The Spatial Pattern of Hop Powdery Mildew in Pacific Northwestern USA

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Introduction

Hop powdery mildew (*Sphaerotheca macularis* [Wallr.:Fr] Lind. (synonym *S. humuli* [DC.] Burrill)) has been a long-time pest in European hop production and was partially responsible for pushing hop production out of the eastern United States and into the Pacific Northwest were it now occurs. Despite its importance, little is known about the biology of the pathogen and even less is known about the epidemiology of the disease. One of the fundamental epidemiological characteristics of a disease is its spatial pattern. The spatial arrangement of a disease results from the pathogens interaction with its host, the environment, its fitness level, and the influence of management practices. Aside from the biological insight a spatial analysis provides, the information is necessary to develop accurate sampling plans, better assess crop loss in relation to disease intensity, or design and analyze experiments more efficiently. The objective of this research is to characterize the spatial pattern of hop powdery mildew.

Materials and Methods

Data collection. Hop yards in Washington and Oregon were randomly selected from yards with a history of powdery mildew for sampling. In Washington State, yards from each of the major hop growing regions within the Yakima Valley were selected. From West to East we refer to the regions as Moxee, Reservation, Mabton, and Prosser. Each yard was partitioned into *H* strata of 20 rows each, i.e., *H*= (# of rows in a yard)/20 [rounded up]. The rows selected for sampling were chosen by randomly selecting a number, *t*, between 1-20 and sampling the t^{th} row in each of the *H* strata. Ten leaves (*n*) were arbitrarily selected from the bottom 2.5-2.75 m of the hop bine of the first 75-100 plants (*N*). For each of the *NH* sampling units (hills), disease incidence (the number of diseased leaves [*x*] of *n* leaves) was recorded. A total of 50 yards were sampled over the course of 2 years (1999 and 2000) and included the varieties Columbus, Tomahawk, Zeus, Perle, Willamette, and Galena. Yards were sampled regularly from shoot emergence through harvest.

Distributional analyses. For incidence data, the binomial and beta-binomial distributions represent the frequency distribution of diseased individuals per sampling unit for several diseases. The binomial has a single parameter representing the probability of disease (π). The beta-binomial has two parameters, *p* (the expected probability of disease) and θ (measure of the variation in disease incidence per sampling unit). The binomial and beta-binomial distributions were fit to the observed frequency distribution of the number of diseased individuals per sampling unit (=x) for: (1) individual rows (herein referred to as >row level=) ***AND*** (2) for all sampling units in all rows sampled in each yard at a given sampling date (herein referred to as >yard level=). Mmultiple verses single rows were used to derive estimates of incidence (and heterogeneity) inorder to provide information on the variability of disease among rows within a yard. This information can be used to designing sampling strategies. An estimate of disease incidence (= *p* or π) for a single row was obtained using $\sum x/nN$; and for a single yard it was obtained using $\sum x/nN$ summed across all *H* for that yard. θ was estimated using the method of maximum likelihood.

Hierarchical analysis. Due to the cluster sampling employed, disease incidence could be calculated at two spatial scales: the leaf scale and the hill scale. At the leaf scale, hills will have from 0 to 10 leaves diseased. At the hill scale, a hill is either diseased or not. A hill is diseased if any one of the 10 leaves is diseased. When disease incidence at the leaf scale is binomially distributed, incidence at the hill scale can be predicted using an equation based on the zero term of the binomial distribution: $p_{su} = 1-(1-p_{leaf})^n$; where p_{su} is disease incidence at the sampling unit scale, p_{leaf} is disease incidence at the leaf scale, and *n* is the number of leaves per hill. If disease at the leaf scale is described by the beta-binomial distribution, *n* can be replaced by a complicated function of *n* and θ. Both functions increase as a saturation-type curves. The purpose of evaluating the information at these two spatial scales was to determine if hill incidence can be used as a predictor of leaf incidence since collecting disease at the hill scale is simpler and less time consuming than collecting information at the leaf scale.

