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**Estimating Russian Wheat Aphid
(Homoptera: Aphididae) Overwintering
Success Using Weather Data**

Estimating Russian Wheat Aphid (Homoptera: Aphididae) Overwintering Success Using Weather Data

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Abstract

The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov), is a significant pest of small grain crops. Since its invasion into the United States a quarter century ago, estimated damage resulting from the Russian wheat aphid has been over a billion dollars. However, aphid abundance and crop damage vary radically from year-to-year. Crop damage is typically much higher from aphid populations that overwinter locally, compared with those that migrate into that location in the spring. Thus, much of the year-to-year and field-to-field variation in crop damage is associated with overwintering aphid populations. We hypothesized that three weather-mediated variables affect aphid populations. Additionally, the correlation between fall and subsequent spring *D. noxia* density was examined. Data collected over three years at two sites in eastern Colorado were used to develop a model for overwintering success of *D. noxia*. Using Akaike's Information Criterion (AIC) based model selection, six weather-mediated models were supported by the data. A model-averaged result from these six models explained 74% of the variation ($R^2 = 0.74$) in spring *D. noxia* densities. Of the tested variables, cumulative degree days above zero and precipitation had the strongest correlation, both of which were positively

associated with *D. noxia* overwintering populations. Fall density was not a strong predictor of spring density.

Key Words

Diuraphis noxia, Russian wheat aphid, Temperature, Precipitation, Overwintering, Predictive model

Introduction

The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov), (Homoptera: Aphididae), is a significant pest of small grain crops. Since its introduction into the United States about two decades ago, cumulative damage is estimated to be over a billion dollars (Webster et al. 1994, Morrison and Peairs 1998). However, aphid abundance varies radically from year-to-year. For example, in the early years following introduction, total losses varied from \$274 million in 1988 to \$12 million in 1991 (Webster and Treat 1997). Understanding the ecological factors that determine the year-to-year variation in *D. noxia* population densities and associated crop damage would be valuable for developing a more comprehensive integrated pest management strategy. One important factor in determining potential crop yield loss is the success of overwintering aphid populations. When *D. noxia* do not overwinter successfully, recolonization must occur in the spring, and crop loss is reduced compared to situations in which *D. noxia* persist throughout the winter (Peairs et al. 2006).

Climate and the severity of winter weather (e.g., cold temperatures and snowfall) have been directly related to overwintering success in *D. noxia* and other aphid species (Dewar and Carter 1984, Messina 1993, Armstrong and Peairs 1996). Undoubtedly linked to climate and local weather conditions, significant spatial heterogeneity in *D. noxia* overwintering mortality exists across North America. In many areas of Canada, complete winter mortality of *D. noxia* populations is commonly observed, and for re-establishment to occur, migration from areas where populations successfully overwintered is necessary (Butts 1992). Even in milder, more southern areas such as Idaho, Montana, and northern Utah, *D. noxia* populations survive only in warmer winters (Feng and Nowierski 1992, Messina 1993, Elliott et al. 1998). On the other hand,

D. noxia has a high probability of overwintering success in areas of northern Texas, southeastern Colorado, eastern New Mexico and the Oklahoma panhandle (Elliott et al. 1998).

Much research has examined the ecological relationship between adult *D. noxia* and environmental conditions that could impact *D. noxia* populations during the overwintering period (e.g., Merrill et al. 2009b). To date, no male *D. noxia* have been reported in North America. Thus, *D. noxia* relies on an anholocyclic (asexual) strategy without the benefit of diapause or an egg stage to survive harsh winter or summer conditions. Despite this, *D. noxia* is considered one of the more winter-hardy aphid pests of small-grains on the Great Plains (Harvey and Martin 1988, Archer and Bynum 1993). Although *D. noxia* can withstand exceptionally cold temperatures, its expected lifespan and fecundity decrease with increasing time spent below 0° C (Knight et al. 1986, Hutchinson and Bale 1994, Armstrong and Peairs 1996, Butts and Schaalje 1997, Merrill 2007, Merrill et al. 2009a).

