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APPLE POWDERY MILDEW: LITERATURE AND RESEARCH OVERVIEW

by

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(ABSTRACT)

Apple powdery mildew, caused by the fungus *Podosphaera leucotricha* (Ell. and Everh.) Salm., is a disease found in apple growing regions world-wide, and is economically important in many of them. Most of the research on this pathogen pertains to various methods of control, particularly with fungicides and host resistance. Fungicide effectiveness and development of new fungicides have been most prominent. A considerable amount of research has been done in epidemiology. Host resistance genetics and mechanisms, components, and development of resistant cultivars have also been emphasized. Aspects of research on apple powdery mildew that have not been explored in as much depth are also reviewed. Some of these areas include the role of cleistothecia and ascospores in life and disease cycles, heterothallism versus homothallism, and growth of the fungus on artificial media. Additional research needs from each aspect are proposed. This report is based on a comprehensive review of the current literature on apple powdery mildew.

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This work is dedicated to the LORD and to the memory of Dellena M. Scamack.

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INTRODUCTION

Apple powdery mildew, caused by Podosphaera leucotricha (Ellis & Everhart) Salmon, is a common fungal apple disease found nearly world-wide, especially in the more humid apple producing areas of the world (25). It is the major foliar disease apple growers must control in some regions; in other areas, it may be only one of ten or more economically important diseases (57).

Podosphaera leucotricha is an Ascomycete in the Erysiphaceae commonly known as the powdery mildews; they are named as such, due to the large number of conidia produced on the surface of the host plant, forming an easily seen powdery coating (1). These wind-disseminated, 22-30 X 15-20 um, are produced in long chains, and are the most common disease propagules (2). Unlike apple scab [Venturia inaequalis (Cke.) Wint.], powdery mildew does not need a film of free water in which to germinate, but germination is favored by high relative humidity. Optimum germination temperatures are 19-22 C, but germination can occur at high relative humidity between 10 and 25 C (2). Slower germination and mycelial growth between 4 and 10 C are possible, and a slight amount of growth can occur over 32 C (24).

Podosphaera leucotricha is an external parasite whose mycelia spread in a prostrate manner over the surface of leaves, flowers, young fruit and immature stems (2). Its nutrient-absorbing haustoria are formed in the cells of the epidermis and anchor hyphae to the leaf, after a germ tube penetrates the cuticle and epidermal cell wall by enzymatic action (54). For production of sexual spores, P. leucotricha develops dark, rounded cleistothecia containing a single ascus of eight ovate to elliptic ascospores; basal and apical, undivided appendages are also present (25).

Alexopoulos and Mims note that this species parasitizes only apple, Malus domestica Borkh., and Toringo crab apple, Malus sieboldii (1). However, it is also found on: peach (Prunus persica L.) and Photinia species (25). This relatively host specific fungus is an obligate parasite, which can survive only on living host tissue (24). Two additional powdery mildews, of little or no economic importance, have been reported on apple: Erysiphe heraclei (DC) St.-Am. and Podosphaera oxyacanthae (DC) de Bary (6).

Damage caused by apple powdery mildew can be significant on highly susceptible cultivars and younger or previously weakened trees; and on less susceptible cultivars, if the surrounding inoculum level has grown to extremes, or has been uncontrolled (24). The parts of the plant usually affected are the terminal growth on immature trees and the leaves, flowers, fruits and shoots on mature ones. The fungus can be identified by observing the following signs: spreading, white, felt-like foliar lesions and a covering of mycelia on emerging leaves, shoots and flowers, from previously infected terminal and flower buds, where it overwinters (24). Symptoms of the disease include: abnormally narrow, longitudinally folded leaves, which become brittle with age; late opening buds which are more susceptible to cold damage; stunted leaves and shoots emerging from infected buds; and russetted, sometimes dwarfed, fruit (especially cv. Jonathan and fruit in a situation of high disease pressure) (24). Therefore, apply powdery mildew can stunt (or even kill) nursery stock, restrict tree growth, reduce yield and cause russetted, poor quality fruit.

HISTORICAL ASPECTS

Prior to 1900, when E.S. Salmon, the authority on apple powdery mildew, published A Monograph of the Erysiphaceae, much of the research involved the proper classification of the fungus (17). Yarwood provides a detailed description of the probable origins of man's recognition and naming of the Erysiphaceae, the powdery mildews. They have been called mould, fen, white mould, egg mildew, field fungus and white rust, by various people over the centuries (55). The word mildew is believed to be of Germanic origin, as mehltau or meal deau, and is mentioned in the Old King James translation of the Bible (I Kings 8:37, 1004 B.C.); it is possible that even Pliny, (about 1000 B.C.) referred to it (55). The justifying characteristics of the genus Podosphaera, that name being coined by Kunze around 1823, are the presence of a single ascus and dichotomously branching appendages (55). Podosphaera leucotricha usually has straight, unbranching appendages, but occasionally dichotomously branching appendages do occur (55).

