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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.

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GROWER SUMMARY

Headline

There are a number of approaches for using cultural control of aerial oomycetes in protected production but more research to optimise their use in commercial systems is required.

Background

Aerial oomycetes pathogens are responsible for a wide range of commercially important diseases in both protected and field horticultural production. They include the causal agents of downy mildews and some *Phytophthora* infections and can be rapidly spread via airborne spores.

A lack of available host resistance due to the emergence of novel pathogen isolates and restriction in the use of chemical control means that alternative approaches should be considered for the control of these diseases. As each stage of the aerial oomycete lifecycle is influenced by climatic conditions, so modification of the growing environment could be used to control diseases associated with these pathogens in protected production.

This review examines the environmental factors affecting aerial oomycete-associated diseases in protected cropping and summarise the cultural control studies made in relation to manipulating these conditions with regards to disease management. The review also discusses the importance of the effect of interactions between the environmental factors on pathogen biology and outline disease modelling studies which aim to aid outbreak prediction.

Summary

The development of aerial oomycetes-associated diseases is strongly dependent upon a range of environmental conditions.

- **Humidity and leaf wetness** aid disease development.
    - Spore germination and infection normally requires free moisture, whilst spore production requires conditions of high relative humidity. If these conditions are not present, other environmental factors are considered to be irrelevant.
    - Overall, low humidity negatively impacts the survival of downy mildew pathogens. Attempts to reduce leaf wetness or RH (such as increased ventilation, air movement

such as fanning or increased plant spacing) could therefore be effective in the reduction of infection or sporulation, respectively.

- It is important to note, however, that a decrease in RH, if applied at the incorrect time of day, could actually trigger spore release from these pathogens.

- The **amount and duration of light** can affect developmental processes such as sporulation and infection in these pathogens.
  - Continuous broad- and narrow-band illumination has been shown to suppress the sporulation of many downy mildew pathogens. Continuous light application can prevent sporulation entirely in some cases, but could also decrease the latent phase of infection.
  - Night break lighting can prove effective against downy mildew diseases but is highly dependent upon the length of light and dark periods used, with the preceding dark period appearing to be of key importance.
  - Effects of white light do not pass to non-illuminated parts of the same leaf or plant. This could mean that parts of the crop which receive lower levels of illumination could prove to be problem areas. In addition, fruiting bodies may still be visible on leaves even if spores are not being produced.
  - For some pathogen species, red and blue light appear equally to be effective in control, in other species, only one of these two colours appears to be effective.
  - UV light, particularly in the UV-B (and perhaps also UV-C) ranges appear to have potential for control of these diseases, including as a ‘priming’ treatment, but careful optimisation of treatments is required to avoid crop damage.
  - Alternatively, polyethylene filters could be used to modify incoming daytime irradiance.
  - However, spore release can also be triggered by light e.g. in the morning as humidity decreases.
- The **temperature** of the growth environment can greatly influence the development of these diseases.
  - Temperature extremes negatively impact aerial oomycetes. Survival of downy mildew pathogens is generally considered to be negatively affected by temperatures above 35°C, but for some species of pathogen, survival can be reduced at lower temperatures.
  - Daytime solar heating, through the closing of ventilation or by covering the growth environment with polyethylene sheets to increase the temperature has been reported to be effective. The effectiveness of heat treatments appears to be dependent upon the stage of the infection.

- Many studies regarding the effect of high temperatures on downy mildew pathogens have been performed in countries with higher climatic temperature and sunlight levels than the UK, so the ability to achieve the required temperatures necessary for pathogen inhibition in the UK could be limited. One possibility could be to employ longer duration treatments at lower temperatures or to augment with supplementary heating provision.

- An important consideration for cultural control of aerial oomycete-associated diseases is the **strong degree of interaction between the different environmental factors** affecting their biology.
  - Such interactions must be considered when designing effective control strategies for these diseases, which may need to combine changes in more than one environmental variable simultaneously. Maintenance of suboptimal temperatures for pathogens in growing environments could potentially allow growers to reduce disease incidence where leaf wetness duration is difficult to modify, or vice versa.
  - It must be also noted that inoculum of downy mildew pathogens spreads better when temperatures are high and RH is comparatively low. This brings clear implications for using heat or humidity to control such diseases, as whilst disease processes such as germination or infection may be reduced, spores may spread more easily, highlighting a need to carefully optimise cultural control treatments and the timing of treatment application in order to obtain maximum efficacy.

- Aerial oomycete pathogens also appear to be **spread via contaminated seed**.
  - Some success has been reported using hot air and hot water treatments of seed.
  - However, as only a fraction of infected seed is required for an outbreak, this approach should be combined with other control methods. Similarly, screening of incoming seed batches is unlikely to be effective in eliminating disease.

- Limited research has been carried out regarding **early warning systems** for vegetable disease occurrence in glasshouses. The effectiveness of such systems will likely depend on how early they are able to predict likely downy mildew outbreaks. If infection has already occurred but symptoms are not yet apparent, i.e. the disease is in its latent phase, then effectiveness may be lower and the system could be more useful for assisting in the timing of fungicide applications rather than eliminating outbreaks altogether.

- **Other potential cultural control approaches** include:

- An increase in plant spacing, avoiding overhead irrigation, rotations, rogueing, avoiding overwatering and hygiene strategies
- Polyethylene mulches to cover the surface of growing media in order to reduce evaporation and humidity.
- Treatment of irrigation water using e.g. hydrogen peroxide or UV.
- Modification of the crop fertilisation regime.
- Maintenance of good crop hygiene, the removal of infected plants, decontamination of the growth system and if possible, the use of rotations.

Control of humidity, leaf wetness, temperature and lighting offer a number of potential strategies for combatting aerial oomycete-associated diseases. It should be stressed that the interaction between these variables remains an important consideration in the design of cultural control methodologies. Despite the promising data produced, further research into optimising novel cultural control strategies tailored to commercial setups is likely to be required.

Financial Benefits

Employment of cultural control versus aerial oomycete pathogens in protected horticulture may aid disease prediction and control. However, as the absolute efficacy of such control measures has yet to be fully established and will require tailored approaches for each pathogen and crop, precise predictions of financial benefits cannot be made at this stage.

Action Points

The control of environmental variables in protected horticulture may offer a number of routes to assist in the control of aerial oomycete-associated diseases such as downy mildews. However, the interaction between these variables and their effect on such pathogens should be considered in the design of cultural control approaches. Pathogen biology is an important aspect and will impact upon the choice of timing and approach for treatment application. Finally, it should be stressed that some areas would benefit from further scientific investigation and optimisation for use in commercial setting and some will prove more cost-effective and economically viable than others. The recommendations here will likely require careful manipulation to provide maximal possible efficacy against different diseases.

- Avoid overhead and excessive irrigation in order to minimise leaf wetness and RH.

- If possible, increase plant spacing to reduce humidity through increased airflow between plants. However, this may not be possible economically or due to space constraints.
- Consider increased natural or forced ventilation (potentially with the use of fanning if economically viable) to reduce RH and shorten LWD. Night time ventilation may be an option. Care should be taken to avoid the morning spore release period so that spore dispersal is not exacerbated. A reduction to around 60-90% RH may prove beneficial, depending on the disease.
- Alternatively, consider maintaining a slight positive air pressure using fans and/or air filters to reduce spore entry to the growth system.
- In some production systems, covering of the growth medium may be possible in order to reduce humidity from evaporation.
- Base or top pipe heating may aid RH reduction but may be prohibitively costly for some producers.
- Increase peak temperatures in the middle part of the day through closure of ventilation, supplementary heating and or film coverings as high temperatures are antagonist to many downy mildews. The temperature and duration required will vary depending on the pathogen and treatment achievable in the growth system. Again, care should be taken to avoid the morning spore release period so that spore dispersal is not exacerbated.
- Achieving low temperatures could be effective but this may delay and not eliminate disease.
- Consider heating the rootzone to e.g. 26-31°C for 2 weeks to combat these diseases.
- Whilst 24 h lighting is unlikely to be economically viable, the use of intermittent night break lighting using a broad (e.g. white) or narrow (e.g. red or blue LEDs) wavelength range may prove useful. Alternatively, polyethylene filters could be used to modify incoming daytime irradiance. The light intensity, timing and duration will likely depend upon the disease in question and unwanted morphological effects such as stretching and crop colour changes will need to be avoided.
- UV light, particularly in the UV-B (and perhaps also UV-C) ranges appear to have potential for control of these diseases, including as a ‘priming’ treatment, but careful optimisation of treatments is required to avoid crop damage.
- Treatment of irrigation water using e.g. hydrogen peroxide or UV.
- Monitoring of dew point leaf temperatures to aid prediction on conditions at risk of disease development.
- Modification of the crop fertilisation regime could prove beneficial but little data is available regarding this approach.

- Seed treatments using hot air or water should be considered for reducing disease incidence. However, as only a fraction of infected seed is required for an outbreak, this approach should be combined with other control methods. Similarly, screening of incoming seed batches is unlikely to be effective in eliminating disease.
- Finally, maintenance of good crop hygiene, the removal of infected plants, decontamination of the growth system and if possible, the use of rotations should also be carried out.

- It is important to remember that there is a strong interaction between the effects of light, humidity and temperature on aerial oomycetes – for example, the temperature optimum of the pathogen can change depending on the humidity and light level. However, this may mean that the use of temperatures which are non-optimal for the pathogen would permit longer LWD or higher RH with reduced disease and vice versa.
- These cultural control strategies may prove more effective when used in an integrated disease management strategy which combines them with chemical and host resistance where possible.

Areas for Further Work:

- Evaluation and optimisation of the potential for RH control of aerial oomycete-associated disease control in UK protected production systems through e.g. ventilation modulation.
- Further optimisation and evaluation of cost-efficiency of a range of lighting approaches for control of such diseases in commercial systems.
- Evaluation and optimisation of the potential for temperature control of aerial oomycete-associated disease control in UK protected production systems.

- The above work should also consider the strong interaction between the effects of light, humidity and temperature on aerial oomycetes and may need to investigate multiple factors simultaneously.
- Investigation of the potential for increased use of base watering in protected production.
- Determination of the potential for increased used of environmental monitoring for disease prediction and control.
- Investigation of disease control using modulation of fertilisation regimes.
- Evaluation of other potential cultural control approaches for aerial oomycete-associated diseases.

