.2 Alternative non-fungicide products

Alternatives are required to the common commercially used fungicides, due to the ever-decreasing number of available fungicides because of stringent legislation and fungal resistance to fungicides. Furthermore, alternative products are essential for scab control in organic orchards.

The use of biocontrol agents (BCAs) against apple scab has been widely investigated in the past couple of decades. For example, an isolate of *Cladosporium cladosporioides* was selected as the most effective fungal coloniser, from a range of those found, at reducing conidial production (Köhl et al., 2009) and then shown to reduce the severity of apple scab on leaf and fruit in orchard conditions (Köhl et al., 2015).

A plant extract product, 1% populin from black poplar (*Populus nigra*), can slow down *in vitro* conidial germination and reduce scab on leaves and fruits when applied to run-off (Bálint et al., 2014). Plant retardant Prohexadione-Ca can reduce scab incidence (Bazzi et al., 2003), most likely by upregulating pathogenesis-related proteins and inducing host resistance (Bini et al., 2008). Several alternative products, including potassium bicarbonate, and products based on extracts from *Quillaja saponaria*, orange peel, grapefruit seeds, *Yucca schidigerra*, and *Camellia oleifera* and *Chenopodium quinoa* seeds, can have good protectant efficacy against *V. inaequalis* when applied at 1% concentration (Laurent, 2011). Copper use, even with low doses, is still necessary to control scab on susceptible cultivars in organic orchards.

Although these alternative methods show promise in lab and field trials, they are rarely adopted in conventional commercial apple production, primarily because of variable and often low levels of control efficacy achieved. Like fungicides, there is the chance that pathogens may develop resistance to

these products. Although BCAs are thought to be more durable than chemical control, the limited available information suggests this assumption is not always justified (Bardin et al., 2015). These alternative products are often compared to fungicides for disease control; this framework of comparison is not justified for BCAs, ignoring BCAs as living organisms and hence that any biocontrol effect is expected to be gradual. These alternative products should be viewed as components of an integrated pest management system rather than straight replacement of conventional fungicides.

4.3 Orchard sanitation

One of the key scab management objectives is to reduce the level of overwintering inoculum in the form of ascospores on leaf litter on orchard floors. Early effective control of scab epidemics in the spring lays the foundation for effective scab management for the entire season.

A practice that is commonly used in commercial orchards is the use of a 5% urea spray, with application recommended between harvest and leaf fall, following a paper in *Nature* (Burchill et al., 1965) that showed urea treatment of leaves in autumn is effective in inhibiting the sexual reproduction of *V. inaequalis* on leaf litter. This reduction may be due to the inhibition of pseudothecium formation by excessive nitrogen, increased bacterial population antagonistic against *V. inaequalis,* and leaves becoming softer, making them more palatable to earthworms for faster degradation. The use of urea has been shown to reduce ascospore number and/or scab incidence to varying degrees in a number of other studies both as an individual treatment and as part of a multifaceted approach (Sutton et al., 2000; Vincent et al., 2004; Holb et al., 2006).

Shredding all leaf litter with a flail mower in autumn reduced the risk of scab by up to 90%, while shredding as little as 65% of the litter could reduce the risk by 50% (Sutton et al., 2000). Sweeping up leaves with a lawn sweeper and ploughing them into the row reduced the incidence of fruit scab by 50%–80% depending on seasons (Gomez et al., 2007). In seasons with conducive conditions for scab development, the effects of removing primary inoculum are less pronounced.

In addition to ascospores on leaf litter as primary inoculum, overwintered conidia in buds and twigs can also be an important source of primary inoculum. However, there are no effective measures to reduce the level of overwintering conidia in buds. Wood scab can also be observed on some cultivars (particularly in organic orchards) and may produce considerable amount of conidia in the spring. The green stems of potted Cox's Orange Pippin trees were susceptible to infection by *V. inaequalis* from June to August and some isolates showed the conspicuous ability to attack the wood (Cook, 1974). These wood scab lesions may be able to produce conidia throughout the growing season and provide a

constant risk of infection. Thus, pruning off these shoots with wood scab lesions can contribute to the reduction of primary inoculum next spring (Holb, 2005), particularly in heavily diseased organic orchards.

Appropriate pruning increases air circulation in the tree canopy and therefore affects tree canopy microclimates, particularly reducing humidity and the length of leaf wetness (Carisse and Dewdney, 2002), contributing to reduced scab development. Tree architecture (Simon et al., 2006) and both winter (Holb, 2005) and summer (Cooley and Autio, 2011) pruning also allow better spray deposition for more effective chemical control. Pruning is carried out predominantly for improved fruit quality with a positive impact on disease control as an additional benefit. However, it should be noted that pruning can also lead to an increase in some diseases such as fire blight (*Erwinia amylovora* – an important disease in North America) and apple canker (*Neonectria ditissima*) (Cooley and Autio, 2011).

4.4 Cultivar mixtures

Reduction of disease development through cultivar mixtures has been shown in a range of crops (Mundt, 2002), predominantly in foliar diseases of cereals, for example, rust diseases (caused by *Puccinia spp.*) of wheat (Cox et al., 2004) and powdery mildew (*Blumeria graminis* f. sp. *hordei*) of barley (Tratwal and Bocianowski, 2018). Disease development in mixtures is reduced through inoculum dilution, barrier effect and induced resistance by non-pathogenic inoculum.

