Hop Powdery Mildew Control Through Alteration of Spring Pruning Practices

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Abstract

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Podosphaera macularis, the causal agent of hop powdery mildew, is a recurrent threat to hops in the Pacific Northwest because of the potential to reduce cone yield and quality. Early-season pruning is a common practice in hop production for horticultural reasons. Studies were conducted over a 3-year period in a commercial hop yard to quantify the effect of pruning method and timing on disease development, yield, and cone quality factors. A 4-week delay in pruning reduced the incidence of leaves with powdery mildew from 46 to 10% and cones from 9 to 1%, with the specific effect being season dependent. Pruning using chemical

desiccants rather than by mechanical means had similar effects on disease levels on leaves. On cones, though, chemical pruning had a small but significant reduction in the incidence of powdery mildew compared with mechanical pruning. Cone yield, levels of bittering-acids, and color were not negatively affected in any individual year or cumulatively over three seasons when pruning treatments were applied repeatedly to the same plots during the study period. Delayed pruning may offer a low-cost means of reducing both the incidence of powdery mildew and early-season fungicide inputs in certain cultivars.

Hop (*Humulus lupulus* L.) is a dioecious, perennial climbing plant grown in a narrow range of latitudes in temperate regions of the northern and southern hemisphere. Each spring, the plant sends out annual shoots from an overwintering root system, and shoots rapidly climb to produce lateral branches that bear the female reproductive structures (cones) during the summer months. After harvest, shoots die back to ground level during autumn and winter. Monocropping of female hop plants is a common practice to ensure maximum cone yield and to prevent cross fertilization by male pollen (Rybáček 1991). The hop cones harbor large numbers of lupulin glands filled with a reservoir of valuable resins and essential oils. These flavorful secondary metabolites are most commonly used by the beer industry to bitter and flavor beer, stabilize foam development, and serve as a natural preservative, extending the shelf life of the product (Hysert 2009). In recent years, hop-derived compounds such as xanthohumol have also received increased attention due to their potential cancer chemopreventive and antimicrobial properties (Stevens and Page 2004; Van Cleemput et al. 2009).

Powdery mildew of hop is caused by *Podosphaera macularis* (Wallr.) U. Braun & S. Takam. and has been of major concern for hop growers in the Pacific Northwest since becoming epidemic in 1997 (Gent et al. 2008; Ocamb et al. 1999). If untreated, the disease can lead to complete loss of marketable crops. Severe outbreaks of powdery mildew have detrimental effects on cone quality and yield and can drastically reduce economic profits (Gent et al. 2008). Regularly scheduled prophylactic fungicide applications are used to

prevent or mitigate foliar powdery mildew and to protect the developing cones from colonization and subsequent deterioration (Gent et al. 2008; Nelson et al. 2015). However, even with regular fungicide applications, crop damage may still occur (Gent et al. 2014b), and incongruent maximum residue limits in key export markets may restrict use of certain fungicides. Furthermore, strains of the fungus capable of infecting previously resistant hop cultivars recently emerged in the Pacific Northwest of the United States. As a result, the overall number of resistant hop cultivars available to hop growers is reduced and the need for alternative powdery mildew management strategies magnified (Wolfenbarger et al. 2014a,b).

Ascocarps of *P. macularis* have not been reported from the Pacific Northwest (Gent et al. 2008; Ocamb et al. 1999), apparently due to the presence of only one mating type of the fungus in the region (Wolfenbarger et al. 2014b). Thus, the fungus overwinters as mycelium in and on crown buds of the dormant host during the winter months (Gent et al. 2008; Liyanage et al. 1976). In early spring, when the plant resumes growth, the overwintering fungus develops on emerging shoots, resulting in the commonly termed “flag shoots” (Gent et al. 2014a). Even though it is estimated that less than 1% of plants produce flag shoots (Gent et al. 2008), these infected shoots produce sufficient primary inoculum to initiate region-wide disease outbreaks on susceptible cultivars (Gent et al. 2008). Infection of young leaves are the first signs of disease onset in hop yards and, even though they are rarely connected to economic loss, provide secondary inoculum to subsequently infect other leaves, developing flowers, and cones (Tureček et al. 2001). Once infected, flowers may abort, leading to reduced cone yield and financial loss. The bloom and the juvenile stages of cone development are particularly susceptible to the fungus and are essential periods of disease control (Nelson et al. 2015; Twomey et al. 2015). Susceptibility of cones decreases with maturity due to the development of partial ontogenic (age-related) resistance, during which cones become progressively less susceptible to the disease but never fully immune (Twomey et al. 2015).

