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A Decade of Hop Powdery Mildew in the Pacific Northwest

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Abstract

Hop powdery mildew, caused by the fungus *Podosphaera macularis*, was confirmed for the first time in hop yards in the United States Pacific Northwest in 1997. The US hop industry experienced significantly crop loss and damage from the disease, but new knowledge, grower experience, and management approaches have allowed the industry to survive the introduction of this damaging pathogen. This review provides an overview of research on and progress towards economically sustainable management of hop powdery mildew in the US, and future directions for research and further innovation.

Introduction

In 1997, hop powdery mildew, caused by the fungus *Podosphaera macularis*, was confirmed for the first time in hop yards in the United States Pacific Northwest (27). The disease had been important in hop production in New York (1), and was responsible, in part, for the decline of the hop industry in that state. The prospects for hop production in the US appeared grim after the 1997 season when greater than 800 ha of crops in Washington were abandoned because of severe infection (37). Sulfur was the only pesticide registered for use on hop with efficacy against powdery mildew, and this product was registered only for suppression of spider mites (*Tetranychus urticae*). The following year, the disease was confirmed in Idaho and Oregon.

In 1998, Yakima Valley growers made aggressive efforts to manage the disease using approaches developed in Europe (26,31), including labor-intensive cultural practices, mechanical removal of spring growth, and rigorous spray programs with the limited fungicides available for use on hop at the time (Table 1). Although successful in limiting disease development, the economic impacts of the added production expenses — estimated at $1400/ha annually in 1998 (15) — were unsustainable given the depressed market for hops at that time. The

United States hop industry seemed threatened by the combined economic impact of addressing an introduced and potentially devastating disease during a period of near record-low crop prices.

Table 1. History of fungicide and herbicide registrations for management of hop powdery mildew in the US since 1997.

Year*	Common name	Registration (Section)
1997	Fenarimol	18
1998	Potassium bicarbonate	3
	Myclobutanil	18
	Tebuconazole	18
1999	*Ampelomyces quisqualis*	3
	Paraffinic oil	3
	Trifloxystrobin	18
2000	*Bacillus subtilis* strain QST 713	3
	Harpin protein	3
	Trifloxystrobin	3
2001	Carfentrazone-ethyl	18
2003	Quinoxyfen	3
2004	Carfentrazone-ethyl	3
	Spiroxamine	3
2005	Pyraclostrobin + boscalid	3
2007	Myclobutanil	3

* Year of first US Environmental Protection Agency emergency registration (Section 18) or full federal (Section 3) registration.

An interesting dynamic that resulted from this situation was that some growers were willing to accept more risk of crop loss and were driven to develop management approaches that minimized fungicide use and production costs. Now a decade later, most US growers have "learned to live with" powdery mildew (14), by adapting European management practices based on new knowledge of the biology (13,14,15) and epidemiology (37) of the disease and availability of new fungicides and herbicides (17,18,19,20,21,22,23,24,25). This review presents a summary of the body of knowledge developed for hop powdery mildew in the Pacific Northwest, new information detailing progress towards economically-sustainable disease management, and future directions for research. The importance of strong public-private partnerships and grower innovations that were essential to successfully addressing an invasive pathogen are highlighted.

Damage from Hop Powdery Mildew

Initially, most cultivars were treated similarly due to the lack of knowledge regarding host susceptibility and understanding of disease progression. However, research, field observations, and grower experience were quickly synthesized into management programs that differed by cultivar and regions. These programs largely were based on perceptions of how disease levels were related to yield and quality factors, individual grower tolerance of disease and risk aversion. Direct estimates of yield and quality losses still remain unclear.

Hop plants appear to produce sufficient foliage so that reductions in photosynthetic activity caused by infection of leaves by *P. macularis* (Fig. 1) causes negligible direct yield loss. However, there is a strong linear relationship between the mean incidence of diseased leaves over the season and incidence of diseased cones at harvest (37). Similarly, there is a strong inverse correlation between the date of the first fungicide application and the area under the disease progress curve for leaf infection and disease incidence in cones (15). These relationships were not apparent to growers when hop powdery mildew was first introduced. As a result, many growers suffered significant crop loss because control measures for the foliar phase of the disease were not implemented until they could find disease easily in a field. Currently, most growers assume that *P. macularis* overwinters annually in most or every yard and begin fungicide applications soon after spring pruning practices. Later season sampling now is used to assess disease levels and assist in adjusting fungicide application intervals (6,36).

