

A review into control measures for blackberry downy mildew (*Peronospora sparsa*)

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Guy Johnson and Ruth D'Urban-Jackson

ADAS Boxworth, Battlegate Road, Cambridgeshire, CB23 4NN

Background

Control of downy mildew in commercial blackberry production is becoming increasingly difficult. Losses of effective spray control products in recent years, particularly close to harvest, have exacerbated the problem. Novel and alternative approaches will be required in future. AHDB has already funded several projects to assess new control measures, but this desk study aims to identify additional ideas.

Summary of main findings

- Use of protected cropping to reduce leaf wetness will help minimise infection
- Good site selection to maximise light interception, maintain good air movement and avoid natural sources of infection is important
- Maintain good air movement by removing weed growth in the crop vicinity and managing the crop to avoid excessive vegetative growth
- Reduce relative humidity below 85%. The use of air fans in glasshouse crops improves air movement
- Manage nitrogen application carefully to avoid excessive leaf growth
- Photosensitive polythene to alter the wavelength of light reaching the crop could affect the infection rate, but this requires further study
- The efficacy of the currently approved biopesticide control agents Serenade ASO, Sonata, Amylo X and Prestop requires further assessment
- Elicitors (such as potassium phosphite) and plant extracts are known to offer varying levels of control, but these need further screening to assess their relative efficacy compared with other control agents
- Any control products showing significant levels of control would need to be registered as plant protection products and require approval before they could be used legally

Introduction

Demand for blackberry fruits (*Rubus fruticosus* L.) in the UK is ever increasing, with national production expanding from 194 ha in 2014, to 284 ha in 2016.^{1,2} Blackberries as fresh products have seen an increase in production, rising from 81% to 95% of total production between the same periods. Alongside this increased production, disease pressure remains a constant challenge, with many growers focusing on developing an integrated pest management (IPM) programme.

Downy mildew, caused by *Peronospora sparsa*, is a major disease of blackberry. If left uncontrolled, it can cause crop losses of up to 50% and, in extreme cases, can result in complete crop loss in the UK,³ amounting to losses of £35,000/ha.⁴ In Mexico, crop losses of up to 70% often occur.⁵ *Peronospora* spp. are considered to be the largest genus in the downy mildew family, with around 450 described species.⁶ They are mostly limited to distinct hosts or a very limited number of hosts.⁷ *P. sparsa* only infects *Rubus* species and the *Rosa* genus. In rose, customers' requirements for high aesthetic standards mean that *P. sparsa* infection can lead to complete crop loss, valued at £29,000/ha.⁴

Regular crop monitoring is an important part of IPM. It requires knowledge of the life cycle and expression of disease symptoms and the conditions favourable to infection and spread. Diagnostic tools present options for early disease detection. Integrating variety selection and cultural practices with selective use of biological and chemical plant protection products leads to improved control. These areas are all covered in this review.

Various academic and commercial resources have been reviewed, using search terms containing “*Peronospora sparsa*”, “downy mildew” and “blackberries” in Web of Science, Researchgate and Google Scholar. For the purpose of this report, literature on *P. sparsa* on blackberry was the main focus, but where relevant, work involving *P. sparsa* on rose was also included. There was no year cap on internet literature searches because there is limited work available on blackberry downy mildew, both in the UK and globally.

Disease symptoms

First symptoms of *P. sparsa* on blackberry occur as foliar discoloration. Starting on the upper leaf surface, yellow angular lesions turn a reddish-brown as they age (Figure 1). These lesions are typically located along a midrib or major vein, but in favourable conditions can expand to cover the entire leaf area, causing leaf abscission. Young, softer leaves are more vulnerable to infection, but lesions can occur on leaves of any age. Foliar symptoms depend on the disease pressure throughout the season and are thought to be associated with the local humidity/temperature around individual leaves, or the cultivar. On well-developed lesions and in conducive climatic conditions, spore-bearing structures emerge on the leaf underside. Occurrence of these on host plants, however, is rarely observed – hence the name *P. sparsa*. Alongside foliar damage, *P. sparsa* can affect the developing fruit, causing premature reddening, irregular ripening, shrivelling and splitting caused by dehydration.

Within commercial production, if susceptible varieties of blackberry do not receive suitable fungicide applications, new lesions can develop throughout the season. In June 2019, the first sightings of *P. sparsa* on blackberry were noted in Kent and, subsequently, in Hertfordshire in early July.⁸



Figure 1. Foliar symptoms of downy mildew (*Peronospora sparsa*) on blackberry, including reddish-brown angular lesions (top and middle-left) on upper leaf surface and grey discoloration on leaf underside (bottom left). Irregular ripening of blackberry fruit (right)

Source: ADAS

Life cycle of *Peronospora sparsa*

Understanding the life cycle and conditions that favour *P. sparsa* infection in commercial blackberry is essential for timing correct fungicide applications to reduce disease progression. Cross-inoculation trials with *P. sparsa* isolates from both rose and blackberry showed that an isolate from either host is capable of infecting the other.⁹ Therefore, research on both crops has been discussed here.

As an obligate biotroph, *P. sparsa* is fully reliant on the metabolites provided by its host for survival.¹⁰ Upon landing on a target leaf, *P. sparsa* spores germinate and hyphae enter the leaf tissue, either by breaking down the plant cell walls via hydrolytic enzymes, or by entering through the stomata.¹¹ Once hyphae enter the leaf tissue and form haustoria, *P. sparsa* becomes nutritionally dependent on the living host cells.¹² The extracellular proteins secreted from *P. sparsa* hyphae and haustoria are key in modulating the host plant's immune responses and metabolism.¹³

Once established within the plant, *P. sparsa* can instigate asexual reproduction, forming spore-bearing structures (sporangiophores) that emerge from stomata (Figure 2¹⁴), stem and flower openings.¹⁵ These sporangiophores produce spores (conidia), which, under ideal conditions, are produced in abundance, quickly spreading the infection. In rose, *P. sparsa* conidia were shown to have a very high potency for infecting leaves: only 40 conidia per leaflet resulted in near-maximum incidence of disease under experimental conditions.¹⁶ This work also confirmed that while free water is essential for initial infection, it is not necessary for sporulation. In

fact, under continuously wet conditions, their isolate of downy mildew sporulated much less than in interrupted wet regimes. Copious sporulation was observed under dry conditions following the infection wet period (Figure 16).