Early spring pruning of the first emerging hop shoots, also known as crowning or cutting, is an integral initial step in the hop growing season for maximizing yield and for disease control (Rybáček 1991). In this practice, shoots are cut back to the ground to encourage vigorous, synchronized growth of bines. Early-season pruning also removes plant remnants from the previous season and can potentially eliminate crown buds with powdery mildew and primary inoculum

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arising from flag shoots (Gent et al. 2012). Pruning also reduces primary inoculum of the downy mildew pathogen, *Pseudoperonospora humuli* (Gent et al. 2012; Rybáček 1991). Spring pruning can be conducted mechanically using specialized farm equipment or chemically by desiccating the leaves of the developing plants (Gent et al. 2008). Mechanical pruning cuts off complete shoots and crown buds but is labor intensive and difficult to apply across large farms, especially when drip irrigation is used. Thoroughly conducted chemical pruning can kill all or most green plant parts but leaves behind woody shoots and associated crown buds that may harbor powdery mildew inoculum (Gent et al. 2012, 2014a). Growers' preference, farm system, economics, and experience will largely determine the method of choice. However, timing and intensity of these cultural practices are largely influenced by cultivar.

It is crucial to establish an appropriate timing of spring pruning, because pruning timing affects subsequent training date and, ultimately, crop development. In addition, thorough spring pruning practices have been linked to both downy and powdery mildew disease reduction (Gent et al. 2012). However, it is unclear whether pruning timing similarly influences powdery mildew development. Conceivably, flag shoots may not yet be emerged if shoots are removed too early or, on the contrary, already may have produced inoculum if spring pruning is conducted too late. Further, the timing of pruning may influence plant vigor and canopy development, which could indirectly influence powdery mildew epidemic development.

The objectives of this 3-year study were to (i) quantify associations of spring pruning timing on season-long powdery mildew development on leaves and cones, (ii) assess the effect of pruning methods (mechanical versus chemical) on disease control, and (iii) evaluate the effect of the above-mentioned modifications on overall cone yield and cone quality factors. The results may be used to modify cultural management strategies to aid in disease prophylaxis.

Materials and Methods

Field site and experimental design. Experiments were conducted from 2012 to 2014 in a 13-ha commercial hop yard planted to 'Tomahawk' hop near Toppenish, WA. Six treatments were replicated four times in a randomized complete block design. Each plot contained three rows encompassing a total of approximately 45 hop plants. Plots were separated by at least one buffer row that was treated according to the cooperating grower's standard spring pruning practices and other crop management inputs.

Spring pruning was conducted on one of three dates in April to represent early, mid, and late pruning times. In each year, early pruning was conducted on 1 to 2 April, mid-pruning treatments were conducted 15 to 16 April, and late-pruning treatments were conducted 29 to 30 April. On each of these dates, plots were either mechanically pruned by the cooperating grower using their standard rotary pruning implement, or the foliage was chemically desiccated. Thus, there was a total of six pruning timing–method treatments and a two-way factorial structure of the three levels of pruning timing and two levels of pruning method. Treatments were applied to the same plots in each year in order to detect multiyear effects of treatments on powdery mildew, cone quality factors, and yield.

Notes were taken on shoot development in each year and shoot length was generally similar across years, being less than 15 cm in the early timing, less than 30 cm in the mid timing, and less than 60 cm in the late timing plots. Degree-days were calculated from 1 February to 30 April using a base temperature of 6°C (Gent et al. 2010) from weather data obtained from a Washington State University AgWeatherNet station located 8 km away at Toppenish, WA. Cumulative degree-days were 100, 214, and 232 in 2012, 2013, and 2014, respectively.

Plots that were chemically desiccated were treated with carfentrazone (Aim EC; FMC Corp., Philadelphia) at 35.9 g/ha amended with 0.5% Mor-Act crop oil (Wilbur-Ellis, San Francisco). Applications were made using a backpack sprayer calibrated to deliver an application volume equivalent to 187 liters/ha (broadcast rate). Chemical applications were conducted twice, first on the date noted above and then 4 to 5 days later to ensure thorough desiccation of the foliage.

