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Review

Epidemiology and control of strawberry powdery mildew: a review

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Summary. Strawberry powdery mildew, caused by *Podosphaera aphanis*, is an economically important disease for strawberry production. Typical symptoms are white mycelium on all aerial parts of affected plants, with young host tissues being the most susceptible. The pathogen overwinters on infected leaves, either as mycelium or chasmothecia, although the quantitative role of chasmothecia in epidemics are not fully understood. In spring, under favourable conditions, the fungus sporulates, disseminating conidia and causing polycyclic infections. The disease is mainly controlled using synthetic fungicides, but there is increasing interest in sustainable alternatives, including microbial biocontrol agents (e.g., *Ampelomyces quisqualis, Bacillus* spp., *Trichoderma* spp.) and substances of plant or animal origin (e.g., *Equisetum arvense*, orange oil, chitosan, whey). Physical methods, (e.g. UV-C, ozone) are also promising alternatives to fungicides. All of these strategies should be combined with appropriate agronomic practices (e.g., overhead irrigation, canopy management) to create unfavourable environments for the pathogen. However, agronomic practices have never been assessed for *P. aphanis*. Disease forecasting models and DSSs, though available, are underutilized due to their complexity and lack of validation across locations. This review presents the current state of knowledge on *P. aphanis* the available methods for control of strawberry powdery mildew, and highlights knowledge gaps relating to this host/pathogen relationship.

Keywords. *Podosphaera aphanis*, natural substances, biocontrol, agronomic practices, disease forecasting models.

INTRODUCTION

Strawberry powdery mildew (SPM), caused by *Podosphaera aphanis* (Wallr.) U. Braun and S. Takamatsu is a common disease, particularly in subtropical and tropical regions where strawberry (*Fragaria* × *ananassa* Duch) is grown (Nakzawa and Uchida, 1998; Amsalem *et al.*, 2006; Gadoury *et al.*, 2010; Carisse and Fall, 2021; Kasiamdari *et al.*, 2021; Palmer and Holmes, 2021). Most strawberry cultivars are highly susceptible to the disease, and only very few are tolerant (Menzel, 2022). Strawberry powdery mildew is mostly managed by synthetic fungicides that are sprayed regularly from emergence of the first leaves to the end of the harvest season (Carisse *et al.*, 2013a). This high use of fungicides fosters the build-up of resistant *P. aphanis* populations and has potentially negative impacts on animal and human health and the environment (Muñoz-Leoz *et al.*, 2011; Rjiba-Touati *et al.*, 2023). Due to increasing concerns relating to pesticides, consumers preferences have changed, and are increasingly opting for food products free of pesticide residues (Rimal *et al.*, 2001). As a result, agrarian systems are moving to sustainable and eco-friendly phytosanitary solutions, which fosters research and development of innovative approaches to disease management (Deresa and Diriba, 2023).

Significant progress has been made to develop alternatives for management of SPM, and many publications confirm this strong scientific commitment. However, strawberry producers still lack effective methods for managing SPM that can be considered as viable substitutes for chemical fungicides (Deresa and Diriba, 2023).

The aim of this review is to summarize current knowledge on SPM, and to highlight gaps in understanding which, if clarified, could contribute to increased effectiveness of SPM management.

METHODOLOGY

This review is structured into the following sections: classification and morphology of *P. aphanis*, and the symptoms of SPM; epidemiology and the most significant stages of the disease cycle; conventional and alternative control methods for SPM; agronomic practices that must be integrated for effective disease control; and the most relevant predictive models, decision support systems (DSSs) and early detection systems for SPM. The review concludes by suggesting future research to improve SPM management.

The relevant literature was reviewed using Google Scholar, Scopus, and Web of Science searches, for reports published from 1962 to 2023. The following keywords were used alone and in combinations in the searches: *Ampelomyces quisqualis*, airborne inoculum, *Bacillus*, basic substances, bioassay, biochar, biological agent, biostimulants, chasmothecia, classification, cleistothecia, conidia, conidiophores, control, cultural practices, decision support system, detection, disease, distribution, environmental conditions, epidemiology, essential oils, field, fungicide, inorganic salts, irrigation, life cycle, low-toxicity compounds, machine learning, model, morphology, mycophagous mite, nutrition, overhead irrigation, overwintering inoculum, ozone treatment, plant extract, *Podosphaera aphanis,* predictive model, resistance, seaweed extract, *Sphaerotheca macularis,* symptoms, strawberry powdery mildew, *Trichoderma*, UV treatment, water stress.

The first search (46 papers) was carried out in order to select the first and the most cited records for the classification of *P. aphanis* (eight papers), its morphology (two papers), and the symptoms it causes (nine papers). A second search (27 papers) focused on the fungus life cycle (18 papers) and SPM epidemiology (11 papers). A third search (104 papers) aimed to identify the fungicides (nine papers) and the alternative products assessed for SPM control (95 papers) by focusing on classical and advanced solutions such as biological control (11 papers), inorganic salts (21 papers), plant extracts (16), seaweeds (10 papers), substances from animal origin (six papers), chitin and its derivatives (12 papers), UV-C (nine papers) and ozone technologies (six papers). The selected papers of the third search were analysed according to the research outcomes, carried out under field or laboratory conditions. When data on *P. aphanis* were lacking and alternatives for management of other powdery mildews could be useful indicators for future research, those alternatives were included in the review. A fourth search was carried out to identify agronomic practices useful for management of SPM, such as canopy management (eight papers), plant nutrition (four papers), overhead irrigation (two papers), genetic resistance (seven papers) or spray equipment (eight papers). In this fourth search, in cases where there was no literature available on SPM, literature related to other powdery mildews was analysed. The fifth search included DSSs (17 papers), and early disease detection systems (six papers). Papers were not included when they showed low quality of experimental designs and data analyses, reported low powdery mildew severity in experimental controls (only for the efficacy trials), or were redundant due to other similar and previous results.

THE PATHOGEN AND THE DISEASE

Podosphaera aphanis (*Erysiphaceae*, *Ascomycetes*) was first reported (sexual stage) in the United States of America (Geneva, New York) in 1886 (Arthur, 1886). In Europe, this fungus was identified a few years later (Salmon, 1900), when its asexual stage was also described. The causal agent of SPM was initially thought to be the same as hop powdery mildew, *Podosphaera macularis* (Wallr.) U. Braun and S. Takamatsu [formerly *Sphaerotheca macularis* (Wallr.) Magnus] (Jhooty and McKeen, 1965). In 1976, Liyanage and Royle discovered that powdery mildews of strawberry and hop were caused by two different pathogens. Recent taxonomic studies have described clear distinction between ascocarp appendages of *Podosphaera* and *Sphaerotheca* (Braun, 1982; Braun and Takamatsu 2000), which neces-

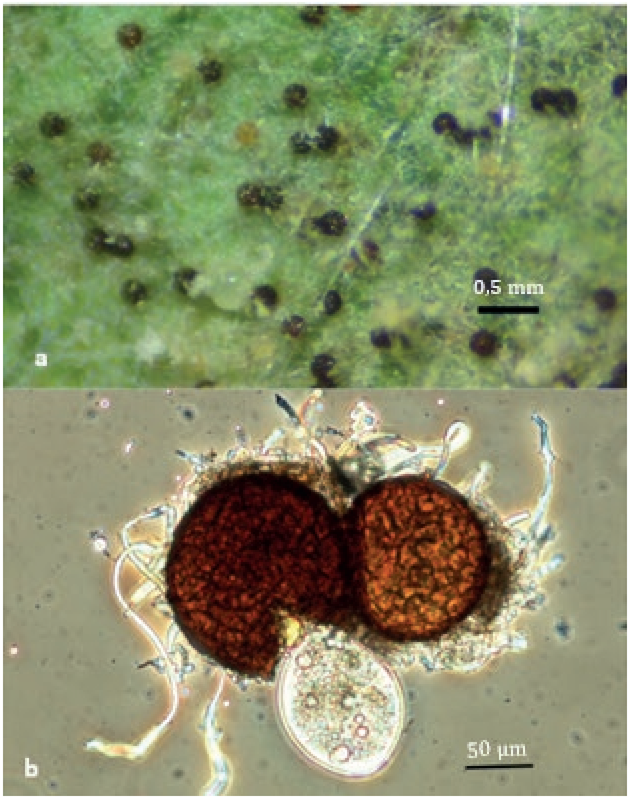

Figure 1. a) Chasmothecia of *Podosphaera aphanis* on an abaxial surface of a strawberry leaf. b) Open chasmothecium and with released ascus.

sitated a change of the genus name of the agent of SPM to *Podosphaera* (Cook *et al*., 1997; Kirk *et al*., 2001).

Morphological characteristics, originally described in 1987 (Braun, 1987), were recently displayed with digital light microscopy (Iwasaki *et al.,* 2021). The hyaline conidia of *P. aphanis* are ellipsoid–ovoid to doliiform–limoniform in shape, and contain oil and fibrosin bodies. Their dimensions are 27–33 × 18–22 µm. The appressoria, which develop on germinated conidia, are 4 µm wide. Conidiophores (dimensions 84–129 × 8–11 µm) each produce six concatenated conidia. Chasmothecia (Figure 1) are dark brown (100–125 × 65–80 µm), and are firmly attached to the surrounding mycelium. Each chasmothecium (Figure 1) contains one ascus (dimensions 60–94 × 55–76 µm), which contains eight ellipsoid to subglobose ascospores.