As sporangiophores develop conidia, they are dislodged from the leaf tissue by moist wind or water splash,¹⁷ and can spread the infection to other parts of the plant, as well as to neighbouring plants and plant debris.

This asexual reproduction will only occur when conditions are favourable, such as in high humidity. At a relative humidity (RH) of 85–100% and temperatures of 15–22°C, germination can be rapid.¹⁸ In work conducted on rose, plants were unaffected by *P. sparsa* when the RH was less than 85%.¹⁹ These spores are responsible for secondary infections on foliage.

Alongside asexual reproduction, *P. sparsa* can undergo sexual reproduction to form oospores – the progeny of sexual reproduction requiring two different mating types and resulting in nuclear fusion and genetic recombination. They form when growing conditions are favourable, producing tougher, robust spores. These resting spores remain viable for many years – far longer than the few days of conidia.

The extensive genetic variation generated by sexual reproduction in the pathogen population has the potential to induce a new epidemic caused by increased virulence and a lack of control of the new species.²⁰ This is important to note because new races have the potential to infect cultivars that are deemed to be resistant. For example, in spinach, existing resistant cultivars are losing their effectiveness against new races of *P. effuse*.²¹

Within a blackberry crop, once leaves have abscised, oospores of *P. sparsa* overwinter in leaf litter. These remain in the soil and are thought to reinfect its host in the following season, but the details of this remain largely unknown.

Disease sources

Various inoculum sources exist for *P. sparsa*, including wild *Rubus* species, which act as hosts and provide a source of inoculum for new plantations.^{16,17} However, the host specificity of *P. sparsa* means these sources are limited and can often be removed easily.

Although not found to be systemic in roses,¹⁶ *P. sparsa* can become well established within its host plant's leaf and stem tissue. *P. sparsa* DNA has been found in the cortex of crown tissue of rose mother plants that were used for propagation, leading to the potential infection of all propagules.²² This is supported by other research,¹⁸ in which intracellular mycelium was found to be responsible for the infection of neighbouring rose leaflets.

Various ways in which *P. sparsa* can overwinter or maintain itself on dormant material have been suggested, but the precise mechanisms employed in this life-stage on blackberry remain unknown.

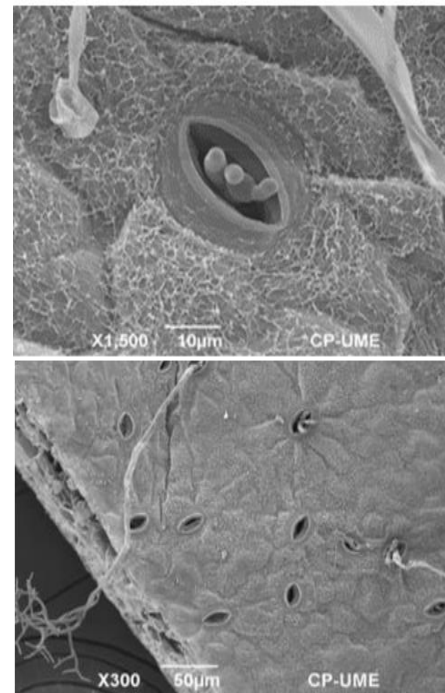


Figure 2. Sporangiophores emerging from stomata

Source: Romero et al.¹⁴

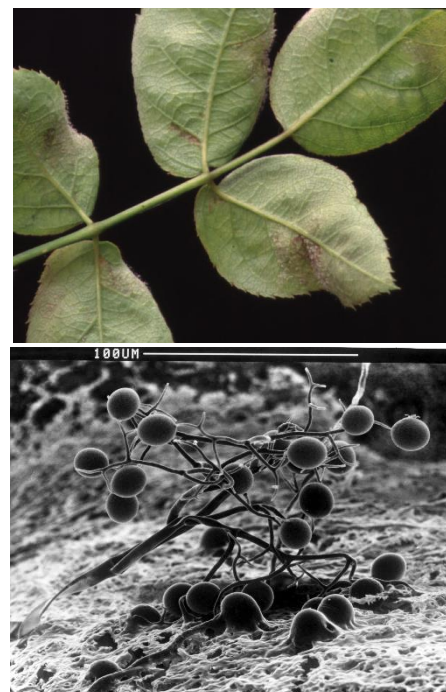


Figure 3. Rose leaflet with sporing *Peronospora sparsa* lesions (top). Scanning electron microscope image of rose downy mildew conidia (bottom)

In roses, *P. sparsa* oospores have been found to form inside the leaf and stem mesophyll, where they have the potential to act as a source of inoculum for future infections. This work also found oospores deposited in particular leaf areas, in relation to discolouration (Figure 4). It would be valuable to confirm whether this is the case in blackberry leaves.

In rose, overwintering oospores of *P. sparsa* in dead leaves and leaf litter were found to be the most important source of disease for the crop, in addition to mycelia on the wood.¹⁶ In blackberry, growers have found it useful to remove the symptomatic bottom leaves from canes when foliar symptoms are spotted.³

It is not clear whether the overwintering oospores of *P. sparsa* in the soil directly go on to infect roots, or if – like *Phytophthora porri* – water splash from the surface of the soil up on to the stems/leaves is required. With an estimated 41% of growers growing directly in soil,² fully understanding the role of oospores in soil could be valuable for identifying better methods of control. Blackberry plantations in substrate/pots would also benefit because plants are typically used for at least 2 years.

