FACTSHEET 18/16

Cross sector

AHDB HORTICULTURE

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Edible crops: recent developments in the management of downy mildew, white blister and aerially spread Phytophthora diseases

Recent advances have been made in the knowledge of downy mildews, white blisters and species of Phytophthora (Oomycete pathogens) that affect above ground tissue in fruit, vegetable and herb crops. This factsheet is the output from a review (CP 157), which highlights information relevant to their management and suggests areas where greater understanding is still needed.

Figure 1. Onion downy mildew (*Peronospora destructor*) causing leaf-tip bleaching in salad onions in October (right hand bed) in contrast to onions receiving a standard fungicide programme (left hand bed)

Action points

- Dispose of crop debris, manage 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 arising from resting spores (oospores) in the soil.
- Where possible, avoid making successive plantings across a single field (or in close proximity) in order to reduce the risk of pathogens moving from established to younger plantings.

- Select varieties with resistance, if available and acceptable to end-users.
- Ensure that seed and propagation material is obtained from sources with good disease management programmes.
- Where available, use 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, adjust 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 so that any disease is quickly detected.
- 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 stages of the pathogen life cycle, 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.

Background

Downy mildews, white blisters and some Phytophthora species are examples of Oomycete pathogens which have spores that can be transmitted aerially to infect above ground tissue, particularly when there is dense, wet, foliage. Infection can remain symptomless for long periods so can be spread in propagation material. Most aerial Oomycetes are able to persist in soil and growing media either as mycelium, or by resting spores, which can release infective swimming spores.

In the UK, preventative applications of fungicides are commonly used to reduce losses to aerial Oomycetes across a range of susceptible plant species. This factsheet is based on AHDB-funded CP 157, which reviewed new findings and potential gaps in the understanding of the biology and control of aerial Oomycetes reported by growers to be of major significance. It covers Brassica, onion, leek, pea, bean, red beet, tomato, cucumber, rhubarb, top fruit, cane fruit and various herb hosts. Potato blight and downy mildews of spinach, grapes and lettuce, although important, are to be reported on via other projects.

Hosts

Edible crops susceptible to downy mildew and reviewed in CP 157 are given in Table 1, together with information on the availability of cultivar resistance.

Figure 2. Basil plant with yellower areas caused by downy mildew (*Peronospora belbahrii*) delimited by leaf veins. Sporulation does not develop on leaf upper surfaces

Table 1. Downy mildew species affecting a number of edible crops, and availability of host resistance

Edible crop host/s	Downy mildew	Resistant cultivars
Allium spp.	*Peronospora destructor*	Yes
Beet	*Peronospora farinosa* f. sp. *betae*	Yes
Brassica spp.	*Hyaloperonospora brassicae*	Yes
Broad (Faba) bean	*Peronospora viciae* f. sp. *fabae*	Limited
Mint	*Peronospora lamii*	No
Parsley	*Plasmopara petroselini*	Limited
Pea	*Peronospora viciae* f. sp. *pisi*	Yes
Rhubarb	*Peronospora jaapiana*	Potentially
Rubus spp.	*Peronospora sparsa*	Yes
Sage	*Peronospora salvia-officinalis*	Limited
Sweet basil	*Peronospora belbahrii*	Potentially

Symptoms

Downy mildew leaves infected by aerially dispersed (detachable) sporangia usually develop pale areas, which on broad-leaved crops are initially delimited by the veins to form angular lesions with velvety sporulation on the underside (Figures 2 and 3). In onions, sporulation is visible on the outside of leaves (Figure 4). Sporulation requires humidity and so may not be seen in dry conditions. It is sparsely produced on Rubus spp. Leaves can become thickened and distorted, a symptom that can be severe in hosts such as peas, Brassicas and beet in which infection can also develop systemically from infested seed or as a result of growing the crop in infested soil.

