

Seasonal Patterns of Aster Leafhopper (Hemiptera: Cicadellidae) Abundance and Aster Yellows Phytoplasma Infectivity in Wisconsin Carrot Fields

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ABSTRACT In Wisconsin, vegetable crops are threatened annually by the aster yellows phytoplasma (AYp), which is obligately transmitted by the aster leafhopper. Using a multiyear, multilocation data set, seasonal patterns of leafhopper abundance and infectivity were modeled. A seasonal aster yellows index (AYI) was deduced from the model abundance and infectivity predictions to represent the expected seasonal risk of pathogen transmission by infectious aster leafhoppers. The primary goal of this study was to identify periods of time during the growing season when crop protection practices could be targeted to reduce the risk of AYp spread. Based on abundance and infectivity, the annual exposure of the carrot crop to infectious leafhoppers varied by 16- and 70-fold, respectively. Together, this corresponded to an estimated 1,000-fold difference in exposure to infectious leafhoppers. Within a season, exposure of the crop to infectious aster leafhoppers (*Macrostes quadrilineatus* Forbes), varied threefold because of abundance and ninefold because of infectivity. Periods of above average aster leafhopper abundance occurred between 11 June and 2 August and above average infectivity occurred between 27 May and 13 July. A more comprehensive description of the temporal trends of aster leafhopper abundance and infectivity provides new information defining when the aster leafhopper moves into susceptible crop fields and when they transmit the pathogen to susceptible crops.

KEY WORDS *Macrostes quadrilineatus*, aster yellows phytoplasma, aster leafhopper, migration, dispersal

Aster yellows (AY) is a widespread disease of plants caused by the aster yellows phytoplasma (AYp), a small, wall-less prokaryotic organism that is currently placed in the provisional genus ‘*Candidatus* Phytoplasma’ (Lee et al. 2000, IRPCM Phytoplasma/Spiroplasma working team – Phytoplasma taxonomy group 2004). The AYp has an extensive and diverse host range infecting over 350 plant species including many common vegetable, ornamental, and agronomically important field crops, and several noncrop plant species (Kunkle 1926; Chiykowski 1965, 1967; Chiykowski and Chapman 1965; Westdal and Richardson 1969; Peterson 1973; Lee et al. 1998, 2000, 2003; Hollingsworth et al. 2008). The most common disease phenotypes are vein clearing, chlorosis, stunting, twisting and proliferation of plant stems, and the development of adventitious roots (Kunkle 1926, Bloomquist 2002). In vegetable crops, these symptoms can lead to direct yield and quality losses and, for root vegetables spe-

cifically, processing problems can result from an inability to obtain clean raw product because of adventitious root growth and associated field soil contamination.

AYp has been reported to be circulative and propagative in the aster leafhopper (Maramorosch 1952, Sinha and Chiykowski 1967, Lee et al. 2000), and vector competence involves acquisition, pathogen replication, and circulation to result in successful transmission to a susceptible host (Matthews 1991). Plant-to-plant spread of AYp in the field can occur as a result of transmission by more than 24 leafhopper species (Mahr 1989, Christensen et al. 2005). However, the aster leafhopper, *Macrostes quadrilineatus* Forbes, is considered to be the primary vector of the AYp because of its prevalence in Midwestern susceptible crops (Drake and Chapman 1965, Hoy et al. 1992).

Similar to most plant pathogens spread by arthropods, risk for spread of AY to a susceptible crop is a function of aster leafhopper abundance and transmission capability, or infectivity (Madden et al. 2000, Jeger et al. 2004). In Wisconsin, aster yellows management has focused primarily on controlling the insect vector, the aster leafhopper, and an AY risk index, known as the aster yellows index (AYI), was developed to describe the maximum allowable numbers of

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infectious leafhoppers and define periods of time when plant protection is most needed (Chapman 1971). The AYI metric is the product of aster leafhopper infectivity (percent of infectious aster leafhoppers) and the magnitude of the aster leafhopper population (number of aster leafhoppers in 100 pendulum sweeps by using a standard 38-cm sweep net). Originally, the AYI was used to make insecticide spray recommendations based on a series of early season leafhopper collections (Chapman 1971, 1973). However, following the observations that aster leafhopper abundance and infectivity, in and around carrot fields, varied spatially and temporally (Mahr et al. 1993), efforts were made to refine AYI estimates for a specific date and field. However, even with the availability of contemporary tools, significant annual and site-specific variation in pathogen detection in the insect vector frequently occurs. In most cases, the relationship between pathogen presence in the vector and the vector's ability to successfully transmit the pathogen is not known. In turn, many producers avoid risk of pathogen spread by using inexpensive, prophylactic insecticide applications, a management practice that circumvents the utility of the AYI.

In Wisconsin, aster yellows typically has been controlled using repetitive applications of insecticidal compounds in the synthetic pyrethroid group. Although successful from the perspective of managing insect pests in a cost-effective manner, this approach presents considerable risk, because these insecticides are older, broad-spectrum compounds with documented mammalian toxicity (Wolansky and Harrill 2008). The chemicals in this group are also harmful to aquatic organisms, are lipophilic, and in aquatic environments, tend to adsorb to organic sediments (Gan et al. 2008). Monitoring surveys in the United States have detected the presence of synthetic pyrethroid residues in the sediment of both agricultural and urban dominated waterways (Werner et al. 2002, Weston et al. 2004). These findings have prompted concerns about pyrethroid exposure to nontarget areas, especially ecologically sensitive areas such as wetlands, which include the lowland muck soils where the majority of Wisconsin carrot is grown. Thus, it has been our goal to reduce the nearly exclusive reliance on synthetic pyrethroid insecticides for the management of aster yellows in carrot. We hypothesize that an improved understanding of the expected AY risk based on historical data, combined with an understanding of the "window" of time during which these events occur, will improve aster yellows management. Specifically, grower adoption of reduced-risk (RR) insecticides may be improved by targeting insecticide applications to periods during which AY risk is high, thereby reducing the number of applications of the more expensive RR insecticides necessary to control aster yellows, improving the cost-efficiency of these newer tools.