Armstrong and Peairs (1996) indicated that 64% of the within-field variation in overwintering survival of *D. noxia* in Colorado was due to variation in weather conditions. They modeled winter mortality of *D. noxia* using two weather variables, temperature and snow cover. They found a strong negative correlation between snow cover and mortality, which was attributed to the effect of insulation by snow cover from colder temperatures, resulting in decreased aphid mortality. While, mechanisms that would allow precipitation to directly increase population growth are difficult to postulate, the insulative properties of snow cover should allow existing *D. noxia* to persist during colder periods. Specifically, cold snaps (e.g., short duration, relative extreme negative temperatures such as -30° C) were shown to have a drastic negative affect on *D. noxia* populations if the populations were not insulated by snow cover (Armstrong and Peairs 1996).

Overwintering mortality is suggested to linearly relate to winter temperatures, with 100% population mortality occurring at ca. 125 degree-days below 0° C (Armstrong and Peairs 1996). Additionally, warm and wet winters should result in greater overwintering survival (Armstrong and Peairs 1996). Conversely, cold and dry winters should reduce overwintering success.

Another important factor influencing overwintering mortality is the longevity of *D. noxia*. The maximum average *D. noxia* lifespan is approximately three months, occurring just above its temperature developmental threshold (Merrill et al. 2009a). Thus, reproduction must occur during the winter because the season lasts longer than maximum aphid longevity. For development and reproduction to occur, aphids must experience temperatures above freezing (Merrill et al. 2009a). Meta-data show a nearly linear increase in fecundity from an average daily temperature of 0° C to 20° C. The developmental temperature threshold for *D. noxia* has been estimated at 4.1° C (Kieckhefer and Elliott 1989), 0.54° C (Aalbersberg et al. 1987), 5.2° C (Nowierski et al. 1995) and -1.57° C (Girma et al. 1990). Pike et al (1991) showed that if temperatures rise above the developmental threshold for only a short portion of the day, some development does occur. For the purposes of our modeling efforts, 0° C was assumed to be the temperature threshold above which development occurs and conversely, below which mortality increases. Meta-analysis (Merrill et al. 2009a) indicates this assumption is reasonable (high variability in developmental thresholds exist because of the inherent difficulty in obtaining data near the threshold values). Additional time at higher temperatures (up to approximately 20° C) increases development and reproduction. Cumulative degree-days above 0° C (DD+0°) are used to quantify developmental units (a combination of temperature and time spent at the temperature). Increases in temperature from 0 to 20° C, which lead to greater degree-day accumulation, also result in increased fecundity (Merrill 2007). Given these considerations, three

weather-mediated variables can be expected to influence overwintering success of *D. noxia* populations: 1) snow cover (or as a surrogate, precipitation) improves overwintering success because snow cover increases longevity, 2) greater accumulation of degree days below 0° (DD-0°) decreases overwintering success because increased accumulation of DD-0° decreases longevity, and 3) greater accumulation of DD+0° increases overwintering success because the increase in fecundity more than offsets the decrease in longevity. Precipitation is used as a surrogate for snow cover because most precipitation in the winter months is in the form of snow.

The factors governing spring density may be density independent (such as temperature). If the effect of such factors predominates, spring density will likely correlate strongly with fall density once abiotic density independent variation is removed. Alternatively, the effect of some factors may be influenced by aphid density (such as habitat availability). With *D. noxia*, for example, only a limited number of aphids may be able to find shelter within a furled wheat leaf during the winter. If density dependent factors play a dominant role, then spring aphid density would not be strongly related to fall density. Assessment of the strength of the correlation between fall density and density in the spring allows for quantification of the importance of density dependent factors. We examined two sets of models for predicting spring *D. noxia* density: one set that explicitly used fall aphid density plus weather covariates and a second set that only used weather covariates (and thus, assumed some effect of density dependent factors during the harsh winter months).

Methods

Two sites were chosen to represent widely differing climates from among eastern Colorado's wheat growing areas (Last Chance: 39°44' N 103°48' W, Lamar: 37°58' N 102°30' W). Each year ca. 80 plots were established at each site. Plots consisted of three consecutive

rows of dryland winter wheat. Plots were infested in late fall with *D. noxia* from the *D. noxia* Biotype 1 colony maintained at Colorado State University. All plots were infested with approximately 450 *D. noxia*, using a Davis Inoculator (Davis and Oswalt 1979).