In order to avoid confounding factors, inputs of water and fertilizer, cultural practices, as well as pesticide and disease control measures, including fungicide applications for powdery mildew, were made by the cooperating grower to the entire yard, including the experimental plots, according to their standard production practices. Therefore, the treatment comparisons in this study measured the cumulative effect of pruning timing and method given standard powdery mildew management tactics. The date of the first fungicide application made to the entire yard and the plots was 17 May 2012, 31 May 2013, and 30 April 2014. In total, 11 or 12 fungicide applications were made in each year.

Disease assessments and cone data collection. One day before treatments were first applied, each plot was assessed for the presence of flag shoots and signs of powdery mildew on emerging plants. Flag shoot and powdery mildew assessments were conducted every 2 weeks until late May. After this time, disease assessments were conducted biweekly at the leaf level until late July 2013 and 2014 or early August 2012 by inspecting 10 leaves from each of 10 plants in the center row of each plot. Disease development over time was expressed as the time-scaled area under the disease pressure curve (AUDPCS) using the equation given by Madden et al. (2007).

On 17 September 2012, 12 September 2013, and 9 September 2014, plots were harvested to estimate the incidence of cones with powdery mildew and yield. Disease assessments were conducted on cones harvested from 10 randomly selected plants in the middle row of each plot. Cones from lateral branches approximately 3, 4, and 5 m above ground were bulked and mixed before arbitrarily selecting 15 cones from each plant, for a total of 150 cones/plot. Each cone was visually inspected for the presence of powdery mildew with the aid of a dissecting microscope ($\times 10$ to $\times 50$), when needed. Ten plants from the center row of each plot were later harvested using a hop-picking machine to estimate cone yield on a per-plant basis. The fresh weight of the cones was recorded, and a subsample of harvested cones (approximately 70 g) was collected and dried for 48 to 72 h at 60°C in order to determine percent dry matter content of the cones. Dry weight per plant was calculated after adjusting for dry matter content.

A second subset of harvested cones, collected and dried overnight to approximately 8 to 10% moisture in an electric dryer, was used to measure bittering acids content by standard spectrophotometric methods (American Society of Brewing Chemists 2009). Color was rated on this subset of cones using a 1-to-10 ordinal scale adapted from a rating system commonly used in hop brokerage, with 10 being the best and 1 being the worst possible color (Twomey et al. 2015).

Statistical analysis. Data were analyzed in two approaches. First, treatment effects were analyzed using mixed-effect models by year. For a given year, data were analyzed considering the factors of pruning timing, pruning method, and their interaction as fixed effects and block as random effect. Analyses were conducted using the GLIMMIX procedure in SAS (version 9.4; SAS Institute, Cary, NC), with the distribution of the response variables specified as normal and with the default link function in GLIMMIX. If a significant treatment effect was found, least-squares means for the factors or their interaction were compared for individual treatments using the lines options in GLIMMIX without adjustment for multiple comparisons. Data from the individual year analyses are given in Table 1.

The experimental design involved repeated measurements on the same experimental units because the same treatments were applied to the same plots in each year. Therefore, data from all years also were analyzed as a repeated-measures design using the GLIMMIX procedure. Multiple covariance structures for the residuals were investigated, and the simplest covariance structures consistent with the data were selected based on Akaike's Information Criterion. Degrees of freedom were estimated by the Kenward-Roger method. Disease incidence data for cones were transformed using an arcsin square root transformation to stabilize variances.

Ordinal cone color ratings were analyzed using an analysis of variance-type statistic in the MIXED procedure in SAS (version 9.4) using the methods described by Shah and Madden (2004). Again, this analysis was conducted individually for each year and also as a repeated-measures analysis over years. Estimated relative

treatment effects and their confidence intervals were calculated using the macros “LD_CT” and “F2_LD_FI” of Brunner et al. (2002).

