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AUTHENTICATION

We declare that this work was done under our supervision according to the procedures described herein and that the report represents a true and accurate record of the results obtained.

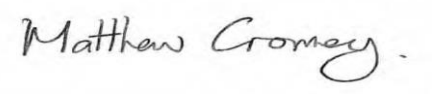
Erika Wedgwood

Project Leader, ADAS

Signature Date 31 March 2016

Matthew Cromey

Project Collaborator, RHS



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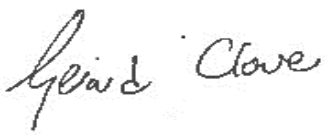

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CONTENTS

GROWER SUMMARY

Headline

Developments in spore detection, disease forecasting and biological treatments are aiding progress towards development of effective IPM strategies for aerial oomycete pathogens, but more work is needed.

Key knowledge gaps remain in our understanding of these pathogens, with implications for their control.

Background

Downy mildews, white blisters and certain *Phytophthora* species are examples of oomycete pathogens which can be transmitted aerially and infect above ground plant tissue. The oomycetes are a group of fungus-like organisms that can cause economically significant losses on a wide range of plant species. They can exist as a range of structures throughout their lifecycle, enabling them to persist aerially, in water and in soil.

Economically significant losses due to oomycetes occur across the majority of horticultural production systems. They are often considered to be fairly ubiquitous in the environment, with most aerial oomycetes also able to persist in soil and growing media as either mycelium or oospores. Temperatures between 5-25°C (varying for individual pathogens) favour diseases caused by oomycete pathogens, with white blister pathogens in general favouring slightly higher temperatures than Phytophthoras and downy mildews. The correct temperature coupled with high humidity and/or foliage wetness can lead to the rapid spread of oomycete diseases throughout a crop once present. There has been recent industry concern over downy mildews new to, or not previously a problem in the UK, including on basil, impatiens and aquilegia and also aerial *Phytophthora* species including *P. ramorum*.

Summary

Information on the main aerial oomycete diseases of horticultural crops, determined by a survey to be currently important to UK growers, was obtained from recent UK and overseas research. In addition to published journals, the outcomes of relevant AHDB projects were evaluated. This review highlights research that has provided new understanding of the pathogens and measures for their control, and the gaps in knowledge remaining. Future threats including pesticide resistance and emerging disease problems were reported. Areas for further investigation related to host range, biology and disease management are itemised below. Thirteen crop-specific reviews of edibles and 11 of ornamentals were carried out and key areas of knowledge for the principal pathogens are tabulated below.

Host range

- Previous understanding of pathogen host interactions has been, in general, simplistic
- Downy mildew species once thought to have a wide host range are showing evidence of increased host preference, with numerous species either being reclassified or split into distinct races.
- Evidence suggests that distinct races which occur within pathogen species do not cause symptoms to the same extent on different cultivars of the same host plant.
- Weed relatives may play a role in acting as reservoirs for inoculum in some systems, but this is an area requiring further investigation.

Biology

- Fundamental gaps need to be filled in the understanding of the biology of some oomycete pathogens of UK importance to further aid integrated crop management.
- The role of oospores in infection is poorly understood. Information is lacking on their durability and viability under field conditions, germination, and role in infection.
- Survival of sporangia in the UK is also not well documented. The extent of aerial travel of viable spores is generally unknown, accepting that it will vary between pathogens and depend on environmental conditions.
- The possibility of spread of predominantly-airborne oomycetes *via* contaminated irrigation water requires further investigation.
- Certain downy mildew and white blister infections can remain without symptoms whilst still having a negative effect on a crop.

Integrated Crop Management

- Advances in spore detection and forecasting are paving the way for the more precise timings of fungicide spray applications.
- Across UK horticulture, limited crop resistance is available against oomycete pathogens. Molecular techniques may identify genes for resistance in wild relatives.
- Currently there is not a definitive system for growers to report suspect cases of fungicide resistance; and no monitoring of sensitivity/resistance levels is undertaken.
- There is increasing potential for the successful incorporation of microbial treatments and elicitors together with chemical fungicides within integrated crop management programmes (see Figure below).

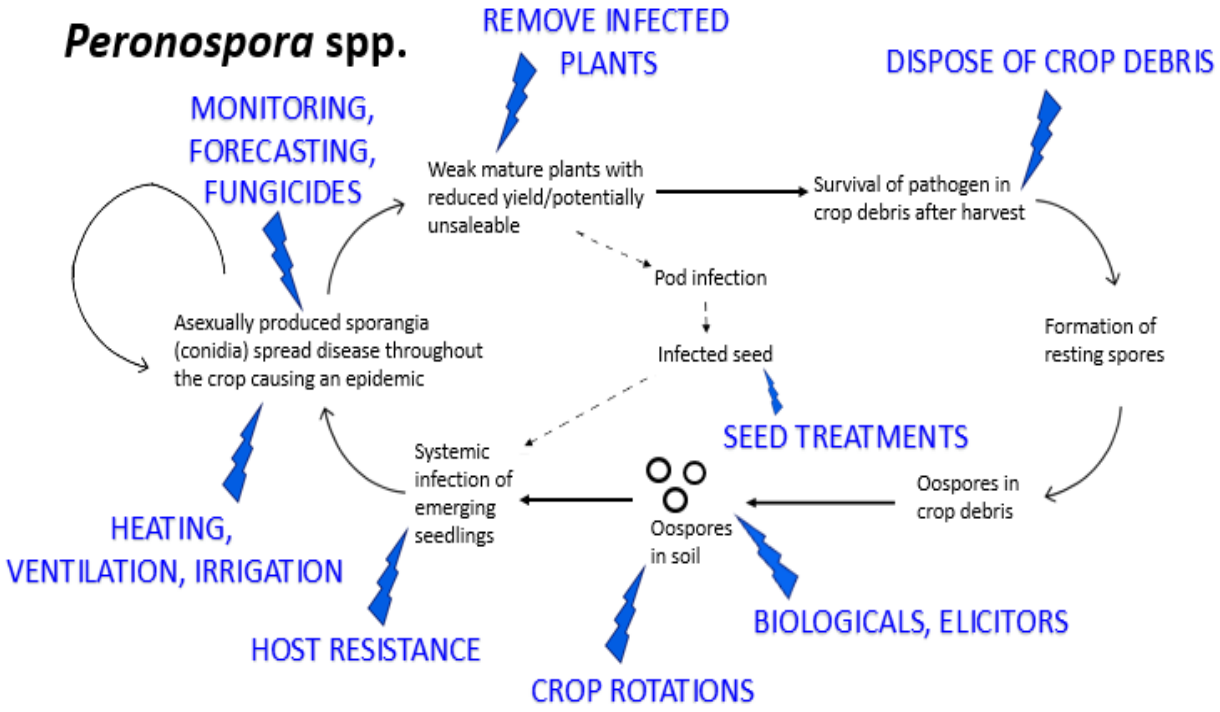

Figure above. General life cycle of a typical *Peronospora* sp. (downy mildew) and integrated crop management. The arrow-flashes shown in blue indicate where control could potentially be achieved by the measures indicated

Financial Benefits

Losses caused by aerial oomycetes can be high, and in many systems, such as salads and herbs, the whole crop can potentially be lost. Preventing disease establishment is the most cost efficient way of combating aerially transmitted oomycete pathogens and this review includes information on recent work on epidemiology and cultural control measures that could help preventative fungicide programmes to be used less frequently (See Summary Table below). The use of resistant cultivars has, for example, the potential to reduce disease incidence by 99% and in broccoli crops was able to increase farm profit by 12%.

Future research towards some of the key knowledge gaps identified in this review, in particular better understanding of the biology of pathogens and their interactions with host and environment, will enable the most effective control methods to be determined.

Action Points

The action points for growers set out how existing information and new understanding gained from the review on the diseases can be applied in integrated crop management programmes.

Effective cultural practices for downy mildew prevention will likely provide wider disease control as a consequence.

- Dispose of crop debris, destroy waste heaps and use other crop hygiene measures
- Remove and destroy volunteer plants as they can be sources of disease inoculum
- Where possible, avoid close proximity of spring plantings to overwintered crops
- Crop rotations of at least five years will minimise infection via oospores
- Where possible avoid making successive plantings across a single field (or in general close proximity) in order to prevent pathogens from moving between them
- Select resistant varieties, if available and acceptable
- Utilise seed treated for the control of oomycete pathogens
- Do not plant too densely, as high humidity within the crop canopy will favour infection and sporulation of many aerial oomycete pathogens
- In protected environments, maintain heating and ventilation to reduce humidity
- Avoid overhead irrigation, or time irrigation for the mornings to reduce leaf wetness
- Utilise disease forecasting systems where available, and monitor crops carefully
- Devise protectant fungicide programmes, consider including biological treatments
- Select fungicides with different modes of action to reduce chemical resistance risk
- Target sprays for at-risk growth stages, if known
- Be alert to any disease symptoms not seen before, or more severe infections, in case of the arrival of invasive pathogens or oomycetes with changed pathogenicity.

Summary Table of key knowledge areas either met or lacking for aerial oomycete pathogens present on UK horticultural crops

Pathogen and host	Active research	Molecular diagnostics developed	Fungicide resistance observed	Optimum growth conditions identified	Resistant cultivars	Progress with bio-logicals	Forecasting	Host specificity	Cultivar specificity (races)
Phytophthora spp. (trees & shrubs)	Yes	Yes	No	Yes	Some information	No	No	Some information	No
Peronospora sp. (*Aquilegia*)	Yes	No	No	No	Unknown	No	No	Unknown	Unknown
Peronospora grisea (hebe)	Yes	No	Possibly	Some	Unknown	Yes	No	Unclear	Unknown
Plasmopara obducens (*Impatiens*)	Yes	Partly	Yes	Yes	No	No	No	Yes	Unknown
Peronospora chlorae (*Lisianthus*)	No	No	No	No	Unknown	No	No	Yes	Unknown
Peronospora hyosami f. sp. *tabacina* (*Nicotiana*)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Peronospora violae (pansy & viola)	Yes	Yes	No	Yes	Yes	No	No	Yes	Unknown
Peronospora spp. (poppy)	Yes	Yes	Yes	No	Yes	No	Yes	Multiple pathogen spp.	Unknown
Peronospora sparsa (rose)	Yes	Yes	No	Yes	Yes	Yes	Yes	Rubus & rose	Unknown
Peronospora antirrhini (*Antirrhinum*)	Some	No	Yes	Yes	Some information	Yes	In part	Yes	No
Pustula sp. (*Senecio*) white blister	Yes	No	No	No	No	No	No	Uncertain (multiple spp.?)	Unknown
Peronospora sparsa (*Rubus*)	Yes	Yes	No	Yes	Yes	Yes	Prediction model	Unconfirmed	Unknown
Pseudoperonospora cubensis (cucurbits)	Yes	Yes	Yes	Yes	Yes	Yes	Not for UK GH cucurbits	No evidence	Several races identified

Peronospora destructor (onion)	Yes	Yes	Yes	Yes	Yes	Limited	Yes	Unconfirmed	Unknown
Peronospora viciae f. sp. *pisi* (pea)	Yes	In develop-pment	Yes	Needs re-evaluating	Yes – race specific	Limited	No	Cultivar specific	Yes
Peronospora viciae f. sp. *fabae* (Faba bean)	Unknown	In develop-ment	No - but reliant on **one** EAMU	No	Limited	No	Yes	Yes	Unknown
Hyaloperonospora sp. (salad rocket)	Unknown	Yes	No	No	No	No	No	Unconfirmed	Unknown
Hyaloperonospora brassicae (vegetable Brassicas)	Yes	Yes	Yes	Yes	Limited	Yes	No	Unconfirmed	Yes
Peronospora jaapiana (rhubarb)	Unknown	No	No	No	Unconfirmed	No	No	Unconfirmed	Unknown
Peronospora farinosa f. sp. *betae* (beetroot)	Unknown	Yes	No	Yes	Yes	No	No	Unconfirmed	Unknown
Albugo candida (veg. Brassicas) w. blister	Yes	Yes	Yes, needs checking.	Yes	Yes	Yes	Yes	Isolate dependent	Yes
Phytophthora. syringae (apples & pears) fruit rot	Unknown	No	No	Yes	No	No	No, but risk of post-harvest rot prediction	Unconfirmed	Unknown
Plasmopara petroselini (parsley)	Unknown	No	No	Some work	Limited	No	No	Unconfirmed	Unknown
Peronospora belbahrii (sweet basil)	Yes	In development	No	Yes	Potentially in near future	No	No	Numerous *Ocimum* spp.	Unknown
Peronospora salvia-officinalis (sage)	Unknown	No	No	Some work	Limited	No	No	Species specific	Unknown
Peronospora lamii (mint)	unknown	No	No	No	No	No	No	Unconfirmed	Unknown
Peronospora porri (leek)	Yes	Yes	Yes	Yes	Yes	In progress	No	Alliums, but leek isolates distinct group	Leek isolates evidence of race?

SCIENCE SECTION

Introduction

The oomycetes are a group of fungus-like organisms related to algae that cause diseases on a range of plant species. Some cause symptoms on aerial plant parts, including *Phytophthora* species such as *Phytophthora ramorum*, *Phytophthora brassicae* and *Phytophthora porri*, *Albugo* species, and downy mildews from genera including *Peronospora*, *Plasmopara*, *Hyaloperonspora*, *Pseudoperonospora* and *Bremia*. For an in depth background on oomycete pathogens please refer to CP 126 (Pettitt et al, 2015, 2014). Recently, foliar infection by some *Pythium* species has been recognised (Denton, 2014). Other *Phytophthora* and *Pythium* species cause emergence failures, damping-off, root rots and stem base diseases. Economically significant losses due to oomycetes occur across the majority of horticultural production systems. They are often considered to be fairly ubiquitous in the environment, with some aerial oomycetes surviving in soil and growing media, but in general they are found where there is high leaf wetness duration. There has been recent industry concern over downy mildews not previously a problem in the UK including on basil, impatiens and aquilegia and aerial *Phytophthora* species including *P. ramorum*.

A large number of projects on oomycete diseases have been commissioned by the AHDB in recent years across the crop sectors. Work specifically targeted against aerial oomycetes has included downy mildews on rose (HNS 173 (Xu, 2013)), hardy nursery stock and herbaceous plants (HNS 186 (O'Neill, 2014)), onions (CP 099c (Wakeham, 2015)) and peas (FV 436 (Maguire, 2015)) plus *Albugo* sp. on Brassicas (FV 053e (Kennedy, 2005)) and *Phytophthora* white tip on leeks (FV 172 (Locke, 1996)). There have been recent investigations monitoring metalaxyl resistance in impatiens downy mildew (PO 011 (Jennings, 2012), PO 011a (Jennings, 2013b), and PO 011b (Jennings, 2015)) and fungicide control (PO 012 (Jennings, 2013a)) and a Basil downy mildew research project PE 024. HNS 185 focuses on understanding and managing crop protection through Integrated Crop Management (IPM) and includes grower responses on crops requiring treatment for downy mildews and the dissatisfaction with the level of control achieved (Wedgwood, 2012).

Research on root and stem rotting oomycetes can also be applicable to oomycetes that show leaf and shoot infection. AHDB Horticulture has funded a recent review of worldwide research on root-rotting oomycetes (CP 126 *(*Pettitt *et al.*, 2015) and provided knowledge transfer of the outcomes (CP 128 (Pettitt, 2015)) with information on diagnostics and monitoring, and chemical and biological control particularly applicable to aerial oomycetes. Diagnostic techniques are being developed to identify, detect or quantify pathogens (CP 136 (Wakeham, 2016)). Molecular methods have been used for roots, substrates and soils (PC 281 (O'Neill,

2011)), conifers (HNS/PO 181 (Wedgwood, 2011)), raspberries (SF 130 (Peters, 2014)), and carrot (FV 353 (Barbara, 2010)) that should apply to aerial oomycetes. Strategies for disease control for organically grown field vegetables were examined in the DOVE project (Gladders, 2002).

Techniques which can be used by growers (baiting and lateral flow devices) for detection of the pathogens in water (HNS/PO 188 (Wedgwood, 2014a)) have relevance to the dispersal phases of aerial *Phytophthora* and *Pythium* species. Work on monitoring *P. ramorum* in the field has led to the development and use by UK plant health inspectors of portable molecular diagnostic equipment. Chemical and biological oomycete control products have been tested for strawberries (SF 121 (Berrie, 2012)), raspberries (SF 123 (Wedgwood, 2014b)) and carrots (FV 391 (Gladders, 2014)). There is a vast body of oomycete research globally. For example, chemical and biological control products have been investigated in the USA IR4 programmes and also in the UK Sustainable Crop and Environment Protection – Targeted Research for Edibles project (SCEPTRE (O'Neill, 2015)). European reviews have been conducted on the use of biocontrol products and integrated crop management (ENDURE, 2009).

Resting spores of aerial oomycetes are formed in plant tissue and will remain in soil and green waste that can be used in mulches. In the UK, composted waste materials, mulching and pathogen control has been the subject of projects in various crops funded by The Waste and Resources Action Programme (WRAP) (Noble and Roberts, 2003).

The nutrient content of the soil can also influence the level of disease caused by oomycete pathogens (Dordas, 2009). For example, the severity of infection by obligate pathogens such as downy mildews and white blisters is increased when plants are grown in a high N environment (Palti and Rotem, 1981; Dordas, 2009). In general, unbalanced nutrition has been reported to facilitate infection by downy mildews; soils rich in organic matter, or a lack of potassium or phosphorus have all been linked to increase the potential for infection by various downy mildew pathogens (Palti and Rotem, 1981; Dordas, 2009). Additionally manganese fertilisation has been linked to giving control of disease caused by downy mildew (Dordas, 2009).

The detachable (caducous) sporangia of most aerial oomycetes means that they can be carried in wind-blown rain and rain-splash and either land on hosts directly or enter irrigation water. The spread of *P. ramorum* in this way to certain trees and shrubs has been of national concern (DEFRA, 2005). Water monitoring and treatment, including the use of slow sand filters and reed beds have been studied at various centres (Pettitt and Hutchinson, 2005).

The EU COST programme has involved work on the diagnostics and control of *Phytophthora* species. In the UK and USA there has been much recent research on *P. ramorum* epidemiology, diagnostics and chemical and cultural control measures.

The current study follows on from work in project CP 126 (Pettitt *et al.,* 2015) and CP 128 (Pettitt, 2015) on root and stem infecting oomycetes and focuses instead on aerial oomycetes. There will be some cross-over between these desk-studies, in particular for *Phytophthora* species with water-borne zoospores and when considering environmental, chemical and cultural control methods. Information from CP 126 and 128 that is relevant to aerial oomycetes has been incorporated within the reviews of the current study emphasising the key aspects relating to above ground infection. Appendix 4 gives the index to topics covered by CP 126.

As other AHDB work is planned on oomycete pathogens belonging to the Genus *Bremia* and those causing downy mildews of spinach these will not be reviewed. Potatoes and grapes fall outside the remit of AHDB Horticulture and so information on *Phytophthora infestans* has only been reviewed where information such as diagnostics and control methods could be applied to other known UK hosts (e.g. tomato). Crops within all of the AHDB Horticulture crop sectors were examined for aerial oomycete problems: field vegetables, protected edibles, soft fruit, top fruit, hardy nursery stock and protected ornamentals. Following industry consultation, a range of aerial oomycete diseases of key importance were selected for review in greater depth.

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Aims and Objectives

The overall aim of this project was to undertake a literature review and collect data and grower comment across a broad range of aerial oomycete pathogens in order to identify where there are gaps in our knowledge, and so direct future research and knowledge exchange work programmes.

Specific objectives were:

1. To survey stakeholders across crop sectors to determine which aerial oomycetes are having the greatest financial impact and specific factors contributing to this

2. To compile a list of AHDB projects and factsheets on the main crop-pathogen interactions and determine key outcomes

3. To assess UK and overseas research publications covering the main UK aerial oomycete diseases and to record the outcomes of those currently most relevant and gaps in scientific knowledge

4. To review future threats including pesticide resistance and emerging disease problems

5. To undertake efficient KT by producing a final report, producing 2 factsheets (one ornamental and one edible), writing an article for AHDB Grower magazine, and delivering multiple grower presentations.

Materials and methods

Literature searches were carried out principally utilising the following web resources:

- Google Scholar
- Web of Science
- Science Direct
- NCBI PubMed
- Google web search
- Endure (A Network for Integrated Pest Management)
- AHDB Horticulture website

In addition to web resources, ADAS Boxworth has a good resource of books and hard copies of journals. In-house expertise was often available to help direct searches towards relevant information. Grower surveys were also used to gain insight into current problems regarding many of the pathosystems described in this review (using the form given in Appendix 3).

Also of note is the IR-4 Project, which since 1963 has been the primary resource for facilitating registrations of conventional chemical pesticides and biopesticides for speciality crops and other minor uses (speciality uses) in the USA.

This review does not seek to include 'text book' information on the pathogens, but to highlight recent knowledge gains and provide references to allow readers to seek greater depth of interest to them. Where knowledge is still lacking, this has been highlighted.

Recent papers, from 2000 onwards, have been the primary focus. However, where deemed necessary and relevant, older literature has been explored, such as when limited recent work has been carried out on certain pathosystems.

The crops and diseases covered in this review were identified as those of primary significance by consultation with pathologists, sector experts and agronomists, however, many of the key principles of disease control are likely to be applicable to other affected crops reported in the grower surveys.

Relevant AHDB Horticulture reports were assessed to highlight new information and where gaps still exist in order to identify where further research or development would be worthwhile. Findings have been summarised as tables towards the back of the report. Unsuccessful projects do not necessarily mean poor quality work as the outcomes of work within biological systems can be unpredictable.

Detailed information on spore types and functions common to all oomycetes was given in the introduction to CP 126, and so a generalised lifecycle has been prepared for the current report as an overview of the various means of spread of aerial oomycetes. Reviews of topics with potentially broad-reaching effects on aerial oomycete control have been presented – spread in irrigation water, elicitors, resistance to fungicides and invasive pathogens. The main reviews of aerial oomycetes that follow have been divided into two sections - on edible and ornamental crops. References to the literature reviewed are given following each disease review. More-general, background, references easily accessible via websites are tabulated at the back of the report. After the reviews section, information from all sources has been used to produce a table with key knowledge areas and gaps for the main pathogens.

Life Cycles

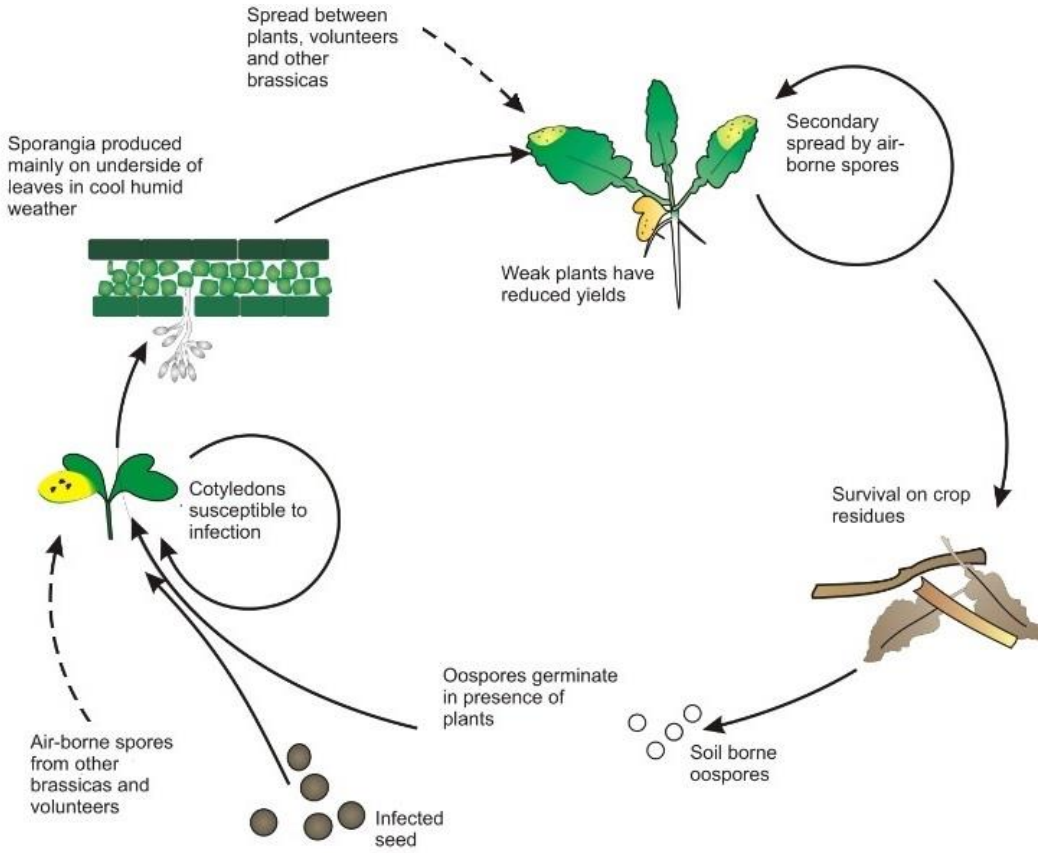

Figure 1. A generalised lifecycle of a downy mildew belonging to the genus *Peronospora*.

While aerial oomycete lifecycles differ, a typical downy mildew lifecycle is shown in Figure 1. This shows both a potential soil-borne phase resulting from root infection (not usually involving rotting) originating from resting spores (oospores) in the soil, and an air-borne / water-splashed phase with sporulation on leaves and stems. Various points within the lifecycle can be uncertain for particular pathogens, e.g. the ability of related hosts to become infected from the same source, or from oospores, and these are mentioned in the reviews.

The downy mildews *Plasmopara* spp. and *Pseudoperonospora* spp. are capable of producing zoospores (swimming spores) from their sporangia, whereas *Peronospora* spp. and *Hyaloperonospora* spp. do not. In general, *Phytophthoras* and white blisters produce zoospores at some stage of their lifecycle, although the timing, frequency, their significance in disease, and the conditions which stimulate their production varies between species (Jeger and Pautasso, 2008). Knowing how the pathogens spread and infect assists their control.

Reference

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Possibilities of spread of predominantly airborne oomycetes via contaminated irrigation water

The presence of infective oomycete propagules in irrigation water sources and their role in plant disease epidemics is well known (Hong *et al*., 2014, also reviewed in CP126, Pettitt *et al*., 2015). Viable propagules of aerial plant pathogens generally are well represented in water samples, especially genera such as *Botrytis* that produce abundant airborne conidia (Pettitt *et al.*, unpublished plant clinic data). Also airborne oomycete species like *Phytophthora infestans* are seen in water samples, sometimes in reasonably large quantities (>50 colony forming units l^{-1}) and spores of this species are known to remain viable and infective for up to 20 days in surface water (Porter & Johnson, 2004). The importance of such inoculum in untreated water in establishing new epidemics on nurseries is not certain although similar concentrations of root-infecting species such as *Phytophthora cryptogea* or *P. cinnamomi* in irrigation water would constitute a significant disease threat. Other airborne *Phytophthora* species that have been detected in water and where such contaminated water has been implicated in disease spread include *Phytophthora cactorum* and *P. ramorum* (McIntosh, 1966; Tjosvold *et al*., 2008; Sutton *et al*., 2009). One feature that these species all appear to have in common is caducous sporangia (Stamps *et al*., 1990), which detach, acting in much the same way as the conidia of the downy mildews. Given the frequent occurrence of the other airborne species mentioned here, it is highly likely that the conidia of downy mildew species are frequently present in significant quantities in untreated open irrigation water sources. As the downy mildews are obligate biotrophs they do not grow on agar media and so are not seen in tests using the conventional membrane filtration-colony plating technique (Pettitt *et al*., 2002). This is unfortunate as this technique generally gives a good picture of species (both pathogens and non-pathogens) present in water samples and their viability, and thus a hint as to their disease-causing potential. Probably, as they are generally considered primarily airborne, few other techniques have been used directly to measure downy mildew inoculum in water samples. A recent exception to this is a study of soils and river water in Northern Spain by Català *et al.* (2015) using genus-specific pyrosequencing of eDNA (environmental DNA). Actually focused on *Phytophthora,* this study also detected inoculum of the downy mildew species *Peronospora aparines, P. aestivalis, P. glomerata, Bremia lactucae, Hyaloperonospora parasitica* and various other, unidentified, *Hyaloperonospora* species in river water. Although the viability and types of propagule present were not assessed, the presence of significant inoculum of a wide range of downy

mildew species was confirmed, and downy mildew propagules may remain viable and infectious in aqueous suspension for hours if not longer. Again, as downy mildews are considered primarily airborne pathogens, their activity and longevity in large masses of water has not been widely studied. Nevertheless, most species are induced to germinate and produce infection structures in free water on leaf surfaces and some genera such as *Bremia* and *Plasmopara* will produce motile swimming zoospores which are able to swim short distances to favourable potential infection sites and (like other oomycete species) can encyst when conditions are not favourable, although whether these spores are polyplanetic (able to encyst and swim multiple times) and able to act as survival capsules like those of *Pythium* and *Phytophthora* species (for full explanation of this see *et al*., 2015) does not appear to have been investigated. Clearly the possibility of contaminated irrigation water being the source of primary infections by pathogens normally considered airborne does exist and needs further investigation with appropriate diagnostic tools (i.e. capable of clearly discerning infective inoculum). However, it is highly likely that such infection potential would be easily eliminated using appropriate water treatment systems – a topic covered in HDC review CP126 (Pettitt *et al*., 2015).

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Elicitors: an overview of their mode of action

Introduction

The response of plants to disease and stress is variable depending on the level of stress encountered and the susceptibility of the plant to the attack or effect of that stress. In nature, when a plant experiences initial disease attack, various defence responses are induced to enhance their resistance. Sometimes this is successful, sometimes, unsuccessful. The discovery of this response has led to gradual investigation on the subject, to look at how domesticated and agricultural plants can optimise their abilities to defend against biotic and abiotic challenges. Plants recognise and respond to defence elicitors which are signal inducing compounds that are perceived by the innate immune system that prime and/or induce defence responses (Weisel *et al.,* 2014). The elicitation of defence responses in plants is a topic that has seen much discussion in relation to the mode of action of particular agents, phyto-hormones and the processes induced within the plant.

Types and pathways of elicitation agents

The main consensus gained from literature on the subject of elicitation is that it rarely results in complete control of pathogens, instead leading to reduced lesion size and/or number (Sillero *et al.*, 2012; Walters *et al.*, 2013). In general terms, there are two main types of induced resistance in plants that have been recognised: systemic acquired resistance (SAR) and induced systemic resistance (ISR). SAR is induced by treatment with a variety of agents (such as Bion, acibenzolar-S-methyl (ASM), beta-amino-butyric acid (BABA) and cis-jasmone) and is mediated by a salicylic acid (SA)-dependent process. ISR develops as a result of the colonisation of plant roots by strains of certain plant-growth promoting rhizobacteria (PGPR) and mediated by a jasmonate (JA) and ethylene (ET)-sensitive pathway (Walters *et al.*, 2013). The induction of plant resistance to biotic challenges can lead to the direct activation of defences, but can also lead to the priming of cells, resulting in stronger elicitation of those defences following pathogen attack, which is termed as ‘priming’ in some literature (Goellner and Conrath, 2008).

There are different types of elicitors that follow their own mode of action depending on the adversary (Figure 2). There are general elicitors, which are designated Pathogen-Associated Molecular Patterns (PAMPs), which trigger signals as a result of pathogen attack on the plant. Wounding by mechanical handling, the creation of lesions by pathogen colonisation or insect

attack may trigger Damage Associated Molecular Patterns (DAMPs). Signalling as a result of application of agents or non-pathogenic microbes comes from Microbe-Associated Molecular Patterns (MAMPs). More detail on these molecular patterns can be found in Henry *et al.* (2012).

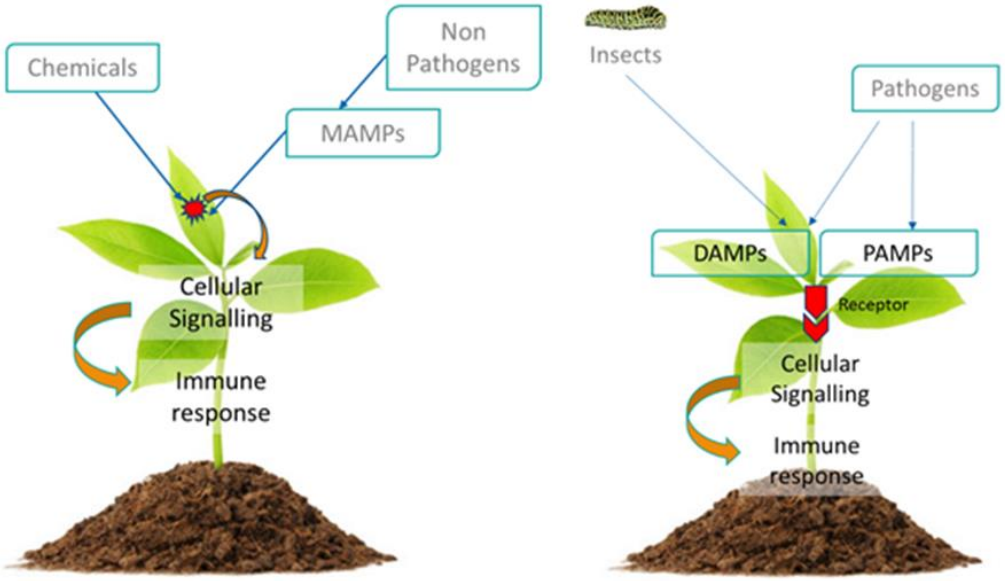

Figure 2. A diagram of the systemic responses from plants that have been triggered by various attacking agents or external inducing agents, which result in induced immunity. The left hand diagram represents the response to non-pathogens or applied chemical agents to trigger signals through MAMPs, inducing an immune response. The right hand diagram shows the signalling response through insect attack via DAMPs, as well as the two types of signalling pathways triggered by pathogens, PAMPs and DAMPs. *(Diagram reconstructed from Henry et al. (2012)).*

The action of elicitation of oomycetes, as well as other biological invaders, has been described in detail in a studies by Weisel *et al.* (2014) and Walters *et al.* (2014). Aspects examined included the type of elicitor or inducer of chemical, pathological or non-pathological nature, the plant that would be effected (i.e., in which the immune response would be induced), the pathogen that has been seen to be controlled or reduced in incidence, and the reference or origin of the information. An abstract of a table adapted from Walters *et al*. (2014) is given below (Table 1) showing studies that have found particular chemical or biological agents controlling or reducing certain oomycetes.

Table 1. Example of some of the chemical and biological elicitors, whether acting by systemic acquired resistance (SAR) and the pathogens they have been found to control or reduce (adapted from Walters *et al*., 2014).