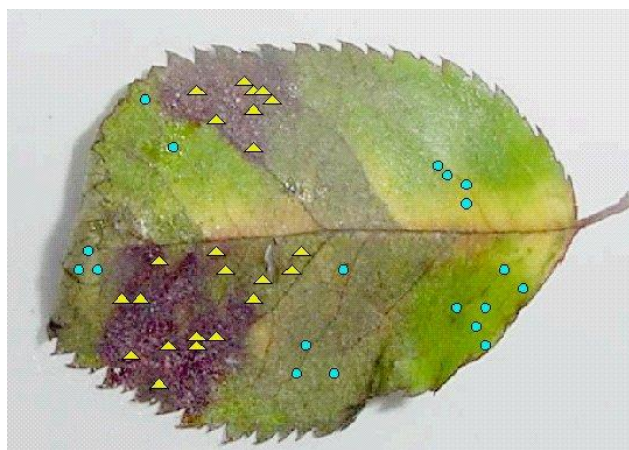


Figure 2. Illustration of *Peronospora sparsa* conidia and oospore distribution on an infected rose leaf. Triangle symbols indicate where oospores were observed, and circles indicate where conidia were observed

Source: Defra¹⁶

Conditions favouring disease development

Leaf wetness is the most important factor in the infection process of *P. sparsa*.²³ Two hours of total leaf wetness is required for conidia to germinate. In addition, on average, 8.4 hours of leaf wetness per day over a 10-day period (within the optimal temperature range) will result in spore germination, with symptoms appearing within 4 days.²⁴ High humidity is also key, where an RH above 85% allows for high production of conidia. The temperate UK climate often results in humid nights and has resulted in at least one UK propagator moving production of the susceptible variety Loch Ness to Europe, where nights are drier and humidity is lower.²⁵ Plant row layout affects the local leaf humidity, so insufficient ventilation can result in an increased risk of *P. sparsa* infection. Some rose growers use fans to better ventilate glasshouse production. Where possible, in outdoor protected blackberry, tunnels should be positioned to face incoming wind to reduce still air and the development of humid conditions.

Temperature is another important factor. *P. sparsa* sporulation and infection below 5°C is poor, but still possible. This is similar at the other end of the spectrum, between 30 and 33°, when new infection still can be initiated.²⁶ Ideal temperature range varies across published work, but in general 15–22°C results in higher rates of *P. sparsa* sporulation.

Environmental monitoring has become financially and logistically possible for some areas of horticulture, such as that seen on the 30 MHz platform. This uses a variety of in-crop sensors to record real-time temperatures and humidity, so while limited actions are possible to manage these climatic conditions in a polytunnel, it will at least show when conditions have been right for the pathogen, so the grower will be alerted to look for symptoms. Prediction models are also an option, giving growers an early indication of disease pressure. Aegerter et al.²⁷ developed a logistic regression model for predicting downy mildew in Californian 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* populations, therefore these parameters could be different in the UK. Within the UK, the free service Blightwatch© for control of *Phytophthora infestans* alerts potato growers when certain climatic criteria are reached.²⁸ A similar system could be established for downy mildew in blackberry.

Control strategies

Detection

Detection of early stage *P. sparsa* infection within a blackberry crop would provide huge benefits to growers. Not only would it reduce the number of misidentified diagnoses (one of the main problems in controlling the disease), but it may also allow infected crops to be identified earlier, before visual symptoms develop.

Certain molecular assays use polymerase chain reaction (PCR) technologies, which use a portion of ribosomal DNA²⁹ specific to *P. sparsa*. Detection assays have been developed that are capable of detecting the pathogen from plant tissue. Aegerter²² designed an assay for use on dormant woody rose rootstocks, which can detect as little as 2 pg of *P. sparsa* DNA.²⁹ Alongside this, nested PCR is also an option, with detection of *P. sparsa* from leaf samples;^{30,31} however the lowest detection limit was unknown. In addition, an enzyme-linked immunosorbent assay (ELISA) is available for testing infected rose leaflets using the primers PS 1/3 and PS 3/4 designed by Schulz and Debener,³² the latter primer giving extreme sensitivity but also a lower specificity.

Wedgwood⁴ discusses various diagnostic options for aerial oomycetes, which relate to *P. sparsa*. Equipment used in molecular testing is becoming smaller and faster, with loop-mediated isothermal amplification (LAMP) and by the portable hand-held DNA sequence generator MinION, moving towards a useful tool for growers. The economic damage that many oomycetes can cause means several genomes have been sequenced to provide a fuller understanding of how they function and proper identification. *P. sparsa* has not been sequenced, but there may be some benefit gathered from sequencing carried out on: *P. effusa*, *Plasmopara viticola*, *Plasmopara halstedii*, *Plasmopara muralis* and *Pseudoperonospora cubensis*.³³

Separate to molecular diagnostics, infrared thermographic imaging has been evaluated as a non-invasive method of *P. sparsa* detection and can also be used before the development of any visible signs of disease.^{18,34}

During the early stages of infection, a significant increase in leaf surface temperature is observed (Figure 3), with a decline in temperature once sporangia production begins (Figure 4). This allows *P. sparsa* to be detected 2 days earlier than a visual assessment, though the method has not been tested in a commercial setting.¹⁵ There is potential for this technology to be used in blackberry production, where it would allow a quicker response time when an infection is found. It may also serve blackberry propagators, who could scan through their young crop and remove pre-symptomatic plants before they are either used for further plugs, or sold on to growers.