Results

Disease assessments and cone data collection. Powdery mildew occurred naturally in all 3 years. However, in 2012, the outbreak was most severe and its onset most rapid, with an average of 97% of plants diseased at the end of May (Fig. 1A). In contrast, natural disease progression was slower and less severe in 2013 and 2014, with an average of 20 and 8% of plants, respectively, diseased by the end of May (Fig. 1B and C). Disease progression in June and July was influenced by treatments and seasonal disease pressure (Figs. 1D to F). In 2012, disease incidence was maximal at the plant scale at the end of May and, on leaves, progressively decreased after late June. In 2013, powdery mildew incidence on leaves increased substantially between day 161 and 175, reaching a plateau of 66% (early-, mid-, and late-pruning timing treatments) at the beginning of July (day 189), and progressively decreased in all treatments. In 2014, no more than 18.9% of plants had powdery mildew in any treatment up to early June. Only slight fluctuations in powdery mildew incidence on leaves were observed in June and July (Fig. 1F).

In 2012 and 2014 but not 2013, powdery mildew was first observed before the last pruning treatments were applied by the end of April (Fig. 1A). At this time, disease incidence in previously pruned plots ranged from 0 to 0.6% of plants (mean = 0.4%) in 2012 and 0 to 4.4% of plants (mean = 1.8%) in 2014. In comparison, powdery mildew incidence in plots that were not yet pruned was 11% in 2012 and 0.6% in 2014. In 2013, powdery mildew was first observed in the middle of May, 2 weeks after the last pruning treatments occurred (Fig. 1B). Flag shoots were not detected in 2012 and 2013. One flag shoot was found on 28 April 2014 in a plot that was pruned mechanically on 1 April.

In the repeated-measures analysis, pruning timing influenced powdery mildew development on leaves ($P < 0.001$), although this effect differed among years (timing–year interaction, $P < 0.001$; Table 2; Figs. 2A and 3A). There was a progressive reduction in powdery mildew incidence with later pruning timing in 2012 whereas, in 2013, only the late-pruning timing reduced disease levels compared with early and midseason pruning. However, there was not a significant difference between the early- and mid-pruning timings that year (simple effect least squares mean comparison, $P = 0.888$; Fig. 2A). Powdery mildew levels on leaves were similar among treatments in 2014 (Fig. 2A). Disease levels on leaves were unaffected by pruning method (mechanical versus chemical; $P = 0.285$; Fig. 3B), and

Table 1. Effect of pruning timing and method on hop powdery mildew, yield, and cone quality factors based on a year-by-year mixed-model analysis of experiments conducted during 2012 to 2014^a

Timing ^d	Method	Disease ^a		Yield ^b			Cone quality factors ^c		
		AUDPCS	Cones (%)	α-Acids (%)	α-Acids (kg)	Cone (kg)	DM (%)	Color	RE (CI)
2012									
Early	Mechanical	0.65	96.2	19.2	0.104	0.54	27.9	5.00	0.19 (0.13–0.29)
Early	Chemical	0.60	93.0	20.1	0.109	0.55	27.8	5.50	0.42 (0.23–0.64)
Mid	Mechanical	0.53	91.6	19.9	0.108	0.54	28.0	5.75	0.49 (0.23–0.77)
Mid	Chemical	0.55	87.0	20.0	0.108	0.54	27.9	5.75	0.53 (0.34–0.71)
Late	Mechanical	0.33	87.3	19.2	0.117	0.62	26.9	6.00	0.65 (0.53–0.74)
Late	Chemical	0.34	84.1	19.9	0.105	0.53	26.7	6.25	0.72 (0.55–0.83)
Model ^e									
T	...	<0.001	<0.001	0.704	0.710	0.525	0.010	...	0.005
M	...	0.471	0.021	0.201	0.612	0.249	0.607	...	0.217
T × M	...	0.079	0.987	0.692	0.309	0.261	0.987	...	0.590
2013									
Early	Mechanical	0.58	98.8	19.2	0.127	0.66	27.6	4.25	0.38(0.21–0.59)
Early	Chemical	0.54	99.0	19.3	0.130	0.67	28.1	5.00	0.65(0.38–0.82)
Mid	Mechanical	0.48	99.3	20.3	0.136	0.67	28.3	4.50	0.48(0.20–0.78)
Mid	Chemical	0.65	99.5	19.0	0.130	0.69	27.0	4.75	0.58(0.37–0.76)
Late	Mechanical	0.48	99.3	19.9	0.140	0.70	27.6	4.75	0.54(0.28–0.78)
Late	Chemical	0.45	99.5	20.2	0.134	0.67	28.9	4.25	0.38(0.21–0.59)
Model									
T	...	0.018	0.261	0.168	0.196	0.792	0.775	...	0.865
M	...	0.216	0.377	0.418	0.459	0.813	0.825	...	0.559
T × M	...	0.009	1.000	0.148	0.525	0.596	0.344	...	0.327
2014									
Early	Mechanical	0.221	87.8	18.1	0.097	0.534	23.7	5.5	0.51 (0.23–0.78)
Early	Chemical	0.279	79.3	18.3	0.095	0.517	23.3	5.5	0.46 (0.23–0.71)
Mid	Mechanical	0.288	90.8	18.4	0.093	0.5	24.9	5	0.28 (0.17–0.47)
Mid	Chemical	0.271	91.5	18.1	0.094	0.521	23.5	6	0.64 (0.33–0.83)
Late	Mechanical	0.224	81.5	18.9	0.099	0.528	23.9	5	0.44 (0.28–0.63)
Late	Chemical	0.228	83.5	19.1	0.105	0.522	23.8	6	0.67 (0.43–0.83)
Model									
T	...	0.165	0.003	0.066	0.337	0.765	0.176	...	0.737
M	...	0.494	0.328	0.881	0.771	0.789	0.047	...	0.115
T × M	...	0.36	0.08	0.698	0.787	0.834	0.245	...	0.315