Power law analyses. The power law is used to characterize the relationship between disease heterogeneity (i.e., variability) and mean disease intensity. The power law can be expressed as a simple relationship between the logarithms of the observed sample variance of diseased leaves (v_{obs}) and the theoretical variance of a random distribution (v_{ran}). With binary data, v_{ran} is the binomial variance, $np(1-p)$, where *p* is the moment estimate of *p* from the beta-binomial distribution. The power law is written: $\ln(v_{obs}) = \ln(A) + b\ln[n(1-p)]$, where $\ln(A)$ and *b* are the intercept and slope of a straight line, respectively, and are parameters to be estimated via regression analysis and v_{obs} is the observed variance for each data set. When *A* and *b* are both equal to 1, randomness as described by the binomial distribution is indicated. When *b* =1 and *A*>1, there is overdispersion, but the degree of overdispersion for each data set (e.g., θ) does not depend on *p*. When *b* and *A* are greater than 1, the degree of overdispersion or heterogeneity changes with *p*.

Results & Discussion

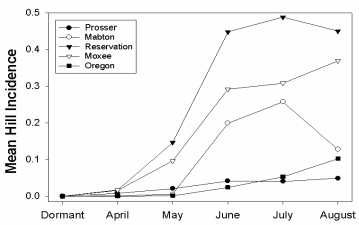

Figure 1. Disease progress curves for hop powdery mildew in the major growing regions in the Washington and Oregon in 2000.

Disease progress curves for hop powdery mildew are shown in figure 1. The disease progress curves represent the average sampling unit (hill) incidence for all rows sampled in the indicated region for the year 2000. In the most heavily infected regions, disease progressed as sigmoid curve with the most rapid or exponential phase of development occurring in the month of May. Hop powdery mildew was noticeable less severe in Oregon and the Prosser region of the Yakima Valley. In the Mabton, a noticeable drop occurred between the months of July and August. This could have been the result of a dilution effect where hot weather creating unfavorable conditions for the development of mildew, but still allowed substantial plant growth. Or this could have been the result of random sampling.

Table 1. Mean values of disease incidence and heterogeneity of hop powdery mildew in the major hop growing regions of Washington and Oregon State in 1999 and 2000.

	Year	Oregon	Prosser	Mabton	Reservation	Moxee	Combined
Disease Incidence (*p*)	1999	0.097±0.128 (7)	0.177±0.188 (14)	0.084±0.126 (18)	0.489±0.165 (5)	N/A	0.162±0.194 (44)
	2000	0.013±0.017 (157)	0.006±0.007 (53)	0.034±0.041 (50)	0.124±0.159 (77)	0.089±0.133 (33)	0.045±0.096 (370)
	Combined	0.017±0.034 (164)	0.042±0.109 (67)	0.047±0.076 (68)	0.147±0.180 (82)	0.088±0.133 (33)	0.057±0.116 (414)
Disease Aggregation (Θ)	1999	0.034±0.037 (7)	0.058±0.064 (14)	0.031±0.052 (18)	0.041±0.031 (5)	N/A	0.041±0.052 (44)
	2000	0.019±0.033 (157)	0.015±0.047 (53)	0.023±0.035 (50)	0.024±0.039 (77)	0.022±0.027 (33)	0.020±0.036 (370)
	Combined	0.020±0.034 (164)	0.024±0.053 (67)	0.025±0.040 (68)	0.025±0.039 (82)	0.022±0.027 (33)	0.023±0.039 (414)

x: mean plus/minus its standard error for individual rows sampled within yards; y: number of rows sampled in each category

Table 2. Mean values of disease incidence and heterogeneity of hop powdery mildew in the major hop growing regions of Washington and Oregon State in 2000.

	Oregon	Prosser	Mabton	Reservation	Moxee	Combined
Disease Incidence (ρ)	0.007±0.012[x] (48)[y]	0.004±0.004 (22)	0.031±0.033 (19)	0.122±0.156 (20)	0.055±0.115 (20)	0.035±0.086 (129)
Disease Aggregation (Θ)	0.033±0.055 (37)	0.009±0.016 (22)	0.038±0.033 (19)	0.056±0.064 (20)	0.023±0.028 (20)	0.031±0.046 (118)

x: mean plus/minus its standard error for individual yards sampled; y: number of yards sampled in each category

The Reservation and Moxee regions of the Yakima Valley are often more heavily infected than the Prosser and Mabton regions, and that all regions in the Yakima Valley are more heavily infected than the Willamette Valley in Oregon. These differences may be a result of more favorable environmental conditions in those regions, a higher population of the pathogen (possibly the result of a greater density of susceptible hosts), a more suitable environment for the pathogen to overwinter, or any combination of these.