SCIENCE SECTION

Introduction

Aerial oomycetes pathogens are responsible for a large number of commercially important crop diseases such as downy mildews and some *Phytophthora* infections (Wedgwood, 2017). Such diseases can be spread by airborne spores enabling widespread aerial infection of above-ground plant parts, particularly under wet conditions. For example, basil (*Ocimum basilicum*) downy mildew (caused by *Peronospora belbahrii*), is one of the most severe basil diseases in many countries (Belbahrii et al., 2005; Thines et al., 2009; Wyenandt et al., 2015) and is found in all growing areas for this crop. This disease causes chlorotic spots on leaf blades and the production of an abundance of spores on both leaf surfaces. Eventually, lesions become necrotic and infected leaves abscise, rendering the plant unmarketable (Cohen et al., 2017). Downy mildew caused by *Pseudoperonospora cubensis* is also the most economically damaging disease of cucurbits (Lebeda and Cohen, 2011). It can lead to significant yield losses (Lebeda and Cohen, 2011; Neufeld and Ojiambo, 2012; Granke et al., 2014) and occurs worldwide, infecting a range of cucurbit crops (Thomas, 1996; Lebeda and Widrlechner, 2003), with cucumber (*Cucumis sativus*) being the most susceptible (Lebeda and Urban, 2007). In addition, spinach (*Spinacia oleracea*) downy mildew (*Peronospora farinosa* f. sp. *spinaciae)* is considered to be the most important threat to spinach worldwide (Correll et al., 2011) and lettuce downy mildew (*Bremia lactucae*) to be the most damaging disease of UK lettuce (K Parker, pers. comm.).

The oomycete causal agents of downy mildews and similar diseases are generally found to behave as obligate pathogens, that is, they can only grow when present on the host plant, for example *P. belbahrii* in basil (Cohen et al., 2017). This makes the study of their biology and development of control strategies more difficult. For example, little is known of the role of the sexual oospores in some downy mildew diseases (Cohen et al., 2017), although in the case of *P. belbahrii*, oospores have been detected on symptomatic leaves in older parts of the infection area and in water washes of the leaf surface (Elad et al., 2016). Oospores have never been found in plant material, seed or soil in association with UK outbreaks of the disease (T. Wood, NIAB, pers. comm.)

The emergence of new isolates of aerial oomycete pathogens can mean that sufficient host resistance is not available in some cases, for example against late blight (*Phytophthora infestans*) in tomato (*Solanum lycopersicum*) (Merk et al., 2012; Nowaki et al., 2012). This means that alternative approaches, such as the employment of cultural control measures, must be considered when contemplating action against such pathogens and the diseases they cause. Each stage of the aerial oomycete lifecycle (germination, infection, sporulation)

is influenced by climatic conditions (Kofoet and Fink, 2007). This brings the potential that modification of the environmental conditions of the growing system could be used to control diseases associated with these pathogens in protected production. Experimental data and simulations suggest that epidemics could potentially be effectively controlled through changes in indoor crop growing conditions (Kofoet and Fink, 2007).

This review will examine the environmental factors affecting aerial oomycete-associated diseases in protected cropping and summarise the cultural control studies made in relation to manipulating these conditions with regards to disease management. The review will also discuss the importance of the effect of interactions between the environmental factors on the pathogens and outline disease modelling studies which aim to aid in disease outbreak prediction.

Materials and Methods

Quick Scoping Review (QSR) methodology has been chosen to search for and screen academic and grey literature pertaining to this topic. QSR is a method of evidence gathering that follows structured, transparent protocols that aim to minimise the bias in the collation and inclusion of evidence (Collins *et al*., 2015). QSRs are seen to be more robust and reliable than traditional literature reviews but quicker and less costly than full systematic reviews. A QSR therefore represents a good compromise for addressing the requirements, timescale and budget of this review. QSR methodology for collating and screening the literature in this review shall be conducted following the Defra/NERC guidelines for the production of Quick Scoping Reviews and Rapid Evidence Assessments (Collins *et al*, 2015).

Primary question:

‘What evidence exists for the cultural control of downy mildew pathogens through manipulation of the protected environment in propagation and protected production?’

Inclusion criteria for search results

All retrieved studies were assessed for relevance against inclusion criteria (what the study must contain to be included in the review) outlined in Table 1.

Table 1. Inclusion criteria

Key element	Inclusion criteria
Population	Aerial oomycete pathogens in protected horticultural production (i.e. glasshouse, polytunnel or 'vertical farming').
Intervention	Cultural control methods through manipulation of the protected environment in propagation and protected production. To include manipulation of: relative humidity, ventilation, thermal heat, light wavelength and night break lighting.
Outcomes	Disease incidence and severity resulting from downy mildew pathogens
Relevant study types	Any study type will be included (e.g. primary research, case studies, unpublished reports, industry articles). Masters and undergraduate theses are ineligible but PhD theses are eligible. Relevant reviews will be screened for relevant studies.
Geographical limits	No geographical restrictions.
Language of searches	English
Date of publication restrictions	No publication date restrictions.

Search string

The search string used to capture literature was formulated using the inclusion criteria above. A number of variations were tested to achieve search results that captured available detail on the required topics whilst minimising irrelevant results.

The search string used was:

("Downy mildew" OR Peronospora OR Pseudoperonospora OR Plasmopara OR Phytophthora OR "Bremia lactucae" OR Albugo OR oomycete*) AND ("Cultural control" OR humidity OR ventilation OR airflow* OR "air circulation" OR temperature* OR heat OR ultraviolet OR "UV" OR "UV-B" OR "UV-C" OR "far-red" OR wavelength* OR photoselective OR light* OR irradiation OR irradiance OR "LED" OR "light-emitting

diode*" OR "night break" OR "dew point" OR "dew period" OR "leaf wetness" OR "solar heating" OR illumination) NOT (fish*)

2,551 and 3,290 initial results were obtained from the Web of Science and CAB databases, respectively.

Searches for published and grey literature

A comprehensive search to capture an un-biased sample of grey literature (popular press) was also undertaken using multiple information sources including: online bibliographic databases, websites of relevant organisations and industry publications to identify where research is being conducted in this area (Appendix 1).

The results of each search on each database (bibliographic and organisational databases) were imported into a separate EndNote X7 library file. Duplicates were removed using the automatic function in the EndNote X7 software. Potentially useful articles from industry news publications were collated and screened separately and used to inform the review.

Screening literature

All retrieved articles were imported into the specialised systematic reviewing software (Eppi-Reviewer 4) and screened for relevance against the pre-defined inclusion criteria at two levels (i) title and abstract (screened concurrently for efficiency) and (ii) full text. The included relevant articles formed the basis of the review.

The review determines current knowledge availability and its potential for implementation of changes in the industry to benefit growers. Gaps in knowledge are identified and suggestions for research priorities that may address such gaps have been made. Liaison with the work project steering group, comprising industry representatives, was used in order to determine the most appropriate and commercially-applicable recommendations based upon the findings of the review.

Results and Discussion

Humidity

The development of aerial oomycete-associated diseases is strongly dependent upon humidity and leaf wetness, typically occurring in cool, moist environments (Choudhury et al., 2016a). For example, in basil downy mildew, propagation occurs by asexual spores produced at night on leaf surfaces under humid conditions. These spores then spread through the air

to other plants, germinate in the presence of water and infect new leaves (Cohen and Ben-Naim, 2016). *P. infestans*, similarly, develops on wet leaves in cool conditions, with leaf wetness deemed ideal for the germination of sporangia (Cohen et al., 2006), with the viability of *P. infestans* spores persisting for longer at high humidity (Rotem and Cohen, 1974). Leaf wetness and RH affect the development of late blight on tomato (Becktell et al., 2005a, 2005b), with the disease increasing in incidence when the RH is greater than 80% (Blume and Jara, 2004). The leaf wetness duration requirements for aerial oomycete infection in protected crops is shown in Table 1.

Table 1. Leaf wetness duration requirements for aerial oomycete infection in protected crops.

Crop	Pathogen	Leaf wetness duration (LWD) required for infection	Reference
Basil (*Ocimum basilicum*)	*Peronospora belbahrii*	4h at 15-20°C (2h in water)	(Garibaldi et al., 2007; Cohen and Ben-Naim, 2016)
		Disease particularly severe with LWD 6-12h.	(Garibaldi et al., 2007)
		Less than 2h depending upon temperature. Longer LWD increases disease severity. No infection above 30°C.	(Jennings et al., 2016b)
Brassica spp.	*Hyaloperonospora parasitica*	0.5h, 7h for maximal infection. Infectivity decreases with increasing spore density.	(Defra, 2005)
Cucumber (*Cucumis sativa*)	*Pseudoperonospora cubensis*	2h, large increase in infection above 6h	(Cohen, 1977; Neufeld and Ojiambo, 2012)
Garden cress (*Lepidum sativum*)	*Perofascis lepidii*	Less than 1h, disease severity increases with LWD	(Farahani-Kofoet et al., 2018)
Lettuce (*Lactuca sativa*)	*Bremia lactucae*	0.5h, 7h for maximal infection. Infectivity decreases with increasing spore density.	(Defra, 2005)
		Infectivity increases with LWD	(Scherm and van Bruggen, 1993)
Parsley (*Petroselinum crispum*)	*Plasmopara petroselini*	1h	(Wright, 2014)
Petunia	*Phytophthora infestans*	Minimum 2h, maximum establishment with 6h LWD	(Becktell et al., 2005a)

Potato (*Solanum tuberosum*)	*Phytophthora infestans*	Minimum 2h, maximum establishment with 6h LWD	(Becktell et al., 2005a)
Spinach (*Spinacia oleracea*)	*Albugo occidentalis*	3h at 12-22°C	(Sullivan et al, 2002)
Tomato (*Solanum lycopersicum*)	*Phytophthora infestans*	Minimum 2h, maximum establishment with 6h LWD	(Becktell et al., 2005a)
Viola	*Peronospora violae*	4-5h	(Jackson et al., 2014)

Unlike infection, sporulation of many foliar downy mildew pathogens does not require free moisture but does need high humidity (Cohen et al., 1971; Rotem et al., 1978; Harrison and Lowe, 1989; Su et al., 2004; Cohen and Ben-Naim, 2016). For example, sporulation of *B. lactucae* requires at least 80% relative humidity (RH) (Powlesland, 1954) and increases dramatically above an RH of 95% (Su et al., 2004), with 90% RH deemed optimal for germination (Yanez Lopez et al., 2012). Interestingly, whilst *Hyaloperonospora parasitica* requires a RH greater than 95.5% for sporulation and its spores germinate when exposed to free water (Hartmann et al., 1983), no infection is noted after 6h at 100% RH at any temperature tested, despite high spore germination levels (Achar, 1998). In basil downy mildew, the fruiting bodies which carry the spores (known as sporophores) emerge from stomata when the air is saturated (Cohen et al., 2013a). In this case, periods longer than 4h with a RH above 95% are thought to be conducive for infection and periods of over 7h with a RH above 95% to be conducive for sporulation (Cohen and Ben-Naim, 2016), although other studies suggest that *P. belbahrii* requires a 24h period of leaf wetness of 24h for sporulation (Garibaldi et al., 2007). Cucumber downy mildew incidence and rate in glasshouses correlates with RH (Zhao et al., 2010). Both disease incidence and rate have a significant positive linear correlation with the cumulative number of days or hours with an RH above 80% (D'Ercole, 1975; Zhao et al., 2010). Sporulation of *P. cubensis* also occurs when leaves are wetted, with sporangia beginning to form after 4h of wetness in the dark at 20°C in a glasshouse (Sun et al., 2017).