Fig. 1. Hop leaves with severe powdery mildew, caused by *Podosphaera macularis*.

Understanding factors influencing cone infection has proven to be difficult. While the risk of severe cone infection increases with the intensity of disease on leaves, low levels of leaf infections may cause unacceptable reductions in cone quality in susceptible aroma cultivars (15). In several yards in 2001, fairly low levels of disease on leaves (<1% incidence) led to levels of cone infection of >3% and rejection by the contracting breweries of 50% of the aroma cultivar Willamette grown in Oregon and Washington. Diffuse, late-season infection of cones by *P. macularis* (Figs. 2 and 3) was associated with cones that turned brown in the kiln, similar to ‘cone early maturity’ (4,9). The host, environmental, and pathogen factors associated with cone early maturity are unclear, but appear to be related to favorable conditions for infection late in cone development, nearby inoculum sources, and cessation of fungicide applications. Unlike leaves, cones do not appear to develop ontogenic (age-related) resistance (33,37). Even yards with near-undetectable levels of disease, cones can have unacceptable levels of infection, particularly in aroma cultivars evaluated on appearance. Quantification of the epidemiological and host factors related to cone infection, yield, and quality loss has potential to assist in disease management.

Fig. 2. Healthy hop cones (**A**), and cones with reddish-brown discoloration caused by powdery mildew (**B** and **C**). Mycelia of the fungus is visible on the cone in **C**.

Fig. 3. Hop cones infected with *Podosphaera macularis* and displaying signs and symptoms of cone early maturity. (**A**) Hop cone browning due to powdery mildew; (**B**) diffuse hyphae and infection of bract; (**C**) Conidiophores and conidia of *P. macularis* on strig of cone; and (**D**) Profuse sporulation of *P. macularis* on strig of cone displaying cone early maturity.

Survival and Overwintering

In the Pacific Northwest, perennation of *P. macularis* appears to occur only as mycelia in infected crown buds, resulting in heavily infected shoots ('flag shoots') in the spring (Fig. 4). Epidemics begin relatively soon after infected shoots emerge, similar to reports in England (31). Where sexual reproduction occurs, the overwintering structures (chasmothecia) form readily on infected leaves and cones in fall (11,12,31) and within crown buds (12). No chasmothecia have been observed in evaluations of over 1 million leaves and 300,000 cones assessed in Oregon and Washington during 1999 to 2006 (5,6,7,36,37), suggesting only one mating type of the pathogen is present or prevalent in the Pacific Northwest.

Fig. 4. Hop shoot (flag shoot) colonized by *Podosphaera macularis* resulting from crown bud infection and perennation.

Little is known of the biology and epidemiology of crown bud infection and perennation of *P. macularis*, such as factors that favor infection and overwintering, timing of bud infection, and dynamics of flag shoot occurrence and incidence. Surveys of commercial yards since 2000 indicate that flag shoots occur on a greater percentage of plants in Washington (mean 0.6%) than Oregon (mean 0.02%), and seldom are found in Idaho. Flag shoot incidence generally corresponds with the regional prevalence and incidence of powdery mildew in these states, but also may be related to differences in cultural practices among the regions or the prevalence of highly susceptible cultivars. In Oregon, many growers practice some form of mechanical pruning in spring where the buds in the top 5 cm of the soil are removed (Fig. 5), which has been shown to reduce flag shoot development in Europe (11,12). This practice is uncommon in Washington. The incidence of flag shoots also varies within and among yards over time (Table 2), which likely is a function of weather conditions during the growing season and over-wintering period (11,12), plant maturity, and/or disease management.

Fig. 5. Spring growth of hop plants (**A**) and plants 'pruned' in early spring by chemical desiccants (**B**) or mechanically (**C**), which removes overwintering buds and shoots infected with *Podosphaera macularis*. Notice in **B** that the hop shoots on the hills are brown and desiccated as a result of an application of paraquat + carfentrazone-ethyl. In **C**, the shoots and several centimeters of the crown have been removed by a modified mower. Both practices aid in eliminating early season inoculum of *P. macularis*.