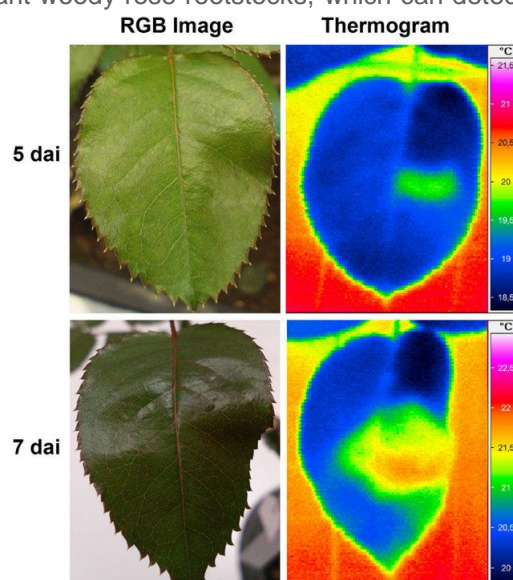


Figure 3. Thermal imaging of rose leaf infected with *Peronospora sparsa*

Source: Mahlein 2015³⁴

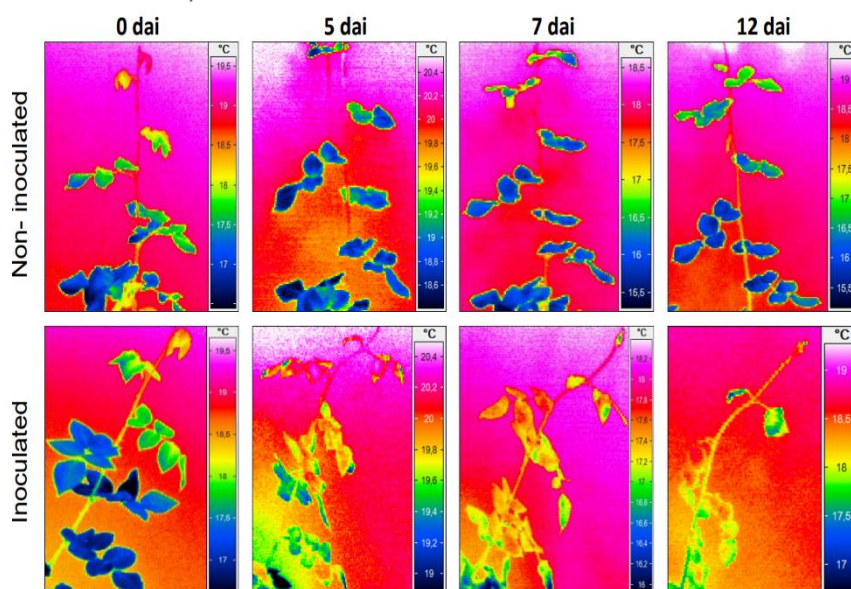


Figure 4. Effect of *Peronospora sparsa* on leaf temperature of rose plant during pathogenesis using infrared thermography

Source: Gómez Caro 2014¹⁸

Variety selection

Although not always top priority in breeding programmes, selecting for disease resistance is important for reducing the amount of fungicide required and preventing the development of chemical resistance in the pathogen.

While some of the most popular blackberry varieties, such as Loch Ness and Black Butte, are very susceptible to *P. sparsa*, others, such as Karaka Black and Navaho, show some levels of resistance to the pathogen. The cultivar Chester Thornless is reported to have good disease resistance and grows well in the UK, but is not prominent in commercial production.³⁵ Globally, no commercial varieties are known to be fully resistant to *P. sparsa*, with other diseases and factors taking priority in current breeding programmes in the UK, such as fruit quality. Lines of arctic bramble (*Rubus arcticus*) have shown some resistance to *P. sparsa*,³⁶ and wild varieties such as *R. cymosus*, recently found in Mexico, could act as a foundation for new resistant varieties.²⁹

In Oregon, USA, a state with similar climatic conditions to the UK, downy mildew on blackberry is a minor issue. This is largely because cultivar resistance (e.g. Marion and Obsidian) and the fact that less than 1% of planted area is in tunnels,³⁷ so humidity is not as big a problem. Growers also have access to more chemical fungicides (Appendix 1) than in the UK.

Cultural control methods

Various cultural management options can reduce sources of downy mildew inoculum and limit in-crop damage. These include;

- Using certified nursery stock that are free of the pathogen
- Proper site selection. Ideal areas are those that receive at least 8 hours of light each day and are not planted too closely to natural woodland or tall hedgerows, which act as a primary natural source for *P. sparsa* from wild *Rubus* spp.
- Removal of suckers and weeds, which, at plant establishment, is essential to allow good airflow around the base of the plant. The lower leaves of mature plants can also be removed for this reason. Removal of debris throughout the season, such as dead plant leaves, is also good practice, as these can host *P. sparsa*, leading to repeat infections
- Protection against rain and avoiding overhead irrigation and/or watering early in the day to ensure leaves are dry by sunset. These actions will all minimise leaf wetness and subsequent spore germination. In the UK, 83% of blackberries produced are grown under tunnels – a key reason being that the plants grow in a drier environment that is free of rain²
- On outdoor blackberry crops, target fungicide sprays before rainfall events
- Sufficient pruning, to improve airflow around plants and reduce relative humidity (RH) to below 85%
- Reducing planting density. Where cultivars are known to be vigorous, ensure suitable spacing to avoid crowded foliage

The use of fans is recommended in glasshouse rose production,³⁸ as this greatly improves airflow around the crop, reducing the infection rate of *P. sparsa*. A similar approach could be adapted for blackberry production, but may not be financially or logistically feasible.

Production of blackberries under protection may reduce the volume of rainfall hitting foliage, but it can also result in increased humidity. Under such conditions, tall grass, weeds and nearby hedgerows provide shade and aid condensation. Growers should ensure tunnel RH is kept below 85%. Where this is not possible, growers could consider growing without protection, such as those in Oregon, but be mindful of rain wetting leaves.

Nitrogen application is another important consideration. Jiang and Caldwell³⁹ found that nitrogen application over 100 kg/ha increased the incidence of downy mildew. The nitrogen prolonged the crop's vegetative stage and increased the young succulent tissue, creating a better environment for *P. sparsa* development. This issue can be avoided in soil-grown crops, depending on the soil type: light sand and shallow soils require 120 kg/ha,⁴⁰ but not over 100 kg/ha for deep silty soils and clay.

Light may also be key in pathogen epidemiology, as seen in the sporulation of *P. belbahrii* on basil. When basil plants are exposed to 10 $\mu\text{mol m}^{-2}\text{s}^{-1}$ of nocturnal illumination, no disease was reported until 18 days after planting; in the control, 32% of plants were infected at the 18-day mark. Further tests showed that light intensity affected disease development, with plants exposed to 8 $\mu\text{mol m}^{-2}\text{s}^{-1}$ appearing 85–97% protected. The level of protection dropped off as shading caused by new growth prevented even light distribution and allowed more

spores to disperse. This trial also found that red light inhibited spore formation more than blue light, which is at odds with previous research, in which blue light was found to suppress *Peronospora* spp.⁴¹ Choudhury⁴¹ found that red light was one of the least favourable wavelengths for spore germination of *P. effusa*. Additionally, light intensity has been shown to be key in the germination of *P. effusa* spores; however, results varied amongst the isolates used. One potential explanation for this is that *Peronospora* spp. all have unique photoreceptors that react to light wavelength and intensity differently.⁴²

With 83% of blackberry production being under tunnels², it may be valuable to assess whether the use of photoselective polythene to alter the wavelengths of light reaching the crop would have an effect on the *P. sparsa* infection rate.

