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Research

Predicting Damage to Hop Cones by *Tetranychus urticae* (Acari: Tetranychidae)

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Abstract

Twospotted spider mite (*Tetranychus urticae* Koch) is a cosmopolitan pest of numerous plants, including hop (*Humulus lupulus* L.). The most costly damage from the pest on hop results from infestation of cones, which are the harvested product, which can render crops unsalable if cones become discolored. We analyzed 14 yr of historical data from 312 individual experimental plots in western Oregon to identify risk factors associated with visual damage to hop cones from *T. urticae*. Logistic regression models were fit to estimate the probability of cone damage. The most predictive model was based on *T. urticae*-days during mid-July to harvest, which correctly predicted occurrence and nonoccurrence of cone damage in 91 and 93% of data sets, respectively, based on Youden's index. A second model based on the ratio of *T. urticae* to predatory arthropods late in the season correctly predicted cone damage in 92% of data sets and nonoccurrence of damage in 77% of data sets. The model based on *T. urticae* abundance performed similarly when validated in 23 commercial hop yards, whereas the model based on the predator:prey ratio was relatively conservative and yielded false-positive predictions in 11 of the 23 yards. Antecedents of these risk factors were explored and quantified by structural equation modeling. A simple path diagram was constructed that conceptualizes *T. urticae* invasion of hop cones as dependent on prior density of the pest on leaves in early spring and summer, which in turn influences the development of predatory arthropods that mediate late-season density of the pest. In summary, the biological insights and models developed here provide guidance to pest managers on the likelihood of visual cone damage from *T. urticae* that can inform late-season management based on both abundance of the pest and its important predators. This is critically important because a formal economic threshold for *T. urticae* on hop does not exist and current management efforts may be mistimed to influence the pest when crop damage is most probable. More broadly, this research suggests that current management practices that target *T. urticae* early in the season may in fact predispose yards to later outbreaks of the pest.

Key words: decision support, hop, *Humulus lupulus*, risk algorithm

The twospotted spider mite, *Tetranychus urticae* Koch, is a polyphagous and prolific pest worldwide that may feed on more than 180 host plants (Huffaker et al. 1969, van de Vrie et al. 1972, James and Barbour 2009). With a generation time as few as 6 d under ideal conditions, there can be a very short period before an outbreak may cause crop damage. In natural conditions, twospotted spider mite often is regulated by a complex of predatory arthropods (James et al. 2001, Gardiner et al. 2003), whereas in modern agricultural systems, this organism is a common secondary pest (van de Vrie et al. 1972). This may be due to use of pesticides that are toxic to important predators or stimulate egg production in *T. urticae*, elimination of refugia for predators, and other predisposing factors such as drought (Bartlett 1968, English-Loeb 1990, Gent et al. 2009, McMurtry et al. 1970). Specific determinants of twospotted spider mite outbreaks and damage on a given host or cropping systems may vary (Costello 2007, Strong et al. 1999, Woods et al. 2012).

On hop (*Humulus lupulus* L.), twospotted spider mites are a recurring pest in most commercial growing regions worldwide (Neve 1991, James and Barbour 2009). Crop damage from twospotted spider mites can be associated with yield loss when the pest feeds on

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the leaves or directly on cones, and also from quality defects due to reductions in brewing quality and cosmetic damage to cones (James and Barbour 2009, Woods et al. 2014). Quality assessment in hops involves subjective assessments and involves in part visual appearance based on cone color. This is a standard practice in the hop industry in the United States because production contracts specify cone color standards that, if not met, can lead to entire crop rejection.

Predicting when cone damage from twospotted spider mites will occur is uncertain, which probably leads to routine overtreatment with miticides (Weihrauch 2005). A central component of successful integrated pest management (IPM) is the ability to make management decisions with relative certainty to avoid crop damage. Presented with a pest issue, a grower could make one of three choices: treat prophylactically (the typical scenario with many hop growers), never treat, or make treatments according to some decision aid. This decision aid could be in the form of an economic injury level based on population density of a pest (Stern et al. 1959, Pedigo et al. 1986), or a warning system based on other risk factors for crop damage. In the absence of a decision aid, growers are forced to make prophylactic applications or never spray (Mumford and Norton 1984, Lindblad 2001). A warning system for predicting pest outbreaks should enable growers to make treatment decisions with greater accuracy, less risk or crop damage, and potentially reduced inputs (Norton 1976, Hughes et al. 1999).

Little work has been published to provide definitive thresholds for twospotted spider mite on hop. A provisional threshold of 10 mites per leaf was suggested by Strong and Croft (1993), although later research in Germany by Weihrauch (2005) suggested that 90 twospotted spider mites per leaf may be tolerated at harvest without economic impact. It is also unclear if action thresholds should be static or dynamic, changing over the course of the season with crop developmental stage or other factors such as predator abundance (Woods et al. 2014). Forecasting cone infestation and damage from twospotted spider mites, even if that damage is only cosmetic, could aid in rationalizing chemical inputs, as well as improve the timing of applications to improve efficacy and reduce the 'guess-work' in using thresholds (Pedigo et al. 1986).

Several statistical methods can predict risk of a pest outbreak based on various risk factors. In the instances of a binary decision (e.g., high vs low risk of an outbreak) risk algorithms may include discriminant analysis, decision trees, and logistic regression to name some of the more common approaches (Morrison 1976). Among these methods, logistic regression is attractive because the assumptions are less restrictive than discriminant analysis (Morrison 1976, Quinn and Keough 2002). Prediction of a pest outbreak by logistic regression is expressed intuitively and explicitly as a probability of an event, unlike decision trees. Multiple applications of logistic regression to develop risk algorithms can be found in entomology and other pest management contexts (Yuen et al. 1996, Hughes et al. 1999, Lindblad 2001, Fabre et al. 2003, 2007).

Logistic regression calculates the probability of a given binary or categorical outcome as a function of a set of explanatory variables (Quinn and Keough 2002, Hosmer et al. 2013). It is impossible to develop a predictive system that is entirely accurate and two types of prediction errors may occur with a dichotomous response variable (Hughes et al. 1999, Gent and Turechek 2015). A false-positive prediction occurs when a model incorrectly forecasts a pest outbreak and unnecessarily calls for management intervention (e.g., a pesticide application). A false-negative occurs when a model incorrectly forecasts no outbreak, potentially leading to lack of a treatment when treatment actually was needed. Positive prediction accuracy is termed sensitivity and negative prediction accuracy is termed specificity (Hughes et al. 1999, Lindblad 2001). The trade-offs in prediction errors for various action thresholds can be expressed graphically in a receiver operating characteristic (ROC) curve to characterize the attributes of a predictive system and identify action thresholds that minimize each type of error (Mumford and Norton 1984, Hughes et al. 1999). In the context of pest management, identifying operational thresholds that minimize various types of errors is an important aspect of developing a logistic regression model used in pest management decision making.

In this research, we had two objectives. First, we sought to identify risk factors for twospotted spider mite infestation of cones and damage to hop cone appearance associated with density of the pest and its key predators. Second, we also sought to develop and validate a risk algorithm to express quantitatively the likelihood of cone damage.

Materials and Methods

Experimental Plots and Data Collection

To identify risk factors for twospotted spider mite infestation of and visual damage to cones, a large data set was needed where a range of levels of twospotted spider mites were observed on leaves at specific times (e.g., before or after bloom) and cone damage from twospotted spider mites was known. This data were derived from multiple sources of previously published data conducted over a 14-yr period. Historical data from five studies were available from the research described in Gent et al. (2009), Woods et al. (2012), Woods et al. (2014), Woods and Gent (2014), and Iskra et al. (2019). A full description of the original studies is available in the original papers, and only a cogent summary is provided here.