Table 2. Density and incidence of flag shoots in hop yards in Oregon and Washington from 2000 to 2007.

	Oregon		**Washington**	
Year	***n****	**Flag shoots (% incidence)**	***n***	**Flag shoots (% incidence)**
2000	8636	1 (0.01)	12582	106 (0.84)
2001	9701	1 (0.01)	9130	88 (0.96)
2002	1337	1 (0.07)	2600	105 (4.04)
2003	800	0 (0)	2000	7 (0.35)
2004	400	0 (0)	2000	0 (0)
2005	6576	4 (0.07)	2800	7 (0.25)
2006	1349	0 (0)	2189	7 (0.32)
2007	15160	0 (0)	13212	2 (0.0002)
Total	43959	7 (0.02)	46513	322 (0.69)

* Number of hills evaluated.

Weather Variables Associated with Infection Risk

Improvements in management of hop powdery mildew have been hastened by a better understanding of weather conditions associated with leaf infection and disease severity. In controlled environments at constant temperature, disease development was optimal at 18 to 21°C and reduced when temperature was 24°C or greater with no disease observed to develop at 30°C (37). Similar trends occur with sporulation density in response to constant and 6-hr exposure to a range of temperatures (28). In experiments conducted with variable temperature regimes, infection was reduced by short exposure (> 2 h) to temperature greater than 30°C (13), and also reduced the susceptibility of leaves to infection. Such super-optimal temperatures are common during late spring and summer in Washington and southern Idaho, and occasionally occur in western Oregon and northern Idaho. Results of growth chamber studies generally parallel observations of disease incidence from field surveys in yards in southern Idaho and Washington, where disease incidence and severity typically decline during extended heat waves.

Rainfall greater than 2.5 mm was associated with reduced disease development in western Oregon yards (15). However, this association appears to be an anomaly associated with long periods of continued wetness and rain. This association does not appear to hold true in other regions (e.g., Germany and eastern Washington) and is not supported by controlled environment experiments. In these experiments, direct effects of wetness on leaf infection and colony survival where ephemeral and established infections were tolerant to even long (24 h) periods of wetness (Gent, *unpublished*). It is possible that a combination of prolonged periods of wetness and rinsing of leaves by rainfall is responsible for the correlation to reduced disease development. However, the, sporulation of other powdery mildew fungi are negatively correlated with rain intensity (2,3,34,40), indicating that the relationship between rainfall, leaf wetness, and disease development is more complex.

Information from controlled-environment studies and field surveys were used to modify the Gubler-Thomas infection risk index for grapevine powdery mildew (caused by *Erysiphe necator*) (8) to assess infection risk for *P. macularis*. The index calculates an infection risk (0 to 100) based on the number of continuous hours when the temperature is between 16 and 27°C or greater than 30°C, and millimeters of rain during the previous 24-hour period. Fungicide application intervals are recommended for different fungicide modes of action depending on the predicted risk level (low, moderate, or high). The index represents the risk of infection for the most susceptible cultivars and does not account for differences in how cultivars respond to environmental conditions. Consequently, the risk index does not accurately represent infection risks for all cultivars. Factors other than temperature and rainfall not considered in the risk index (e.g., inoculum density, solar radiation) likely moderate infection risk in some yards.

Dissemination of the risk index outputs were delivered to US hop growers via websites operated through public-private partnerships with agricultural consulting and management companies, which were made possible by industry funding and grant support. Later, disease forecasts were linked to five-day, site-specific weather forecasts generated by Fox Weather LLC (Fortuna, CA), which improved the utility and adoption of the risk index. In 2001, growers using the risk index reported they made 9.1 fungicide applications resulting in an average of 9.3% incidence of diseased cones, while growers that did not use the risk index made 10.3 applications and had 23.9% incidence of diseased cones. Mahaffee et al. (15) stated that the risk index was adopted widely in the industry, and was used to aid in disease management on approximately 60% of hops produced in the US. Sustaining weather station networks, forecasts, and websites for risk index delivery over time has been a challenge because of annual expenses associated with hardware and software maintenance, and information delivery. Currently, the risk index is available publicly through the Washington State University AgWeatherNet and Oregon State University Integrated Plant Protection Center websites, which should provide long-term stability and improve access to risk index outputs. However, many growers and crop consultants appear to have developed an intuitive sense of the risk index and no longer monitor index results closely, but rather adjust application intervals based on their knowledge of weather conditions and disease severity. Perhaps this behavior modification is the best indicator of the success and adoption of this innovation for improving disease management.