ENVIRONMENTAL RELATIONSHIPS

Another important aspect of powdery mildew research has been its relationship to moisture and free water. Yarwood details findings on the ability of various powdery mildews to germinate under low relative humidity (although apple powdery mildew prefers high R.H. for germination), but not in water (55). He also discusses other aspects of powdery mildews and moisture relationships, such as water and lipid content of spores, water requirements for spore production, soil moisture relationships and control by spraying with water (55). Fisher (17), in 1918, described dissemination of the fungus as being very dependent on the dews in the Wenatchee Valley of the Pacific Northwest, and correctly attributed conidial dispersal to the wind. In 1927 Woodward compiled information on the perennation and some host-parasite relationships of P. leucotricha (54). The general method of perennation is for the mycelia to overwinter among the folds of the terminal buds. One study demonstrated that most primary infection sites developed in apical vegetative buds, and only 2% involved blossoms (5). The first mention of mycelial overwintering was in 1889 by Sorauer in Germany, of Sphaerotheca castagnei Lev. (44), and of apple mildew by Galloway in America (18). He explains the process of mycelial invasion into the buds in the leaf axils of the current season growth, the distribution of mycelia within that bud, and the emergence of infected leaf and flower buds the following season (54).

The production, location and development of perithecia, now called cleistothecia, on the current season's terminal growth, suckers or non-fruiting stems and leaf stalks, mid-ribs and large veins are also discussed in detail (54). In 1889, Galloway was the first to note the seeming unimportance of the sexual cycle in apple powdery mildew, with which many later researchers concurred (54). Also discussed are: conidia germination conditions; the mechanism of germ tube penetration (which Woodward proposes is by unidentified chemical means, not mechanical), the reduced importance of secondary infections (which Yoder (57) notes as an important part of the disease cycle), external and physiological symptoms (i.e., browning of invaded leaf cells); and the non-specialization of races (54).

CHEMICAL CONTROL

Chemical control is the most common means of managing this disease today and is therefore quite heavily researched. Compounds labeled for use in this country are sulfur, oxythioquinox, dinocap, benomyl, thiophanate methyl and ergosterol biosynthesis inhibitors (EBIs), such as fenarimol, triadimefon, triforine and myclobutanil;

other countries allow the use of bupirimate, nitrothal-isopropyl and pyrazophos (57).

In England, as many as 10-12 fungicide applications may be needed each season (3). In the mid-Atlantic region of the United States, starting applications at the tight-cluster stage provides adequate control of this disease (22). The need for frequent applications is due to the fungus' short generation time and ability to infect leaves under a relatively wide range of climatic conditions (48). Close interval sprayings are useful, especially in the spring, to reduce current season build-up and the amount of infection top overwinter in buds (19). Also noted is the use of disease forecasting and assessment systems in Europe, in combination with preventive EBI applications (22); this practice is currently used to combat apple scab in the United States. Assessing disease conditions in a particular orchard provides a basis for the need and timing of fungicide sprays, an important factor in integrated pest management; Butt (7) has devised an objective method, more accurate than a cursory observation (7).

Sulfur, oxythioquinox and dinocap are regarded as general, surface active toxicants. Sulfur has had a long history in plant protection, used in ancient times as a fumigant and first recorded as a fungicide in 1802 (3). Fisher notes some susceptible older varieties of apple, and the types and results of sulfur sprays used for control (17). In his brief discussion of chemical control, Yarwood noted that even though the powdery mildews developed resistance to some fungicides, they had developed none to sulfur in more than 150 years (55). Sulfur provides adequate protection against the powdery mildews on vine and tree crops (3). Its mode of action on them is difficult to study due to the obligate parasitism of these fungi (3).

Oxythioquinox has protective, curative and antisporulant action, and despite its good control, can have phytotoxic effects (3). Its mode of action has not been investigated in depth (3).

Dinocap's mode of action has been more thoroughly researched on plant and animal tissue, than it is on fungi, as an inhibitor of oxidative phosphorylation. It too provides good protection against apple powdery mildew (3).