During studies from 2005 to 2018, arthropod and visual cone damage data associated with twospotted spider mite feeding were collected from plots located near Corvallis, OR. The plots were not treated with miticides. The hop yard used for data collection was planted in April 2005 to the cultivar 'Willamette'. The total area of the yard was ≈0.75 ha and was surrounded by mowed grass, cereals, or vegetable crops. Plants were arranged on a 2.1-m grid pattern and under a 5-m trellis.

Standard production practices for hops in western Oregon were followed in all years, minus the use of miticides. Basal foliage and weeds were controlled during 2006–2018 with herbicides according to commercial standards. In 2005, 2006, and 2007 irrigation was supplied by sprinklers every 7–14 d as needed for crop development, whereas in subsequent years, irrigation was supplied daily by a surface drip system. Granular nitrogen, phosphorous, and potassium were broadcast applied (2006–2013) or applied by hand (2005, 2014–2018) during April, May, and June. During 2005–2013, this was according to standard commercial recommendations (Gingrich et al. 2000, Gent et al. 2009), whereas plot-specific nitrogen rates were applied during 2014–2018 as detailed in Iskra et al. (2019) and below.

Within a given year and experiment, varying densities of twospotted spider mites and other arthropods were generated within specific plots, with a plot consisting of at least eight plants that were separated by at least one row of plants that did not receive any insecticides or miticides with the exception of 2017, as detailed below. In all years, experiments were arranged in a randomized complete block design with each treatment replicated four or five times. These treatments varied depending on the purpose of a given study, but involved fungicides that induce twospotted spider mite outbreaks to varying degrees (Gent et al. 2009, Woods et al. 2012, Woods and

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Gent 2014) or altered rates of nitrogen fertilizer (Iskra et al. 2019). During 2014–2018, four nitrogen rate treatments were evaluated, with the total nitrogen applied ranging from 44.8 to 269.0 kg/ha as described in Iskra et al. (2019). In all of these years, a uniform application of 16-16-16 fertilizer was broadcast-applied to the entire field during mid-April, delivering 44.8 kg/ha of nitrogen, 44.8 kg/ha of P_2O_5, and 44.8 kg/ha of K_2O. Then on two later dates in mid-May and mid-June, additional nitrogen was delivered by applying 40-0-0 (2014 study) or 46-0-0 (2015–2018 studies) at a rate of 0, 22.4, 67.3, or 112.1 kg/ha banded over plants in each plot.

During these studies, some selective insecticides with minimal impact on twospotted spider mites were applied in most years as needed to reduce confounding effects from hop aphid *Phorodon humuli* (Schrank) (Hemiptera: Aphididae) and hop looper (*Hypena humuli* Harris) (Lepidoptera: Noctuidae). Application methods, dates, and rates are described in detail in Woods et al. (2012), Woods et al. (2014), and Iskra et al. (2019). In 2017, an application of bifenthrin (22.4 g a.i./ha as Brigade 2EC, FMC Corporation, Philadelphia, PA) was made to the entire hop yard to induce a twospotted spider mite outbreak (Iskra et al. 2019). Bifenthrin is nonselective for the predator complex that regulate twospotted spider mite and also may increase fecundity in *T. urticae* (Gerson 1989). No other miticides or insecticides were applied to the sampled plots or directly neighboring plants during the other 13 yr.

Arthropod Sampling

In all experiments, except 2012, leaf samples were collected every 1–2 wk beginning in mid-April to early May and continued until cone harvest during late August. In 2012, four biweekly samples were collected beginning in mid-July, due to labor constraints. On each sampling date, at least 10 leaves were collected from each plot and motile twospotted spider mite stages, twospotted spider mite eggs, apterous hop aphids, predatory mites (Phytoseiidae), mite-eating ladybeetles (*Stethorus* spp.) (Coleoptera: Coccinellidae), and minute pirate bugs (*Orius* spp.) (Hemiptera: Anthocoridae) were identified and enumerated as described below. Nonacarine, winged, or mobile natural enemies are referred to herein as macropredators.

Leaves were collected using standard methods as described in Gent et al. (2009), Woods et al. (2012), and Iskra et al. (2019). Briefly, lower canopy (<2 m) and upper canopy (>2 m) samples were collected from four to six plants in the middle of each plot to reduce plot-to-plot interference from other treated plots in the yard. Leaves were collected into paper bags, promptly transported to a laboratory, and refrigerated until processed. Enumeration of arthropods was conducted under a stereomicroscope, observing organisms either directly on the leaves or after transferring to glass plates using a mite brushing machine (Leedom Engineering, Twain Harte, CA; Macmillan 2005).

Assessment of macropredators from canopy shake samples was as described in Woods et al. (2014). In brief, macropredators of twospotted spider mites and aphids were enumerated from canopy shake samples collected during 2006–2009 and 2012–2018, with shake samples occurring every 7–14 d from mid-June to mid-August. In 2012, shake samples began in mid-July due to labor constraints.

Cone Assessments

As noted previously, crop damage caused by twospotted spider mites on hop can be due to direct losses in yield, changes in brewing characteristics typical for a given cultivar, and reductions in cone appearance due to direct feeding of the pest on cones. These forms of crop damage may occur independently (Weihrauch 2005). In the present study, yield data and common measures of brewing quality such as alpha-acids and oil content and composition were not available, and we focused only direct infestation of cones and the associated visual defects. This is still highly relevant for understanding the risk of crop damage and management because production contracts for hops specify standards for cone color and appearance. In practice, hop producers in the western U.S. manage twospotted spider mites at levels that minimize occurrence of the pest in cones and impacts on cone appearance. We do not consider the question of whether this management objective is sound for maximizing yield or brewing quality attributes. Rather, we take as a starting point that maintaining a green and uniform color of hops is the current management objective.

During 2005–2010, cones were assessed for mite damage either directly, as described in Gent et al. (2009) and Woods et al. (2014), or inferred from cone color. In 2005–2007, 2010, and 2014–2018, a four-point scale was used to determine twospotted spider mite damage based on the degree of discoloration associated with mite feeding, where 1 = no damage, 2 = slight discoloration or damage on one or a few bracts, 3 = moderate levels of discoloration or damage (greater than '2' rating but <25% of cone exhibiting damage), and 4 = severe cone discoloration (damage on >25% of cone or cone abortion). In 2008–2009, cones were evaluated by a third-party commercial hop merchant using their standard hop rating scale, where 1 = 'excellent', 2 = 'excellent (–)', 3 = 'good (+)', 4 = 'good', 5 = 'good (–)', 6 = 'poor', and 7 = 'poor (–)'. In 2011–2013, cone color was assessed using a 1–10 scale, where 1 = brown/red cones and 10 = green cones as depicted in Twomey et al. (2015). Mite damage was inferred from this scale.

Although multiple rating systems were used in different years, it was possible to dichotomize all of these scales to represent cones with or without visual feeding damage from twospotted spider mites. To standardize cone damage ratings for all years, cone damage ratings were converted to a binary scale, with '0' indicating no damage and '1' indicating an appreciable level of visual damage from twospotted spider mites. For samples rated using the four-point scale, cones rated > '2' were classified as damaged and cones rated ≤ '2' were considered nondamaged. For the 7-point scale, any sample with a rating of ≥'6' was classified as damaged and cones rated < '6' were classified as nondamaged. In studies during 2011–2013, cone color ratings assessed on a 10-point ordinal scale were always ≥7 and thus all were classified as nondamaged.