Chemical fungicides, biopesticides and elicitors

Chemical fungicides

Fungicide use is becoming increasingly restricted. Repeated use of fungicides within the same Fungicide Resistance Action Committee (FRAC) groups risks resistance developing in pathogen populations, which further compounds the issue of limited chemical control options. In consequence, products have the maximum number of applications stipulated. Further restrictions on the selection of products within programmes results from the long harvest intervals of some products, so they cannot be used during fruiting, although this is when conditions can be particularly favourable for downy mildew.

Depending on the plant protection product used, sprays can be applied to new foliage, flowers and developing berries. Issues can arise when there is a need to protect developing primocane (May/June) and avoid leaving residues on developing fruit (as was seen with chlorothalonil).

Of the current chemical fungicides available for blackberry downy mildew, only pyrimethanil, dimethomorph and fluazinam have known activity against downy mildew pathogens. However, the product Tizca (fluazinam), granted Extension of Authorisation for Minor Use (EAMU) on 13 May 2019, can only be applied via drip irrigation, or sprayed directly on the base of the plant because it targets raspberry root rot (*Phytophthora rubi*). It can also only be used during stages 1 and 3 of propagation, so is not applicable for use on mature blackberry plantations.

Recent work on downy mildew control in sunflower found Plenaris (oxathiapiprolin) to be highly effective.⁴³ In vitro testing found strong suppression of zoospore release and cyst germination by Plenaris. Syngenta currently markets Plenaris as a seed treatment in the USA.

Biopesticides

Alongside approved chemical fungicides, the biopesticides Serenade ASO, Sonata (protected crops only), Amylo X and Prestop are also available, through EAMU.

Serenade ASO (*Bacillus subtilis* strain QST 713) was recently approved for use on blackberries, but data on its efficacy against *P. sparsa* on UK blackberry is limited. Over 3 years of testing in Mexico, Boyzo-Marín et al.⁵ found *B. subtilis* to provide low level control on blackberry. In work conducted in India on downy mildew on maize, Sireesha and Velazhahan⁴⁴ found a 54% reduction in disease incidence on seedlings that had received a *B. subtilis* seed treatment. *B. subtilis* has also been found to give significant control against the oomycete *Pseudoperonospora cubensis* on cucumber under greenhouse conditions.^{45,46} Together, these findings indicate potential efficacy of *B. subtilis* against *P. sparsa* on UK blackberry, so is something that should be explored in further work.

Sonata (*B. pumilus*) is also authorised for use on blackberry but, although extensive work has evaluated its use for powdery mildew control, limited information is available about its control of oomycete downy mildew plant pathogens. El-Gremi et al.⁴⁷ confirmed loss of turgor and osmolysis of *P. cubensis* sporangia on cucumber leaves treated by liquid culture of *B. pumilus*. Amylo X WG (*B. amyloliquefaciens*) has been trialled against the fungal powdery mildews, but not so extensively against downy mildews. Palmer and Veal⁴⁸ found that typically, *Bacillus* strains offer poor control of the *Peronospora* genus.

A recent study exploring the use of biological control on downy mildew in grape vine found that use of *Streptomyces viridosporus*, a currently unregistered active, showed an increase in phenol content and increased activity of the antioxidant enzyme peroxidase. *Trichoderma harzianum* has shown control against downy mildew in grapes.⁴⁹ The product Trianium P (*T. harzianum* strain 22) has approval for use on blackberries, in both propagation and cultivation, under EAMU 3433 of 2016.⁵⁰ However, since it is not native to the UK, it can only be used under permanent protection with full enclosure, so is not an option for all UK growers.

Closely related to *Trichoderma* is *Gliocladium catenulatum*, the component of Prestop (*G. catenulatum* strain J1446). Work on tomato late blight (*Phytophthora infestans*, a close relative of the downy mildew *Peronospora* spp.) found *G. catenulatum* to have no curative activity.⁵¹ *G. catenulatum* did show activity against *Phytophthora* and *Pythium*,⁵² but further work is required to investigate its effect on *Peronospora* spp.

In work investigating the use of *Aneurinibacillus migulanus* strains, gramicidin secondary metabolites were identified.⁵³ The work highlighted *A. migulanus* strain NCTC 7096, which showed potential as a biocontrol agent against plant diseases and this led to efficacy work on cucumber downy mildew (*Pseudoperonospora cubensis*). Here, Schuster and Schmitt⁵⁴ demonstrated that both the biosurfactant of *A. migulanus* liquid culture and *A. migulanus* spores containing the metabolite gramicidin-S contributed to the control of *P. cubensis*. The authors reported a 90% reduction in *P. sparsa* disease when the spores and liquid culture of *A. migulanus* were used in a preventative manner rather than curatively. This was achieved through the reduction in time taken for the leaf to dry, thus reducing the number of conidia produced by the pathogen. The authors also found similar efficacy against *Phytophthora infestans*, suggesting this product has good potential for control of downy mildew and other foliar oomycete diseases.

Elicitors

With limited fungicides available, other modes of action for control of *P. sparsa* are being investigated. One set of products includes elicitors that induce plant immune responses.⁵⁵ They trigger defence reactions in plants by copying the way in which plants' natural elicitor defence signalling molecules respond to infection, or by interrupting other defence signalling components. These plant immune responses can be the direct activation of defences and can lead to the priming of cells, which results in stronger elicitation of those defences. While elicitors rarely give complete control of pathogens, they can often reduce the severity of the attack.

Potassium phosphite is a well-known plant elicitor. In cucumbers, treatment with potassium phosphite prior to infection by downy mildew (*P. cubensis*) was found to be more effective than treatment after infection.⁵⁶ Potassium phosphite works as an elicitor, increasing thaumatin-like proteins, which have been found to inhibit hyphal growth. Additionally, potassium phosphite increases phenolic and flavonoid components, both of which are considered important defence compounds and occur in higher concentrations in resistant varieties of various crops.⁵⁷ Concerns over residue levels were addressed in 2018, with a modification of the existing maximum residue level from 100 mg/kg to 300 mg/kg of fosetyl (or 200 mg/kg of phosphonic acid).⁵⁸

Frutogard is a potassium phosphite product registered in the UK for use on table and wine grapes, with a harvest interval of 24 days and a maximum of six applications per year. This product has been trialled in several SCEPTREplus efficacy trials (2018/19). Soriale is a potassium phosphate fungicide, produced by BASF for use on apple and pears, with a maximum of six applications and a minimum of 35 days between the last application and harvest. For apples, it can be used up to 81 on the BBCH scale: the beginning of ripening at the first appearance of cultivar-specific colour. While no potassium phosphite products are currently on the market for blackberries, the availability of products for other crops means there is potential for extensions of use to blackberries. However, if given a long harvest interval, they may only be of use in propagation.