Figure 3. Purple sporulation of downy mildew sporangia on the underside of basil leaves and distortion caused to the new shoot

There are a few aerial Oomycete pathogens that are not downy mildews. Infection of Allium species by *Phytophthora porri* causes water-soaked spots on leaves, which become dry and bleached. In leeks, the leaf tips become white and distorted so giving this disease the name of white tip (Figure 5). Other Phytophthora species, mainly *P. syringae* in the UK or *P. cactorum* in the USA, infect apples and pears to cause a firm dark brown storage rot. *Phytophthora infestans* causes blight on tomato as well as potato, causing water-soaked lesions, which quickly progress to tissue blackening and plant collapse.

White blister is found on Brassica species, with the raised white scab-like structures (Figure 6) as a result of infection by Albugo species, principally *A. candida*, causing crop quality issues.

Identification of infection by Phytophthora species can be aided by the use of lateral flow devices (LFDs) in the field. The affected tissue is broken up in a buffer solution and dropped into the device, which will produce a coloured stripe if positive. There have also been rapid advances in molecular diagnostics and hand-held sequencers currently in use by researchers to test soil and plant tissue are predicted to become a tool for growers.

Figure 4. Velvety grey downy mildew (*Peronospora destructor*) sporulation on onion

Figure 5. White tip on leeks caused by *Phytophthora porri*, showing the white lesions that have caused the collapse of many leaf tips

Figure 6. Pustule of white blister on cabbage caused by *Albugo candida*, seen from both sides of the same leaf. The shiny white surface of the pustule ruptures when the sporangia are ready to release zoospores

Pathogen populations

Races exist in both the downy mildews of Brassicas (*Hyaloperonospora brassicae*) and pea (*Peronospora viciae* f. sp. *pisi*) and cultivars differ in their resistance to different races. The downy mildew affecting lettuce, *Bremia lactucae*, is a very adaptable pathogen, having the ability to develop new races that can overcome the genetic resistance bred into lettuce varieties. Downy mildew, *Peronospora farinosa* f. sp. *spinaciae* recently overcame spinach cultivar resistance to races one to four, with a further 11 races identified by 2015. Races of *H. brassicae* differ in their virulence to different Brassica species. In contrast both tomato and potato can be infected by the same strains of *P. infestans*, however, since the 1980s a second mating type of *P. infestans* has been present in Europe allowing sexual reproduction and multiple clonal lineages in the UK. It is not known if this has led to the development of more-aggressive isolates, so leading to the recent upsurge of reports of tomato blight in glasshouses. All Lamiaceae were thought to be infected by the same species of downy mildew, *Peronospora lamii*, but this species is now only listed on mint, whereas basil is infected by *P. belbahrii* and sage by both *P. salviae-officinalis* and *P. belbahrii*.

White blister infects a wide and diverse range of hosts and the host specificity of *A. candida* has recently been defined as due to distinct species instead of the previous assumption of different physiological races of the pathogen. It is likely that further host and cultivar specificity will be found in other aerial Oomycetes and this has implications for plant breeding for resistance.

Disease sources and spread

The life cycle of Peronospora species (Figure 7) shows how and where infection of a host can potentially take place via airborne and soil-borne spores, seed-borne infection and from debris. Downy mildews that are Peronospora and Hyaloperonospora species produce airborne and splash dispersed sporangia (or conidia) that germinate and enter the host tissue. Plasmopara and Pseudoperonospora species are capable of producing many swimming spores (zoospores) out of one sporangia to splash onto susceptible tissue. The longevity of sporangia and zoospores of various species is, in general, not well documented. Phytophthora and Albugo species produce zoospores at some stage, but their significance and the conditions that stimulate production varies between species, and knowledge gaps exist in their life cycles.

Thick-walled resting spores (oospores) are formed as the pathogen exhausts the supply of nutrients in the host tissue. If the debris is left to decay then the oospores are released into the soil and can survive for at least five years, but information is lacking on their durability under various field conditions. Downy mildew oospores can also be formed on seeds in pods and infect the emerging seedling. Oospores have not yet been found in *P. belbahrii*, but seed batches from which infected basil crops had grown have been shown to contain the pathogen internally. *Pseudoperonospora cubensis* in the UK only has one mating type so cannot sexually reproduce by oospores and so how it persists between cucumber crops is uncertain. In blackberry, oospores are formed, but their role in the overwintering of *Peronospora sparsa* is unclear.