In 10 yr (2005–2010 and 2015–2018), twospotted spider mites were extracted from 30 cones per plot using an ethanol extraction method (Gent et al. 2009) to relate visual cone damage rating to the number of spiders mites present at harvest. To extract mites, bracts and bracteoles were removed from the cones and washed with 70% ethanol. The samples were sonicated for 30 s and then the solution was passed through a 20-µm filter to collect twospotted spider mites. Each filter was assessed using a stereomicroscope to determine the number of twospotted spider mites.

Development of a Risk Algorithm

Preliminary Data Analysis

Candidate risk factors for visual cone damage were generated from data from each plot for each year. We summarized arthropod-days for twospotted spider mites, *Stethorus* spp., and predatory mites on leaves and *Anystis* (Trombidiformes: Anystidae), Coccinellidae, predatory Hemipteran, *Stethorus* spp., and total predators recovered in shake samples. We selected these organisms because of their association with and importance in regulation of twospotted spider

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mite on hop (Calderwood et al. 2015, 2017; Woods et al. 2014). Mite-days and arthropod-days for the predator complex were calculated for various periods of time, namely: over the entire growing season (April or May to August); before training of shoots in early spring (April and May); during vegetative development during late spring to early summer (1 June–15 July); during bloom to harvest (15 July to harvest); and during cone development (late July to harvest). From these data, a summary data set over all years was constructed that had each of the variables for arthropod abundance and resulting visual cone damage as a dichotomous classification (damaged or nondamaged). The summary data set covered a period of 14 yr (2005–2018) and a total of 312 individual plots (4–32 per year).

Preliminary analyses were conducted to identify potential predictors of twospotted spider mite damage to cones. This was done by creating scatter plots of the variables with the number of twospotted spider mites recovered from cones for the years when these data was collected. Correlations between variables were expressed by Spearman's nonparametric rank correlation coefficient, and in linear or polynomial regression models fit using the CORR and REG procedure in SAS version 9.4 (SAS Institute, Cary, NC). For categorical variables, the distribution of potential predictor variables in plots with or without visual cone damage from twospotted spider mites was summarized in box plots. The median values of the predictor variables were compared using the Kolmogorov–Smirnov (K–S) test in the NPAR1WAY procedure in SAS.

Logistic Regression

Following the preliminary analysis, variables expected to be associated with visual cone damage from twospotted spider mites were evaluated as predictors in logistic regression models. Candidate models were fit and evaluated based on Akaike's information criterion (AIC) and the Hosmer and Lemeshow goodness-of-fit test (Stokes et al. 2012). Classification accuracy was summarized as overall accuracy, positive prediction accuracy (sensitivity), and negative prediction accuracy (specificity). Parsimonious models with low AIC values, high prediction accuracy, adequate fit diagnostics, and biologically logical combinations of variables were selected as the final models. Logistic regression models were fit and examined using the LOGISTIC procedure and its options in SAS. For each model, the cut point where the overall error rate was smallest was determined by Youden's index, J, which identifies the point on the ROC curve at the greatest geometric distance from the line representing a noninformative predictor (Metz 1978). Youden's index is a commonly used measure of overall diagnostic effectiveness and is calculated as J = sensitivity + specificity − 1.

Path Analysis

Path analysis was conducted to quantify possible interactions among variables and develop a conceptual model of the seasonal progression of twospotted spider mites that can lead to cone infestation and visual damage. Path coefficients are standardized partial regression coefficients (β weights) that indicate the magnitude and sign (positive or negative) of direct effects of variables when other variables are held constant. Path coefficients can be summarized as direct and indirect effects of an exogenous variable (analogous to a predictor variable in linear regression) on an endogenous variable (analogous to a response variable). Direct effects are the standardized path coefficients of a path denoted by an arrow directly connecting two variables. Indirect effects are the association of one variable with another mediated through one or more other variables. Indirect effects are calculated as the sum of the product of the path coefficients linking two variables. The total effect is the sum of direct and indirect effects (Loehlin 1987).

To conduct the analysis, a correlation matrix of the variables used in the models was constructed using the CORR procedure in SAS version 9.4 and analyzed using the CALIS procedure. Goodness-of-fit of the models was assessed with a χ^2 test and by inspection of residual diagrams.

Validation in Commercial Hop Yards

The risk algorithms that were developed utilized an extensive data set from one experimental yard of cv. 'Willamette'. To ensure the validity of the risk algorithms in commercial hop yards, we established nontreated plots in 7–8 yards during each of 2017, 2018, and 2019, representing three to four different farms each year and 23 hop yards in total. The majority of the yards were planted to cv. 'Willamette' (20 yards) and two other cultivars with similar sensitivity to *T. urticae*, cv. 'Fuggle' (2 yards), and cv. 'Tettnang' (1 yard). These cultivars are harvested at approximately the same time and are generally similar in their sensitivity to twospotted spider mites. Production practices varied by yard and farm, although all were typical for western Oregon.

In each yard, a plot was established that ranged in size from three to five rows wide by approximately 30 plants in length. Plots were situated at least three rows from the field border to reduce edge effects. Each plot was left untreated with miticides and insecticides that had any miticidal activity for the entire year. Rows bordering the plot were only treated with pesticides directed outward from plots by the application equipment to minimize drift. Leaf and canopy shake samples were collected as described in Woods et al. (2011). Leaf and canopy shake samples were collected from the middle row of each plot biweekly beginning in late June to early July and continuing until cone harvest in mid-August to late August. On each sampling date, 30 leaves were collected arbitrarily from the lower and upper canopy and evaluated for arthropods as described previously. Canopy shake samples were conducted on each of 10 hop bines per plot as described previously. Arthropods were identified and enumerated from each shake sample and standardized as the mean per plant for each plot. Cones were collected from each plot and evaluated for spider mite feeding damage using the 4-point ordinal scale described previously. Twospotted spider mites were extracted from 30 cones per plot using the ethanol wash method described above.

Predictor variables identified during model development were calculated from each commercial yard plot and used to calculate estimated risk of cone damage from twospotted spider mites. Estimated probability of visual cone damage from twospotted spider mites was compared to the actual damage (damaged or not) and expressed in a two-way contingency table.

Results

Abundance of Arthropods in Experimental Plots

During 2005–2018, populations of twospotted spider mites varied substantially between years. Averaged over all plots within a year, populations of twospotted spider mites expressed as seasonal mite-days ranged from 0.84 to 8.89 log-units (Fig. 1). As is typical, twospotted spider mites were more numerous in the upper canopy (mean 7.4 log-units) than the lower canopy (mean 4.6 log-units). Visual cone damage from twospotted spider mites was recorded in at least some plots in 2005, 2008, 2010, and 2017; no plots were rated as damaged in the other 10 yr (Fig. 1). Generally, the years where

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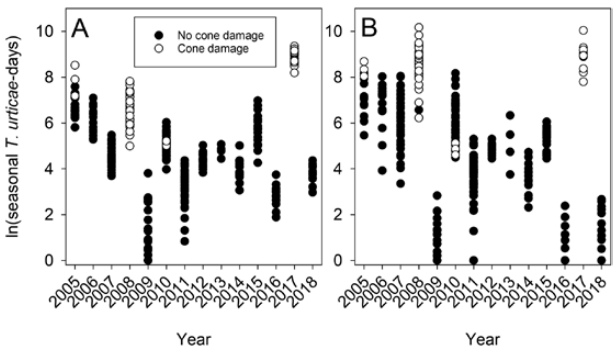

Fig. 1. Seasonal abundance of *Tetranychus urticae* expressed as arthropod-days by year and plot in data sets used to identify risk factors for damage to hop cones. Each point represents populations measured in an individual plot. Data from lower canopy leaves are presented in (A) and upper canopy data are presented in (B).

visual cone damage occurred were years with overall more severe outbreaks of twospotted spider mites based on seasonal mite-days. However, casual inspection of seasonal mite-days suggested that factors other than seasonal mite-days were associated with cone infestation and associated damage.