Starting in the early 1970s, much research was done on systemic fungicides, the benzimidazoles, including benomyl and thiophanate-methyl. Increased selectivity and less phytotoxicity are two of the benefits of systemic fungicides; more selective compounds would have less toxic impact on the environment (14). One aspect investigated was transcuticular movement; abaxial (bottom) and adaxial (top) cuticles were removed from apple leaves for this experiment (43). Both of these fungicides were found to move within the lamina, and transcuticular movement, from adaxial to abaxial surface, was more efficient with thiophanate-methyl than with benomyl (43). This movement was enhanced with benomyl, by making it more soluble in acidified water (43). Benomyl and thiophanate-methyl, both good performers (48), were found to have similar fungitoxic activity (16). Possibly the obligately parasitic nature of powdery mildews leads them to be well controlled by systemic fungicides, since obligate parasites draw on transpiration fluids, and hydrophilic compounds move to leaf margins; model systemic compounds apparently shift the hydrophilic-lipophilic balance (16).

The use and development of EBIs, in the past three decades has been a great leap forward in chemical protection of many crop plants, apple powdery mildew control being no exception. Research in the areas of EBI efficacy, fungal sensitivity and effect on host crop plants has been heavy.

Of those EBIs labelled for use on apple powdery mildew, triademifon gave excellent protection against the fungus, and its vapor gave very good protection on unsprayed trees in the greenhouse; on apple scab it provided an eradicative action (47). The systemic nature of triademifon, an EBI was investigated on powdery mildew in grape leaves (33). In some apple production regions, one means of early season control is the pruning of infected terminals to reduce primary inoculum (10). Postsymptom activity against apple powdery mildew of triademifon, triforine, sulfur, dinocap and benomyl were tested to aid in reducing the need for pruning (10). Of these tested, triademifon and sulfur provided the best reduction in new viable spore production (10). The systemic nature of triademifon was later investigated on powdery mildew in grape leaves. Myclobutanil provided highly suppressive action on growth and sporulation of P. leucotricha when tested on the commonly grown cultivar, 'Rome Beauty' (20). On a 14-day spray schedule, it controlled primary and secondary infections (37). Triademifon, triforine and fenarimol were found to be significantly more effective than dinocap and benomyl under climatic conditions in the mid-Atlantic states (21).

The side-effect of EBIs on the host crop plants is another important area of research. One study, using fenarimol and triademifon among other EBIs, showed that an evening application generally decreased the unsaturated free fatty acid content of apple leaves, and morning applications increased it (38). Unsaturated fatty acids reportedly harm sterol synthesis and hormone production, which are involved in vegetative and fruit development (38). However earlier studies asserted that vegetative growth was stimulated by the use of triademifon, a highly effective fungicide (29). The author attributes this effect to the excellent control of the fungus and its harmful effects on generative capacity of the tree (29). Yet another study reports that none of the mildewcides used, including triademifon and dinocap, affected percent floral buds or fruit set, size or shape (45). Additionally, trees treated with dinocap had a greater yield than those treated with triademifon (45). Spotts emphasizes the usefulness of short term data, on crop effects, such as his and Kolbe's, reported here, but also believes long-term studies are as important (45).

One of the most recent challenges in EBI research is that of fungal resistance to the fungicides. Early reports of powdery mildew decreases in sensitivity came from the Netherlands, and were noted on powdery mildew of cucurbits, Sphaerotheca fuliginea, and on wheat powdery mildew, Erysiphe graminis f. sp. tritici. In the study on cucurbit powdery mildew, it is noted that reduced sensitivity did not result in full failure of control (41). Another point of interest in the resistance problem is in cross-sensitivity. Such a phenomenon in wheat powdery mildew control came about between the two triazoles triademifon and propiconazole; no cross-sensitivity was present between the triazoles and fenpropimorph, a morpholine compound (15). Koller discusses the need for a set of guideline defining the terms: resistance (a stable and heritable reduced sensitivity), adaptation (an unstable and non-heritable reduced sensitivity), and field sensitivity (an increase in frequency of resistant strains) (30). Due to the speed and extent of resistance development to EBIs, he encourages more study of these site-specific fungicides (30).

EPIDEMIOLOGY

Epidemiological studies on apple powdery mildew go hand-in-hand with research on chemical control. One has to know how, when and at what rate the fungus is disseminated to know what chemical control strategy to use. One of the most important epidemiological aspects of P. leucotricha is the production and dispersal of asexual spores; conidia from previously infected fruit and vegetative buds, and secondary infections are its primary means of infection (22).

Conidia maturation and release cycles, environmental effects, the role of secondary infections and the role of ascospores have been investigated.