Elicitor Agent	Effective on	Pathway	Host plant	Reference
acibenzolar-S-methyl (ASM)	*Pseudoperonospora cubensis*	SAR	Cucumber	Ishii *et al.* (2001)
	Phytophthora infestans		Tomato and petunia	Becktell *et al.* (2005)
beta-amino-butyric acid (BABA)	*Peronospora parasitica* (*Hyaloperonospora parasitica* / *H. brassicae*)	SAR	Cauliflower	Silue *et al.* (2002)
Harpin Protein	*Peronospora parasitica* (*Hyaloperonospora parasitica)*	SAR	*Arabidopsis thaliana*	Dong *et al.* (1999)
Chitosan	*Pythium ultimum*	Unknown	(plate study)	Palma-Guerrero *et al.* (2007)
	Pythium aphanidermatum		Cucumber	Weisel *et al.* (2014)

Degree of elicitation can vary with host genotype

The efficacy of elicitor agents varies with host genotype. A study by Sharma *et al.* (2010) found that tomato genotypes varied significantly in their expression of BABA-induced resistance to *Phytophthora infestans*. In this study, the level of induction was not always related to the resistance rating of the tomato accession, and was significantly influenced by the pathogen isolate. The degree of resistance induction tended to decrease with increasing leaf age, possibly reflecting the effect of BABA from root to shoot. Sharma *et al.* (2010) also found that, though BABA performed well on one isolate, it was less effective on two or three mixed isolates. In this case, it was suggested that studies focusing on one isolate or a single host genotype might lead to a misleading conclusion concerning the effectiveness of the elicitors in practice (Walters *et al.,* 2013).

Some agents, which are available in the commercial market, that have been investigated for their efficacy in inducing resistance include: ASM, Bion (Syngenta), Milsana (*Reynoutria sachalinensis* extract), Elexa (chitosan), β-aminobutyric acid (BABA) and Messenger (harpin protein, Plant Health Care). ASM is widely reported to be effective in inducing resistance against a broad range of pathogens in many plant species. Studies on algae-based agents

have found that extracts from *Ulva armoricana* give high elicitor activity from their complex sulphated heteropolysaccharides (Jaulneau *et al.*, 2011; Walters *et al.*, 2013). The majority of the literature focuses on the effect of elicitors on fungi and bacteria. This highlights the relatively limited amount of literature found on the efficacy of elicitors on oomycetes.

Potential drawbacks of elicitors

Understanding how elicitors prime plants against pathogens is required to determine the fitness costs to the plant which could result in reduced yield, or whether or not priming could negatively affect the quality of the crop (taste, texture, appearance). Phytotoxicity of some elicitors has been observed and therefore plant safety is also an issue which needs addressing (Gladders, P., pers. comm.) The types and levels of secondary metabolites produced and their effect on human health also need evaluating to check for any potential risks (or indeed benefits (Alghasham, 2013)). Cucurbitacins are defence related chemicals produced primarily by cucurbits when stressed and which are amongst the bitterest tasting substances to humans, and can even be toxic (Huckle, A., pers. comm.). If priming of plants increases the levels of these chemicals in fruit, the quality of the produce might be greatly reduced. At the same time, certain cucurbitacins have been identified to have potential health benefits (Hsu et al., 2014; Alghasham, 2013) and as such, growing crops under stress to induce cucurbitacin production for use in pharmaceuticals may (perhaps some time in the future) open up a whole new market to cucurbit growers.

Conclusion

It is important to note that it is generally accepted that elicitors do not give 100% control (Sillero *et al*., 2012; Walters *et al.*, 2013) and that they are best used preventatively, with the aim of reducing the requirement for synthetic pesticide usage. It is therefore important to determine the timescale of induced resistance as frequent reapplications would prove expensive (Gladders, P., pers. comm.), especially when complete control is unlikely. In relation to studies on oomycetes, Sharma *et al*. (2010) found that BABA provided almost complete control of late blight (*P. infestans*) in tomato. In van der Wolfe *et al.* (2012), seed treatments of BABA did not significantly reduce *P. parasitica* on cabbage (*Brassica oleracea*), however, there was a greater degree of pathogen reduction when BABA was applied to the leaves. In a study by Ji *et al*. (2011), ASM was found to supress *P. capsici* on squash by an average 75%, and by about 80% when used in conjunction with standard fungicides such as Ridomil Gold (metalaxyl-M and mancozeb; Syngenta) and Revus (mandipropamid; Syngenta). Some agents, such as *Ulva armoricana*, were applied with a wetting agent (Jaulneau *et al.,* 2011) which may alter their efficacy through enhanced tissue coverage. It is suggested in literature that it would be more useful to study the effect of particular, or more

successful eliciting agents on various crop types against multiple pathogens. In nature, plants will experience more than one pathogenic or insect challenge during the growing period, it would be beneficial to create a programme that would assist the obligation to sustainable cropping by minimising synthetic fungicide use, but also to study the practicality of the use of elicitors in a commercial setting. In relation to this, the integration of priming (applying an eliciting agent or non-pathogenic inducer pre-pathogen attack) into a conventional fungicide programme could be of some use to growers and industry, and aid better understanding of the interaction between elicitation, fungicides and plants against pathogen attack.

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Changes affecting the incidence and severity of aerial oomycete diseases

Fungicide resistance in aerial oomycetes and product availability

The AHDB Horticulture review of root infecting oomycetes (CP 126, Pettitt *et al.,* 2015) determined that fewer examples exist of their resistance to fungicides than for foliar infecting oomycetes, but the reason for this was unclear. Both have a rapid turnover of generations associated with asexual sporulation (by either sporangia or zoospores) and the consequent increased opportunities for mutations and selections.

Fungicide groups active against oomycetes, their target site of action, and the risk of resistance developing in each were given in Table 8 of CP 126 (Pettitt *et al*., 2015), along

with The Fungicide Resistance Action Committee issued FRAC codes that should be used by growers to develop programmes alternating different modes of action. The review of fungicide modes of action and resistance of downy mildews by Gisi and Sierotzki (2008) gives further detail. FRAC has published a book, available online, detailing the management of fungicide resistance in general (Brent and Hollomon, 2007). Information on known cases of resistance to fungicides used against oomycetes, or the potential for this occurring, are given below.

Quinone outside inhibitors (QoIs) (which include azoxystrobin and fenamidone) (having cross resistance shown between all active ingredients within the QoL group) have a high resistance risk, with resistant isolates obtained of *Plasmopara viticola* from grape and *Pseudoperonospora cubensis* from cucurbit (Gisi and Sierotzki, 2008).

Phenylamides also have a high resistance risk. Field populations of the Peronosporales have been found with resistance to phenylamides in 13 hosts and include metalaxyl resistance by *P. cubensis* in 1980, *Phytophthora infestans* in potato in 1981, *Bremia lactucae* in lettuce in 1983 and *Peronospora destructor* in onion in 2004, with resistance to phenylamide seed treatment found against *Peronospora viciae* in pea (Gisi and Sierotzki, 2008). More recently a metalaxyl-M resistant strain of *Plasmopara obducens* was introduced into the UK in 2011 and resulted in widespread downy mildew infections of Impatiens that were difficult to control. Monitoring in project PO 011 in 2012, 2013 and 2015 found no further resistant *P. obducens* isolates, with reduced incidence of the pathogen through cultural measures (Jennings, 2015).

Quinone “x” inhibitor (QxI) potato blight fungicide active ingredient ametoctradin has a medium-high risk. Other fungicide groups are thought to have a lower risk of pathogens developing resistance to them. However, although the carboxylic acid amides (CAA) fungicides (which in include dimethomorph and mandipropamid) have a low to medium risk (with cross resistance between group members) resistance is known in *P. viticola* (grape downy mildew) although not *P. infestans* (potato blight). Isolates of *P. infestans* causing lower field efficacy of fluazinam (Shirlan), a pyridinamine with low resistance risk, have been found in the Netherlands.

Numerous widely used conventional chemical pesticides have already or are predicted to become unavailable over the next few years. Some were lost by failing to make the Annex I list of active substances permitted in the EC following a review under the pesticide Registration Directive (91/414EEC) and the implementation of Regulation EC 1107/2009 requiring the assessment of inherent hazard as well as risk has meant more losses. Work within CP 077, SCEPTRE, sought to broaden the range of active ingredients available to horticulture to assist resistance management. Infinito (fluopicolide + propamocarb) was found

to be effective against *P. destructor* and EAMU 1142/2015 for use on bulb onions has subsequently been obtained. This product belongs to a different mode of action group than those named above. A mixture of dimethomorph and pyraclostrobin (Cassiopeia) also gained approval for use on this crop and pathogen following work in SCEPTRE which also found a reduction in Brassica downy mildew and root-infecting *Phytophthora cactorum* (strawberry crown rot). Non-conventional products were also tested against Brassica and onion downy mildews in SCEPTRE. A biostimulant gave significant control on Brassicas, but it has become unlikely this will become available to UK growers. Two fungal biopesticides were found effective as drenches against *P. cactorum*, and could be tested against soil-borne aerial sporulating oomycetes such as *P. viciae* on pea.

Natural products with potential to control oomycetes, in particular downy mildews, were reviewed in HNS 135 (O'Neill, 2006). Various chemical salts, plant extracts, beneficial fungi and bacteria and other named products had reports of efficacy. In subsequent efficacy testing on rose and blackberry downy mildews (both *Peronospora sparsa*) a product containing grapefruit oil reduced the leaf area affected more than the then standard product (Aliette 80 WG, fosetyl-aluminium). For commercial reasons fosetyl-Al is now only available as a mixture with fenamidone in Fenomenal against downy mildews and oomycete root rots. Biofungicides with activity against oomycetes have become available in the UK in the last decade, with recommendations for drench application against oomycete root rots for Serenade ASO (*Bacillus subtilis* strain QST713) and Prestop (Gliocladium catenulatum strain J1446). The USA label for Serenade ASO includes the suppression of various downy mildews – the plant defence mechanism of biofungicides can give general benefit. Experimental uses of beneficial micro-organisms are noted in the pathogen reviews in this report. Examples of beneficial micro-organisms classified by their potential allochemical activities against oomycetes were summarised in Table 9 of CP 126.

Potassium phosphites are a commonly used a root drench in soft fruit production in the UK, and have been shown to have some effect against *P. sparsa* (O'Neill, 2006). Products are thought to induce host disease resistance, while phosphorous acid is the anionic metabolite of fosetyl-aluminium. A new EC regulation has been drafted that may mean that phosphite products may not continue to be allowed to be sold as fertilisers. There is current concern that as some have now been approved as fungicides, edible crops are subject to maximum residue levels and higher rates and late season use of phosphite fertilisers may risk breaching the limits.

Invasive pathogens

A detailed summary of key UK horticultural crops with species of oomycete rot and / or stem rot pathogens in the UK or only in mainland Europe was provided in Table 2 of CP 126. Some of these spread from aerial sporulation, such as *Phytophthora ramorum* and *Phytophthora kernoviae*.

The UK Plant Health Risk Register rates pests and pathogens for the likelihood and impact of their becoming established in the UK, or for spreading further within the UK. The Register records organisms against which actions have been recommended by the European and Mediterranean Plant Protection Organisation and also those for which UK action has been considered (e.g. following the production of a Pest Risk Analysis). There are currently 17 oomycetes listed showing their host range, which countries they are present, risk to the UK and action recommended against them, nine having the ability to spread aerially (Appendix 5). Of highest concern are *P. ramorum* and *P. kernoviae* (which are reviewed in the ornamentals section of this report) plus the likelihood of the introduction of new resistant or more virulent races of *P. infestans* causing potato and tomato blight. The Forestry Commission and Defra carried out 17 research projects on *P. ramorum* / *P. kernoviae* between 2002 and 2013. Of high concern are two *Phytophthora* species not in the UK which can infect the needles of *Pinus radiata*; *P. pinifolia* and *P. pluvialis* (Ganley *et al*., 2014) and so there is prohibition of pine planting material coming in from outside the UK. Another *Phytophthora* species, *P. pseudosyringae*, causing bleeding canker and root rot of a number of broadleaved tree species is present in the UK in limited areas, but from the assessed combination of likelihood, impact and value it is not currently considered of major concern to the UK. In the USA, it is reported to spread aerially, but in Europe it has only so far been reported as soil-borne.

Three downy mildews are listed in the UK Plant Health Risk Register; *Plasmopara halstedii* on sunflower is absent from the UK, but is present across the rest of Europe, *P. obducens* was first found in the UK in 2003 and drastically reduced the popularity of *Impatiens balsamina* and *Impatiens walleriana* (as reviewed in this ornamentals section of this report). *Peronospora belbahrii* is now found on basil in the UK, but no statutory action is required if it seen (this disease is reviewed in the edibles section of this report).

Recently, growers have reported downy mildews on aquilegia and rhubarb, although not seen before in these crops (for more details see crop sections). Biosecurity measures, such as given in the protocols produced for ornamentals (Slawson, 2012), are important, particularly when importing plants. Ensuring that unfamiliar symptoms are checked by a plant clinic, or

possibly utilising diagnostic devices on-site, and being alert to unexpected failures in fungicidal control are measures necessary to prevent problems escalating.

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Edible Crop Reviews

Vegetable Brassica Downy Mildew

Hyaloperonospora brassicae (also referred to as *Hyaloperonospora parasitica* and *Peronospora parasitica* throughout the literature (Göker *et al.*, 2004; Göker *et al.*, 2009)) is the causal organism of downy mildew in Brassica species (Koike *et al.*, 2007). The disease is common on many species of *Brassica oleracea* including (but not limited to) Brussels sprouts, cauliflower, broccoli, cabbage, marrow-stem kale, and kohlrabi. The disease is most severe in young plants, especially in protected environments, and can have serious economic implications for propagators as often the whole crop may die (Koike *et al.*, 2007; Rimmer *et al.*, 2007). Young plants can also become systemically infected but remain symptomless until they are in the field, an occurrence also of economic significance due to reductions in yield

and quality (Rimmer *et al.*, 2007), with cauliflower and calabrese usually showing the most severe infections (Gladders *et al.*, 2002).

Due to the high susceptibility of seedlings to downy mildew, disease at this stage is most important and will likely influence the impact of the downy mildew on mature crops (Gladders, P., pers. comm.). Symptoms are most common on the leaves, but the disease can affect all aerial parts of the plants, importantly the inflorescence of cauliflower and broccoli which can develop symptoms in storage. Downy mildew is common, but good quality crops can still be achieved at low levels of disease and do not require treatment; adult plant resistance can prevent infection carried through from propagation from turning into an epidemic (Gladders, P., pers. comm.). The extent of post-harvest and field losses of vegetable Brassicas resulting from downy mildew have not yet been accurately quantified. It would be beneficial to determine the trends of downy mildew epidemics in Brassica crop systems by utilising disease progress curves (assessing shape and time course); with disease cycling at 3-5 days, time to 100% disease incidence within a crop can be rapid (Gladders, P., pers. comm.).

Temperature optima for many stages of disease development have been well researched (Minchinton, 1998a) and there is evidence that the disease can be spread by contaminated seed. With seed contamination, depending on the crop, the pathogen can be internal or external (Minchinton, 1998a) and insight into the location of the pathogen may help identify the origin of infection while also helping to establish the most efficient method for its control. Good hygiene in propagated crops including growing on plastic or concrete to avoid soil contact, should remove the risk of infection via oospores found in soil and crop debris and therefore windblown spores are likely to be responsible for the majority of infections. The survival period of conidia from *H. brassicae* is not well documented (Nordskog and Hermansen, 2008; Hladilová, 2011). Standard cultural control methods are advised such as crop rotations, rogueing, avoiding over watering, etc. (Minchinton *et al.*, 1996; Minchinton and Hepworth, 1998; Koike *et al.*, 2007).

The sources of initial inoculum vary depending on whether the crop is in propagation or in the field. In the field, root infection by oospores can lead to systemic infection of the plant and the production of sporangia on the above ground parts, which are disseminated throughout the crop. Additionally it has been hypothesised that wild members of the *Brassicaceae* family such as *Capsella bursa-pastoris* (shepherds-purse), and indeed cultivated members of *Brassica napus* may be a source of windblown inoculum for vegetable Brassicas (Minchinton and Hepworth, 1998). However, the role of this source of inoculum is not fully understood due to increasing evidence of phylogenetic distinction (Göker *et al.*, 2003; Göker *et al.*, 2004; Göker *et al.*, 2007; Göker *et al.*, 2009; Monot and Silué, 2009) and understanding regarding

host specialisation is not well documented (Nordskog and Hermansen, 2008; Hladilová, 2011).

Significant race variation within *H. brassicae* has been seen and consequences of such specialisation on aspects such as virulence and cultivar resistance are not yet fully understood. For example, one race which is particularly virulent on one vegetable Brassica host, may only be weakly virulent on others (Nashaat and Awasthi, 1995; Silué *et al.*, 1996; Koike *et al.*, 2007), and cultivars resistant to certain strains of the pathogen may be susceptible to others (Agnola *et al.*; Monot and Silué, 2009; Coelho *et al.*, 2012). Further insight into the specificity of race-cultivar interactions is required so that the development of resistance and other control methods, both cultural and product based, can be targeted against relevant UK strains (Wang *et al.*, 2000; Coelho *et al.*, 2012).

In recent years a lot of research has looked into Brassica resistance to *H. brassicae*, often at the genetic level (Monteiro *et al.*; Nashaat and Awasthi, 1995; Silué *et al.*, 1996; Farinhó *et al.*, 2004; Monot and Silué, 2009; Carlier *et al.*, 2011; Vicente *et al.*, 2012; Singh *et al.*, 2013; Bahcevandziev *et al.*, 2015). Vicente *et al.* (2012) identified one resistance gene from certain lines of *B. oleracea* which conferred resistance to all UK isolates of *H. brassicae* tested during the study, and several other genes which provided partial resistance to various isolates. The study also found that plants containing these R genes are fully susceptible to Portuguese *H. brassicae* isolates, illustrating that the pathogen can be geographically specialised.

Currently, there are very few commercial varieties of vegetable Brassicas which show high levels of resistance against downy mildew. However, available varieties showing some level of downy mildew resistance include: cv. Puntoverde (romanesco cauliflower; Rijk Zwaan) which is described as having ‘high partial resistance’ versus downy mildew; cv. Bosworth (Brussels sprouts; Tozer Seeds) is described as having ‘intermediate’ downy mildew resistance; cv. Zen and cv. Typhoon (broccoli; Tozer Seeds) described as having ‘some’ downy mildew resistance; cv. Marathon (broccoli; various suppliers) which is ‘partially tolerant’ to downy mildew. Due to the apparent limited availability of resistant cultivars, effective cultural control methods are essential, and often both biological and chemical treatments are also required. Control is primarily focused at the propagation stage, as virtually all Brassica crops get downy mildew but few require field treatment (Gladders, P., pers. comm.).

Little work has been done regarding forecasting for downy mildew in vegetable Brassicas. This is because of the short duration of moisture required over frequently seen temperature ranges and as such, infection conditions occur in the crop canopy on most days (or nights) (Kennedy, R., pers. comm.). Additionally, in-field disease may be of minor importance,

compared with infection in propagation, although relative losses are yet to be quantified. It could be that field crop treatments against *Alternaria* and *Phoma* diseases, such as Amistar Top (Syngenta; azoxystrobin and difenoconazole), are also having an effect on *H. brassicae* and so the disease does not show its full effect.

There may be scope for the development of a forecasting system within propagation so that when the environment becomes conducive to infection, growers could trigger protective fungicide applications and hence save time and money. However, as little as 30 minutes of leaf wetness is required for infection with Brassica downy mildew (Gladders, P., pers. comm.) and so forecasting would likely need to be based primarily on spore presence within the system, potentially utilising lateral flow-type tests. Cultural and chemical control methods should minimise the risk of sporulation on diseased tissue under protection, however certain areas of the glasshouse may be more susceptible, perhaps where ventilation is slightly compromised. Logging of environmental conditions suitable for sporulation and infection in these areas (including leaf wetness), twinned with the use of lateral flow tests to detect aerial spore concentrations (Kennedy, 2012; Wakeham, 2015a; Wakeham, 2015b) to enable the confirmation of sporulation events, could enable fungicide sprays to be timed only as and when they are needed. Additional lateral flow tests may be required to detect the presence of significant spore concentrations originating from outside the propagation crop.

Chemical and biological elicitors of plant defence have shown good potential for protecting against downy mildew pathogens in Brassicas (Jensen *et al.*, 1998; Godard *et al.*, 1999; Sun *et al.*, 2015); one study by Monot *et al.* (2002) showed avirulent strains of '*Peronospora parasitica*' were able to induce systemic resistance in broccoli. The majority of propagators apply chemical treatments active against downy mildew as seed treatments or as drenches. Due to the reported emergence of metalaxyl-resistant strains of downy mildew (Koike *et al.*, 2007), a close watch of the efficacy of these treatments must be maintained. Any cases of apparent resistance of downy mildew on vegetable Brassicas to in-field fungicides should be recorded and isolations could be made to check chemical resistance. However, there is no proactive monitoring scheme in place in the UK.

Various biological treatments with inhibitory effects on *H. brassicae* have been identified. Seed and leaf treatment with novel bacterial substances have shown significant reductions in disease severity (van der Wolf *et al.*, 2012). Additionally, certain plant extracts have also been shown to have activity against *H. brassicae* (Lawson and Kennedy, 1998). More work is required to progress some of these identified leads into utilisable biological treatments.

Research into light treatments under protection to protect against downy mildew epidemics during propagation has shown promising results (Reuveni and Raviv, 1997; Cohen *et al.*,

2013), with blue light frequencies being inhibitory to *H. brassicae* sporulation (Cohen and Eyal, 1977; Reuveni and Raviv, 1997; Minchinton, 1998a; Minchinton, 1998b). Practices utilising these principles are reportedly already being used in Israel (Minchinton, 1998a; Minchinton, 1998b), and their potential for incorporation into IPM programmes in the UK should be assessed.

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Vegetable Brassica White Blister

Albugo candida (and other closely related *Albugo* species) is the causal agent of white blister, which affects a wide range of vegetable Brassicas and is widespread in the UK Brassica growing industry. Symptoms of white blister include: raised white or cream blisters on leaves, stems, and flower stalks, tissue can become distorted and turn yellow or red and leaves may wither and die (Koike *et al.*, 2007). Broccoli, Brussels sprouts, cauliflower, radish, mustard, Chinese cabbage and turnip can all be infected (Kennedy and Gladders, 2012) and as the symptoms are primarily cosmetic, infection can render crops unmarketable (Kennedy and Gladders, 2012). *A. candida* can infect a diverse range of hosts (over 200 species of plants, over a range of families) and host specificity is primarily thought to be down to different physiological races of the pathogen (Rimmer *et al.*, 2000). Recently however, various pathogens previously described as *A. candida* have been redefined as distinct species and it is likely that we still have a generalised understanding of white blister pathogens (Thines *et al.*, 2009; Ploch *et al.*, 2010; Thines, 2014). Currently, 24 physiological races of *A.* candida have been defined (McMullan *et al.*, 2015) and race 9 is thought to be the primary cause of infection in *Brassica oleracea* (Wakeham, 2015b).

Initial inoculum is primarily from sexually produced oospores in soil and plant debris which germinate into multiple zoospores that cause infection (Koike *et al.*, 2007). The detailed process of primary infection, including the infection plane, is unclear. A study by Jacobson *et al.* (1998) on wild crucifers has also provided evidence to suggest a role for seed-borne transmission of the disease. The white pustules associated with the disease are primarily due to zoosporangia development within the plant tissue and when they burst, release the asexual propagules and spread the disease throughout the crop (primarily via wind and water splash, although invertebrates may also play a role) (Singh *et al.*, 2002; Koike *et al.*, 2007). The optimal temperatures for spore development is around 20-25°C when symptoms can occur within three days of infection; below 8° C symptoms do not develop (Kennedy and Gladders, 2012). Zoosporangia release zoospores which infect the plant, leaf surface moisture is

required and infection takes around 4 hours in optimal conditions (Koike *et al.*, 2007). It is advised to bury crop residues after harvest to minimise disease spread to nearby crops, to plant resistant cultivars, and to rotate with non-*B. oleracea* crops (Koike *et al.*, 2007). Scheduling overhead irrigation in the morning as opposed to in the evening has been shown to reduce disease incidence by 58% and increase farm profit by 3% per hectare (Minchinton *et al.*, 2013).

Infection with *A. candida* has been shown to suppress host defences and increase the likelihood of secondary infections (Cooper *et al.*, 2008; Kamoun *et al.*, 2015; McMullan *et al.*, 2015). This includes infection by the downy mildew pathogen *Hyaloperonospora brassicae* which as a result, has a close association with white blister (Bains and Jhooty, 1985; Koike *et al.*, 2007). Host defence suppression also means that after infection with a compatible *A. candida* race, other usually non-compatible races may also infect (McMullan *et al.*, 2015). The mechanism(s) by which this host defence suppression arises is yet to be determined (Kamoun *et al.*, 2015).

Recent data from experiments on non-vegetable Brassicas has suggested that a significant amount of *A. candida* infections may remain latent and symptomless, and that the oomycete may persist as an endophyte (Ploch and Thines, 2011). Many cases of infection by *A. candida* could therefore remain unnoticed and be vertically transmitted via infected seed, removing the need for spore production (Jacobson *et al.*, 1998; Ploch and Thines, 2011). This scenario needs to be investigated within *B. oleracea* – white blister pathosystems. The level of defence suppression being caused by the pathogen in these systems needs to be determined and insight gained into any influence on secondary infections (Kamoun *et al.*, 2015). Could these symptomless plants potentially become reservoirs for *A. candida* races not specific to the host, or even targets for other plant pathogens not normally associated with the affected host?

In the case of an infected crop remaining symptomless, there may be an increased risk of secondary infections, perhaps even with pathogens not normally found on the host or that the host was believed to be previously resistant to. For example, Cooper *et al.* (2008) found that when *Arabidopsis thaliana* was pre-inoculated with *Albugo laibachii* (closely related to *A. candida*) specific to this host, previously resistant plants were now susceptible to *Hyaloperonospora arabidopsidis* (Arabidopsis downy mildew), and were even susceptible to *Bremia lactucae* (lettuce downy mildew), the latter illustrating a loss of species level resistance. Significant disease associated losses could then occur if plant protective products are not targeted against a pathogen to which the crop is thought to be resistant, which would be especially important in cases where disease prevention is relied upon for effective control.

Understanding the relationship between latent *A. candida* infections, reductions in host defences, and their consequential effect on secondary infections is vital in determining both the extent of the damage caused by the disease, and the best way to control it. Due to the vast number of plant species susceptible to white blister, it might be possible that weeds infected with compatible *A. candida* isolate may be subject to secondary infection by a race 9 isolate which can now proliferate on this non-host due to reduced defences, and act as a reservoir of inoculum. Understanding the parameters associated with a shift from an asymptomatic to a symptomatic interaction of white blister with its host is pivotal in progressing our understanding of this pathogen.

Various levels of cultivar resistance are available within *B. oleracea* crops. For example Rijk Zwaan offer a romanesco cauliflower with 'high partial resistance to white blister' (cv. Puntoverde), and Bejo Zaden offer the Brussels sprout cultivar Neptuno F1 which is 'very good' versus white blister. Minchinton *et al.* (2013) illustrated the effectiveness of cultivar resistance; growing the resistant cultivar 'Tyson' reduced disease incidence in broccoli heads by 99% compared to the susceptible 'ironman' cultivar and increased farm profit by 12% per hectare. Advances in molecular techniques has enabled further insight into the mechanics underlying host resistance (Piquerez *et al.*, 2014) and will hopefully accelerate the development of cultivars with effective and durable white blister resistance (Borhan *et al.*, 2008; De Geus *et al.*, 2013; Singh *et al.*, 2015).

Various biological control measures have shown promise in their ability to combat white blister. Singh *et al.* (1999) found that inoculation with a non-compatible isolate of *A. candida* induced both local and systemic protection against infection by a compatible isolate. Tirmali and Kolte (2013) showed that a wide range of biotic and abiotic plant defence activators applied as a spray to Indian mustard pre-inoculated with *A. candida* were able to significantly reduce the incidence and extent of blister development. The treatments included *Trichoderma harzianum*, *Pseudomonas fluorescens*, potassium sulphate, calcium sulphate, salicylic acid, borax and talc powder. Salicylic acid and calcium sulphate offered the most control but none of the treatments were able to prevent blister development completely. Kumar *et al* (2014) showed that essential oils from various plants were able to significantly inhibit spore germination of *A. candida* (Kumar *et al.*, 2014a; Kumar *et al.*, 2014b). de Souza *et al.* (2003) showed that isolates of *Pseudomonas fluorescens* were able to exhibit zoosporicidal properties; *A. candida* zoospores were rendered immobile within 30 seconds and subsequently lysed within 60 seconds.

Brassica$_{spot}$ is a disease risk forecaster computer programme based on meteorological data developed (Kennedy, 2005) and until recently, run by the National Pollen and Aerobiology Research Unit at the University of Worcester; the programme is currently unavailable.

Economic analysis has shown that utilising the Brassica$_{spot}$ predictive model to time sprays against white blister can increase farm profits by 15% per hectare compared to weekly spray applications (Minchinton *et al.*, 2013). Wakeham (2015a) determined the risk threshold for bio-aerosol concentrations of white blister zoosporangia and developed an in-field lateral flow test able to detect *A. candida* race 9 spore concentrations relevant to disease forecasting. 'Brassica Alert' is a forecasting system available through Syngenta UK's website but as yet does not take into account spore presence within the crop. Combination of meteorological conditions and risk thresholds of spores could help growers save even more on disease control inputs by further increasing the precision of fungicide applications.

Most of the current research on white blister in Brassicas is being carried out in non-vegetable crops such as *Arabidopsis thaliana* and *Brassica juncea*. Although this research is likely largely transferable to vegetable Brassica crops, more work is required.

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Onion Downy Mildew

Peronospora destructor, the causal agent of downy mildew on both bulb and salad onions, is widespread in the UK (Richardson *et al.*, 2011). The pathogen can cause premature defoliation, reduced bulb swelling, and can also negatively affect bulb storability, all of which can contribute to yield losses of up to 60-75% in bulb onions (Wakeham, 2015). Salad onion crops can be lost entirely due to the symptoms rendering the crops unmarketable (Wakeham, 2015). Seeds from onion plants infected with *P. destructor* show poor germination rates yet opinion on the role of seed transmission in the spread of disease is divided. (Stuart and Newhall, 1935; Glushchenko, 1980; Brewster, 1994; Sugha *et al.*, 1996).

Expected cultural control measures such as removing infected plants (including bulbs), avoiding overcrowded crops, and a four year rotation are advised (Koike *et al.*, 2007). Volunteer plants surviving the winter and carrying over disease is thought to be linked to disease outbreaks the following year (Gladders, P., pers. comm.). Additionally it is advised not to grow crops of autumn bulb onions near spring crops (Gladders, P., pers. comm.). However, the origin of infection foci and the role of oospore persistence in the soil is unclear (Sugha *et al.*, 1996; Parkunan *et al.*, 2013); can downy mildew oospores in soil infect roots directly and lead to systemic infection, or do these require water splash onto the above ground parts before they can cause infection as is the case with *Phytophthora porri* in leeks (Koike *et al.*, 2007)? It is feasible for the pathogen to remain active in different Allium crops throughout the year, with spring onions and both spring and autumn sown ware onions. *P. destructor* also infects leeks, shallots, chives and Ransoms (*Allium ursinum*) (FRDBI database). Insight into the mechanisms of initial infection, including the role of infested seed, will help determine the best cultural control methods to be implemented for disease reduction.

Infection requires temperatures below 22°C and leaf wetness of at least 3 hours. The optimum temperature for spore germination is between 10-12°C and sporangia can survive on leaf surfaces for up to 3 days. As well as surviving in the soil as oospores, the pathogen can persist as mycelium inside infected bulbs (Palti, 1989; Koike *et al.*, 2007). It has been observed that particularly cold winters appear to reduce the severity of disease the following season, probably by reducing the viability of overwintering structures (Koike *et al.*, 2007).

Resistant onion varieties are available: cv. Hylander (spring sown bulb onion), and cv. Performer (salad onion) are currently available from Elsoms Seeds Ltd.; cv. Toughball (autumn sown bulb onion) and cv. Santero (spring sown bulb onion) are available from various suppliers. Varietal resistance will become more important in the future as a result of the increasing constraints on the use of chemical fungicides, placing an emphasis on IPM.

Various uncultivated Allium species have been shown to be a potential source of resistance against *P. destructor* (Kofoet and Zinkernagel, 1990; Keller *et al.*, 1996) and work needs to be done to identify specific sources of utilisable resistance and consequently accelerate the development of resistant cultivars.

Disease forecasting has the potential to aid in the prevention of severe disease outbreaks, while reducing both financial and environmental costs. MILIONCAST is a forecasting model which takes into account environmental factors conducive for sporulation of *P. destructor*, but it does not take into account the disease presence in the crop (Gilles *et al.*, 2004). Combining environmental forecasting with in-field spore detection systems such as lateral flow device tests, can enable the precise timing of fungicide application only as and when it is needed (Kennedy, 2012; Wakeham, 2015). A lateral flow test for *P. destructor* sporangia utilising monoclonal antibodies able to detect components of the spore wall was developed by Kennedy and Wakeham (2008). Treatment based upon this type of detection system coupled with an environmental forecasting model has shown the potential to reduce downy mildew prevention inputs by up to 50%, whilst reducing the incidence of leaf infection by over 95% compared to the untreated control and was shown to be equally or more effective than the growers standard spray regime (Kennedy, 2012; Wakeham, 2015).

Globally, there is some evidence that the continued use of phenylamide fungicides (e.g. metalaxyl-containing fungicides) is leading to populations of resistant *P. destructor* isolates (Wright, 2004). In the UK however, no such cases of resistance have been documented, and other non-phenylamide fungicides are available with anti-downy mildew activity, and their use is likely helping to delay resistance development. Such fungicides tend to be broad spectrum however, and are advised to be used in rotation with specific oomycete fungicides that are likely to be phenylamide based. Alternative oomycete specific fungicides would be welcomed, in particular if products could be found with curative activity.

Work in SCEPTRE has identified two fungicide products, Cassiopeia (BASF; dimethomorph (11) + pyraclostrobin (40)) and Infinito (Bayer; fluopicolide (43) + propamocarb hydrochloride (28)) which have since been approved for use on bulb onion; Cassiopeia has on label approval, Infinito has approval through EAMU 1142/2015. Limited work assessing the efficacy of biological control agents on downy mildew of onion has been carried out and identification of any effective biological controls would help build an effective IPM strategy for disease prevention and control. One potential biological candidate was identified as significantly reducing disease in the recent AHDB ‘SCEPTRE’ project (O'Neill, 2015) and more work is needed to progress its development.

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White Tip of Leeks

White tip of leeks is caused by *Phytophthora porri* and has been responsible for losses of >50% in Europe (Plantwise). The pathogen causes severe foliar symptoms which include the blanching of the leaf tips, which then die rapidly. Leaves often also become distorted and twisted. The first signs of infection are water-soaked spots on the leaves surrounded by a green, transparent, water-soaked region, which later become white, dry and crisp (Plantwise;

Koike *et al.*, 2007). Despite being soil borne, *P. porri* can only infect above ground parts of the plant (Declercq *et al.*, 2012); many infections originate in the leaf basin usually present near the leaf axils, but symptoms tend to be seen at a distance above the leaf basin due to the growth of the leaves during the incubation period. Both mature and immature plants are affected, and severe infections can result in the leaves rotting off at the soil level (Plantwise). The pathogen also infects onions with similar symptoms, where white spots surrounded by green water-soaked patches are present all over the leaf. Severely damaged leaves will die off and sometimes, *P. porri* will cause shanking in onions and shallots, where the base or bulbs will become water-soaked and soft (Plantwise).