Sampling was designed to obtain specimens over three growing seasons at two sites with one sample date in the late fall and two sampling dates in the late winter or early spring per site per growing season (the unit of one sample date per site per year will henceforth be referred to as a sample set or SS). However, during the 2002-2003 growing season, the fall and one spring SS at the Lamar field site were not obtained because of equipment failure. Wheat tillers were clipped from plots, placed into ziplock bags, and transported to Colorado State University's Agricultural Research Development and Education Center (ARDEC, Fort Collins). Sample design was for randomly selected tillers to be clipped from plots at a rate of eighteen tillers per plot (six tillers per row by three rows). If tiller density was low (e.g., from poor crop emergence), tillers were removed to maximize the number of tillers obtained in all sample periods. For example, if only eight tillers existed on a subplot during the first spring sample period, half of the tillers were removed allowing the second set of four tillers to remain for sampling during the second spring sample period. After being transferred from the field sites, tillers were removed from the ziplock bags and placed into Berlese funnels for approximately 24 hours to extract the aphids for counting under a dissecting microscope. *Diuraphis noxia* densities were calculated per tiller. Mean *D. noxia* density per SS (Table 1) was calculated as the mean of the plot averages per SS, and a log transformation ($\ln(\text{mean } D. noxia \text{ density})$) per SS was used to normalize the data. Each SS mean *Diuraphis noxia* density was calculated from approximately 58 *D. noxia* plot density averages (poor wheat emergence caused many plots to be lost).

Temperature and precipitation data were obtained from the Colorado Agricultural Meteorological network (CoAgMet) Stations on or near each field site (<http://ccc.atmos.colostate.edu/~coagmet/index.php>). CoAgMet stations provided maximum temperature, minimum temperature, and precipitation on a daily basis. DD+0° and DD-0° were calculated for all days between December 1st and the sampling date. If the average daily temperature ($[\text{high temperature} - \text{low temperature}] / 2$) was greater than 0° C, that average temperature was used in the calculation of the DD+0° total. Conversely, if the average daily temperature was below 0° C, that temperature was used in the calculation of the DD-0° total. One DD-0° was calculated as 1° C below zero for one day. DD-0° accumulated with any combination of temperature below zero degrees and days spent at such temperatures. For example, 10 DD-0° could be accumulated by a temperature of -10° C for 1 day or -1° C for 10 days. Corresponding to DD-0°, a DD+0° is the equivalent of 1° C above zero for one day.

Model Development and Selection. A set of *a priori* models was developed using all subsets of the variables of interest (Fall *D. noxia* density (FDnD), precipitation, DD-0°, DD+0°, and interaction terms between weather covariates) (Burnham and Anderson 2002). Pearson's Correlations Coefficients were calculated for each of the independent weather variables. DD+0° and precipitation were highly correlated ($r = 0.74$, $p = .0094$, $df = 10$). Instead of removing one of these variables or risking losing information if only one variable was allowed during model selection procedures, an index was created by averaging the normalized values for precipitation and DD+0° (hereafter referred to as the PD Index) (Normalization for precipitation (max = 13.94 cm, min = 0.28 cm) and DD+0° (max = 771.81, min = 208.28) were calculated by: $(X_i - X_{\min}) / (X_{\max} - X_{\min})$). Additionally, DD+0° and DD-0° were scaled down by 1000 to avoid small betas during parameter estimation.

The PD Index predictor variable was added to the candidate variable set. Thus, combinations of four variables (DD+0°, DD-0°, precipitation, and the PD Index) were used to develop candidate models. However, because precipitation, DD+0°, and the PD Index were highly correlated, any candidate model that included more than one of these variables was discarded. Candidate models were compared using an Information Theoretic approach (Burnham and Anderson 2002, 2004). All candidate models were ranked based on Akaike's Information Criterion (AIC) (Akaike 1973, 1981, Burnham and Anderson 2002, 2004). As is recommended for small sample sets, a correction to AIC was used (AICc). AICc values were calculated for all candidate models in the model data set and were used to select the models that would best approximate *D. noxia* densities. AICc values, Δ AICc, and AICc weights (Burnham and Anderson 2002, 2004) were calculated for each candidate model.