Symptoms of strawberry powdery mildew

The typical symptoms of SPM are white powdery patches of mycelium and conidia, spread across all aerial parts (leaves, runners, flowers, fruit) of affected host plants (Figure 2, a to i). Host tissues can be affected at all stages of development, although young organs (e.g., not fully expanded leaves, flowers, green berries) are more susceptible than older tissues (Carisse and Bouchard, 2010; Asalf *et al*., 2014). As the disease progresses, leaf edges curl upwards, and purple to reddish irregular blotches may develop on the leaf surfaces (Lambert *et al*., 2007) (Figure 2, c and d). Round black chasmothecia may be visible on abaxial leaf surfaces, in late summer/autumn (Gadoury *et al*., 2010).

Severe infections can cause strawberry yield losses of up to 30% (Carisse *et al.,* 2013b), due to the white mycelium covering ripe and unripe fruit, fruit deformation (Figure 2, g, h and i), hardening and dehydration, achene exposure (Figure 2 g), and eventual fruit decay. Beside negative impacts on fruit quality, photosynthesis reduction, plant stunting and flower abortion are also associated with SPM (Peries, 1962a; Jhooty and McKeen, 1965; Gooding *et al*., 1981; Maas, 1998; Amsalem *et al*., 2006), although no data are available on the yield losses caused by these types of symptoms.

The disease cycle of Podosphaera aphanis

The disease cycle of strawberry powdery mildew (Figure 3) has been extensively investigated. The pathogen overwinters as mycelium on living infected leaves, and sporulation recommences in spring, leading to conidium dissemination and consequent polycyclic infections (Gadoury *et al*., 2010; Iwasaki *et al*., 2021) (Figure 3). Nevertheless, *P. aphanis* can also overwinter as chasmothecia, which developed in late summer/autumn (Gadoury *et al*., 2010; Jin *et al*., 2012) on the infected host leaves, in commercial fields or in the nurseries (Peries, 1962b). In spring, commonly from early March to late May in the northern hemisphere, mature chasmothecia release ascospores, which are responsible for the early infections on plants (Gadoury *et al*., 2010) (Figure 3).

Asexual reproduction

Extensive research has been conducted on the processes of asexual reproduction during host vegetative growth, including laboratory and field studies on conidiation and polycyclic infections. These have provided insights into the dynamics of fungal development and dissemination. After infection, temperatures between 18 and 25°C at 97–100% relative humidity (RH) favour enlargement of the lesions, leading to conidiation (Miller *et al*., 2003; Amsalem *et al*., 2006). Conidiophores each develop from a generative cell that after a gradual

Figure 2. Strawberry powdery mildew symptoms. a-b) white patches on the abaxial and adaxial leaf surface, c) red blotches on the leaf surface, c-d) leaf curling, e-f) white patches on leaf and flower petioles, g) fruit deformation, h-i) white mycelium and white patches on unripe and ripe fruits.

upward elongation, produces conidium chains. Conidia are released when mature, following the individual order of development. Each time a conidium is released, the generative conidiophore cell starts to form a new conidium. The lifetime of conidiophores, from generative cell formation until the first conidium release, is approx. 125 to 150 h. At 22°C and 45–55% RH, with wind speed of 0.5 m s^{-1} (necessary for conidial detachment), each

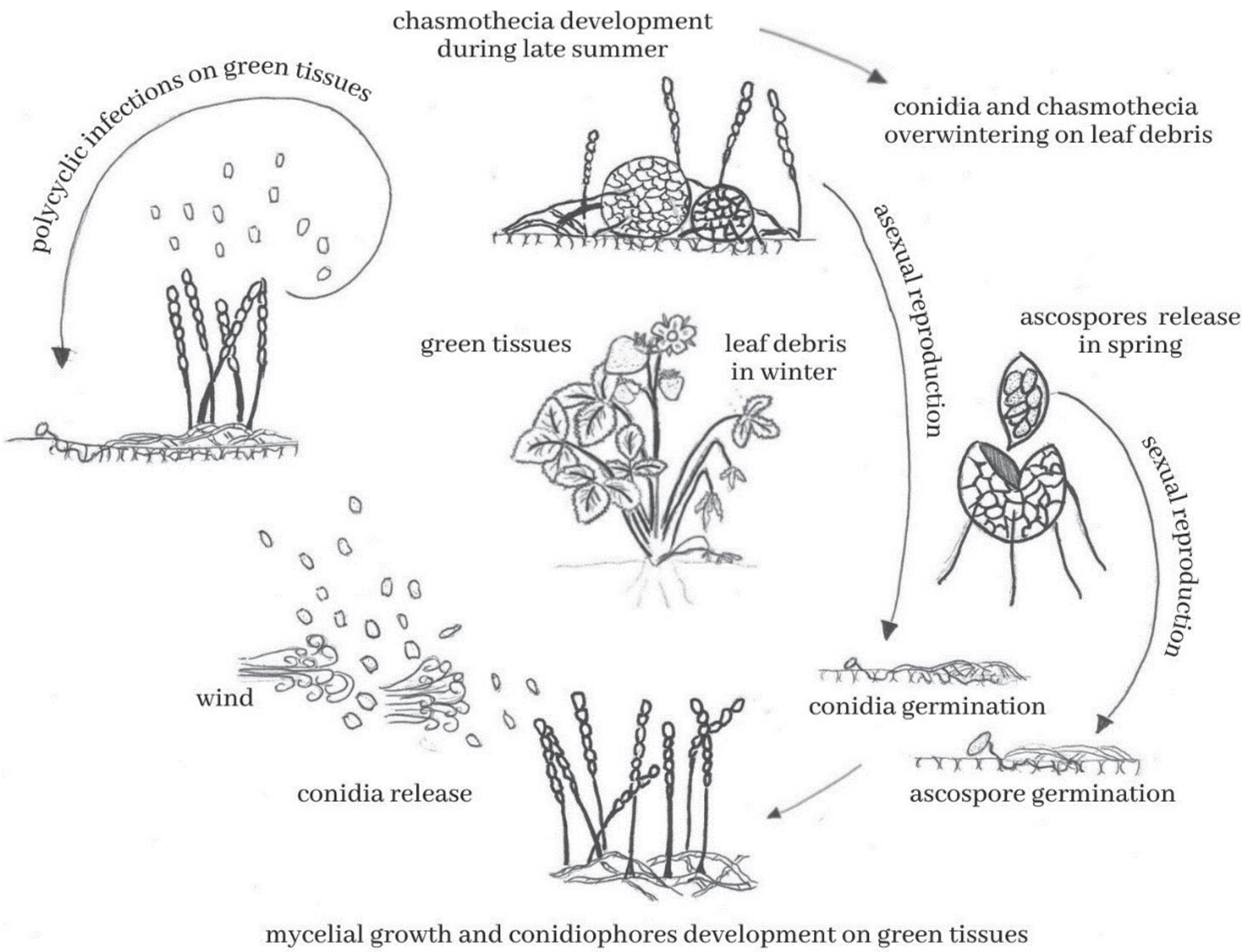

Figure 3. Disease cycle of strawberry powdery mildew.

conidiophore releases an average of 38 progeny conidia within 96 h (Iwasaki *et al.*, 2021). Within a colony lifetime (35 d after inoculation) each colony can release an average of 6.7×10^4 conidia (Ayabe *et al.*, 2022).

Under laboratory conditions (22±1°C, 45–55% RH), conidia of *P. aphanis* germinate within 4–5 h after inoculation, with each conidium forming a germ tube that develops into an appressorium (Iwasaki *et al.*, 2021). After successful host penetration, achieved by enzymatic and mechanical processes, a haustorium forms within the host epidermal cell, and typically invades the host plasma membrane 1 d after inoculation, and hyphal growth commences. Conidiophores develop 3–5 d after inoculation, and conidiation usually commences 6 d after inoculation (Peries, 1962a; Jhooty and McKeen, 1965; Iwasaki *et al.*, 2021).

Conidia can germinate between 3 and 32–38°C (Jhooty and McKeen, 1965; Sombardier *et al.*, 2009), and temperature influences the rate and speed of germination. For example, between 15 and 25°C germination of conidia varies between 85 to 88% (Amsalem *et al.*, 2006), while only 1% germination was recorded at 5 or 35°C (Amsalem *et al.*, 2006). At 5, 10, and 15°C, minima of, respectively, 25, 15 and 12 h were required for conidium germination, while between 18 and 30°C only 5 h were necessary (Peries, 1962a). Conidium germination rates are also influenced by different leaf surfaces, with is 20% greater germination on abaxial than adaxial surface (Maas, 1998; Sombardier *et al.*, 2009). As for many powdery mildews, free water is detrimental to conidia and mycelium of *P. aphanis* (Peries, 1962a; Sombardier *et al.*, 2009).