Outbreaks of diseases such as cucumber downy mildew and late blight in tomato depend primarily on inoculum, temperature, high RH and LWD, but the presence of leaf wetness is considered to be the limiting factor in disease development (Shtienberg et al., 2010). As discussed, free moisture is required on the leaf surface for germination of sporangia and zoospores and for host penetration, whilst high RH is needed for sporulation. If these are not present, other environmental factors are reported to become irrelevant (Cohen, 1977; Thomas, 1977; Palta and Cohen, 1980; Cohen, 1981; Fry et al., 2001; Becktell et al., 2005a). Therefore, it is thought that preventing leaf wetness and high RH can stop disease development (Shtienberg et al., 2010).

The survival of downy mildew pathogens is generally negatively affected by low humidity (Cohen and Rubin, 2015). For rose (*Rosa* spp.) downy mildew (caused by *Peronospora sparsa*), for example, where leaf wetness is considered the most important factor in infection (O'Neill, 2009), the disease is reportedly absent in conditions below 85% RH (Minchinton 1998). Reducing the RH of the growing environment through ventilation has been considered to be a cost-effective and practical strategy (Marx et al., 2010), for example against cucumber downy mildew, where wetting of leaves should also be avoided (Varady and Ducrot, 1985). Reduced humidity (below 90%) has been found to reduce *P. cubensis* spore production and downy mildew incidence on cucumber (Marx et al., 2010; Sun et al., 2017). In such situations, infection can occur on lower leaves only (Kral and Gebelein, 2000), presumably due to the more humid environment resulting from transpiration from leaves and evaporation from growing medium for these leaves. Spore dispersal of *P. belbahrii* is strongly inhibited by low (15-20%) RH (Cohen et al., 2017), whilst significantly fewer spores are produced at RH lower than 95% and none below 75% (Cohen and Ben-Naim, 2016). However, sporangia of *P. infestans* have been reported to survive for as long as 10h when the RH is only 31% (De Weille, 1964), whilst rewetting of partially desiccated *P. infestans* sporangia can promote germination in a manner dependent on the rate of subsequent rewetting, with a low rewetting rate favouring spore survival (Minogue and Fry, 1981). Such results have implications for the use of low RH as an aerial oomycete-associated disease control measure, as subsequent rewetting could permit disease development if an insufficient or suboptimal humidity treatment has been employed. It should also be noted though, that a return to moisture under illumination did not allow infection to initiate from heat treated *P. belbahrii* spores (Cohen and Rubin, 2015). Furthermore, RH had no effect on the survival of *P. belbahrii* mycelium inside infected leaves (Cohen and Rubin, 2015), indicating that successful restriction of downy mildew diseases using RH control likely requires treatment at stages prior to pathogen establishment in the host.

In order to obtain lower levels of RH to aid downy mildew and other aerial oomycete-associated disease control, it is recommended that plants be adequately ventilated (D'Ercole, 1975; Jarvis, 1989). Increasing natural ventilation for 3h in the morning and at night, every day from the end of April to the first 10 days of May reduced the dew duration on cucumber leaves in Beijing glasshouses, whilst the use of natural ventilation for the whole night within the second 10 days and the last 10 days of May reduced downy mildew by 86% and 46%, respectively (Chen et al., 1989). Furthermore, in plastic tunnel production of cucumber, downy mildew disease severity was reduced in two different cultivars by daily 4h side ventilation (Bhat et al., 2013). In lettuce, night time ventilation reduced the number of lettuce leaves infected by *B. lactucae* by around 90% (Morgan, 1981). This approach was suggested to be

a useful control measure in the 14 days prior to harvest. The use of high tunnels has been reported to reduce late blight severity on tomato by leading to non-optimal RH and temperature for *P. infestans* (Inglis et al., 2009, 2011; Kumar and Srivastava, 1998; Tumwine et al., 2002). However, tomato late blight did not consistently correlate with RH in some studies of open-ended high tunnels and open-field production systems (Powell et al., 2014).

Air movement is another factor that can reduce leaf wetness, affect the RH in the leaf surface boundary layer (Harrison, 1992) and decrease infection and disease development (Scherm and van Bruggen, 1993, 1994a). It has been reported that wind reduces sporulation of foliar pathogens such as *P. infestans* and *B. lactucae* in outdoor production (Harrison, 1992, Su et al., 2004). Indeed, in the case of *B. lactucae* under controlled indoor conditions, a study found that air movement prevented dew formation and no sporulation was noted at wind speeds in excess of 0.5 m/s, regardless of RH (Su et al., 2004). This was in comparison to still air, where the number of sporangiophores per cotyledon increased linearly with RH from 81-100%. In addition, *P. infestans* did not produce sporangia at wind speeds of 0.3 x 10^{-3} ms^{-1} even under conditions of 80-88% RH, nor at speeds of 5.5 to 13.7 x 10^{-3} ms^{-1} at 80-95% RH (Harrison and Lowe, 1989). Forced-ventilation has also been used in an attempt to control humidity in plastic houses containing spinach crops (Park et al., 2011). The treatments used did not cause large differences in temperature, however, forced ventilation reduced the RH by 9.2% compared to the control treatment. Spinach growth was found to be good with the forced ventilation treatment and the incidence of downy mildew was reduced to 4.0% with forced ventilation, down from 34.7% in the control treatment (Park et al., 2011).

Fanning of crops at night in a net house has been examined in order to reduce humidity and dew deposition in basil (Cohen and Ben-Naim, 2016). The fans were spaced 7.2m apart, placed 1 m above canopy level and were inclined 30 degrees towards the ground. They provided a wind speed of 1.5 ms^{-1} 1m away from the crop, 0.7 ms^{-1} 6m away and 0.4 ms^{-1} to the side of the crop and were operated from 8pm to 8am (Cohen and Ben-Naim, 2016). Artificially inoculated inoculum spreader plants were used to initiate infection spread. Fanning had only a small effect on the temperature of the net house but caused a large reduction in RH. Fanning reduced the percentage of sporulating leaves from around 90% to less than 2% in three different trials, by reducing the frequency of optimal RH conditions. Leaves were also observed to be dry when fanned, versus wet when not fanned. Turning the fans on at 70% and off at 65% RH was found to provide excellent disease control, however, if the fans were only turned on at 80% RH and off at 70% RH, disease control was poor (Cohen et al., 2017). In addition, interrupting the infection process with a 10 min fanning period at 30°C during the dew period significantly reduced infection, from 70% to 10-15% sporulating leaf area, when

applied 3 or 4h post inoculation when spore germ tubes were at the critical stage of leaf penetration and could reduce or eliminate later spore production (Cohen and Ben-Naim, 2016). However, the ability to successfully time such an application in a commercial setting remains to be proven. Covering cucumbers rows with a plastic tunnel and filling the tunnel with filtered air to a slightly positive pressure has also been found to eliminate downy mildew (Lego, 2009). This approach has also been combined with fanning of air inside the tunnel (SARE, 2012). A 100 ft by 26 ft high tunnel was maintained at slight positive pressure by drawing in air through a bank of 15- 20X25 inch 3M Filtrete Allergen Reduction Filters. A fan was used to move air through the tunnel at either 6,500 or 13,300 cubic feet per minute. This system was found to prevent downy mildew occurrence on cucumbers, in contrast to plants outside the tunnel (SARE, 2012). By contrast, fan assistance in a tunnel was only found to have limited benefit against *Hebe* downy mildew (caused by *Peronospora grisea*) and requires further investigation (O'Neill, 2000). It should also be considered that the fans could potentially increase airborne dispersal of spores and encourage the spread of infection.

Finally, it is also important to note, that a decrease in RH, if applied at the incorrect time of day, could actually trigger spore release from these pathogens. In *B. lactucae*, for example, reducing the RH to 94% for 2h before the start of the morning light period, increased spore release within one hour and again after light application started (Su et al., 2010). Humidity control approaches would therefore require optimisation for fan speed, location and timing in commercial production systems.

Light

There is a strong interaction between illumination and the biology of aerial oomycete pathogens. Both the quantity and period of light can affect developmental processes such as sporulation and infection (Cohen et al., 2013). For example, maximum sporulation of *B. lactucae* requires a minimum of 6 h of darkness 7 days after inoculation (Raffray and Sequiera, 1971). Sporulation of *P. belbahrii*, meanwhile, requires at least 7.5h in the dark in saturated air at 10-27°C, with sporophores beginning to emerge after 4h (Cohen et al., 2013). Similarly, whilst *P. cubensis* is able to infect cucumber plants in either light or dark conditions, infection is enhanced by low light levels (Cohen and Eyal, 1977, 1980). Interestingly, however, *P. cubensis* zoospores locate stomata more rapidly in the light than the dark (Cohen and Eyal, 1980).

Light inhibits the growth and spore production of many fungi (Tan and Epton, 1974; Roberts et al., 2020). Continuous broad- and narrow-band illumination spectra have been shown to

suppress the sporulation of many downy mildew pathogens (Patel et al., 2019) such as *P. belbahrii* (Cohen et al., 2017). Incandescent (3.5 µmol m^{-2} s^{-1}) or cool white fluorescent light (6 µmol m^{-2} s^{-1}) prevented all spore formation by *P. belbahrii* on the lower leaf surface, even when only the corresponding upper leaf surface was exposed to light (Cohen et al., 2013). However, this inhibitory effect did not pass to non-illuminated parts of the same leaf or plant. Nocturnal illumination in the field in a net house (4-10 µmol m^{-2} s^{-1} from 7pm to 7am) also suppressed sporulation of *P. belbahrii* and reduced epidemics of basil downy mildew (Cohen et al., 2013). Light exposure during the wet period reduced the rate of infection of *H. parasitica* and, to a greater extent, *B. lactucae*, where light reduced infection by around 30% (Defra, 2005). Continuous light applied at 7 days post inoculation (dpi) has been reported to completely prevent sporulation of *B. lactucae* in some studies (Raffray and Sequiera, 1971), but not in others (Verhoeff, 1960; Nordskog et al., 2007). If no dark period was allowed immediately after inoculation, there was an apparent inhibition of penetration and establishment of the pathogen (Raffray and Sequiera, 1971). In addition, *B. lactucae* spores were found to survive for much longer periods of time at lower radiation levels (Bashi and Aylor, 1983). This could mean that parts of the crop which receive lower levels of illumination, such as lower leaves, could prove to be problem areas, especially as the effects of light may not be systemic. Light treatments may therefore need to maximise light application to all plant parts to achieve optimal efficacy.