Δ AICc values were calculated as the difference between the candidate model of interest and the candidate model with the lowest AICc value (i.e., the best approximating model). AICc weights (w_r) were assigned to each of the candidate models based on their distance from the candidate model with the lowest AICc. If no single candidate model distinguished itself as the best approximating model ($w_r > 0.9$), model averaging was used to reduce model selection bias (Burnham and Anderson 2002).

AICc weights were used to assess the relative importance of each predictor variable (e.g., DD+0°) in explaining variation in aphid density (Adair 2005). Variable relative importance weight ($w_{+(i)}$) is the sum of the AICc weights for predictor variable i over all models in which predictor variable i occurs (Burnham and Anderson 2002). The resulting $w_{+(i)}$ can range from 0 to 1, with the more important variables having higher values.

Parameter Estimates. Weighted average parameter estimates ($\beta_{+(i)}$) were calculated using w_r s in conjunction with parameter estimates from each model in the model selection set:

$$\beta_{+(i)} = \sum w_r * \beta_{r(i)} \dots \text{for all models } r = 1 \text{ to } R$$

where w_r is the AICc weight for model r and $\beta_{r(i)}$ is the parameter estimate for variable i in model r .

When examining the strength of density dependent factors, data from the Lamar field site in 2003 were not used (equipment failure led to no fall aphid density samples). Therefore, there were 10 spring SS used in the analysis of density dependent factors. Examining the affect of weather-mediated variables allowed for the use of 11 SS (i.e., inclusive of the single Lamar SS from the spring of 2003). AICc values are not comparable between candidate model sets that use different data sets (i.e., model AICc values can only be compared relative to other models using identical data). Therefore, two complete sets of candidate models were developed: One candidate model set was developed using data from 10 SS to examine the effects of density dependent factors (These candidate models included the variables: $FDnD$, $DD+0^\circ$, $DD-0^\circ$, precipitation, the PD Index and interaction terms between weather covariates). Additionally, this candidate model data set included the following non-linear model forms:

$$\text{Form 1: } \ln(SDnD) = \beta_0 + \beta_1 * \ln(FDnD) * (\beta_i * WMVs)$$

$$\text{Form 2: } \ln(SDnD) = \beta_0 + \beta_1 * \ln(FDnD) * (\beta_i * WMVs) + (\beta_j * WMVs)$$

$$\text{Form 3: } \ln(SDnD) = \beta_0 + \beta_1 * FDnD^{(\beta_i * WMVs)}$$

$$\text{Form 4: } \ln(SDnD) = \beta_0 + \beta_1 * FDnD^{(\beta_i * WMVs)} + (\beta_j * WMVs)$$

Examples of Forms 1-4:

$$\text{Example Form 1: } \ln(SDnD) = \beta_0 + \beta_1 * \ln(FDnD) * (\beta_2 * PPT + \beta_3 * DD-0^\circ)$$

$$\text{Example Form 2: } \ln(SDnD) = \beta_0 + \beta_1 * \ln(FDnD) * (\beta_2 * PPT + \beta_3 * DD-0^\circ) + \beta_4 * DD-0^\circ$$

$$\text{Example Form 3: } \ln(SDnD) = \beta_0 + \beta_1 * FDnD^{(\beta_2 * PPT + \beta_3 * DD-0^\circ)}$$

$$\text{Example Form 4: } \ln(SDnD) = \beta_0 + \beta_1 * FDnD^{(\beta_2 * PPT + \beta_3 * DD-0^\circ)} + \beta_4 * DD-0^\circ$$

where $SDnD$ and $FDnD$ are spring and fall *D. noxia* density estimates, respectively. PPT is precipitation. WMVs are all subsets of the weather-mediated candidate variables precipitation, $DD-0^\circ$, $DD+0^\circ$, and the PD Index, exclusive of variable combinations that were highly correlated (e.g., $DD+0^\circ$ and precipitation). Non-linear forms 3 and 4 use the non-transformed variable $FDnD$ instead of $\ln(FDnD)$ because power transformations of value less than 1 (four $FDnD$ values were less than 1 when log transformed) rapidly converges to zero as the exponent increases, which therefore creates a lack of convergence in model parameterization.