White tip of leeks primarily affects crops that overwinter as the disease is most prevalent under cool, wet conditions (Plantwise; Koike *et al.*, 2007; Declercq *et al.*, 2012). Temperatures between 4°C and 22°C (optimum around 8°C) and the presence of free water facilitate oospore germination (Declercq *et al.*, 2012), so it is advised to plant in well-draining beds (Koike *et al.*, 2007). Oospores can survive in infested soil for up to four years (Declercq *et al.*, 2012) and so a minimum four year rotation is advised. Oospores germinate to give zoosporangia which burst open releasing large numbers of motile zoospores. Zoospores infect leaf tissue when they get splashed onto the plant, encyst and either invade via stomata or directly via appressoria (Declercq *et al.*, 2012). Zoospores can remain viable for over seven weeks between temperatures of 0°C and 24°C (Declercq *et al.*, 2012) as long as free water remains. Smilde *et al.* (1996), in agreement with the findings of Yokoyama (1976), found that disease increase was correlated with both temperature and rainfall. It appears that rainfall is important for initial infection, but less important in subsequent disease spread (Smilde *et al.*, 1996).The role of sporangia in disease spread is not well understood due to their infrequent recovery from the field (Declercq *et al.*, 2012). This therefore raises questions about the mechanisms and dynamics of field epidemics of *P. porri*.

Covering crops with hoop greenhouses was able to significantly reduce disease incidence most likely by minimising rain splash mediated infection via zoospores (Declercq *et al.*, 2012). This practice may have additional consequences however due to the likelihood of increased humidity in such a system, potentially providing conducive environments for other pathogens such as *P. destructor* (downy mildew) to infect and cause disease.

Declercq *et al.* (2010) grouped *P. porri* isolates from leek in a distinct group, which had little variation and were separate from those isolates from other allium species. This evidence for high host specificity poses queries about the virulence of leek isolates on other allium species and *vice versa* and consequent roles as sources of inoculum for alternate hosts. Cross inoculation experiments might provide some insight.

Due to the presence of metalaxyl-resistant *P. porri* isolates, HDC project 172 advises not to grow leeks in areas which has extensively used metalaxyl based fungicides (Locke, 1996). Prevention is key to controlling white tip because once symptoms have been observed it is too late to effectively treat (Declercq *et al.*, 2010). As a result, growers will tend to monitor meteorological conditions and apply preventative sprays accordingly. Disease control can be challenging as both young and mature crops can become infected, and so modelling of infestation and monitoring of environmental conditions are important.

Varieties of leek which are stronger and more vigorous, such as cv. Lexton and cv. Pluston (Nunhems) are more resilient to *P. porri* and shorter, stockier leek varieties tend to have more tolerance to white tip than those with a taller shaft. However, growers are increasingly planting taller-shafted leeks for the pre-pack market and therefore many UK crops are at high risk from the pathogen. Smilde *et al.* (1995) and Smilde *et al.* (1997) illustrated the presence of genes conferring resistance traits in wild and cultivated relatives of winter leek but these have not yet been incorporated into commercial crops.

The threat of losing fungicide actives to resistance and deregistration is driving the search for novel methods of *P. porri* control. A project funded by HDC in 1995-6 (FV 172 (Locke, 1996)) investigated the presence of metalaxyl-resistant strains of *P. porri* in leeks and tested a number of fungicides as well as a non-chemical approach to preventing disease. The effectiveness of a straw-covering around the base of the leeks to prevent rain splash was evaluated, but this proved ineffective as the straw degraded over time. The use of straw in this way was also trialled (Alofs and Pijnenburg, 1988) and gave some positive results, which lead to about 10% of the Dutch leek acreage to be mulched on the surface with straw. The most effective chemical against the pathogen tested in FV 172 was Invader (BASF; dimethomorph + mancozeb) which is now available for use on outdoor leeks as a ground spray. An adjuvant was also tested in combination with the fungicides, but this had little effect on the efficacy of the chemicals. A new AHDB Horticulture project (FV 446) investigating fungicide efficacy on leek white tip has been funded and is due to start later this year (2016).

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Pea Downy Mildew

Downy mildew on peas caused by *Peronospora viciae* f. sp. *pisi* can have serious implications on yield and quality, and in the UK losses of up to 50% have been reported (Biddle *et al.*, 1988; Clark and Spencer-Phillips, 2004; Liu *et al.*, 2013). Infection by *P. viciae* f. sp. *pisi* is most serious in seedlings and infection results in reduced vigour, stunted growth and in severe cases death (Falloon *et al.*, 2000; Koike *et al.*, 2007). Infection later in the season can result in low quality produce (Maguire, 2015). Symptoms include yellowing of leaf surfaces, corresponding grey to purple sporulation on the underside of leaves and yellow blotches on pods (Koike *et al.*, 2007).

Infection foci originate from oospores in the soil and from infected plant debris (Van Der Gaag and Frinking, 1997a; Chang *et al.*, 2013). The disease can be seed borne but these seeds are unlikely to germinate (Koike *et al.*, 2007) and therefore oospores in the soil are the primary source of initial inoculum and germinate to infect the hypocotyls and upper parts of the roots (van der Gaag and Frinking, 1997b; Stoddard *et al.*, 2010). Sporangia can be spread efficiently by rain-splash and wind, leading to downy mildew epidemics (Stegmark, 1994; Koike *et al.*, 2007; Liu *et al.*, 2013). A minimum five year rotation is advised (Stegmark, 1994; Maguire, 2015), however oospores of *P. viciae* have been shown to survive for up to 15 years (Olofsson, 1966; Liu *et al.*, 2013) and therefore the efficacy of this cultural control is uncertain. Homothallic and heterothallic isolates have been described (Stegmark, 1994) and it is unclear which pathotypes currently predominate in the UK. The Processors and Growers Research Organisation (PGRO) is currently carrying out research investigating the races of downy mildew present in UK pea crops (Maguire, 2015).

Physiological specialisation has been reported for *P. viciae* f. sp. *pisi* isolates found in the UK (Taylor *et al.*, 1989). Therefore although resistant pea cultivars are available, they appear to

only be resistant to certain races of the pathogen (Sillero *et al.*, 2006; Davidson *et al.*, 2011). With the emergence of new pathogen strains able to overcome plant defences, novel cultivars will continue to require development (Koike *et al.*, 2007) and understanding the population dynamics of UK isolates will help to achieve durable resistance (McDonald and Linde, 2002). Resistance ratings of pea varieties currently available in the UK can be viewed in the 'PGRO Recommended list 2016'. Additional pea lines showing resistance have been identified by Maguire (2015) and the group plan to pursue gene-specific markers to identify resistant cultivars; the work is ongoing.

Work using specific primers in this pathosystem has highlighted the potential for molecular diagnosis of pea downy mildew. The primers are highly specific and can amplify pathogen DNA direct from plant tissue to enable pathogen identification. This technique has been the focus of other promising attempts to identify obligate pathogens in the field by utilising PCR (Cao *et al.*, 2007; Faggian and Strelkov, 2009; Liu *et al.*, 2013). There is a current project at NIAB focused on advancing downy mildew diagnostics, and included in this is the detection of pea and bean downy mildew resting spores in soil. Additionally, the use of lateral flow tests like those described by Alison Wakeham in 2014 and 2015 for *Peronospora destructor* detection could be implemented for the detection of airborne *P. viciae* sporangia. Though there is currently no recognised forecasting system for downy mildew in peas, the system described by Wakeham (2015) for *P. destructor* forecasting, combining meteorological thresholds and spore concentrations, could be applicable. Meteorological parameters for infection and sporulation were determined 45 years ago (Pegg and Mence, 1970) and likely need to be re-evaluated due to the subsequent recognition of distinct *P. viciae* f. sp. *pisi* races.

There are no available foliar fungicides in the UK specifically targeting pea downy mildew (PGRO Pulse Agronomy Guide 2015 (Biddle, 2000)) and seed treatments with phenylamide fungicides are advised in areas which have had a history of the disease or when a particularly susceptible variety is grown. Resistance to phenylamide fungicides such as in Wakil XL has been observed in New Zealand isolates of *P. viciae* f. sp. *pisi* (Falloon *et al.*, 2000) and strategies are required to prevent the build-up of resistance in UK populations of the pathogen. In Canada, Chang *et al*. (2013) found that non-approved fungicide products applied as seed treatments and foliar applications were able to reduce disease caused by *P. viciae* f. sp. *pisi*. Identification of biological seed treatments or novel conventional seed treatments would reduce the selective pressure on *P. viciae* f. sp. *pisi* populations to develop resistance to phenylamide compounds. There is limited published work on biologicals in the control of pea downy mildew, however one study carried out by Okorski *et al.* (2008) found that application of EM 1™ (a formulation of 'effective microorganisms' including lactobacilli, yeasts, and autotrophic bacteria marketed by Greenland Technologia in Poland) to soil had

a significant effect on reducing pea downy mildew. Plants grown in soil treated with EM 1™ showed a 25% reduction in the incidence of leaf symptoms compared to the untreated control. This study illustrates the potential to develop effective biologicals for incorporation in treatment programmes for pea downy mildew.

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Broad Bean Downy Mildew

Peronospora viciae f. sp. *fabae*, is particularly prevalent in susceptible spring sown broad bean crops (*Vicia faba*) and does not infect phaseolus bean crops. Symptoms include small yellow/greyish green spots on young leaves which eventually turn brown. Sporulating structures are also evident as light grey downy growth on the underside of the leaves (Glasscock, 1963; Dixon, 1981). Oospores of bean downy mildew seem be less durable than those causing pea downy mildew (~3 years) (Dixon, 1981; van der Gaag and Frinking, 1997b; van der Gaag and Frinking, 1997a) perhaps making crop rotation a more successful control method. The reasons behind this variation is unclear. In addition, bean plants seem to be most susceptible to airborne sporangia in the period immediately prior to flowering (Biddle *et al.*, 2003) rather than at the seedling stage and foliar sprays should be targeted at this growth stage. A spring sown field bean downy mildew forecasting programme is available; CropMonitor™ a project led by FERA (CropMonitor, 2016), utilises untreated reference crops in combination with meteorological data to identify days with high infection risk. Additionally, like for pea downy mildew, there is a current NIAB project looking to develop techniques to detect resting structures in soil. Developing in-field lateral flow tests to determine the presence of *P. viciae* sporangia when conditions for infection are conducive (Wakeham, 2015b; Wakeham, 2015a) would require more work. It is uncertain as to whether such tests would be able to distinguish between the downy mildew pathogens of pea and bean due to their close phylogenetic relationship.

Field beans are also a host of *P. viciae* f. sp. *fabae* and may provide a source of inoculum for broad bean crops. However, *P. viciae* f. sp. *pisi* which infects pea is cultivar specific and it remains unclear whether the bean pathogen displays similar specificity.

In summary, limited research has been carried out since the turn of the millennium despite the bean downy mildew being common and having potentially significant impacts on yield with limited control options. The only control option currently available is an extension of minor

use for Syngenta's SL567A (metalaxyl-M) due to Fubol Gold being revoked in 2013 (Clarke, 2013). Reliance on one fungicide is less than ideal when attempting to prevent pathogen resistance, especially when *P. viciae* isolates with resistance to phenylamides have already been reported (Falloon *et al.*, 2000). Varietal resistance is available but limited; the only spring bean cultivars with good downy mildew resistance found on the PGRO recommended list 2016 are 'Lynx' (field bean) and 'Maris Bead' (tic bean). These are not broad been varieties but illustrate that development of downy mildew resistance in fava bean crops is achievable.

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Cucumber Downy Mildew

Pseudoperonospora cubensis, the causal agent of cucurbit downy mildew, is an economically important pathogen all over the world (Lebeda and Cohen, 2011; Cohen *et al.*, 2015). In the UK, downy mildew on cucumbers is only an occasional problem with only a small numbers of outbreaks most years usually in non-heated or partially heated crops. These outbreaks are often associated with persistent wet weather (O'Neill, T., pers. comm.). According to the Cucumber Growers Association (CGA) the total area of UK glasshouse cropped with commercial cucumbers is around 120 hectares, with a value of £350,000 per hectare of crop.

Cucumber crops require a high financial input and, as a result of reducing profit margins, there is an increased requirement for growers to impose tight management controls to make sure maximum yields can be achieved. Early infections with downy mildew can cause plant stunting and even death in severe cases while in later infections fruit production, maturation and flavour may also be affected and therefore strict controls are needed to prevent pathogen derived reductions in quality and yield (Bennison *et al.*, 2013).

The vast majority of *P. cubensis* isolates are heterothallic (Cohen *et al.*, 2015) meaning they can only produce oospores as a result of sexual reproduction with an isolate of a different mating type. Oospore production by *P. cubensis* has not been witnessed in the UK probably because only one mating type is believed to be present (Lebeda and Cohen, 2011) (for a comprehensive review of the sexual reproduction of *P. cubensis* see Cohen and Rubin (2012); for a general review of the disease see Lebeda and Cohen (2011)). Some homothallic isolates have however been reported by Y. Cohen and A. E. Rubin in Vietnam but the data remains unpublished (Cohen *et al.*, 2015) and these isolates would be able to produce oospores within their own mycelium (without meeting hyphae of another mating type). If homothallic isolates were to become persistant in the UK, then the entire disease cycle of *P. cubensis* in UK growing systems would alter, removing the need for extrinsic windblown sporangia due to the potential persistence of the pathogen as oospores on site. The primary structures associated with disease spread are asexually produced sporangia, and these can be disseminated by wind, water splash and physical transfer (Lebeda and Cohen, 2011; Savory *et al.*, 2011). Sporangia can germinate directly via a germ tube, or alternatively germinate to produce motile zoospores (Lange *et al.*, 1989; Lebeda and Cohen, 2011). The 'overwintering' mechanism for this pathogen is unknown; oospores are not produced and mycelia, zoospores, and sporangium do not appear to persist in the soil or in plant debris (Lebeda and Cohen, 2011). A recent study by Cohen *et al.* (2014) has however suggested that seed transmission of *P. cubensis* may occur. Another study by Runge and Thines (2009) has identified *Bryonia dioica* (White Bryony) as a potential wild perennial host of *P. cubensis*. White bryony frequents British hedgerows but its role in the epidemiology of cucumber downy mildew remains unclear.

It may be the case that as sequential crops are being grown in a single year in the same glasshouse, that sporangia from one infected crop may be able to survive the changeover period between crops. If this is the case then the disease will always be present within a system unless measures are taken to remove it. In the UK this possibility seems unlikely as there is generally a period of about 8 weeks over the winter months were no crop is grown (perhaps 6 weeks without debris) (Hargreaves, D., pers. comm.). Research regarding the outdoor survival of sporangia in the USA, and their survival *in vitro* has been carried out

(Cohen and Rotem, 1971; Cohen, 1981; Kanetis *et al.*, 2010), but understanding longevity within a controlled growing environment is key to establishing the best cultural control methods for the eradication of this pathogen in the UK. Research into the source of the initial infection is required when new instances are reported. Likely origins of UK outbreaks include introduction on plants at planting, possibly as latent infections, and air dispersal of sporangia from the near continent (Hargreaves, D., pers. comm.; O'Neill, T., pers. comm.).

In 2012, two downy mildew resistant varieties of outdoor grown cucumber were made available in the USA by Seminis, cultivars SV3462CS and SV4719CS. These two varieties have been described as equal to the leading cucumber varieties in terms of yield, quality, storability and colour, while providing 'really good' resistance to downy mildew (Scaduto, 2012) and allowing the number of spray applications to be reduced. Although these varieties are not well suited to the UK's protected cucumber industry, they illustrate that there is significant potential for the development of downy mildew resistance in the UK by utilising conventional breeding methods. The variability of *P. cubensis* is uncertain; variability of pathotypes, and the presence of physiological races has been suggested (Lebeda and Cohen, 2011) yet analysis of the ITS region of numerous isolates from different hosts showed them to be almost identical (Choi *et al.*, 2005; Lebeda and Cohen, 2011). Molecular evidence supports that *P. cubensis* has made a host 'jump' and can now infect the ornamental plant *Impatiens irvingii* (Vogalmayr *et al.*, 2008), and may well be one step towards a speciation event. The sequencing of the cucumber genome in 2009 (Huang *et al.*, 2009), discovery of several quantitative trail loci (QTL) responsible for resistance to downy mildew (Zhang *et al.*, 2012; Pang *et al.*, 2013), and identification of numerous markers associated with these QTL's (Horejsi *et al.*, 2000; Pang *et al.*, 2013) will enable the use of marker-associated selection to greatly enhance development of resistant cucumber cultivars. Powdery mildew resistance seems to be a priority in cucumber breeding currently and this is perhaps due to the success of effective chemical and cultural control methods against the downy mildew pathogen.

At an optimum of 22^{o}C, *P. cubensis* requires a minimum of two hours leaf wetness for spore germination and successful infection (Cohen, 1977). The majority of UK glasshouses are heated all year round (Hargreaves, D., pers. comm.) helping to prevent this window of infection by aiding leaf drying. Also, controlled irrigation and good ventilation are antagonistic for disease development. The main chemical treatments currently used are metalaxyl-M and azoxystrobin. These treatments are currently still effective and the majority of UK cases of downy mildew on cucumber are seen in organic crops (Hargreaves, D., pers. comm.). Both metalaxyl resistance and azoxystrobin resistance has been observed globally (Urban and Lebeda, 2006; Colucci, 2008) and efficacy of these compounds needs to be monitored by growers. However, although cases of suspected resistance can be reported to FRAC, there

is no UK action plan to effectively address the issue. Applying fungicide programmes utilising fungicides of varying modes of action is advised (Urban and Lebeda, 2006) as part of a wider IPM programme. Oxathiapiprolin, a novel oomycide compound has been shown to be effective in controlling *P. cubensis* in cucurbits (Cohen, 2015), however it is uncertain whether fungicides containing this active (from Syngenta and DuPont) will be made available in the UK. A new range of actives will become available in the UK in 2016 and includes isopyrazam and proquinazid (Hargreaves, D., pers. comm.).

Numerous biological treatments have also shown activity against *P. cubensis*. Extracts of the plants *Macleaya cordata* (Schuster and Schmitt, 2015), *Glycyrrhiza glabra* (Scherf *et al.*, 2012) and *Salvia officinalis* (Scherf *et al.*, 2010) have shown effective antagonism against the pathogen. *Aneurinibacillus migulanus* (Scherf *et al.*, 2010), *Bacillus licheniformis* HS10 (Wang *et al.*, 2014) and a *Bacillus* species most closely related to *B. asahii* (Sun *et al.*, 2013) are examples of different bacterial strains which have also shown activity against downy mildew on cucumber. Further work is needed to progress these biologicals towards a commercial use, including commercial efficacy trials, phytotoxicity assessments, and the effect of these biologicals on human health.

There may be scope for the development of a forecasting system for downy mildew of various protected crops to enable growers to efficiently co-ordinate fungicidal applications, saving time and money. Cultural control methods such as heating and effective ventilation should minimise the risk of infection within the system, however certain areas of the glasshouse may be more susceptible to persisting leaf wetness, perhaps where ventilation is slightly compromised etc.. Logging leaf wetness in these areas, twinned with the use of lateral flow tests to detect aerial spore concentrations (Kennedy, 2012; Wakeham, 2015b; Wakeham, 2015a) could enable the prediction of infection and sporulation events, enabling fungicide sprays to be timed only as and when they are needed. Additional lateral flow tests may be required to detect the presence of significant spore concentrations originating from outside the propagation crop if indeed this does occur.

Yang *et al.* (2007) identified the threshold parameters for *P. cubensis* infection and symptom development as part of an early warning model for cucumber downy mildew in unheated greenhouses in China. For infection, these were: a daily temperature range of no more than 5°C, a daily mean temperature of 15-25°C and a relative humidity (RH) of ≥80%. An average temperature over the previous night of 15-20°C, and an average RH ≥83%, leads to symptom development within 24 hours. Neufeld and Ojiambo (2012) constructed 'risk charts' estimating potential risk of field infection by *P. cubensis* based on temperature and leaf wetness duration. The results of this study mainly agreed with the findings of Yang *et al.* (2007) but for the first time witnessed infection at 30°C, a temperature previously thought to be antagonistic for

infection. Due to the majority of UK glasshouses being constantly heated, ventilation can be kept high while still maintaining adequate temperatures, reducing the likelihood of meeting the identified parameters for infection and progression.

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Tomato Late Blight

Historically, late blight, caused by *Phytophthora infestans*, has not occurred frequently on commercial protected tomato sites, especially as humidity is kept down by venting and use of heating pipes. However, in recent years the incidence of late blight outbreaks has been observed to be on the increase and it is not uncommon for an entire crop to be lost (McGrath, 2015). Outbreaks most commonly occur because of breakdowns in heating infrastructure, leaks in glass and irrigation systems or introduction on plants at planting. As the pathogen also infects potato, outbreaks have been associated with the presence of potato in the area surrounding the glasshouse. However, over the 2015 cropping season, several outbreaks were reported where these circumstances were not present. Additionally, growers have reported that outbreaks in 2015 proved difficult to control or eradicate, being more aggressive than previously observed. As such, late blight is becoming a more important problem on commercial tomato crops, and has also been implicated as a problem at propagation.

Symptoms of late blight in tomato tend to start at the top of the plant and include small, pale green, water soaked leaf lesions which become darker as they grow. White mycelium may be present in humid conditions on the undersides of the lesions. Infected tissue quickly blackens, collapses and dies. Infected fruit show dark lesions which grow quickly to cover the whole fruit and become easily colonised by secondary pathogens (Seebold, 2011).

Current control options are based on glasshouse management to prevent leaks or high humidity hotspots occurring. In the event of an outbreak, increasing heating pipe temperatures can effectively drive off humidity and prevent disease progression, however this is usually prohibitively expensive. For growers with older glass, glasshouse conditions may also be difficult to control absolutely. With regard to plant protection products, there is currently an over-reliance on a very small number of approved products with proven efficacy. This includes Amistar (azoxystrobin) and Cuprokylt (copper oxychloride), which is currently under revocation. Recent research also illustrates the potential of fungal biocontrol agents to control *P. infestans* in tomato and chilli seedlings; Loliam *et al.* (2012) showed that a *Streptomyces rubrolavendulae* isolate was able to significantly increase the survival of colonised tomato and chilli seedlings in *P. infestans* infested peat. A number of ‘grey-area’ products are also likely to have good activity against late blight, for example potassium

phosphite, which was shown to be effective at suppressing disease in a trial by Becktell *et al.* (2005). The same trial also identified the plant defence activator as having potential to help control disease. Physical control methods such as wrapping stem lesions (e.g. with newspaper) with the aim of preventing sporulation and delaying lesion spread are also sometimes practiced. At what point removal of whole plants, rather than curative treatments, becomes practical is worth further investigation.

Extensive research has been carried out on the late blight pathogen, *Phytophthora infestans*, on potato, and on populations of *P. infestans* in the UK and overseas. It is likely that this research could be better utilised for disease control on tomato in the UK. The heterothallic *Phytophthora* species, *P. infestans*, is thought to have originated in wild *Solanum* species in Mexico (Goodwin *et al.*, 1994). Until the 1980s only one of the two mating types (A1 and A2) was present in Europe, with mating type A2 present only in Mexican populations (Gisi and Cohen, 1996). Around this time resistance to phenylamide fungicides also developed, though it is thought this resistance became established in A1 populations before arrival of the A2 type (Gisi and Cohen, 1996). Resistant isolates express equal or greater fitness than sensitive isolates, and resistant isolates have been observed to be maintained in populations even when use of the chemicals has ceased (Cohen *et al.*, 1987). The movement of exotic strains of the pathogen, and the ability to sexually reproduce in Europe has resulted in a population capable of rapid changes, and has presented challenges to successful management (Fry and Goodwin, 1997). Pathotype is thought to evolve rapidly, such that mating type, and neutral molecular and biochemical markers are more reliable descriptors of *P. infestans* populations (Fry and Goodwin, 1997).

The presence of both mating types and multiple clonal lineages in the UK may have led to the development of more aggressive isolates, which may explain the recent flurry of outbreaks in propagation and on commercial nurseries. A large number of virulence factors have been found in *P. infestans*, not all of which are necessary for pathogenesis (Fry and Goodwin, 1997). It has also been discovered that environmental conditions may affect what mating type dominates, with the A2 mating type favouring semiarid conditions (Gisi and Cohen, 1996; Miller and Johnson, 2000). In another study on isolates from France and Switzerland, the A2 type was found at very low incidence in potato populations, but at higher incidence in tomato crops. Races isolated from tomato also tended to have simpler race structure than potato (Knapova and Gisi, 2002). However, strains isolated more recently from both potato and tomato were shown to exhibit little host specialisation (Stroud *et al.*, 2016). In populations investigated over two years in Michigan, only one mating type was found (Rojas and Kirk, 2015). As the make-up of late blight populations is continually changing, updated knowledge of the state of the UK population in tomato will allow management actions to be tailored to

the lineages found. In the UK, populations of *Phytophthora infestans* on potato have been monitored annually since 2003 for AHDB Potatoes. This monitoring identified an increase in two strains, 13_A2 and 6_A1, which now dominate the population in contrast to the more mixed populations pre-2006. Both strains have been shown to be more aggressive and have a shorter latent period than isolates representing other genotypes (Cooke *et al.*, 2011). Whether these strains are those responsible for causing outbreaks on tomato remains unknown and warrants further investigation. Over the last 10 years several isolates from tomato have been sent by ADAS to David Cooke at the James Hutton Institute (JHI) for characterisation and comparison with potato isolates. Isolates from tomato sent by ADAS to JHI in 2015 were identified as a novel strain. More information on the isolates currently infecting tomato may help to determine if changes in the populations are occurring.

Control of blight in potato may help to inform control in tomato, though the cropping system of tomato presents a number of challenges. A number of fungicides are available for blight control in potato, which are not currently permitted for use in tomato. In the UK, where tomato is a protected crop, a number of factors to fungicide use are potentially more hazardous than in outdoor cropping, such as re-entry periods and operator exposure limits. This may restrict the number of products whose authorisation may be extended. Additionally, control in potato is informed by the use of BlightCast, a computer model that reports the occurrence of Smith Periods (Syngenta). This highlights to growers that favourable conditions for blight have occurred, and that a preventative spray should be applied. Though this could be applied to late blight in a protected environment and used to augment glasshouse controls, the use of environmental models in a glasshouse presents multiple challenges. Tomato varieties are known to differ in susceptibility, and varieties containing blight resistance genes have been developed. It has been demonstrated experimentally that utilising varieties with good resistance to late blight in combination with low doses of fungicides can provide good control of late blight on potato (Bain *et al.*, 2009) and may be an option for protected use. However, recent outbreaks have been observed on multiple varieties of tomato and it is likely other factors would more strongly affect a grower's choice of variety than blight resistance. Isolates have also been reported that have developed the ability to overcome varietal resistances (Sujkowski *et al.*, 1996).

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Wild and Salad Rocket Downy Mildew

A singular species of oomycete, *H. parasitica*, was believed to be the causal agent of downy mildew in the *Brassicaceae* (Rimmer *et al.*, 2007). However, by using ITS sequence comparison techniques (Cooke *et al.*, 2000), Choi *et al.* (2010) found that a Korean isolate of downy mildew isolated from salad rocket (*Eruca sativa*) was clearly distinct from *H. parasitica* isolated from *Capsella bursa-pastoris* (*Brassicaceae* family) but not from other *Hyaloperonospora* sp. found on rocket. This evidence suggests that the pathogen causing downy mildew in rocket is, as with the pathogen causing downy mildew in vegetable Brassicas, a different species to the pathogen believed to be causing downy mildew in other members of the *Brassicaceae* (Choi *et al.*, 2010). The causal agent of downy mildew in wild rocket (*Diplotaxis tenuifolia* and *D. muralis*) remains to be determined.

The disease is a serious problem in baby leaf crops and seedlings are particularly susceptible. Rocket crops are grown at high density and as such the disease can spread rapidly and the whole crop can be lost (Gladders, 2009). Symptoms include small, irregular, dark speckling on leaves correlated with white fungal growth on the lower leaf surface. The symptoms can be confused with those of bacterial blight caused by *Pseudomonas syringae* pv. *Alisalensis*. Gladders (2009) identified several wild rocket varieties which showed good resistance in field trials, including the variety SSC2501 from the breeder Shamrock, which had almost complete resistance to downy mildew. SSC2501 is not a typical commercial wild rocket variety and is a spicier wasabi type but does however show that breeding for resistance is possible. There were other, more typically commercial varieties, which also showed good levels of downy mildew resistance. Varietal resistance in salad rocket was also compared in this study but no differences between varieties were observed. Fungicidal seed treatments have shown strong potential for disease control in both salad and wild rocket in the early stages of plant growth yet plants may still be susceptible to late infection (Gladders, 2009). Varietal resistance can vary based on geographical area and what might be resistant for one grower in one location may not have resistance for another grower located elsewhere (Huckle, A., pers. comm.), perhaps indicating the presence of distinct pathogen races.

The biology of the *Hyaloperonospora* sp. causing downy mildew in both salad and wild rocket needs to be evaluated in light of its recent phylogenetic distinction. If the biology of this new Hyaloperonospora species is substantially different to that of *H. brassicae*, then cultural control methods will need to be re-evaluated. PCR techniques were able to detect downy mildew DNA in seed batches obtained from breeders, however as PCR does not determine

the viability of DNA, further research is required to see if plants grown from these seeds develop disease under controlled conditions (Gladders, 2009).

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Red Beet Downy Mildew

Peronospora farinosa f. sp. *betae* (formerly *Peronospora schachtii*) is the causal agent of downy mildew in red beet, sugar beet, mangold, Swiss chard, and wild sea beet (Koike *et al.*, 2007). The disease is believed to be responsible for root malformation disorder (RMD) in red beet, where symptoms include the severe distortion of roots as crops reach maturity, an elongated neck, and a thickened tap root (McPherson, 2003; McPherson, 2004; McPherson, 2005). This pathogen can cause marketable yield losses of more than 50% to the beet root (Kioke *et al*., 2007). Infection is systemic and initial symptoms include the chlorosis and distortion of young leaves (Koike *et al.*, 2007) which may later wilt and die. In moist conditions, grey mycelium can become visible on the leaf surfaces (Koike *et al.*, 2007). Older plants may recover from infection by producing new, healthy leaves, but in seed crops infection leads to distortion and stunted growth giving a 'witches broom' type symptom (Koike *et al.*, 2007). Infection can leave plants vulnerable to secondary infections (PacificNorthwestHandbooks, 2016)

Infection can arise via soil borne oospores, airborne sporangia, or as a result of infested seed. Seed infection rates as low as 1% can result in infected plants which act as disease loci. (Koike *et al.*, 2007). Sporangia produced by overwintering mycelium in weed hosts, volunteer plants, and seed crops can infect and cause disease in red beet crops (Byford, 1981; Koike *et al.*, 2007). Several historical reports on sugar beet identified seed crops as the main source of infection (Byford and Hull, 1967; Byford, 1981). Optimum conditions for sporulation to occur in sugar beet are 12°C and 85% relative humidity (Byford, 1981; Koike *et al.*, 2007). For infection to occur, at least six hours of leaf wetness are required with temperatures between 7°C and 15°C; temperatures over 20°C are not conducive for infection (Byford, 1981; Koike

et al., 2007). Under favourable conditions (low temperatures and high relative humidity) sporangia from infected sugar beet can remain viable for over seven days (Byford, 1981).

The majority of work investigating the biology of this pathogen has been carried out using isolates from sugar beet, not red beet. In light of recent insights into the host specificity of other *Peronospora* spp. it is possible that different strains of this pathogen cause disease in different hosts. That being said, Kim *et al.* (2010) isolated a pathogen causing downy mildew-like symptoms on Swiss chard in Japan and when sequenced, its ITS region was found to be identical to that of the pathogen causing downy mildew on sugar beet. Cross inoculation experiments comparing the virulence of different isolates on different hosts would shed light on this query. If the pathogen demonstrates host (or even cultivar) specificity, then the biology of specific strains need to be re-evaluated to provide a platform for the implementation of effective cultural control methods. However it is worth noting that since a range of oomycete fungicides were approved for use on beet in the UK, neither downy mildew nor RMD have been of commercial significance (Koike *et al.*, 2007).

Cultural control methods can aid in reducing disease incidence and include planting in well drained soils, irrigating in the mornings and avoiding overhead irrigation where possible, spacing plants to improve air circulation and reduce humidity in the canopy (Hortsense, 2016), removing crop debris after harvest, and using disease free seed (Koike *et al.*, 2007). Resistant red beet cultivars are available including the variety 'F. M. Detroit Dark Red' (Hortsense). Klosterman *et al.* (2014) developed a '*P. effusa*' and '*P. schachtii*' (more often referred to as *P. farinosa* f. sp. *spinaciae* and *P. farinosa* f. sp. *betae* respectively) specific real-time quantitative polymerase chain reaction (qPCR) assay to detect airborne sporangia. This technology could be used in conjunction with meteorological data to forecast disease outbreaks and increase the precision of spray timings. However, no such system is currently commercially available.

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Rhubarb Downy Mildew

Rhubarb downy mildew in the UK is a recently emerging issue (Creed, C., pers. comm.). Due to the limited amount of work into this disease, uncertainty remains as to the identity of the causative pathogen (Howard and Ormrod, 1994; Koike *et al.*, 2007; Horst, 2008), but it is generally accepted to be *Peronospora jaapiana* (Koike et al., 2007; Cunnington, 2008). Seedlings grown in cold frames are most vulnerable to the disease, but plants of all growth stages can be affected (Koike *et al.*, 2007). Symptoms include small yellow (early) to large brown (late) lesions on the leaves with corresponding white/violet mycelial growth on the lower surface, and often a rough edge to the leaf where lesions have died and torn away from the remaining healthy tissue (Koike *et al.*, 2007). Symptoms appear to vary between varieties, but as yet there has been no formal work carried out on varietal resistance (Huckle, A., pers. comm.).

Disease can be spread by sporangia either by wind or rain splash, and cool wet weather facilitates rapid reproduction (Howard and Ormrod, 1994). The longevity of the sporangia is yet to be determined, however they are thought to be short lived if humidity and temperature become unfavourable (Howard and Ormrod, 1994). The origin of initial infection is unknown, as is the role of oospores in the disease cycle. It is important to determine if the infection becomes systemic, due to the perennial nature of the crop and the potential influence of infection on yield in subsequent years. Propagation material should be checked for signs of infection before planting (Howard and Ormrod, 1994) and affected leaves should be removed and destroyed (Mycobank).There is an EAMU for Fubol Gold WG (2283/13) currently available for treating downy mildew on rhubarb (Creed, C., pers. comm.).