As sporulation of *P. belbahrii* reaches a maximum after 10-11h of darkness (Cohen et al., 2013; Lopez-Lopez et al., 2014), so shortening or interrupting the dark period using "light breaks" could present a control approach for this and similar pathogens. In downy mildew-infected basil plants, 24h illumination with white light resulted in no sporulation (Cohen et al., 2013; Lopez-Lopez et al., 2014). However, continuous light has also been found to reduce the latent phase of basil downy mildew infection to just 5 days (Cohen et al., 2017). This is an important consideration as the latent phase determines the number of disease cycles possible during crop production (Kofoet and Fink, 2007). Interruption of the dark period with light periods (4h in middle of dark period or alternating 2h light and dark periods) led to reduced or absent sporulation (Lopez-Lopez et al., 2014). However, in another study, whilst basil plants exposed to 4 h of night time illumination with incandescent lighting (approximately 10 µmol m^{-2} s^{-1}) showed lower downy mildew disease severity than non-illuminated plants, the differences were not statistically significant (Jennings, 2017).

For *Peronospora tabacina*, the causal agent of tobacco (*Nicotiana* spp.) blue mould, continuous illumination using incandescent bulbs (40 µmol m^{-2} s^{-1}) provided total inhibition of sporulation (Cohen et al., 1978), whilst illumination treatments of 10 min h^{-1}, 15 min h^{-1} or 15 min 2 h^{-1} provided 47, 94 and 42% reductions in conidia number, respectively. This effect

increased with higher light intensity or temperature and with both increased duration and/or frequency of the interrupting dark periods (Cohen et al., 1978). Intermittent illumination (less than 1h light followed by less than 2h dark) with broad spectrum light at a moderate irradiance (9.8 µmol m^{-2} s^{-1}) gave better sporulation reduction than longer intermittent light treatments (more than 2h light followed by more than 3h dark) at the same irradiance (Cruickshank; 1963). In another study, increasing the dark intervals between lighting periods to 2 or 3 h meant that light was no longer effective against sporulation of *P. cubensis* and *P. tabacina*, respectively (Cohen et al., 1978). Against *P. tabacina*, 1 min of illumination every 15 min was more effective in reducing spore production than longer intervals of 1 min of illumination every 30 min (80 and 55% reduction, respectively) (Cohen et al., 1978). Similarly, shorter dark intervals were also more effective against *P. cubensis*. A 62% reduction in sporulation was achieved using 5 min of illumination followed by 15 min of darkness versus 49% reduction for 5 min of illumination followed by 25 min of darkness (Cohen et al., 1978). This, together with other studies, suggests that dark duration must be sufficiently limited and/or irradiance sufficiently high in order to reduce downy mildew pathogen sporulation (Radetsky et al., 2020). Very short intermittent periods of incandescent light (cycles of 13 or 30s of light, followed by 30s of darkness), meanwhile, reduced spore production by *P. cubensis* by 74 to 91%, whilst 10 min h^{-1} light treatments provided only around a 50-77% reduction (Cohen and Eyal, 1977; Cohen et al., 1978).

Light effects on downy mildew biology are also dependent upon wavelength and investigations have studied disease control using different colours of light in the visible spectrum. In basil downy mildew, narrow band illumination showed that red light (λ_{max} 625nm, 12 µmol m^{-2} s^{-1}) was the most inhibitory versus sporulation of the pathogen and could reduce disease incidence by around 50%, whilst blue light (λ_{max} 440nm) was the least inhibitory, suggesting that light reception in *P. belbahrii* could act through a red light photoreceptor (Cohen et al., 2013a; Patel et al., 2016; Patel and Zhang, 2016). Red light also increased the efficacy of fungicidal products such as Actigard (acibenzolar-S-methyl) and Organocide (sesame oil) against basil downy mildew, although Prophyt (potassium phosphite) remained the most effective treatment regardless of lighting regime (Patel et al., 2016). It should be noted that none of these fungicide actives are currently approved (July 2020) as plant protection products for control of basil downy mildew in the UK. In more recent studies, continuous and intermittent applications of red (λ_{max} 670nm) and blue (λ_{max} 458nm) LED top lighting (60 µmol m^{-2} s^{-1}) to *P. belbahrii* were compared (Patel et al., 2019; Radetsky et al., 2020). Continuous (10h) illumination with either colour of light suppressed sporulation by over 99%. At lower doses, the efficacy was lower, with continuous illumination proving more effective than intermittent application (either 4h of illumination in the middle of the dark period

or three 1.3h duration illumination periods, each separated by 3h darkness), with no apparent difference in efficacy between red and blue light (Radetsky et al., 2020). Red light has reportedly been used by some basil producers to reduce downy mildew severity in glasshouses (Choudhury et al., 2016b). Application of blue light (λ_{max} 450nm) for 24h reduced the *P. cubensis* sporangia yield at 20°C as the light level increased from 5-50 µmol m^{-2} s^{-1}, providing up to 80% disease reduction at the highest light level (Cohen and Eyal, 1977). Red light (λ_{max} 650nm) was reported to be the least effective, with green light (λ_{max} 550nm) having an intermediate effect (Cohen and Eyal, 1977). Fluorescent blue light (3.7 µmol m^{-2} s^{-1}) also inhibited sporulation of *P. tabacina,* by 99% at 20°C (Cohen, 1976). Under conditions of continuous light, sporulation of *P. tabacina* is sensitive to very low light intensities, with an effective dose (ED)50 for inhibition of sporulation of 16 uW cm^{-2} for incandescent light and 0.58 uW cm^{-2} for a monochromatic light source (469 nm) in the region of maximum effectiveness (450-525 nm) (Cruickshank, 1963). Blue light (λ_{max} 450 nm) was also found to be the most inhibitory against *P. infestans* sporangia production (Cohen et al., 1975). A low intensity of blue light (3.7 µmol m^{-2} s^{-1}) induced about 85% inhibition of sporangia production, while red light (λ_{max} 650 nm) was ineffective in inhibiting sporangial formation (Cohen et al., 1975). Finally, two 3h night time periods of red (670nm) but not blue (473nm) light may be effective against lamb's lettuce downy mildew but this result could not be repeated with both colours of light leading to an increase in symptoms in a second experiment (Herforth-Rahme et al., 2017).

Interestingly, whilst high light levels caused the production of abnormal sporangiophores by *P. cubensis*, the pathogen was able to produce sporangia upon returning to dark conditions, an important consideration for the employment of light treatments against such pathogens (Cohen and Eyal, 1977). In addition, whilst some data suggest that red light application may be able to eliminate sporophore emergence from stomata (Patel et al., 2016), broad-spectrum light appears not to inhibit this process (Cohen and Eyal, 1977; Cohen et al., 2017). This could still therefore lead to a crop with unsaleable appearance in some circumstances. In addition, wavelength range will need to be carefully considered to avoid potential impacts on crop appearance and morphology such as leaf colour changes and stretching. Unlike the effect of white light on *P. belbahrii* (Cohen et al., 2017), the inhibitory effect of blue light on sporangia production by *P. cubensis* was able to spread to non-irradiated parts of the leaf and provide around two thirds of the reduction effect of the illuminated part (i.e. about 58% vs 91%) (Cohen and Eyal, 1977). Other potential benefits from light treatments could include growth rate increases. A 10h night time (2000 to 0600h) exposure to red light (60 µmol m^{-2} s^{-1}) increased the number of greenhouse-grown basil leaves per plant, plant height, leaf size

(length and width), and leaf fresh and dry weight compared with plants in darkness at night (Patel et al., 2018).

The preceding dark period prior to the use of illumination treatments appears to be a critical consideration for the deployment of light against aerial oomycete-associated diseases and will be important in the choice of night break lighting regime. For example, fluorescent light of 300 lx at 23°C and incandescent light of 4000 lx at 24°C could suppress sporangia production of *P. cubensis* on detached cucumber leaves, but not if the leaves were taken from the glasshouse at certain times of night (21.00 to 24.00h) (Kajiwara and Iwata, 1959). Furthermore, preceding dark treatments of 2-4h reduced the inhibitory effect of blue light against *P. cubensis,* but inhibition could be restored using a preceding dark treatment of 6h duration (Cohen and Eyal, 1977). This meant that blue light could induce between 13-93% disease inhibition according to the preceding darkness time applied before the onset of dew formation. This effect was seen better at 20 and 30°C than at 10°C (Cohen and Eyal, 1977). For *B. lactucae* on lettuce (Raffray and Sequiera, 1971) and *P. tabacina* on tobacco, (Cruickshank, 1963; Cohen, 1976), light-induced inhibition of spore formation could be reduced or reversed by applying a preceding dark treatment. For *P. tabacina*, the dark treatments induced sporulation under otherwise continuous light conditions in a manner directly proportional to the length of the exposure to darkness (Cruickshank, 1963). However, in contrast, preceding dark treatments did not remove the inhibitory effect of blue light on *P. infestans* sporulation, suggesting perhaps that sporulation of this species is not induced by darkness (Cohen et al., 1975).

For *P. tabacina,* the time of day at which sporulation occurred could be modified by adjustment of the time of day at which darkness was initiated (Cruickshank, 1963), revealing another potential control route through the use of illumination. However, for *B. lactucae,* in one study, a light and dark-independent diurnal pattern of sporulation was found for infected whole plants at 15°C (Nordskog et al., 2007). When high RH coincided with the expected ‘night’ period, sporulation occurred regardless of the presence or absence of illumination. Light treatments were not effective at reducing sporulation under such circumstances, nor could darkness induce sporulation during the expected ‘day’ period. Such results were again noted when the lighting period was reversed, such that plants were conditioned to expect night during normal daytime hours. Spores produced in the light had a lower germination efficiency than those produced in darkness and showed a rate of around 50% abnormally small and pigmented spores (Nordskog et al., 2007). Such findings have clear implications for the use of lighting treatments against these pathogens, during which control of RH may also be required. It remains to be determined how widespread this effect is and under which range of environmental conditions it is present. It is not known how long this effect persists

and whether the inherent circadian rhythm of the pathogen will eventually change to coincide with the new lighting regime.