A second candidate model set used data from 11 SS to examine the influence of weather-mediated variables (The candidate models were limited to the weather-mediated variables: $DD+0^\circ$, $DD-0^\circ$, precipitation, the PD Index and their interaction terms).

Results

Substantial variation occurred within the observed *D. noxia* densities (Table 1). The Lamar field site had more aphids on average (whole study average = 3.5 aphids per tiller) than the Last Chance field site (whole study average = 0.81 aphids per tiller). Conditions during the 2001-2002 overwintering season produced an average across both sites of 1.4 aphids per tiller. The 2002-2003 overwintering season produced the lowest average density at ca. 1.0 aphid per tiller. And the 2003-2004 season produced the highest average density (ca. 3.3 aphids per tiller).

A substantial proportion of the overall 2003-2004 high can be attributed to the Lamar field site where on average 5.7 *D. noxia* per tiller were found during the 2003-2004 winter.

The three overwintering seasons had relatively dry conditions (Table 1) with no extreme temperatures observed (e.g., temperatures never dropped below -30° C). Winter temperatures ranged from a high average daily temperature of ca. 4° C for the Lamar field site from December 2003 to April 2004 to a low daily average of 0.9° C at the Last Chance field site from December 2001 to April 2002. No extremely harsh conditions or prolonged cold snaps were observed during the study.

Analysis of the Effect of Density Dependent Factors: Model Selection and Model Averaging. No single model distinguished itself as the best approximating model. Five models had $\Delta AICc$ s less than seven, with a combined $AICc w_r$ of 0.947 (i.e., of the tested models, there was approximately a 95% probability that one of the top five models was the best approximating model). Of these five models none included the variable $FDnD$. The best model that included the variable $FDnD$ had an $AICc w_r$ of 0.013. Combined variable weight of $FDnD$ was 0.036, indicating that fall aphid density is not strongly associated with spring *D. noxia* densities.

Analysis of Weather-Mediated Variables: Model Selection and Model Averaging. As in the above analysis, no single model distinguished itself as the best approximating model. The model with the lowest $AICc$ ($\ln(D. noxia \text{ density}) = -1.85 + 4.36*DD+0^\circ$) had an $AICc w_r$ of 0.587 ($\Delta AICc = 0$), the second best approximating model ($\ln(D. noxia \text{ density}) = -0.56 + 1.52*PD \text{ Index}$) had an $AICc w_r$ of 0.241 ($\Delta AICc = 1.777$) (Tables 2 & 3). Other models had higher $\Delta AICc$ values and lower relative $AICc$ weights indicative of lower likelihoods of being the best approximating model. Because more than one model had support in the data for being the best approximating model, a model-averaged result was calculated using the six models with

$\Delta AICc$ values less than seven (i.e., models that had a good likelihood for being the best approximating model to the data (Burnham and Anderson 2002)). Models were averaged using their respective $AICc$ w_i s to form the following model-averaged result:

$$\ln(D. noxia \text{ density}) = -1.491 + 0.393 * (\text{PD Index}) + 3.707 * (\text{DD}+0^\circ) \\ + 0.596 * (\text{DD}-0^\circ) + 0.025 * \text{PPT} - (4.456) * (\text{DD}+0^\circ) * (\text{DD}-0^\circ)$$

where PPT is precipitation. The model-averaged result explains 74% of the variance in *D. noxia* density ($R^2 = 0.74$) (Fig. 1).

Analysis of Weather-Mediated Variables: Variable Importance. Each of the predictor variables was examined to clarify its strength and importance for explaining variation in *D. noxia* density. After renormalizing using the top six models, $\text{DD}+0^\circ$ had the highest variable weight, $w_{\text{DD}+0^\circ} = 0.681$ (Table 4). The PD Index had the second highest weight of the included variables ($w_{\text{PDIndex}} = 0.259$). $\text{DD}-0^\circ$ was third highest of the included variables ($w_{\text{DD}-0^\circ} = 0.110$). Precipitation and the interaction terms had low weights indicative of a lack of support for being good predictors of spring *D. noxia* density.