The potential for mixed apple cultivar orchards to reduce scab development was first assessed by simulation (Blaise and Gessler, 1994). A field trial with mixed susceptible and R-gene-carrying resistant cultivars demonstrated that scab lesion density is lower in mixture than in monoculture (Bousset et al., 1997). Similar results were also obtained in later studies (Didelot et al., 2007; Parisi et al., 2013), showing that the magnitude of mixture effects depends on season (climatic conditions), mixture structure and orchard management practices. In general, the higher the disease pressure, the lower the mixture control efficacy is.

Although often significant, the reductions in scab observed in mixed cultivar orchards are usually insufficient for disease control in commercial production. However, they could be of benefit if implemented as part of an integrated disease management programme alongside other strategies, such as sanitation, use of BCAs, and backed up by the use of fungicides in high-risk periods. Mixture could be more appropriate for cider apple production as disease control is not as stringent as for dessert apple. The management costs of a mixed cultivar orchard are likely to be higher than that of monoculture due to differences in the timing of bud-break, flowering and fruit development between cultivars, leading to complications in pest and disease control, crop

husbandry (e.g. irrigation, fertilisation) and harvesting. Furthermore, dessert cultivars are sold as named varieties and therefore fruit needs to be separated into individual cultivars on harvesting.

A major concern in adopting mixtures in commercial agriculture is the emergence and subsequent rapid build-up of a scab 'super race' combining virulence factors that overcome most or all of the resistance genes in the host cultivars present in the mixture, rendering the mixture ineffective as a means of managing scab. A simulation study suggested that a super race is not likely to occur within the life time (ca. 20 years) of a perennial tree plantation of cultivar mixtures where annual fungal population crashes occur during overwintering (Xu, 2012). However, the formation of super races is real as artificial crossing showed that it is possible for ascospore progenies to be produced that combine virulence factors to overcome resistance in different cultivars (Barbara et al., 2008).

Recent studies on fungal population structures of *V. inaequalis* over time show that a super race is unlikely to occur in the length of a commercial orchard (Xu et al., 2013; Passey et al., 2016). One likely explanation as to why a super race of *V. inaequalis* is unlikely to occur and become dominant in an orchard is because there is insufficient sexual mating between isolates from different cultivars. Mating among strains of opposite types is more likely to occur and succeed for lesions on the same leaf than on different leaves, resulting in more mating among strains with similar genetic (in terms of virulence factors) background.

5 Future trends

Given the polycyclic nature of apple scab, it is critically important to predict and reduce the level of primary inoculum. Currently, prediction of potential primary inoculum is primarily based on severity of visible scab lesions in autumn and winter conditions. As there are old leaves harbouring micro-scab colonies that are not visible to the naked eye, further research is needed to elucidate the role of these symptomless colonies in overwintering of *V. inaequalis* and in production of ascospores.

Recent research on population changes of *V. inaequalis* in a cultivar mixture orchard suggests that the risk of a super fungal race emerging in the mixture is much less than we anticipated based on the assumption of random mating. One plausible explanation is the lack of mating among strains on different leaves compared to those on the same leaf. We need to study the dynamics of the mating process in terms of successful production of ascospores in relation to time and physical location of lesions. This could have a significant impact on the adoption of mixtures in commercial production.

There is an urgent need to develop alternative products, which are not necessarily a straight replacement of fungicides. In particular, we need to

explore the biocontrol options and develop multiple biocontrol products, targeting specific stages of the pathogen life cycle integrated with forecasting models. Availability of multiple products with different epidemiological modes of actions will reduce the risk of over-reliance on individual products. Similarly, long-term large-scale demonstration is necessary to implement an integrated pest management approach and demonstrate the feasibility and benefit of such an approach in commercial horticulture.

6 Where to look for further information

The monograph by MacHardy (1996) is the best resource for apple scab research up to 1996, whereas a brief introduction to the disease can be found in the paper by Bowen et al. (2011) and the website hosted by the American Phytopathological Society on apple scab (https://www.apsnet.org/edcenter/disandpath/fungalasco/pdlessons/Pages/AppleScab.aspx). The following publications are a good starting point for research synopsis on more specific topics on apple scab: (1) host resistance against *V. inaequalis* – Bus et al. (2011), (2) epidemiology of *Venturia* diseases – González-Domínguez et al. (2017), and (3) fungicide resistance management – Beckerman et al. (2015). There are several chapters in this book that also deal with specific areas relevant to apple scab: use of disease forecasting models for practical management (Chapter 9), breeding for resistance (Chapter 10), use of fungicides (Chapter 12) and biocontrol (Chapter 13).

Apple scab is the most important disease on apple worldwide and thus studied in most research institutes/centres globally where apple is grown. Leading research organisations on apple scab include: (1) New York State Agricultural Experiment Station, USA; (2) NIAB EMR (East Malling Research), UK; (3) Plant & Food Research, New Zealand; (4) INRA, Université d'Angers, France; and (5) Research Institute of Horticulture, Skierniewice, Poland. Although scab related research can be presented in many horticultural and plant pathological conferences, the conference with most contributions on apple scab is the workshop organised by the IOBC-WPRS Pome Fruit Disease Subgroup in the Working Group of Integrated Protection of Fruit Crops (https://www.iobc-wprs.org/expert_groups/02_wg_fruit_crops.html).

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