Although sporulation processes in oomycete pathogens such as *P. infestans* occur predominantly at night, spore release itself occurs in the day and is triggered by light as well as other factors described below (Populer, 1981; Su and van Bruggen, 1998). For *P. infestans* in the field, spore release starts at sunrise and peaks at 1000-1200h (Fletcher, 1976; Scherm and van Bruggen, 1995). Spore release coincides with decreasing humidity, rising temperature and the evaporation of leaf wetness (Populer, 1981; Sutton and Hildebrand, 1985). Therefore, another consideration for the use of lighting treatments against these diseases is that whilst sporulation can be inhibited through the use of illumination, spore release from the pathogens responsible could be initiated by light at certain times of day. For example, a study of *B. lactucae* using three different light periods (0400-1600, 0600-1800 and 0800-2000h, with a RH of constant 99-100%) indicated that whilst few spores were released in the dark period, spore release increased sharply at start of the light period, reaching a maximum 1-2h after the start of light application, followed by a rapid decline (Su et al., 2000). Lighting treatments will therefore need careful timing management to avoid the stimulation of spore release from aerial oomycete pathogens. Furthermore, modelling of downy mildew in lettuce under field conditions highlighted that high solar radiation from 0500 to 0600 h together with leaf wetness at 0900 to 1000 h was associated with infection (Wu et al., 2002).

Despite this, solar radiation is also considered the main cause of death for dispersed spores of pathogens such as *P. infestans* (De Weille, 1964; Rotem et al., 1970; Bashi et al., 1982). On sunny days, about 95% of *P. infestans* spores were inactivated after 1h (Mizubuti et al., 2000). Solar radiation has also been reported to be the main factor affecting survival of *Peronospora destructor* (causal agent of *Allium* downy mildew) and *P. tabacina* in the field (Bashi and Aylor, 1983). Ultraviolet (UV) light is the main component of solar radiation affecting spore survival (Wu et al., 2000). For *B. lactucae*, the germination percentage of spores was significantly reduced after exposure to sunlight, with a 90% reduction found with a sunlight dose equivalent to 0.6 MJm^{-2} of UV (Wu et al., 2000). However, less than 9% of solar radiation is comprised of light at UV wavelengths (UV-A (320-400nm), UV-B (290-320nm) and UV-C (below 290nm)). The effect of UV-A is thought not to be particularly strong, with most of the effect of sunlight on oomycete spores thought to be due to UV-B (Coohill, 1989; Diffey, 1991; Cullen et al., 1992). The amount of UV-B present in sunlight depends on the ozone amount, the angle of the sun in the sky and the degree of cloud cover (Wu et al., 2000).

UV light has therefore also been investigated as a potential control measure for aerial oomycete-associated diseases due to its potential to inhibit plant pathogens (Rotem, 1985:

Wu et al., 2000). *For P. tabacina*, sporangia treated with UV-A light at 366 nm survived for more than 4 h (Sukanya and Spring, 2013). UV-C light at 254 nm, however, killed spores within 30–40 min, although sporulating leaves exposed to UV-C remained infective to other plants if the irradiation time was below 40 min (Sukanya and Spring, 2013). In *B. lactucae*, UV-B (280-315nm, λ_{max} 305-310nm, 1.5 or 7.0 Wm^{-2}) significantly reduced sporangium viability and infection, but fluorescent and UV-A (315-400nm, λ_{max} 340-350nm, 6 or 12.5 Wm^{-2}) had no effect (Wu et al., 2000). In another study, exposure of lettuce plants to supplementary ultraviolet radiation (UV-B at 280-320 nm) prior to inoculation with a conidial suspension of *B. lactucae* led to a significant reduction in the subsequent sporulation of the pathogen (Wargent et al., 2006). This suggests a possible priming effect of host defence systems which could prove beneficial as a prophylactic application of UV-B light to the crop to prevent or reduce disease incidence. In addition to disease control, UV treatments increased the leaf thickness, reduced the leaf area and increased leaf pigmentation in a red-leaved lettuce cultivar. Such changes in leaf area and thickness are important quality factors that would be expected to improve plant performance if subsequently transplanted into the field (Wargent et al., 2006). UV-C has been found to be 100 times better at killing *P. tabacina* spores than either UV-A or UV-B (Rotem et al., 1985), however UV-C is practically absent in sunlight reaching the earth's surface (Wu et al., 2000). Therefore, like UV-B, studies have investigated the use of artificial UV light sources. In a commercial setting, a UV-C light (10 mJ cm^{-2}) has been used to try and control *P. infestans* in ornamental bulbs and potatoes using a Cleanlight machine in the field travelling at 6 km/h (Anon, 2007). Custom made Narva UV-C machines are being trialled in connection in commercial setting after evaluation with Wageningen University for mildew control (Hortidaily, 2020). Other automated UV-C based research projects include UV-ROBOT (Interreg NW Europe, 2019). This project aims to use UV-C application as part of an Integrated Pest Management (IPM) approach and is being studied in lettuce, basil, tomato, cucumber and strawberry crops.

However, care must be taken with UV dose rates as application of too strong a treatment can lead to plant damage. In basil, UV-B LEDs (λ_{max} 292nm, placed 4 cm from the plants) were used to apply an average dose of 16 kJ m^{-2} day^{-1} for 0, 3 or 6 days to one side of 48-day old basil plants prior to inoculation with *P. belbahrii* (Patel et al., 2017). A 3 or 6 d exposure significantly reduced the percentage of the plant exhibiting *P. belbahrii* sporulation at 9-12 dpi from around 5% to around 2%. There was no difference in effectiveness between the 3 and 6 d treatments. The fresh and dry weight of the plants was not significantly affected, but some leaf burning was seen on the leaves closest to the UV-B source. The authors consider that a more uniform application of UV-B, rather than from just one side could help reduce burning symptoms by allowing increased spacing between LEDs and plants (Patel et al., 2017). In

another study, high UV-B doses (68 kJ m^{-2} day^{-1}, 4 h exposure) severely inactivated photosynthetic processes and eventually killed the basil plants, whilst low level UV-B doses (8.5 kJ m^{-2} day^{-1}, 30 min exposure) did not show any signs of stress (Mosadegh et al., 2019). In another study, green and purple basil plants grown at two photosynthetic photon flux densities (PPFDs) of 160 and 224 µmol m^{-2} s^{-1} were treated with five different doses of UV-B at 16 µmol m^{-2} s^{-1} (Dou et al., 2018). The UV-B doses suppressed plant growth and reduced yield, reducing fresh weight by 12-51% and 6-44% for green and purple basil, respectively. Under the higher PPFD level, a 1h day^{-1} for 2d UV-B treatment was sufficient to cause a reduction in fresh weight and at low PPFD, a 2h day^{-1} for 2d UV-B treatment was sufficient. In addition, UV-B treatments increased the concentrations of phenolics and flavonoids in the basil leaves, reflecting their stressed status.

Filters have also been used in order to obtain different wavelengths of light for studies of aerial oomycete-associated diseases. When filtered light at 90 µmol m^{-2} s^{-1} was used to inhibit sporulation of *B. lactucae*, 400-450nm was found to be the most effective wavelength range, providing a 75% reduction in sporulation (Nordskog et al., 2007). Wavelength ranges of 450-500 and 500-550nm also exhibited smaller inhibitory effects. Interestingly, a daylight filter provided an even better efficacy of 90% sporulation reduction. Three spectrally modifying filters (polyethylene films) with contrasting UV transmission were used to filter ambient sunlight in lettuce fields (Paul et al., 2012). Interestingly, both UV inclusive and zero UV-B filters reduced the severity of lettuce downy mildew. UV filters may also be beneficial against stocks downy mildew (Sampson, 2001). The effect of light on germination of the broad spectrum downy mildew pathogen *Peronospora effusa* was investigated using boxes covered with colour correction gels on the top, with the base and sides covered in foil (Choudhury et al., 2016b). Unfiltered light from fluorescent or incandescent lamps significantly reduced *P. effusa* germination compared to either the absence of light or low intensity light provided by half power fluorescent lamps (Choudhury et al., 2016b). Blue light significantly reduced germination compared to red, yellow or no light, whilst green light was effective at higher light intensities. At 18°C, but not 4°C, yellow and red light actually increased germination (Choudhury et al., 2016b). Photoselective foils (light and dark red, yellow and green) have also been used for tomato crops in high tunnels (Manole et al., 2009). Dark red foil led to the most severe late blight, dark green the least and yellow foil an intermediate level of disease. Six types of polyethylene sheet with or without a blue pigment (maximum absorbance at 580nm) were used in combination with three levels of UV-B (280-320nm) absorbance to investigate their effect on cucumber downy mildew (Reuveni and Raviv, 1997). All sheets contained an infrared absorber. The presence of the blue pigment significantly inhibited colonisation and sporangia production of *P. cubensis* and delayed the appearance of

cucumber downy mildew symptoms. Filtration of UV-B, meanwhile, enhanced colonisation by the pathogen but did not affect sporulation (Reuveni and Raviv, 1997). In a subsequent study, the blue/UV-B ratio of the transmitted light was altered from 4:1, as measured in commercial polyethylene sheets, to 40:1 in a modified sheet which was developed and tested under glasshouse conditions and manufactured as 'Anti-Fungi' and later as 'Anti-Virus' film (Reuveni and Raviv, 1998) although whether commercial uptake of this product has occurred is not clear to the author. A significant reduction in sporulation of *P. cubensis*, as well as a slower rate of epidemic development on cucumbers was obtained in glasshouses covered with the improved blue sheet having a high ratio of blue/UV-B transmittance. These results were achieved with minimal absorption of the light required for normal photosynthesis and plant morphogenesis, without decreasing the yield potential (Reuveni and Raviv, 1998).