Development of a Risk Algorithm

Preliminary Data Analysis

Potential predictors of twospotted spider mite abundance in cones and subsequent damage had varying strengths of association and often were interrelated. The number of twospotted spider mites in cones at harvest was associated with prior occurrence of the pest on leaves during May to mid-July (mid-season mite-days) and during mid-July to harvest (late-season mite-days; Table 1). However, we did not find evidence of correlation between levels of twospotted spider mites in April (termed early-season mites) and the number of spider mites in cones at harvest ($S = 0.07$; $P = 0.513$; Table 1). Correlations between the number of twospotted spider mites in cones and predatory arthropods captured in canopy shake samples were not always significant and the sign of the Spearman rank correlation coefficient was not always positive. However, the ratio of twospotted spider mites on leaves to predatory arthropods captured in canopy shake samples during mid-July to harvest was positively correlated with the number of *T. urticae* in cones ($S \geq 0.60$ depending on canopy height; $P < 0.001$), as was the ratio when restricted to a single time point in late July ($S \geq 0.54$; $P < 0.001$). With only a few exceptions, the relative magnitude, sign, and significance of the correlations were similar for measurements of twospotted spider mites made on leaves in the lower or upper canopy.

When plots with visual cone damage were compared to plots without visual damage, all variables differed based on the K–S test (Table 2). Expectedly, the number of spider mites in cones at harvest was strongly associated with cones damaged by the pest (Table 2; Fig. 2A). More informative, though, was the association between antecedents of spider mites in cones and visual cone damage, specifically late-season mite-days (K–S = 0.33; $P < 0.001$), mid-season mite-days (K–S = 0.25; $P < 0.001$), early-season populations of *T. urticae* (K–S = 0.22; $P < 0.001$), and the ratio of *T. urticae* to predatory arthropods late in the season (K–S = 0.32–0.36 depending on canopy level; $P < 0.001$; Figs. 2 and 3).

Among these variables, late-season populations of *T. urticae* were investigated more closely. Late-season populations of *T. urticae* on leaves were predictive of the number of *T. urticae* in cones at harvest (Fig. 2B and C). A quadratic regression yielded the model: ln(*T. urticae* in cones) = 0.012 −0.084(ln(*T. urticae* days mid-July to harvest)) + 0.027(ln(*T. urticae* days mid-July to harvest))^2 with $R^2 = 0.36$ (intercept $P = 0.914$, $t = 0.108$; b_1 $P = 0.149$, $t = -1.448$; and b_2 $P < 0.001$, $t = 4.202$).

Logistic Regression

Since the variables measured in the upper and lower canopy shared similar statistical trends we focused our attention on presentation of variables associated with upper canopy samples for simplicity and economy of space here. Various logistic regression models were fit to the data to describe the relationship between risk factors identified in the preliminary analyses and the likelihood of visual cone damage. The most predictive model was based on *T. urticae*-days during mid-July to harvest (Table 3; Fig. 4A). Area under the receiver operating characteristic curve, a measure of classification accuracy that ranges from 0 to 1 (Stokes et al. 2012), was 0.96. This indicates very high prediction accuracy. The model indicated a precipitous increase in the risk of visual cone damage as late-season populations of *T. urticae* increased. Assuming a nominal probability threshold of 0.5 for classifying an observation as having visual cone damage or not, the sensitivity (positive prediction accuracy) was 0.83 and specificity (negative prediction accuracy) was 0.96. A cut point corresponding to 0.32 probability maximized Youden's index (sensitivity 0.91 and specificity 0.93; Fig. 5A).

A second logistic regression was constructed using the ratio of *T. urticae* to predatory arthropods late in the season (Table 3; Fig. 4B). We selected this model based on classification accuracy, fit diagnostics, and biological considerations. Although late-season populations of *T. urticae* is more strongly correlated with the number of *T. urticae* that invade cones and subsequent visual cone damage, we sought an antecedent of this variable that could provide earlier warning of the risk of visual cone damage and also considered predatory arthropods explicitly. The logistic regression model using the prey–predator ratio as the only predictor had area under the receiver operating characteristic curve of 0.88. Again assuming a nominal operational threshold of probability 0.5 for classifying events, sensitivity was 0.17 and specificity was 0.94. At this threshold, the model underpredicted cases where twospotted spider mites damaged cones. Youden's index was maximized at the cut point corresponding to 0.16 probability of visual cone damage, where sensitivity was 0.92 and specificity was 0.77 (Fig. 5B).

A third model using only prey–predator ratios in July, a single time point expected to be important for later development of *T. urticae*, was the poorest predictor of visual cone damage (Table 3; Fig. 4C). The parameter estimate for the predictor variable was not significantly different from 0 ($P = 0.267$; $\chi^2 = 1.233$; df = 1; Table 3), although the area under the receiver operating characteristic curve was 0.84 (Fig. 5C). Inspection of the measured versus predicted values indicated that prey–predator ratio at this single time point alone was inadequate for predicting visual cone damage (Fig. 4C).

Path Analysis

A simple path diagram conceptualizing the determinants of twospotted spider mite invasion of hop cones considered populations of the pest to progress directly from early to mid to late season on leaves, with mid-season levels of *T. urticae* associated with the prey:predator ratio and the prey:predator ratio in turn influencing late-season populations of the pest (Fig. 6). Fit of this model was questionable, however, as the absolute index χ^2 was 21.93 (df = 5; $P < 0.001$) and the root mean square error of approximation (RMSEA) was 0.31.

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Table 1. Spearman rank correlation of candidate predictor variables in the upper canopy (above diagonal) and lower canopy (below diagonal) associated with the number of *Tetranychus urticae* in hop cones at harvest[a]

Variable	Mites in cones	Early-season mites	Mid-season mite-days	Late-season mite-day	Mid-season predators	Late-season predators	Prey:predator ratio	Prey:predator ratio July
Mites in cones	—	0.07 (0.513) 92	0.15 (<0.024) 219	0.74 (<0.001) 219	−0.09 (0.308) 123	0.52 (<0.001) 123	0.60 (<0.001) 123	0.54 (<0.001) 99
Early-season mites	0.07 (0.513) 92	—	0.27 (0.010) 92	0.11 (0.314) 92	0.28 (0.007) 92	−0.11 (0.289) 92	0.03 (0.78) 92	−0.45 (<0.001) 73
Mid-season mite-days	0.008 (0.226) 219	0.56 (<0.001) 92	—	0.59 (<0.001) 312	−0.08 (0.321) 160	0.08 (0.322) 160	0.77 (<0.001) 160	0.70 (<0.001) 128
Late-season mite-day	0.79 (<0.001) 219	0.16 (0.130) 92	0.37 (<0.001) 312	—	−0.12 (0.142) 160	0.35 (<0.001) 160	0.94 (<0.001) 160	0.85 (<0.001) 128
Mid-season predators	−0.09 (0.308) 123	0.28 (0.007) 92	0.05 (0.533) 160	−0.09 (0.243) 160	—	0.28 (<0.001) 160	−0.30 (<0.001) 160	−0.33 (<0.001) 124
Late-season predators	0.52 (<0.001) 123	−0.11 (0.289) 92	0.02 (0.813) 160	0.34 (<0.001) 160	0.28 (<0.001) 160	—	0.07 (0.36) 160	0.30 (<0.001) 124
Prey:predator ratio	0.66 (<0.001) 123	0.21 (0.043) 92	0.66 (<0.001) 160	0.96 (<0.001) 160	−0.17 (0.031) 160	0.13 (0.106) 160	—	0.91 (<0.001) 124
Prey:predator ratio July	0.60 (<0.001) 104	−0.13 (0.249) 76	0.50 (<0.001) 154	0.83 (<0.001) 154	−0.12 (0.162) 139	0.40 (<0.001) 139	0.86 (<0.001) 139	—

[a]*P*-values are presented parenthetically. *N* for each correlation is shown below the correlation coefficient and *P*-value. Note that upper and lower canopy distinctions are relevant only for variables involving enumeration of *T. urticae* as predators were assessed from shake samples conducted over the entire canopy. Prey:predator ratio was calculated for the entire period of mid-July to harvest, and also only for late July (indicated as prey–predator ratio July).