We have previously examined factors that contribute to the variability of aster leafhopper abundance and infectivity (Frost et al. 2012). However, we did not directly model the patterns of variation associated

with those factors. An outcome of our previous analysis noted significant residual trends in the seasonal patterns of aster leafhopper abundance and infectivity that could be directly modeled. Nonparametric regression and additive models are extensions of linear models that allow for nonlinear relationships between the response variable and multiple predictor variables. In these models, the goal is primarily to describe the data in a way in which complex functions serve as best predictors making the models flexible and preserving model interpretability (Hastie et al. 2009). Recently their application to examine trends in long-term data sets has become useful. For example, these methodologies have been used to examine environmental drivers affecting long-term trends in water quality (Ferguson et al. 2008), sperm whale habitat preference (Pirodda et al. 2011), shifts in insect phenology because of climatic variation (Hodgson et al. 2011), and seasonal trends of aphid dispersal into agricultural fields (Nault et al. 2009). Our primary goal in the current study is to identify periods of time in the growing season when crop protection is most needed. In this paper, generalized additive mixed models are used to: 1) describe the pattern that represents the expected seasonal aster leafhopper abundance and infectivity in the carrot crop, 2) predict the expected seasonal aster leafhopper abundance and infectivity to deduce a seasonal AYI that best represents the periods of risk for exposure to infectious leafhopper, and 3) retrospectively quantify the frequency and magnitude of aster leafhopper infestation events. For integrated pest management (IPM) practitioners, the identification of temporal trends of abundance and infectivity can improve our knowledge of where leafhoppers acquire the pathogen, when they move into susceptible fields, and when they spread the pathogen to susceptible crops.

Materials and Methods

Data Description. A detailed description of the data set, sample sites, and sampling methodologies, previously has been reported (Frost et al. 2012). Briefly, field sampling was conducted using sweep nets in commercial carrot fields to monitor the relative abundance of aster leafhopper in the common carrot production areas of Wisconsin from 2001 to 2011. In total, 237 fields were sampled over the 11-yr span of this survey. Abundance was estimated for an average of 31 fields per year with several fields resampled in multiple years because of crop rotation practices. Abundance was determined by sweep net sampling along two to 18 transects that were walked into the carrot crop toward the middle of the field. Twenty-five to 100 (pendulum) sweeps per transect were conducted using a standard sweep net (38 cm in diameter) and aster leafhoppers were counted and enumerated as aster leafhoppers per 25 sweeps. Decimal values were rounded to the nearest integer. Aster leafhopper infectivity was monitored using an infectivity bioassay in the commercial carrot production areas and records of infectivity were available from 1994 to 2007.

The prevalence of infectious aster leafhoppers was estimated for 378 insect populations in total from 1994 through 2008. Approximately 25 populations were collected and assayed per year with multiple geographic locations and several dates represented throughout each growing season. At each sample location and date, aster leafhoppers were collected in sweep nets and placed onto oat (*Avena sativa* L.) seedlings for transport back to the laboratory. When possible, 204 leafhoppers were placed, in pairs, onto 102 Chinese aster [*Callistephus chinensis* (L.) Nees], plants and allowed to feed for the duration of the experiment. Disease symptoms were assessed after a 2-wk incubation period and percent infectivity was calculated as:

$$\text{infectivity} = \frac{\text{number of diseased plants}}{\text{number of leafhoppers}}$$

The total number of leafhoppers was used as the denominator because infectivity levels are low, usually between 0 and 3%, and a diseased plant was more likely because of a single infective leafhopper rather than the presence of two infective leafhoppers on the same plant.

Statistical Analysis. We used generalized additive mixed models (GAMM) to describe the annual and seasonal trends of aster leafhopper abundance and infectivity. A GAMM is an extension of a generalized additive model that relaxes the underlying assumption that the data are independent by allowing observations to be correlated (Zuur et al. 2009). One advantage of using a GAMM to describe seasonal leafhopper abundance is that we can estimate the underlying trend from the data without assuming the trend has any specific functional form (Wood 2006). In these models, the goal is primarily to describe the data in a way in which complex functions serve as best predictors—without needing to understand the complex mathematical representation of the model; trends are represented by mathematical functions, but those mathematical representations are not particularly intuitive when written down (Wood 2006, Agresti 2007). Therefore, to examine the form of the function, or trend in the data, we produced model predictions given a new set of data containing all model covariates. From our models, the seasonal predictions of leafhopper abundance and infectivity were used to deduce the expected AYI for the average growing season to define the interval in which elevated risk for crop exposure to infectious leafhoppers was greatest. In addition, the strategy we used to confront the presence of annual variability associated with leafhopper abundance and infectivity was to include seasonal estimates for the years with the highest and lowest observed annual abundance and infectivity. This approach is in contrast to our previous study where we chose to characterize the distributions for each level of grouping in our data.

Aster Leafhopper Abundance. A GAMM was used to describe the seasonal pattern of aster leafhopper abundance (Y_{ij}) as a function of calendar day (x_i) with each field–year combination and observation repre-

sented as a random effect in the model. This GAMM could be represented as:

$$Y_{ij} \approx \text{Poisson}(g[\mu_{ij(abc)}]) \quad (\text{model 1})$$

$$g(\mu_{ij[ab]}) = \log_e(\mu_{ij[abc]}) = \text{offset}(\text{INt}) + \beta_i$$

$$+ f(d_j) + \varepsilon_{(a)} + \varepsilon_{(b)} + \varepsilon_{(c)}$$

$$\varepsilon_{(a)} \approx N(0, \sigma_{\text{farm}}^2),$$

$$\varepsilon_{(b)} \approx N(0, \sigma_{\text{field}}^2),$$

$$\varepsilon_{(c)} \approx N(0, \sigma_c^2),$$

where β_i corresponded to the average abundance estimate for each year (i) and $f(d_j)$ was a smoothing function (penalized cubic regression spline) of the calendar day covariate (d_j). The model contains an offset corresponding to the log-transformed number of transects (INt) used to estimate leafhopper abundance, and $\varepsilon_{(a)}$, $\varepsilon_{(b)}$, and $\varepsilon_{(c)}$ are the random effects for each farm, field, and observation, respectively. The model was specified using the *gamm4* function in the *gamm4* package (Wood 2006) of R (version 2.15.0; R Development Core Team 2012) and generalized cross validation was used to estimate the value of the smoothing parameter for the unknown scale parameter (Wood 2004, 2006; Zuur et al. 2009).