The pathogen is similar to *Peronospora polygoni* and *Peronospora rumicis*. Cross inoculation experiments have not yet been conducted but would provide insight into the nature of these pathogens (Mycobank). There are many gaps in our knowledge of this pathogen and much more work is required to enable the development of effective control strategies.

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Blackberry Downy Mildew

The UK blackberry industry has been expanding in recent years due to an increase in public demand, increasing from 140 ha in 2011 (Bennison, 2011) to 194 ha in 2014 (Garthwaite *et al.*, 2015). Novel cultivars producing larger, sweeter fruit have become more popular amongst UK growers as supermarkets try and move blackberries towards the fresh fruit market as opposed to use only for cooking (Anon, 2014). 81% of the blackberries grown commercially in 2014 were sold on the fresh market (Garthwaite *et al.*, 2015). As a result of this shift, there is increasing requirement for high quality, disease free produce.

Downy mildew, otherwise known as ‘dryberry’ of blackberry (*Rubus fruticosus* L), is caused by *Peronospora sparsa* and is the same pathogen widely accepted to cause downy mildew on rose (O'Neill *et al.*, 2002). It is not unusual for losses of 50% to occur as a result of the disease and in extreme circumstances entire crop losses may occur. The pathogen is most recognisable by its foliar symptoms, primarily reddish angular lesions on leaves, but it also affects developing fruit causing premature reddening, irregular ripening, and shrivelling of berries due to dehydration (O'Neill *et al.*, 2002; Boyzo-Marín *et al.*, 2015). Severe disease can lead to the death of the infected plant (O'Neill *et al.*, 2002).

Like other downy mildew pathogens, wet weather facilitates disease caused by *P. sparsa* with optimum environmental conditions of >80% relative humidity and temperatures between 15-22°C (Ellis *et al.*, 1991; Boyzo-Marín *et al.*, 2015). Sub-irrigation as opposed to overhead irrigation showed a significant reduction in disease in the absence of fungicide applications (O'Neill *et al.*, 2002). Harsh pruning is also carried out by some growers to prevent excessive humidity in the canopy. *Rubus* spp. infected with the pathogen may remain asymptomatic but this can still result in significant losses (Boyzo-Marín *et al.*, 2015). Therefore, diagnostic techniques other than assessing the presence or absence of foliar symptoms are required;

variations of PCR such as nested PCR, have been shown to detect the pathogen in leaves (Hukkanen *et al.*, 2006; Rebollar-Alviter *et al.*, 2012). Chemical treatment of well-established infections is ineffective and an early detection system to time fungicide sprays would be beneficial (O'Neill *et al.*, 2002). 58% of crops are now grown under tunnels (Garthwaite *et al.*, 2015) and it is important to determine what effects this has on the epidemiology of the disease.

The pathogen is disseminated primarily by airborne sporangia (Hukkanen *et al.*, 2006), but oospores have been observed in leaves (Hall and Shaw, 1982; Williamson *et al.*, 1995) and roots (Tate, 1979) of infected plants. The overwintering role of oospores and their role in disease spread is unclear in this pathosystem and more work is required. Windblown leaves containing oospores may have potential to spread the disease, leaving oospores in the soil which could potentially go on to infect roots. Highly susceptible blackberry cultivars can become systemically infected and it is thought that *P. sparsa* may survive in stems between seasons as dormant mycelium (O'Neill *et al.*, 2002). This characteristic of the pathogen needs to be explored further as with the sometimes asymptomatic nature of the disease, it could have implications on the vegetative propagation of new plants.

The host specificity of this disease is uncertain. While it is believed that it is the same pathogen causing downy mildew in both rose and blackberry this view may be outdated. This comes from increasing evidence of high host specificity in other oomycete pathosystems and a shift in understanding towards race based population dynamics. It is important to determine the UK population structure of *P. sparsa* and if applicable, identify races of commercial significance. This information will allow the effective targeting of resistance, and also enable evaluation of wild *Rubus* spp. for their role in disease transmission.

Aegerter *et al.* (2003) developed a logistic regression model for the prediction of downy mildew in rose nurseries based on three microclimatic variables calculated over the previous 10 days: hours of leaf wetness when temperatures were less than 20°C, hours between 15 and 20°C, and hours when temperatures exceeded 30°C. The study also suggested that there may be geographical specialisation within *P. sparsa* and therefore these parameters could be different in the UK. Kim *et al.* (2013) developed a prediction model for seasons with high and low risk of disease in blackberry, boysenberry and rose utilising weather data from standard weather stations. Other forecasting systems have been developed for *P. sparsa* on rose and may also be applicable to *rubus* spp. (Xu, 2013; Filgueira and Velasquez, 2014). Some UK growers are utilising potato blight forecasting systems to help time protective sprays and finding this of some use.

Resistance to downy mildew in blackberry cultivars is limited with spine free erect or semi-erect spined cultivars appearing particularly susceptible (Allen, J., pers. comm.). Cv. Loch Ness was one of the principal varieties grown in 2014 (Garthwaite *et al.*, 2015) despite its widely known high susceptibility to *P. sparsa*. A study assessing the genetic resources of wild blackberry species in Michoacan, Mexico has identified several cultivars as potential sources of disease resistance including resistance to downy mildew (Segura *et al.*, 2012). A similar study conducted in the UK could provide new directions for the development of resistant blackberry cultivars. Lines of arctic bramble (*Rubus arcticus*) showing some resistance have also been identified (Kostamo *et al.*, 2015). While cultivars from overseas showing resistance to *P. sparsa* may provide a resource for developing cultivars for growth in the UK, care needs to be taken that the resistance is targeted against UK isolates of *P. sparsa*.

The range of fungicides available to control downy mildew in *Rubus* spp. is limited, partly due to the latest EU legislature (Kostamo *et al.*, 2015). O'Neill (2010) showed that tebuconazole had activity versus downy mildew but there is uncertainty over its future availability due to the tightening stance on endocrine disruptors. This is especially interesting as tebuconazole is not recognised as having activity versus downy mildews (Gladders, P., pers. comm.). Copper oxychloride is no longer permitted for use on cane fruit and therefore cannot be used by growers to treat for blackberry downy mildew (Allen, J., pers. comm.). Signum (BASF; boscalid and pyraclostrobin) was shown to provide some control of downy mildew by O'Neill (2010) as part of the AHDB project SF 085. However the subsequent off label approval states an approved rate of application for Signum as only 1.25kg/ha on protected crops, which is much lower than the rate of 1.8kg/ha applied during the study.

The fertiliser potassium phosphite (and phosphorous acid) has been shown on numerous occasions to effectively control *P. sparsa* (Walter *et al.*, 2004; Rebollar-Alviter *et al.*, 2012; Boyzo-Marín *et al.*, 2015). In other pathosystems, potassium phosphite has been shown to have both a direct effect on pathogens, as well an effect promoting plant defence responses (Garbelotto, 2007; King *et al.*, 2010). However, recent concerns about residues has led to uncertainty about the future of potassium phosphite use on blackberries and other horticultural crops. Repeated applications of potassium phosphite (as a fertiliser) as a foliar spray or via fertigation fertiliser may as a consequence no longer be possible due to the constraints of maximum residue levels (MRL's), which if exceeded could lead to the rejection of produce by the end purchaser. The loss of this product during the high risk harvest period, a period where Amistar also cannot be used for control due to its harvest interval, will leave crops vulnerable to the disease (Allen, J., pers. comm.).

Boyzo-Marín *et al.* (2015) showed glutathione-oligosaccharin-based compounds (used as elicitors) to be effective at controlling blackberry downy mildew, a strategy shown to be

effective in viticulture (Dagostin *et al.*, 2011). Hukkanen *et al.* (2008) also found that Bion (acibenzolar-S-methyl), a 'plant activator' produced by Syngenta, was able to provide protection against *P. sparsa* in arctic bramble. This product is registered as Insimmo in the UK, but is not currently marketed. Effective use of biologicals to control *P. sparsa* in blackberry crops is not yet reported; Boyzo-Marín *et al.* (2015) found a *B. subtilis* strain (Serenade Max; Bayer CropScience) and *Trichoderma harzianum* (T-22; PHC) to be ineffective at controlling disease. Non-conventional alternatives to chemical foliar sprays, such as effective elicitors and biologicals, would be beneficial to the industry as dense canopies can hamper spray coverage, and consequently control.

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Apples and Pear Phytophthora Fruit Rot

In the UK, *Phytophthora* fruit rot in apples and pears is primarily caused by the homothallic oomycete *Phytophthora syringae* (Erwin *et al.*, 1983; Fujita *et al.*, 1994; Erwin and Ribeiro, 1996). Symptoms may vary according to variety, but generally include a firm, dark brown rot with a diffuse boundary and mycelial growth on rotted fruits may occur if there is sufficient moisture (Jones and Aldwinckle, 1990). In the USA, *Phytophthora* fruit rot in apples and pears is primarily caused by a different *Phytophthora* species, *P. cactorum* (Jones and Aldwinckle, 1990) and this tends to be the focus of the literature. Limited work has been done on *P. syringae* fruit rots of apples and pears in recent years.

P. syringae is suited to low/mild temperatures with an optimum growing temperature of 10-14°C (Cross and Berrie, 2001). The pathogen is believed to have a saprophytic phase where it survives in fallen apple leaves on the ground. Oospores produced in these leaves are the pathogen's means of survival and soil containing infected leaf debris can remain infective for many years (Erwin *et al.*, 1983). Oospores require moisture (but not free water) to germinate to form zoosporangia, which in turn require free water to produce zoospores. It is the

zoospores which get splashed onto growing fruit and cause infection (Erwin *et al.*, 1983). The fungus does not appear to infect growing leaves and the reasons behind this are unknown (Erwin *et al.*, 1983). The fungus is not prolific in the summer months due to the often warm and dry conditions but is mainly active from September through to May (Erwin *et al.*, 1983), although it has been found that temperatures between 10-16°C optimally facilitate oospore germination and lead to soil 'activation' (Harris and Xu, 2003). Consequently, disease is most prolific during the months of September, October, and November which coincides with fruit harvest (Erwin *et al.*, 1983) and has caused issues associated with post-harvest rot (Spotts and Grove, 2002; Harris and Xu, 2003). If fruit is infected near to harvest, the crop may remain symptomless until harvest, where it can spread by contact to other fruit and post-harvest losses of up to 88% have been seen for Cox apples (Cross and Berrie, 2001). The pathogen can grow in storage temperatures of 3-4°C (Cross and Berrie, 2001).

Chemical treatments are available and cultural control techniques are also advised. These include disposing of dropped fruit, mulching the soil surface to lower the risk of soil splash and selectively harvesting fruit over 0.5 m off the ground where a high risk of infection has been determined. Scheduling fruit for earlier marketing following a high risk harvest to minimise post-harvest losses is advised. Applying a 5% urea spray prior to leaf fall, and macerating leaves after they have fallen will encourage rapid breakdown and help prevent colonisation by *P. syringae* (Cross and Berrie, 2001).

The dwarfing of trees has meant that fruit is now lower to the ground and consequently more vulnerable to infection by rain splashed zoospores (Erwin *et al.*, 1983; Harris and Xu, 2003). The use of herbicides around the bases of trees leaves soil exposed and enhances the efficacy of infection by rain splash (Erwin *et al.*, 1983; Harris and Xu, 2003). A minimum pesticide control strategy utilising data on orchard rot history, fruit quality, % bare ground, % of fruit less than 0.5m above the ground, and rainfall, was developed by Berrie *et al.* (1996) and an integrated disease management programme proposed. As part of a thesis on the incidence and severity of pear cankers, Laywisadkul (2008) tested various novel controls for antagonism against *P. syringae*. Two phosphonate containing treatments, BioPhos (Eco-Right) and Phyto FOS (Sipcam Agro USA), effectively prevented stem infection by *P. syringae* when sprayed onto the plants prior to stem inoculation. Fruit infection varies significantly from this experimental system, however the ability of phosphonate treatments to suppress the pathogen is demonstrated and supports further work.

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Downy Mildew of Herbs

The value of the Herb industry in the UK is estimated at around £100 million per annum. There are no available statistics on current herb areas grown in the UK but a rough estimate based on a BHTA survey of its members estimates that somewhere between 4000ha and 4500 ha of culinary herbs are grown. Many crops are cut multiple times in one growing season and multiple crops are possible for certain herbs within the same season (Davies, T., pers. comm.). Downy mildew has ranked as the number one disease of importance to UK herb growers as the leaf blemish symptoms it causes can lead to the rejection of entire crops at buyer's quality control. The herbs most seriously affected are basil, sage, mint, parsley, and chives. The biggest problems with basil have been observed under protection, whilst concern with sage, mint, parsley and chives is in field grown crops.

There is a best practice guide for protected herbs on the AHDB website (Bennison and Parker) and while much of this content is also applicable to outdoor grown herbs, many issues differ between the two systems (Davies, T., pers. comm.). There are various chemical treatments available for use on herb crops to combat downy mildew infections and additionally there was a recent EAMU for the use of Fenomenal (Bayer CropScience Limited; fenamidone and fosetyl-aluminium) to treat downy mildew on fresh herbs (0109/2016). Understanding the best ways of using these products is key for effective disease control, but a better knowledge of the epidemiology and biology of these pathogens is required to best know how and when to control. Knowing how best to utilise current chemical controls and combining these with effective cultural controls is particularly important in herb crops as downy mildew can appear in an explosive form throughout a crop. Improving recognition of

the initial symptoms of the disease may facilitate more timely application of chemical controls. Forecasting disease might be possible if meteorological parameters facilitating the different stages of the pathogen life cycle are determined and it is important to note that these parameters vary between pathogen species infecting different hosts (Wright, 2014)(Davies, T., pers. comm.).

Basil

About 30 ha of Basil (*Ocimum* spp.) are grown in the UK, but as each crop can be cut multiple times the value of basil grown is thought to be well over £10m. *Peronospora belbahrii*, the causative agent of downy mildew on basil (Belbahri *et al.*, 2005; Thines *et al.*, 2009), was first identified on *Agastache* sp. in the UK in 2009 and the following year on *Ocimum basilicum* (sweet basil) (Henricot *et al.*, 2010; Budge, 2011). There is currently an AHDB funded project (PE 024) on the epidemiology and control of basil downy mildew which is aiming to answer some fundamental questions associated with the disease including identifying the origins of infection and determining optimum conditions for spore production, as well looking into host specificity, spore longevity, and diagnostics.

The most serious issues with basil downy mildew to date have been associated with protected crops (Davies, T., pers. comm.). Early symptoms of basil downy mildew can easily be confused with magnesium deficiency with the development of chlorotic spots (Budge, 2011) so observing spores on the underside of leaves is key to diagnosis (McGrath, 2015). Sporulation corresponds to the blemishes on the leaf surface (Budge, 2011) and occurs at night, making early morning the optimum time to inspect basil for downy mildew. Suspected infected plants with chlorotic symptoms resembling downy mildew but that lack spores may be stimulated into sporulation by placing in a dark and humid environment, for example placing the sample upside down on wet paper towel inside a closed plastic bag in the dark for 24 hours (McGrath, 2015). Like most downy mildews, *P. belbahrii* favours cool, moist conditions so cultural controls involve heating and maintaining good crop ventilation (Budge, 2011). Timing irrigation for mornings may also provide some control. Garibaldi *et al.* (2007) found that disease was most severe when leaves were kept wet for at least 6-12 hours immediately after inoculation, that at temperatures outside the range of 12°C - 27°C disease did not develop, and that at least 24h of leaf wetness was required for sporulation.

Cohen and Rubin (2015) showed that temperatures of 35-45°C for six to nine hours were antagonistic to *P. belbahrii* and that these conditions could be achieved by covering glasshouses with transparent infra-red-impermeable, polyethylene sheets. This practice raised the temperature of the system sufficiently so that when applied for a few hours on consecutive days it was able to suppress the disease caused by the pathogen and enhance

crop growth. Work in the USA on plant resistance inducers has shown them to have potential for providing control of downy mildew in basil (Mersha *et al.*, 2013; Patel *et al.*, 2014).

Seed transmission of *P. belbahrii* is suspected (Garibaldi *et al.*, 2004). In the USA, Eurofins STA Laboratories (http://www.eurofinsus.com) have started testing basil seed for *Peronospora* spp. and seed companies are introducing novel techniques of treating basil seed such as steam treating (McGrath, 2015). Sweet basil is particularly susceptible to *P. belbahrii* and there are no commercially grown resistant varieties. Other *Ocimum* species, such as *O. americanum*, *O. kilimanadascharicum*, *O. gratissimum*, *O. campechianum*, *O. tenuiflorum*, and *O. ×citriodorum* have been shown to have a degree of resistance to the pathogen (Wyenandt *et al.*, 2010; Koroch *et al.*, 2013; Ben-Naim *et al.*, 2015). Progress has been made towards identifying the sources of downy mildew resistance in these species and determining the feasibility of developing resistant varieties of sweet basil (Wyenandt *et al.*, 2010; Ben-Naim *et al.*, 2015; Pyne *et al.*, 2015). Ben-Naim *et al.* (2015) crossed a sweet basil variety with high susceptibility to downy mildew with 27 tolerant non-sweet basil varieties from various *Ocimum* spp. The crosses yielded two hybrids with high downy mildew resistance, 24 hybrids with moderate downy mildew resistance and only one hybrid which remained highly susceptible. One hurdle with breeding resistance to downy mildew from related species into sweet basil is maintaining the characteristic appearance, aroma and taste of the herb, a feat which researchers at Rutgers University in New Jersey, USA have reportedly achieved, with varieties likely becoming available to growers in 2017 or 2018 (McGrath, 2014; Higgins, 2015).

Sage

Multiple different pathogens cause downy mildew on specific *Salvia* spp. (Choi *et al.*, 2009; Thines *et al.*, 2009) but it is the recently described *Peronospora salviae-officinalis* which causes the disease on *Salvia officinalis* (common sage) (Choi *et al.*, 2009). Downy mildew on common sage was previously believed to be caused by *P. lamii* (Thines and Choi, 2015). The overwintering mechanisms of the pathogen is not well understood but it is believed it may be able to persist in woody tissue between growing seasons (Wright, 2014). Symptoms include lesions on the lower side of leaves, varying in colour from grey to violet to dark brown and can merge to form large areas of diseased tissue. Lesions are angular and clearly limited by vasculature (Choi *et al.*, 2009). The economic impacts of this disease to UK growers as a whole is yet to be determined although losses of up to 80% were reported in 2009 as a consequence of downy mildew (Wright, 2014).

Varietal resistance is limited but implementation of chemical and cultural controls should help prevent severe outbreaks of disease. As with other downy mildew pathogens, irrigating in the

morning as opposed to the evening is advised, and crops should be sufficiently spaced to allow good airflow and prevent the crop becoming overly humid. Plant only symptom free plants, and if an outbreak does occur, remove all infected plants and debris. For protected crops consider treating relevant structures and apparatus with a disinfectant (Bennison and Parker).

Parsley

Downy mildew in parsley (*Petroselinum crispum*) is caused by the pathogen *Plasmopara petroselini* (also referred to as *Plasmopara umbelliferarum*) (Amein *et al.*, 2006; Soylu *et al.*, 2010; Wright, 2014) and, as with other downy mildews, is favoured by wet and humid conditions (Amein *et al.*, 2006). This pathogen does however differ from downy mildews belonging to the genus *Peronospora* in that sporangia from members of the genus *Plasmopara* can germinate to produce zoospores (motile spores). Symptoms of disease start off as faint chlorotic spots on the upper leaf surfaces which can grow rapidly and whole leaves can rot. White/grey sporulation on the underside of leaves develops in appropriate conditions which corresponds to the blemishes on the upper leaf surface (Amein *et al.*, 2006; Soylu *et al.*, 2010). The pathogen appears to favour low temperatures with periods as short as 1 hour leaf wetness were sufficient for infection. Wright (2014) found that despite prolonged periods of leaf wetness and high humidity throughout the summer months, infection did not occur until autumn, perhaps highlighting that temperature is a more important factor in disease development than humidity, or that the disease potentially has a latent period. More work is needed on these aspects.

Marthe *et al.* (2012) identified numerous potential sources of resistance to *P. petroselini* but more work is needed in identifying and developing durable cultivar resistance to this pathogen. ‘Felicia’ is a variety which has been shown to have good tolerance to downy mildew (Krauthausen and Leinhos, 2007). The seed company Rijk Zwaan markets the variety ‘Amsterdamse Snij-Felicia RZ’ which is described as ‘very strong against downy mildew’.

Chives

Downy mildew of chives (*Allium schoenoprasum*) is believed to be caused by the same pathogen which causes downy mildew on other allium species, *Peronospora destructor*. The symptoms of downy mildew on chives are similar to those shown in infected onions, chlorotic regions begin to develop at the tips and down the length of the leaves. Eventually, entire leaves become brown and under optimum conditions purple/brown sporulation structures develop (Bennison and Parker). *P. destructor* may also survive on chive seeds, however as with onion seeds, the role of this inoculum remains undetermined (Bennison and Parker; Glushchenko, 1980; Brewster, 1994; Sugha *et al.*, 1996). Due to the numerous recent

reclassifications of downy mildew pathogens, either into distinct species or races, cross inoculation experiments would provide insight into onion (and other Alliums) and chive hosts as alternate sources of inoculum for their respective pathogen.

As with other downy mildews high humidity in the capony favours disease development so where possible allow adequate spacing between plants and keep weeds to a minimum to maintain airflow through the crop. If overhead irrigation is used time this for the morning as opposed to the evening so the crop does not stay damp throughout night. Resistance to this pathogen, *P. destructor*, has been achieved in onion cultivars but as yet is not a focus of chive breeding.

Mint

Peronospora lamii was believed to be the causative agent of downy mildew in the *Lamiaceae* family of plants (to which mint, *Mentha* spp., belongs) (Voglmayr, 2008). This classification needs re-evaluating as downy mildews on sage and basil (both hosts belonging to *Lamiaceae)* have now been identified as distinct species, *P. salviae-officinalis* and *P. belbahrii* respectively.

As with other herb downy mildews, the disease of mint causes leaf blemishes and under conducive conditions (yet undetermined) sporulation can be seen on the undersides of the leaves. The pathogen causing downy mildew on mint has not been well researched and much information on its biology and epidemiology is lacking, however it is thought to persist between seasons in-host (Davies, T., pers. comm.).

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Aerial *Phytophthora* on Ornamental and Amenity Trees and Shrubs

The genus *Phytophthora* is well known for causing root, crown and basal stem rots. Some species are associated with disease on aerial plant parts. The best known of these is *Phytophthora infestans* (which is outside the scope of this review) but several new species have become important diseases of trees and shrubs. This review focuses on two species of particular importance in the UK – *P. ramorum* and *P. kernoviae*. Both of these pathogens are under regulatory control by the Animal and Plant Health Agency (APHA), meaning that outbreaks must be notified to the relevant Plant Health authority. Other aerial *Phytophthora* species at risk of affecting ornamentals in the UK include *P. acerina* on acer (not yet reported in the UK) (Ginetti *et al*., 2014), and *P. austrocedri* (previously *P. austrocedrae*) on juniper (Green *et al*., 2012).

The first European record of sudden oak death, also known as ramorum dieback (caused by *P. ramorum*) was in Germany and the Netherlands in 1993, but the causal organism (a new species) was not described until 2001 (Jones, 2003). Since then, it has become widespread in Europe and North America. It has a wide host range and symptoms vary between hosts. Jones (2003) describes the hosts and symptoms in the UK as at 2003. Symptoms vary according to host, and can be hard to distinguish from those of some other pathogens or abiotic conditions. Typical symptoms on rhododendron are brown to black lesions on shoots, blackening along the leaf stalk and into the leaf and blackening of the leaf tip. Symptoms on trees include bleeding cankers, which can result in tree death. Asymptomatic infections have also been reported on various hosts (Beinapfl and Balci, 2014), a finding that has implications for means of spread. The pathogen favours wet environments which facilitate spore production, dispersal, germination, and infection (DEFRA, 2008).

Since 2003, another new species of *Phytophthora*, *P. kernoviae* (formerly known as *Phytophthora* taxon C or PTC), was found attacking beech, rhododendron and several other plant species in England and Wales in woodland and, later, in nurseries (Turner, 2006).

By 2006, In England and Wales, there had been a total of over 582 confirmed outbreaks of *P. ramorum* in England and Wales, ~75% of which (434) were in nurseries (Turner, 2006). These outbreaks proved costly to the nursery industry as they resulted in the destruction of large numbers of plants. If infected material is found at a nursery or garden centre, current regulations require destruction of infected plants and all plants within a 2 m radius, holding all susceptible plants within a 10 m radius for 3 months and inspection of all susceptible plants

on the premises. Such requirements are both costly and disruptive. By 2008 the number of confirmed outbreaks on nurseries in England and Wales had reached 510 for *P. ramorum* and four for *P. kernoviae* (Jennings, 2008). Confirmed cases of regulated *Phytophthora* spp. in home gardens usually requires the destruction of infected plants. Infected trees in the wider environment have been destroyed to limit the spread of the pathogens (Forestry Commission http://www.forestry.gov.uk/forestry/infd-5ubesn).

In spite of much research, not all the potential means of spread of aerial *Phytophthora* spp. have been confirmed. Movement of infected plants is known to be a key means of spreading the pathogens over long distances (Bienapfl and Balci, 2014). Local dispersal within plants and to neighbouring plants occurs primarily through rain splash of sporangia from leaves and soil (Kliejunas, 2010). Wind-driven droplets during storms have been shown to be associated with medium distance spread. In the UK, *P. ramorum* has been detected in spore traps at least 50 m from the nearest source of inoculum (Turner *et al*., 2008a, reported in Kleijunas, 2010). Other known means of spread include footwear, dogs' paws, bicycles wheels, tools and equipment (Forestry Commission http://www.forestry.gov.uk/forestry/infd-5ubesn). The role of *P. ramorum* oospores as survival structures is unknown, as they have not been observed in the field, although oospores of other *Phytophthora* species typically serve as survival structures (Kliejunas, 2010).

Jones (2003) described measures to manage and control *P. ramorum* in an AHDB review, soon after the species was described. At that stage, eradication of confirmed outbreaks, both in nurseries and further afield, was attempted. Quarantine measures were recommended in nurseries and garden centres and included the use of plant passports, avoiding the use of disease suppressants within six weeks of shipping, careful inspection for symptoms, establishing quarantine areas and implementing hygiene measures (similar to those used for soil-borne *Phytophthora* spp.) and avoiding overhead irrigation where possible.

Quarantine *Phytophthora* spp. continue to be an issue in nurseries and control methods will not prevent plant destruction being required when these species are introduced on infected bought-in plants (Jennings, 2008). Bienapfl & Balci (2014) showed that several *Phytophthora* spp. could be found in nurseries in association with infested potting media of asymptomatic plants.

There has been a considerable amount of work (particularly in the USA, but also in UK and Europe) examining the diversity of foliar *Phytophthora* spp. in nurseries and in woodlands (Knaus *et al*., 2015; Schlenzig *et al.,* 2015). There are various issues in detecting and managing the various species. There are several known species present, but also as yet unnamed species whose significance is yet to be determined. *Phytophthora* spp. may be

asymptomatic in some hosts, but cause serious disease in others. Their presence in asymptomatic hosts will be difficult to detect. For instance, 15 different *Phytophthora* spp. from 77 plant genera were identified in a study of nurseries and the managed environment in Scotland (Schlenzig *et al*., 2015), including important aerial pathogens. Frequency and species diversity were higher in trade premises than in gardens or amenity landscapes.

Eradication attempts have had only limited success (Peterson *et al*., 2015), indicating the need for prompt action.

Composting has been shown to have the potential to eradicate *P. kernoviae* and *P. ramorum* from infected material, but temperature during the composting process is important (Noble *et al*., 2011). The ability to eradicate these pathogens via composting could reduce the costs of disposing of infected material and also reduce the risk of spreading infection via undetected infections (such as in asymptomatic material).

Xu *et al*. (2009) carried out a spatio-temporal analysis of *P. ramorum* in England and Wales and concluded that statutory actions had reduced the extent of its long-distance spread among garden centres and nurseries, but not short distance spread between garden centres/nurseries and semi-natural environments, and *vice versa*.

Aerial *Phytophthora* spp. show considerable variation. For instance, *P. kernoviae* isolates from the UK had a higher overall virulence than those from New Zealand (Widmer, 2015). *Phytophthora ramorum* is made up of lineages which differ in host preference and environmental requirements (Eyre *et al*., 2014). King *et al*. (2015) reviewed the current status of *P. ramorum* lineages in Europe and further afield. Until recently, three largely clonal lineages were recorded. One (EU1) was found in Europe and North America, while the other two (NA1 and NA2) were found exclusively in North America. Lineage EU1 mostly infects ornamental shrubs, such as Rhododendron, explaining differences in primary hosts in Europe and North America. More recently, a second European lineage (EU2) was identified and has been found infecting Japanese larch (*Larix kaempferi*), non-native red oak (*Quercus rubra*), bilberry (*Vaccinium myrtillus*) and rhododendron. This new lineage explains recent serious epidemics on larch. Such results support measures to minimise the spread of *Phytophthora* spp. between regions, for example Natural Resources Wales note that around 6 million larch trees are to be felled in Wales over the next few years to try and stop the spread of the pathogen (https://naturalresources.wales/media/4136/cwmcarn-faqs-1-may.pdf).

While there is information available on the relative susceptibility of host species to *P. ramorum* there is little known about within-species variation in susceptibility. Grunwald *et al*. (2006) found that Viburnum species and cultivars vary in resistance to *P. ramorum*. If the regulations around *P. ramorum* are lifted, there will be the potential to manage the disease in gardens

through cultivar and species selection. Such information should therefore be obtained in readiness for a change from an eradication approach to one involving management of the disease. Given the existing variation in resistance, there is the potential to select for resistance to *P. ramorum* in ornamental shrub and tree breeding programmes.

A leaf bait diagnostic test combined with a lateral flow device (LFD) test showed potential to provide a quick and easy method to detect *Phytophthora* spp., including *P. ramorum* and *P. kernoviae* (Jennings, 2008).

Considerable research has been done to develop rapid assays for the detection of *Phytophthora* spp. in plant tissue, soil, debris and water. These include PCR for trees and soil (Hughes *et al*., 2011; Mulholland *et al*., 2015), isothermal amplification assays for plant tissue (Miles *et al*., 2015) and microarrays for identification of multiple species using padlock probes (Sikora *et al*., 2012) or as a 'lab on a chip' (Julich *et al.,* 2011). The need for monitoring for *Phytophthora*, even in the absence of clear symptoms, is likely to lead to the uptake of new grower-friendly methods. Commercially available immunoprinting kits and lateral flow devices (LFDs) are amongst the first tools available (De Boer and Lopez, 2012). Such methods could be of great value in detecting asymptomatic disease in plants while still in quarantine and also to ensure the clean-up is effective following an outbreak. The only device currently available for use in the field is a simple disposable LFD test kit, which detects *Phytophthora* but not to the species level. Samples of known hosts, with likely symptoms that are positive for *Phytophthora* need to be sent to a laboratory for confirmation of species. The availability of a commercial, species-specific, test kit would enable on-site monitoring for *P. ramorum* and improve speed and certainty of possible diagnoses.

AHDB funded two projects (Turner, 2004; Turner, 2006) between 2003 and 2006 to evaluate fungicides and disinfectants for the control of *P. ramorum*. A number of fungicides with protectant (SL 567A (metalaxyl), Amistar and Sonata were most effective) and eradicant (especially SL 567A, Standon Etridiazole, Tanos, Amistar and Sonata) properties were identified and potential resistance management strategies were developed. These were unable to be implemented due to regulatory measures aimed at avoiding infections being masked, which could result in the spread of the disease. Jeyes Fluid was shown to be an effective disinfectant. Delano *et al*. (2012) identified further disinfectants that were effective for nursery surfaces that were contaminated with *P. ramorum*. Further work has been carried out on fungicide efficacy (Elliott *et al*., 2015). They found that systemic fungicides were the most effective at preventing mycelial growth and zoospore germination of *P. ramorum*.

Rolando *et al*. (2014) showed that the use of adjuvants can improve the uptake of phosphorous acid applied to control a needle disease caused by *P. pluvialis* in *Pinus radiata*.

Kanaskie *et al*. (2011) showed the potential for phosphorous acid to control outbreaks of sudden oak death, caused by *Phytophthora ramorum*.

Widmer & Dodge (2013) found that leaf necrosis caused by *P. ramorum* could be reduced when certain fungal epiphytes were applied. Bailey *et al*. (2012) examined commercial biofungicides for the suppression of *P. ramorum*, but found effectiveness was dependent on host species and isolate (maximum reduction in disease severity, using the product Actinovate®, which is based on the bacterium *Streptomyces lydicus,* was 50%).

If and when a management approach is adopted towards the regulated aerial *Phytophthora* diseases, knowledge of efficacy of plant protection products will be required.

Slow sand filtration and disinfectant treatment were shown to be effective against both *P. ramorum* and *P. kernoviae* (Jennings, 2008). Several disinfectants gave full decontamination of infested composts when applied as a drench, while only 'Unifect G' was effective against established infections on detached leaves.

Management of outbreaks of regulated *Phytophthora* spp. has included plant destruction, although re-sprouting of stumps can be an issue. Herbicides were shown to be more effective than a bioherbicide at reducing re-sprouting of *Rhododendron ponticum* following cutting to prevent disease spread in a UK study (Willoughby *et al*., 2015).

Yakabe & MacDonald (2010) noted that ramorum leaf blight re-emerged at several Californian nurseries after removal of infected material, and attributed this to inoculum (in particular chlamydospores) surviving in soil beds. They found that soil fumigation treatments such as chloropicrin, Vapam and iodomethane were effective at reducing *P. ramorum* propagules below detection limits. Heat treatments above 40^0C for 3 days were also effective. Similarly, Linderman & Davis (2008) showed that aerated steam treatment or fumigation with metam sodium can effectively sanitise soil-less potting media infested with *P. ramorum*, (recovery dropping from 75% to 0%) thereby reducing its survival with a nursery or its transfer between locations.

There is further potential to integrate strategies to minimise the likelihood of arrival and spread of aerial *Phytophthora* species within the nursery industry, based on existing knowledge as well as new detection and management methods.

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Antirrhinum Downy Mildew

Antirrhinum production in the UK is primarily in the pot and bedding sector. Cut flower antirrhinums are usually imported but have potential to be tunnel- or field-grown in the UK (Hanks, 2014). There is little information on antirrhinum downy mildew (*Peronospora antirrhini*) in the UK; it was first observed in 1937 and was seen regularly throughout England and Wales since then until 1952, when the last available report was made (Moore and Moore, 1952). More recently, it has been noted that antirrhinum downy mildew can be troublesome in the UK and it is recommended to avoid overhead watering and high humidity (Hanks, 2014).

Antirrhinum downy mildew is mainly a disease of seedlings and young plants, although conidia may cause secondary infections (these appear as pale yellowish spots) under high humidity (Francis, 1981). Infection is systemic and affected plants appear stunted and pale yellowish green (Francis, 1981). Systemically infected plants rarely survive (Anon., 1988).