Sexual reproduction

Podosphaera aphanis is heterothallic, so initiation of chasmothecia begins when antheridium and ascogonium are formed from the mycelium of different mating types. Myceloid appendages extended from the outer chasmothecia wall are directed downward to the mycelium and tenaciously attached (Asalf *et al.,* 2013). Initiation of ascocarps is regulated by temperature. The most favourable temperature for chasmothecium development is approx. 13°C, that occurs 10 to 14 days after inoculation (Asalf *et al.,* 2013). Up to 400 chasmothecia per cm^2 of leaf form after 14 d incubation at this temperature. However, chasmothecium development is largely suppressed at temperatures >13°C. For example, at 20°C the mean number of chasmothecia per cm^2 was up to 21, and the incidences of leaves bearing chasmothecia at 9 or 12°C were much greater (respectively, 92 and 93%) than at 15, or 18°C, (respectively, 7 and 6%) (Asalf *et al.*, 2013). Chasmothecia have different developmental stages: white, brown, and black when mature. Rupture of the ascus and ascospore release generally occurs within 5 min at 22 to 25°C provided that the ascocarp remains in contact with a film of water (Gadoury *et al.,* 2013).

EPIDEMIOLOGY OF STRAWBERRY POWDERY MILDEW

Environmental factors influencing the disease

Primary infections

The role and quantitative contribution of chasmothecia in initiation of SPM epidemics is not clear, and in some regions the asexual stage prevails over the chasmothecia, which are rare or absent (Howard and Albregts, 1982). This indicates a secondary role of chasmothecia in the SPM epidemiology. One possible reason is that geographically discontinuous distributions of mating types may prevent/reduce sexual reproduction (Gadoury *et al.*, 2010). A second reason could be unsuitable temperatures for the ascocarp initiation (Gadoury *et al.*, 2013). Temperature is a key environmental factor influencing ascocarp formation.

While the most favourable temperatures for the development of chasmothecia are well-documented, the conditions for chasmothecium survival during winter, and the related viability of ascospores, have been little studied. In a 4-year survey carried out in New York State and Norway, proportions of chasmothecia containing viable ascospores (i.e. positively reacting to fluorescein diacetate stain) consistently exceeded 80%. In contrast, ascospore germination on glass, investigated in the last two years of the same experiment, was highly variable, ranging from 42% to 98% (Gadoury *et al.,* 2010). This variability underscores the need to explore the factors affecting ascospore germination and infection rates. Integration of such data into powdery mildew predictive models could increase prediction precision to assist commencement of disease control treatments at the beginning of strawberry production seasons. However, quantitative estimation of initial inoculum is a challenge for all forecasting models that have been developed in other powdery pathosystems (Gubler *et al.*, 1999; Caffi *et al.,* 2011).

Secondary infections

As with the majority of *Erysiphales*, *P. aphanis* releases conidia mainly during daytime (Blanco *et al.*, 2004), and conidium release is affected by temperature and RH fluctuations. The release of conidia is directly correlated with increase in temperature and decrease in RH (Blanco *et al.,* 2004). For example, Blanco *et al.* (2004) showed, in a 2-year experiment, that in the first year minimum conidium release occurred at 12°C and 86% RH, and maximum release was at 14°C and 73% RH. In the second year release was at 13°C and 82% RH, and maximum release was at 18°C and 54% RH.

The quantity of conidia and the timing of their release are key for development of SPM epidemics (Willocquet *et al.,* 1998; Van Maanen and Xu, 2003). As for other *Erysiphales*, populations of airborne SPM conidia depend on the quantity of infected organs in a crop. For example, there is a close correlation between the weekly average aerial concentration of conidia (conidia/m^3) and the weekly average number of diseased leaves and berries (Blanco *et al.*, 2004; Van der Heyden *et al.,* 2014). As the number of conidia in the air and the infected organs in a field are closely related, the number of conidia in the air and the first visible symptoms on plants are also closely related. If promptly recognized, the critical conidium concentration threshold at which crops must be treated could be crucial to avoid field disease outbreaks. First SPM symptoms likely to become visible after 7-14 d, when the airborne conidium concentration captured with an air sampler has recorded more than 500 conidia m^{-3} d^{-1} (Carisse and Bouchard, 2010).

Because SPM is a wind-borne disease, understanding patterns of conidium dispersal under field conditions is important for implementing disease control strategies. However, accurate models of pathogen spread over time from specific inoculum sources have not been developed, although there have been attempts to measure conidium dispersal. For example, after 3 d of exposure, the dispersal radius from infected plants used as inoculum sources was 1.2-1.5 m (Peries, 1962b). The dispersal of conidia from an infected source changes according to the environment. For example, dispersal is greater under plastic tunnels than in greenhouses (Willocquet *et al.*, 2008), and is greater in open fields than in plastic tunnels (Carisse *et al.*, 2013a). The hypothesis for these effects is that wind is less in greenhouses than in plastic tunnels, and less in tunnels than in open fields (Willocquet *et al.*, 2008; Carisse *et al.*, 2013a). In addition, this may explain why SPM dispersal in an open field is difficult to determine, because dispersal has heterogeneous patterns (Van der Heyden *et al.*, 2014).

Agronomic factors influencing the disease

Cropping systems and crop cultivars

In response to growing market demand for strawberries, cropping systems have evolved from classical field production to highly complex approaches. The need to provide high-quality product throughout the year has led to progressive replacement of short-day (June-bearing) varieties with day-neutral (or everbearing) varieties, that produce fruit for the entire season. Both varieties June-bearing and everbearing are susceptible to powdery mildew, but the latter are more exposed to pathogen infections during their life cycle in summer (Maas, 1998). Whereas June-bearing varieties produce fruit until late spring, the growing season of day-neutral varieties coincides with optimal conditions for disease development in midsummer (Maas, 1998; Blanco *et al.,* 2004; Carisse and Bouchard, 2010). Risk of infection is further enhanced where June-bearing and day-neutral varieties coexist. There is an overlapping production at the beginning of the season of new transplanted day-neutral plants with overwintering infected June-bearing varieties, which are sources of inoculum (Fall and Carisse, 2022). In subtropical regions, to ensure high yields, June-bearing varieties are planted in mid-summer for the first harvest, in late summer, and, after overwintering in the field, these crops each produce a second harvest in the following late-spring. The day-neutral varieties, on the other hand, are planted in mid-spring for a single growing season, that partially overlaps with the growing cycle of the June-bearing plants (Carisse and Fall, 2021).

As well as high susceptibility of everbearing strawberry varieties, the adoption of soilless production on raised beds in plastic tunnels or greenhouses gives environmental conditions that are conducive to powdery mildew (Xiao *et al.*, 2001). Under coverage, SPM is not inhibited by rain and/or prolonged leaf wetness, which can stop conidium germination and eventually kill conidia in open fields. In addition, polyethylene/glass shading decreases sunlight intensity, favouring powdery mildew development because these pathogens are strongly photosensitive (Amsalem *et al.*, 2006; Elad *et al.*, 2007).

Plant water stress

Effects of plant water stress on *P. aphanis* infections has not been extensively studied, although for other powdery mildews host water stress reduces hyphal growth, slowing colonisation of new tissues, and also disrupts conidiation (Ayres and Woolacott, 1980; Caesar and Clerk, 1985). Xu *et al.* (2013) and Rossi *et al* (2020) showed positive correlations among plant hydration, disease susceptibility, and pathogen fitness. For example, 21 d after inoculation, water stressed plants showed slight reductions in disease severity on abaxial leaf surfaces compared to the well-hydrated plants (Rossi *et al.,* 2020). Host water stress also affects conidium germination. Germination rates differed for conidia collected from plants grown at different soil moisture levels. Germination, assessed on water agar, increased linearly from 0 to 30% for conidia collected from plants grown in soil moisture levels ranging from 0 to approx. 53%.

CONTROL METHODS AND APPROACHES

Fungicides

In the European Union, synthetic fungicides authorised for the control of SPM and categorised based on their modes of action (Frac Code List, 2022) (Table 1), belong to the following groups: hydroxy-(2-amino-) pyrimidines (A2), succinate dehydrogenase inhibitors (C2), quinone outside inhibitors (QoIs; C3), (C5), demethylation inhibitors (G1), and others with unknown modes of action (U). To reduce risks of selecting resistant pathogen populations, fungicides with different modes of action must be combined in appropriate disease management strategies (Palmer and Holmes, 2021). The majority of active substances authorised for the use against *P. aphanis* belong to few mode of action groups, resulting in recurrent use of a limited number of products with the same modes of action. Some of these fungicides, such as the triazoles (demethylation inhibitors) have favoured emergence of resistant *P. aphanis* populations (Sombardier *et al.*, 2010; Palmer and Holmes, 2021).

Among the authorised active ingredients, only sulphur has multisite mode of action, which can be used to mitigate emergence of fungicide resistant *P. aphanis* populations (Peres and Mertely, 1969). However, although sulphur has low mammalian toxicity and has a long use history, including in organic farming, this

Table 1. Fungicides authorised for use against strawberry powdery mildew in at least one European Union Member State (EU pesticide database, April 2023). The active ingredients are grouped according to the FRAC Code list, 2022.