The component smooth function $f(d_j)$, centered on the scale of the linear predictor, was plotted versus calendar date (d_j) together with the partial residual of the model to represent the seasonal trend of aster leafhopper abundance. Thus, the period of elevated leafhopper abundance was estimated by visual examination of the plotted data (i.e., $f_1[d_j]$ versus d_j). Predictions (P_A) of leafhopper abundance, and associated standard errors (SE) of the predictions, were obtained from the fitted GAMM for each calendar day in low, typical, and high abundance years. Confidence intervals for each day were estimated as $P_A \pm 2*SE$. Confidence intervals were back-transformed to the response scale and multiplied by four, to obtain leafhoppers per 100 sweeps, before being used in the calculation of the seasonal AYI.

ALH Infectivity. A GAMM also was used to examine seasonal trends of leafhopper infectivity. This model was used to fit aster leafhopper infectivity (Y_i ; sqrt-transformed) to calendar day (x_i) with year represented as a random effect in the model. This GAMM could be represented as follows:

$$Y_i \approx N(g[\mu_i], \sigma^2) \quad (\text{model 2})$$

$$g(\mu_{ij}) = \mu_{ij} = \beta_i + f(d_j) + \varepsilon_i + \varepsilon_{ij}$$

$$\varepsilon_i \approx N(0, \sigma_i^2)$$

$$\varepsilon_{ij} \approx N(0, \sigma_r^2),$$

where β_i corresponded to the mean infectivity estimate for each year (i) and $f(d_j)$ was a smoothing function (penalized cubic regression spline) of calendar day (d_j). In this model, ε_a corresponded to the random effects term for farm and ε_{ij} represented the residual error. The method used to fit this function was the same as the one described previously.

The component smooth function, $f(d_i)$, of the model fit was plotted versus calendar date (d_i) representing the seasonal trend of aster leafhopper infectivity. Again, the period of elevated infectivity was estimated by visual examination of the plotted data (i.e., $f_1[d_i]$ versus d_i). Predictions (P_i) of leafhopper infectivity, and associated standard errors (SE) of the predictions, were obtained from the fitted GAMM for each day in low, typical, and high infectivity years. Similar to abundance, infectivity confidence intervals were estimated for infectivity as $P_i \pm 2*SE$. Predictions and confidence intervals were squared and expressed as percentages before being used in the calculation of the seasonal AYI.

Aster Yellows Index. The number of aster leafhoppers and the associated rate of infectious individuals in the leafhopper population affect the exposure of a crop to infection by a pathogen and subsequent disease development. Therefore, the seasonal AY risk was deduced using the daily model predictions of aster leafhopper abundance (P_{Ai} ; model 1 above) and infectivity (P_{fi} ; model 2) into an AYI metric as follows:

$$AYI_i = P_{Ai} * P_{fi} \text{ (model 3)}$$

where i indexes calendar day. The seasonal AYI was calculated for low, typical, and high abundance and infectivity years to represent the range of the observed data. Because the calendar day range of the infectivity data set was shorter than the abundance data set, predictions of infectivity after calendar day 228 were estimated as the prediction on day 228. The AYI is essentially an assessment of the potential annual and seasonal "risk" of crop exposure to aster leafhoppers capable of transmitting AYp. In the results section, we define the relative exposure "risk" as the exposure of the carrot crop to infectious leafhoppers relative to the exposure of some reference group, usually the low-exposure AYI. For example, holding infectivity constant, a field with an abundance of two leafhoppers (per 100 sweeps) has a twofold greater exposure to infectious leafhoppers than a field with an abundance of one leafhopper (per 100 sweeps). Similarly, a field in which the rate of infectious leafhoppers is 3% has a threefold greater exposure to infectious leafhoppers than a field in which only 1% of the leafhoppers are capable of transmitting AYp.

Correlation of Abundance and Infectivity. The correlation between annual estimates of leafhopper abundance and infectivity was calculated for the years in which the data overlapped (2001–2008). To examine if the average seasonal abundance and infectivity were correlated, a preliminary examination of the cross-correlation between leafhopper abundance and infectivity model predictions was conducted. Because infectivity was only measured weekly, model predictions were extracted for the weeks in which infectivity estimates were available. The cross-correlations were calculated and plotted versus the weekly time lags. For example, a time lag of -2 represents the correlation of the weekly abundance predictions with weekly infectivity predictions from 2 wk earlier in the growing season. Thus, the peaks in the cross-correlations rep-

resent the phase shift between leafhopper abundance and infectivity within the growing season.

Quantifying the Frequency of Leafhopper Influxes. We defined an influx event as an occurrence when the observed number of aster leafhoppers at a field was greater than the allowable number of leafhoppers calculated using predetermined AYI values of 25, 50, 75, and 100, corresponding to high, medium, medium-low, and low susceptibility, respectively. These AYI values represented the nominal thresholds that have been determined based on professional experience and experiments examining host plant resistance to aster yellows (Pedigo 1989, Foster and Flood 2005). For this calculation, infectivity was allowed to vary across the growing season as predicted by model 2 for the typical growing season. Allowable leafhoppers were calculated as follows:

$$\text{allowable leafhoppers}_i = AYI/P_{fi}$$

where i indexes calendar day. Indicator variables were used to code the occurrence of an event or nonevent (allowable leafhoppers _{i} < observed leafhoppers _{i} = 1; allowable leafhoppers _{i} > observed leafhoppers _{i} = 0). The total number and proportion of events in each magnitude category was calculated for each year, week, farm, and field. A GAMM (family = binomial) was used to examine the seasonal probability of detecting leafhopper abundances above an AYI threshold value given an average seasonal infectivity. These models could be represented as follows:

$$Y_{i(abc)} \approx \text{Binomial}(\mu_{i[abc]}, n_{i[abc]}) \text{ (model 4)}$$

$$g(\mu_{i[abc]}) = \text{logit}(\mu_{i[abc]}) = f(d_i) + \varepsilon_{i(a)} + \varepsilon_{i(b)} + \varepsilon_{i(c)}$$

$$\varepsilon_{i(a)} \approx N(0, \sigma_a^2),$$

$$\varepsilon_{i(b)} \approx N(0, \sigma_b^2),$$

$$\varepsilon_{i(c)} \approx N(0, \sigma_c^2),$$

where $f(d_i)$ was a smoothing function (penalized cubic regression spline) of calendar day (d_i). In this model, $\varepsilon_{i(a)}$, $\varepsilon_{i(b)}$, and $\varepsilon_{i(c)}$ corresponded to the random effects term year, farm, and field, respectively. As described above, this model was specified using the *gamm4* function in the *gamm4* package (Wood 2006). The component smooth function, $f_1(d_i)$, on the scale of the response, was plotted versus calendar date (d_i) to represent the expected seasonal probability of observing aster leafhopper abundance that would prompt a control practice.