Table 2. Kolmogorov–Smirnov statistic testing the equality of distributions of candidate predictor variables of hop cone damage from *Tetranychus urticae*

	Variable							
Canopy height[a]	Mites in cones	Early-season mite-days	Mid-season mite-days	Late-season mite-days	Mid-season predators	Late-season predators	Prey:predator ratio	Prey:predator ratio July
Upper canopy	0.31 (<0.001) 219	0.22 (<0.001) 92	0.25 (<0.001) 312	0.33 (<0.001) 312	0.17 (<0.001) 160	0.34 (<0.001) 160	0.32 (<0.001) 128	0.32 (<0.001) 128
Lower canopy	0.31 (<0.001) 219	0.22 (<0.001) 92	0.19 (<0.001) 312	0.32 (<0.001) 312	0.17 (<0.001) 160	0.34 (<0.001) 160	0.36 (<0.001) 160	0.32 (<0.001) 154

[a]*P*-values are given parenthetically. *N* for the test is below the test statistic and *P*-value. Note that variables associated with predators are identical for both canopy heights because predatory insects were collected from shake samples irrespective of canopy height.

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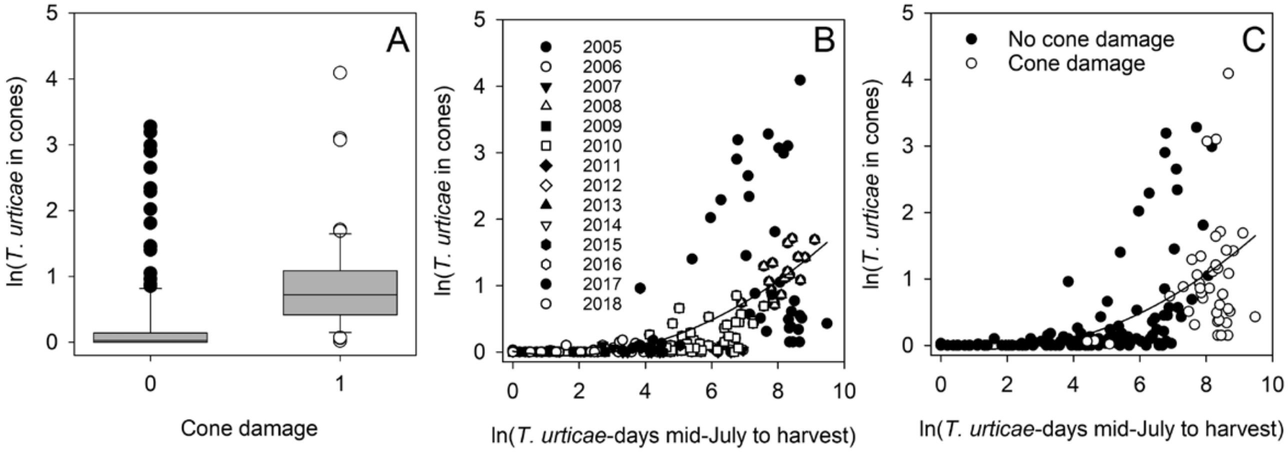

Fig. 2. Association between number of *Tetranychus urticae* in cones at harvest and cone damage rating (0 indicates insignificant damage, 1 indicates damage) (A), and relationship between *T. urticae* on leaves during late July to harvest and subsequent spider mites in cones at harvest (B and C). The regression in (B) and (C) is as follows: ln(*T. urticae* in cones) = 0.012 – 0.084 (ln(*T. urticae*-days mid-July to harvest)) + 0.027 (ln(*T. urticae* days mid-July to harvest))^2 (R^2 = 0.36; intercept P = 0.914; b_1 P = 0.149, and b_2 P < 0.001).

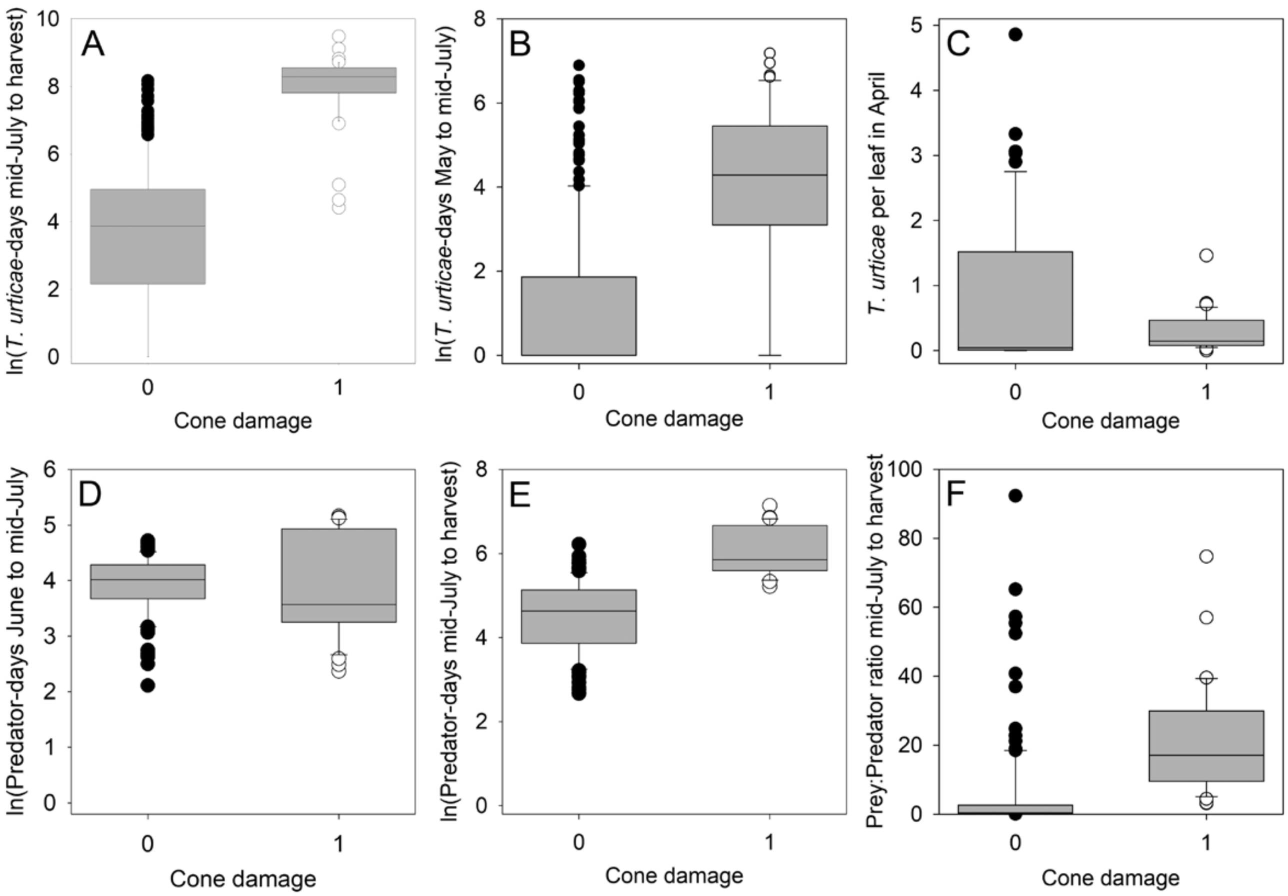

Fig. 3. Association between *Tetranychus urticae* populations on leaves (A–C) and predator populations (D–F) at various times during the growing seasons and hop cone damage at harvest from *T. urticae*. For cone damage ratings, 0 indicates insignificant damage and 1 indicates damage.