Active substance	Target Code	Group name
Bupirimate	A2	Hydroxy- (2-amino-) pyrimidines
Boscalid	C2	Succinatedehydrogenase inhibitors
Cyflufenamid	U6	Phenylacetamides
Difenoconazole	G1	Demethylation inhibitors
Fluopyram	C2	Succinatedehydrogenase inhibitors
Fluxapyroxad	C2	Succinatedehydrogenase inhibitor
Meptyldinocap	C5	Uncouplers of oxidative phosphorylation
Penconazole	G1	Demethylation inhibitors
Pyraclostrobin	C3	Quinone outside inhibitors
Tetraconazole	G1	Demethylation inhibitors
Trifloxystrobin	C3	Quinone outside inhibitors
Sulphur	M02	Inorganic

chemical can negatively impact beneficial arthropods (Beers *et al*., 2009).

In addition to selection of resistant pathogen populations, some compounds, such as the triazoles (demethylation inhibitors; G1), are posing risks for animals and humans (Muñoz-Leoz *et al*., 2011; Rjiba-Touati *et al*., 2023). Also because of slow environmental degradation of these chemicals (EFSA, 2010), they have been associated with detrimental human health consequences, including infertility and disruptions in neurobehavioural functioning (Menegola *et al*., 2006; Zhang *et al*., 2016).

Bioprotection

There has been increased research to develop alternatives to synthesized fungicides. However, intrinsic bias often occurs, with tendency to publish positive results while ignoring the negative outcomes. This leaves an important gap in understanding of effectiveness of these alternatives, which may result increased expectation for efficacious products. When applied in the field, these products fail to control target diseases, either due to overestimation of efficacy or to lack of knowledge of factors that may reduce their effects, such as optimal concentrations, and timing and frequency of applications. This underlines the importance considering negative results which could contribute realistic evaluations. There are also discrepancies between published research and results obtained by the industry. While a range of commercial products have been officially authorised for the use in SPM control (and are therefore of proven efficacy), this often lacks robust confirmation in the scientific literature. Industry operators may not disclose efficacy data, which hinders the advancement of research efforts. This lack of information impedes collective progress in SPM control and raises concerns about the "robustness" of the effectiveness of these active substances.

Several categories of alternatives to fungicides have been defined. Although their analysis is beyond the scope of the present review, the suggestion of Stenberg *et al.* (2021) is relevant: *"bioprotection can be used as an excellent umbrella term that encompasses protection provided by either living agents or non-living substances of biological origin […] with low impact on human health and the environment'*. In the present review we divide the alternatives into groups based on their nature and/or origins.

Inorganic salts

Several inorganic salts have been tested for efficacy in suppressing fungal pathogens, but when considering powdery mildews, potassium and sodium bicarbonates (Homma *et al*., 1981; Crisp *et al*., 2006a), potassium silicate (Menzies *et al*., 2019) and potassium phosphate (Reuveni *et al.,* 1995; Reuveni and Reuveni, 1998) have been the most investigated. For SPM, there are fewer reports, and only potassium and sodium bicarbonates and silicates have been sufficiently assessed. For example, potassium and sodium bicarbonates (4 g L^{-1}) showed promising efficacy, in leaf bioassays, for control of *P. aphanis*, with, respectively, 87% and 84% reductions in hyphal biomass (Pertot *et al.,* 2007). The promising laboratory results were not fully confirmed in the field, where prolonged applications of a combination of potassium bicarbonate and potassium silicate at 6 g L^{-1} gave 85% disease incidence compared to 88% for untreated controls (Gomez *et al.,* 2017). A much greater rate of potassium bicarbonate (20 g L^{-1}), if integrated with fungicides, has given promising outcomes. Two applications of potassium bicarbonate were as effective as the systemic fungicide myclobutanil, suggesting a potential role for potassium bicarbonate in integrated disease management (Dodgson, 2007). Comparative studies assessing the effectiveness of inorganic salts versus conventional fungicides or their combinations, could improve their application strategies. Even if mode of action has yet to be fully defined (Deliopoulos *et al*., 2010), activity of bicarbonates likely occurs when the salts come into contact with the pathogen. This interaction inhibits sporulation and fungal development due to detrimental osmotic effects of K^+ imbalance, spore dehydration and increases in leaf surface pH (Ziv and Zitter, 1992; Kettlewell *et al.*, 2000; Pertot *et al.*, 2007). Bicarbonates need frequent applications to be effective, as is emphasized in label guidelines of commercial products (e.g., Karma 85, Certis Europe), that suggest 7-10 d interval between treatments. However, these repetitive treatments can possibly cause residual deposits and phytotoxicity.

Potassium silicate is another inorganic salt that has been extensively tested against SPM. Silicon (Si) is associated with beneficial effects on mechanical and physiological characteristics of plants, depending on whether it is applied to roots or to canopies. For example, potassium silicate 100 mg L^{-1} applied once to strawberry roots in hydroponics decreased disease severity by 17% (Kanto *et al.,* 2004). This compound at 500 mg L^{-1}, applied at an average of 0.86 g m^{-2} d^{-1} during cultivation (Kanto *et al.,* 2006) also suppressed SPM in soil by up to 15%. Kanto *et al.* (2007) demonstrated that hydroponic Si fertilization decreased disease severity and reduced fungal fitness. This was shown by reductions in germination of conidia collected from Si-treated plants compared to the controls. Germination rates were 49.7% for Si-treated plants and 67.2% for the controls. This protective role of root Si fertilization was attributed to Si accumulation in leaves, which hinders cuticle penetration by pathogens (Seal *et al.*, 2018). This theory was supported by identification of Si transporters in strawberries, providing genetic evidence that strawberry is receptive for Si fertilisation (Ouellette *et al.*, 2017). However, silicic acid is the only soluble form that plants can absorb to successfully store Si in leaves and decrease disease severity (Ouellette *et al.,* 2017). Under a daily potassium silicate fertilization (1.7 mM Si) leaf accumulation can reach up to 3% Si on a dry weight basis (Ouellette *et al.,* 2017). Silicon is also as an elicitor of plant resistance, and induces several defence-related reactions, such as the over-production of enzymes (e.g., polyphenoloxidase and peroxidase) and antifungal compounds (e.g., flavonoids and phytoalexins) (Wang *et al.*, 2017).

Elicitation of resistance to SPM in strawberry has yet to be assessed. Although potassium silicate is promising when applied to plant roots, when applied to leaves this compound was less effective (Palmer *et al.,* 2006; Jin, 2015; Gomez *et al.,* 2017). Root applications influence various aspects of plant physiology and defence mechanisms, which may have greater disease suppression effects than foliar applications. The mode of action of foliar-applied potassium silicate for reducing powdery mildew has not been determined, but formation of physical barriers and osmotic effects on leaf surfaces may contribute to disease suppression (Bowen *et al.,* 1992; Rodrigues *et al.,* 2009).

Plant extracts

Plant extracts are complex mixtures containing bioactive compounds, that are obtained by physical processes such as distillation and extractions of/from leaves, stems, of fruit (SANCO, 2012). In the EU, plant extracts used as plant protection products are authorised according to Regulation (EC) No 1107/2009 (EU, 2009). Several plant extracts have shown promising results for suppressing powdery mildews, with various mechanisms including inhibition of spore germination and mycelium growth, and disrupting fungal reproductive structures (Marei *et al.,* 2012; Silva *et al.,* 2020). Among plant extracts, essential oils and aqueous extracts are promising groups for disease management.

Essential oils are concentrated hydrophobic liquids extracted from plants, by distillation with water or steam, mechanical processes (e.g., pressing or grinding), or dry distillation (ISO 9235, 2021). These oils contain volatile compounds (ISO 9235, 2021) that have diverse biological activities, including antifungal properties (Cavanagh, 2007; Ferraz *et al.,* 2022). Among these, oils from *Thymus* spp. L., *Mentha* spp. L., *Melaleuca alternifolia* (Maiden and Betche) Cheel (tea tree oil) and *Citrus sinensis* (L.) Osbeck (orange oil) have been tested against several powdery mildew species (Reuveni *et al.,* 2020; Mostafa *et al.,* 2021; Frem *et al.,* 2022), but limited information is available for SPM.

Orange oil is the only essential oil authorized in the EU and in at least one European Union Member State for control of SPM (European Pesticide Database, 2023). However, only a few papers report efficacy of orange oil against SPM (Prodorutti *et al.,* 2019). For example, orange oil, if applied weekly, was as effective against SPM as most conventional fungicides. Disease severity was reduced from 81% (untreated control) to 14% by penconazole and 19% by orange oil (Prodorutti *et al.,* 2019). The active component of orange oil is limonene, a volatile compound that disrupts fungal cell membranes and inhibits spore germination (Marei *et al.,* 2012; Silva *et al.,* 2020). Beside antifungal properties, orange oil has insecticidal properties, as is common with essential oils in general (Isman, 2020), possibly affecting beneficial insects and disrupting ecosystem balance. This highlights the importance of holistic pest management strategies that target pathogens but also do not generally impact the field environment.

Aqueous plant extracts may include secondary metabolites, phenolic compounds and enzymes that can directly affect pathogen physiology and growth (Tavares *et al.,* 2021). For example, *Equisetum arvense* L., and *Salix* spp. L. cortex extracts can control some powdery mildew species, although with slight efficacy (Marchand *et al.,* 2014; Frem *et al.,* 2022). Among plant aqueous extracts, those from *E. arvense* are authorised in the EU as basic substances and in at least one European Union Member State for control of SPM (EU Pesticide Database, 2023). Although the mode of action is unknown, silicon as a major component of *E. arvense* reduces effects of excessive moisture on leaves and inhibits fungal growth. This involves creation of physical barriers of Si on leaf surfaces combined with osmotic effects that absorb excessive moisture favouring fungal proliferation (Bowen *et al.*, 1992; Rodrigues *et al.,* 2009).