The frequency distribution of the beta-binomial parameters *p* (disease incidence) and θ (index of aggregation) at the yard (Figure 2A, B) and row levels (Figure 2C,D) are skewed heavily to the right and their median values are close to zero. For disease incidence, this indicates that the majority of rows/yards had relatively low levels of disease. The low incidence is a result of the numerous assessments that were made early in the season when incidence was low in combination with several assessments being done in regions where powdery mildew was not as problematic, such as Oregon (see Fig. 1). For heterogeneity, the skewed distribution is indicative of a very low degree of aggregation. This conclusion is supported by the observation that over half of the assessments could be described by the binomial distribution (θ=0), indicating a random distribution of disease.

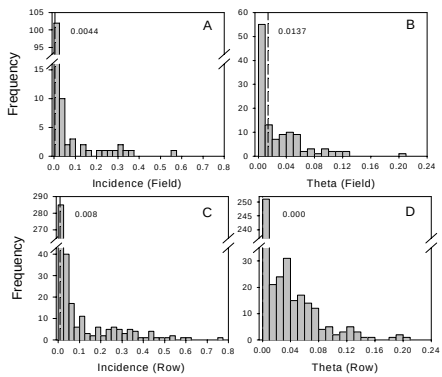

Figure 2. Frequency distribution of the beta-binomial parameters *p* (disease incidence) and θ (index of aggregation) at the yard (**A** and **B**) and row levels (**C** and **D**). Median values are shown on the Figure as a broken line.

Table 3. Estimated intercept and slope parameters from the power law analysis at the row and yard levels

	ln(A)	*b*
Row	0.285	1.07
Yard	0.418	1.09

Results of the power law analyses (Table 3) indicate hop powdery mildew is slightly aggregated at both the row and yard level. The slope parameters are very close to 1 suggesting that the low level of aggregation that does exists is nearly constant across the range of incidence encountered, rather than changing systematically with incidence. Both parameters are, however, very close to the nominal for a random distribution of disease. Estimating means, variances, sample sizes, and many other population level statistics is much simpler when dealing with randomly dispersed populations.

The results of the hierarchical analyses indicate a very close relationship between incidence at the leaf scale and incidence at the hill scale (Figure 3). At the row level **(A),** the relationship was well-predicted by the beta-binomial function. This was not quite as evident at the yard level (**B**). The variability among rows in a given yard tended to increase as average incidence increased (Figure 4). This was more prominent at the hill scale than the leaf scale. The variability becomes important when deciding on threshold values for sampling. When the variability is small, it is easier to define a threshold which would allow all estimates of disease incidence to fall either above or below the threshold value. For example, in figure 3A, a threshold of 0.12 was chosen. Note, that the threshold value only intersects 6 yards in this case, (e.g., yard 88) mainly in yards located in the Reservation. This means for those 6 yards, either threshold decision is possible depending on which row was sampled. Compare this to an equivalent threshold (i.e., based on the binomial equation above) when hills were considered diseased or not and notice that the same 6 fields fall out (Fig. 4B). The bottom line is that the sampler would arrive at the same decisions irrespective if he/she would have sampled leaf level or hill level. However, sampling at the hill level would be easier and save a considerable amount of time but, as figure 3A shows, one can still predict the level of leaf incidence rather precisely from information collected at the hill scale.

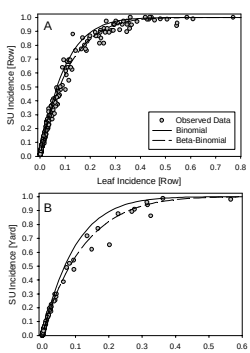

Figure 3. Relationship between hop powdery mildew incidence at the leaf scale and the hill scale for data collected at the row level (**A**) and the yard level (**B**). Grey symbols represent the observed data, the binomial prediction of SU incidence is shown as a solid line, and the beta-binomial prediction of SU incidence is shown as a broken line.

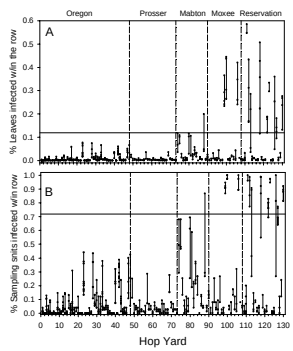

Figure 4. Variability in disease incidence of individual transects sampled within a single yard. Data were collected over two years from 50 different yards (sampling was performed at least twice in each yard). The solid line represents an arbitrary threshold (discussion in the text). Dotted lines indicate the data from different regions regions.

Acknowledgements

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