Temperature

The temperature of the growth environment can greatly influence the development of aerial oomycete-associated diseases such as cucumber downy mildew (Neufeld and Ojiambo, 2012). Infection by *P. cubensis* in cucumber has been reported at 17-22°C (D'Ercole, 1975). However, more recent studies in cucumber cotyledons in controlled environment conditions indicated the possibility of infection over a wider temperature range of 5-30°C, with a model-estimated temperature optimum of 18.8°C for infection and 16.2°C for sporulation from lesions (Sun et al., 2017). In *P. lepidii*, which infects *Lepidium*, sporangia germinated best in vitro at 5-10°C with a post-inoculation temperature of 15-25°C found to be optimal for disease development (Farahani-Kofoet et al., 2018). For *P. petroselini* (causing parsley downy mildew), lower temperatures are favoured with a 5°C optimum for disease development and no infection apparent at 20°C (Wright 2014). For *P. effusa*, germination in the dark declines as the temperature increases from 5-25°C (Choudhury et al., 2016b), although an earlier study suggested high levels of germination occurred at 10 and 25°C, with lower efficiency at 20°C (Frinking et al., 1981). *P. infestans* has similar temperature requirements for sporulation on tomato, petunia and potato, with an optimum of 18°C and temperatures of 13-23°C generally being conducive to disease establishment (Becktell et al., 2005a). The viability of *P. infestans* spores, meanwhile, declines more slowly at low temperature (Rotem and Cohen, 1974). For *B. lactucae*, sporulation occurs from 4-20°C (Verhoeff, 1960), with the optimum temperature for sporulation being reported to be 15°C (Grogan et al., 1955; Su et al., 2004) or 6-11°C (Powlesland, 1954). *A. occidentalis* exhibits a temperature optimum of 12-18°C (Sullivan et al., 2002), with around 22°C deemed optimal for sporangia production (Correll et

al., 1994) and 12-16°C for germination (Raabe and Pound, 1952). However, the optimum temperature for spore germination in this species has been reported to be just 10°C (Yanez Lopez et al., 2012), reflecting differing optimal conditions for different stages of the pathogen life cycle. Conidia of *H. parasitica* can germinate in the range of 5-30°C, but a range of optima have been suggested (Kofoet and Fink, 2007). Germination can occur within 1h under favourable conditions (Weis, 1994). Prolonged incubation (48h) at 20-25°C enhances *H. parasitica* infection rates (up to 100%) (Achar, 1998), with 20-24°C considered optimum for disease development (Lakra, 2001). Sporulation of this pathogen, meanwhile, occurs at night from 4-24°C (Felton and Walker, 1946) with an optimum of 12-16°C (Felton and Walker, 1946; Hartmann et al., 1983; Jang and Safeeulla, 1990). Temperature did not affect the minimum latent period but low temperatures did slow the end of the latent phase (Kofoet and Fink, 2007). By contrast, in *B. lactucae*, the minimum latent period was longer at low temperature and shorter at higher temp (requiring 14 d at 10°C and 5 d at 22°C) (Scherm and van Bruggen, 1994b). The relationship between the minimum latent period and temperature was not as strong under conditions of fluctuating (diurnally alternating) temperature. For *Antirrhinum* downy mildew (caused by *Peronospora antirrhinin*), the optimum temperature for sporangia is 13°C, whilst infection and disease development are most severe at 4-16°C (Anon, 1988). In aquilegia downy mildew, germination of spores occurs over a wide temperature range, with an optimum at 10-15°C, whilst infection is optimal at 5-20°C (Jennings, 2016a)

As a result of the temperature-dependent nature of developmental processes in aerial oomycetes, temperature extremes have been found to negatively impact aerial oomycete-associated diseases. Survival of downy mildew pathogens is generally considered to be negatively affected by temperatures above 35°C (Cohen and Rubin, 2015). For example, increasing the temperature from 29 to 33°C reduced downy mildew in glasshouse cucumber (Kawashiro et al., 2010) whilst *B. lactucae* sporangia survived much longer on lettuce leaves at 23°C (over 12h) than at 31°C (2-5h) (Wu et al., 2000). *B. lactucae* spores germinated well in water at temperatures between 0-20°C, but germination has been found to decrease with increases in temperature above 20°C (Sargent and Payne, 1974). In *Aquilegia* downy mildew, no infection occurred at 25°C (Jennings, 2016a). By contrast, *P. valerianellae* is reportedly unable to sporulate at temperatures above 15°C (Herforth-Rahme et al., 2017). High air temperature also affects the development of late blight on tomato (Becktell et al., 2005a, 2005b). Above 28°C sporulation of *P. infestans* is nearly absent and little disease establishment occurs (Becktell et al., 2005a). *P. tabacina*, however, would possibly appear to be an exception, with sporangia reportedly surviving on tobacco? leaves for 48h at 50°C (Sukanya and Spring, 2013), although another study suggested that survival of *P. tabacina* inside leaves is lost after 24h at 35-45°C (Rotem and Cohen, 1970).

The temperature sensitivity of aerial oomycete spores appears to be situation-dependent – i.e. whether they are tested *in vitro* or on plant surfaces and whether they have been inoculated onto the plant by the researcher, naturally dispersed by air currents, or have passed through a wetting-drying process (Cohen et al., 2017). For example, extremes of temperature reduced the ability of *P. belbahrii* spores to infect basil plants, with a shorter heat treatment duration being required at the highest temperatures tested (Cohen et al., 2017). No survival of *P. belbahrii* spores was found after 48h at 45°C, 72h at 35-45°C or 96h at 25-45°C. Whilst infection by *P. belbahrii* can occur from 5-25°C (Jennings et al., 2016b), some data suggest that a temperature of 30, 35 or 40°C for 72h can eliminate infectivity of *P. belbahrii* spores on plants (Cohen et al., 2017; Jennings et al., 2016b), whilst another study reported no disease at either 12°C or 27°C (Garibaldi et al., 2007). In the case of naturally dispersed *P. belbahrii* spores on basil plants, only around 20% infectivity remained after 48h at 25°C, with no infectivity remaining after 48h at 30°C (Cohen and Rubin, 2015). Wetted-dried spores lost infectivity after 9h at 40°C, 20h at 30°C or 55h at 25°C (Cohen and Rubin 2015). The heat tolerance of *P. belbahrii* mycelium in intact plants and detached leaves was also assayed. 6 or more hours at 40-45°C or 12h at 35-45°C was highly detrimental for *P. belbahrii* in detached leaves from infected plants, with 9h at temperatures over 35°C or 27h at 30°C required for a near total reduction in the appearance of sporulating leaves in whole inoculated plants (Cohen and Rubin, 2015). Three 3h consecutive daily exposures or one longer exposure to 30, 35 or 45°C was strongly suppressive towards *P. belbahrii* sporulation (especially so at the higher temperatures tested) (Cohen et al., 2017). In addition, spore dispersal in basil downy mildew is strongly inhibited by high temperature, perhaps due to effects on spore survival (Cohen et al., 2017). In another study, no sporulation of this species was found at 5°C or 28°C (Cohen and Ben-Naim, 2016), raising the possibility of using low, as well as high, temperature extremes for disease control, so long as disease progression does not resume upon return to optimal growing conditions.

Interestingly, the efficacy of heat treatments appears to be dependent upon the stage of the infection process. In basil, heat treatment of infected plants was more successful when used later in the infection process (Cohen and Rubin, 2015). A temperature of 35°C eliminated *P. belbahrii* mycelium at 7 or 9 dpi, with 30°C conferring partial control (Cohen and Rubin, 2015). By contrast temperatures above 35°C were required for good levels of spore reduction at 5 dpi. In addition, three consecutive daily heat exposures of 3h duration were more suppressive at 4-6 dpi than at 2-4 dpi. A 50% reduction in pathogen viability required a temperature of 40°C at 4-6 dpi and 45°C at 2-4dpi (Cohen and Rubin, 2015). This suggests that older mycelium may be more susceptible to the inhibitory effects of heat (Cohen and Rubin, 2015)

and that unlike in the case of RH, heat treatments at later stages on infection, once the pathogen is inside the host, could still prove effective.

Daytime solar heating to control basil downy mildew has been investigated in net-houses in Israel (Cohen and Rubin, 2015). Covering the net-house with transparent, infrared (IR)-impermeable polyethylene (PE) sheets raised the daily maximum temp by 11-22°C, reaching 40-58°C. Applying this treatment for several hours for 1-3 consecutive days killed the pathogen and suppressed disease progress, while also enhancing plant growth (Cohen and Rubin, 2015). Similarly, in plastic tunnels, a high air temperature (above 25°C), combined with a lowered relative humidity (RH) of 65-85% and a high soil temperature (above 21°C) was found to be negatively related to downy mildew severity (Elad et al., 2016; Cohen et al., 2017). However, symptomless plants from tunnels with temperatures of 45-48°C still exhibited disease symptoms when transferred to conditions promoting basil downy mildew development, suggesting that infection is still possible at even very high temperatures but that symptom development and/or tissue colonisation is suppressed (Elad et al., 2016). It should be noted that in this study, the increase in air temperature to above 40°C did not cause a significant increase in leaf temperature, with the crop canopy surface temperatures only reaching 30°C, which could explain this effect.

Heat shock has been reported to reduce the need for fungicide application in cucumber crops (Sato and Kubo, 2015). In plastic houses, closing doors and ventilation openings to allow the temperature to rise to 40-47°C for 2 h every other day has been used to combat downy mildew in cucumber (Ma et al., 1990). This procedure is reported to increase cucumber production by around 45%. In glasshouses, almost complete closure from 9:30 to 12:00 on a sunny day created a heat shock treatment which reached a maximum temperature of around 45-48°C for 2h. After 12:00, the windows were gradually opened over a period of 30 minutes then remained open (Ding et al., 2016). Heat shock of cucumber seedlings at the 20-leaf stage in this manner reduced the downy mildew disease severity index by more than 50%, with the effect increased up to two weeks after the heat shock (Ding et al., 2016). However, the heat shock also significantly reduced cucumber net photosynthetic rate, photochemical efficiency and starch content. It also increased stomatal conductance (potentially aiding pathogen entry), transpiration rate and antioxidant content, indicating plant stress, in both infected and control leaves (Ding et al., 2016). A similar study found effective disease suppression and yield increases using heat shock, but a higher number of dead or malformed fruits were reported (Sato et al., 2003). The authors recommend that such treatments be halted prior to harvest to aid fruit set and growth. In another study, however, setting the glasshouse ventilation temperature to 45°C from 11.30 to 13.30, to generate a heat shock treatment which reached temperatures of 40-45°C, still allowed downy mildew to cause serious damage to

cucumber crops (Sato and Kubo, 2015). Such approaches could also lead to an increase of RH in the growing environment by limiting ventilation, which could limit the effectiveness of disease control.

However, many studies regarding the effect of high temperature on downy mildew pathogens have been performed in countries with higher climatic temperature and sunlight levels than the UK, so the ability to achieve the required temperatures necessary for pathogen inhibition in the UK could be limited. One possibility could be to employ longer duration treatments at lower temperatures or to augment with supplementary heating provision. It should be noted though, that in *B. lactucae*, for example, the effect of heat treatments on spore germination at around 25-28°C may only represent a delaying effect (Sargent and Payne, 1974). Whilst spore viability of this species decreased significantly above 25°C with no germination occurring after 24h at 28°C, if these spores were subsequently cooled to 15°C, they were then able to germinate and had apparently remained in a state of quiescence (Sargent and Payne, 1974). Alternatively, heating the rootzone to 26-31°C, whilst keeping the above ground zone at ambient temperature (20°C) was also found to suppress downy mildew in basil (Elad et al., 2016). This effect lasted for 1-2 weeks after returning to conditions conducive to basil downy mildew development (22+/-2°C, RH above 95%). In this case, the authors suggest that heat may also act to improve host resilience rather than merely exerting a direct effect on the pathogen.