Sampling for Hop Powdery Mildew

In practice, disease risk assessments based on weather factors are integrated with scouting information on disease levels in individual yards to determine the need for fungicide applications. Fixed and sequential sampling plans for powdery mildew on leaves and cones (6,7) have been used developed from spatial patterns of disease incidence obtained over several years of intensive disease assessments (5,6,7,36). An important finding of this work was that the greatest variability in disease incidence occurred between yards rather than within yards, suggesting that sampling efforts should focus on sampling a greater number of yards rather than focusing sampling in any particular yard (36). The work also indicates that relatively few plants need to be assessed to obtain a precise estimate of disease incidence when disease is above 2.5% leaf or cone incidence (6,7). Detecting disease below this level is possible but requires a much greater sampling effort, and likely is impractical on a commercial scale.

Disease Management

Arguably the greatest success story since the introduction of hop powdery mildew into the Northwestern US has been the development of cost-effective and practical approaches to managing the disease. The association of early season grower practices with disease incidence on leaves, and subsequently cones, were noted soon after research was initiated. Turechek et al. (37) found that disease incidence was relatively low in yards with low incidence of flag shoots or that were pruned thoroughly in spring, and suggested that disease management practices prior to pruning likely were not needed if the pruning was done such that no green plant tissue was left. Similar analysis of flag shoot density and pruning quality indicates that cone infection is greater in poorly pruned yards (Gent, *unpublished*). Potential savings for this practice are estimated at $148 to $296/ha, depending on the method of pruning and irrigation. A caveat to this recommendation is that the pruning must be done very well if fungicide applications are to be delayed until after spring pruning, which can be difficult to achieve in practice because of logistical constraints. A strong correlation also was found between the date of the first fungicide application and the incidence of cone infection in a yard, although correlations between cone infection and the total number of applications or amount of active ingredient applied were not apparent (15). These studies suggest that management of powdery mildew in cones is dependent on the success and thoroughness of early season control measures.

Numerous fungicide and desiccant herbicide trials have been conducted in the past 10 years that provided data to support pesticide registrations and develop management programs for growers (17,18,19,20,21,22,23,24,25). These data have supported registration for 11 products, all with different modes of action, with full federal use labels (Section 3), and five products for emergency (Section 18) registrations (Table 1). The rapid registration of so many products with diverse modes of action highlights the organization of the US hop industry and effective cooperation among public and private sectors.

Fungicide programs for powdery mildew vary among growers and regions, but, in general, most programs include a rotation of inorganic fungicides (e.g., horticultural oils, potassium bicarbonates, sulfur) and synthetic fungicides (e.g., myclobutanil, spiroxamine, strobilurins, quinoxyfen). Inorganic fungicides are used heavily because, in part, of their relatively low cost as compared to synthetic fungicides. The synthetic fungicides tend to be used more heavily during cone development because of buyer restrictions on sulfur use after flowering.

Among the fungicides now registered for management of hop powdery mildew, quinoxyfen appears to be highly efficacious, especially under moderate disease intensity. In 10 fungicide trials in Washington, treatments that included quinoxyfen alone or in programs with other fungicides have provided an average of 74% disease control compared to non-treated plots [derived from (17,18,19,20,21,22,23,24,25)]. However, under high disease pressure no fungicide or fungicide program provided satisfactory control of powdery mildew on cones [derived from (17,18,19)]. Conversely, under low disease pressure most fungicides provide similar disease control. Research currently is underway to develop more efficient management programs based on crop phenology and fungicide physical mode of action.