Path coefficients were positive and significant for all endogenous variables (path coefficients ≥ 0.33; P ≤ 0.038), but were negative and nonsignificant for the only exogenous variable, early-season *T. urticae* (path coefficient = –0.13; P = 0.44). Mid-season populations of *T. urticae* had indirect effects (0.27; P = 0.012) on infestation of cones, mediated by influencing the ratio of prey-to-predator and late-season populations of *T. urticae*. The ratio of prey-to-predator had a significant direct effect on late-season populations of *T. urticae* (0.42; P = 0.008), and indirect effects mediated by the same variable on infestation of cones (0.19; P = 0.045).

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Table 3. Maximum-likelihood estimates of logistic regression parameters, significance, and area under the receiver operating characteristic (ROC) curve for two logistic regression models for predicting damage to hop cones from *Tetranychus urticae*

Model	Parameter	df	Estimate (SE)	Wald χ^2	*P*-value	Area under ROC curve (SE)
Late-season mite-days	Intercept	1	−13.7699 (1.874)	53.9965	<0.0001	0.96 (0.015)
	Late-season mite-days	1	1.7614 (0.243)	52.4067	<0.0001	
Prey–predator ratio	Intercept	1	−1.8580 (0.260)	51.1807	<0.0001	0.88 (0.026)
	Ratio	1	0.0540 (0.013)	16.6109	<0.0001	
Late-July prey–predator ratio	Intercept	1	−1.0307 (0.213)	23.4250	<0.0001	0.84 (0.033)
	Ratio	1	0.0053 (0.005)	1.2330	0.2668	

Validation in Commercial Hop Yards

In the 23 plots established in commercial yards, only two had visual cone damage due to *T. urticae*. The mean of *T. urticae*-days during mid-July to harvest was (on a natural log scale) 3.5 (range −0.4 to 9.0) with SD = 2.4. Using the logistic regression model based on this variable, the presence or absence of visual cone damage (overall accuracy) was predicted correctly in 21 of 23 yards. There was one false-positive prediction and one false-negative prediction. The proportion of true positive and true negative predictions was identical when using a cut point of 0.32 based on Youden's *J* or a nominal cut point of 0.5 (Fig. 7A).

We also evaluated the logistic regression model based on the ratio of *T. urticae* to predatory arthropods late in the season. Among the 23 yards, this variable averaged 69.1 (range 0.13–596.3) with SD = 157.4. Using the cut point of 0.16 based on Youden's *J*, the model correctly predicted visual cone damage in 12 of the 23 yards. The 11 instances of misclassification were all false-positive predictions. When a nominal cut point of 0.5 was used, visual cone damage was predicted correctly in 21 of 23 yards. The two misclassifications were again false-positive predictions (Fig. 7B).

Discussion

We have identified risk factors associated with infestation of hop cones by twospotted spider mite and developed probabilistic risk algorithms for predicting the damage to cones from the pest. Apart from a direct measure of twospotted spider mite presence in cones, the most predictive risk factors for visual cone damage is density of twospotted spider mites on leaves during cone development. An important aspect of this risk factor is that the timing of spider mite occurrence relative to cone development is central to when cones may be damaged by the pest. Elevated populations of the pest earlier in the growing season, even in early July just before bloom, are not necessarily associated with elevated risk of late-season outbreaks. In fact, the opposite may be the case in that twospotted spider mite levels in spring had either no significant association or a negative association (based on the K–S test) with the risk of visual cone damage at harvest (Fig. 6). As late-season twospotted spider mite populations are those most likely to lead to cone infestation and damage, management efforts should be focused on this crop stage to minimize crop damage.

A provisional economic threshold for twospotted spider mites on hop is 10 motile mites per leaf, which has been presented in literature and used for years (e.g., Strong and Croft 1993). The biological basis of this threshold is unclear as it is invariant to time of year and other dynamic factors that may influence twospotted spider mite populations (Woods et al. 2014). The risk algorithm based on late-season populations of twospotted spider mite is probabilistic and we identified the threshold probability (cut point) that maximizes prediction accuracy as 0.32. This threshold has a direct relationship to late-season mite-days as it is the only variable in the model. An estimated probability of 0.32 translates into 7.4 log-units or 1634 mite-days from mid-July to harvest. Arthropod-days are a time-weight cumulative density of an organism over time, but growers and other pest managers often discuss twospotted spider mite populations in terms of single point measurements that are easily measured and conceptualized such as pests per leaf (Strong and Croft 1993; Weihrauch 2005). A population of 1,634 mite-days translates into a weekly mean density of approximately 33.4 *T. urticae* per leaf, assuming sampling is evenly spaced from 15 July to 1 September. Thus, a weighted average of 33.4 *T. urticae* per leaf in the upper canopy may be considered the economic injury level for visual cone damage on

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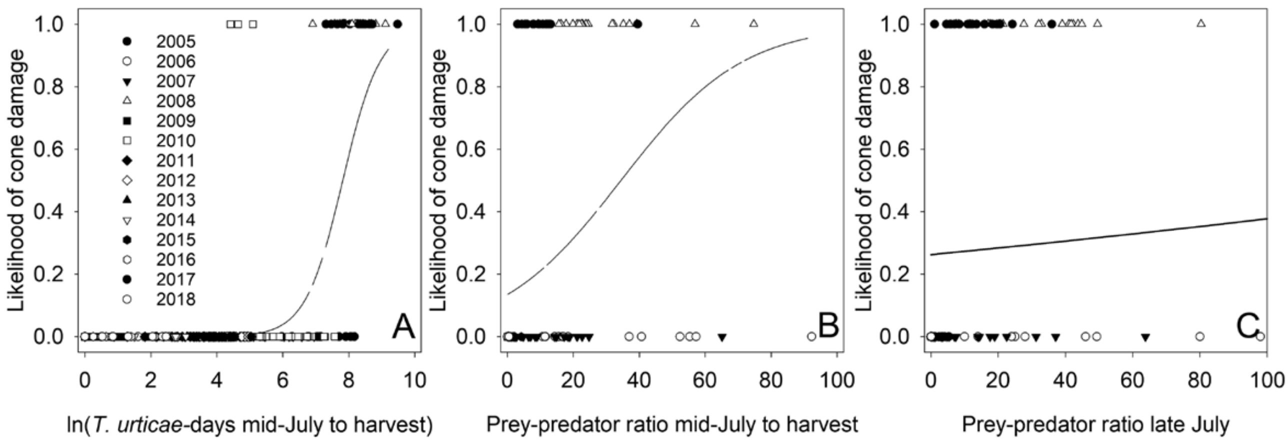

Fig. 4. Predicted probability of hop cone damage from *Tetranychus urticae* based on logistic regression models that consider late-season pest populations (A), the ratio of *T. urticae* to predatory arthropods captured in canopy shake samples from mid-July to harvest (B), or the ratio of *T. urticae* to predatory arthropods measured only during late July (C). All of the models utilize populations of *T. urticae* measured in the upper canopy. Note that in (C), two data points (114, 1; 500, 0) are not presented to improve legibility.