Results

Abundance Trends. Annual. Here we chose to present year modeled as a fixed effect because we were primarily interested in characterizing the within season trends, and the annual trends also can be inferred from the graphical presentation of the annual means (Fig. 1). Overall, the average annual aster leafhopper abundance decreased from 2001 to 2011, but also varied greatly among years with average abundance ranging from 0.08 to 1.27 insects per 25 pendulum sweeps

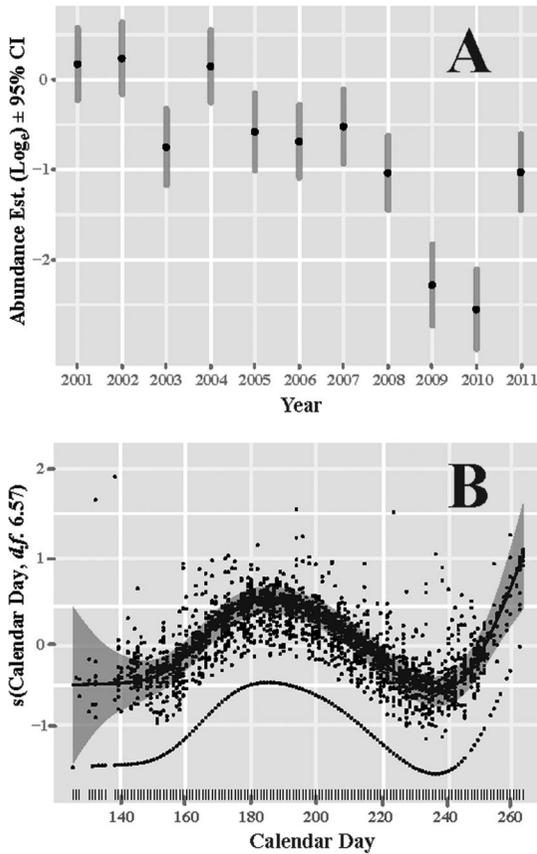


Fig. 1. A) Model coefficients ($\pm 2 \times$ SE) representing the average annual leafhopper abundance (log-scale) for 2001 through 2011. B) Component smooth function representing the trend of aster leafhopper abundance as a smooth function of calendar day plotted with partial residuals from model 1. Partial residuals for a well-fitting model should be scattered evenly around the curve to which they relate.

(Table 1; Fig. 1A). This variation implies that, for the year with the highest observed aster leafhopper abundance, the exposure of the crop to infectious individuals would be ≈ 16 -fold greater than the year with the lowest leafhopper abundance (i.e., holding infectivity constant).

Seasonal. Within year, a plot of the component smooth function for abundance versus calendar date indicated that periods of above average aster leafhopper abundance occurred between 11 June and 2 August (Fig. 1B). Holding infectivity constant, the component smooth function for aster leafhopper abundance ranged from -0.6 to 1.0 (log_e-scale), which represents a fivefold change in the exposure of the crop to infectious leafhoppers over the entire growing season and a threefold change in the exposure of the crop to infectious leafhoppers for the period in which a pest management practice would be implemented, 1 June through 31 August. Residual plots indicated that some seasonal (within year) trends remained after fitting model 1. These trends could be removed by fitting separate smoothing functions for

Table 1. Model coefficients (model 1) estimated by fitting fixed effects for year and a smooth function of calendar day (day of year) to aster leafhopper abundance

Parameters	Abundance estimate \pm SE	z-value	P value
Fixed			
β_{2001}	0.17 (0.20)	0.85	0.39
β_{2002}	0.24 (0.20)	1.17	0.24
β_{2003}	-0.75 (0.21)	3.49	<0.001
β_{2004}	0.14 (0.20)	0.72	0.47
β_{2005}	-0.58 (0.22)	2.66	<0.008
β_{2006}	-0.69 (0.20)	3.35	<0.001
β_{2007}	-0.52 (0.21)	2.48	0.013
β_{2008}	-1.04 (0.21)	4.97	<0.001
β_{2009}	-2.28 (0.22)	9.91	<0.001
β_{2010}	-2.55 (0.21)	11.36	<0.001
β_{2011}	-1.03 (0.21)	2.32	0.02
Smooth	df	Chi-square	P value
s(calendar day)	6.57	109	<0.001
Random			
σ_a	0.38		
σ_b	0.19		
$\sigma_{a,b}$	0.99		
σ_c	0.93		

Year effects represent the average annual leafhopper abundance (per 25 sweeps) on the scale of the linear predictor (i.e. log_e). P values are approximate. R-sq. (adj.) = 0.15.

each year (not shown); however, the overall pattern observed by year was described by the simpler model. In addition, we presented the simpler model here because it was more consistent with the objectives of our study to determine if, on average, there was a critical time interval when crop protection is most needed.