^a Time-standardized area under the disease progress curve (AUDPCS) for powdery mildew development on leaves.

^b Bittering acids content, as percentage and kilograms per string (kg), was determined using standard spectrophotometric methods provided by The American Society of Brewing Chemists (2009).

^c Color was rated using a 1-to-10 ordinal scale, where 1 is the worst possible color and 10 is the best (Twomey et al. 2015). DM = dry matter. Relative marginal effect (RE) and associated 95% confidence interval (CI) are as explained by Shah and Madden (2004).

^d Spring pruning was conducted biweekly on one of three dates in April to represent early, mid, and late pruning times. On each date, developing vines were pruned off either mechanically or with a chemical desiccation.

^e Model factors were timing (T), method (M), and their interaction.

there was only weak evidence that pruning method and timing interacted ($P = 0.061$; Table 2; Fig. 3C).

On cones, pruning timing similarly influenced powdery mildew incidence ($P < 0.001$) in a year-dependent manner (timing–year interaction, $P < 0.001$; Figs. 2B and 3D). Powdery mildew incidence on cones was reduced in a stepwise manner with later pruning in 2012 whereas, in 2013, no effect due to pruning timing was observed. In 2014, significant disease reductions in cones were found only compared with plots with the mid-pruning timing (Table 2; Fig. 2B). However, even in years when pruning timing effects were observed, variation in powdery mildew incidence was modest and never exceeded 9%. There was a small (2%) but statistically significant ($P = 0.024$) reduction in the incidence of cones with powdery mildew in plots pruned chemically versus mechanically (Fig. 3E). This effect

was consistent over all years (method–year interaction, $P = 0.079$) and independent of pruning timing (timing–method interaction, $P = 0.085$; Fig. 3F). Cone color varied among years ($P < 0.001$) but was not affected by the treatments in a repeated-measures analysis (Table 2).

Yield of α -acids varied by year ($P < 0.001$; Table 2). However, yield was independent of pruning timing and method ($P \leq 0.313$; Fig. 4). Furthermore, no evidence of negative effects on cone yield or α -acids yield associated with pruning timing or method were found in any given year (Table 1).

Discussion

How and when to prune are two major considerations for early-season disease prophylaxis in hop cultivation. This study establishes

Fig. 1. Powdery mildew disease progression on A, B, and C, plants and D, E, and F, leaves when mechanically or chemically pruned on three different dates in April 2012, 2013, and 2014.