Discussion and Conclusions

Fall *D. noxia* density does not appear to be a good predictor of spring density. This result is surprising and could result as an artifact of a low number of samples or a low variation in the fall density samples. While low importance of density dependent factors was observed in this data set, it is unlikely that these factors play no role in overwintering survival. For example, some minimal density is necessary for population survival. While additional sampling may show the importance of fall aphid density, our data suggest overwinter weather conditions have a much stronger influence than initial fall densities.

Modeling results suggest that two variables, precipitation (mediated through the PD Index) and cumulative DD+0°, strongly correlate with overwintering survival. A third variable, cumulative subzero overwintering temperatures, was weakly correlated with overwintering success. Variable effect directions were parameterized as expected. That is, increasing the variables DD+0°, precipitation, and the PD Index correlated in a positive direction with *D. noxia* overwintering success, and increasing DD-0° had a net negative correlative effect on *D. noxia* overwintering success when combined with the DD+0°*DD-0° interaction term (Table 4). Overall, weather-mediated variables that contribute to population survival and growth during the winter are more likely to be important variables (i.e., they have higher variable weights) and each have a larger influence on overwintering success than the weather-mediated variable associated with mortality. Our findings contrast with previous research which suggested that low spring aphid densities are primarily caused by mortality associated with cold temperatures (e.g., Messina et al. 1993, Armstrong and Peairs 1996). For example, Armstrong and Peairs (1996) found that *D. noxia* populations decreased linearly as DD-0° increased (however, the variable DD°0 was not included in their model). There are many possible reasons for the low weight of the DD-0° in our study. Among the most likely reasons are: 1) DD-0° is not a strong indicator of *D. noxia* overwintering mortality. 2) Data collected during this study period did not include weather conditions under which DD-0° would have a strong effect (e.g., exceptionally cold winters). 3) DD-0° effects may be non-linear. For example, accumulation of DD-0° may have a minimal influence on *D. noxia* density until a threshold value has been reached, after which the accumulation of additional DD-0° has a strong effect. Or 4) the precision of the DD-0° data did not capture the influence of DD-0° on *D. noxia* mortality. For example, using degree hours to measure the influence of negative temperature accumulation on *D. noxia*, instead of using degree

days, would distinguish between days that experienced large daily temperature fluctuations versus days where temperature remained relatively constant. Temperature patterns may be important factors for explaining variation in overwintering success. For example, years with more temperature variation may result in different overwintering success from years with the same mean temperature but less variation. That is, mild weather punctuated by intense cold snaps may equate to the same number of DD-0° as a year with constant cold temperatures, yet result in different overwintering mortality. In addition there may be other, unknown reasons that the data used in this study did not capture the signal generated by DD-0°. Surprisingly, the precipitation variable was not included in the final model results. However, variation associated with precipitation may have been captured by the PD Index. While the Armstrong and Peairs (1996) model was not explicitly tested (snow cover data were not available), a model using precipitation (as a surrogate of snow cover) and DD-0° model was tested. The precipitation and DD-0° model did not perform as well as the described model-averaged result using this data set.

The model appears to generate better predictions when observed densities are low (i.e., less than two *D. noxia* per tiller). However, because of the small number of high density values observed in this study, determining the quality of the model fit at high aphid densities is difficult.

No extreme events (such as cold snaps, heavy rain storms or prolonged exposure to snow cover) occurred during this study and modeling results do not directly incorporate extreme events. However, extreme events have been shown in other studies to have dramatic effects on overwintering population dynamics. For example, cold snaps (ca. -30° C) had a drastic negative effect on *D. noxia* populations if the insects were not insulated (e.g., by snow cover) (Knight et al. 1986, Armstrong and Peairs 1996). Kriel et al. (1984) found a rapid decrease in *D. noxia* abundance associated with heavy rainfalls. Armstrong and Peairs (1996) found that prolonged

exposure to snow cover (e.g., greater than 40 days) appeared to have negative effects on *D. noxia* survival, even though the temperature to which they were exposed may have been relatively mild. These negative effects may result from disruption or inhibition of feeding behavior under snow cover over the extended time period. Additional work to incorporate these and other extreme events into the model would likely increase its overall usefulness.