Infectivity Trends. Annual. Similar to abundance, aster leafhopper infectivity varied among years and the average annual infectivity ranged between 0.09 and 6.25% (Table 2). Thus, the exposure of the crop to

Table 2. Model coefficients (model 2) estimated by fitting fixed effects for year and a smooth function of calendar day (or day of year) to square root-transformed aster leafhopper infectivity estimates

Parameters	Infectivity estimate \pm SE	t-value	P value
Fixed			
β_{1994}	0.12 (0.01)	11.7	<0.001
β_{1995}	0.14 (0.01)	14.4	<0.001
β_{1996}	0.19 (0.01)	17.8	<0.001
β_{1997}	0.18 (0.02)	11.1	<0.001
β_{1998}	0.18 (0.01)	13.2	<0.001
β_{1999}	0.10 (0.01)	8.9	<0.001
β_{2000}	0.22 (0.01)	19.5	<0.001
β_{2001}	0.13 (0.01)	10.1	<0.001
β_{2002}	0.13 (0.01)	10.1	<0.001
β_{2003}	0.08 (0.02)	5.5	<0.001
β_{2004}	0.20 (0.01)	13.7	<0.001
β_{2005}	0.03 (0.01)	2.8	0.005
β_{2006}	0.09 (0.02)	4.2	<0.001
β_{2007}	0.10 (0.02)	4.8	<0.001
β_{2008}	0.25 (0.03)	8.4	<0.001
Smooth	df	F	P value
s(calendar day)	5.41	6.6	<0.001

P values are approximate. R-sq. (adj.) = 0.36.

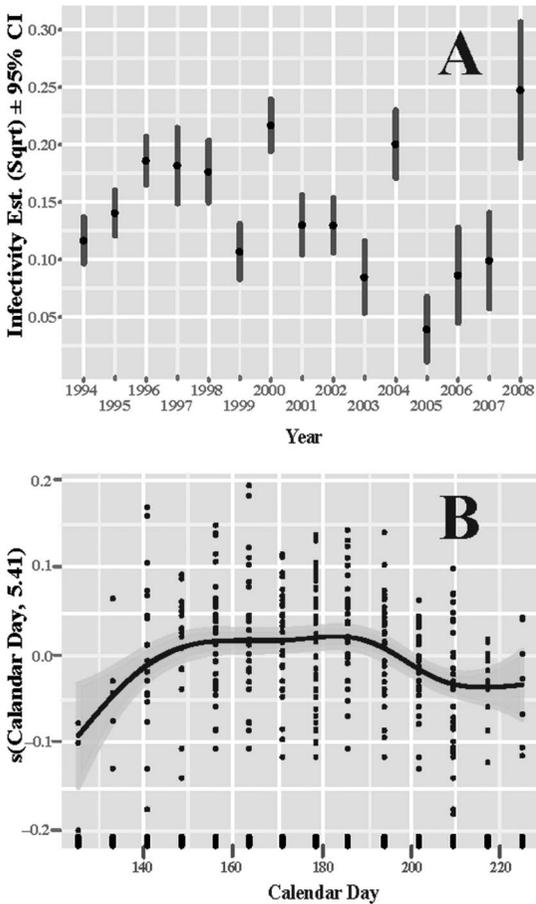


Fig. 2. A) Model coefficients ($\pm 2 \times$ SE) representing the average annual leafhopper infectivity (square root-transformed) for 1994 through 2008. B) Component smooth function representing the trend of aster leafhopper infectivity as a smooth function of calendar day plotted with partial residuals.

infectious leafhoppers in the year with the highest rate of infectivity was 75-fold higher than the year with the lowest rate of infectivity (i.e., if leafhopper abundance was held constant). Visually, there was no overt trend in the average annual leafhopper infectivity from 1994 to 2008 (Fig. 2A).

Seasonal. Within year, plots of the component smooth function of infectivity versus calendar date indicated that periods of above average infectivity occurred between 27 May and 13 July (Fig. 2B). Similar to leafhopper abundance, residual plots indicated that some seasonal (within year) trends remained after fitting model 2. These trends were removed by fitting separate smoothing functions for each year (not shown). Our rationale for presenting the simpler model remains as stated previously.

Seasonal Aster Yellows Risk. From May to August, the typical (or expected) seasonal aster leafhopper abundance ranged from 1 to 3 leafhoppers per 100 sweeps (Fig. 3A). However, for the year with the highest observed leafhopper population sizes, the ex-

pected leafhopper abundance varied between 3 and 9 leafhoppers per 100 sweeps. Similarly, the typical infectivity between May and mid-August ranged from 0.3 to 2.6%, representing a ninefold increase in exposure of carrot to infectious individuals because of seasonality (Fig. 3B). The deduced AYI for the state of Wisconsin incorporates the seasonal variability of leafhopper abundance and infectivity estimates (Fig. 3C). In a typical year, the seasonal AYI ranged from approximately one to eight. In years when both leafhopper abundance and infectivity are high, the expected AYI peaks at 60, although an AYI of 130 is not unexpected given the error associated with the seasonal trend. Taken together, estimates of a critical "risk window" or timing interval in which aster leafhopper management could be focused, were similar to previous estimates (Table 3; Frost et al. 2012).

Correlation of Abundance and Infectivity. There was no correlation between annual estimates of leafhopper abundance and infectivity for the time interval 2001 through 2008 ($R = 0.05$, $P = 0.90$). Within a season, the correlation between the aster leafhopper abundance and infectivity was examined using a cross-correlogram (Fig. 4). On average, over the 11-yr term of this data set, within-season leafhopper abundance and infectivity estimates were negatively correlated at time lags that ranged between -3 and -5 wk. In contrast, leafhopper abundance and infectivity were positively correlated at time lags of 0–3 wk.

Frequency of Occurrence of Aster Leafhopper Influxes. Over the 11 yr of this data set, there were 583 occasions when the observed aster leafhopper abundance (an "influx" event) was greater than the allowable abundance (established AYI thresholds) given an average expected seasonal infectivity (Table 4). This corresponds to ≈ 1.8 events per field across all years. However, the highest number of influx events (146) occurred in 2002, corresponding to an average of 4.4 events per field. In contrast, only one influx event occurred in 2009 for all 25 fields sampled corresponding to an estimated 0.04 events per field. In general, the number of influx events has decreased since 2001, which is consistent with the trend of the annual leafhopper abundance over the same time, and the magnitude of the aster leafhopper events also has decreased. Among farms, influx events, determined as a proportion of total observations, were not evenly distributed and ranged from 3.5 to 29.5% (Table 5).