Seaweed extracts

The first report of seaweed against powdery mildews was that of Stephenson (1966), and research on these extracts has expanded (Li *et al.*, 2020; Elagamey *et al.*, 2023). Abundant and common brown seaweeds such as *Ascophyllum nodosum* (L.) Le Jolis, *Ecklonia maxima* (Osbeck) Papenfuss and *Laminaria digitata* (Hudson) J.V. Lamouroux, are the most frequently used for their plant growth promoting activities (Khan *et al.*, 2009). In the EU, most seaweed extracts used in agriculture are considered as fertilizers (EU, 2019). However, seaweeds have also been acknowledged as potential alternatives for plant protection products, due to their capacity to enhance plant disease resistance by interacting with secondary metabolism and defence-related processes (EIBC, 2012; OECD, 2017). For example, laminarin, a storage glucan extracted from *L. digitata*, is an authorised active substance for SPM in the EU, with demonstrated positive results in laboratory and field tests. In leaf assays, laminarin decreased *P. aphanis* conidium germination by 75% (Bajpai *et al.,* 2019), while in greenhouse tests laminarin with a reduced chemical dosage, gave 1.7% SPM infestation, which was similar to the complete chemical scheme (Melis *et al.*, 2017).

The laminarin mode of action against SPM not been investigated. However, its plant protection activity has been studied for several plant species and involves several key elements. The compound elicits production of defence compounds, such as phytoalexins (Aziz *et al.,* 2003), and synthesis of pathogenesis-related proteins (Tziros *et al.,* 2021). It may also directly interact with the pathogen, reducing conidium germination and fungal growth (Hu *et al.,* 2012; de Borba *et al.*, 2022).

Substances from animal origins

Cow's milk and whey have been studied for their plant growth-promoting activity (Sharratt *et al.,* 1959; Ahmed Hashim, 2019), and as alternatives to synthetic fungicides. Fresh cow's milk, at concentrations greater than 10% in water, applied twice a week, was as effective (10% severity) as fenarimol and benomyl (9%) for reduce powdery mildew of zucchini squash, compared to the water control (56% severity), after 1 month since treatment (Bettiol, 1999). Similarly, 10% whey applied twice a week powdery mildew severity (caused by *Podosphaera xanthii* (Castagne) U. Braun and Shishkoff) by 71-94% in cucumber and 81-90% in zucchini, compared to experimental controls (Bettiol *et al.*, 2008). Cow's milk and whey are already authorized in the EU as basic substances and in at least one European Union Member State for use against several powdery mildews (EU Pesticide Database, 2023).

Effects of milk and whey against powdery mildews may involve more than one mode of action. Electron spin resonance and scanning electron microscopy showed that fresh milk and whey applied to grape leaves infected by *Erysiphe necator* Schwein. led to the collapse of fungal hyphae and conidia within 24 h after treatments, likely because of release of free radicals, fatty acids, and lactoferrin by the milk microbial community (Crisp *et al.*, 2006b). Despite high efficacy, the European Food Safety Authority has raised concerns about potential food allergies associated with lactose and milk proteins derived from the use of whey for plant protection (SANTE, 2021). Consequently, its application is restricted in the EU only to approved crops during plant growth stages devoid of fruit (EU Pesticides Database, 2023). Without additional safety data, milk/whey for SPM control could be authorized only in the EU at the beginning of crop growth, when disease outbreaks are commonly rare, making the alternative of little use for growers.

Chitin and chitin derivatives

Chitin, an amino polysaccharide, is a structural supporting components of fungal cell walls, and insect, nematode, and crustacean exoskeletons (Latgè, 2007). Chitin and chitin oligosaccharides have been assessed as plant protection agents (Li *et al.*, 2020), because they are environmentally friendly and highly degradable (Yeul and Rayalu, 2013). These compounds have antimicrobial activities and elicit host defence mechanisms. When recognized by plant cells, they trigger several immune responses (Xing *et al.*, 2015; Li *et al.*, 2020), including lignification and cytoplasmic acidification (Barber *et al.,* 1989).

Chitosan, the N-deacetylated derivative of chitin, is the most extensively studied among chitin fragments. Chitosan is a family of molecules with different sizes and compositions, so it has ductile chemical and physical properties (Aranaz *et al*., 2021). Chitosan stimulates plant defences and growth (Chakraborty *et al*., 2020), but also has filmogenic and fungicide properties against spore and mycelium growth (Martínez-Camacho *et al*., 2010; Meng *et al*., 2010). Chitosan is effective against several powdery mildew pathogens. *Sphaerotheca fuliginea* (Schltdl.) Pollacci on cucumber cotyledons in Petri dishes was inhibited by one preventive treatment of 2.5% chitosan (Moret and Muñoz, 2009). Similarly, a weekly foliar treatment of 0.5% chitosan on cutting roses decreased infections by *Podosphaera pannosa* (Wallr.) de Bary (Wulf *et al*., 2023). However, field studies with chitosan suggest it should be applied when pathogen levels are low (Wulf *et al*., 2023). Although chitosan has been authorised in the EU as a basic substance and in at least one European Union member state for SPM control, there are no reports of efficacy in scientific literature.

Chitosan fragments known as chitooligosaccharides (COS) have been tested in combination with pectin (oligogalacturonides, OGA) as elicitors of plant resistance in a formulation referred to as COS-OGA (Ferrari *et al*., 2013). Because of proven efficacy (van Aubel *et al*., 2014), COS-OGA has been authorised in the EU for the use against several powdery mildews, including SPM. However, no efficacy data are available for chitosan against SPM.

Microbial biocontrol agents

Microbial biocontrol agents (BCAs) are microorganisms that act against phytopathogens with various mechanisms (e.g., competition for resources, antibiosis, hyperparasitism, and induced resistance), and can control plant diseases (Köhl, *et al*., 2019). Several BCAs with different modes of action have been studied against SPM: *Ampelomyces quisqualis* Ces., *T. harzianum* Rifai, and *Bacillus* spp. Cohn are the most investigated. *Ampelomyces quisqualis* is a hyperparasite of several powdery mildew fungi (Sundheim, 1982; Falk *et al*., 1995). *Trichoderma* spp. strains are mycoparasites that can produce antifungal metabolites, and can induce host resistance (Vinale *et al*., 2008). *Bacillus* spp. produce many antimicrobial compounds and can induce resistance on plants (Pérez-García *et al*., 2011). The microbes commonly have good efficacy when applied under controlled laboratory/greenhouse conditions, but their efficacy decreases under commercial field conditions. For example, *in vitro*, *A. quisqualis* AQ10 and *T. harzianum* T39 decreased SPM hyphal biomass by, respectively, 46 and 74%, compared to untreated controls, but these organisms were not as effective as *B. amyloliquefaciens* (formerly *B. subtilis)* QST 713 Cohn that achieved results that were similar to those from to chemical pesticides (99% inhibition of hyphal biomass) (Pertot *et al*., 2007). However, under field conditions, the exclusive use of these microorganisms throughout crop growing seasons without integrating fungicides has been proven insufficient. Contrary to bioassay results, *T. harzianum* T39, in an integrated programme, had the greater activity than *A. quisqualis*. The average fruit incidence in the two locations was 25% for *T. harzianum* and 44% for *A. quisqualis* (Pertot *et al*., 2008). In contrast, their efficacy against leaf severity was variable across locations. Currently, *A. quisqualis* AQ10 and *B. amyloliquefaciens* QST 713 are authorized in the EU and in at least one European Union Member State for SPM control (EU Pesticide Database, 2023).

Inhibition of SPM conidiation (80.7% reduction) on leaf discs was also obtained combining *B. subtilis* ABiTEP GmbH FZB24 and *Metarhizium anisopliae* (Metschn.) Sorokīn (Sylla *et al*., 2013). However, no studies have reported assessments under field conditions. *Bacillus pumilus* Meyer and Gottheil QST2808 is also authorized in the EU and in at least one European Union Member State for SPM control (EU Pesticide Database, 2023). This microorganism, under field conditions, demonstrated high consistency against SPM compared to other tested BCAs. It showed better efficacy compared to a 14 d fungicide application regime, but not in comparison with a 7 d fungicide application schedule (Berrie and Xu, 2021). No data are available for efficacy of *B. pumilus* QST 2808 against *P. aphanis* under controlled conditions.

Understanding the epidemiology of SPM disease and the environmental conditions for survival and/or optimal growth of BCAs in the field are considered key factors for successful control strategies (Pertot *et al*., 2008). Variability in BCA efficacy under field conditions often stems from misuse of these living organisms, treating them as if they were synthetic fungicides, so use of BCAs is more complex than for chemical agents (Legein *et al*., 2020). Applying BCAs at specific stages of the pathogen cycle could be more strategic than frequent treatments during crop growth seasons, when environmental conditions may not be favourable for BCA growth. For example, *A. quisqualis* AQ10, when applied at the end of a crop growth season under suitable temperature and RH conditions can reduce inoculum for the following growing season. Ensuring BCA efficacy also includes assessing compatibility with conventional fungicides when developing integrated pest management programmes. For example, *A. quisqualis* is incompatible with commonly used chemicals against SPM, including penconazole, pyrimethanil, tebuconazole, cyprodinil, fosetyl-aluminium, azoxystrobin, and metalaxyl (Roberti *et al*., 2002). Research on biocontrol agents has a long history, but there has been little recent research focusing on SPM. The research community may have recognized that the previous approaches are not productive for addressing this issue.