Seed transmission has been suggested but, prior to 1981, not demonstrated (Francis, 1981).There appears to be no more recent information and, if still unknown, this is an important knowledge gap, as seed-borne inoculum could contribute to outbreaks.

In a UK study from 1950 to 1952, outbreaks were reported to have a crippling effect on young plants raised under humid conditions, while plants raised under relatively dry conditions suffered little damage (Moore and Moore, 1952). Antirrhinum downy mildew is most common on seedlings and young plants growing in very humid, poorly ventilated greenhouses where low temperatures exist (Anon., 1988). The optimum temperature for sporangia production is 13^{o}C, while infection and disease development are favoured by temperatures of 4^{o}C to 16^{o}C (Anon., 1988). The disease can be destructive in the US and guidelines for its management are available in several states (Anon., 1988; Anon., 2015). Cultural measures to manage antirrhinum downy mildew in the US (Anon., 1988; Anon., 2015) include reducing greenhouse humidity to below 80 to 85% (via heating, venting, air circulation), planting in areas with adequate sunlight and spacing plans to foster air flow, avoiding overhead irrigation and using clean seed and seedlings. Oospores develop in dead plant parts, so removing and destroying infected plants and plant debris is recommended. It is also recommended to sanitise tools, seed trays and other containers as well as to plant in steamed soil. Minimisation of primary inoculum is regarded as a key to avoiding downy mildew epidemics, especially on young plants where the systemic infection is most serious. Optimising such measures for the UK growing environment would have benefits for efficient management of the disease.

No races of *P. antirrhini* have been reported (Francis, 1981). Dark varieties of Antirrhinum have been reported to be less severely affected than light ones (Moore and Moore, 1952), but early attempts to produce snapdragons resistant to mildew in California were unsuccessful (Francis, 1981). More recently, differences in susceptibility to downy mildew have been shown amongst US antirrhinum cultivars (Byrne *et al*., 2004). The authors suggest that, with the implementation of resistant cultivars, growers can significantly reduce downy mildew, and identification of snapdragon cultivars that are especially susceptible to downy mildew is also important in the development of a disease management program. Information on variation in downy mildew susceptibility in current UK antirrhinum cultivars appears to be lacking. Such information could enable the most susceptible cultivars to be avoided, thus improving the feasibility of using cultural measures to manage the disease.

Early and frequent scouting is considered important in the USA because signs of the disease may go unnoticed on the undersides of leaves (Byrne *et al*., 2005). Methods for improved early detection of downy mildew would enable measures to be taken before an epidemic became established.

Byrne *et al*. (2005) examined the influence of environment on spore release in field-grown snapdragon, with the aim of developing a forecasting model to prompt fungicide applications (thus improving the efficiency of fungicide programmes, avoiding unnecessary applications and delaying the development of pathogen resistance). While useful information was gained on spore release patterns and factors affecting them, further progress is required for the development of a viable forecasting model. Such a model would also need to be tested under UK conditions. Hanks (2014) noted that 'antirrhinum downy mildew can be troublesome in the UK and it is recommended to avoid overhead watering and high humidity' There appears to be no more information available regarding the frequency of problems attributable to this pathogen.

Fungicides are regularly applied to antirrhinum in the USA for downy mildew control. Recommendations in the USA include drenching seedlings in the greenhouse with mefenoxam (Anon., 2009). Mancozeb-based products are also (as at 2005) recommended, applied preventatively and in alternation with a strobilurin-based fungicide, dimethomorph, or fosetyl-Al (Byrne *et al*., 2005). Sprays are typically applied every 1 to 3 weeks through the growing season to manage downy mildew. However, calendar spraying can lead to fungicide resistance (Byrne *et al*., 2005).

Palmer and Vea (2010) conducted two experiments in the USA. In the first experiment (in 2003), most effective treatments were fosetyl-AL + mancozeb, fenamidone, fenamidone + mancozeb, mancozeb and pyraclostrobin + dimethomorph. The second experiment (in 2009) included other products with the most effective treatments found to be fluopicolide, fenamidone, azoxystrobin, Regalia (extract of *Reynoutria*) and dimethomorph.

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Aquilegia Downy Mildew

Aquilegia downy mildew is caused by a currently unnamed *Peronospora* sp. It was first recorded by FERA in 2011 (Anon., 2015), while outbreaks in UK gardens began to be reported to RHS Gardening Advice in 2013 (Denton *et al*., 2015). It does appear to be a single species, but without knowing its origin there are questions as to its host range.

Symptoms of downy mildew on aquilegia leaves are angular, yellow patches which spread, eventually resulting in the whole leaf curling and turning brown (Denton *et al*., 2015). Fungal mycelium may be visible on the lower leaf surface. Symptoms are also seen on flowers, which become distorted and appear water-soaked. Flower stalks develop purple blotches. If infection occurs after flowering, the seed pods can develop brown patches and fail to set seed (Denton *et al*., 2015). Affected plants are often killed. The disease can devastate plantings of aquilegia and has resulted in the death of large numbers of plants in two National Collections (Anon., 2015; McCann, 2015).

Prompt action is advisable if downy mildew is detected on aquilegia. As a minimum, removal of infected leaves is recommended, but digging out infected plants and destroying them by burning or commercial composting is more likely to restrict its spread (Anon., 2015; McCann, 2015).

Cultural measures currently recommended by the Royal Horticultural Society (RHS 2015) are based on minimising the survival of resting spores by disposal of affected plants. It is also recommended to avoid planting aquilegia in affected areas for at least a year to give time for resting spores to lose viability (although there is as yet no information on how long the resting spores remain viable). Where plants are grown in pots, it is recommended to replace compost and disinfect containers between uses. More information is needed on the role of oospores in survival of the aquilegia *Peronospora* sp.

It is not yet known if aquilegia downy mildew is seed borne, so in the meantime it is recommended to try to source disease-free seed (Denton et al., 2015). AHDB are currently funding research (Projects HNS 196 and HNS 196a) to identify inoculum sources, in particular

whether infected seed could act as a primary source of infection. Final results of this study are not yet available. Preliminary results have shown low levels of oospores can be present on the outer surfaces if seed, but transmission from seed to plant has not yet been shown.

The origin of the *Peronospora* sp. infecting aquilegia is unknown and it remains unnamed. It appears to have a unique DNA sequence and so it is thought to be a new or previously unidentified species.

The apparently sudden appearance of downy mildew on aquilegia suggests that there has been little opportunity for natural selection for disease resistance to occur in the UK aquilegia population. No aquilegia cultivars resistant to downy mildew are known (Denton *et al*., 2015). Given the devastation the disease has caused to two National Aquilegia Collections, crosses and selections from surviving plants may provide plants with a degree of resistance.

The disease was first brought to the attention of FERA in the UK in 2011 (Anon., 2015) and, as yet, globally there are no monitoring programmes or diagnostic tests.

As this is a recently recognised disease as yet there are no products specifically tested for the treatment or protection of aquilegia against downy mildew.

Further studies (AHDB Project 196a) are examining factors which influence infection and control of this newly emerged disease.

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Hebe Downy Mildew

First found in the UK in 1914, Hebe downy mildew (*Peronospora grisea*) has had a major impact on the production of certain varieties for many years. O'Neill (2004, 2014a) states that losses in Hebe are estimated to exceed £200,000 annually, though he also notes that downy mildews in general have been less damaging in the last 10-15 years, probably due to new fungicides and improved management practices (O'Neill, 2014b).

The disease is much more damaging in nursery production than when plants are subsequently planted out in gardens or landscaping schemes, although the RHS does have a number of records of infected Hebe samples sent in for diagnosis by its members. Pscheidt and Ocamb (2015) state that in the Pacific Northwest of America the disease is rare in the landscape, but plants that are subject to heavy shade can be infected.

*S*ymptoms of downy mildew infection vary according to cultivar. Large-leaved varieties often show leaf distortion and yellowing, with copious mildew growth present on the undersides of leaves, whereas smaller-leaved varieties often exhibit shoot tip dieback with little obvious mildew growth (O'Neill, 2014b).

Cultural practices that avoid periods of extended leaf wetness (such as good ventilation and the use of sub-irrigation) will reduce the risk of severe attacks (O'Neill, 2014b). Some of these aspects were investigated by O'Neill (2000) who found only a limited benefit from fan-assisted ventilation in a low tunnel, and suggested that alternative fan systems resulting in better air movement through the crop would warrant further investigation.

P. grisea sometimes produces oospores within the leaves of affected plants (Whipps and Linfield, 1987), but the role (if any) played by these in the epidemiology of the disease has not been investigated.

The use of polytunnels is common in Hebe production, but no references can be found investigating the effects against *P. grisea* of cladding materials containing spectral filters; research suggests that this aspect may be worth pursuing. For example, Sampson (2001) investigated the effects of UV-blocking films on a number of crops (predominantly on pests and biological control organisms) and found that a downy mildew infection that developed on stocks was significantly reduced by two of the products.

Whilst it is well known that there are differences in varietal susceptibility to *P. grisea*, no specific research on resistance breeding or identification of sources of resistance was found. O'Neill (2014b) lists some of the most susceptible varieties and states that *H. ochracea* 'James Stirling' appears to have some natural tolerance to the disease.

Plants in the genus Hebe are more correctly classified as shrubby species of the genus Veronica*.* This latter genus is now confined to annuals, perennials and some mostly deciduous sub-shrubs. Whilst *P. grisea* is also found on some herbaceous Veronica species (Francis and Berrie, 1983), there also are a number of other species of *Peronospora* found on Veronica. The precise number is unclear; four species are listed (including *P. grisea*) by Francis and Berrie (1983), but others are mentioned in the British Mycological Society Fungal Records Database. Voglmayr (2013) carried out genetic analyses of three *Peronospora*

species (*P. agrestis, P. arvensis* and *P. grisea*) found on herbaceous Veronica species and confirmed that they were distinct but closely related.

It is unclear whether host-specific strains exists within *P. grisea*, and whether reported wild herbaceous hosts of *P. grisea* such as common speedwell (*V. officinalis*) and brooklime (*V. beccabunga*) play any role in perpetuating the disease in and around nurseries. Neither is it clear whether the downy mildew that affects cultivated herbaceous Veronica species such as *V. spicata* and *V. longifolia* is always *P. grisea* nor whether cross-infection can occur between cultivated herbaceous Veronica species and Hebe species (which may be grown at the same nursery).

No forecasting system currently exists for *Peronospora grisea*, and detailed knowledge of the precise environmental conditions required for infection by this pathogen is still lacking. It would be worthwhile evaluating the effectiveness against downy mildews of Hebe and other nursery stock subjects of the forecasting system recently developed for rose downy mildew (Xu, 2012).

A TaqMan PCR test developed to detect the downy mildew species *Peronospora farinosa* f. sp. *betae* in red beet as part of HDC project 226c (McPherson, 2005) was subsequently shown to be capable of detecting both pansy and impatiens downy mildew DNA in seed and plant material. If, as seems likely, the test will also detect DNA of *P. grisea* it has potential for use in studies on disease development, and also in the detection of latent infection in mother plants and/or cutting material.

Control of Hebe downy mildew has been the subject of HDC research projects (O'Neill, 2000; O'Neill, 2014a) that demonstrated the effectiveness of a number of different products (fungicides, coded biological controls and potassium phosphite fertiliser) and investigated their use in spray programmes. These results have been communicated to growers in factsheets (O'Neill 2004; O'Neill, 2014b). Unfortunately, the disease was absent or at low levels in most of the trials conducted in the most recent project (O'Neill, 2014a), so information on the performance of some of the newer products under higher disease pressure would be welcome.

O'Neill (2000) states that the results of one of the trials in project HNS 79 suggested that a metalaxyl-resistant isolate of *P. grisea* may have been present, although this was not confirmed. Testing of UK *P. grisea* isolates for their sensitivity to this fungicide would have merit, as if confirmed this would influence product choice in spray programmes (as has been the case with the occurrence of resistant isolates of Impatiens downy mildew).

Work carried out in France showed that the phytostimulant Semafort (containing phosphite, algal extract and amino acids) gave good control of *P. grisea* in field trials (Stapel *et al,* 2011).

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Impatiens Downy Mildew

Impatiens species can be infected by three downy mildews. *Plasmopara constantinescui* is found in North America and Russia. *Pseudoperonospora cubensis* was found on *I. irvingii* in Cameroon in 2007 (Voglmayr *et al.,* 2008). *P. cubensis* also cause downy mildew of cucurbits in many countries, including the UK, but there is no evidence to suggest that it has caused downy mildew on impatiens here.

The significant downy mildew problem affecting bedding busy lizzies (*Impatiens walleriana*) in the UK and elsewhere is caused by *Plasmopara obducens.* It was first found in the UK in 2003 and was suspected (but not proven) to have arrived on imported cutting material. Symptoms include yellowing, downward curling and loss of leaves, stunting, lack of flowering and often death of affected plants. Infection can become systemic.

The impact of the disease has been devastating. Prior to the downy mildew problems UK impatiens production was estimated to have a financial value in the UK of £40M/annum (Jennings, 2013). The disease led to a collapse in production of *I. walleriana*, together with a loss of consumer confidence in the product.

Impatiens downy mildew has been the subject of extensive HDC research, resulting in the production of numerous disease updates and factsheets summarising current knowledge and giving recommendations for both cultural and chemical control (e.g. McPherson and Brough, 2009). The disease has become widespread in the US, resulting in similar guidelines (Hansen *et al*., 2013).

Information remains limited on the issues of seed transmission and infection from soil-borne oospores. *Plasmopara obducens* has been reported as seed-borne on *I. balsamina* in India, being found as mycelium and oospores (Srivastava and Singh, 1988). Jennings (2011) germinated seed lots of *I. walleriana* identified as 'infected' by a PCR test (see below) to see if the resultant plants became infected. No disease symptoms developed, but further PCR testing showed that pathogen DNA was present in the plants derived from the seed lots with the highest levels of pathogen DNA. The significance of this is unknown.

Production of oospores by *P. obducens* in infected plant tissues is widely reported. These were found to be capable of overwintering in soil under UK conditions when assessed using a viability stain (Jennings, 2011), but because they could not be germinated it was not possible to assess their potential role in plant infection. The role of overwintering oospores as inoculum sources under UK conditions remains unknown. Latent infection by *P. obducens* has been demonstrated (Jennings, 2011). Good nursery hygiene is therefore important to minimise the risk of asymptomatic plants being sold.

The role of 'wild' hosts in perpetuating the disease would warrant further investigation. A number of Impatiens species found growing wild in the UK are recorded hosts of *P. obducens*, including the introduced and now widespread Himalayan balsam (*I. glandulifera*) (Tanner *et al.,* 2008), although to date there are no UK records of the pathogen on this host.

Brielmaier-Liebetanz and Idczak (2012) tested 52 cultivars of *I. walleriana* from nine series for susceptibility to *P. obducens* under standard conditions and found all of them to be highly susceptible. Identification of sources of resistance that would result in the production of disease-resistant *I. walleriana* cultivars is clearly required. In the meantime, the introduction of claimed mildew-resistant interspecific Impatiens hybrids such as the 'Bounce' series may have some potential to replace *I. walleriana* as a shade-tolerant and free-flowering bedding impatiens with a spreading habit.

No forecasting system currently exists for *Plasmopara obducens*. A TaqMan PCR test developed to detect the downy mildew species *Peronospora farinosa* f.sp. *betae* in red beet as part of HDC project 226c (McPherson, 2005) was shown to be capable of detecting Impatiens downy mildew DNA in seed and plant material (Turner, 2009).

Jennings (2011; 2013) identified a number of fungicides (and a phosphite product) with activity against *P. obducens* and evaluated them as single-product treatments and in spray programmes, carrying out tests using both metalaxyl-sensitive and metalaxyl-resistant isolates of the pathogen. Products worked better as protectants, having limited eradicant activity. The identification of the metalaxyl-resistant isolate in 2011 has complicated fungicidal control programmes, particularly as both resistant and sensitive isolates have been detected in subsequent years. Monitoring of the resistance status is continuing until 2018 (Jennings, 2014). Metalaxyl-M (also known as mefenoxam) resistance has also been reported in isolates of *P. obducens* from Holland (Warfield, 2012).

Given the worldwide distribution of impatiens downy mildew it is unsurprising that research into chemical and biological control measures has been carried out elsewhere, including over thirty trials reported from the United States since 2011. It is beyond the scope of this review to summarise these; many of the trial results are available online as Plant Disease Management Reports for a small subscription. Control options for the pathogen have been researched under the IR-4 Project (Palmer, 2014). Many of the active ingredients evaluated in these US trials are available in the UK (although often at a different concentration of active ingredient and in different formulations, and note that the reported trial results usually list the fungicides by US product name rather than active ingredient).

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Lisianthus (Eustoma) Downy Mildew

Downy mildew of lisianthus (Eustoma) and *Blackstonia* is caused by *Peronospora chlorae* (Hall, 1994). The disease resulted in significant economic losses to lisianthus in the late 1990's to the early 2000's (O'Neill, 2003). It was only recently reported from China (Yang *et al*., 2015), where it is regarded as a serious threat to production of *Eustoma grandiflorum*.

Symptoms are similar to many other downy mildews. Sparse mycelial patches develop first on shoots and buds under wet conditions, followed by heavy greyish-brown fungal growth on foliage, leaf necrosis and defoliation (Yang *et al*., 2015).

Peronospora chlorae is transmitted by conidia dispersed by wind or rain-splash (Hall, 1994). As with many other downy mildews, it is suggested that disease incidence can be reduced by avoiding excessive watering or manuring and with careful management of humidity by ventilation (Hall, 1994).

Sources of primary infection have not been demonstrated but identification of these sources would target management strategies. The role of oospores in disease transmission is unknown, but may enable the pathogen to survive in the absence of a living host (Hall, 1994). There is circumstantial evidence that *P. chlorae* can initiate epidemics of lisianthus downy mildew from seed borne infection (O'Neill, 2003), but this has not been confirmed. There is also no information on the existence of oospores.

Control of downy mildew of lisianthus was examined in an AHDB project (O'Neill, 2003). It was noted that there is a lack of precise knowledge of environmental conditions conducive to pathogen development, but there is likely to be potential to minimise these conditions by manipulating ventilation, heating, plant spacing, airflow, and the timing and duration of overhead watering. Determining these precise environmental conditions would enable them to be minimised.

There appears to be no information available on variation in susceptibility of lisianthus cultivars to downy mildew, pathogenic variation, or the potential of breeding cultivars with a degree of resistance to the disease.

O'Neill (2003) suggested that there is the potential to develop forecasting systems for lisianthus downy mildew, as has been done for rose downy mildew. The availability of chemicals with some curative activity allows some flexibility in timing fungicide applications once a disease warning has been issued (O'Neill, 2003).

Fungicide efficacy was tested, with results reported, in an AHDB-funded project (O'Neill, 2003).

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Nicotiana Downy Mildew

Downy mildew, or blue mould, of Nicotiana is caused by *Peronospora hyoscyami* f. sp. *tabacina*. The synonym *P. tabacina* is often used in reports of the disease, but Hall (1989) suggested that it should be a 'special form' within *P. hyoscyami*, rather than a separate species. Both commercial and ornamental varieties of tobacco are affected by downy mildew (Hall, 1989). It is one of the most important foliar diseases of tobacco, causing significant losses in the Americas, Europe and the Middle East (Borras-Hidalgo *et al*., 2010; Zipper *et al*., 2009). It is also common and can be a serious disease in ornamental *Nicotiana* plantings in the UK, both in nurseries and in gardens.

Chlorotic leaf spots develop on leaves of susceptible seedlings, which become deformed (Hall, 1989). The pathogen sporulates on the underside of leaves, producing the characteristic blue-grey mould. Infection is often severe, with apical growth ceasing following the rapid development of light-brown tissue necrosis (Hall, 1989). The entire plant may be destroyed within 3 – 4 weeks, leaving only a blackened stem (Hall, 1989).

Peronospora hyoscyami f. sp. *tabacina* is transmitted by airborne spores, which are reported to be transported over distances of 1,600 km (Hall, 1989). It is unclear whether the pathogen is capable of overwintering in infected debris and the role of oospores in disease is not clearly

understood (Ivors and Mila, 2007). It is also not certain whether the disease can be seed-borne. Clarifying these aspects could be valuable in developing improved cultural means of control of the disease.

Recommendations for nursery stock production in the US include manage temperature and ventilation systems to minimize leaf-surface moisture by reducing relative humidity and condensation, irrigating beds early in the day to allow drying before nightfall and using a regular preventative-fungicide spray program in greenhouses and plant beds (Ivors and Mila, 2007).

Sukanya and Spring (2013) examined the influence of temperature and ultra-violet light on the viability and infectivity of *P. hyoscyami* f. sp. *tabacina* in commercial tobacco. While much of this post-harvest research is not readily transferable to disease management in living plants, the use of short-term irradiation with 254 nm UV light to kill sporangia could be investigated.

Analysis of the genetic structure of the *P. hyoscyami* f. sp. *tabacina* populations in the Americas and Europe showed that migration occurred within regions (USA, central America, Europe) but less so between regions (Blanco-Meneses *et al*., 2008). Measures to minimise the movement of the pathogen between regions will reduce the likelihood of spread of fungicide resistance and of different pathotypes.

Physiological specialisation has been reported (Hall, 1989), the three forms differing in pathogenicity to different *Nicotiana* spp. Some *Nicotiana* spp. are resistant to downy mildew and molecular linkage mapping has shown the potential for marker assisted selection in breeding (Zhang *et al*., 2012). Tobacco cultivars have also been shown to differ in resistance to downy mildew (Blanco-Meneses and Ristaino, 2011). There is potential to use real-time PCR assays to quantify host resistance in breeding programs (Blano-Meneses and Ristaino, 2011).

Blue mould is difficult to diagnose before the appearance of symptoms and so can easily be spread in non-symptomatic seedlings (Blanco-Meneses and Ristaino, 2011). A PCR assay has been developed to detect the pathogen in leaves, roots and systemically infected seedlings (Blanco-Meneses and Ristaino, 2011).

January temperatures have been shown to be useful to predict the need for early-season fungicide applications in the USA (La Mondia, 2010). Disease forecasts were available to US growers, but appear to have been discontinued after 2011.

Systemic acquired resistance has been reported against this disease (Borras-Hidalgo *et al*., 2010). The use of a systemic acquired resistance activator (acibenzolar-S-methyl) in

combination with fungicides has been investigated to control tobacco blue mould and shown to increase fungicide efficacy (Perez *et al*., 2003; La Mondia, 2008; La Mondia, 2009). A plant growth-promoting rhizobacterium (PGPR) was also shown to provide a degree of systemic protection against blue mould in tobacco (Zhang *et al*., 2004). There is potential for further work on resistance elicitors. Fungicide treatment with phenylamides in commercial tobacco is often used to control the disease, although fungicide resistance is a problem (Spring *et al*., 2013).

PCR-based methods have been used to differentiate between metalaxyl-sensitive and metalaxyl-resistant isolates of *P. hyoscyami* f. sp. *tabacina* in Europe (Zipper *et al*., 2009). Experiments on isolates of *P. hyoscyami* f. sp. *tabacina* in Germany showed that metalaxyl-M-resistant isolates were less virulent than the susceptible isolates (Spring *et al*., 2013). However, the population in Germany comprised almost only the resistant strain between 2002 and 2004, due to the widespread use of this product. With a change in disease management in Germany, the metalaxyl-sensitive strain increased proportionately from 2005 and dominated the population by 2010. This, and infection experiments, indicates that the previous high frequency of metalaxyl resistance in Germany was due to selection pressure caused by the continuous use of the fungicide (Spring *et al*., 2013).

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Poppy Downy Mildew

Poppies are grouped into three genera. The genus *Papaver* contains many species of annual poppy, including the opium poppy, while poppies in the genus *Meconsopsis* can be annual, biennial or perennial. The California poppy (genus *Eschscholzia*) is also a popular garden plant in the UK. Downy mildews are recorded on species of Papaver and Meconopsis, while Eschscholzia is generally regarded as disease free. Poppy downy mildew is distributed widely around the world (Francis, 1981). Downy mildew is one of the most economically limiting diseases of opium poppy (*Papaver somniferum*) worldwide (Calderon *et al*., 2014). Most research on poppy downy mildew focuses on the opium poppy, which is the most commercially important species around the world. Poppy downy mildew is also one of the most common downy mildews recorded amongst garden enquiries from the UK.

Six *Peronospora* spp. have been recognised on *Papaver* spp. (Voglmayr *et al*., 2014). There is still some confusion over species and host ranges, but the named species are *P. arborescens*, *P. argemones*, *P. cristata*, *P. meconopsidis*, *P. apula* and *P. somniferi* (Voglmayr *et al*., 2014). Differentiation of *Peronospora* spp. on poppy using morphological criteria can be difficult, so PCR-based methods have been used to carry out phylogenetic analysis of the species (Scott *et al*., 2004; Landa *et al*., 2007). This has been important as the different species, as well as strains within species, differ in their host ranges.

Symptoms of downy mildew on poppy vary, but systemic infection can be severe. Systemic infection can affect leaves, stems, buds and capsules (Francis, 1981), with the leaves appearing greenish-yellow, thickened and deformed. The pathogen can be seen on the

undersides of infected leaves, showing as a greyish violet felt. Local secondary infections also occur on the lower leaves, where angular chlorotic blotches appear on the upper leaf surface (Francis, 1981).

Oospores of *P. arborescens* form prolifically in leaves and it has been demonstrated that oospores in infested soil or leaf debris are effective sources of infection through underground plant tissues early in poppy seedling growth (Montes-Borrego *et al*., 2009). This gives rise to systemic infections that led to stunting and chlorosis of plants. The longevity of poppy downy mildew oospores appears not to be well understood and so the feasibility of crop rotation for control of the disease is unknown.

Montes-Borrego *et al*. (2011) validated a qPCR downy mildew detection protocol for quarantine purposes. PCR protocols have been used to show that *P*. *arborescens* can be transmitted from seeds to seedlings, indicating the value to diagnosing the pathogen in commercial seed stocks and facilitating the avoidance of spreading the pathogen in seeds (Landa *et al*., 2007).

There is little information on cultural control of poppy downy mildew because most research has been focused on large-scale plantings of opium poppies, where management measures will be very different from those in smaller-scale horticulture.

Symptomless infection has been recorded and could be a means for the unwitting spread of the pathogen.

Voglmayr *et al*. (2014) state that there is high host specificity of *Peronospora* on Papaver and that wild *Papaver* spp. cannot play any role as primary inoculum source for downy mildew epidemics in cultivated opium poppy crops. However, the *Peronospora* populations on poppy in the UK need to be characterised.

Given the importance of downy mildew in opium poppy, it is not surprising that there is a considerable amount of research identifying host resistance in *P. somniferum* (Dubey *et al*., 2009; Dubey *et al*., 2010; Dubey *et al*., 2014). It has been established that there is the potential to develop highly resistant cultivars. There appears to be no information available on differences in downy mildew resistance amongst garden poppy cultivars.

The feasibility of high-resolution thermal and multi-spectral imagery as an indicator of downy mildew infection in opium poppy crops has been demonstrated (Calderon *et al*., 2014).

A quantitative polymerase chain reaction (qPCR) assay has been developed to quantify downy mildew infection in poppy (Montes-Borrego *et al*. 2011). The method has allowed quantification of the pathogen in symptomless plant samples.

The DOWNCAST forecasting model (originally for onion downy mildew) has been modified for use in opium poppy downy mildew, where it is reported to have the potential to predict early season events and thereby reduce inoculum loads later in the season (Scott *et al*., 2008).

Efficacy tests of systemic and non-systemic fungicides for the control of opium poppy downy mildew showed that a degree of control of non-systemic infection was possible with Ridomil-ZM and Alliete (Doshi and Thakore, 2002). Effective seed treatments would reduce the likelihood that poppy downy mildew will be transported to new sites, but issues of fungicide resistance have been reported. A recent study (reported in the Australian news media - http://www.abc.net.au/news/2015-09-03/tch-poppy-fungicide/6745872) identified a new seed treatment that provided very good protection for poppies in early seedling stages up to about four to six-leaf. Opium poppy is an important crop in Australia and management measures developed there for poppy downy mildew should be monitored for their applicability in the UK.

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Pansy and Viola Downy Mildew

Pansies and violas are arguably the most important bedding plant species grown in the UK (Jackson *et al*., 2014). Downy mildew of pansy and viola is caused by *Peronospora violae*. It is one of the most common and destructive diseases of *Viola* spp. Control of this disease, along with other leaf and root diseases of pansy and viola (which together can result in losses of 5 – 10% of batches of plants), was recently reviewed by Jackson et al. (2014).

Conditions favourable to downy mildew on pansy and viola are similar to other downy mildews. It is most common in spring and autumn, associated with cool weather, high humidity and leaf surface moisture for infection (Jackson *et al*., 2014).

In the early stages of the disease, a light covering of sporangia and sporangiophores may be seen on the undersides of leaves (Hall, 1989), which can easily be missed as there are no symptoms on the upper surface of the leaves. Development of ways to more easily detect early infections would aid prompt actions for disease management. Dull yellowish or grey-green blotches later appear on the upper leaf surface, but inspection of lower leaf surface is necessary to detect early infections (Jackson *et al*., 2014). Downy mildew can result in a lack of vigour, delayed flowering and reduced growth in pansy and viola (Jackson *et al*., 2014).

Jackson *et al*. (2014) note that spores are disseminated on air currents and via water splash. Boudier (1987) noted that ‘spectacular attacks of mildew follow sprinkler watering in dry autumn weather’. This also suggests that spores can be dispersed by water splash (Hall, 1989) although the sprinkler irrigation might also provide the leaf surface moisture necessary for infection. Fans in the glasshouse can dislodge and disseminate the spores, although 4 to 5 hours of leaf wetness is needed for germination and infection (Jackson *et al*., 2014). The disease can be hard to eradicate if infection is not controlled early (Jackson *et al*., 2014). Spores are produced during darkness and released the following morning (Minchinton, 1998).Overhead watering of seedlings in the morning, especially after a dew, lengthens the time leaves are wet during the critical spore release and infection period (Minchinton, 1998).

Therefore, if overhead watering is required, it is better carried out later in the day, in particular when leaves will dry more rapidly. Further research on the interactions of water, temperature and light with spore production, spread and infection would enable more specific recommendations to be developed.

It is not clear whether thick-walled resting spores (oospores) are associated with survival of the pathogen in the absence of a living host. Knowledge of this would help determine requirements for sanitation between crops.

Given the importance of environmental conditions for development of downy mildew on viola and pansy, Jackson *et al*. (2014) suggest that cultural methods are key to its management. Measures include managing environmental conditions (such as glasshouse humidity and avoiding overhead watering), cleanliness and hygiene (cleaning glasshouse areas and using new trays where possible), and quarantining and examining plants before they are introduced (to enable rapid diagnosis). The importance of rapid and accurate diagnosis is stressed.

Boudier (1987) notes that cultivars range between very resistant and very susceptible, suggesting that there is the potential to use cultivar resistance as a management tool (even partial resistance would be a useful addition to cultural measures). Boudier (1987) grouped cultivars into four categories: highly susceptible; moderately susceptible; slightly susceptible; and apparently resistant. Cultivars with variegated flowers were less susceptible than those with yellow, light blue or white flowers. There appears to be no information on whether pathotypes of *P. violae* exist. Such knowledge would be important if cultivars were to be marketed as resistant to downy mildew.

Jackson *et al*. (2014) suggest that a routine protectant spray programme is important when conditions are conducive to the disease as it is hard to control when established.

Jennings (2009), in an AHDB-funded study, used molecular methods to show that 66% of pansy seed samples tested contained downy mildew DNA. Where downy mildew DNA was detected in seeds, it was also detected in seedlings once grown-on. When seed from batches in which pathogen DNA had been detected were germinated in humid conditions conducive to downy mildew sporulation these seedlings did not express downy mildew symptoms. In other tests, levels of downy mildew DNA in leaf tissue were shown to increase until the point when symptoms were expressed. Further research is needed on latent infections and the triggers for symptom development.

Various plant protection products are listed in Jennings (2009) and in Jackson *et al*. (2014), who note the problem of fungicide resistance in downy mildews and suggest alternating fungicide groups rather than relying on one. They also outline the use of chemicals for

disinfecting surfaces. Identification of other effective products would be of value in case metalaxyl resistance becomes established.

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Rose Downy Mildew

Rose downy mildew (*Peronospora sparsa*) is a disease that occurs sporadically, but can be very damaging under suitable environmental conditions. O'Neill (2009) states that if just 1% of the UK crop was unmarketable due to downy mildew, financial losses would equate to £192,000 per annum. The disease may sometimes render an entire crop unmarketable.

Symptoms of downy mildew infection are variable, and can sometimes be confused with spray or weather damage. Purplish red to brown spots or blotches are found on leaves. Spore production is often sparse, although it has been shown experimentally that low numbers of spores can still result in extensive infection (Xu and Pettitt, 2002). Spores may sometimes be produced on leaves that appear otherwise healthy (Xu and Pettitt, 2002). A particularly damaging symptom is extensive leaf fall, often including visually healthy leaves. The pathogen can also affect petioles, stems, flower buds and flowers.

In addition to the UK, much of the recent research on rose downy mildew has been carried out in the United States or South America (particularly Colombia).

Leaf wetness is the most important factor in the infection process (O'Neill, 2009). Cultural practices that avoid periods of extended leaf wetness (such as good ventilation and the use of sub-irrigation) will reduce the risk of severe attacks (O'Neill, 2014a). Temperature is less critical and the pathogen can be active over a wide temperature range. O'Neill (2009) states that spore germination occurs at temperatures up to 26°C. In recent work reported from Colombia (Filgueira and Zambrano, 2014), however, some production and germination of spores occurred at temperatures up to 33°C. The authors state that this may show adaptation of the pathogen to the higher temperatures experienced in Colombia. The disease spreads rapidly under appropriate conditions and the period between infection and symptom

production (latent period) has been shown to be as little as three days at 18-22°C (Gomez and Arbelaez, 2005).

Various ways in which the pathogen can overwinter or maintain itself on dormant material have been suggested, but the precise importance of each of these is still unknown. It has been known for many years that the pathogen can produce oospores in leaf and stem tissues, and Xu and Pettitt (2002) regarded oospores in leaf debris as the most likely means by which the pathogen overwinters. However, DNA analysis techniques have shown the fungus to be present in rootstock stems, and also sometimes in stems without visible symptoms (Thomas, 2009). The same DNA probes were used to detect *P. sparsa* in stems and roots of symptomatic plants, and in the crowns of symptomless mother plants used for propagation (Aegerter *et al*., 2002). This latter finding has potential implications for the movement of infected propagation material in the nursery industry. The importance of systemic infection is also still unclear – it was not found by Xu and Pettitt (2002), but movement of the pathogen through petioles and its presence in the vascular tissues of leaves has subsequently been reported by other workers (Gomez 2014, Gomez and Filgueira 2012).