Removal of infected leaves and stems has proven to be a very important component of managing powdery mildew (Fig. 6), in a practice referred to as 'stripping.' Prior to the introduction of *P. macularis*, stripping was practiced for control of basal growth primarily for downy mildew (caused by *Pseudoperonospora humuli*) in western Oregon and northern Idaho where downy mildew is endemic. Stripping rarely was practiced in Washington and southern Idaho where downy mildew is not an annual threat (10). Chemical desiccants (i.e., paraquat) were available prior to the introduction of powdery mildew, but because of issues related to paraquat efficacy during cool weather in spring there was an urgent need to identify new desiccants to aid in stripping. Research conducted in 2002 identified carfentrazone-ethyl (Aim EC and Aim EW, FMC Agricultural Products, Philadelphia, PA) as an effective herbicide to remove basal growth. Field trials compared the incidence of powdery mildew on leaves and cones in relation to basal foliage control programs consisting of two applications of endothall (Desicate II, Cerexagri Inc., King of Prussia, PA) and paraquat (Gramoxone Max, Syngenta Crop Protection, Greensboro, NC) three applications of carfentrazone-ethyl, and non-stripped controls, in the absence of fungicide application. The incidence of disease on leaves was similar for the majority of the season, but differences among treatments were evident in mid-August, when the incidence of powdery mildew on leaves was reduced from 46.9% without stripping to 17.4 or 9.7% using endothall + paraquat or carfentrazone-ethyl, respectively (Fig. 7). Reduction in the incidence of infected cones, compared to the non-treated plots, also was reduced 10.9 and 22.0% with endothall + paraquat and carfentrazone-ethyl, respectively (Table 3). Reduction in yield was not detected in this trial, although previous work in England reported a reduction from chemical stripping (39). Uncertainty still exists about the effect of chemical stripping on yield loss for cultivars grown in the US.

Fig. 6. Hop plants where basal growth has been removed by carfentrazone-ethyl (**A**) or left untreated (**B**). Removal of basal foliage with chemical desiccants effectively reduces inoculum of *Podosphaera macularis*, and is important for reducing later infection of leaves and cones. Achieving adequate cover of dense basal growth, as in **B**, during fungicide applications is difficult.

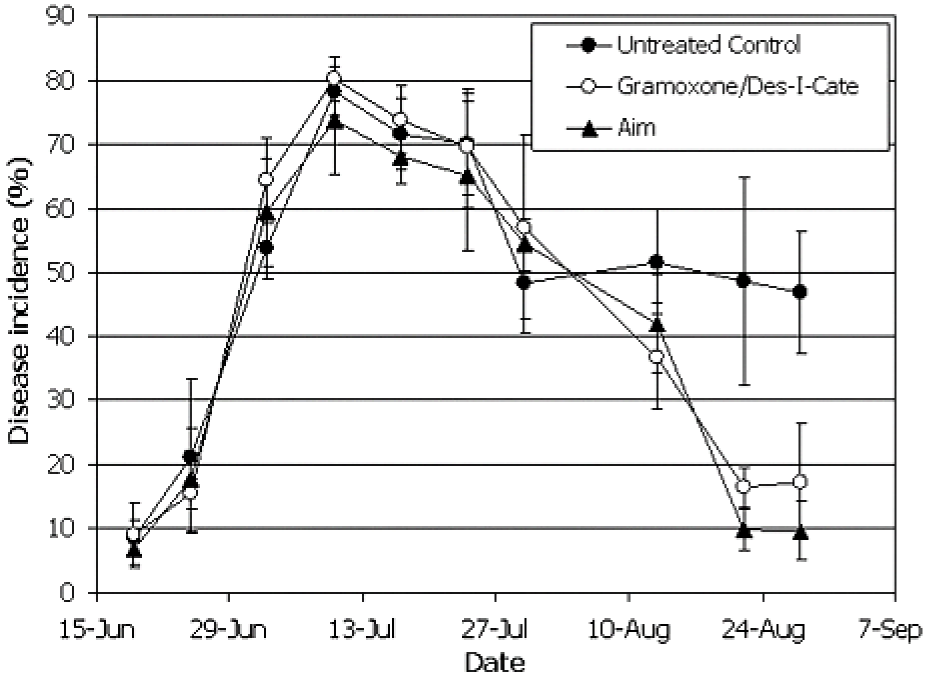

Fig. 7. Incidence (%) of hop leaves with powdery mildew in relation to herbicide treatments to remove basal leaf growth, Granger, Washington, 2002. Applications of Aim EW (carfentrazone-ethyl) were applied 6 July, 3 August, and 20 August. Applications of Gramoxone Max (paraquat) + Desicate II (endothall) were applied 6 July and 3 Aug 2002. Data are means of three replications ± standard error.