Fungivorous biocontrol agents

While microbial BCAs have predominantly dominated biocontrol efforts against powdery mildews, fungivorous insect biocontrol agents, have recently emerged as potential contenders (IBMA, 2022). Pijnakker *et al*, (2022) reported that the mycophagous mite *Pronematus ubiquitus* McGregor gave promising results against tomato powdery mildew (*Oidium neolycopersici* L. Kiss), by decreasing disease severity to 4%, compared to 32% for untreated controls, 8 weeks after mite release. The mites were in greater numbers where powdery mildew was severe. In addition, Pijnakker *et al.* (2022) suggested that for effective disease control this mite must be released preventatively. For SPM control, *P. ubiquitous* has not been assessed scientifically, but is currently being investigated by the industry, and is at first stages of market development (IBMA, 2022). Although the precise contribution of conidium nutrition and plant-mediated effects on powdery mildew resistance, remain unclear, there is potential for determining these interactions. It is also important to develop understanding of whether *P. ubiquitus* is present in each territory of investigation, as potential field releases of alien mites may not be permitted (Heimpel and Cock, 2018).

Other control means

Crop canopy management

Plant canopies have important roles in the development of powdery mildew diseases, which are favoured by host vigour and high plant density in many host species (Jarvis *et al.,* 2002). Dense canopies create microclimates (i.e., high humidity, low ventilation, low light penetration) that favour pathogen growth (Aust and Hoyningen-Huene, 1986; Keller *et al*., 2003), and suitable canopy management can reduce infection risks. Direct effects of canopy management on SPM control have not been validated in robust research. However, some studies indicate positive correlations between SPM severity and canopy density. For example, breeding for SPM resistance is leading to the selection of cultivars with reduced canopy densities due to consistent genetic correlations observed between host susceptibility and high canopy density (Kennedy *et al*., 2014). Although research on SPM is lacking, studies on other powdery mildews suggest practices that can be also tested for strawberry. For powdery mildew of hop (*P. macularis*) removal of highly susceptible climbing shoots and reductions in canopy density improved disease management and fungicide distribution (Gent *et al*., 2012; Gent *et al*., 2016). In grapevine, vertical trellis system and spring pruning reduced powdery mildew by up to 32% (Austin and Wilcox, 2011). Canopy thinning in strawberry crops has been assessed for yield optimization (Sønsteby *et al*., 2021), but has not been comprehensively investigated for SPM management. Similarly, removal of highly susceptible strawberry runners could reduce risks of SPM (Eccel *et al*., 2010), but this is yet to be precisely quantified.

Host nutrition

Balanced mineral nutrition is important for plant self defense, and when specific elements are either deficient or over-abundant, plants can become vulnerable to particular pathogens (Huber and Haneklaus, 2007). High nitrogen inputs have been associated with increased risk of fungal diseases. For SPM under experimental conditions, Xu *et al.* (2013) reported a 54% increase of nitrogen above fertigation standard (from 128 to 197 mg L^{-1}) applied from the beginning of bloom resulted in an 8% increase in disease severity. For deficiencies in the other macro- and micro-elements, there are no published reports relating to SPM susceptibility.

Some soil amendments may enhance plant defence against biotic stresses. For example, biochar can induce plant resistance by improving chemical and physical soil properties (e.g., water holding capacity, nutrient availability, soil texture), and by enhancing soil microbial activity such as plant growth promoting rhizobacteria (Schmidt *et al*., 2021). For strawberry, incorporation of 3% biochar into potting mixture resulted in high expression of defence-related genes and a related decrease of SMP (Harel *et al*., 2012).

Overhead irrigation

Although *P. aphanis* develops well under high RH (Amsalem *et al*., 2006), free water prevents conidium germination (Peries, 1962a). Water sprays on plant canopies can control SPM but could also promote pathogenic fungi that are favoured by a wet canopy, such as *Botrytis cinerea* Pers. and *Colletotrichum* spp. Corda. However, since micro-sprinklers are commonly used to spray water to reduce high temperature stress during summer (Liu *et al.,* 2021), well-balanced overhead irrigation can be used to reduce SPM. For example, application of pulsed water mist has shown promising results: applications of 660 mL min^{-1} for 1 min four times a day was as effective as standard fungicide treatments, in high tunnel and open field conditions (Asalf *et al.*, 2021). Overhead irrigation also reduces SPM severity when applied for long periods. For example, after 67 d of mist treatments, severity of powdery mildew decreased from 80 to 17% in high tunnels and from 73 to 22% in the open field, compared to untreated controls. Application of pulsed misting for 1 min four times a day did not increase in *B. cinerea* infections, indicating that if water was correctly applied, grey mould could be reduced (Asalf *et al.,* 2021). Although overhead irrigation reduced the disease, procedures (i.e., frequency, volume, application methods) were not fully explored for maximizing efficacy.

Fungicide spray equipment

Spray equipment can also affect pest control (Ebert and Downer, 2006), and this is particularly the case for SPM because applied fungicide must reach the undersides of leaves, lower leaves and the fruit. This is particularly difficult when strawberry plants develop dense canopies. Low technology devices (i.e. hand-held and cannon sprayers) may not provide adequate and even fungicide distribution (Balsari *et al*., 2008; Bondesan *et al*., 2015). These devices are widely used in strawberry high-tunnels in Mediterranean regions (e.g., Italy and Spain) (Sánchez-Hermosilla *et al*., 2012; Cerruto *et al.,* 2018), because they are inexpensive and easily adaptable to horticultural crops. Cannon sprayers also distribute plant protection agents at high pressure (>20 bar) and rates (1500–2500 L ha^{-1}), producing spray drift that can contaminate soil and may increase operator exposure (Sánchez-Hermosilla *et al*., 2011, 2012; Cerruto *et al*., 2018). In technologically advanced greenhouses, sprayers with increased efficiency, such as vertical booms (Braekman *et al*., 2010), or autonomous pesticide spraying robots (Abanay *et al*., 2022), have been associated with improved better canopy coverage and reduced application volumes compared with cannon and hand-held sprayers (Braekman *et al.,* 2010).

Ultraviolet light

Light is an important factor for minimising fungal development and stress responses in plants, and ultraviolet light (UV) can suppress powdery mildews in several crop plant hosts (Gadoury *et al*., 1992; Suthaparan *et al*., 2012; Pate *et al*., 2020). For strawberry, the application of UV once or twice per week during night-time (60 s followed by 4 h dark period) resulted in up to 90% reduction of SPM incidence and severity compared to the controls (Janisiewicz *et al*., 2016). However, UV-based methodology is still at early commercial development, and has various challenges. For example, UV technology is not adaptable to diverse rural growing systems, such as high-tunnels and open fields. In some cases, machines may not be able to access tunnels and/or move between benchtop rows. Application parameters (UV dose, light exposure durations, treatment frequencies) are not yet optimised and standardised. A range of doses spanning from 30 to 200 J m^2, administered once or twice per week, or at 10 d intervals, have been assessed (Van Delm *et al*., 2014; Janisiewicz *et al*., 2016; Suthaparan *et al*., 2012; Ledermann *et al*., 2021), without determining the best application schedule. Antifungal effects also only occur only irradiated host surfaces and UV light poorly penetrates crop canopies, and uniform light distribution is difficult in multi-layered crop canopies, giving limited SPM control on abaxial leaf surfaces (Delorme *et al*., 2020). Implementing UV light technologies is expensive: beside the initial costs that include purchase of UV equipment, installation, and the necessary modifications to the existing infrastructure, there are extra costs for electricity and frequent replacement of UV lamps (Rea *et al.,* 2022). For these reasons, growers must carry out careful cost/benefit analyses when evaluating the feasibility of UV light for SPM control.

Ozone

Ozone (O_3) has antimicrobial activity and is rapidly decomposed in the environment. In the food industry O_3 is used to safely disinfect food, and as postharvest treatments to increase shelf-life of fruit and vegetables (Tzortzakis and Chrysargyris, 2017). For plant protection, O_3 has been tested against powdery mildews of several horticultural crops under controlled conditions, both as fumigant and as ozonated water (Hibben and Taylor, 1975; Rusch and Laurence, 1993; Khan and Khan, 1999; Fujiwara and Fujii, 2002; He *et al*., 2015). Effects of O_3 on powdery mildews and plants depends on concentration: at too low levels powdery mildews may be not harmed, while at too high levels host phytotoxicity may occur. For example, increasing concentrations of gaseous O_3 (from 50 to 200 ppb) applied intermittently (7 h d^{-1} for 7 d) on cucumber plants in closed-top chambers, decreased powdery mildew colonization from 70 to 23%. In addition, 50 ppb of O_3 increased the germination conidia collected from treated plants, while conidia exposed to greater concentrations (100 and 200 ppb) were smaller and had reduced germination compared to untreated controls. High O_3 concentrations (i.e., 200 ppb) can cause foliar necroses (Khan and Khan, 1999). Ozonated water gives similar results (Fujiwara and Fujii, 2002). Although some growers currently use ozonated water, its efficacy against SPM has not yet been assessed (Fujiwara and Fujii, 2004). Devices to spray ozonated water are available (e.g., MM-Biozono, MMSpray, Italy; Mowat, Gr Gamberini, Italy), and are also tailored for strawberry production (e.g., GZO-D, ZonoSistem, Spain), but no definitive data are available (e.g. minimum exposure times, effective dosage) (Fujiwara and Fujii, 2004).