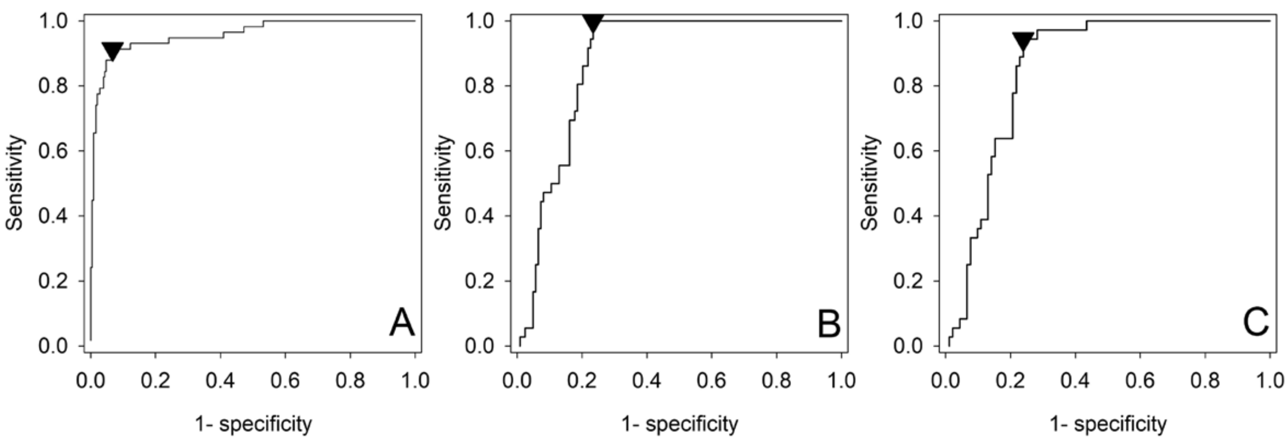

Fig. 5. Receiver operating characteristic curves for logistic regression models that predict hop cone damage from *Tetranychus urticae* based on late-season pest populations (A), ratio of *T. urticae* to predatory arthropods captured in canopy shake samples from mid-July to harvest (B), and ratio of *T. urticae* to predatory arthropods only during late July (C). The filled triangle in both plots indicates the cut point that maximizes overall prediction accuracy based on Youden's index.

cv. Willamette and similar cultivars in western Oregon. Studies on other cultivars with varying sensitivity to *T. urticae* are needed to understand the generalizability of this estimated threshold.

Of course, the economic threshold for management intervention is more complicated and depends on other dynamical processes. Producing a model for predicting pest outbreaks that goes beyond simple theoretical parameters is the weakest link in utilizing a predictive model in IPM (Pedigo et al. 1986, Foster et al. 1997). An economic threshold should be predictive of damaging pest levels in the future. Often, though, an economic threshold is a single value of a pest sampled at a single point in time without explicit consideration of environment-, time-, and situation-dependent factors. Thus, a single threshold value is an oversimplification (Pedigo et al. 1986, Rhodes et al. 1986, Brown 1997, Nyrop et al. 1999). Numerous factors may contribute to pest regulation and can be difficult to quantify, such as natural enemy suppression, changing crop susceptibility throughout the season, and economics (Mumford and Norton 1984, Rhodes et al. 1986, Zhang and Swinton 2009). The logistic regression models developed implicitly integrate multiple factors over time and express the risk of cone damage probabilistically. This is an intuitive means to translate pest (and predator) levels into a single value to express risk. Probabilistic outputs also are appealing as these may more closely align to pest management actions that are intended to reduce risk (Fabre et al. 2007, Gent and Turechek 2015). However, we recognize that the models developed here still oversimplify the multiple processes that may influence the risk of crop damage from twospotted spider mite.

Importantly, we were not able to consider direct losses in yield and focused only on visual damage caused by twospotted spider mite feeding. As we discussed previously, this is a highly relevant and important aspect of current management efforts for the pest but still only one of multiple ways that twospotted spider mites can cause economic damage. Therefore, we view the present analyses and models as stepping stones that can guide future research to derive damage functions and economic injury levels based on both yield loss and cone quality defects.

In the present analyses, the most important risk factor for visual cone damage is twospotted spider mite populations present on leaves in the upper canopy late in the season. The risk of cone infestation and visual damage is clear when relatively high populations of the pest are present late in the season. A more uncertain situation for hop growers is whether twospotted spider mite populations present prior to mid-July actually will be suppressed or continue to develop into the critical stages of cone development. The ratio of twospotted

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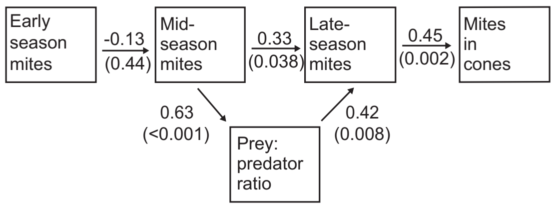

Fig. 6. Path diagram illustrating a conceptual model of *Tetranychus urticae* (termed mites for brevity) seasonal development leading to infestation of hop cones. The abundance of twospotted spider mites in cones is modeled as due to direct effects of twospotted spider mite populations in April (early-season mites), subsequent populations on leaves during May to mid-July (mid-season mites), and mid-July to harvest (late-season mites). The ratio of twospotted spider mites to predatory arthropods (prey:predator ratio) is modeled as having an indirect effect on the abundance of twospotted spider mites in cones through moderating late-season populations of the pest. Path coefficients are presented numerically and the associated *P*-value is presented parenthetically. The analysis was conducted on data from leaves in the upper canopy when these leaves were present and using log-transformed values to normalize variances.

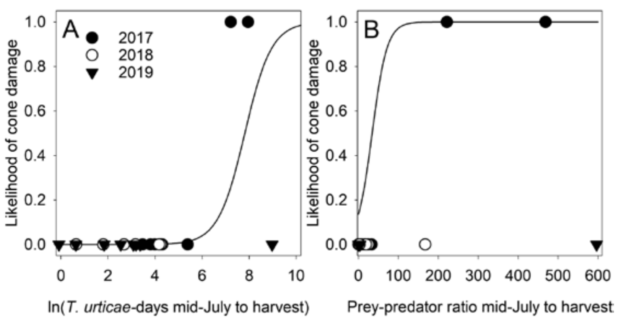

Fig. 7. Validation of two logistic regression models that estimate the probability of hop cone damage from *Tetranychus urticae* based on late-season pest populations (A) or the ratio of *T. urticae* to predatory arthropods captured in canopy shake samples from mid-July to harvest (B). Points in each curve are from nontreated plots established in 23 commercial hop yards in Oregon during 2017–2019. Instances where cone damage actually occurred are plotted on the y-axis at 1; nonoccurrences of cone damage are plotted at 0.

spider mites to certain predatory arthropods predicts (but with less certainty) the trajectory of the pest population and the likelihood of subsequent cone damage. Week-to-week decision making on the need for a miticide application thus requires information on both abundance of twospotted spider mite and their predators. In the logistic regression model based on prey–predator ratio, the cut point identified by Youden's index was 0.16, which corresponds to a mean ratio of about a 4:1 ratio of *T. urticae* to predators recovered from canopy shake samples during mid-July to harvest.