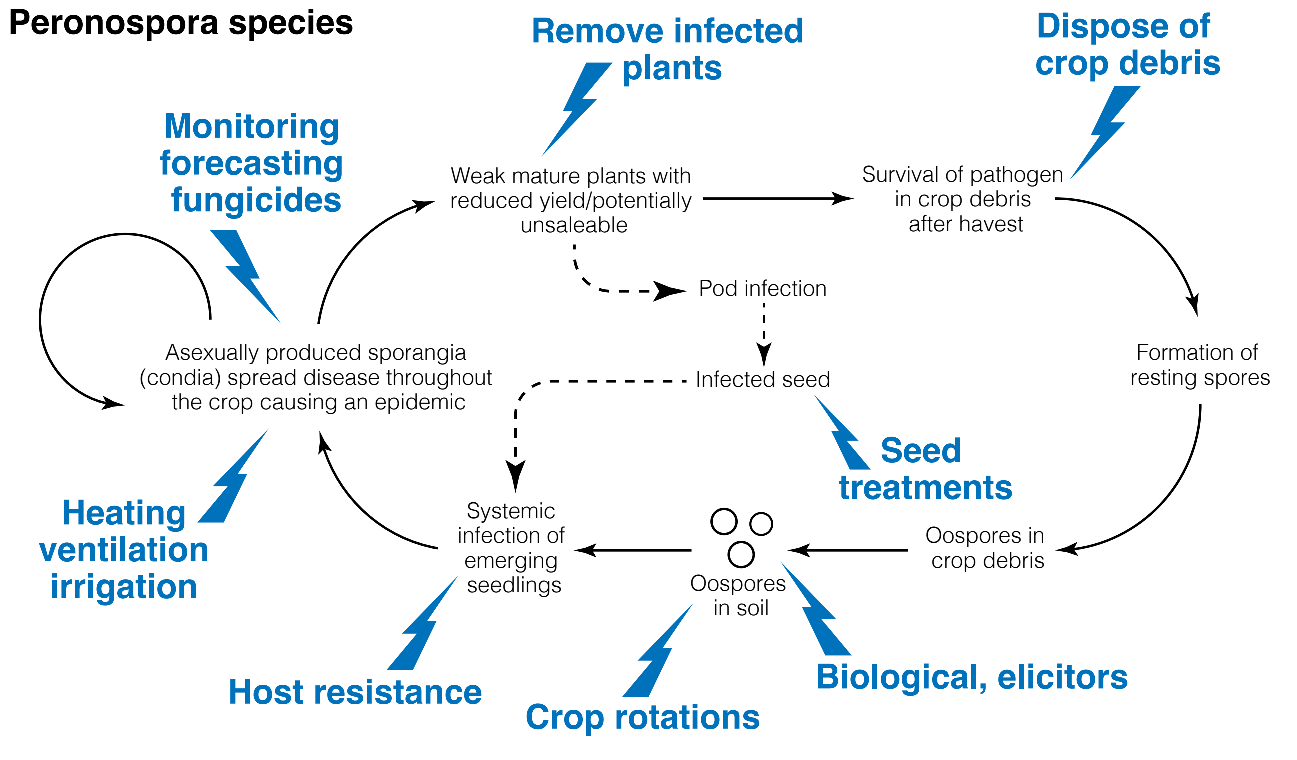

Figure 7. Generalised life cycle of a typical Peronospora species. (downy mildew) and integrated crop management. The arrow-flashes shown in blue indicate stages where control could potentially be achieved

Infection by *P. porri* on Allium species originates from zoospores released by oospores splashed from the soil. Sporulation has only been found infrequently on leek leaves in the field and the involvement of sporangia in subsequent disease spread is unclear. *P. syringae* infection of apple and pear fruit is as a result of zoospore release from oospores produced following saprophytic growth in fallen apple leaves. It is known that Phytophthora species can contaminate irrigation water and cause plant infection, however, this transmission mode is uncertain for downy mildews, although they have been detected in water.