Chitosan hydrochloride has been listed as a basic substance for use as an elicitor of plant defences against fungal and bacterial pathogens. It has demonstrated effectiveness in the control of *P. sparsa* on rose.⁵⁹ Products such as HortiPhyte, Fortify 30-20 and Fortify Cu are marketed as plant fertilisers and contain phosphites, but are not currently registered as plant protection products.

Plant extracts

Plants extracts are another target in the search for plant disease control because plants have honed certain compounds to naturally fend off pathogen attack.

In the related oomycete *Plasmopara viticola*, the potential for plant extracts to offer control of downy mildew control on grape is being explored. Arysta LifeScience is developing a plant extract-based product that works like a typical elicitor, offering increased hydrogen peroxide production and the upregulation of pathogenesis-related proteins. In work conducted by Krzyaniak et al.,⁶⁰ their coded plant extract gave rise to an accumulation of resveratrol, a natural phenol produced by plants in response to injury or pathogen attack. The plant extract also left a dried residue on the leaf surface, impairing zoospores' ability to reach the stomata.

In other work on *P. cubensis* in cucumber, which took place in greenhouse trials in Egypt across two seasons, castor and clove oils were found to significantly reduce disease severity.⁴⁵

In consultation with the manufacturers, evaluation is required of newer fungicides and oomycides lacking approval for use on soft fruit, as well as biological products such as foliar feeds and plant extracts. **Table 1** summarises candidate products discussed in this review that have shown efficacy against downy mildew plant pathogens on horticultural crops.

Table 1. Preliminary list of candidate products to test for efficacy against blackberry downy mildew

Candidate product	Active ingredient	Manufacturer	Product type
Frutogard	Potassium phosphonate	Certis	Biological
Soriale	Potassium phosphonate	Syngenta	Biological
Plenaris	Oxathiapiprolin	Syngenta	Chemical
Chitosan hydrochloride	Chitosan hydrochloride	Numerous	Basic substance
HortiPhyte	Phosphite	Hortifeeds	Plant fertiliser
Fortify 30-20	Potassium Phosphite	EngageAGRO	Plant fertpliser
Serenade ASO	<i>Bacillus subtilis</i> strain QST 713	Bayer	Biological

Conclusions

This review has highlighted our lack of understanding of some aspects of the life cycle of *P. sparsa*.

Proper understanding of the role that oospores play when overwintering in the roots and soil is important for better control of the pathogen because it is not known whether they aid in the repeat infections in the following year. Control of persistent oospores could be a key aspect in reducing the impact of downy mildew on blackberry, but requires further investigation.

Breeding resistant varieties should be a key focus and would act as a foundation on which to build the rest of the integrated management plan. Products with a slower or incomplete control of the pathogen, including microbial and elicitor products, would be able to work in conjunction with varietal resistance to provide a satisfactory level of control.

Growers who produce outdoor blackberries could consider moving to a protected cropping system, whereby the use of polytunnels will reduce leaf wetting by rainfall, creating a less favourable environment for disease development. However, husbandry may also be needed to reduce humidity in the canopy. The installation of fans or vents could be considered, since this method has proven useful for disease control in other protected crops.

Early detection of *P. sparsa* is very important: the use of diagnostic thermal imaging could facilitate this and allow better control of the disease. It could be particularly worthwhile during propagation. Additionally, the current lack of plant protection products needs attention. Work must be done on the use of elicitors and their role in the control of *P. sparsa* in blackberries and the potential for securing EAMUs for products registered for other crops (such as those for potato blight, caused by *Phytophthora infestans*).

Light manipulation, such as the use of photoselective polythene, may offer some disease control, but further work is required to identify the light spectrum or spectra that would effectively control *P. sparsa* in the UK.

Chemical fungicides remain limited, but biostimulants acting as plant elicitors and biological control agents should be considered in screening trials in a commercial crop setting.

Further work

This literature review has found several gaps in our knowledge of *P. sparsa* on blackberries.

Further work is required to:

1. Identify whether oospores located in the soil in autumn cause repeat infections in the next growing season
2. Determine any link between the leaf position of oospores and leaf discolouration
3. Test thermographic imaging for early detection of infection in a commercial crop
4. Trial early detection methods, such as ELISA or infrared imaging, in a commercial crop setting
5. Validate PCR assays for *P. sparsa* with a view to provide a laboratory service that will determine thresholds in soil and plant tissue that require control measures
6. Evaluate forecasting programmes in use for other oomycetes and whether they could be utilised in blackberry
7. Investigate whether photoselective polythene can reduce disease pressure, further reducing reliance on fungicides
8. Test potential fungicides and biopesticides in efficacy trial work against *P. sparsa*, such as those mentioned in this report, for potential registration for use on blackberries. Biopesticides should be tested, making allowance for the conditions they may require for optimal performance and how these match to the environmental conditions for disease establishment in the crop
9. Compare commercial varieties such as Karaka Black, Victoria and Loch Ness and use these results to inform growers of varieties that could be used in an integrated management programme