The diurnal cycle of conidia maturation and release has long been known. Some of the earliest work on this aspect of a powdery mildew was done in 1905 by Massee on Sphaerotheca humuli, which appeared to have nocturnal dissemination patterns (9). Later work by Childs provided details on this process for some conidial-chain-bearing powdery mildews, including P. leucotricha (9). Abstrictions of the conidiophore occurred from early morning to late afternoon, and formation of the next crop of conidia occurred in between those hours (9). Release of apply powdery mildew conidia begins shortly after daybreak, peaks around noontime and gradually declines through the afternoon and early evening (39). An additional subsidiary peak after dark was shown in studies carried out in the orchard, unlike earlier work which was done in the greenhouse (46). Increasing wind speed, warm temperatures and a puff or splash dispersal at the onset of rain, encourage spore dispersal; whereas high relative humidity, low temperatures and leaf wetness, from fog, dew or rain, are unfavorable conditions for spore dispersal (46).

Secondary infections arise from conidia produced at primary infection sites, which are diseased terminal shoots or flower clusters grown out from infected buds. Development of a forecasting model for the fungicide concentration needed to control secondary infections, may be based on the level of primary mildew (34).

Higher levels of primary inoculum indicated greater rates of disease progression and higher carrying capacities for disease, which is reached when the host ceases production of young tissue (34). The square root of the rate of severity (average number of lesions per leaf per tree) was determined to be proportional to the incidence (proportion of infected leaves per tree); this formula aids in severity assessment (42).

Another phenomenon of apply powdery mildew epidemiology is the occurrence of late season infection sites (4). They arise from a new flush of leaves late in the growing season, which are infected by inoculum from present primary and secondary infections (4). These sites have much lower survival rates, produce more vegetative than fruit buds and are possibly an inoculum source for infection of overwintering buds (4).

Included in epidemiological research is the role of cleistothecia in the disease cycle. Since conidia are the primary source of dispersal and infection, more research has been done in this area, correlating it to control measures. However, ascospores appear to play a less apparent role in the disease cycle, and less research effort has been applied to further study of this. Cleistothecia are produced by mid-summer on heavily infected shoots and leaves (57), and have also been observed, in an immature state, on fruit (40). Ascospore germination has been low under controlled experimental conditions, as is resulting foliar infection (57).

Development and differentiation of the ascospores is favored by warm, dry weather conditions; this process continues in the spring after overwintering within the cleistothecium (35). A study in Japan resulted in a maximum germination of 12.5% at 25 C (51), and demonstrated the need of a four to seven month period for maturation of germinable ascospores, after initial formation of cleistothecia (51). Molnar also refutes earlier statements that apple cultivar susceptibility is involved with cleistothecial occurrence (35). Further study in this area is needed to determine the real purpose for cleistothecia, such as genetic variation, since it appears to play no role in survival. Future studies on the effects of freezing, and possibly outsurviving mycelia in infected buds, have been suggested (56). The heterothallic nature of P. leucotricha is yet another aspect for study. In 1974, Coyier (12) demonstrated this in a trial mating of 14 different cultures, each derived from a single conidium (12). Evidence is in formation of cleistothecia where randomly paired cultures were inoculated, and the lack thereof where single cultures were inoculated (12). Studies on the thallism of other powdery mildew genera showed that both heterothallism or homothallism may occur within a species, depending on the particular host (12). The fact that P. leucotricha is shown to be heterothallic, suggests the value of cleistothecia, where genetic recombination takes place.

HOST RESISTANCE

Studies of host resistance to apple powdery mildew tend to take at least a few growing seasons to obtain meaningful results (13). Varying weather conditions, plus the fact that few genetic sources of resistance are known, also complicate the screening process (13). Another impediment to resistance research is that under optimum disease conditions, even resistant cultivars show some susceptibility (13).

In a survey of 62 cultivars grown in New York, five (Baldwin, Cortland, Granny Smith, Jonathan and Mutsu) were rated very susceptible; 29 (including Empire, Golden Delicious, McIntosh, Rome Beauty, Stayman and York Imperial) were susceptible; nine (including Delicious, and the apple scab resistant cultivars Liberty and Prima) were resistant; none were very resistant, where no control was needed (52). Several small-fruited *Malus* species and crab apple cultivars have been investigated in the search for resistance (26). One evaluation involved controlled crosses between *M. domestica* cv. Golden Delicious and other *Malus* species. Other studies have been done with open-pollinated seedlings from many *Malus* species, including *M. robusta* and *M. zumi* crossed with cultivated apple (26). Because the presence of races or strains of the fungus has not yet been proven, continuous cultivar evaluations in varying environments should be carried out (32).