This model was parameterized for the winter wheat / fallow agroecosystem. Areas outside of this system or *D. noxia* on different plant species may show different population dynamics. More studies should be undertaken to determine if increasing the number of samples and changing the geographic region of study would reconfirm precipitation and overwintering temperatures above zero as dominant variables or perhaps elucidate other signals influencing spring *D. noxia* densities.

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Fig. 1. Model-averaged predictions for *Diuraphis noxia* density per tiller compared to observed density data (black diamonds). Model predictions and observed data have been back transformed (i.e., $e^{(x)}$) to illustrate data in *D. noxia* density per tiller. The depicted line is the 1:1 line (i.e., the line on which perfectly correlated observed data and model predictions would fall).

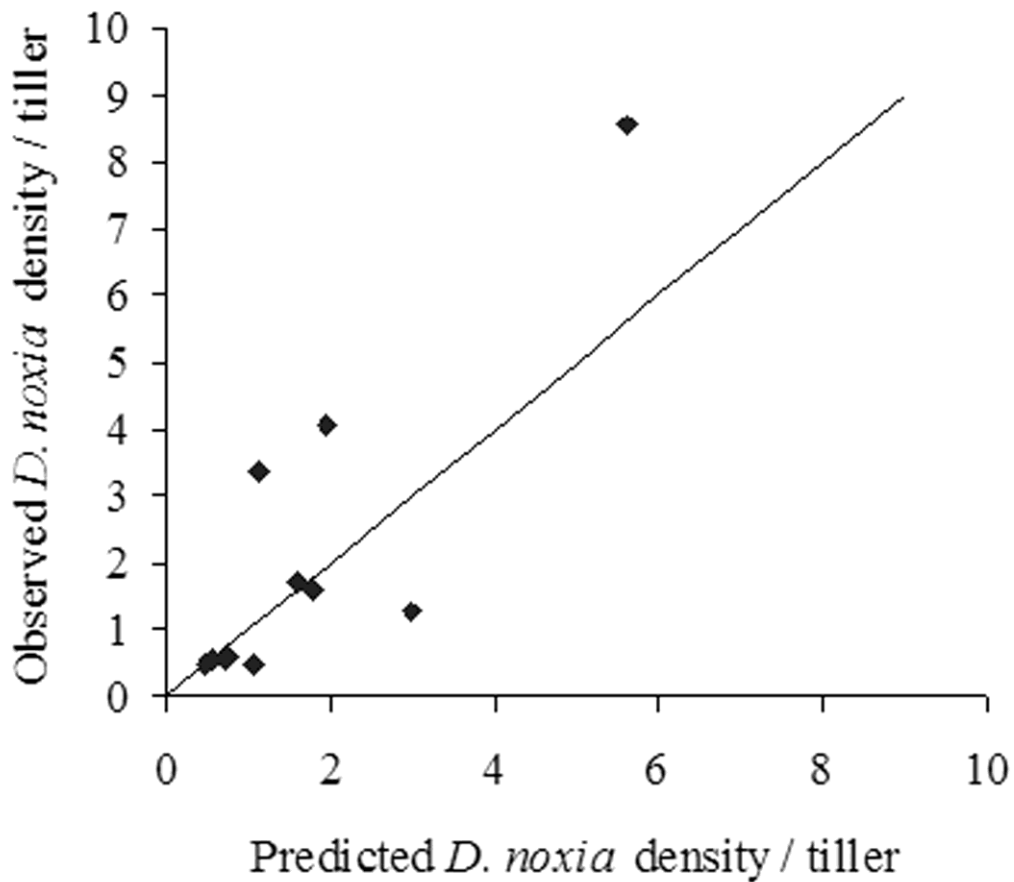


Table 1: Data for candidate model development.