Interactions Between Environmental Factors

An important consideration for cultural control of aerial oomycete-associated diseases is the strong degree of interaction between the different environmental factors affecting their biology. Such interactions must be considered when designing effective control strategies for these diseases which may need to combine changes in more than one environmental variable simultaneously. In addition, the impact of interacting environmental variables will vary depending on stage of the pathogen life-cycle (e.g., sporangial formation, sporangia release, infection and disease development) (K Parker, pers. comm.). For rose downy mildew, for example, a degree of control was achieved by reducing the RH to less than 90% using ventilation and simultaneously increasing the temperature to over 27°C (O'Neill, 2009). With *P. cubensis* in cucumber, the minimum, maximum and optimum levels of temperature, inoculum concentration and LWD all depend upon each other (Cohen, 1977). The minimum temperature required for infection decreased from 20°C to 5-10°C as LWD increased from 2 to 12 h. In addition, the minimum dew period required was increased by lowering the temperature, presumably due to slowed zoospore release and germination (Cohen, 1977).

Furthermore, higher *P. cubensis* inoculum levels were required for disease under less favourable conditions (Cohen, 1977). In aquilegia downy mildew, infection required 90% RH at 5-10°C, but only 70% RH at 15-20°C (Jennings, 2016), meaning that decreasing the RH to control such diseases may be less effective at higher temperatures. Furthermore, temperature and humidity interact strongly to determine the overall disease severity present in basil downy mildew (Jennings et al., 2016b).

In another example of the interaction of environmental variables on aerial oomycete-associated diseases, the inhibitory effect of light on sporulation in basil downy mildew and tobacco blue mould was temperature-dependent, with full inhibition occurring at 15-25°C, but not at 10°C (Cohen, 1976; Cohen et al., 2013). Similar results were found regarding the inhibitory effect of blue light upon sporulation of *P. infestans* (Cohen et al., 1975) and white light upon sporulation of *B. lactucae* (Nordskog et al., 2007), which increased in efficacy with a rise in temperature from 10 °C to 25 °C. Blue light inhibition of *P. cubensis* was also strongly temperature dependent, with inhibition of 27, 70 and 93% at around 15, 20 and 24°C, respectively (Cohen and Eyal, 1977). Of importance to note is that at a temperature of 10°C, light application stimulated, not inhibited, sporangia production of this species (Cohen and Eyal, 1977). For *P. cubensis*, whilst the optimal temperature for infection in the dark at 2 and 4 h of wetness was 25°C and 15°C respectively, in the light it remained at 20°C regardless of this variation in LWD (Cohen and Eyal, 1980). Sporulation of *H. parasitica* is affected by temperature, humidity and light and their interactions (Kofoet and Fink, 2007), being favoured by 15°C at night and 20°C in day (Kofoet and Fink, 2007). For *P. tabacina*, 15 min h^{-1} illumination was not effective against sporogenesis at either 10 or 15°C and actually led to increased spore production at 10°C (Cohen et al., 1978), indicating the potential importance of obtaining a sufficiently high temperature for lighting treatments to be effective.

In addition, light-based suppression of sporulation in *B. lactucae*, appears to be highly dependent upon pathogen isolate, with light levels of 13 and 30 µmol m^{-2} s^{-1} required for an 80% reduction in sporulation in two different isolates (Nordskog et al., 2007). Isolate differences have also been noted for *Peronospora sparsa* and *P. rubra*, two rose-infecting downy mildew species, which exhibit variation in optimal germination temperature (Breese et al. 1994). Furthermore, it should be noted that varietal effects in the response to light treatments of aerial oomycete-associated diseases have been recorded. In tomato, late blight disease incidence and severity was not influenced by light intensity (240 or 120 µmol m^{-2} s^{-1}) in one variety (Nova) but was in another (Beefsteak), where growth under low light significantly increased the disease. Both varieties behaved similarly under high light in terms of disease incidence and severity (Bradford et al., 1982).

In addition to direct effects on the pathogen and host, heating of the growing environment can be used to dry the canopy and reduce the RH in order to combat foliar diseases (Morgan, 1985; Hausbeck et al., 1996). For *B. lactucae* sporangia, there was a significant effect of the interaction between temperature and RH on germination from 5-25°C (Yanez Lopez et al., 2012). In addition, exposure time in relation to temperature, but not RH, had a significant effect on sporangia production in this species (Su et al., 2004). In cucumber downy mildew, the minimum LWD required for infection and downy mildew development is also highly temperature-dependent (Neufeld and Ojiambo, 2012). LWD requirements for cucumber downy mildew have been reported as 12, 4, 2.5, 1, 1 and 6h for 5, 10, 15, 20, 25 and 30°C, respectively (Sun et al., 2017), indicating that a longer wetness duration is required at suboptimal temperatures. Similar results have also been reported for spinach white rust (Sullivan et al., 2002). This raises the possibility that maintenance of suboptimal temperatures for pathogens in growing environments could potentially allow growers to reduce disease incidence where leaf wetness duration is difficult to modify, or vice versa. In addition, in cucumber downy mildew, host type, temperature, LWD and their interactions have significant effects on both pathogen germination and disease severity (Neufeld and Ojiambo, 2012). The germination of sporangia was found to be highest on cantaloupe (*Cucumis melo* var. *cantalupo*) and lowest on acorn squash (*Cucurbita pepo* var. *turbinata*). Disease severity was highest on cucumber and lowest on cantaloupe. Based on data modelling, at 20°C, 15% leaf area infection was expected after 2, 4 and 8h LWD for cucumber, squash and cantaloupe, respectively. The effect of host type on germination and infection is thought to be due to differences in the upper temperature limit of the pathosystem (Neufeld and Ojiambo, 2012). The growing medium also influences the effectiveness of cultural control. For cucumber downy mildew, growth in vermiculite vs soil increased blue light inhibition of the disease from 80% to 98% after a 24 h treatment at 30 µmol m^{-2} s^{-1} (Cohen et al., 1975). Similarly, *Phytophthora megasperma* f. sp. *medicaginis*, which infects alfalfa (*Medicago sativa*), but has also been reported on hollyhock (*Alcea* spp.), exhibits different temperature optima on different *in vitro* growth media.

However, it must be also noted that inoculum of downy mildew pathogens spreads better when temperatures are high and RH is comparatively low, as has been found, for example, in field cucumbers (Granke and Hausbeck, 2011). This brings clear implications for using heat or humidity to control such diseases, as whilst disease processes such as germination or infection may be reduced, spores may spread more easily, highlighting a need to carefully optimise cultural control treatments and timing of applications.

Such results bring clear implications for the design and use of cultural control strategies for these diseases, which must ensure that treatments are applied under appropriate environmental conditions in order to obtain maximum efficacy.

Seed Treatment

Fungicidal seed treatment using metalaxyl-M can be effective for control of downy mildews on some crops, however, development of resistance to this active and increasing restrictions on its use, make this an unsustainable solution. In the absence of other effective fungicides available as seed treatments for downy mildews, there is interest in physical methods for this purpose.

Aerial oomycete pathogens also appear to be spread via contaminated seed (Minchinton, 1998; Jennings, 2019). For example, pansy and viola downy mildew has been reported to be seedborne (Jennings, 2009). The sudden appearance and rapid spread of basil downy mildew also suggests the possibility of seed transmission of this disease (Cohen et al., 2017). Indeed, *P. belbahrii* has been detected in seed samples (Jennings et al., 2017) including one study reporting presence in 25% of seed samples at an incidence of 0.33-0.66% (Garibaldi et al., 2004). This has serious consequences for the grower as very low levels of seed infection could lead to a disease outbreak. This also means that conventional growing-on tests are unlikely to detect the pathogen.

Diagnostic PCR approach for basil downy mildew have been reported (Farahani-Kofoet et al., 2012; Jennings et al., 2017) and are able to detect the causal agent in artificially inoculated seeds at a level of DNA equivalent to 1 spore per seed (Farahani-Kofoet et al., 2012). This method was used to screen commercial seed and found *P. belbahrii* to be present in 80-90% of randomly chosen samples, independent of harvest year. In another study, however, *P. belbahrii* DNA could be detected in seeds by PCR but the pathogen itself could not be identified on or in the seed (Belbahri et al., 2005). This could be due to limited viability of spores present in seed lots. As part of AHDB project CP 184, a PCR-based viability assay is being developed in order to determine the levels of living spores present in seeds and so likely disease severity.

When seeds were collected from infected basil plants in the glasshouse and re-grown, 23% of the following plants were infected. Some of these plants were symptomless but the pathogen DNA was found to be present in stems or leaves, indicating that systemic infection is possible (Farahani-Kofoet et al., 2012). Indeed, movement from an infected to an uninfected leaf, leading to sporulation at that second leaf has been reported in a proportion (6-12 out of 60) of plants tested (Cohen et al., 2017). Another study, however, could not detect

seed transmission and seeds collected from infected plants gave healthy plants when grown (Cohen et al., 2017), however this study used only microscopy for pathogen detection rather than PCR. Such studies have clear implications for hygiene in seed production facilities.

The screening of incoming seed batches is a possibility but as only a tiny fraction of infection is sufficient for outbreaks (Jennings, 2019), seed treatments are likely to be required. Heat treatment of seed at 48-50°C for 20 min reduced disease incidence caused by *H. parasitica* from 42.5% to 2.5% (Minchinton, 1998). Seed treatment with hot air (65°C for 10 min) before sowing has been reported to significantly reduce disease incidence of basil downy mildew in naturally infected seeds from around 5% to 1% (Gilardi et al., 2015). Seed germination did not appear to be affected by this treatment, however, the effectiveness of seed treatments varied considerably between trials. This study used a single layer of seeds in Petri dishes in an incubator, and so the methodology may require adaptation for use with larger volumes of seed. In addition, heat treatment of lamb's lettuce seeds at 40-55°C for 10-30 min (Gullino et al., 2012) or hot water treatment at 50°C for 30 min (but not 53°C, which negatively affects germination) (Nega et al., 2011) was somewhat effective against *P. valerianellae*, but the hot water treatment was not effective against highly infected seed (Nega et al., 2003). Sodium hypochlorite was also found to be effective against this pathogen, when compared to ethanol, calcium hydroxide and compost pellet treatments, although hot water was the only treatment tested that completely eliminated *P. valerianellae* (Herforth-Rahme et al., 2017). For spinach, immersion in 50°C water for 25 min eradicated *P. farinosa* f. sp. *spinaciae* (Gullino et al., 2012). Unfortunately, basil seeds are not considered suited to hot water treatment as they produce a gelatinous exudate (McGrath, 2019).

However, for diseases like downy mildew, where a small infection rate (less than 0.1%) may lead to complete crop loss, preventative measures at other production stages are likely to be required in addition to seed treatments (Herforth-Rahme et al., 2017).