Moreover, predicted influx events were not evenly distributed throughout the growing season (Fig. 5). The seasonal dynamics of the probability of observing an influx event was similar to the pattern observed for the expected seasonal abundance with the peak probability (14.8%) of observing any event occurring on 2 July (184). However, the timing of the peak probability of observing an influx event was earlier for larger influx events. For example, the peak probability of observing an event with an associated AYI of 25, 50, 75, and 100, occurred at 11 July (193), 5 July (187), 1 July (183), and 26 June (178), respectively.

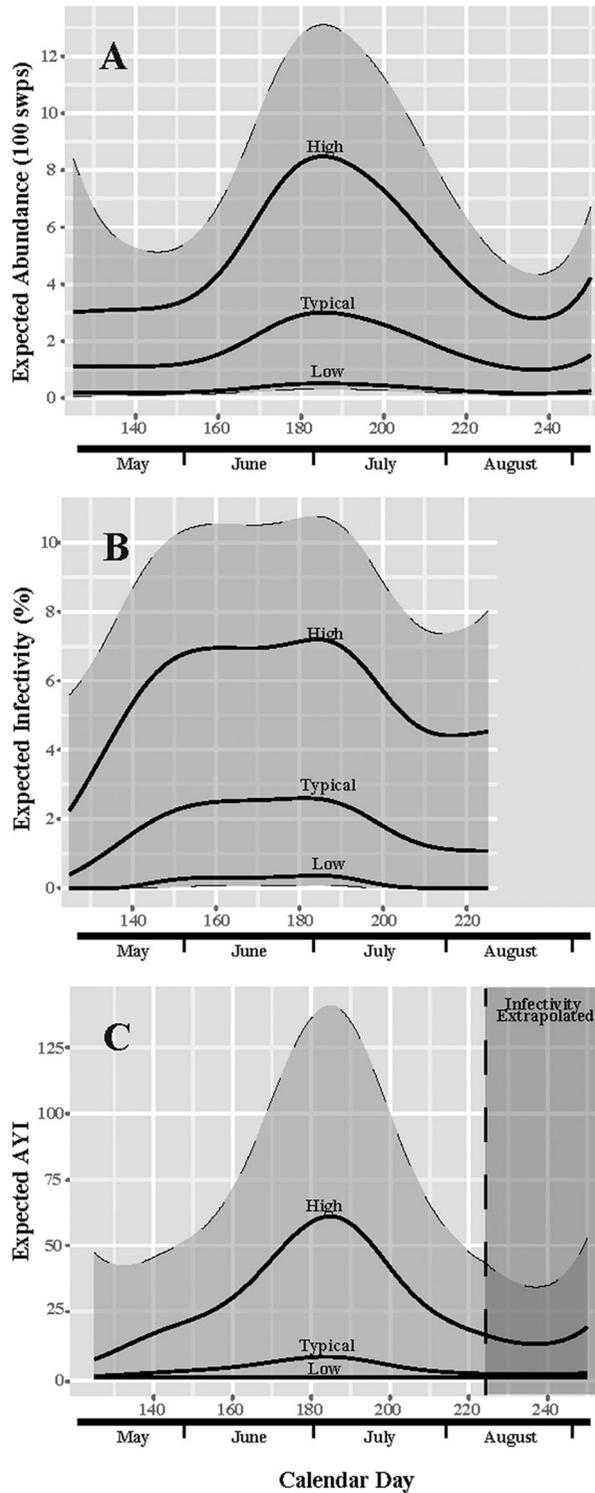


Fig. 3. A) Model 1 prediction representing the average seasonal leafhopper abundance. Predictions are on the data scale and have been multiplied by four to obtain an estimate of abundance per 100 pendulum sweeps. y (square root-transformed) for 1994 through 2008. B) Component smooth function representing the trend of aster leafhopper infectivity as a smooth function of calendar day plotted with partial residuals. C) Expected aster yellows index (AYI) values in example seasons with high, typical, and low estimated AYI values computed from abundance and infectivity estimates.

Table 3. Windows of risk for aster yellows phytoplasma spread

	Calendar day		Window length	Model source
	Start	End		
Aster leafhopper abundance	163	214	51	Frost et al. (2012)
	11 June	1 Aug.		
	163	214		
Aster leafhopper infectivity	11 June	1 Aug.	57	Frost et al. (2012)
	140	197		
	19 May	15 July		
	145	196		
AYI	24 May	14 July	51	Current paper (model 2)
	155	210		
	3 June	28 July	55	Current paper (model 2)

Discussion

For aster yellows management in Wisconsin, the aster yellows index combines insect vector abundance and transmission capability to describe the maximum allowable numbers of infectious leafhoppers that can be tolerated on a susceptible crop, providing an indication of when crop protection is most needed (Chapman 1971, 1973). In this paper, we used a multiyear data set, and multilocation modeling approach, to generate reliable estimates for the expected seasonal patterns of aster leafhopper abundance and transmission capability, or infectivity. The predicted seasonal leafhopper abundance and infectivity then were used to deduce a seasonal aster yellows index to represent the expected seasonal exposure to infectious aster leafhoppers that may spread AYp to a susceptible crop. In addition, we used the expected seasonal infectivity to retrospectively determine the frequency at which the observed insect abundance would have exceeded the established AYI thresholds, resulting in an insecticide application.

Annual Trends of Abundance and Infectivity. The exposure of a carrot crop to infectious aster leafhoppers was ≈ 16 -fold greater in the year with the highest observed aster leafhopper abundance than the year with the lowest leafhopper abundance. Similarly, the exposure of the crop to infectious leafhoppers was 70-fold higher in the year with the highest rate of infectivity when compared with the year with the lowest rate of infectivity. Taken together, these observations suggest that years in which high aster leafhopper abundance occurs co-incidentally with high infectivity can result in 1000-fold greater exposure of the carrot crop to infectious leafhoppers when compared with years in which low leafhopper abundance is co-incident with low infectivity. These observations are consistent with the large annual variability of aster yellows pressure reported previously in Wisconsin (Chapman 1971, 1973; Mahr et al. 1993) and consistent with our previous findings of large annual variability of leafhopper abundance and infectivity (Frost et al. 2012).