Genetic resistance to strawberry powdery mildew

Breeding for resistant varieties is an effective disease management strategy, provided that plants bear high-quality fruit, are well-suited to local cultivation regions and have adequate and long-lasting tolerance or resistance to pathogens. Resistance in strawberry to *P. aphanis* has low durability and is variable under different environmental conditions (Menzel, 2022). Whether this behaviour is related to unstable resistance genes or different virulence of SPM strains is unknown (Nelson *et al.,* 1995). Several genes may control levels of infection, and under natural conditions inoculum density varies leading to differential elicitation of systemic resistance (Kennedy *et al*., 2013). In a plant breeding programme, beside inoculum level, other variables (e.g., climatic conditions, growing systems, time of season) may influence strawberry responses to pathogens, making comparison of results obtained in different breeding programmes challenging. Defining the optimum breeding methodology and conditions for development of resistant strawberry cultivars could be helpful (Menzel, 2022). Marker-assisted selection can accelerate cultivar improvement, but SPM resistance in strawberry is probably regulated by complex genetics with several additive genes involved. To date, several genes have been associated with SPM resistance (Menzel, 2022), including nine QTL genes (Cockerton *et al*., 2018; Sargent *et al*., 2019), seven TGA genes (Feng *et al*., 2020a) and 68 MLO sequences (Tapia *et al*., 2021).

Predictive models and Decision Support Systems

Reductions of fungicide use can also be achieved by optimizing, and thus reducing, numbers of spray applications, and predictive models and Decision Support Systems (DSSs) can help growers identify optimum timing of pesticide applications. Predictive models are based on empirical data collected from the field and/or under controlled conditions, and forecast disease development (Van Maanen and Xu, 2003). DSSs are interactive computer-based systems, which use predictive models, data analysis techniques, and recommend/support actions for farmers to manage diseases (Sprague and Carlson, 1982). Both of these tools are useful to schedule fungicide treatments, thereby avoiding unnecessary applications (Lázaro *et al*., 2021). For SPM, several predictive models (Carisse *et al*., 2013a, 2013b) and DSSs (Table 2) have been developed (Gubler *et al.,* 1999; Eccel *et al*., 2010; Bardet and Vibert, 2011; Dodgson *et al*., 2021; Carisse and Fall, 2021; Fall and Carisse, 2022). However, the developed models, excepting that of Gubler *et al.* (1999), have not been validated in different locations. This decreases the reliability of the models, as agricultural conditions can vary widely from one region to another. Without validation it is therefore difficult to assess model robustness and accuracy in different environmental contexts.

Predictive models

Several models, as mentioned in the epidemiological section of this review, have been developed in Canada. For example, Carisse *et al.* (2013a) characterized a close relationship between SPM incidence and severity to define an economic loss threshold for fungicide interventions. In another model, Carisse *et al.* (2013b) described a strong positive linear relationship between seasonal crop losses, disease severity and daily mean airborne conidium concentration, to potentially define a severity and airborne conidium concentration threshold for fungicide interventions. Carisse and Bouchard (2010) defined windows of high leaf and berry susceptibility for June-bearing and everbearing strawberry cultivars.

DSS developed by Carisse and Fall

From these models, Carisse and Fall in 2021, modelled a DSS based on a decision tree forecast (the outcome of several algorithms that offered a model, following a subset of classification rules visualised and exemplified as a tree) (De Ville, 2013). This model forecasts risk of infection, firstly from airborne inoculum concentration and number of susceptible leaves, and then using mean RH, mean daily number of hours at temperature between 18 and 30°C, and mean daily number of hours at saturation vapour pressure between 10 and 25 mmHg

Table 2. Decision support systems developed for management of strawberry powdery mildew.

Reference	Aim	Input drivers	Output	Validation	Treatment reduction	Commercial application
Dodgson *et al.* (2021)	Disease development forecast based on the number of hours with favourable conditions	T°, RH%	Daily risk predicted on cumulative h of conducive conditions, recommendation of action	2009-2020, under tunnels, UK	30% fungicide reduction	Agri-tech
Bardet and Vibert (2011)	Disease development forecast based on favourable conditions for fungal stages	T°, RH% and rainfall	Graphical representation of disease progression and infection risk in 4 d period	2006-2007 under tunnels and glasshouse, 2010 under tunnels, France	Not available	Inoki
Eccel *et al.* (2010)	Disease development forecast based on weather data, growing system, agronomic practices, host susceptibility.	T°, RH%, daily disease incidence, type of sprayer, tunnel height, overhead irrigation, cultivar susceptibility, time of disease onset, time since last treatment, presence of runners	Daily risk of disease outbreak and risk forecast in the next 3 d, recommendation of action	2007 under tunnels, Italy	60% fungicide reduction	Not available
Hoffman and Gubler (2002)	Ascosporic infection and disease development forecast based on whether data	T° and leaf wetness	Treatment interval threshold according to risk index	2002 in open field, California, in 2008 in open field, Quebec	40% fungicide reduction in California, 0% in Quebec	Not available
Fall and Carisse (2022)	Dynamic simulation of inoculum load and fungal development based on weather data	T°, rainfall, RH%, plant density, initial airborne inoculum concentration	Daily SPM severity, warning and action threshold and related crop loss	2006, 2007, 2008, 2015, 2016 and 2018 in raised beds open field, Quebec	Not available	Not available
Carisse and Fall (2021)	Decision tree forecast of infection based on weather data	Airborne inoculum concentration, susceptible leaves, RH%, T°, vapour pressure	Daily infection risk, warning	2015, 2016, 2018 in raised beds open field, Quebec	Not available	Not available

during the previous 6 d. Carisse and Fall (2021) noted that the main characteristic of their prediction system was understanding that groups of variables can affect SPM e development, and that different combinations of these variables can result in similar disease severities. For example, low inoculum amounts and a limited number of susceptible leaves, but conducive weather, may yield the similar severities as scenarios of high inoculum, few susceptible leaves and less favourable weather conditions. The factor potentially hindering use of the model could be detection of airborne conidium concentrations, that Carisse and Fall (2021) suggested analysing manually, twice weekly using microscopy, for each strawberry field.

DSS developed by Fall and Carisse

Fall and Carisse (2022) developed a DSS according to a dynamic simulation model, which simulates the asexual life cycle of *P. aphanis* and its related severity. This model considers at which rate *P. aphanis* changes growth stage with time, according to weather conditions, simulating daily conidium production and resulting disease severity. In the model *P. aphanis* stages (initial inoculum, conidium germination dropout population, germinated conidia, cumulative proportion of diseased leaf area, secondary inoculum) are regulated and influenced by rate variables, such as sporulation rate, germination rate, lesion increase rate (defined by algebraic equations), that in turn are influenced by intermediate variables such as daily temperature, rainfall, RH and the number of leaves per plant (35,000 plant ha^{-1} in a 0.91 m row spacing field), estimated on a daily basis. The model is based on evidence that in May at least one lesion m^{-2} of strawberry field is sporulating, and the initial inoculum load in 1 ha of strawberry is assumed to be 1,000,000 conidia (Blanco *et al.,* 2004; Carisse *et al.*, 2013a, 2013b). According to the initial inoculum value, the model starts running each day, estimating inoculum load based on weather data and fungal development, thus predicting powdery mildew severity and related crop loss. According to disease severity, warning and action thresholds are simulated on a daily basis. For cost-effective management of SPM, crop managers in Quebec may tolerate 1% yield losses (warning) but not more than 5% losses (action).

UC Davis DSS

In California, a DSS developed by UC Davis (Gubler *et al.*, 1999) was another attempt to forecast SPM epidemics, assessing risks and action thresholds. This model was developed for grape powdery mildew (caused by *E. necator*) and then applied for SPM (Hoffman and Gubler, 2002). The model focuses on forecasting ascospore infection to refine fungicide application timing at the start of each cropping season (Gubler *et al.*, 1999; Hoffman and Gubler, 2002). This model assesses ascospore release according to leaf wetness and temperature, considering that at least 12–15 h of continuous leaf wetness at 10-15°C average temperatures are necessary for release. After the ascospore infection occurs, the model changes into the risk assessment phase, relying solely on temperature impacts on pathogen reproductive rate. To start an epidemic, the pathogen requires three consecutive days with at least 6 h between 21 and 30°C. If these conditions are not met, the index resets to zero; otherwise, the model initiates estimation of an infection index (from 0 to 100). Thresholds of action and frequency of intervention depends on risk. If the risk index remains low (<30), interval between treatments decreases (between 14 and 21 d). If risk index is increases (>60), shorter intervals between applications are recommended (maximum, 7 d interval). The model was validated in 2002 under open field conditions, reducing 40% of fungicide treatments, compared to a calendar-based programme. However, after several tests in Quebec, the model did not accurately predict SPM at the beginning of the season, probably due to the wide range of favouring conditions, This resulted in similar numbers of fungicide applications prescribed as for calendar-based schedules (Bouchard, 2008).