Modelling Aerial Oomycete-Associated Diseases

Overall, limited research has been carried out regarding early warning systems for vegetable disease occurrence in glasshouses (Zhao et al., 2011). As aerial oomycete spores can be present in air in the absence of visible disease, a rapid spore detection and measuring system for airborne brassica and lettuce downy mildew spores has been developed (Defra, 2005). This antibody-based immunological test (enzyme-linked immunosorbent assay, ELISA) can provide results within 3 h and could be used as part of an early warning system. Also, combining a heating control unit with a dew condensation sensor has been reported to reduce

the incidence of cucumber downy mildew in glasshouses from 78 to 51% (Ushio and Takeuchi, 2006).

Some studies have attempted to mathematically model the behaviour of downy mildew diseases in order to develop early warning systems that aid prediction of disease outbreaks. The effectiveness of such models will likely depend on how early they are able to predict likely downy mildew outbreaks. If infection has already occurred but symptoms are not yet apparent, i.e. the disease is in its latent phase, then effectiveness may be lower and the system could be more useful for assisting in the timing of fungicide applications rather than eliminating outbreaks altogether.

Mathematical models of the germination and infection of *B. lactucae* have been made using variables of 0-24h LWD and six different temperatures ranging from 5 to 30°C (Scherm and van Bruggen, 1993). Spore germination of *B. lactucae* showed a broad optimum of 5-20°C when the LWD was greater than or equal to 8h. When the LWD was shorter (4 vs 12h), a higher temperature was required for spore germination (10-15°C vs 5°C) (Scherm and van Bruggen, 1993), further illustrating the interaction between multiple environmental factors on downy mildew biology. Additional studies of mathematical models which summarise the effect of leaf wetness duration, temperature and spore density on infection by *H. parasitica* and *B. lactucae* have been made (Defra, 2005). Such studies may help to model such diseases when multiple interacting factors important and could be useful for predicting disease outbreaks and scheduling control approaches.

Modelling has been used to create risk threshold charts for cucumber downy mildew (Aruz et al., 2010; Ojiambo et al., 2011) in order to assist with the timing of fungicide applications (Neufeld and Ojiambo, 2012). A model for cucumber downy mildew for use in early warning systems in solar glasshouses (known as EWMPICDW) has been developed (Zhao et al., 2011). This model is based on monitoring data and published disease epidemiology data. In an improvement over earlier forecasting models (Xu, 2004; Ju, 2006; Yang et al., 2007; Li et al., 2010), the study combined a leaf wetness sensor and RH threshold model to estimate LWD. LWD predictions were then combined with temperature to generate an infection condition model. Temperature was chosen as a warning indicator for disease incubation. The success of predicting disease for the early warning model was 94% in one location and 57% in another, with 0-3d of lead time before disease occurrence. In the low success location, these results are considered to be likely due to lower RH making LWD prediction insufficient to trigger a warning. However, the latent phase for this disease has been reported to be 2d at 22-25°C, 3-4d at 26-30°C, 7d at 15-16°C and 10d at 12-15°C (Fu and Yao, 1983). This means that infection could already be underway by the time the warning is raised. Such a model may therefore be useful for timing fungicide applications but may not provide sufficient

notice to prevent infection unless growth conditions can be changed to inhibit further disease development and so the occurrence of visible symptoms.

Other Potential Cultural Control Approaches

In addition to control measures such as reducing RH to 80-85% through heating, venting and air circulation; an increase in plant spacing and hygiene strategies are recommended for a range of downy mildew diseases (Anon, 1988; Anon 2015; Jackson et al., 2014; Jennings, 2019; McGrath, 2019). Standard control measures such as rotations, rogueing and avoiding overwatering have been recommended to combat pathogens such as *H. parasitica* (Minchinton et al., 1996; Minchinton and Hepworth, 1998; Koike et al., 2007). Avoiding high humidity and overhead watering in order to minimise leaf wetness have been recommended to control a wide range of downy mildew diseases, for example, of roses (O'Neill, 2014a), *Antirrhinum* (Hanks, 2014), *Aquilegia* (Jennings, 2016a), lisianthus (*Eustoma*; Hall, 1994; O'Neill, 2003), *Viola* (Jackson et al., 2014), basil (Jennings, 2019) and (O'Neill, 2014b).

An integrated management for aerial oomycete-associated diseases has been described (Minchinton 1998). This strategy recommends the use of controlling watering, where the watering of seedlings in the morning is avoided, particularly after dew evaporation due to coincidence with spore release. Short, heavy watering is considered preferable to longer, lighter periods of watering. The maintenance of ventilation in order to reduce humidity and aid leaf drying, in combination with adequate plant spacing and lower seedling density is also recommended, together with providing a balanced programme of plant nutrition. Regarding crop nutrition, results suggested that cucumber downy mildew was significantly decreased in a manner comparable to fungicide application on plants grown with 200 or 300 ppm N and either 300 or 400 ppm K fertilisation, but the inhibitive effect was only recorded with increasing K levels at low N rates, indicating an interaction between the effects of N and K levels on downy mildew (Papadaki, 2009). Glasshouse hygiene is also considered to be key to minimising such diseases with the removal of heavily infected plants or outbreaks where necessary together with the eradication of cruciferous weeds, which may act as a reservoir of inoculum for brassica hosts (Minchinton, 1998). Such control measures are recommended to form part of a combinatorial approach which also includes fungicide application where permitted (D'Ercole, 1975).

Polyethylene mulches have also been used to cover the surface of growing media in order to reduce evaporation and so humidity, with an aim to controlling downy mildew. The covering of soil with reflective polyethylene reduced the RH, LWD and the frequency of nights with dew formation, suppressing late blight infection in tomato by up to 84%, particularly when

temperatures exceeded 30°C (Shtienberg et al., 2004, 2010). The colour of mulch used (bicolour aluminised, clear or black) was not considered to affect treatment efficacy (61-96% efficacy of control) (Shtienberg et al., 2010). Such polyethylene mulches have also been investigated in cucumber production. Plastic mulching on whole ground was compared to that for ridge surfaces only (Ding et al., 2014). Compared to ridge mulching, mulching on whole ground raised the soil temperature by around 2°C and decreased RH by around 11.5%. It also improved the fresh weight per unit leaf area, leaf chlorophyll content and net photosynthetic rate, increasing yield by 17-24%. Mulching on whole ground reduced the disease index of downy mildew by 22-24% and reduced water use by 40% (Ding et al., 2014). In a similar study, an efficacy of around 35% disease reduction was obtained (Shtienberg et al., 2010). These techniques have been used for crops which are planted directly in the ground and drip irrigated, but this or similar approaches could be considered for reducing evaporation from growing media in other protected horticulture systems.

Some aerial oomycete pathogens such as *P. cubensis* predominantly enter the leaf via stomata (Iwata, 1938). In addition, at lower RH, fewer open stomata are seen in lettuce leaves and this is thought to contribute to the lower numbers of *B. lactucae* sporangiophores found under such conditions (Su et al., 2004). Therefore, factors affecting stomatal opening may be key to the initiation of the infection process and could represent control routes through the modulation of stomatal opening, for example through reduced humidity, as already discussed, or through transient drought treatments, for example, intended to reduce stomatal opening.

It should also be noted that doubling the CO_2 concentration in controlled environment growth cabinets significantly increased basil downy mildew incidence and severity (Gilardi et al., 2016). Modification of glasshouse CO_2 provision could also therefore be investigated as a means to control aerial oomycete-associated diseases.

It is also thought that spores present in irrigation water could represent a source of downy mildew infection (Wedgwood, 2016 and for monitoring and control options Pettitt CP 126). A 10-day ultrasound treatment showed some effectiveness against spores of *P. infestans* in water (Anon, 2011) but such a duration of treatment is unlikely to be of practical use. Other water treatments such as UV irradiation or slow sand filters could be investigated for their efficacy against aerial oomycete spores.

Finally, other potential treatments include calcium oxide, K-phosphite and orange oil with ascorbic acid, which controlled basil downy mildew with efficacies of 58%, 40% and 26%, respectively (Gilardi et al., 2020) but these products are not currently approved for use in the UK. This data was used to develop a spray programme consisting of 2 to 4 applications of calcium oxide in succession to one application of azoxystrobin. This programme reduced

downy mildew severity by up to 80% under a reduced crop density and provided comparable control to a conventional fungicide programme based on the alternation of azoxystrobin, fluopicolide + propamocarb and mandipropamid (Gilardi et al., 2020).

Conclusions

The environmental sensitivity of aerial oomycete pathogens provides an opportunity to develop cultural control practices to aid in their management. The manipulation of humidity, leaf wetness, temperature and lighting offer a number of potential control strategies for aerial oomycete-associated diseases. A number of studies have investigated the effects of environmental changes in aerial oomycete pathogen behaviour and disease biology and a number of potential approaches have been developed for protected horticulture. It should be stressed that the interaction between these variables and other factors such as pathogen and host species remains an important consideration in the design of cultural control methodologies. Despite the promising data produced, further research into optimising novel cultural control strategies tailored to commercial setups is likely to be required.

Knowledge and Technology Transfer

Aspects of this review have been presented at the Basil Downy Mildew Workshop (Stockbridge Technology Centre) 05/03/20 and CP 184 Downy Mildew and Blight Control Strategies Update Meeting 22/06/20.

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Appendices

Appendix 1.

Databases and websites used in the literature search.

Bibliographic databases:

Thomson Reuters Web of Science Core Collection [http://ipscience.thomsonreuters.com]
CAB abstracts [http://www.cabi.org/]
Dart e theses [http://www.dart-europe.eu/]

Ethos [https://ethos.bl.uk/]

Organisational websites

- Defra online databases [https://www.gov.uk/government/organisations/department-for-environment-food-rural-affairs]
- NERC Open Research Archive [https://nora.nerc.ac.uk/]
- FERA
- NIAB
- The cut flower centre [[https://www.thecutflowercentre.co.uk/?s=downy+mildew]
- United States Department of Agriculture [https://www.usda.gov/]
- AHDB [https://ahdb.org.uk/]
- SARE Sustainable Agriculture Research and Education [https://projects.sare.org/search-projects/]
- NFU
- Philips Lighting [https://www.lighting.philips.com/main/products/horticulture]
- Light and Plant Health [http://www.lightandplanthealth.org/]
- Stockbridge Technology Centre
- James Hutton Institute
- Lancaster University
- Nottingham University
- Worcester University
- Warwick University
- Cornell University
- Clemson University
- Wageningen University
- HAS University,
- UC Davis University
- NC State University
- University of Arizona

Online Industry news and other potentially useful publications:

- Farmers Weekly
- Farmers Guardian
- Commercial Glasshouse Grower

- The Vegetable Farmer
- Hort News
- Hortidaily
- Greentech
- Fruitnet (Eurofruit)
- Fresh Plaza
- New Scientist
- Nature
- Science
- British Herb Trade Association
- British Leafy Salad Association