References

1. Garthwaite, D. et al. (2014). *Pesticide usage survey report 264: soft fruit in the United Kingdom 2014*. York: Fera. Available from: secure.fera.defra.gov.uk/pusstats/surveys/documents/softFruit2014.pdf. Accessed 03/03/2020.
2. Garthwaite, D. et al. (2016). *Pesticide usage survey report 274: soft fruit in the United Kingdom 2016*. York: Fera. Available from: secure.fera.defra.gov.uk/pusstats/surveys/documents/softfruit2016.pdf. Accessed 03/03/2020.
3. Allen, J. ADAS Fruit Consultant. Personal communication.
4. Wedgwood, E. (2016). Aerial oomycetes: assessing management and control options needed in UK edible and ornamental crops. Project number CP 157. Kenilworth: Agriculture and Horticulture Development Board. Available from: <https://ahdb.org.uk/cp-157-aerial-oomycetes-a-review-of-management-and-control-options-available-for-the-uk-horticulture-industry>. Accessed 03/03/2020.
5. Boyzo-Marín, J., Silva-Rojas, H. V., Rebollar-Alviter, A. (2015). *Biorational treatments to manage dryberry of blackberry caused by Peronospora sparsa*. Crop Protection 76: 121–126.
6. Thines, M., Choi, Y. J. (2015). *Evolution, diversity, and taxonomy of the Peronosporaceae, with focus on the genus Peronospora*. Phytopathology 106: 6–18.
7. Spring, O. et al. (2018). *Biological characteristics and assessment of virulence diversity in pathosystems of economically important biotrophic oomycetes*. Critical Reviews in Plant Sciences 37: 439–495.
8. Newman, S. ADAS Fruit Consultant. Personal communication.
9. Breese, W. A. et al. (1994). *In vitro spore germination and infection of cultivars of Rubus and Rosa by downy mildews from both hosts*. Annals of Applied Biology 125: 73–85.
10. Judelson, H. S. (2017). *Metabolic diversity and novelties in the oomycetes*. Annual Review of Microbiology 71: 21–39.
11. Blackman, L. M. et al. (2015). *RNA-Seq analysis of the expression of genes encoding cell wall degrading enzymes during infection of lupin (Lupinus angustifolius) by Phytophthora parasitica*. PLoS One 10: e0136899.
12. Schornack, S. et al. (2009). *Ten things to know about oomycete effectors*. Molecular Plant Pathology 10: 795–803.
13. Meijer, H. J. et al. (2014). *Profiling the secretome and extracellular proteome of the potato late blight pathogen Phytophthora infestans*. Molecular and Cellular Proteomics 13: 2101–2113.
14. Romero, P. I. Á. et al. (2018). *Identificación y alternativas de manejo del mildiu veloso en rosal*. Revista Mexicana de Ciencias Agrícolas 9: 1577–1589.
15. Salgado-Salazar, C. et al. (2018). *Downy mildew: a serious disease threat to rose health worldwide*. Plant Disease 102: 1873–1882.
16. Horticulture Research International. (2002). *Final project report (HH1749SHN): Biology and epidemiology of rose downy mildew (Peronospora sparsa)*. London: Department for Environment, Food and Rural Affairs. Available from: randd.defra.gov.uk/Document.aspx?Document=HH1749SHN_2670_FRP.doc. Accessed 03 March 2019.
17. O'Neill, T. M., Pye, D., Locke, T. (2002). *The effect of fungicides, irrigation and plant density on the development of Peronospora sparsa, the cause of downy mildew in rose and blackberry*. Annals of Applied Biology 140: 207–214.
18. Gómez Caro, S. (2014). *Infection and spread of Peronospora sparsa on Rosa sp. (Berk.) - a microscopic and a thermographic approach* [Dissertation]. Bonn, Germany: University of Bonn. Available from: hss.ulb.uni-bonn.de/2014/3473/3473.pdf. Accessed 03/03/2020.

19. Horst, R. K., Cloyd, R. (2007). *Compendium of rose diseases and pests*. 2nd ed. St. Paul, MN: American Phytopathological Society.
20. Kandel, S. L. et al. (2019). *Spinach downy mildew: advances in our understanding of the disease cycle and prospects for disease management*. Plant Disease 103: 791–803.
21. Feng, C. et al. (2018). *New races and novel strains of the spinach downy mildew pathogen Peronospora effusa*. Plant Disease 102: 613–618.
22. Aegerter, B.J., Nunez, J.J., Davis, R.M. (2002). *Detection and management of downy mildew in rose rootstock*. Plant Disease 86: 1363–1368.
23. O'Neill, T. (2009). *Control of rose downy mildew*. AHDB factsheet 15/09. Kenilworth: Horticulture Development Company.
24. Mabbett, T. (2018). *Managing downy mildew on African roses*. International Pest Control Magazine 60: 228–230.
25. UK soft fruit propagator. Personal communication.
26. Filgueira D., Juan, J., Zambrano, A. (2014). *Temperature effect on rose downy mildew development under environmental controlled conditions*. Agronomía Colombiana 32: 29–36.
27. Aegerter, B.J., Nuñez, J.J., Davis, R.M. (2003). *Environmental factors affecting rose downy mildew and development of a forecasting model for a nursery production system*. Plant Disease 87: 732–738.
28. Agriculture and Horticulture Development Board, Met Office. (2019). *Blightwatch* [online]. Available from: blightwatch.co.uk/. Accessed 01 December 2019.
29. Rodríguez-Díaz, K. J. et al. (2017). *Molecular detection of Peronospora sparsa in sources of primary inoculum and components of resistance in wild blackberry species*. European Journal of Plant Pathology 149: 845–851.
30. Hukkanen, A. et al. (2006). *Quantification of downy mildew (Peronospora sparsa) in Rubus species using real-time PCR*. European Journal of Plant Pathology 116: 225–235.
31. Rebollar-Alviter, A. et al. (2012). *Fungicide spray programs to manage downy mildew (dryberry) of blackberry caused by Peronospora sparsa*. Crop Protection 42: 49–55.
32. Schulz, D. F., Debener, T. (2005). *Screening for resistance to downy mildew and its early detection in roses*. IV International Symposium on Rose Research and Cultivation 751: 189–198.
33. Fletcher, K. et al. (2019). *Genomic signatures of heterokaryosis in the oomycete pathogen Bremia lactucae*. Nature Communications 10: 2645.
34. Mahlein, A. (2015). *Plant disease detection by imaging sensors – parallels and specific demands for precision agriculture and plant phenotyping*. Plant Disease 100: 241–251.
35. Fernández, F. NIAB EMR. Personal communication.
36. Kostamo, K. et al. (2015). *Control of downy mildew (Peronospora sparsa) in arctic bramble (Rubus arcticus ssp. arcticus)*. Annals of Applied Biology 167: 90–101.
37. Strik, B. Extension Berry Crop Specialist, University of Oregon. Personal communication.
38. O'Neill, T., Thomas, J. (2010). *Control of rose downy mildew*. Project numbers HNS 135 and HNS 150. Agriculture and Horticulture Development Board.
39. Jiang, Y., Caldwell, C. D. (2016). *Effect of nitrogen fertilization on camelina seed yield, yield components, and downy mildew infection*. Canadian Journal of Plant Science 96: 17–26.
40. Agriculture and Horticulture Development Board (AHDB). (2017). *Nutrient management guide (RB209)*. Kenilworth: AHDB. Available from: <https://ahdb.org.uk/nutrient-management-guide-rb209>. Accessed 03/03/2020.
41. Choudhury, R. A., McRoberts, N. (2018). *Temperature and light effects on in vitro germination of Peronospora effusa sporangia*. Tropical Plant Pathology 43: 572–576.
42. Cohen, Y. et al. (2013). *Light suppresses sporulation and epidemics of Peronospora belbahrii*. PLoS One 8: e81282.