The idealistic idea of 'universal' resistant genes, providing protection against apple powdery mildew and apple scab (52), from M. floribunda and other Malus species is noted, but earlier work by Mowry (36) espouses the genetic independence of susceptibility to these two diseases (26). Work on an interdependent group of cultivars, linked by common parents, had indicated the governing of susceptibility inheritance to be on a single, dominant gene, and supported the idea of independence of susceptibility to scab and mildew mentioned earlier (36). Dayton later provides evidence of a single, heterozygous dominant gene, providing heritable resistance (31). More recent research has indicated the presence of polygenically controlled resistance with additive gene effects (32), contrary to some earlier reports (31 and 36). Dayton also believes that bud hardiness and related characteristics may factor into the degree of host susceptibility (36). A later study showed that leaf hairiness, which varies greatly between cultivars, did not act as a spore trap or as a barrier to infection (23).

The intensified presence of hydrolytic enzymes (acid phosphatase and non-specific esterase), produced by the host at the site of fungal penetration pegs, has been cited as helping barley, Hordeum vulgaris L. cv. Proctor, to resist entrance of barley powdery mildew, Erysiphe graminis D.C. f. sp. hordei Em. Marchal (49). These enzymes were localized most intensively in a layer of oversized host wall papillae, corresponding to sites of unsuccessful penetration, and may degrade components of the penetration pegs (49).

Components of resistance to P. leucotricha, determined in a set of experiments, include: lower leaf surfaces have more colonies; colonies on younger leaves produce more conidia; minimal incubation period on a cultivar corresponds with a high disease incidence, many colonies and high spore production; and older leaves had a higher number of colonies, shorter incubation periods and a greater proportion of the leaf surfaces were covered with the fungus (23). Their research methods gave the following results: there was no interaction between cultivar and inoculum concentration; greenhouse grown colonies had a shorter incubation period and covered a larger area, than orchard grown; and conidia concentration (number of conidia per square cm of colony area) differed significantly between cultivars only in the greenhouse (23).

IN VITRO GROWTH

Because P. leucotricha is an obligate parasite, any study on the fungus usually involves, in some way, host tissue, which may be whole trees, seedlings, excised stems, excised leaves or leaf fragments. Special single-plant isolation chambers have been employed in apple powdery mildew studies, for long term greenhouse use (11). This chamber provides greater flexibility, than larger multi-plant isolation units (11). Non-isolated plants can be kept free of the fungus, without the use of chemicals, under a constant water mist (50), however, this does not prevent other pathogens and insect pests from invading. Neither does it absolutely prevent all powdery mildew infections; they can occur on leaf tissue shielded from the mist.

Another attempt at in vitro culture of the fungus involved ground up leaves and liquid culture medium, which is then combined with sterilized, dissociated conidia (8). This mixture is then combined with a gelled medium (8). Low rates of slow germination were attained, as were small amounts of mycelia and a few conidiophore initials (8).

BIOLOGICAL CONTROL

Concern about hazardous, toxic chemicals in the environment has been a factor in public thinking for the past 30 years. As residents of our planet and as members of the public, researchers bear the responsibility of developing control measures that are as safe as possible. One possibility is to exploit naturally occurring substances and organisms. Hyperparasitism and antibiotic production are a couple ways for this to take place.

Little has been done in this area with P. leucotricha at this point. Only two possible avenues have been found: the hyperparasitic fungus, Cicinnobolus cesatii De Bary (27), and a fungivorous cecidomyid larva (54). There is potential for mildew suppression by the fungal hyperparasite (27); and fungicidal effects on it and the mildew have been investigated (28). The effect of the insect's feeding on powdery mildew incidence has not been noted (54). Here again, further investigation is warranted.

CONCLUSION

In little more than a century, research on apple powdery mildew has taken tremendous strides, as have many areas of the plant sciences. The development of very disease-specific, low toxicity and systemic fungicides has revolutionized disease control, but not all the details are completely understood. For example, long-term effects of ergosterol biosynthesis inhibitors, on host and fungal populations, are not yet known. Exact modes of action of some very useful fungicides still remain a mystery. And there is always value in developing new weapons in the fungicide arsenal, to protect crops against resistance in the pest population. In the area of host resistance to apple powdery mildew, the exact mechanisms (which can vary between cultivars) are not understood; again, developing new disease resistance cultivars, new weapons to protect our crops, is desirable. Greater flexibility in handling the fungus in the lab, and eliminating the need for live host tissue, would aid in preliminary fungicide investigations and development, and in other areas of research. Finally, the realm of biological control of powdery mildew of apple is yet another great unknown, yet one that shows some potential. Our rapidly improving biotechnology: the possibility of genetic engineering (albeit an area in which researchers must proceed cautiously), advanced plant physiological and biochemical methods, provide the necessary tools for researchers to meet the needs in apple powdery mildew investigation.

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VITA

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