Downy mildew spore germination requires water on the tissue surface, with the wetness duration required before infection occurs varying between pathogen species and with the temperature. For example, *P. belbahrii* infection of basil takes four hours at either 15°C or 25°C but eight hours at 5°C or 10°C; in *Peronospora sparsa* on Rubus species, optimum spore germination occurs at 19°C; whereas optimum infection by *P. destructor* of onion takes place in cooler temperatures of 10–13°C. In parsley, infection is also favoured by low temperatures with *Plasmopara petroselini* requiring only an hour of leaf wetness. Losses to downy mildew are common in propagation and other protected cropping and here forecasting can be used to trigger air circulation before critical conditions are reached. In basil, infection by *P. belbahrii* only occurs when humidity is over 70%, when plants are in darkness. Downy mildew infections can become systemic, particularly after seedling infection and, importantly, some can infect without producing visible symptoms, but still have a negative effect on the crop.

Phytophthora porri zoospore release from oospores is optimal at 8°C and infection seems to require rainfall, possibly by facilitating the splashing of inoculum into leek leaf axils. The role of sporangia in subsequent disease spread is not well understood. In white blister, the infection process of *A. candida* by zoospores from oospores is also unclear, but zoospores released from aerial sporangia require moisture and temperatures around 20–25°C and then infect within four hours. Further investigation is needed to determine the importance to crop production of the significant proportion of *A. candida* infections that can remain symptomless and the ability of *A. candida* to suppress host defences so that pathogens (such as *H. brassicae*) have a greater likelihood of infecting.

Disease management strategies

Integrated management

Established control strategies for downy mildews are shown in Figure 7, with most also applying to aerially dispersed Phytophthora species and white blister. The first step is to understand as much as possible about the life cycle of the particular pathogen on the specific host, in particular if disease transmission arising from infestation in crop debris or soil can be stopped. Removal of infested crop waste, crop rotation intervals of at least five years and any available seed treatment should be used. If aerial infection is likely to be the primary source then crop spacing, and field or protected crop irrigation timing can be set to reduce the period of leaf wetness and so reduce the risk of spore germination and infection; increased ventilation and heating to reduce humidity is also possible under protection. Fungicide programmes, whether chemical or biological, need to be protectant. Alternate chemical modes of action, and continue throughout the crop life or high risk periods, although it may be possible to reduce field applications if a period of dry weather is forecast. Where seed infection is possible then all practical measures should be taken to avoid it. Molecular techniques being developed, including soil sampling for oospores, ongoing aerial spore monitoring, detection of latent infection and breeding for resistance are likely to play an increasingly important part in integrated crop management.

Biosecurity

Biosecurity should always be a priority in crop protection, especially so where propagation material is moved between countries. Unusual symptoms on crops, or poor response to fungicides should be subjected to further investigation in case invasive aliens (or new races) are involved. Recently, downy mildews on basil (*P. belbahrii*) and on rhubarb (*P. jaapiana*) were found to be causing problems in the UK and information on their life cycles has to be elucidated to formulate suitable control plans.

Varietal resistance

Pea variety lists with resistance ratings for downy mildew are published, but similar tables do not exist for most crops as resistance is unknown or not common. That breeding or selecting for resistance traits is possible is shown by the presence of some examples across the crops in Table 1. In cucumber, the resistant cultivars are currently not glasshouse crops. In onion and Brassicas there are a handful of downy mildew resistant commercial cultivars. Advances in molecular techniques, such as gene-specific markers and the association of resistance to particular pathogens with specific physical traits, should accelerate the development of cultivars with effective resistance, spurred on by the loss of chemical fungicides through both legislative changes and loss of efficacy.