Casual inspection of Fig. 3F suggests this threshold is quite conservative, which is intuitive given the considerable overlap of prey–predator ratios in plots that had cone damage versus those that did not (Fig. 4B). When validated in commercial hop yards, the frequency of false-positive predictions for cone damage based on prey–predator was sensitive to the threshold used to predict cone damage or not (Fig. 7B). It is relevant to note here again that the logistic regression model utilizing prey–predator ratio was calculated as the mean ratio overall sampling periods from mid-July to harvest; less conservative ratios of prey to predator may be useful for predicting the trajectory of twospotted spider mite populations on a weekly basis. To demonstrate this, we also examined prey–predatory ratios only during the 2-wk period from mid-July to late July in the experimental plots (Fig. 8). The median prey–predatory ratio in the plots with cone damage was approximately 20:1, whereas the ratio was 1:1 in plots without damage. Prey–predator ratio at this specific time point was not significant in a logistic regression model (Table 3) and predictions associated with this model were inadequate (Figs. 4C and 5C). This may indicate that pest and predator populations are too dynamic for a single time to capture the risk of cone damage effectively.

Notwithstanding this, regular assessment of prey–pest ratios and their trend over time likely are predictive of the trajectory of populations of twospotted spider mites and the likelihood of cone damage. Thus, several pieces of information appear necessary to make an informed decision on the need for late-season treatment for twospotted spider mites. We suggest that sampling occur on a regular basis for both twospotted spider mites and their natural enemies, and both algorithms based on abundance of the pest and the prey–predator ratio be used jointly to estimate risk with the most recent measurements of these organisms. Situations deemed high risk (i.e., those where the estimated probability of cone damage exceed the cut points) would warrant management interventions. However, situations where estimated risk is below the cut point based on previous and current sampling could later develop into high-risk situations if pest populations develop in the future. In these situations, estimation of the prey–predator ratio on a weekly basis could provide some indication of the likely trajectory of the pest population over time. This would give some confidence that treatment could be delayed until the next sampling period without exposing a grower to an unacceptably high risk of later cone damage.

Most IPM decision guides do not explicitly consider the value of natural enemies (Pedigo et al. 1986, Zhang and Swinton 2009, Zhang and Swinton 2012). Detailed knowledge of how natural enemies interact with pests dynamically over time is difficult to collect and synthesize, and most crop-pest scenarios are too poorly understood to include this level of information in pest management decision making (Musser et al. 2006). This is true of the hop-twospotted

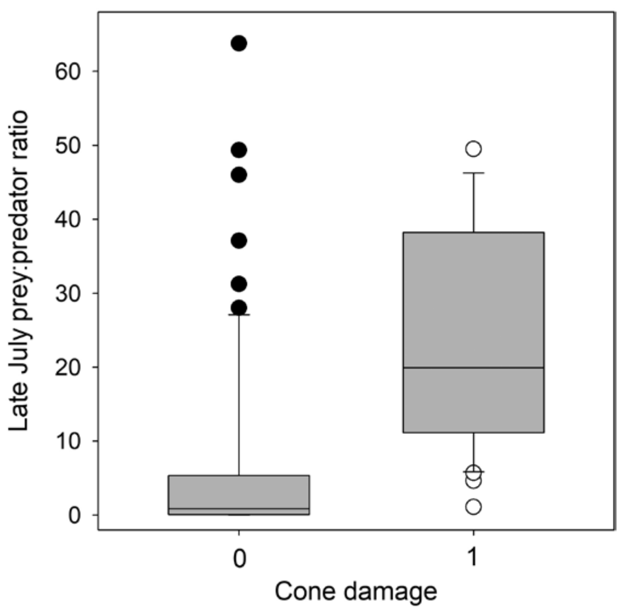

Fig. 8. Ratio of *Tetranychus urticae* to predatory arthropods captured in canopy shake samples in late July. For cone damage ratings, 0 indicates insignificant damage and 1 indicates damage.

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spider mite system as well, and the present research provides only general guidance or a rule-of-thumb for the ratios of pest and prey associated with successful biological control of late-season spider mites on one cultivar in one environment. Note also that the prey–predator ratio calculated here does not explicitly consider predatory mites. Predatory mites are important in spider mite suppression in multiple systems (Strong et al. 1997, 1999). In hop, a complex of predatory arthropods beyond predatory mites regulate twospotted spider mites. Predatory mites are often present at low abundance and in many years may be of secondary importance to the overall complex of predatory insects (James et al. 2006; Woods et al. 2014; Iskra et al. 2019). Given that the ratios calculated here do not consider predatory mites explicitly, the prey–predator ratios presented in fact are quite conservative measures of biological control potential. Development of an index of biological control potential that considers the complex of predatory mites and insects would help to generalize the findings of the present study.

This study has implications for understanding the antecedents that contribute to elevated populations of spider mites late in the season and provides hints at the characteristics of production systems that reduce the overall risk of cone damage. Blattný and Osvald (1950) stated that overwintering populations of predatory arthropods in hop yards are related to the severity of later outbreaks of twospotted spider mites. In the present analysis, cone infestation from twospotted spider mites was conceptualized as the result of a sequential set of events beginning at the earliest stages of plant growth in spring. Abundance of twospotted spider mites in spring and early summer (termed mid-season in this analysis) and the relative population of specific predator groups during vegetative stages of crop development were correlated with later spider mite abundance during cone development and invasion of cones by *T. urticae*. Thus, factors that eliminate twospotted spider mites (and their predators) well before cones develop may in fact predispose hop yards to late-season mite outbreaks, which are the outbreaks most likely to result in cone damage. Early-season control measures may not only be unnecessary but may actually increase the risk of later crop damage from twospotted spider mite when predators are present.

We recognize there are potential limitations to these data set given that the data were collected from one hop cultivar, from one location, and from experimental plots that were minimally treated with pesticides when compared with commercial hop production (Sherman and Gent 2014). We intentionally avoided more complicated situations where miticide residues may be present. Nonetheless, validation in 23 commercial yards over 3 yr indicates that the risk algorithms are predictive of cone damage in commercial situations with similar cultivars. Future validation in commercial hop yards with a variety of cultivars, environmental conditions, and disturbance levels typical of commercial production is important to understand whether the risk factors and risk algorithms identified here are more broadly generalizable. Also, the present analyses focused only on the risk of cone damage from *T. urticae* because this is the most costly damage caused by the pest. Again, we did not collect yield data and yield may be reduced by twospotted spider mite feeding even when cones escape damage. In Germany, however, no significant yield damage from twospotted spider mites was found from as many as 90 spider mites per leaf near harvest (Weihrauch 2005).

A challenge to the adoption of a predictive system by growers and their advisors is the perceived risk from not treating and added management complexity as compared to prophylactic treatment (Wearing 1988; Gent et al. 2011). The present research has produced simple, intuitive risk algorithms that make the likelihood of visual crop damage explicit. However, there are broader management implications of this research than operational use of the risk algorithms. We quantified associations between early-season spider mite, later predator and pest populations, and the consequent risk of cone infestation. Based on this, growers' current practices, even those that rely on provisional thresholds for miticide application, may in fact be increasing their risk for later season outbreaks of twospotted spider mite and cone damage. Thus, the findings from this research should help to refocus management attention away from control decisions based on simple thresholds and stimulate research on the predisposing factors that cause hop yards to be vulnerable to outbreaks of spider mites in the first place.

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