Safeberry DSS

In Italy, Eccel *et al.* (2010) modelled the SafeBerry DSS, based on forecasted daytime temperatures over 3 d, and risk factors including daily disease incidence in a tunnel, type of sprayer, tunnel height, overhead irrigation, cultivar susceptibility, time of disease onset, time since last treatment, and presence of runners. Suitability of weather conditions for disease development was categorised according to day-time temperature as follows: low suitability (≤18 or >26°C), medium suitability (18 < T° ≤ 20 or 25 < T° ≤ 26°C), and high suitability (20 < T° ≤ 25°C). Outputs of this model are daily assessment of disease outbreak risk at the daily time/temperature during the previous 6 d and forecasted in the next 3 d, the favourability of temperature for disease in the next 3 d, and then a recommendation for action. The model includes two action possibilities: either 'Do not spray today' or 'Apply as soon as possible'. In the second scenario, a selection of recommended fungicides is provided, based on their modes of action, risks for pathogen resistance development, and timing restrictions prior to harvest. With this system in 2007, under tunnel conditions, up to 60% reductions in fungicide treatments were obtained.

DSS developed by Bardet and Vibert

In France, Bardet and Vibert (2011) developed a DSS that modelled five stages of the *P. aphanis* life cycle (inoculum dispersal, infection, mycelium growth, sporulation, and disease progression), as influenced by meteorological variables of temperature, RH, and precipitation. The model was based on evidence that conidium germination occurs between 5 and 32°C, mycelium growth is interrupted above 35°C, sporulation occurs between 7 and 28°C. and conidium dispersal occurs in low humidity conditions. The maximum threshold accepted by the model is set at RH <65% over a minimum duration of 8 h. At RH >85% for at least 5 h, germination occurs rapidly. The index risk separately considers the conditions favourable for infection, mycelium establishment with sporulation, and lesion development, and each stage has a 0 to 5 value. For example, 5 is assigned to infection under favourable conditions for the fungus (temperature between 20 and 26°C, and 85% < RH < 99%). For strawberry cultivars that are particularly susceptible, the model allows additional risk to be set. The model gives graphical representation of periods suitable for pathogen dissemination, infection and mycelium growth for a 4 d period. Fungicide treatments can appear on the graph provided their application dates and effectiveness duration are entered. The model was validated with experiments conducted in 2006 and 2007 under tunnel and glasshouse conditions, and in 2010 under tunnel conditions. This DSS is available for growers through the web platform Inoki (Ctifl, 2023).

Strawberry Powdery Mildew Forecasting Model DSS

In the United Kingdom, a DSS implementing 15 years of historical data was developed by Dodgson *et al*., (2021). The model is based on laboratory and field evidence that *P. aphanis*, under optimum conditions (>15.5 and <30°C, 60% RH), takes 144 h (disease conducive hours) to complete a cycle from conidium germination (6 h) to growth of elongating secondary hyphae and sporulation (138 h). The system then extends according to weather conditions (15.5°C, the minimum temperature for spore germination; 18°C, the minimum temperature for sporulation, at 60% RH). According to sensitivity analysis under field conditions, temperature is the main factor influencing fungal development and sporulation. Other secondary weather parameters with lower impacts on the prediction system, such as leaf wetness, were removed to simplify the rules of the forecast. Once one cycle is completed, a daily risk is predicted and used for guiding fungicide applications. The prediction system uses a 'traffic light' colour scheme indication to represent the progression of accumulated hours of conducive conditions. When 125 accumulated hours are reached, the line changes from yellow to red, indicating high risk of conidium production. A fungicide should normally be applied before the elapsed time reaches 144 accumulated hours, to prevent *P. aphanis* sporulation. When a fungicide application is made, the growers record this manually in the software, and reset the system to zero and the process repeats. Unlike the Carisse and Fall (2021) decision tree, the Dodgson *et al.* (2021) model does not essentially require accurate estimation of susceptible leaves and airborne inoculum, and these variables are deemed to be limiting. Instead, the Dodgson *et al.* (2021) forecast always assumes a standard presence of inoculum, and susceptibility for all crops. To effectively manage powdery mildew, growers are required to start each growing season with a *clean-up spray* treatment, as this was also confirmed by greater infection in crop where clean-up spray was neglected. Relying on these assumptions and the risk forecast, control of powdery mildew was demonstrated with 30% fungicide reduction. The model has been validated from 2009 to 2020 under tunnel conditions. To date, the Dodgson *et al.* (2021) online real-time web-based prediction system is used and sold with commercial licencing (Strawberry Powdery Mildew Forecasting Model, Agri-tech Service, United Kingdom).

New tools for early detection

Early disease detection is often complex and time-consuming, and for SPM, prompt recognition of the disease in the field is difficult (Carisse *et al*., 2013a). However, rapid development of advanced agricultural technologies, such as machine learning and vision, has helped capture of disease images, and, therefore, detection of pathogen presence and abundance in the field (Liu and Wang, 2021). Machine vision-based recognition may replace traditional naked eye identification with computing science. Robust models have recently been developed to detect SPM on strawberry leaves with high accuracy (>94%) (Shin *et al*., 2020, 2021).

At research level, analyses of volatile organic compounds released by diseased crops is another potential machine learning technique for disease detection. These compounds are potential biomarkers for warning and forecasting disease spreading in fields (Li *et al*., 2019). The approach is based on plant emission of unique profiles of Volatile Organic Compounds (VOCs) when attacked by a pathogen, which differ from profiles from undamaged plants, allowing interactive signalling with neighbouring plants and release of danger signals. Nearby undamaged plants may recognise this novel profile and activate physiological changes that enhance their readiness to future pathogen attacks (Effah *et al*., 2019). For powdery mildew detection, this has only been studied for *B. graminis*, where sensitivity and specificity of six wheat VOCs have been identified as possible biomarkers for disease detection (Hamow *et al*., 2021). SPM identification and detection by VOC analyses has not been assessed, although greenhouse-grown strawberry plants could be excellent candidates for VOC analyses.

CONCLUSIONS

This review has critically considered the extensive research on SPM, attempting to identify knowledge gaps that warrant further investigation. Given the similarities of SPM with the other powdery mildews, the available data on other species could be used to inspire future research. In addition, factors related to growers' approaches to plant protection strategies could be considered. For example, natural substances are used as supplementary and marginal tools in disease management spray programmes, which are still largely based on synthetic fungicides. To overcome this problem, data on natural substance efficacy under various environmental conditions should be generated and made available in the public domain. Exploring new more effective application methods may also increase farmer confidence on alternative products. Natural substances and antagonistic microorganism often have limited field persistence, and frequent and/or appropriate timing of applications are required. Exploration of solid set spraying systems, especially in greenhouses and tunnels, could provide valuable new direction for SPM management. Assessment of the impacts of agronomic practices on SPM, and validation of SPM forecasting models across diverse strawberry-producing regions also deserve research effort.

Genomic, transcriptomic, and metabolomic technologies could provide powerful tools for development of innovative plant protection strategies. Although promising, biotechnological tools remain underexplored for SPM control. These technologies could be useful for assisting the breeding for resistant host varieties. For example, naturally occurring or experimentally induced inactivation and/or mutation of MLO genes (e.g., by gene silencing and genome editing) may provide strong and long-lasting immunity/resistance to the fungus (Wan *et al*., 2020).

Transcriptomics and metabolomics can offer unique approaches for identifying host resistance traits (Castro-Moretti *et al*., 2020). When transcriptomic information is coupled with metabolomic analyses, plant defence mechanisms can be better understood (Wink, 1988), and this knowledge could guide targeted interventions. For example, metabolomics can guide selection or breeding of plant cultivars with increased levels of defence molecules. For example, SPM infections influence strawberry plant metabolism (Duan *et al*., 2022): alongside phenols, ten chitinases are upregulated in infected plants, indicating the role of chitinase in reaction to *P. aphanis* (Duan *et al*., 2022). For example, determining substances that can mimic pathogen effects on strawberry chitinase overexpression, or identifying cultivars that are can further overexpress these enzymes, could result in new tools for disease management, as has been demonstrated by some reported attempts (Feng *et al*., 2020b; Zhang *et al*., 2021; Yin *et al*., 2022). Alongside overexpression of plant defence related pathways, gene silencing with expression of RNAi constructs against host and/or pathogen target genes could be assessed (Capriotti *et al*., 2020). Through the utilization of host and/or pathogen RNA interference (RNAi), specific pathogen genes could be silenced by degrading their messenger RNAs. This process can hinder translation of the RNA into proteins, thereby disrupting pathogen ability to carry out normal biological processes (Zotti *et al*., 2018). RNAi-based fungicides are at early stages of development, but they have already been assessed against grape powdery mildew (*E. necator*), giving up to 64% reduction in conidium production compared to experimental controls (McRae *et al*., 2023).

These new biotechnologies, although powerful, may be of limited use due to high costs (both for research and implementation), and because of existing restrictive regulations. Therefore, innovative investments and policy interventions are necessary to guarantee sufficient knowledge advancements from research on SPM.

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