We found a low correlation among annual estimates of aster leafhopper abundance and infectivity, which would support the hypothesis that aster leafhopper abundance and infectivity are independent quantities varying among years. It has been determined that

fitness is increased in aster leafhopper individuals infected by AYp (Beanland et al. 2000, Sugio et al. 2011), but it is not known how the increase in fitness translates to the in-field population dynamics of infectious insects. Our correlations were calculated using the 8 yr of data for which we had estimates of both abundance and infectivity. However, it is likely that a fitness effect may appear in the field as a lagged correlation (i.e., high abundance lags high infectivity by a year or two) and this would require many more paired annual estimates of leafhopper abundance and infectivity than are currently available.

Nevertheless, a year when the aster leafhopper is abundant and a high proportion of the population is capable of transmitting AYp may occur with a relatively low frequency, and many years may pass before the two conditions coincide (Magnuson 1990). Assuming independent events and using previous estimates of among year variability, i.e., $\log_e(\text{abundance}) \approx N(-0.82, 0.860^2)$ and $\text{sqrt}(\text{infectivity}) \approx N(0.14, 0.047^2)$; (Frost et al. 2012), we simulated values for the average annual leafhopper abundance and infectivity. These abundance and infectivity values then were back-transformed and used to calculate AYI values to represent 1,000 yr. We found that an average annual AYI that was 2-, 3-, 5-, and 10-fold greater than the median annual AYI would occur, on average, every 4, 6, 13, and 53 yr, respectively. These time estimates may represent a null model from which the assumption of independence among years may be tested. Finally, the high among year variability of abundance and infectivity is also consistent with the hypothesis that the spring migration of the aster leafhopper contributes to the annual risk of AY epidemics in Wisconsin. However, the large annual variability in the rate of infectious leafhoppers further suggests that, in addition to weather events affecting insect trajectories and deposition (Hurd 1920, Huff 1963, Westbrook and Isard 1999, Zhu et al. 2006), the prevalence and heterogeneity of AYp-infected feeding hosts of the leafhopper in the landscape along the migratory route, or acquisition trajectory, may also be important factor contributing to annual infectivity (Carter 1961, Lee et al. 2003).

Seasonality of Abundance and Infectivity. Aster leafhopper abundance varied by approximately threefold during the period of the growing season in which

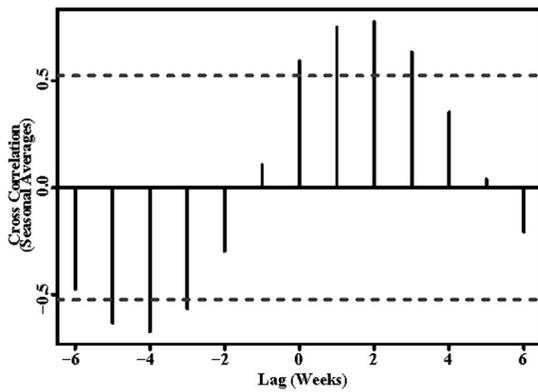


Fig. 4. Cross-correlation of the weekly abundance and rate of infectious leafhoppers for the average season.

pest management normally would be implemented. In addition, the exposure of the carrot crop to infectious leafhoppers within a year varied by as much as nine-fold. Taken together, carrot growers can expect the relative exposure to infectious aster leafhoppers to vary by as much as 30-fold throughout the growing season. However, the periods during which aster leafhopper abundance and infectivity tend to be above average often overlap within the growing season. Thus, without information about insect abundance and infectivity for a specific field, the coincidence of these expected periods of high population sizes and increased infectivity represent a timing interval in which management of the insect could be focused to limit pathogen spread.

Within a season, however, it is unlikely that aster leafhopper abundance and infectivity are independent. In theory, the mixing of aster leafhopper populations with differing proportions of infectious aster leafhoppers can result in variable proportions of infectious leafhoppers in the population. Recently, Bressan et al. (2011) described a pathosystem in which the abundance of the planthopper, *Pentastiridius leporinus* (Linnaeus), was directly related to the proportion of individuals carrying the pathogen, ‘*Candidatus Ar-*

Table 4. Number of influx events, in each year, when the observed ALH abundance was greater than the allowable abundance as calculated using an AYI of 25, 50, 75 and 100, provided an average seasonal infectivity estimate

Year	AYI 25	AYI 50	AYI 75	AYI 100	No. events	No. fields	No. obs.
2001	78	28	15	23	144	34	438
2002	69	31	16	30	146	33	478
2003	25	6	2	2	35	21	309
2004	52	13	7	14	86	34	548
2005	33	1	2	1	37	26	386
2006	28	15	8	4	55	35	477
2007	28	6	2	2	38	31	415
2008	15	9	2	5	31	34	420
2009	1	0	0	0	1	25	315
2010	3	0	0	0	3	28	403
2011	12	3	1	1	17	35	442
Total	344	112	55	82	593	336	4,631

Table 5. Number of influx events, on each farm, when the observed ALH abundance was greater than estimated allowable abundance calculated using an AYI of 25, 50, 75 and 100, given the average seasonal infectivity

Location	AYI 25	AYI 50	AYI 75	AYI 100	No. events	No. obs.
Farm 1	142	44	14	11	211	2,060
Farm 2	18	6	8	11	43	146
Farm 3	120	47	23	53	243	1,029
Farm 4	2	1	0	0	3	17
Farm 5	32	11	10	6	59	409
Farm 6	30	3	0	1	34	970
Totals	334	112	55	82	583	4,631

senophonus phytopathogenicus,’ in the population. A key difference between the system that Bressan et al. (2011) described and our system is that transovarial, or vertical, transmission is not known to occur in our system. Bressan et al. (2011) also measured the proportion of insects carrying the pathogen, which may be different than the proportion of infectious planthoppers.