Fungicide resistance

The risk of resistance developing to phenylamine fungicides is high, with metalaxyl resistance known to occur in *P. cubensis* in cucurbit, *P. destructor* in onion, *Bremia lactucae* in lettuce and *P. infestans* in potato and tomato. Resistance risk to quinone outside inhibitors (QoIs) (which include azoxystrobin, pyraclostrobin, fenamidone and kresoxim-methyl) is also high and has been found in *P. cubensis* and *Plasmopara viticola* from grape. Even though the carboxylic acid amine fungicides (which include dimethomorph and mandipropamid) have only a low to medium resistance risk, resistance is known in *P. viticola*. Some newer chemical fungicides with activity against downy mildews, such as Infinito (fluopicolide + propamocarb) and Cassiopeia (dimethomorph + pyraclostrobin) have recently become available to horticultural crops via Extensions of Authorisation for Minor Use (EAMU). When using plant protection products it is important to follow guidelines that help to limit resistance development, such as alternating activity groups in plant protection programmes.

Biofungicides

Integration of partially resistant varieties with biofungicide application is likely to improve disease control, but few products are available in the UK and Oomycete biological plant protection products are currently marketed only for Phytophthora and Pythium root infection rather than any aerial infection. The level of protection that biological products offer against aerial Oomycetes and how best to use them requires more investigation. The AHDB AMBER Project CP 158 examines the application and management of biopesticides for both efficacy and reliability. Products are currently being evaluated against leek white tip, and evaluation of biofungicides against other aerial Oomycetes is a priority. Biofungicides have multiple modes of action (so reducing the chance of resistance), including competition for space and nutrients, direct attack by hyphal penetration or enzymatic activity and stimulation of the host's natural defence mechanisms, often systemically. Various different bacterial species have shown activity against *H. brassicae*, *P. cubensis* and *P. viciae* f. sp. *pisi*, but require development as commercial products. Similarly, potential for chemicals that work as plant defence stimulants, some of which are plant extracts, has already been shown in *H. brassica*, *P. cubensis* and *P. sparsa*.

Disease forecasting

Forecasting infection by aerial Oomycetes is possible where the conditions required for infection are known and the availability of in-field meteorological stations with data transfer to a distant electronic device means that information on local weather conditions can be acted on promptly by fungicide spray operators. A number of programmes for UK farmers have been set up (Brassica$_{spot}$ and currently Brassica Alert for white blister of Brassicas, MILIONCAST for onion downy mildew, CropMonitor for spring bean downy mildew and BlightCast for potato). A research goal is to speedily add in information from sampling for the presence/absence of spores in monitored crops to forecasting programmes, meaning that sprays potentially could be saved for higher risk timings. However, because infection can take place, in optimum wet conditions within three hours of a spore landing, then stopping this infection in time is difficult. Reactive sprays triggered by a positive result from spore sampling may thus best protect against the subsequent spore dispersal to other plants following sporulation, which can occur a week after the initial infection.

Diagnostics

In-crop visual diagnosis of Oomycete foliar infections is relatively easy when there is sporulation, and is essential for selecting the correct plant protection products. Lateral flow devices (LFDs) using antibodies to confirm the presence of Phytophthora species are available commercially. One issue with both LFDs and molecular tests is that they also show positive for dead pathogens, however recent research with root-infecting Phytophthora species has created antibody cell lines that can discriminate between zoospores (which should be alive) and mycelium (potentially dead) in water samples and this could further be developed for aerial Oomycetes. The technique of propidium monoazide (PMA™) based qPCR is currently being explored in research on Phytophthora species in order to seek to quantify viable (living) pathogen material. Molecular (DNA) methods based upon the polymerase chain reaction (PCR) to replicate and multiply DNA sequences to allow accurate identification can also be used quantitatively and there is potential to use this to assess oospore levels in soil. The equipment used in molecular testing has become smaller and faster with loop-mediated isothermal amplification (LAMP) and the hand-held DNA sequence generator called MinION and is moving towards being a tool for use by growers. Next generation sequencing (NGS), which allows the sequencing of whole populations of microbes (such as in soil), differs from other diagnostics in not looking for specific organisms and will be able to warn growers which of multiple potential pathogens present in a soil are likely to be reducing crop performance.