SS	Date	n	DD+0°	DD-0°	PPT	PD Index	Location	Mean <i>D.</i> <i>noxia</i>
W1	Nov 01	65	N/A	N/A	N/A	N/A	Lamar	0.60
W2	Dec 03	55	N/A	N/A	N/A	N/A	Lamar	1.33
W3	Nov 01	66	N/A	N/A	N/A	N/A	Last Chance	2.93
W4	Dec 02	81	N/A	N/A	N/A	N/A	Last Chance	0.71
W5	Dec 03	62	N/A	N/A	N/A	N/A	Last Chance	1.38
1	Feb-02	72	208.28	120.05	0.62	0.05	Lamar	0.49
2	Apr-03	43	571.33	187.08	4.09	0.94	Lamar	1.59
3	Mar-04	60	444.53	164.44	2.26	0.55	Lamar	3.35
4	Apr-02	66	616.92	161.39	1.45	0.65	Lamar	4.06
5	Apr-04	51	771.81	164.44	13.94	2.48	Lamar	8.56
6	Mar-03	54	431.39	186.56	2.97	0.63	Last Chance	0.45
7	Mar-04	65	340.20	188.12	0.28	0.16	Last Chance	0.54
8	Mar-02	65	273.06	233.72	1.07	0.18	Last Chance	0.56
9	Apr-02	40	359.90	243.94	1.40	0.33	Last Chance	0.58
10	Apr-03	64	703.58	187.83	6.10	1.37	Last Chance	1.26
11	Apr-04	61	578.05	188.29	1.37	0.60	Last Chance	1.69

DD+0° are the degree days above 0° C, DD-0° are the degree days below 0° C, PPT is precipitation in centimeters, and PD index is an index created from PPT and DD+0°. n is the number of plots sampled. Winter sampling dates occurred approximately at or before the start date for temperature and PPT accumulation; thus, those sampling dates are marked with N/A.

Table 2: Top candidate models tested for value in estimating *Diuraphis noxia* density assuming density dependence.

Model	K	MSE	AICc	ΔAICc	$\mathcal{L}(g_i/\text{data})$	AICc Weight
						Renormalized (w_r)
DD+0°	3	0.430	0.135	0.000	1.000	0.587
PD Index	3	0.505	1.911	1.777	0.411	0.241
PPT	3	0.650	4.688	4.554	0.103	0.060
DD+0° & DD-0°	4	0.409	4.835	4.700	0.095	0.056
DD+0° & DD-0° with Interaction terms	5	0.226	5.616	5.482	0.065	0.038
PD Index & DD-0°	4	0.504	7.134	6.999	0.030	0.018

K is the number of estimated parameters in the model. Akaike's Information Criterion for small sample sizes (AICc), and AICc weights (w_r) quantify the support in the data for each of the models (Burnham and Anderson 2002). $\mathcal{L}(g_i/\text{data})$ is the likelihood of the model (g_i) given the data and is also a measure of the support in the data for model (g_i). PPT is precipitation in centimeters.

Table 3: Parameterized models, renormalized AICc w_r and R^2 for all models with $\Delta AIC < 7$.

Model: $\ln (D. noxia \text{ density}) =$	AICc w_r	
	Renormalized	R^2
$-1.85 + 4.36 * (DD+0^\circ)$	0.587	0.62
$-0.56 + 1.52 * (PD \text{ Index})$	0.241	0.55
$-0.29 + 0.42 * (PPT)$	0.060	0.42
$-0.44 + 4.20 * (DD+0^\circ) + (-7.24) * (DD-0^\circ)$	0.056	0.67
$-6.34 + 24.14 * (DD+0^\circ) + 28.90 * (DD-0^\circ) +$ $(-117.70) * (DD+0^\circ) * (DD-0^\circ)$	0.038	0.84
$0.72 + (-6.74) * (DD-0^\circ) + 1.45 * (PD \text{ Index})$	0.018	0.60

AICc weights were renormalized using all candidate models with $\Delta AICc < 7$. PPT is precipitation in centimeters.

Table 4: Variable weight ($w_{+(i)}$), parameter estimate and direction for weather-mediated variables selected as likely to predict *Diuraphis noxia* overwintering pressure.

Variable	AIC _c Variable Weight ($w_{+(i)}$)	Parameter Estimate
DD+0°	0.681	3.707
PD Index	0.259	0.393
DD-0°	0.112	0.569
PPT	0.060	0.025
DD+0° * DD-0°	0.038	-4.456
Intercept		-1.491

Note: DD+0° and DD-0° were divided by 1000 before modeling efforts to avoid problems associated with small parameter estimates (e.g., with exceptionally small parameter estimates, a small change in value can lead to large differences in predictions). PPT is precipitation in centimeters.

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