Table 2. Mixed-model repeated-measures analysis of the effect of pruning timing method and timing on the incidence of hop leaves and cones with powdery mildew, yield, and cone quality factors in Tomahawk hop during 2012 to 2014^a

Effect	Leaves with powdery mildew ^b				Cones with powdery mildew ^b				Yield of α -acids ^b				Cone color ^c			
	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P	NDF	DDF	F	P
Timing (T)	2	18	44.94	<0.001	2	26.36	13.76	<0.001	2	18.98	1.24	0.313	1.74	15.6	0.96	0.372
Method (M)	1	18	1.21	0.285	1	26.36	5.73	0.024	1	18.98	0.13	0.721	1	1	2.31	0.129
T $\times$ M	2	18	3.27	0.061	2	26.36	2.71	0.085	2	18.98	0.24	0.789	1.74	15.6	0.22	0.768
Year (Y)	2	17	123.24	<0.001	2	24.93	145.14	<0.001	2	34.52	87.32	<0.001	1.62	1	18.24	<0.001
T $\times$ Y	4	19.62	22.03	<0.001	4	26.96	8.05	<0.001	4	35.01	0.32	0.862	2.9	28.8	1.5	0.214
M $\times$ Y	2	17	1.32	0.293	2	24.93	2.82	0.079	2	34.52	0.25	0.778	1.62	1	0.77	0.438
T $\times$ M $\times$ Y	4	19.62	1.71	0.188	4	26.96	1.21	0.329	4	35.01	0.75	0.563	2.9	28.8	1.88	0.133

^a NDF and DDF = numerator and denominator degrees of freedom, respectively.

^b Treatments were deployed and measurements were repeated each year during 2012 to 2014. Covariance structures for the factor “Year” were selected based on minimizing Akaike’s Information Criterion. The covariance structures selected for Year in the analysis of leaves with powdery mildew, cones with powdery mildew, and yield were unstructured, heterogeneous compound symmetry, and autoregressive, respectively. Leaves with powdery mildew was expressed as relative area under the disease progress curve.

^c Analysis of cone color was conducted using ranks of cone color rating and an analysis of variance-type statistic as described by Shah and Madden (2004).

that spring pruning practices can influence development of powdery mildew throughout the season, although the overall effect on disease is subject to seasonal effects. These seasonal effects may be related to disease onset and overall disease pressure, thoroughness of pruning in a given year, and occurrence of flag shoots. The greatest powdery mildew control was achieved with late-pruning timing. The benefits

of delayed spring pruning are twofold. There was a general reduction in disease severity, particularly on leaves, from delayed pruning. Furthermore, because fungicide applications for powdery mildew commence after foliage regrows after pruning, delaying pruning also avoids one or more fungicide applications simply due to avoiding several weeks of powdery mildew-favorable weather in early spring.

Fig. 2. Suppression of powdery mildew on **A**, leaves and **B**, cones in relation to pruning timing and year. Data are from a commercial hop yard of Tomahawk hop near Toppenish, WA during 2012 to 2014. Within a year, means with different letters are significantly different ($P = 0.05$) according to a mixed-model repeated-measures analysis. Bars without letters were not significantly different.

Fig. 3. Combined 3-year incidence of powdery mildew on **A**, **B**, and **C**, leaves and **D**, **E**, and **F**, cones in relationship to pruning timing and method. Means with different letters are significantly different ($P = 0.05$) according to a mixed-model repeated-measures analysis. Data are from Tomahawk hop in Toppenish, WA during 2012 to 2014. Bars without letters were not significantly different.

In this study, pruning method had little effect on powdery mildew development. The use of chemical desiccants significantly reduced powdery mildew disease incidence on cones compared with mechanical pruning, independent of application timing. However, the numerical differences were quite small, averaging only about 2%. The delay between application dates of the chemical desiccant, with the second chemical application applied 4 to 5 days after the initial treatment, could be a contributing factor because the plots pruned chemically were effectively pruned slightly later than the mechanically pruned plots.

Although we did not detect large differences in disease control related to pruning method, we caution that this may not always be the case. In the present study, plots that were chemically desiccated had essentially no susceptible leaf tissue present for 7 days or longer, including shoots on the sides of plants. Thoroughness of spring pruning is of great importance, independent of pruning method (Gent et al. 2012; Turechek et al. 2001). Complete removal of plant material reduces primary inoculum levels and delays disease development (Turechek et al. 2001). Mechanical pruning, as conducted in this study, did not remove all foliage and shoots on the sides of plants. This was especially apparent on the later pruning dates, when more plant material was present. This may be important when inoculum of *Podosphaera macularis* is present because, without susceptible host tissue, inoculum of *P. macularis* is removed and development of powdery mildew is delayed because primary inoculum must be introduced from another hop yard. Therefore, pruning method and timing likely interact with the thoroughness of pruning, and ensuring complete removal of host tissue is critical regardless of how or when pruning is conducted.