These molecular techniques are currently more applicable to research rather than field applications because of their cost, but hand-held sequencers are predicted to become a tool for use by growers in the future.

Key knowledge areas

Project CP 157 identified eight key knowledge areas that are important to achieving effective and sustainable control of aerial Oomycete pathogens in UK horticultural crops. These are: host specificity, cultivar specificity (races), resistant cultivars, optimum conditions, forecasting, molecular diagnostics, fungicide resistance and biocontrol. The reports listed below made significant advances in particular areas, and it is anticipated that recently commissioned work will further fill some of these knowledge gaps.

Further information

AHDB Horticulture factsheets and publications

AHDB Factsheet 08/11 'Downy mildew of basil'.

AHDB Factsheet 14/12 'Downy mildew on vegetable Brassicas'.

AHDB Factsheet 23/12 'White blister on vegetable Brassicas'.

AHDB Factsheet 01/13 'Practical measures to prevent and manage insecticide, fungicide and herbicide resistance in horticultural crops'.

AHDB Factsheet 20/13 'Fungal diseases on canes, foliage and fruit of cane fruit crops'.

AHDB Factsheet 18/14 'Getting the best from biopesticides'.

AHDB Crop Walkers' Guides are available for most crops and describe disease symptoms.

AHDB website: Best Practice Guidelines to Integrated Pest and Disease.

Management on Protected Herbs (Herb Best Practice Guide). **herbs.ahdb.org.uk**

AHDB Horticulture grower summaries and reports with knowledge advances relevant to aerial Oomycetes

CP 077 – Sustainable crop and environment protection – targeted research for edibles (SCEPTRE) (O'Neill, 2015).

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, 2015).

CP 099b – Evaluation of the horticultural industry requirement for on-site diagnostic tests for crop pathogens and their use within disease management systems (Wakeham, 2013).

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, 2015).

CP 126 – A desk study review of global knowledge on best practice for Oomycete root-rot detection and control (Pettitt, 2015).

CP 157 – Aerial Oomycetes: Assessing management and control options needed in UK edible and ornamental crops (Hamilton, Wedgwood, Cromey, Scrace, Denton, van Sprang and Pettitt, 2016).

CP 158 – Application and management of biopesticides for efficacy and reliability (AMBER) (Chandler, 2017).

FV 053e – Brassicas: Further development of a spray-timing model for white blister (*Albugo candida*) in vegetable Brassica crops within the $\text{Brassica}_{\text{spot}}$ system (Kennedy, 2005).

FV 172 – Leeks: control of white tip (*Phytophthora porri*) (Locke, 1996).

FV 189a – Onions: development of detection systems for conidia of *Peronospora destructor* (downy mildew) in onion crops (Wakeham and Kennedy, 2006).

FV 189b – New products for the control of downy mildew (*Peronospora destructor*) in bulb and salad Onions (Richardson, 2006).

FV 215 – Vining Peas: downy mildew control (Biddle, 2000).

FV 226a – Red beet: further elucidation of the cause, epidemiology and control of root malformation disorder (RMD) (McPherson, 2003).

FV 284 – Improving the value of downy mildew resistance information for UK spinach growers (Thomas, 2009).

FV 293 – Evaluating new fungicides for the control of downy mildew on spinach (Thomas, 2007).

FV 313 – Brassicas: Integrating fungicide usage with risk assessment for ringspot, dark leaf spot and white blister (Kennedy, 2010).

FV 316 – Baby leaf crucifers: Improving control of downy mildew (Gladders, 2009).

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).

FV 357 – Outdoor lettuce: evaluation of novel fungicides for downy mildew control (Gladders, 2010).

FV 436 – Pea downy mildew diversity in the UK (Maguire, 2015).

FV 446 – Leeks: White tip control (*Phytophthora porri*) (Wedgwood and Huckle, 2017).

PE 024 – Basil: Improving knowledge and control of downy mildew in protected and outdoor crops (Jennings, 2016).

SF 085 – Blackberry: evaluation of fungicides for improved control of downy mildew and purple blotch (O'Neill, 2010).

Acknowledgements

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