The use of spectral filters against rose downy mildew does not appear to have been investigated – other work suggests that this aspect may be worth pursuing. For example, Sampson (2001) investigated the effects of UV-blocking films on a number of crops (predominantly on pests and biological control organisms) and found that a downy mildew infection that developed on stocks was significantly reduced by two of the products.

The effects of different feeding regimes (concentrations of major and minor nutrients, applied singly or in combination) on the development of the disease were investigated by Castillo *et al* (2010). Differing effects on disease severity were noted, although a varietal effect was also evident.

In addition to *Rosa* spp., *Peronospora sparsa* is known to affect a range of *Rubus* spp. (including raspberry, blackberry and loganberry) and cherry laurel (*Prunus laurocerasus*) (CABI, 2015). Cross-infection can occur between Rubus and Rosa species; it is not known whether this is the case between *P. laurocerasus* and Rosa. There is no information available on the potential role played by *Rubus* spp. (wild or cultivated) or *Prunus laurocerasus* in the epidemiology of downy mildew on roses. However, research carried out on *P. sparsa* on *Rubus* spp. could be applicable to rose downy mildew.

It is well known that rose varieties vary in their susceptibility to *Peronospora sparsa*, and some varieties have been bred specifically for resistance (O'Neill, 2009). However, such varieties will need careful monitoring over time to determine if their resistance is robust, and there is

currently no information on the structure of rose downy mildew populations in the UK (O'Neill, 2009). Schulz *et al*. (2010) screened 183 wild rose accessions and identified 19 resistant accessions. They were able to introduce this resistance (based mainly on the hypersensitive response) into the progeny of some crosses between resistant wild rose varieties and cultivated varieties. In a review on resistance breeding in roses Debener and Byrne (2014) discuss the use of biotechnological tools such as marker assisted selection to accelerate the production of rose varieties resistant to the most damaging diseases, including downy mildew.

A forecasting system for *P. sparsa* has been developed in the UK by Xu (2012), based partly on a previous model by Aegerter *et al*. (2003), but this has not yet been evaluated under field conditions. Kim *et al*. (2014) report on an empirical forecasting model that does not require leaf wetness data. This provided a significant degree of agreement between predicted and observed risks for *P. sparsa* outbreaks on rose, boysenberry and blackberry in Mexico, the US and New Zealand. A simple model to predict spore production by *P. sparsa*, based on temperature and relative humidity values measured the previous night, has been developed by Filgueira and Velasquez (2014).

The PCR diagnostic test developed in the US by Aegerter *et al*. (2002) was used subsequently by Thomas (2009) in UK research. In addition to using PCR, Schulz *et al*. (2007) also developed a serological ELISA test based on polyclonal antisera developed against *P. sparsa.* In Finland, Hukkanen *et al*. (2006) developed a quantitative real-time PCR method for the detection of *P. sparsa* in Rubus species and roses.

Gomez (2014) used a thermographic approach to identify infected rose material prior to symptom expression and to study the progress of the disease.

Control of rose downy mildew has been the subject of HDC research projects (O'Neill, 1994; O'Neill, 2009; Thomas, 2009) demonstrating the effectiveness of a number of different products (fungicides, biostimulants and natural products) and investigating their use in spray programmes. The results of the 2009 work were communicated to growers in factsheet 15/09.

Chase and Daughtrey (2013) summarise the results of fifteen trials carried out in the US against rose downy mildew in the previous fifteen years. Many of the active ingredients rated as 'good, very good or excellent' have also performed well in UK trials on *P. sparsa*, with some active ingredients (for instance metalaxyl, azoxystrobin, mandipropamid and boscalid + pyraclostrobin) registered in the UK. Effective active ingredients that have not been evaluated in the UK against *P. sparsa* included cyazofamid, and dimethomorph + ametoctradin (although a UK product containing dimethomorph + ametoctradin was evaluated with some success against downy mildews of *Geum* and *Hebe* (O'Neill, 2014b)). It

should be borne in mind that US fungicide products will often contain different rates and formulations of active ingredients to those used in the UK.

Aegerter *et al*. (2002) had some success in reducing levels of rose downy mildew by dipping hardwood rootstock cuttings in mefenoxam (metalaxyl-M). Hot water dips were also sometimes effective but further work was recommended, to determine temperature and treatment times that were optimal for control of the pathogen without causing damage to the plant tissues.

Other alternative treatments to fungicides, not used in UK trials but evaluated overseas with some success against *P. sparsa*, include electrolysed oxidising water (Fernandez *et al*. 2011), chitosan (Wojdyla, 2004) and acibenzolar-S-methyl (Yang *et al*. 2013).

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Senecio cineraria White Blister

White blister (sometimes known as white rust or white blister rust) can cause extensive damage to the leaves of the bedding plant *Senecio cineraria*. While this plant is more correctly named *Jacobaea maritima* the name *S. cineraria* will be used here as it is still in common usage. The precise financial impact caused by this disease is unknown and there has been little in the way of research on the epidemiology or control of white blisters of ornamental plants.

Blister-like pustules develop on the leaves, predominantly on the underside, bursting open to produce numerous powdery spores that appear white *en masse*. In severe attacks the leaves can turn yellow and shrivel. Related pot plants such as florist's cineraria (*Pericallis x hybrida*) and Gerbera can also be affected by white blister, although due to extensive and ongoing revisions of both the identity and the host ranges of the white blister pathogens it is currently unclear whether the same species is found on these plants as that on *S. cineraria*.

Thines and Spring (2005) transferred the white blister pathogens of the *Asteraceae* and some other plants into a new genus: Pustula*.* The white blister pathogen of *S. cineraria* is currently

known as *Pustula* sp. (Ploch *et al.,* 2011; Rost and Thines, 2012). It was known previously as *Pustula tragopogonis*, and before that as *Albugo tragopogonis*. The precise identification and host ranges of white blister pathogens is currently in a state of considerable flux as a result of ongoing work into both the genetics and morphology of the pathogens. For many years the white blister disease of plants such as *Senecio cineraria* in the family *Asteraceae* was ascribed to *Albugo tragopogonis.* It was assumed to have a host range in excess of 300 plants, although host specialisation was known to occur (Whipps and Cooke, 1978b).

Pustula on Senecio acts in a similar way to other white blister pathogens, producing zoosporangia (the white spores) that germinate on the leaves under wet conditions to produce infectious swimming spores (zoospores). It therefore follows that avoidance of extended periods of leaf wetness is likely to reduce the amount of infection. Optimal temperatures for germination of the zoosporangia are 10-15°C (Whipps and Cooke, 1978a). Resting spores (oospores) have been found within the tissues of a range of affected hosts, but their role in the survival and spread of white blister on *S. cineraria* has not been investigated. White blister pathogens of many hosts are known to be seed-borne, but again no specific information can be found for *S. cineraria.*

Based on the genetic analyses carried out so far it is likely that what were thought to be host-specific races may in many cases turn out be new species; Thines and Voglmayr (2009) mention the possibility of a 'plethora of unknown species'. White blister of sunflower, thought for many years to be caused by *Pustula* (*Albugo*) *tragopogonis*, has already been identified as a new species, *Pustula helianthicola* (Rost and Thines, 2012). Ploch *et al* (2011) found that isolates of *Pustula* obtained from Senecio species (including *S. cineraria*) formed a distinct genetic lineage from isolates obtained from a range of other ornamental genera from the same family. These developments mean that at present it is not possible to state with certainty whether cross-infection could occur between white blister on *S. cineraria* and related cultivated or wild hosts in the *Asteraceae*. Caution must also be applied when extrapolating from research into white blister on other hosts in this plant family.

Uncertainty over the taxonomy and host ranges of white blister fungi make it difficult to determine the role of alternative hosts as sources of inoculum. Species of Albugo have been shown to be asymptomatic endophytes in natural populations of *Brassicaceae* (and so could, conceivably, act as sources of inoculum to cultivated types).

No specific diagnostic tests or forecasting systems are currently available for Pustula on Senecio species. It is possible that the Brassica$_{spot}$ forecasting system developed for white blister (*Albugo candida*) and other diseases of Brassicas may have some relevance for white blister pathogens of other crops, including *Pustula* on *S. cineraria*.

No records could be found of research evaluating fungicides or biological control products specifically against *Pustula* (or its previous incarnation *Albugo tragopogonis*) on *S. cineraria*. Products used on nurseries against this pathogen tend to be the same as those used against other oomycete pathogens such as downy mildews (e.g. those from the phenylamide and strobilurin groups). Lava *et al* (2015) found metalaxyl-M and azoxystrobin to be effective against the white blister pathogen of sunflower (as mentioned previously, now known to be a distinct species: *P. helianthicola*).

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Summary tables of common UK pathogens, knowledge areas and gaps

The potential economic losses to aerial oomycetes will vary widely between each of the host crops, with key factors including the age at which plants become affected and whether symptoms are on the marketable part of the crop and the damage tolerances. Once symptoms are seen on some plants then the decision can be taken to destroy the whole crop. In propagation there can be rapid spread across large numbers of plants. The sections on each crop disease gave further details on crop damage symptoms and tolerances. Information from the survey and industry contacts on potential maximum crop losses (if a preventative fungicide programme were not in place) and any literature sources is summarised in Table 2. Farm-gate prices are based on either the Defra "Basic horticultural statistics dataset" https://www.gov.uk/government/statistics/basic-horticultural-statistics-2014 for either 2013 or 2014 (not the projected year) or grower or agronomist information for crops not covered by the dataset. Information on the areas of production are available from the dataset. Standard area conversion formulas have been used for container ornamental crops not field grown.

Table 2. Aerial oomycete diseases affecting commonly grown edible and ornamental crops in the UK and farm-gate losses based on the highest estimated % crop loss if fungicide programmes were not in place. Losses will vary greatly with individual situations.

Crop	Pathogen	Disease	Estimated maximum potential loss (%)	Cost of loss (£/Ha)
Apple	*Phytophthora syringae*	*Phytophthora* post-harvest rot	88%	£11,988
Basil	*Peronospora belbahrii*	Downy mildew	50%	£400,000 (modules)
Beetroot	*Peronospora farinosa* f. sp. *betae*	Downy mildew	50%	£9,250
Blackberry	*Peronospora sparsa*	Downy mildew	>50%	>£35,000
Broad bean	*Peronospora viciae f. sp. fabae*	Downy mildew	50%	£1,361 processing
Broccoli	*Hyaloperonospora brassicae*	Downy mildew	100% (propagation)	£400,000
Broccoli	*Albugo candida*	White blister	100%	£6,910
Brussels sprouts	*Hyaloperonospora brassicae*	Downy mildew	100% (propagation)	£400,000
Brussels sprouts	*Albugo candida*	White blister	100%	£16,750
Bulb onion	*Peronospora destructor*	Downy mildew	75%	£8,150
Cabbage	*Hyaloperonospora brassicae*	Downy mildew	100% (propagation)	£300,000

Crop	Pathogen	Disease	Estimated maximum potential loss (%)	Cost of loss (£/Ha)
Cauliflower	*Hyaloperonospora brassicae*	Downy mildew	100% (propagation)	£400,000
Cauliflower	*Albugo candida*	White blister	100%	£4,650
Chives	*Peronospora destructor*	Downy mildew	50%	£400,000 (plugs)
Cucumber	*Pseudoperonospora cubensis*	Downy mildew	33%	£116,666
Kale	*Hyaloperonospora brassicae*	Downy mildew	100% (propagation)	£300,000
Leek	*Peronospora destructor*	Downy mildew	50%	£8,730
Leek	*Phytophthora porri*	White tip	>50%	£8,730
Mint	*Peronospora lamii* (sp. determination needed)	Downy mildew	50%	£400,000 (plugs)
Parsley	*Plasmopara petroselini*	Downy mildew	50%	£400,000 (plugs)
Pea (green)	*Peronospora viciae* f. sp. *pisi*	Downy mildew	50%	£673
Pear	*Phytophthora syringae*	Phytophthora fruit rot	33%	£2943
Rhubarb	*Peronospora jaapiana* (species determination needed)	Downy mildew	30%	£18,605
Rose	*Peronospora sp.*	Downy mildew	100%	£29,000 (HONS)
Sage	*Peronospora salvia-officinalis*	Downy mildew	5%	£40,000 (plugs)
Salad onion	*Peronospora destructor*	Downy mildew	100%	£14,740
Salad rocket	*Hyaloperonospora sp.*	Downy mildew	50%	£7500
Spinach	*Peronospora farinosa* f. sp. *spinaciae*	Downy mildew	100%	£15,000 (baby leaf)
Susceptible UK tree & shrub species	*Phytophthora ramorum*	Ramorum dieback	2% (notifiable so depends on Order)	£9,860 (container)
	Phytophthora kernoviae	Dieback	2% (notifiable so depends on Order)	£9,860 (container)
Antirrhinum	*Peronospora antirrhini*	Downy mildew	100%	£580,000
Aquilegia	*Peronospora sp.*	Downy mildew	100%	£288,000
Hebe	*Peronospora grisea*	Downy mildew	100%	£288,000
Impatiens	*Plasmopara constantinescui; Pseudoperonospora*	Downy mildew	100%	£580,000

Crop	Pathogen	Disease	Estimated maximum potential loss (%)	Cost of loss (£/Ha)
	cubensis; Plasmopara obducens			
Lisianthus (Eustoma)	*Peronospora chlorae*	Downy mildew	20%	£37,000
Nicotiana	*Perononspora hyoscyami f. sp. tabacina*	Downy mildew	50%	£144,000
Poppy	*Peronospora arborescens*; *P. argemones*, *P. cristata*; *P. meconopsidis*; *P. apula*; *P. somniferi*	Downy mildew	100%	£288,000
Pansy	*Peronospora violae*	Downy mildew	75%	£292,500
Viola	*Peronospora violae*	Downy mildew	60%	£234,000
Senecio cineraria	*Pustula sp.*	White blister	10%	£58,000

Table 3 summarises information from throughout the whole review for each of the pathogens that have been reported on. This gives a quick reference to the information already available for each disease including the availability of molecular diagnositics, observations of pathogen resistance to certain fungicides, the existence of resistant cultivars of the host and pathogen specificity. Whether or not there information is lacking on optimum growth conditions of the pathogens and the capability for disease forecasting is shown. This table therefore highlights some of the research gaps and shows where active research on the pathogen is still ongoing (or recent).

Table 3. Summary of some key knowledge areas on aerial oomycete pathogens found on horticultural crops in the UK

Pathogen and host	Active research	Molecular diagnostics developed? (not necessarily commercial)	Fungicide resistance observed	Optimum growth conditions identified	Resistant cultivars	Progress with biologicals	Forecasting	Host specificity	Cultivar specificity (races)
Phytophthora spp. (trees & shrubs)	Yes	Yes	No	Yes	Some information	No	No	Some information	No
Peronospora sp. (*Aquilegia*)	Yes	No	No	No	Unknown	No	No	Unknown	Unknown
Peronospora. grisea (hebe)	Yes	No	Possibly	Some	Unknown	Yes	No	Unclear	Unknown
Plasmopara. obducens (*Impatiens*)	Yes	Partly	Yes	Yes	No	No	No	Yes	Unknown
Peronospora chlorae (*Lisianthus*)	No	No	No	No	Unknown	No	No	Yes	Unknown
Peronospora hyosami f. sp. *tabacina* (*Nicotiana*)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Peronospora violae (pansy & viola)	Yes	Yes	No	Yes	Yes	No	No	Yes	Unknown
Peronospora spp. (poppy)	Yes	Yes	Yes	No	Yes	No	Yes	Multiple pathogen spp.	Unknown

Pathogen and host	Active research	Molecular diagnostics developed? (not necessarily commercial)	Fungicide resistance observed	Optimum growth conditions identified	Resistant cultivars	Progress with biologicals	Forecasting	Host specificity	Cultivar specificity (races)
Peronospora sparsa (rose)	Yes	Yes	No	Yes	Yes	Yes	Yes	Rubus as well as rose	Unknown
Peronospora antirrhini (*Antirrhinum*)	Some	No	Yes	Yes	Some information	Yes	In part	Yes	No
Pustula sp. (*Senecio*) white blister	Yes	No	No	No	No	No	No	Uncertain (possibly multiple spp.)	Unknown
Peronospora sparsa (*Rubus*)	Yes	Yes	No	Yes	Yes	Yes	Prediction model available	Unconfirmed – geographical specialisation suggested in *Rubus* sp.	Unknown
Pseudoperono-spora cubensis (cucurbits)	Yes	Yes	Yes	Yes	Yes	Yes	Not for UK cucurbits grown under protection	No evidence to suggest narrow host range	Several races identified
Peronospora destructor (onion)	Yes	Yes	Yes	Yes	Yes	Limited	Yes	Unconfirmed	Unknown
Peronospora viciae f. sp. *pisi* (pea)	Yes	In development	Yes	Over 45 years ago – need re-evaluating	Yes – race specific	Limited	No	Cultivar specific	Yes

Pathogen and host	Active research	Molecular diagnostics developed? (not necessarily commercial)	Fungicide resistance observed	Optimum growth conditions identified	Resistant cultivars	Progress with biologicals	Forecasting	Host specificity	Cultivar specificity (races)
Peronospora viciae f. sp. *fabae* (Faba bean)	Unknown	In development	No - but reliant on **one** EAMU	No	Limited	No	Yes	Yes	Unknown
Hyaloperonospora sp. (salad rocket)	unknown	Yes	No	No	No	No	No	Unconfirmed	Unknown
Hyaloperonosporab rassicae (vegetable Brassicas)	Yes	Yes	Yes	Yes	Limited	Yes	No	Unconfirmed – increasing evidence of phylogenetic distinction	Yes
Peronospora jaapiana (rhubarb)	Unknown	No	No	No	Unconfirmed	No	No	Unconfirmed	Unknown
Peronospora farinosa f. sp. *betae* (beetroot)	Unknown	Yes	No	Yes	Yes	No	No	Unconfirmed	Unknown but races reported for *P. farinosa* f. sp. *spinaciae*
Albugo candida (veg. Brassicas) w. blister	Yes	Yes	Yes???	Yes	Yes	Yes	Yes	Isolate dependent	Yes
Phytophthora. syringae (apples & pears) fruit rot	Unknown	No	No	Yes	No	No	No, but risk of post-harvest rot can be predicted	Unconfirmed	Unknown
Plasmopara petroselini (parsley)	Unknown	No	No	Some work done (FV 390) – more needed	Limited	No	No	Unconfirmed (could corn parsley be an alternate host?)	Unknown

Pathogen and host	Active research	Molecular diagnostics developed? (not necessarily commercial)	Fungicide resistance observed	Optimum growth conditions identified	Resistant cultivars	Progress with biologicals	Forecasting	Host specificity	Cultivar specificity (races)
Peronospora belbahrii (sweet basil)	Yes	In development	No	Yes	Potentially in near future	No	No	Numerous *Ocimum* spp.	Unknown
Peronospora salvia-officinalis (sage)	Unknown	No	No	Some work done (FV 390) – more needed	Limited	No	No	Species specific	Unknown
Peronospora lamii (mint)	unknown	No	No	No	No	No	No	Unconfirmed	Unknown
Peronospora porri (leek)	Yes	Yes	Yes	Yes	Yes	In progress	No	Alliums, but leek isolates thought to be a distinct group	Leek isolates may be a distinct group –could be evidence of race

AHDB Funded Research on Aerial Oomycete Pathogens (Edible Crops)

Table 4. A Review of HDC/AHDB funded research on aerial oomycetes (Edible Crops) 1996-2015

Star ratings **DO NOT** reflect the quality of the work carried out. They merely reflect whether or not the objectives set out at the start of the project were achieved. Not achieving objectives is often down to the unpredictability of living systems – for example a disease only being present at low levels during the time of study – **NOT** due to poor work.

*	objectives largely not achieved
**	some/most objectives achieved
***	vast majority of objectives achieved

Report	Objectives	Any specific pathogen host interactions?	Objectives achieved?	Comments (what next)
FV 053e - Brassicas: Further development of a spray-timing model for white blister (*Albugo candida*) in vegetable Brassica crops within the Brassica$_{spot}$ system (Kennedy, 2005)	• Evaluate a disease forecasting model - time sprays to control white blister • Programme into Brassica$_{spot}$ disease forecasting suite of models (within MORPH) • Insight into development time for white blister	White blister on vegetable Brassicas	**	• Rapid symptom development between 20-24^{o}C identified; No symptoms at <8^{o}C • Forecasting model developed using MORPH standards so that it is fully integrated into the MORPH framework • Addition of disease development forecasts for white blister to Brassica$_{spot}$ (within MORPH) – coordinate multiple crop treatments • Limited validation of white blister model due to time constraints

CP 099 - Diagnostics: Validation of the lateral flow detection devices for the light leaf spot and powdery mildew vegetable Brassica pathogens and testing of white blister detection test prototypes (Wakeham, 2015a)	• Measure spore concentrations in field aerosol samples for light leaf spot, powdery mildew and white blister. And evaluate the effect on infection and symptom development in commercial Brassica cropping systems • Provide tests which can be used directly (in field tests by UK growers or consultant) or indirectly (laboratory analysis) to identify presence of these three diseases in the air. Identify the spore concentrations likely to cause disease at a commercial scale. • Ability to detect white blister, Brassica powdery mildew and light leaf spot in field bioaerosols before disease is visible in the crop. • Improved use of fungicide applications within vegetable Brassica production systems and the reduced likelihood of tebuconazole resistance within light leaf spot	Light leaf spot, powdery mildew, and white blister on Brassicas	**	• An in-field lateral flow test for daily testing of crop based bioaerosols has been used successfully in conjunction with the MORPH Brassica Spot system to identify when commercial Brassica crops are at risk to White blister disease. • A laboratory ELISA has been developed giving participating growers a weekly disease risk of light leaf spot and white blister disease from MTIST collected field bioaerosols. Risk thresholds for both pathogens have been developed during this project. • In Scotland, the system has been used in a commercial cropping system for the timed application of light leaf spot control measures. Good control has been achieved with minimal pesticide application.

	populations (already been reported). • Assess the potential to develop a multiplex test to identify risk of multiple pathogens on a single test device			
CP 099b - Evaluate the Horticultural Industry requirement for on-site diagnostic tests for crop pathogens and their use within Disease Management Systems (Wakeham, 2013)	• Evaluate the UK Horticultural Industry requirement for on-site diagnostic tests to monitor crop pathogens and their use within Disease Management Systems.		***	• A comprehensive review
CP 099c - Bulb and Salad Onion: Evaluation of an integrated disease management system to ascribe risk of downy mildew disease on commercial crops in the UK (Wakeham, 2015b)	• Provide validation of the onion downy mildew 'in field' lateral flow tests in onion crops to help reduce fungicide inputs • Use of 'in field' tests (lateral flows) will be evaluated in commercial cropping systems for their accuracy in monitoring airborne downy mildew disease transmission events • Assess the benefit of applying fungicides in	Downy mildew on bulb and salad onions	***	• The timed application of downy mildew controls according to bioaerosol concentrations of *Peronospora destructor* reduced crop protection inputs by 50% and provided either the same or increased levels of disease control. • This strategy should reduce the reliance on mancozeb-based fungicides, which are being withdrawn • Using this approach will help growers satisfy the Sustainable Use Directive (SUD) by demonstrating alternate Integrated Pest Management (IPM) measures for control of downy mildew

	coordination MILIONCAST and lateral flow tests			
FV 172 - Leeks: control of white tip (*Phytophthora porri*) (Locke, 1996)	• Evaluate a range of fungicides/control measures for their efficacy including a range of new potato blight products, and a physical barrier control system using straw mulch	White tip on leek (*Phytophthora porri*)	***	• 'Invader' was identified as the best candidate to pursue for specific off-label approval • One trial highlighted the overwhelming presence of metalaxyl-resistant strains of *Phytophthora porri* at that site • Use of a straw mulch as a physical barrier to prevent leaf infection from soil-borne inoculum proved ineffective due to decay • Metalaxyl-resistance may be responsible for problems with control and growers should avoid the production of leeks in fields where this fungicide has been extensively used – needs further investigation
FV 226a - Red beet: further elucidation of the cause, epidemiology and control of root malformation disorder (RMD) (McPherson, 2003)	• Elucidate the primary cause of RMD using a series of field-scale trials • Evaluate the efficacy of a soil sterilisation treatment in conjunction with a range of novel and existing fungicides • Carry out a literature search in an attempt to determine whether or not downy mildew on wild *Chenopodiaceae* can also infect commercial beet crops	Downy mildew on Red Beet leading to Root Malformation Disorder (RMD)	**	• Substantial evidence that systemic infection with downy mildew is responsible for RMD • Literature search found that *P. farinosa* isolates are host specific and wild *Chenopodiaceae* are unlikely a source of infection for commercial crops. • None of the fungicides tested showed particularly effective control of downy mildew and both trial sites were effected by other diseases • Evidence that RMD symptoms had been suppressed by soil sterilisation, suggesting a possible soil borne component to the disorder

FV 226c - Red Beet: Further Elucidation of the Cause, Epidemiology and Control of Root Malformation Disorder (RMD) (McPherson, 2004)	• Evaluate a range of fungicides for RMD control in terms of their efficacy and timing • fully integrate a PCR technique for quantifying the downy mildew pathogen in distorted roots	Downy mildew on Red Beet leading to Root Malformation Disorder (RMD)	*	• Little success in fungicide trials due to very low levels of the pathogen in beet crops during 2004 attributed to a warm, dry spring • One trial did provide some indication that oomycete fungicides may have a significant effect at reducing the number of roots with RMD • Both trials eventually abandoned • Molecular testing during the growing season correlated RMD with the presence of downy mildew biomarkers however the testing is for *Peronospora* sp. not specifically for *P. farinose* • Project extended – see FV 226d
FV 226d - Red Beet: Further Elucidation of the Cause, Epidemiology and Control of Root Malformation Disorder (RMD) (McPherson, 2005)	• Undertake a replicated fungicide timing trial in a high risk unsprayed beet crop (in the hope that RMD would be problematic) • Undertake cross-reaction studies with the molecular PCR test to see if positive reactions were gained against other fungi commonly found on red beet, particularly other oomycetes • To validate and use the molecular PCR test to check seed-lots of commercial red beet for	Downy mildew on Red Beet leading to Root Malformation Disorder (RMD)	*	• Lack of disease in 2005 hampered the fungicide trial and no conclusions could be made • Lack of disease also prevented the molecular testing of crop samples • Downy mildew DNA was identified in all of the seed-lots tested however the test requires further validation and therefore firm conclusions could not be made • Still unable to confirm with 100% certainty that RMD is a result of systemic infection by downy mildew

	the possibility of seed-borne downy mildew.			
FV 316 - Baby leaf crucifers: Improving control of downy mildew (Gladders, 2009)	• Evaluate cultivars and selections of the major types (wild and salad) of rocket for susceptibility to downy mildew • Evaluate the efficacy of downy mildew seed treatments • Investigate the influence of crop covers on downy mildew development in rocket • Develop a molecular diagnostic test for seed-borne downy mildew in rocket and determine the occurrence of downy mildew in seed stocks	Downy mildew on rocket	***	• Varietal resistance has potential to provide good control of downy mildew in wild rocket • Downy mildew was less severe in salad rocket than in wild rocket yet there were no significant differences in downy mildew severity between varieties • Promising results for successful seed treatment control of downy mildew however seed treatments appear to be unable to protect crops against late downy mildew epidemics - more work is needed • Phytotoxic effects were caused by seed treatments in both wild and salad rocket experiments • Enviromesh, Ultrafine and Fleece covers provide an acceptable balance of features by reducing pest damage, increasing yield (or earlier harvest dates) whilst slightly increasing downy mildew risk • A molecular (PCR) diagnostic test detecting seed-borne downy mildew in wild and salad rocket has been developed using nested PCR and this is available for use by breeders and growers
FV 390 - Outdoor herbs: epidemiology and control of downy mildew in sage, parsley, mint and basil under protection	• Determine the environmental conditions posing the greatest risk for downy mildew infection	Downy mildew on sage, parsley, mint, and basil	*	• Progress regarding optimal environmental conditions for disease development but more work is needed to validate (repeated experiments failed due to absence of

(Wright, 2014)	• Develop a forecasting model based on the above • Determine whether disinfestation of crop debris and soil can mitigate against infection • Assess efficacy of control measures against parsley and basil downy mildew			suitable inoculum) – no forecasting model developed • Current fungicides appear to have limited success once the disease is established in these crops • Assessment of pathogen persistence in soil and crop debris largely unsuccessful – results inconclusive • In sage, the pathogen may persist in the woody tissue making environmental conditions less significant for initial infection but likely still play a role in disease development – more work needed • Fungicide treatment of soil and crop debris unsuccessful in suppressing infection – suggests limited role for inoculum from this source • Fungicide programme efficacy in small pot trails was unsuccessful due to lack of inoculum
FV 436 - Pea Downy Mildew diversity in the UK (Maguire, 2015) Expected completion date – March 2018	• Provide information about downy mildew race structure • Assess geographic spread in the UK • Assess varietal resistance to different races of downy mildew	Downy mildew on pea	**ONGOING**	• Few actively sporulating samples received in 2014 due to low disease presence limited the capacity to identify races and build an isolate collection • A literature review identified lines showing partial or strong resistance to downy mildew • Seed multiplication has been carried out on potentially resistant lines

FV 356 - Onions: Further development and calibration of detection tests for conidia of onion downy mildew in combination with the Morph forecast model MILIONCAST (Kennedy, 2012)	• Develop a 10 minute in-field detection system to monitor airborne concentrations of onion downy mildew disease inoculum	Downy mildew on onion	***	• Critical date for applying fungicides can be determined by using both environmental forecasting and in-field spore concentration testing • Disease potential can be identified prior to symptom development • Precisely timed applications could reduce inputs and enhance control • Lateral flow tests to become commercially available by 2014
FV 189a - Onions: development of detection systems for conidia of *Peronospora destructor* (downy mildew) in onion crops (Wakeham and Kennedy, 2006)	• Enable better detection of onion downy mildew in the field before disease is visible in the crop • Develop detection tests which can be used "in field" to determine the level of risk to the onion crop posed by onion downy mildew	Downy mildew on onion	***	• "in field" tests for conidia of onion downy mildew were developed utilising antibodies • Tests for pathogenic inoculum can be carried out in the field (using lateral flow devices), therefore the system meets the criteria necessary for its uptake by the onion industry • See FV356 and CP099c for progress in this area
FV 189b - New Products for the Control of Downy Mildew (*Peronospora destructor*) in Bulb and Salad Onions (Richardson, 2006)	• Compare existing and new actives for the control of downy mildew on onions	Downy mildew on onion	**	• Mancozeb or mancozeb based products afforded the best control of onion downy mildew, particularly for severe disease • The study found that the then commercial standard, was not significantly different from the water control at one of the sites • Extended – see FV 189c

FV 189c - New Products for the Control of Downy Mildew (*Peronospora destructor*) in Bulb and Salad Onions (Richardson, 2007)	• Evaluate four new products for efficacy against Downy Mildew • Evaluate three new products identified in FV189b in commercially comparative spray programmes for efficacy against Downy Mildew • Assess a silicone wetter and a wax based adjuvant and determine their effect on Downy Mildew susceptibility • Evaluate the effectiveness of two new resistant bulb onion varieties against Downy Mildew	Downy mildew on onion	*	• Low levels of downy mildew at all three sites meant that there were no significant differences between either individually applied fungicide products or fungicide programmes • A new coded product UK958 showed promise at all three trial sites • Resistant variety BGS from Bejo Zaden showed lower levels of downy mildew infection than the commercial standard Red Baron but is late maturing making its suitability in the UK questionable • Results for both the wetter and the wax varied between sites with no effect observed at 2 sites and a minor positive effect observed at the other
SF 085 - Blackberry: evaluation of fungicides for improved control of downy mildew and purple blotch (O'Neill, 2010)	• Evaluate a range of fungicides for downy mildew control • Devise and test sustainable spray programmes	Downy mildew on blackberry	**	• Numerous treatments identified which reduced downy mildew on container grown plants, including various fungicides, potassium phosphite, and a wetter • Lack of disease in the third year prevented the evaluation of spray programmes
FV 284 - Improving the value of downy mildew resistance information for UK spinach growers	• Carry out independent assessment of R gene content in various cultivars • Predict the risk of attack on different varieties in	Downy mildew on spinach	**	• Resistance claims for spinach varieties are reliable. However growers need to remain aware that new races continue to emerge that could rapidly overcome cultivar resistance • 2 new races were detected over the course of the 3 year study

(Thomas, 2009)	the main UK production areas			• Very few samples were received from growers • Some varieties although predominantly resistant, saw a variable number of plants show susceptible reactions
FV 402 - Brassicas: pre-adaptation of seedlings for increased resistance to pest and pathogen attack (Mulholland, 2013)	• Summarise current approaches to downy mildew control • Assess physiological and growth response of untreated and pre-adapted plants challenged with downy mildew • Quantify resistance of pre-adapted seedlings to selected levels of downy mildew inoculum	Downy mildew on Brassica	*	• Pre-treatment with NaCl had limited effect on plants ability to resist infection from downy mildew • Refining the pre-adaptation process may improve increase the potential for non-chemical control of downy mildew • Project primarily focussed on CRF rather than downy mildew
SF 099 - Sustainable control of crown rot (*Phytophthora cactorum*) in strawberry (Berrie, 2011)	• Develop an integrated sustainable approach for control of strawberry crown rot based on cultural controls, fungicide treatments, alternative chemicals and biological treatments.	Crown rot (*Phytophthora cactorum*) in strawberry	**	• Revus, Ranman, and Fenomenal applied as one spray or drench, significantly reduced the incidence of crown rot compared to the untreated control and were as effective as the standards Aliette and Paraat • The biocontrol agents Serenade and Prestop showed no significant difference compared to the untreated controls • An integrated approach was not able to be assessed due to the lack of disease in the first year which meant the experiments had to be repeated in the second
FV 215 - Vining Peas: Downy mildew control	• Evaluate field resistance of current varieties of vining peas	Downy mildew on vining peas	**	• Field trials at locations with a high risk of disease, and artificially inoculated propagation trials found that Barle, Kermit

(Biddle, 2000)	• Compare seed treatments for ability to control downy mildew • Compare foliar treatments for ability to control downy mildew			and Pinnacle varieties showed the lowest levels of infection • For seed treatment comparisons Apron Combi, which contains metalaxyl as the active ingredient for mildew control, gave poor control compared with Apron Elite (cymoxanil + oxadixyl) and Triple Pea (fosetyl aluminium) potentially highlighting the presence of metalaxyl resistance • In the foliar tests there were no consistent reductions of mildew from any of the treatments
FV 293 - Evaluating new fungicides for the control of downy mildew on spinach (Thomas, 2007)	• Establish a comparative test of a number of new products for effectiveness against downy mildew	Downy mildew on spinach	***	• The most effective products overall were 'BUK 98800' (boscalid plus pyraclostrobin), now available off label as 'Signum' (outdoor spinach); 'EXP 11047' (propamocarb & fosetyl-al) and 'Folpet' (phaltan) • While differences between products were small, 'BUK 98800' gave the largest improvement in marketable yield. • Only a single spray was used in the experiment to allow clear differentiation between products and levels of disease at harvest were therefore higher than would be expected with commercial fungicide practice.
FV 313 - Brassicas: Integrating fungicide usage with risk assessment for ringspot, dark leaf spot and white blister	• provide information on the effect of application time post-infection in combination with dosage and product type on the effectiveness of fungicide applications against dark	White blister on Brassicas	***	• Spray timing trials using the infection and symptom development model in MORPH demonstrated that it can be used to effectively control white blister in crops of Brussels sprouts whilst reducing the numbers of spray applications

(Kennedy, 2010)	leaf spot, ringspot and white blister			
FV 357 - Outdoor lettuce: evaluation of novel fungicides for downy mildew control (Gladders, 2010)	• To confirm methods that ensure consistent development of lettuce downy mildew in screening experiments using artificial inoculation with *Bremia lactucae* • To determine the crop safety and activity of novel and standard fungicides against lettuce downy mildew • To define the dose response activity of the most promising products and • To quantify the persistence of products, to guide timing of treatments.	Downy mildew on lettuce	***	• Trial set up ensured consistent development of downy mildew disease • Previcur Energy, Revus, Signum and Valbon were most effective at reducing disease incidence and severity, with Invader and coded product HDC F3 being moderately effective. • There was a significant effect of timing, irrespective of fungicide treatment. • Disease incidence was not affected by halving fungicide dose. For disease severity, Invader and Valbon were more effective when applied at half dose, while efficacy of Previcur Energy, Revus and Signum was unaffected when the dose was halved. • At spray intervals of 10 and 14 days, all products reduced downy mildew incidence to <50% for up to 20 days. • Under high disease pressure, 10 day intervals are likely to be more robust.
CP 077 - Sustainable crop and environment protection – targeted research for edibles (SCEPTRE) (O'Neill, 2015)	• Identify effective plant protection opportunities with the potential to fill current gaps and to develop integrated pest, disease and weed management programmes compliant	Wide range of systems covered – those of interest to this study include: Downy mildew on Brassicas	***	• Over the project life, a total of 92 conventional synthetic plant protection products and 67 biopesticides were evaluated. • Potential new plant protection products were identified for all the priority disease, pest and weed problems examined. • A biofungicide with treatment efficacy equal to the reference synthetic

	with the new Sustainable Use Directive.	Downy mildew on onion		conventional fungicide was identified for Brassica downy mildew • Cassiopeia (test code 24) was registered during the project's life with on label approval for use on bulb onions to treat downy mildew. • Infinito (test code 20) shown affective against *Peronospora destructor* and now has an EAMU (1142/2015) for use on bulb onion. • There was a demonstrable benefit of multiple (3 or 4) different actives in each spray application for control of spring onion downy mildew, rather than using a single active

Table 5. A Review of HDC/AHDB Funded Research on Aerial Oomycetes (Ornamental Plants) 1996-2015

Star ratings **DO NOT** reflect the quality of the work carried out. They merely reflect whether or not the objectives set out at the start of the project were achieved. Not achieving objectives is often down to the unpredictability of living systems – for example a disease only being present at low levels during the time of study – **NOT** due to poor work.