43. Cohen, Y., Rubin, A. E., Galperin, M. (2019). *Novel synergistic fungicidal mixtures of oxathiapiprolin protect sunflower seeds from downy mildew caused by Plasmopara halstedii*. PLoS ONE 14: e0222827.
44. Sireesha, Y., Velazhahan, R. (2016). *Biological control of downy mildew of maize caused by Peronosclerospora sorghi under environmentally controlled conditions*. Journal of Applied and Natural Science 8: 279–283.
45. Mohamad, A., Hamza, A., Derbalah, A. (2016). *Recent approaches for controlling downy mildew of cucumber under greenhouse conditions*. Plant Protection Science 52: 1–9.
46. Essa, T. A., Manal, A. H. E-G., Afifi, M. M. I. (2017). *Control of cucumber downy mildew by some plant growth promoting rhizobacteria under greenhouse conditions*. Middle East Journal of Agriculture Research 6: 395–408.
47. El-Gremi, M. et al. (2013). *Mode of action of Bacillus pumilus in suppressing Pseudoperonospora cubensis, the pathogen of downy mildew of cucumber*. Egyptian Journal of Pest Control 23: 71–77.
48. Palmer, C., Vea, E. (2016). *Downy mildew fungicide efficacy. IR-4 Ornamental Horticulture Program*. Available from: ir4.rutgers.edu/Ornamental/SummaryReports/DownyMildewDataSummary2016.pdf. Accessed 03/03/2020.
49. El-Sharkawy, H. H. A., Abo-El-Wafa, T. S. A., Ibrahim, S. A. A. (2018). *Biological control agents improve the productivity and induce the resistance against downy mildew of grapevine*. Journal of Plant Pathology 100: 33–42.
50. Health and Safety Executive. (2020) Extension of Authorisation for a Minor Use of a Plant Protection Product. Extension of Authorisation Number: 3433 of 2016
51. Pettitt, T. (2014). *A desk-study to review global knowledge on best practice for oomycete root-rot detection and control*. Available at: ahdb.org.uk/cp-126-a-desk-study-to-review-global-knowledge-on-best-practice-for-oomycete-root-rot-detection-and-control. Accessed 03/03/2020.
52. Niemi, M., Lahdenperä, M. L. (2000). *Gliocladium catenulatum J1446 - a new biofungicide for horticultural crops*. DJF Rapport, Havebrug 2000 12: 81–88.
53. Alenezi, F. N. et al. (2017). *Increased biological activity of Aneurinibacillus migulanus strains correlates with the production of new gramicidin secondary metabolites*. Frontiers in Microbiology 8: 517.
54. Schuster, C., Schmitt, A. (2018). *Efficacy of a bacterial preparation of Aneurinibacillus migulanus against downy mildew of cucumber (Pseudoperonospora cubensis)*. European Journal of Plant Pathology 151: 439–450.
55. Bektas, Y., Eulgem, T. (2015). *Synthetic plant defense elicitors*. Frontiers in Plant Science 5: 804.
56. Ramezani, M., Rahmani, F., Dehestani, A. (2017). *Study of physio-biochemical responses elicited by potassium phosphite in downy mildew-infected cucumber plants*. Archives of Phytopathology and Plant Protection 50: 540–554.
57. Gogoi, R., Singh, D. V., Srivastava, K. D. (2001). *Phenols as a biochemical basis of resistance in wheat against Karnal bunt*. Plant Pathology 50: 470–476.
58. Brancato, A. et al. (2018). *Modification of the existing maximum residue levels for potassium phosphonates in certain berries and small fruits*. EFSA Journal 16: e05411.
59. Wojdyła, A. T. (2004). *Chitosan (biochikol 020 PC) in the control of some ornamental foliage diseases*. Communications in Agricultural and Applied Biological Sciences 69: 705–715.
60. Krzyzaniak, Y. et al. (2018). *A plant extract acts both as a resistance inducer and an oomycide against grapevine downy mildew*. Frontiers in Plant Science 9: 1085.
61. Pacific Northwest Pest Management Handbooks. *Blackberry (Rubus spp.) – Downy mildew*. Available from: pnwhandbooks.org/plantdisease/host-disease/blackberry-rubus-spp-downy-mildew. Accessed 04 November 2019.

Appendix 1

Plant protection products, available to US growers, recommended in the Pacific North West Factsheet on downy mildew on blackberry (2013).⁶¹ Products not available to UK growers

Product name	Active	Spray applications	FRAC group	Comments
Aliette WDG	Fosetyl aluminium salt	2x in Autumn before rainfall events and 2x in Spring	P7	Do not mix with surfactants or foliar fertilisers.
Fosphite	Potassium phosphate	-	P7	Do not use copper products within 20 days of treatment Do not use spray adjuvants
OxiPhos	Potassium phosphate	-	P7	-
Phostrol	Phosphorus acid	-	P7	Registered for root rot control and may be effective for downy mildew
Rampart	Potassium phosphite	-	P7	-
Ridomil Gold Copper	Mancozeb + metalaxyl-M	Can be applied the day of harvest.	4 + M1	Repeat after 7 days Do not apply with an adjuvant
Tanos	Cymoxanil + famoxate	-	11 + 27	Tanos plus a copper-based fungicide is registered for this crop, but not for downy mildew

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