In addition to disease control, adverse effects on cone yield and quality factors caused by altered pruning timing are a primary consideration for growers. Over a 3-year period, neither yield nor cone quality factors were negatively affected by any pruning treatment. We also found no evidence of a cumulative effect of late spring pruning over a 3-year period on yield or cone quality metrics.

Hop plants are extremely fast growing and, if chemical pruning methods are applied late, both time and a second application of desiccant are needed to ensure that all green foliage has been thoroughly desiccated. A dual approach of mechanical pruning followed by chemical desiccation may be useful when flag shoots are present. This combined treatment would first physically remove surface crown buds from plants and subsequently desiccate remaining foliage in areas that are difficult to access with a mechanical pruning implement. Indeed, previous studies have reported that the most thorough pruning methods in commercial hop yards typically involve at least two pruning operations (Gent et al. 2012).

The general suppression of powdery mildew on leaves and, to a lesser extent, cones due to delayed pruning is likely due to multiple factors, including escape of early-season inoculum. A similar effect

has been observed with powdery mildew disease development on grapevines where the date of first infection, and a delay thereof, was strongly related to final severity of disease (Calonnec et al. 2006). Another study conducted by Valdés-Gómez et al. (2011) also showed that earlier vegetative growth led to more disease in grape clusters at harvest.

Hop plants pruned later in the season also tend to produce less foliage due to altered vigor. It is not possible to disentangle the relative contribution of pruning timing on later host susceptibility, inoculum dose, and epidemic duration from the present experiments. More detailed studies and modeling are needed to resolve the mechanisms underlying the overall less-severe disease development associated with delayed pruning.

Disease pressure on both a seasonal and geographical level appears to affect the overall effects of spring pruning practices on powdery mildew progression. During this 3-year investigation, the greatest treatment differences due to chemical desiccation and modified pruning timing were apparent early in the season in 2012, when disease was extremely high. Modified pruning timing may be most effective in seasons with high disease pressure due to the massive production of inoculum early in the season.

Seasonal disease severity obviously is influenced by numerous factors, including the onset and dose of primary inoculum. It is well known that sanitation measures that reduce primary inoculum delay epidemic development (Madden et al. 2007). Depending on the pathosystem, the timing of disease onset may interact with environment to effectively enable disease escape during periods of greatest host susceptibility (Moyer et al. 2014). To this end, early-arising flag shoots are of central concern for disease management in hop yards because flag shoots present a point source of inoculum that may initiate outbreaks of powdery mildew essentially at emergence of hop shoots (Liyange and Royle 1976). As demonstrated here, modification of pruning practices can delay powdery mildew development, which may have important implications for later-season management of the disease. Hop cones tend to be most susceptible to powdery mildew during bloom and juvenile stages of cone development, generally corresponding to late July and early August (Twomey et al. 2015). Minimizing early-season inoculum density may enhance the efficacy of disease control measures later in the season because the efficacy of fungicides for control of the disease on cones is moderated by the incidence of disease on leaves (Nelson et al. 2015).

In the case of powdery mildew, cultural methods alone generally are unable to eliminate the use of preventative fungicide applications but can help to avoid the earliest applications and reduce the severity of later disease outbreaks. Modifying common cultural practices to serve multiple goals is highly desirable because they do not present additional costs. The data presented here on early-season management modifications are only a first step in a well-rounded disease mitigation program. Integrated disease management approaches should

Fig. 4. Combined analysis of data from 2012 to 2014 on the effect of pruning timing and method on α -acids yield at harvest. Significant differences among means ($P = 0.05$) are indicated by the presence of a letter according to a mixed-model repeated-measures analysis. Bars without letters were not significantly different.

involve reduction of early-season inoculum by adjusting pruning timing as well as other tactics such as well-timed fungicide application (Nelson et al. 2015), midseason basal foliage removal (Gent et al. 2008; Mahaffee et al. 2009), and timely harvest (Gent et al. 2014b).

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