*	objectives largely not achieved
**	some/most objectives achieved
***	vast majority of objectives achieved

Report	Objectives	Any specific host-pathogen interactions studied	Objectives achieved?	Comments (what next)
HNS 079 – Hebe: control of downy mildew on container-grown plants (O'Neill, 2000)	• Evaluate new fungicides in comparison with standard products, and to develop a spray programme providing effective and reliable control.	Hebe downy mildew	***	• Fungicide spray programmes developed and evaluated • Cultural control through plant spacing and air circulation investigated • Possible (not confirmed) presence of metalaxyl-resistant strain • Report suggests further work required to investigate relationship between leaf wetness duration and infection

HNS 186 – Control of downy mildew on shrub and herbaceous plants (O'Neill, 2014)	• Determine the effectiveness of selected novel fungicides and biofungicides • Devise and determine the effectiveness of some simple alternating programmes • Screen novel fungicides and biofungicides with good potential for control of downy mildew diseases for their safety to a range of susceptible ornamentals	Hebe downy mildew Geum downy mildew	***	• Programmes developed including use of fungicides, coded biological controls and phosphite fertiliser • Two new EAMU's obtained as a result of the trials • Crop safety evaluated • Hebe trials had low levels of infection, products therefore not tested on hebe under high disease pressure
PC 230 – Detection and control of downy mildew of ornamentals (Jennings, 2009)	• Develop a sensitive molecular method for detection of downy mildews, especially *Plasmopara obducens* and *Peronospora violae,* in seed/young plants. • Evaluate the safety and efficacy of a range of fungicides for effective disease prevention and control. • Develop an integrated GHP (Good	Downy mildew on impatiens	**	• TaqMan PCR test originally developed for downy mildew of red beet shown to detect impatiens d.m. DNA in seeds and plant material • Crop safety tests carried out • Unable to carry out efficacy tests on impatiens d.m. due to lack of pathogen isolates and infected host material

	Horticultural Practice) strategy which minimises the resistance risk and which can be quickly adopted by seed-houses, propagators/plug raisers, growers and commercial end-users of plants.	Downy mildew on pansy		
PC 230a – Control of downy mildew (*Plasmopara obducens*) an economically important foliar disease on impatiens (Jennings, 2012a)	• Evaluate the efficacy of a range of fungicides for control of infection by *P. obducens* on impatiens	Impatiens downy mildew Pansy downy mildew	***	• Range of products evaluated for protectant and eradicant activity • Fungicide programmes evaluated • Metalaxyl-M resistant isolates detected
PC 230b – Source of downy mildew (*Plasmopara obducens*) infection on impatiens (Jennings, 2012c)	• Gain a better understanding of the epidemiology and biology of impatiens downy mildew, especially in relation to the risk posed by potential sources of infection, in particular from seed-borne infection and oospore survival.	Impatiens downy mildew	**	• Impatiens d.m. DNA detected in seed and tissues of subsequent plants • No visible infection resulted when plants were raised from affected seed lots • Oospores demonstrated to overwinter under UK conditions • Significance of oospores could not be investigated as they could not be germinated

PO 011/11a – Monitoring metalaxyl-M sensitivity in impatiens downy mildew isolates from 2012 infections (Jennings, 2012b)	• As per title of project	Impatiens downy mildew	**	• Isolates tested during 2012 were sensitive to metalaxyl-M • Difficult to draw conclusions due to small sample size (10) • Monitoring of isolates will now continue until 2018 (as ongoing project PO 011b); no isolates received in 2013, 2014 isolates (5) a mixture of resistant and sensitive
PO 012 – Evaluation of the non-metalaxyl-M based fungicides/programmes against metalaxyl-M resistant strains of *Plasmopara obducens* (Jennings, 2013)	• As per title of project	Impatiens downy mildew	***	• Fungicide programmes developed that provide good (although not total) control of the metalaxyl-M resistant strain
PC 179 – Lisianthus (*Eustoma*): Control of downy mildew (*Peronospora chlorae*) (O'Neill, 2003)	• Evaluate existing and novel fungicides for the control of *P. chlorae* and to provide grower guidelines for the use of the most effective and crop-safe chemicals.	Lisianthus downy mildew	**	• (Fungicide spray programmes developed and evaluated) • (Cultural control through plant spacing and air circulation investigated) • (Report suggests further work required to investigate relationship between leaf wetness duration and infection)
HNS 053 – Container-grown roses: control of downy mildew by manipulation of cultural factors and timely use of fungicides (O'Neill, 1994)	• Evaluate a range of fungicide sprays and drenches for efficacy and crop safety • Investigate the effect of plant spacing on	Rose downy mildew	***	• Effective products (several no longer available) and programmes identified • Basic information obtained on effects of spacing and orientation according to prevailing wind direction

	development of downy mildew			
HNS 135 – Container-grown rose: evaluation of natural products for prevention and control of downy mildew (*Peronospora sparsa*) and improved shelf life (O'Neill, 2007)	• Evaluate biostimulants and natural products for prevention and control	Rose downy mildew	***	• Some products identified with activity against rose d.m. Potassium phosphite (with wetter) gave equivalent control to fungicides at low-moderate disease pressure, but less effective at high pressure.
HNS 150 – Managing downy mildew epidemics in rose by early detection and treatment of infection sources (Thomas, 2008)	• Identify potential sources of downy mildew in production environments • Identify and evaluate potential new fungicide products • Investigate the potential of varietal resistance	Rose downy mildew	**	• PCR used successfully to detect pathogen DNA in leaves, petioles, stems, roots (but not budwood) • No commercial or on-site rapid test yet available for growers to test propagation or suspect material • New fungicides evaluated – Valbon & Signum most effective • Differences in varietal susceptibility demonstrated
HNS 173 - Epidemiology and prediction of rose downy mildew (Xu, 2013)	• Develop a prediction system for rose downy mildew • Evaluate the system in practice	Rose downy mildew	**	• Standalone computer programme for disease prediction developed. • Possible 25% reduction in fungicide use against powdery mildew demonstrated as a result of prediction system for that disease. More difficult to predict benefit against downy mildew due to more sporadic nature of the disease • Not validated against downy mildew in field due to unfavourable weather conditions • Advised not to time sprays based on downy mildew predictions until validations done

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Grower survey responses

Growers returned 18 completed questionnaires. Over 30 different propagation and over 50 different post-propagation crop systems were reported on (indoor and growing outdoor systems of the same crop are classed as two separate crop systems) with regards to problems to aerial oomycete pathogens and are summarised in Table 6. Information was obtained via links to the form sent out via the AHDB Horticulture mailing system in additon to the survey form being available to all members visiting the AHDB website. Growers and advisors subscribing the ADAS Crop Technical Notes, and ADAS clients were also reminded of the survey. Additional information was obtained from a further 10 sources such as consultants who for various reasons did not complete a questionnaire but still provided valuable information.

The majority of reports were of downy mildews. One nursery reported having had nursery stock infected by a notifiable *Phytophthora* (most likely to have been *P. ramorum* and/or *P. kernoviae*). When growers were asked to give an indication for each of the diseases they had named of its frequency of occurrence and the severity of crop loss experienced (using a 0 to 5 index, see Appendix 3), and also what the potential scale of the problem could be, the vast majority of growers viewed various aerial oomycete diseases as a serious concern. Growers often said that the diseases were common, and occasionally a problem when present (index 3) and consistently said that crop damage would potentially be common and often lead to economic damage (index 5) if they did not have their fungicide spray programmes in place. Information on the severity of any crop losses provided by growers was utilised in Table 2.

Table 6. List of propagation and post-propagation crops in the UK reportedly affected by various aerial oomycete pathogens according to the survey responses by growers in 2016

Crops in propagation (and diseases reported)	**Post-propagation crops (and diseases reported)**	
	Indoor	**Outdoor**
Ajuga (downy mildew)	Acer (*Phytophthora*)	Aquilegia (downy mildew)
Blackberry (downy mildew)	Ajuga (downy mildew)	Baby leaf lettuce (downy mildew)
Brassicas (various)	Anemone (downy mildew)	Beetroot (downy mildew)
Buddleja (downy mildew)	Arabis (white blister)	Blackberry (downy mildew)
Ceanothus (*Phytophthora*)	Aquilegia (downy mildew)	Brussels sprouts (white blister)
Cineraria (downy mildew/white blister)	Blackberry (downy mildew)	Buddleja (downy mildew)

Crops in propagation (and diseases reported)	Post-propagation crops (and diseases reported)	
	Indoor	**Outdoor**
Fenugreek (downy mildew)	Buddleja (downy mildew)	Geum (downy mildew)
Geranium (downy mildew)	Cineraria (downy mildew)	Greens (downy mildew)
Hebe (downy mildew)	*Cornus controvelsa* (*Phytophthora*)	Hebe (downy mildew)
Helichrysum (downy mildew)	Digitalis (downy mildew)	Hellebore (downy mildew)
Herbs (various)	Erysimum (downy mildew)	Hops (downy mildew)
Hops (downy mildew)	Geum (downy mildew)	*Parthenocissus tricuspidata* (downy mildew)
Ilex (*Phytophthora*)	Hebe (downy mildew)	Peas – fresh pick (downy mildew)
Impatiens (downy mildew)	Lemon balm	Pointed cabbage (downy mildew)
Kale (white blister)	Lettuce	Ribes (*Phytophthora*)
Lemon balm	Nepita (downy mildew)	Rose (downy mildew)
Lettuce (downy mildew)	*Parthenocissus tricuspidata* (downy mildew)	Sage (downy mildew)
Nepita (downy mildew)	Pieris (*Phytophthora*)	Salad onion (downy mildew)
Pansy (downy mildew)	Poppy (downy mildew)	Spinach (downy mildew)
Papaver (downy mildew)	Prunus (downy mildew)	Vaccinium (*Phytophthora*)
Parsley (downy mildew)	Rhamnus (*Phytophthora*)	Viburnum (*Phytophthora*)
Parthenocissus tricuspidata (downy mildew)	Rhododendron (*Phytophthora*)	Wild rocket (downy mildew)
Prunus (downy mildew)	Rose (downy mildew)	Winter onion (downy mildew)
Rose (downy mildew)	*Salvia* spp. (downy mildew)	
Salvia spp. (downy mildew)	Strawberry (downy mildew)	
Scabiosa (*Phytophthora*)	Various Brassicas (downy mildew)	
Strawberry (downy mildew)	Verbascum (downy mildew)	
Tomato (*Phytophthora*)	Veronica (downy mildew)	

Crops in propagation (and diseases reported)	Post-propagation crops (and diseases reported)	
	Indoor	**Outdoor**
Veronica (downy mildew)	Viola (downy mildew)	
Viola (downy mildew)		
Winter onions (downy mildew)		

In order to aid the future dissemination of information from the current review, growers were asked which means of knowledge exchange they had found most useful to date for disease information. The number of growers who gave opinions and their ratings on how useful they had found each information source are shown in the charts comprising Figures 3a and 3b. Replies given per grower are summarised in Appendix 2.

Of the 18 surveys received, only five acknowledged the AHDB website as 'acceptable (score 2)' or 'good (score 3)' with the others either not giving a rating (suggesting perhaps that it was not used) or rating it as 'poor (score 1)' (giving a mean rating of 1.9). Some comments were also given stating that the website is not specific enough, is hard to use, and difficult to search. Few respondents commented on blogs, and those who did found them to be a poor source of information on diseases caused by aerial oomycetes.

Only eight surveys gave feedback for 'training courses' with an average rating where used of 1.88 ('acceptable' = 2). Comments included that they take up too much time for the benefit that growers get out of attending, that they are too infrequent and that they only cover a limited range of topics.

AHDB Factsheets and AHDB Grower magazine was rated highly by the growers with mean ratings of 2.25 (16 responses) and 2.14 (14 responses) respectively. Visits by specialists, where used, were rated joint top along with AHDB project reports by 13 growers, each having a mean rating of 2.46.

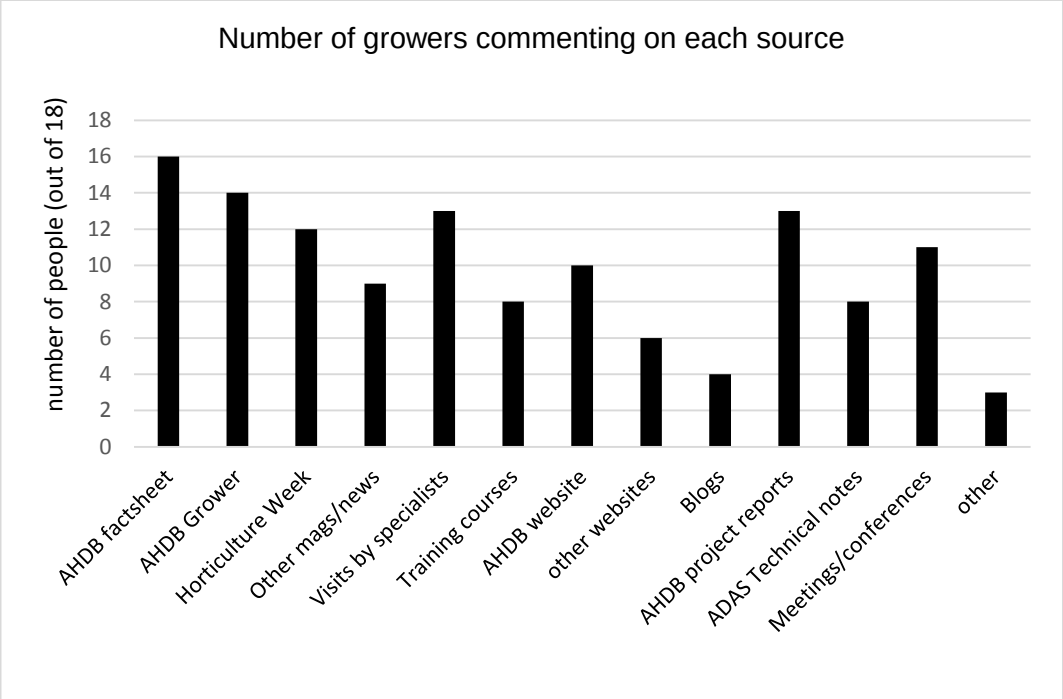

Figure 3a. The number of respondents who made comments on the usefulness to them of each knowledge source

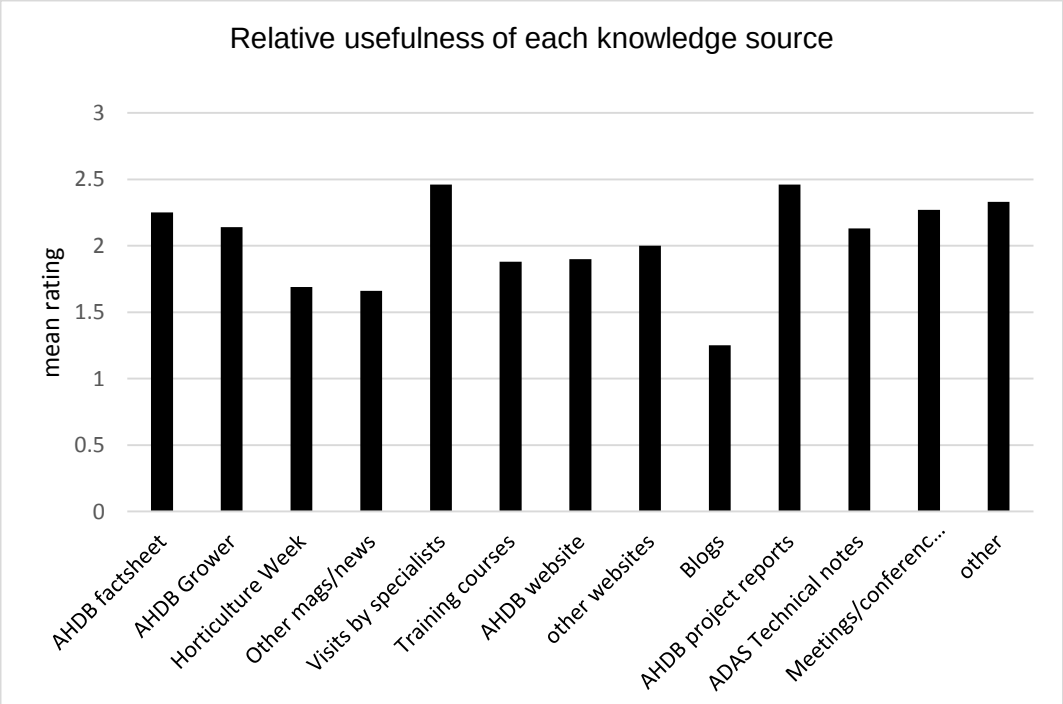

Figure 3b. The average usefulness (1 = poor, 2 = acceptable, 3 = good) of each knowledge source to survey respondents (the number of respondents commenting on a source is shown in Figure 3a)

Most growers were carrying out a full range of cultural control measures. Crop inspections were usually carried out by themselves or advisors, with visual inspections by advisors sometimes resulting in samples being sent for laboratory diagnosis. On-site diagnosis was not done and the type of any laboratory diagnosis used was not known.

In general, growers used preventative fungicides from across the range of Fungicide Resistance Action Committee (FRAC) groups, thus utilising a range of modes of action to reduce the chance of pathogens developing resistance to active ingredients. Products targeted against oomycetes included Fubol Gold (Syngenta; mancozeb (FRAC code M3) + metalaxyl-M (4)), Fenomenal (fenamidone (11) + fosetyl-aluminium (33); Signum (boscalid (7) + pyraclostrobin (11)), Revus (mandipropamid (40)), and Infinito (fluopicolide (43) + propamocarb hydrochloride (28)). Growers also used Horti-Phyte (potassium phosphite). There were no indications given of failures in chemical disease control.

Ware and salad onion downy mildew control was identified by two respondents as requiring improvement. Work in SCEPTRE has identified two fungicide products, Cassiopeia (BASF; dimethomorph (11) + pyraclostrobin (40)) and Infinito (Bayer; fluopicolide (43) + propamocarb hydrochloride (28)) which have since been approved for use on bulb onion; Cassiopeia has on label approval, Infinito has approval through EAMU 1142/2015.

Grower overview of potential issues with aerially sporulating oomycetes in propagation and methods used on a nursery for pathogen control.

Information on the cultural control of aerial oomycetes in propagation was provided in a telephone interview with Andrew Gretton of R.A. Meredith Nursery. This propagator mainly buys-in herbaceous plants as micropropagated plants, rather than as cuttings. Bedding plants are mainly grown from seed, with the remainder from cuttings. Vegetables are grown from seed at the nursery.

To reduce the risk of all diseases, the nursery concentrates on hygiene, careful selection/sourcing of seed and cuttings, rejection of poor material, careful damage-free production and giving the correct growing conditions.

Downy mildew

Problems can arise because of systemic infection in or on the seed, and in the cuttings used. Pansies have been grown from seed and shown systemic infection. Nicotianae are not now grown at this nursery because it was believed that systemic downy mildew infection from the seed had resulted in every glasshouse with the crop showing infection when the temperature reached 30°C in August. The lack of clean Nicotiana seed was said to be known in the industry. Tissue culture has been used to successfully clean up hebe with downy mildew and there is potential for wider use of micropropagation for this purpose.

Downy mildew has not been seen on this nursery on basil. Downy mildew has not been seen on cucumbers, only powdery mildew. Sweet peas have not been seen with downy mildew, but most are sold when a few weeks old.

Tomato blight (*Phytophthora*) has been seen, but not in the last few years, and is controlled by the use of phosphites.

Phytophthora and *Pythium* root/stem rots occur and can be encouraged by high salts, cold and wet and compacted fine growing media, but infected material at production and hand-planting damage are more likely causes of losses. Parsley used to be grown and if it was not sprayed against *Phytophthora* then it rotted. It was possible that infection originated from the seed, or from the river water used to irrigate. Growing a high number of seeds per pot and the seedlings standing cold and too wet probably encouraged the disease. Geraniums grown from rooted cutting material delivered to the nursery can exhibit occasional *Phytophthora* or *Pythium*. Geraniums from seed do not normally have a problem with either pathogen unless either there is damage at planting or if they are grown in too wet or cold conditions, although cheap F1 seed can have more disease.

The optimum conditions for aerial infection are removed by watering first in the morning in summer, unless there is sub-irrigation. Plants grown outside do, however, have to contend with rain. In winter, irrigation is not done first thing, but late morning, and only if it is sunny, and the vents are then kept down as much as possible to warm the air to dry the leaves before opening fully again (unless raining or gales). Watering should not be done on a dull wet day. It is important the leaves and flowers are fully dry by night time.

Ventilation, fans and leaf blowers are used to dry the leaves. If a wetter is used in the irrigation water then this creates a thinner water layer on the leaves so hastens drying. Stock plants have dense foliage because of pinching to produce a high number of shoots for cuttings and this increases the humidity which can favour downy mildew, but irrigation is given from below so that the leaves do not get wet. It is necessary to hand-operate the vents otherwise they can close when it is raining and the humidity builds up. For cold crops the computer controls

on the vents do not give the required control. If vents are not closed when it is raining then crops can be quickly spoilt. Automatic vent operation is used more for heated crops. Vents are never fully shut unless the heat is on. Vent operation is important so that the plants do not get too wet, especially in winter when it will take longer for the leaves to dry out.

It is important to keep the plants growing well and this can be achieved by careful fertiliser use e.g. high potash and low phosphate. Every plant variety is different, but fertilisation is based around 12 4 40 plus Mg for autumn/winter and 16 4 32 plus Mg for late spring/summer, with growing media base fertiliser use at only 200 g/litre. FortifyCu (phosphite + copper) is used every two to three weeks for downy mildew and other diseases. Phosphite is used mainly on pansies. Outdoor hebe are given fungicide sprays every two to three weeks, the interval being less if there is more rain. If leaves are to be wetted with a spray for a pest, then for crops particularly prone to diseases (such as pansies and impatiens to downy mildews), a chemical or biological fungicide will always also be added preventatively. Pesticides (e.g. Mycotal) or growth regulators that have to dry slowly in order to work result in favourable conditions for disease infection. Products requiring high humidity to work are not used at this nursery.

Plants are kept strong by using blowers which keep the vegetable crops short. Automatic brushes on booms are used that move across the herbs to strengthen them.

White blister

Cineraria gets white blister particularly if the leaves touch the growing media as it seems to need moisture to develop. If necessary Fubol Gold (mancozeb + metalaxyl) is used as it has systemic activity. It is not clear whether infection arrives from the air.

A cultural control measure for all overwintered or autumn flowering plants has been to fill the pot to the brim with growing media and have the plug slightly raised above the surface so that the leaves do not touch the growing media and stay wet.

Biofungicides

Serenade ASO (*Bacillus subtilis*) has been used, but the recommendation is to use this in a programme with chemical fungicides. Products that work best in humid conditions are not ideal, even in propagation as even here humidity is kept down by just watering between the trays and covering with fleece instead of polythene sheet.

Trianum G (*Trichoderma harzianum*) has been used in growing medium for years. With hebe this has given better rooting. This is still used in propagation, but T34 Biocontrol (*Trichoderma asperellum*) is cheaper and now put in the growing medium of cyclamen and dianthus against

Fusarium. Prestop (*Gliocladium catenulatum*) product has to be stored in a fridge so it is logistically more difficult to place it in crop protection programmes.

Agronomist overview of prevalence and problems in edible crops in the UK

Information on aerially sporulating oomycetes across a wide range of principally vegetable crops was obtained in a meeting with Chris Wallwork of UK agronomy company Agrii.

Downy mildews

Infection on outdoor courgettes has not yet been seen in the UK. Pumpkins and squash suffer from *Phytophthora* blight and the only products available in the UK against *Pythium* and *Phytophthora* spp. on these crops is Serenade ASO (*Bacillus subtilis*) under an EAMU (0306/15) and Prestop on outdoor pumpkin under an EAMU (2773/2015).

Downy mildew is very important on broad beans, but uncommon on phaseolus beans. Plants grown for pea shoots for restaurants can suffer, in addition to vining peas, but additional issues with pesticide harvest intervals arise with “baby leaf” crops.

This disease is very important in rocket, continuing to be seen even when fungicides have been applied. This is in contrast to lettuce where treatment programmes are more effective. Lettuce downy mildew symptoms can appear on the leaf present at planting a week after planting-out and it is speculated that infection may have occurred at the propagators perhaps from carry-over on the seed coat. Evidence of seed-borne infection of spinach has been seen in a field, where a cotyledon leaf showed infection, with the rough-textured seed coat perhaps aiding the carriage of spores. Salad onions can be re-cropped in the same field and infection occurs from debris and early symptoms are then seen. Information for growers on whether there is a risk to subsequent crops from oospore infection would be helpful.

Downy mildew on red beet is uncommon. Radish can become infected on the shoulder, with some symptoms on the leaves. Chard can also have problems with downy mildew.

On Brassicas the close proximity of plants in modules in propagation means downy mildew is a big issue. Curd infection on cauliflowers was a big issue for many years, but this is not seen on the current varieties and may be because of resistance. Downy mildew is important on broccoli because of quality reduction, but there is an increasing issue with bacteria. Pointed cabbage and spring greens have greater issues with downy mildew than other types of cabbage. Field infection of Brussels sprouts is less important than infection in propagation. When crucifers are grown for “baby leaf” it has been observed that not all those in the mixture show downy mildew and one explanation of this might be that there is pathogen strain specificity as the conditions for infection should be the same. It would be useful to also be

able to use Cassiopeia (dimethomorph + pyraclostrobin) on Brassicas against white blister as an alternative to SL 567A (metalaxyl-M) because of the risk of resistance developing.

Parsnips get downy mildew from time to time. Neither carrot nor celery are affected.

Basil does not tend to get downy mildew outdoors, only under protection, whereas parsley is found with symptoms in both crop locations.

Bulb and salad onion downy mildew is very important. The resulting quality loss in salad onions can mean that crops are destroyed rather than harvested. AHDB recently gained an EAMU for use of Cassiopeia (dimethomorph + pyraclostrobin) on bulb onions. One problem with onions is the restricted range of fungicides. There are sufficient products available for application to potatoes against blight to allow sprays at four to five day intervals, but if this interval was used for onion downy mildew, which is at least as aggressive, then the programme would run out half way through the crop life. Following work in SCEPTRE Infinito (fluopicolide + propamocarb) has gained an EAMU for bulb onions.

Outdoor lettuce crops have a useful wide range of fungicides including Invader (dimethomorph + mancozeb), Fubol Gold WG (mancozeb + metalaxyl-M), two strobilurins, Infinito, Paraat (dimethomorph), Revus (mandipropamid) and Karamate (mancozeb). Mancozeb is a useful active ingredient to have for resistance management, but the maximum amount able to be applied has been reduced and the harvest interval increased for some crops. In spring onions, as there is no approval for Karamate (only for bulb onions) it means that to be able to use mancozeb it has to be used with metalaxyl in Fubol Gold and it would be better if straight mancozeb could be used to save the risk of building up metalaxyl resistance.

In the 1980's lettuce downy mildew resistant to metalaxyl was found across most major lettuce-producing regions in the UK, in particular protected crops. It can be advised to avoid use of Fubol Gold in preventative fungicide programmes, but to save it for when symptoms start to be seen, perhaps 14 days from harvest.

Phosphite nutrient products are widely used on crops and reduce downy mildews, particularly when applied in the higher temperatures of summer. Benefit has also been seen against white blister. In alliums, a silicon wetter and a reduced dose of the product is used because the leaves are waxy, whereas no wetter is needed for lettuce and spinach.

Biofungicides may be best applied at times of wetter weather to aid their survival. They are only likely to be effective when applied before spores land on the plant, as oomycetes grow only inside the plant (unlike powdery mildews). There could, however, be a plant disease stimulant effect that will work internally.

White tip

Onion white tip (*Phytophthora porri*) would be more common if it were not for the application of fungicides against downy mildew.

White blister

Occurs quite commonly on cabbage. It is problematic on sprouts and hard to eradicate. As radishes are fungicide treated for downy mildew then white blister is not often seen.

Financial impact

It is not easy to evaluate potential crop losses because fungicides are used to prevent crop loss. Even a low incidence can mean the whole crop becomes unmarketable, e.g. from white blister in Brassicas unless incidence is low enough to allow sorting out of infested material.

A key message is that the potential cost of not applying a fungicide is in general much higher than any financial loss from having sprayed when it was not necessary.

Forecasting

It is feasible to utilise in-field electronic meteorological stations to gather localised data and transmit it for use with programmes such as MORPH to give warnings that conditions favourable for diseases have occurred. MORPH takes account of sporulation risk, infection risk and the latent phase of disease development. The Allium and Brassica centre run five weather stations and run models. There are however issues of where to place the sensor in the crop as relative humidity will vary across the field and this is a key measure for disease development. In the Netherlands, the Darcom fee-paid service provides forecasting information to growers three times a week. Forecasting programmes can be obtained for use by UK growers, but it is the experience at Agrii that few growers utilise this because when the model shows a risk of infection then fungicide application should already have been carried out. For example, on onions there are only protectant fungicides, or at most curative activity against newly-landed spores, available against downy mildew. Information from the weather stations can assist in spraying decisions, but cannot be used alone to trigger a spray, it is important a farmer or agronomist first considers other factors. There is often a requirement to justify the use of fungicides for audit purposes and then station data can show that conditions in the crop merited a spray (particularly if the field is some way from the office, as weather at either location may differ).

Improving the timing of applications is important, rather than aiming to reduce the number of applications. The spray interval can however be increased if the conditions in the crop are hot and dry and the pathogen is known to require different conditions. In Lincolnshire it is possible for lettuce growers to not require the full possible fungicide programme, but in the

West of England and Northern Ireland the wetter conditions mean that an intensive spray programme is needed.

Crop Consultants' evaluation of aerial oomycete prevalence in the UK on edible and protected ornamental crops and potential crop losses

ADAS crop consultants and plant pathologists were consulted to evaluate the frequency over at least the last 15 years or so of various downy mildews, *Phytophthora* blights and rots and white blisters on edible and ornamental outdoor and protected crops in the UK. These included crops that were not under fungicide spray programmes. The potential proportion of the crop that would not be able to be marketed given the maximum spread seen by them was noted. The two indices below (1 to 4 for frequency, and low to high for loss) were utilised to enable comparison between the crops and the results presented in Table 7 (edibles) and Table 8 (ornamentals). This evaluation guided the selection of crops reviewed in this project. Severity and spread in any particular situation will depend on many factors, once the pathogen inoculum is present then aerial oomycetes are particularly favoured by high humidity, misty conditions and water splash.

Frequency of occurrence in fields of conventionally grown crops across the UK

0 = not seen in the UK

1 = rare, only seen "once in a blue moon"

2 = uncommon, throughout the UK, i.e. noteworthy when it occurs

3 = locally common only, perhaps related to regional weather

4 = Usually seen (or feared and treated) annually in most crops.

Crop loss from maximum spread seen in the UK across leaves and or fruit / between plants

H = High loss – 40% or more of a field crop unmarketable

- more than 20% of glasshouse crop produce unmarketable

M = Medium loss – 11% to 39% of a field crop unmarketable

- 5% to 20% of a glasshouse crop produce unmarketable

L = Low loss – 10% or less of a field crop unmarketable

- less than 5% of a glasshouse crop produce unmarketable

Table 7. Edible crops and the frequency with which each pathogen has been reported seen in the UK and the potential maximum loss that could occur once the pathogen was present (utilising assessment indices).