Table 3. Effect of sucker growth control with herbicides on incidence of powdery mildew on cones in Washington in 2002.

Treatment*	**Cone infection** (%)**
Carfentrazone-ethyl	64.9 a
Endothal + paraquat	75.4 ab
Non-treated	86.0 b

* Applications of carfentrazone-ethyl were applied 6 July, 3 August, and 20 August 2002. Applications of endothal + paraquat were applied 6 July and 3 August.

** Numbers followed by the same letter are not significantly different (Fisher's protected $LSD_{0.05}$)

Host resistance is considered to be one of the most efficient way to manage plant disease (16), but is difficult to employ in hops due to the time required to develop new cultivars and market factors. Laboratory studies indicate that isolates of *P. macularis* capable of overcoming the resistance genes (*R*-genes) R_B, R_3, and R_5 are prevalent in the Pacific Northwest, while strains that can infect cultivars with R_2, R_6 or a combination of $R_B/R_1/R_3$ are relatively uncommon (C. M. Ocamb, *unpublished data*). Novel sources of powdery mildew resistance also have been identified in wild *Humulus* accessions collected in North America, western Europe, and Kazakhstan (35).

Outlook and Future Directions

Development of management approaches for hop powdery mildew has created a new set of IPM issues for growers to address. The registration of numerous powdery mildew fungicides has led to a need for resistance management research and development of complete fungicide management programs. Additionally, several fungicides (e.g., petroleum oils, sulfur) and cultural practices (e.g., spring pruning) used commonly for powdery mildew management can adversely affect arthropod natural enemies of spider mites and potentially exacerbate mite outbreaks (29,30,38). Thus, new challenges for growers and researchers are to assemble the current information into an integrated and profitable production system that optimizes multiple production goals. Systems approaches to managing powdery mildew will require refinement of management approaches, greater efficiency, and reduced reliance on chemical controls.

Achieving these goals will require enhanced understanding of the epidemiology of hop powdery mildew. An exciting area of current research is development and deployment of novel PCR-based detection technologies for *P. macularis* in air samples and plant tissues in semi-real time. Currently, fungicides are applied prophylactically assuming that inoculum is always present, which may not be true in all fields or situations. These technologies may improve the efficiency of disease management by targeting control measures only to periods when the pathogen is actively sporulating and present in air samples. Predicting inoculum availability could be automated by deriving equations to model aerial conidial density and dispersal as a function of disease incidence and/or weather factors.

Much work remains to be done on characterizing pathogenic variability in *P. macularis* and integrating disease resistance into cultivars with brewing qualities that will be accepted by the brewing industry. R-gene pyramiding may be an effective strategy to breed for resistance (32), especially if new R-genes are incorporated. Also underutilized is broad spectrum, horizontal resistance to powdery mildew, which likely would provide more durable resistance than resistance based on single R-genes (32). Progress towards integrating horizontal resistance into hop is hindered by the lack of molecular markers and an understanding of the genetic traits underlying quantitative trait loci, as well as slow acceptance of new cultivars by the brewing industry. Identification and characterization of the genes underlying quantitative resistance could speed selection and breeding efforts, and avoid the "boom-and-bust" cycle of disease resistance based on a single major gene.

The introduction and establishment of *P. macularis* in the Northwestern US undoubtedly has changed the US hop industry, but the response by public researchers, private industry, and individual growers provides a model for partnership in addressing pest outbreaks and threats in the future. Much of the innovation and progress towards management of powdery mildew has come from the collaboration of individual growers and researchers in integrating and balancing research findings with economic and logistic realities of hop production. Clearly, much of this work has not or cannot be documented. Perhaps the most important measure of the success of growers and the US hop industry to respond to hop powdery mildew is that 10 years after the establishment of powdery mildew the impact of powdery mildew has been reduced significantly (15), and the hop industry was able to endure the introduction of a new and, locally, poorly understood disease during a time of depressed hop prices. Efforts to further reduce input costs and develop systems approaches to hop production and IPM are underway with the goal of enhancing the profitability and sustainability of powdery mildew management and hop production in the US.

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