In Wisconsin, a dilution of aster leafhopper infectivity may occur as aster leafhoppers that overwinter in Wisconsin as eggs (local population) begin to emerge from their habitats in early June, although we have no direct evidence for this phenomenon (Drake and Chapman 1965). A preliminary examination of the cross-correlation of the average within season dynamics of aster leafhopper abundance and infectivity showed that infectivity was negatively correlated with abundance with a -3 to -5 wk lag. This examination is counterintuitive given that leafhopper fitness is increased by AYp infection (Beanland et al. 2000, Sugio et al. 2011). However, the negative correlation could be because of grower management resulting from plant protection practices implemented when infec-

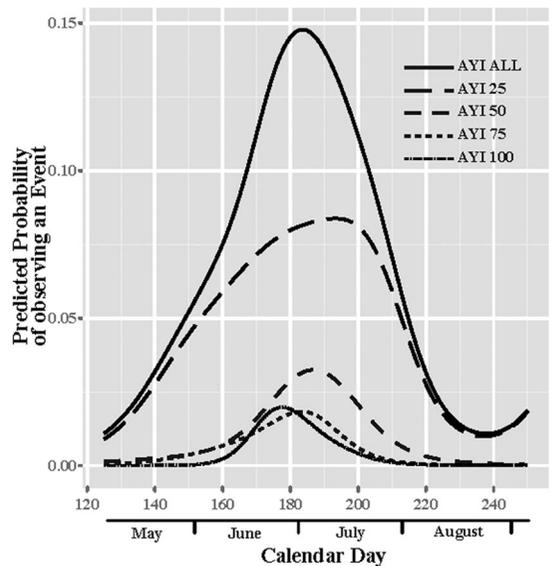


Fig. 5. The seasonal probability of detecting leafhopper abundances above an AYI of 25, 50, 75, or 100 given an average seasonal infectivity.

tivity is known to be high. Leafhopper abundance was positively correlated with infectivity at a 0–3-wk lag, suggesting that higher vector abundance results in AYp spread and higher rates of infectious leafhoppers in subsequent generations, an observation consistent with the findings of Sisterson (2009). In general, more research is needed to examine the within season relationship between leafhopper abundance and infectivity in the field to determine the reasons for the correlations at time lags of 3–4 wk, which is approximately the generation time of the aster leafhopper (Mahr 1989). Thus, the emergence of local populations, or offspring from early migratory populations, variability in birth and death rates between inoculative and noninoculative individuals, and insect management practices could all contribute to the observed phase shifts between abundance and infectivity within the growing season.

Frequencies and Magnitudes of Aster Leafhopper Influxes. The arrival of large numbers of insects into a field (or an influx) has the potential to affect epidemic progression, and the spring migration of the aster leafhopper has long been considered the principle source of early season infectious aster leafhoppers (Chiykowski and Chapman 1965, Hoy et al. 1992). We have defined a leafhopper influx as an aster leafhopper abundance that exceeds a predetermined AYI threshold, given the expected seasonal aster leafhopper infectivity. The selected AYI thresholds are used by growers to make spray decisions and are nominal thresholds determined by practitioner experience and known cultivar resistance to aster yellows (Pedigo 1989, Foster and Flood 2005). We found that the occurrence of insect influxes that would elicit an insecticide application coincided with the period of time when higher numbers of leafhoppers are expected. Our approach did not distinguish between an increase of insect numbers occurring because of population growth, local insect movements, or long-distance insect movements. However, the probability of influx events occurring in May is lower than the probability of influxes occurring in mid to late-June. A similar phenology has been observed for *Circulifer tenellus* (Baker) (beet leafhopper), *Psammotettix alienus* (Dahib) (European grass-feeding leafhopper), and *Graephophala atropunctata* (Signoret) (blue-green sharpshooter), all of which achieve peak abundance in June followed by population declines in late July and August (Lindblad and Arenó 2002, Munyaneza et al. 2010, Gruber and Daugherty 2012). It may be that these leafhoppers all overwinter, or diapause, in the same life stage (i.e., eggs) and have to develop through a similar number of instar stadia (i.e., four to five instars), leading to a reasonably synchronous emergence as adults among species. Alternatively, the occurrence of the observed leafhopper influxes beginning in early June may be because of the emergence and dispersal of the local leafhopper population from their overwintering host (i.e., winter wheat, *Triticum aestivum* L.) to more succulent irrigated vegetable crops present in the landscape at that time (Carter 1961).

The number of occurrences when a spray would be recommended has decreased since 2001, which is consistent with the overall decrease in the annual aster leafhopper abundance occurring over this time period. In addition, the number of occurrences when a spray would be recommended varied among farm (or farm locations). This variation could be because of the differential influence of the landscape surrounding each farm and its effect upon the reproductive capability of the aster leafhopper in these local environments. For example, the aster leafhopper uses over 300 different plant species for food, oviposition, and shelter (Lee and Robinson 1958, Wallis 1962, Peterson 1973), and the distribution and abundance of these species surrounding each farm likely differs. It could also be due, in part, to differences in grower management of their crop where some growers tolerate higher insect abundances before applying an insecticide; some growers tolerate a modest, but ephemeral leafhopper population prior an insecticide application, and finally other growers may prefer to apply more regular, prophylactic insecticide treatments that functionally maintain low leafhopper populations.

Management Implications. Control of pathogens transmitted by insects in a persistent manner tends to be less difficult than pathogens transmitted nonpersistently (Chapman 1973, Madden et al. 2000). The decision to intercede and implement a pest control action requires an understanding of the level of insect infestation a crop can tolerate without incurring economic loss (Pedigo 1989). In Wisconsin, growers currently achieve adequate control of aster yellows in their crops using repetitive applications of insecticidal compounds in the synthetic pyrethroid group. In a given year, it is common for as many as five to seven applications of an insecticide to be applied on a 7–10-d calendar schedule on the same crop. In part, the rationale behind these repetitive spray applications results from the fact that a single insecticide application is inexpensive when compared with newer, reduced-risk, and less broad spectrum insecticides that target fewer hemipterous pests.

In this study, we identified a timing interval in which management of the aster leafhopper could be focused. This interval, or “risk window” results from the coincidence of above average leafhopper abundance and higher observed infectivity. In addition, because this timing interval occurs early in the season, there exists the opportunity to deploy newer, reduced-risk, systemic insecticides with flexible application methods (i.e., seed treatments, in-furrow, or layby incorporation) as potential pest management alternatives for long-term control of the aster leafhopper. When compared with current management practices (and if successful), the use of these new insecticides and associated delivery systems have the potential to increase the sustainability and profitability of carrot production, enhance natural enemy populations and biological control, and reduce adverse effects on farm workers and applicators, as well as the local environment.

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