Crop	Pathogen	Frequency seen	Loss when present
Strawberry	*Phytophthora* fruit rot	1	L
Raspberry	Downy mildew	1	M
Blackberry	Downy mildew	3	M
Grape	Downy mildew	4	H
Apple	*Phytophthora* fruit rot	2	L
Pear	*Phytophthora* fruit rot	2	M
Sweet Chestnut	*Phytophthora* blight	1	L
Broad bean	Downy mildew	3	M
Pea	Downy mildew	3	H
Cucumber	Downy mildew	2-3	M
Lettuce	Downy mildew	4	H
Rocket	Downy mildew	4	H
Red Beet	Downy mildew	3	M
Spinach	Downy mildew	4	H
	White rust	1	L
Chard (baby leaf)	Downy mildew	3	M
Calabrese	Downy mildew	2-3	M
Cabbage	Downy mildew	2-3	L
	White blister	2	M
Cauliflower	Downy mildew	3	M
	White blister	2	M
Brussels sprout	White blister	4	M
	White blister	4	M
	Downy mildew	2	M
Radish	Downy mildew	3	M
	White blister	2	L
Swede	Downy mildew	3	L
Turnip	Downy mildew	3	L
Parsnip	Downy mildew	2	L
Tomato	*Phytophthora* blight	2	H
	Phytophthora (stem)	2	M
Basil	Downy mildew	3	H
Parsley	Downy mildew	3	H
Sage	Downy mildew	3	H
Mint	Downy mildew	2	H
Bulb onion	Downy mildew	4	H
Salad onion	Downy mildew	4	H
Leek	White tip	3	H
Shallots	Downy mildew	3	H

Rhubarb	Downy mildew	1	L

Table 7. Ornamental crops and the frequency with which each pathogen has been reported seen in the UK and the potential maximum loss that could occur once the pathogen was present (utilising assessment indices).

Crop	Pathogen type	Frequency seen	Loss when present
Pansy	Downy mildew	4	M
Impatiens	Downy mildew	4	H
Nicotiana	Downy mildew	4	H
Lisianthus (Eustoma)	Downy mildew	3	M
Digitalis	Downy mildew	4	H
Veronica	Downy mildew	4	H
Aquilegia	Downy mildew	4	H
Lamium	Downy mildew	4	H
Papaver	Downy mildew	4	H
Hebe	Downy mildew	4	M-H
Geum	Downy mildew	4	H
Buddleia	Downy mildew	4	M-H
Salvia (perennial)	Downy mildew	4	M_H
Potentilla (herbaceous)	Downy mildew	4	M_H
Scabiosa	Downy mildew	3	M_H
Rosa	Downy mildew	4	M_H
Geranium (hardy)	Downy mildew	4	M_H
Meconopsis (Poppy)	Downy mildew	4	M_H
Helleborus	Downy mildew	3	M
Gallardia	Downy mildew	3	M-H
Erysimum	Downy mildew	3	M
Coreopsis	Downy mildew	3	L
Aucuba	*Phytophthora* blight	1	L
	Downy mildew	3	M
Juniperus	*Phytophthora austrocedri*	3	M
Ceanothus	Phytophthora blight	2	L
Choisya	Phytophthora blight	2	L
Various shrubs and trees	*Phytophthora ramorum/ kernoviae*	1 or 3	H
On ornamentals, but pathogen is mostly on edible crops			
Honesty	White blister	3	L
Wallflower	Downy mildew	3	L
Ornamental cabbage	Downy mildew	3	L
Cineraria	Downy mildew	3	L
Antirrhinum	Downy mildew	3	M-H
Disease of lesser importance or little information on prevalence in the UK			
Primula	Downy mildew	1	L
Aubretia	Downy mildew	1	L or M
Alyssum	Downy mildew	0	L
Verbena	Downy mildew	3	L

Salvia (annual)	Downy mildew	4	L
Myosotis	Downy mildew	1	L
Sweet pea (annual)	Downy mildew	2-3	L
Cineraria	White rust	3	L
Delosperma	White rust	3	L
Brunnera	Downy mildew	2	L
Agastache	Downy mildew	2	L
Campanula	Downy mildew	0	L
Rock rose (*Helianthemum*)	Downy mildew	3	M
Ilex	Phytophthora blight	2	L
Laburnum	Downy mildew	1	L
Alnus	Phytophthora blight	2	L
Prunus	Phytophthora blight	0	L
Malus	Phytophthora blight	1	L

Discussion

Recent research into oomycete pathogens is beginning to illustrate how diverse these organisms really are. Utilisation of molecular techniques enabling DNA sequencing and comparison is revealing a new level of specificity within the group, and showing that previous understandings about pathogen-host interactions are, in general, simplistic. There is increasing evidence to suggest that the majority of interactions are likely cultivar-race specific, and different races of the same pathogen do not cause symptoms to the same extent on different cultivars of the same host plant. In light of this, how we understand the disease, including the role of weedy relatives as reservoirs for inoculum, needs to be re-evaluated.

An effective framework is needed to facilitate the reporting and recording of any suspected cases of fungicide resistance development, cases of new pathogen races (perhaps with heightened virulence), and any infection of apparently new hosts. This might enable a more rapid response to potential threats to UK horticulture.

Molecular technologies may be able to address another issue associated with certain downy mildew pathogens: the prolonged asymptomatic nature of certain interactions. Certain species, such as *P. sparsa*, can cause reductions in yield while remaining primarily asymptomatic and an early detection method to identify infected plants is required so that appropriate action can be taken, e.g. destroying infected batches before resources are invested into plants with reduced potential and their sporulation leads to infection of other batches of the same host. An additional area which would benefit from an early detection system is white blister infections of vegetable Brassicas, where the microorganism can influence the nature of secondary infections and potentially compromise any resistance traits

of the host. Symptomless infection increases risk that infected plants are moved, in particular nursery stock, and the potential of secondary disease spread from these plants needs to be better understood. Developing molecular techniques for the reliable detection of asymptomatic infection by aerial oomycetes will also enable the weak points in nursery stock production systems to be identified and acted upon. Some species of *Phytophthora*, such as *P. ramorum*, are regulated against and there can be considerable costs associated with their presence in a nursery.

There still remain some fundamental gaps in our understanding of the biology of oomycete pathogens and their interactions with respective hosts, insight into which could help determine effective control strategies. For example, the infection plane of oospores of many downy mildews remains unclear, as does the role and nature of seed transmission, both of which are important in implementing successful cultural control procedures. Oospore durability and viability under field conditions is another topic which is not well documented in the literature with regards to specific downy mildew pathogens; insight into which would provide guidance for the most appropriate sanitation and crop rotation methods to reduce primary inoculum within a growing system. Our understanding of the processes surrounding oospore germination is limited; what stimulates oospores to germinate, is it environmental factors or biotic factors or a combination of both. More research is also needed into the survival of sporangia in both outdoor and protected crops as this would provide insight as to the sources of initial inoculum in outdoor crops and whether oospores play a significant role in protected environments.

The ability of a pathogen to persist is another area requiring more work. Some species of oomycete pathogen, for example *P. cubensis* the causal agent of downy mildew in cucumber, is unable to produce oospores in the UK due to the absence of one of the two known mating types. The ability of this pathogen to persist in the UK is unclear. It may be able to survive the changeover period between crops as viable sporangia, be a consequence of infected seed, survive on an alternate host, or be re-introduced each year e.g. on symptomless infected plants or by windblown conidia from Europe. Understanding long distance spore movement will help determine the importance of primary inoculum within versus outside the production systems. More work in this area is required to better target inoculum elimination.

Recent advances in spore detection and disease forecasting from the University of Worcester should revolutionise how certain diseases are protected against. Lateral flow tests able to detect aerial spore thresholds for disease combined with meteorological parameters allow the precise timing of sprays only at those times when the disease is a real threat, saving time, resources, and consequently financial inputs. To this end, it would be beneficial for different control methods to undergo economic analysis to determine the financial benefits of their

implementation. This kind of analysis was carried out by Minchinton *et al.* (2013) with regards to the benefits of cultivar resistance, timing fungicide sprays in accordance to a disease forecasting system, and irrigating crops in the morning as opposed to the evening. Work into forecasting within a protected environment to increase the precision of fungicide spraying is a priority, especially in light of the study by Minchinton *et al.* (2013) which showed that fungicide application based on a forecasting system for outdoor crops could increase farm profits by 15% compared to weekly spray applications.

The protected environment has particular risks and opportunities for the management of aerial oomycetes. While the glasshouse and tunnel conditions can be perfect for downy mildew development, there are opportunities to modify the environment to make it less favourable to disease. Current recommendations tend to be generic, but further research on the interactions of water, temperature and light with spore production, spread and infection for specific host-pathogen combinations would enable more targeted recommendations to be developed.

The principles of existing forecasting systems should be evaluated for their relevance to alternate and emerging diseases. Such systems would then require validation before being incorporated into an IPM strategy. If adaptations are unsuccessful effort should be put into developing novel systems, as accurate forecasting consequently facilitates more precise timing of protective sprays which can economise disease prevention. The location of an individual grower's crops may be spread over large distances and therefore are subject to varying meteorological conditions and as such, in-field monitoring may be required; this implies that practical logistics need to be considered when developing forecasting systems.

Identifying sources of resistance has also benefitted from the advent of molecular sequencing techniques. Additionally the advent of molecular plant breeding, utilising molecular markers and high throughput sequencing techniques, allows the development of novel cultivars with the potential for durable resistance. Identifying the genes responsible for disease resistance in wild relatives and breeding them into commercial crops is an important area for research. Minchinton *et al.* (2013) showed that using a disease resistant cultivar of broccoli was able to reduce the incidence of an oomycete disease by 99% compared to a susceptible cultivar. With the recent insight into the cultivar specificity found in an increasing number of oomycete pathogens, stacking of resistance genes within a species may be possible to create durable, widely resistant crops. An understanding of the variability within oomycete species will be needed to predict the likely durability of cultivar resistance. One particular sector requiring development of resistant varieties is the UK herb industry. These crops are highly vulnerable to downy mildew and disease can lead to the rejection of entire crops.

There is currently a heavy reliance on phenylamide fungicides (FRAC code 4) in the treatment and prevention of crop diseases caused by oomycete pathogens and resistance has long been observed to this group of fungicides, both in UK pathogen races and worldwide. Currently however, there is not a definitive system in place in UK horticulture for monitoring and reporting of cases of suspected chemical resistance; guidelines on reducing the likelihood of resistance development is available through the Fungicide Resistance Action Committee (FRAC; www.frac.info). Fungicides with novel modes of action need to be developed and used in combination to reduce the selective pressure on pathogen populations to develop resistance. Recently, in the AHDB project 'SCEPTRE', a range of fungicides were identified as effective against downy mildew on both Brassicas and onions; four products significantly reduced disease incidence and severity on cauliflower seedlings with FRAC codes of 11+40, 43+28, 7+11 and 40+45, and four products significantly reduced disease incidence and severity in salad onions with FRAC codes of 11+40, 43+28, 40+45 and one biofungicide (O'Neill, 2015). Two fungicide products, Cassiopeia (BASF; dimethomorph (11) + pyraclostrobin (40)) and Infinito (Bayer; fluopicolide (43) + propamocarb hydrochloride (28)) have since been approved for use on bulb onion; Cassiopeia has on label approval, Infinito has approval through EAMU 1142/2015.

Numerous control methods based on biological substances have been identified and proven to have potential in combatting disease caused by oomycetes. Some pathosystems, for example downy mildew on pea, have had limited research into the potential of biological control and this is an area for future work. Studies which have identified potentially effective biological treatments for other pathosystems need to be followed up, testing UK isolates of the pathogen in UK cropping systems. The development and approval of biological treatments, used in combination with chemical fungicides, would reduce the selective pressure on the pathogen for resistance development. Studies for the development of biological treatments will need to be in depth and detailed, providing insight into efficacy and wider environmental effects, as well compatibility with other control measures and financial viability; this is currently a major gap.

There are currently no foliar fungicides approved in the UK for use against downy mildews on pea crops, a system which relies on seed treatment with a phenylamide compound for control. Only Broadsheet (AgChem Access Holdings; chlorothalonil + metalaxyl-M) and Folio Gold (Syngenta; chlorothalonil + metalaxyl-M) are available for foliar treatment of downy mildew in broad (faba) beans, with Wakil XL (Syngenta; cymoxanil + fludioxonil + metalaxyl-M) available as a seed treatment. All of these rely primarily on phenylamide modes of action and so new treatments need to be made available against oomycete pathogens in these crops.

There is increasing evidence to suggest a beneficial role for elicitors and priming in IPM strategies. Pre-treatment of crops with certain substances elicits a defence response priming it for challenge by a pathogen. For example it was shown that pre-inoculation of a plant with a non-compatible strain of *A. candida* was able to induce resistance against a compatible *A. candida* isolate. In this scenario, the non-compatible oomycete acted as an elicitation agent, priming the plant for attack by the compatible isolate. Elicitors do not necessarily have to be pathogen derived and can be varied in nature and origin. Plants likely encounter more than one pathogen/pest before harvest and as such it would be beneficial to understand the role of elicitors in the context of more than one pest/pathogen interaction. As with biologicals, insight into elicitors would require detailed scientific studies and this is currently a major gap. These studies would ideally provide insight on aspects such as efficacy, modes of actions, compatibility with other control mechanisms, as well as helping to understand the durability of induced resistance caused by specific elicitors, all of which have implications on economic viability.

Aerial oomycetes, collectively, infect a wide range of crop species. Some are important crops, where extensive research has been carried out. Others are minor crops, where little is known. While the smaller crops will always struggle to fund extensive research, it will be important to determine what research is applicable to them and how it can be used to optimise disease management.

The development/identification of new fungicides for the treatment of aerial oomycetes will be a challenge. Therefore progress with breeding, elicitors and biologicals, seed treatments, and cultural controls should be a pursued.

References

Minchinton, E.J., Auer, D.P.F., Thomson, F.M., Trapnell, L.N., Petkowski, J.E., Galea, V., Faggian, R., Kita, N., Murdoch, C., and Kennedy, R. (2013). Evaluation of the efficacy and economics of irrigation management, plant resistance and Brassicaspot™ models for management of white blister on Brassica crops. Australasian Plant Pathology 42, 169-178.

O'Neill, T. (2015). Sustainable Crop and Environment Protection – Targeted Research for Edibles (SCEPTRE). AHDB Final Report for project CP 077.

Conclusions

Host range

- Previous understanding of pathogen host interactions has been, in general, simplistic
- Downy mildew species once thought to have a wide host range are showing evidence of increased host preference, with numerous species either being reclassified or split into distinct races.
- Evidence suggests that distinct races which occur within pathogen species do not cause symptoms to the same extent on different cultivars of the same host plant.
- Weedy relatives may still play a role in acting as reservoirs for inoculum in some systems, but this is an area requiring further investigation.

Biology

- Fundamental gaps need to be filled in the understanding of the biology of some oomycete pathogens of UK importance to further aid integrated crop management.
- The role of oospores in infection is poorly understood. Information is lacking on their durability and viability under field conditions, germination, and role in infection.
- Survival of sporangia in the UK is also not well documented. The extent of aerial travel of viable spores is generally unknown, accepting that it will vary between pathogens and depend on environmental conditions. The possibility of spread of predominantly-airborne oomycetes *via* contaminated irrigation water requires further investigation.
- Certain downy mildew and white blister infections can remain without symptoms whilst still having a negative effect on a crop.

Integrated Crop Management

- Advances in spore detection and forecasting are paving the way for the more precise timings of fungicide spray applications.
- Across UK horticulture, limited crop resistance is available against oomycete pathogens. Molecular techniques may identify genes for resistance in wild relatives.
- Currently there is not a definitive system for growers to support suspect cases of fungicide resistance; and no monitoring of sensitivity/resistance levels is undertaken.
- There is increasing potential for the successful incorporation of microbial treatments and elicitors together with chemical fungicides within integrated crop management programmes (Figure 4).

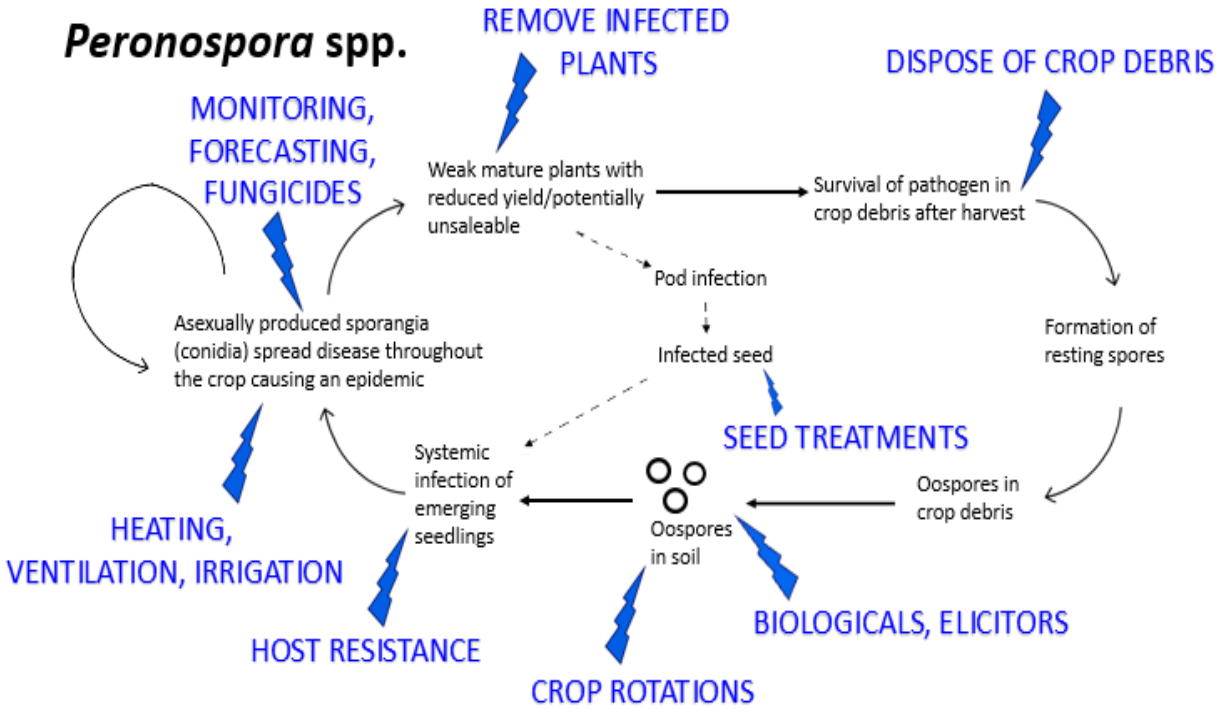

Figure 4. General life cycle of a typical *Peronospora* sp. (downy mildew) and integrated crop management. The arrow-flashes shown in blue indicate where control could potentially be achieved by the measures indicated.

Knowledge and Technology Transfer

Poster presentation at Ornamentals Pest, Disease, and Weed Control Conference: Devising sustainable solutions (Stoneleigh, 23rd February 2016).

Two AHDB Factsheets are due to be submitted by 31 May 2016.

Appendices

Appendix 1. Table of useful websites

Contents	Web address
'Crop Modules' (production protocols) on different crops. These provide general production guidance including aspects of disease management. Also useful templates e.g. 'Plant Protection Products Application Record' (UK)	http://assurance.redtractor.org.uk/rtassurance/schemes.eb
Daily crop forecasts including: temperature, crop relative humidity, leaf wetness, rainfall, soil temperature, etc. (EUROPE)	http://www.weatheronline.co.uk/weather/agriculture/Europe/UK/0.htm
An ecological pest management database (USA)	https://attra.ncat.org/attra-pub/biorationals/index.php
Information on pest management for numerous crop sectors including: vegetables, trees, ornamentals, fruit, greenhouse crops. Also information on IPM (USA)	http://edis.ifas.ufl.edu/
EU pesticides database	http://ec.europa.eu/food/plant/pesticides/index_en.htm
Fact sheets on diseases of vegetable crops (USA)	http://vegetablemdonline.ppath.cornell.edu/cropindex.htm
Well illustrated fact sheets and also includes a guide for rapid diagnostic testing (USA)	http://entoplp.okstate.edu/

Pesticide factsheets and self-study tutorials (USA)	http://psep.cce.cornell.edu/facts-slides-self/Factsheets.aspx
Database of factsheets and abstracts	http://www.cabi.org/cpc
Disease factsheets	http://learningstore.uwex.edu/Lawn-Garden-C2.aspx
Pest management guidelines	http://www.ipm.ucdavis.edu/PMG/crops-agriculture.html
Information on the UK cucumber industry (CGA)	http://www.cucumbergrowers.co.uk/
Disease factsheets and pest distribution information	http://www.plantwise.org/KnowledgeBank/Home.aspx
Profiles for many diseases	www.rhs.org.uk/science/plant-health-in-gardens/pathology
Fact sheets on plant diseases of various hosts (USA) including disease control information	http://extension.psu.edu/pests/plant-diseases
Fact sheets on plant diseases of various hosts (USA) including disease control information	http://hortsense.cahnrs.wsu.edu/Home/HortsenseHome.aspx
Database of DEFRA scientific reports	http://sciencesearch.defra.gov.uk/
AHDB Horticulture news, reports, factsheets etc.	http://horticulture.ahdb.org.uk/
Resource for fungicide product efficacy with relation to *Phytophthora infestans*	http://euroblight.net/

Appendix 2. Knowledge Exchange; grower evaluation of various methods

	Survey No.																		Average rating where used	people who use
KE mechanism	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
AHDB factsheet	**	***	**	***	**		***	*	*	**	***	***	***	***	*		*	***	2.25	16
AHDB Grower	**	*	***	***	**		***	**	*	**	***	**	***	**	*				2.14	14
Horticulture Week	**	***	**	**	*		***		*	*	***	*	**		*				1.69	12
Other magazines/newspapers	**	**		**			**	**	*	*	**				*				1.66	9
Visits by specialists		**	***	***		***	**		**	**	***	**	***	***	*			***	2.46	13
Training courses		***	***	**			**		*	**	*				*				1.88	8
AHDB website		* not spec	***	**	* not easy to search		***		*	**	***				*			**	1.9	10
other websites		**					**		*		***				*			***	2	6
Blogs		*					**		*						*				1.25	4
AHDB project reports		***	***	***	**		***	***	*	**	***		***		*	***		**	2.46	13
ADAS Technical notes		**		***		**	***		*	**			***		*				2.13	8
Meetings/conferences		***	***	***	**		***		*	***	***		**		*		*		2.27	11
other				*** being involved v		*** EU minor crops CEG									*				2.33	3

Key: *=poor, **=acceptable, ***=good

Eighteen respondents to the CP 157 grower survey rated how useful/beneficial various methods of knowledge exchange had been to them at providing crop information, particularly on aerial oomycetes (Phytophthora diseases, downy mildews and white blisters).

Appendix 3. Grower Survey Form

AHDB Project CP 157. Aerial oomycetes: a review of management and control options available for the UK horticultural industry

As part of this new AHDB project to bring together current knowledge and to identify knowledge gaps regarding airborne oomycete pathogens (namely **downy mildews**, **Phytophthora species producing spores on leaves or stems** (not root rots), and **white blister**) we (ADAS) would like to ask if you would complete this questionnaire. Insight into your experiences of these pathogens will help us to direct our review down the most beneficial paths for the industry across the AHDB Field Vegetables (not potatoes), Protected Edibles, Ornamentals, Soft Fruit and Top Fruit sectors.

Please could complete the survey with as much detail as possible and return it to us as soon as you are able via either e-mail to Erika.Wedgwood@adas.co.uk or post to:

Dr Erika Wedgwood
ADAS Boxworth, Battlegate Road,
Boxworth, Cambridge, CB23 4NN

If you would also like, or prefer, to talk with us over the phone to discuss your experience with these pathogens then please either e-mail or call Erika Wedgwood (Tel. 01954 268231).

To follow up this survey you may be contacted by telephone by ADAS to discuss your experience with, or freedom from this type of disease. Please tick if you do not wish to be contacted ☐

Returned survey forms will be held by ADAS researchers and any information you provide to us will be anonymised before being included in reports to the AHDB.

Business name and address	
County where your crops are mainly grown	

Your name	
Contact telephone number/s	
Email address	

If you do not wish to give your details, please can you let us know the County in which you mainly grow your crops?

Q1 Crop loss

What is the significance of crop losses in your UK crops due to either downy mildews, white blister, or Phytophthora species that sporulate on leaves, stems or fruit (aerial oomycetes)?

What do you envisage could be the potential loss if you had no spray programmes in place?

Please attach another sheet if you have had a greater number of crops with these diseases.

Crop - propagation stage *If none, please go to next table*	**Disease**	**Problem** Rank 0 - 5 *		**Mean % crop loss**	**Highest % crop loss**
		Actual	**Potential**	**Actual estimated**	

*Frequency of disease occurrence and severity of crop loss, please rank 0 - 5 as follows:

0 = Never seen in your crops
1 = Rare, only seen “once in a blue moon”
2 = Uncommon

3 = Common and an occasional problem
4 = Common and serious problems can occur
5 = Common, and often leads to economic damage

Crop - after propagation stage	Outdoor (O) or Indoor (I)	Disease	Problem Rank 0 - 5 *		Mean % crop loss	Highest % crop loss
			Actual	Potential	Actual estimated	

Q2 Crop loss contd.

Any additional information on disease frequency and severity e.g. effects of crop location (including in storage), irrigation, variety, time of year:

Q3 Crop areas

What approximate areas do you generally grow of the crops you have listed in Q1?

In propagation	Out of propagation

Crop	Area (state ha or m²)	Crop	Area (state ha or m²)

Q4 Knowledge exchange

How useful have you found information sources at providing information, particularly on the pathogens in this survey? Please rate source as; * = Poor, ** = Acceptable, *** = Good

Information source	Star rating	Please comment, or give more details
AHDB Factsheets		
AHDB Grower magazine		
Horticulture Week		
Other magazines, newspapers		
Visits by specialists		
Training courses		
AHDB website		
Other websites (please name)		
Blogs		
AHDB Project reports		
ADAS Technical Notes		
Meetings/conferences		
Other- please specify below;		

Q5 Disease management

Please select three aerial oomycete diseases from Q1, if possible covering a disease control success range. For an average year rate the level of control;

***** = Improvement needed, ****** = Satisfactory, ******* = Very good

	Disease A	**Disease B**	**Disease C**
Crop			
Disease			
Level of control			

Please indicate which measures you have utilised in their management by stating Yes or No:

Control measures	**Has this control measure been utilised for the disease Y/N?**		
	Disease A	**Disease B**	**Disease C**
Resistance/varieties			
Hygiene			
Irrigation scheduling			
Ventilation of protected crops			
Crop rotation			
Chemical fungicides			
Biopesticides			

Growth promoters			
Routine Protectant Programmes			
Diagnostics (on or off-site)			
Monitoring / crop walking			
Forecasting based on experience			
Forecasting by computer program			
Other/s (please specify)			

Q6 Plant protection products

Of the chemical and/or biological fungicides, or similar, you have you used against the three diseases named in Q5, please give information on the **best three** products for each disease.

Target disease	Effective product name (up to 3 per disease)	Crop location Glasshouse (G) Tunnel (T) Field (F)	Protectant (P) or curative (C) application	Comments on why they were good e.g. long or quick acting, worked well, no deposit
A				

B				
C				

If you have found any products ineffective please also name and comment on them below:

Target	Ineffective product name	G, T or F location	P or C application	Comments on why you consider they were poor
A				
B				
C				

Q7 Poor disease control

If fungicide control has been less than anticipated for particular aerial oomycete disease/s (not necessarily of those named above), do you believe it to be due to the development of pathogen resistance, spray coverage or other cause/s?

Crop	Disease	Products used	Suggestions on why you consider disease control has been problematic

Q8 Disease diagnosis

How do you carry out diagnosis of aerial oomycetes on stems, leaves or fruits in your crops? Please state (if known) how frequently you, or services you use, employ these methods;

N = Not used, ***** = Rarely, ****** = Sometimes, ******* = Usually ?

By whom	Naked eye / Hand-lens	Micro-scope	Damp box	Culture	Lateral flow kit (LFD)	Mol-ecular / DNA / PCR	Other
In-house staff							
Visiting Advisor							
Direct to laboratory							

Q9 Suggestions for further research or other information

Are there any specific disease management problems that you would like to see answers to, or areas of knowledge that you (or your staff) would like to be better informed on?

Examples might include: effective use of biofungicides; how pathogens disperse/survive etc.

We would be grateful if we could either receive a completed form back from you, or you could contact us if you prefer to complete this form by telephone. Please could we have your replies back at the latest by 4th January 2016?

We will contact you to arrange a suitable day and time to speak with you if you have requested a phone-call, or if we have queries. We may also seek to speak with you towards the end of November if you have not returned this form, as we wish to obtain information from growers of as wide a cross-section of crops and business types as possible.

Results from this survey will be presented to AHDB in a final report at the end of March 2016. The information from the report will be used to guide decisions on the funding of particular areas of research or development, factsheets and other publications, and training events.

Thank you for your help with this survey. Please return it to me as detailed on the first page.

E. F. Wedgwood

Dr Erika F. Wedgwood

Appendix 4. Contents of CP 126 – A desk study to review global knowledge on best practice for oomycete root-rot detection and control.

Contents

Appendix 5. Information on oomycete pathogens on the UK Plant Health Risk Register including where they are present and their UK risk rating based on 1-125 scale of likelihood x impact x value (60+ high risk). Action to be taken to prevent spread, and their principle infection route.

Pest Name and Major Hosts	UK presence, & risk rating	EU presence	Global presence	Action in the UK	Aerial or root as principle or only infection route. Comments on pathogen impact, spread and control
Peronospora belbahrii (Downy mildew) on *Agastache; Ocimum basilicum; Solenostemon scutellarioides*	Present 4	Hungary, Italy	Africa, Asia		**Aerial.** Identified by RHS; consultation on PRA concluded no statutory action should be taken.
Phytophthora acerina (Bleeding canker and dieback) on *Acer pseudoplatanus*	Absent 30	Italy		Statutory action against findings.	**Root.** Affects sycamore and present in an Italian forestry plantation. Closely related to other phytophthora species so could be more widespread than reported.
Phytophthora alni (Alder bleeding canker; Alder Phytophthora root disease) on *Alnus*	Present (Widespread) 48	16 countries		No statutory action against findings.	**Root.** Damaging pathogen of Alder; first detected in the UK in 1993; subsequently spread to most areas. No prospect of eradication or containment but possible co-ordinated action to mitigate impacts to be considered with stakeholders.
Phytophthora austrocedri (Dieback) on *Chamaecyparis lawsoniana; Chamaecyparis nootkatensis; Juniperus communis ssp. communis; Libocedrus chilensis*	Present (Limited) 48		South America	Prevent spread via nurseries. Protect rare juniper habitats.	**Root.** Significant threat to juniper and a need to work with stakeholder and statutory conservation bodies to mitigate risk and protect unaffected areas where possible. Keep EU informed because other countries may wish to establish pest free areas.
Phytophthora fragariae (Red core) on *Fragaria ananassa (F. x ananassa)*	Present (Widespread) 48	19 countries	Asia		**Root.** Present (widespread) in field grown strawberries; but well controlled through clean propagating material; no longer meets the definition of a quarantine pest. EFSA are conducting a risk assessment as part of the review of IIAII organisms.
Phytophthora infestans (Late blight of potato and tomato) on *Solanum tuberosum*	Present (Wide-spread) 100		N. & S. America, Oceania, Africa, Asia	Encourage develop-ment of resistant varieties.	**Aerial.** A serious pest of potatoes currently managed by chemical control and crop production practices in the UK. Concern about loss of current effective fungicide treatments. Likelihood of introduction of new resistant or more virulent races.

Phytophthora kernoviae (Dieback) on *Drimys winteri; Liriodendron tulipifera; Magnolia; Quercus; Rhododendron ponticum; Vaccinium myrtillus; Fagus sylvatica*	Present (Limited) 100	Ireland	Oceania	Keep regulatory status under review. Continue current measures	**Aerial.** Five year programme to remove key sporulating host ended in 2014. Containment of *P. kernoviae* is more realistic than for *P. ramorum*.
Phytophthora lateralis (Root rot) on *Chamaecyparis lawsoniana*	Present (Limited) 30	France, Ireland, NL	North America, Asia	Regulation as by EPPO.	**Root.** Recommended for regulation by EPPO; therefore should be considered for regulation by EU. Limited findings in UK which are either being eradicated or action taken to prevent further spread.
Phytophthora pinifolia (Needle cast) on *Pinus; Pinus radiata*	Absent 60		South America		**Aerial.** Significant risk; mitigated by prohibition of Pines from South America. Include in sentinel tree project for *P. sylvestris* in Chile
***Phytophthora* pluvialis** (Red Needle Cast) on *Lithocarpus densiflorus; Pinus radiata*	Absent 60			Statutory action against findings.	**Aerial**. Affecting mainly Monterey pine. Prohibition on pine planting material from outside the EU and restrictions on soil imports help to mitigate the risk of introduction to the UK.
Phytophthora polonica (in association with Alder decline) on *Alnus glutinosa*	Absent 20	Czech Republic, Germany, Poland		No statutory action against findings.	**Root.** Pathogen present in parts of the EU and beyond. Not known to be present in the UK; but unlikely to be damaging if introduced.
Phytophthora pseudosyringae (Bleeding canker and root rot) *Acer macrophyllum; A. glutinosa; Arctostaphylos; Carpinus betulus; Castanea sativa; L. densiflorus; Malus pumila; Nothofagus alpina; Pieris floribunda; Quercus agrifolia; Quercus cerris; Quercus robur; Umbellularia californica; Vaccinium myrtillus; Fagus sylvatica*	Present (Limited) 36	Germany, Spain, France, Italy	N. & S. America		**Root.** Soil-borne in Europe, but spores semi-caducous so able to spread aerially and aerial spread reported in the USA. Present in UK since 1930s. Consultation in 2012 concluded statutory action was not appropriate.
Phytophthora ramorum on *Acer pseudoplatanus; Aesculus hippocastanum; Castanea sativa; Larix; Larix kaempferi; L. densiflorus;*	Present (Limited)	19 countries	North America		**Aerial**. Five year programme to remove key sporulating host ends in 2014; consultation on further action continues (Sept 2013). Containment of *P. kernoviae* is more realistic than for *P. ramorum*.

Quercus; Rhododendron; Rhododendron ponticum; U. californica; V. myrtillus; Vaccinium ovatum; Viburnum; F. sylvatica 125					
Phytophthora rubi (Root rot) on *Rubus idaeus*	Present (Widespread) 40	7 countries	N. & S. America, , Oceania		**Root**. Present (widespread) in field grown raspberries; but well controlled through clean propagating material; does not meet the definition of a quarantine pest.
Phytophthora siskiyouensis (Canker and stem lesions) on *Alnus; L. densiflorus; U. californica*	Present 36			Statutory action to contain current outbreak	**Root**. Disease of Alder and other tree species in the USA and Australia; now in the UK. Could possibly be mistaken for *P. alni*. Further work needed to assess risk and extent of findings to be developed into a risk assessment.
Plasmopara halstedii (Downy mildew) on *Helianthus annuus;* Asteraceae	Absent 6	15 countries	N. & S. America, Oceania, Africa, Asia	Survey to follow up UK outbreak.	**Aerial.** Sunflowers could be a more important crop in UK in future; consider some targeted survey and developing European risk assessment.
Plasmopara obducens (Downy mildew) on *Impatiens balsamina; Impatiens walleriana*	Present 12	12 countries	N. &S. America, Asia		**Aerial.** Serious disease of bedding Impatiens; a decision taken in 2008 to allow industry to manage the disease, but the disease has reduced the popularity of the crop.

