Modeling Spatial Variation of Russian Wheat Aphid Overwintering Population Densities in Colorado Winter Wheat

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ABSTRACT The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov), is a pest of small grain crops that has caused hundreds of millions of dollars of damage since it was first reported in the United States in 1986. Much is known about *D. noxia* population dynamics during the spring and early summer when most of the crop damage occurs, whereas little is known about the system during the overwintering period. Using a spatially explicit model developed from field observations in a wheat/fallow agroecosystem, we sought for predictable variation in overwintering success of *D. noxia* based on environmental factors such as topography and soil type. Successful modeling of densities of *D. noxia* would facilitate early control efforts targeting locations where *D. noxia* successfully overwintered. *D. noxia* density data were collected over 3 yr at two sites in eastern Colorado. The model incorporates georeferenced data from soil surveys, topography, and satellite imagery as predictor variables. Our approach links an information theoretic approach for model inference and model selection to landscape ecology, allowing for the examination of multiple candidate models and variables within each of the candidate models. Results were used to create trend surface models for *D. noxia* density in winter wheat agroecosystems. The model has the potential for use in site specific pesticide applications. Using site specific pesticide applications, pesticide inputs could be reduced by an estimated 30%, reducing input costs to the producer, increasing natural enemy refuges, reducing environmental contamination, augmenting pesticide resistance management practices, and reducing exposure of agricultural workers.

KEY WORDS *Diuraphis noxia*, spatial modeling, topography, satellite imagery, precision agriculture

The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov), is a major pest of wheat, *Triticum aestivum* L., and barley, *Hordeum vulgare* L. Damage estimates are in excess of a billion dollars since their invasion into the United States (Webster et al. 1994, Morrison and Peairs 1998). There has been extensive research into elucidating its population dynamics during the spring and early summer, when most of the crop damage occurs to the small grain crops. However, little has been published regarding *D. noxia* overwintering population dynamics with the exception of two articles (Messina et al. 1993, Armstrong and Peairs 1996). Quantitative, spatially explicit knowledge of the interaction between *D. noxia* and their environment is limited, indicative of a need for exploring variables that may explain variation in *D. noxia* densities within the winter wheat agroecosystem.

No male *D. noxia* have been reported from North America. Consequently, *D. noxia* are believed to rely on parthenogenic reproduction throughout the year, and these aphids overwinter as adult females. During the winter, *D. noxia* are relatively dormant but are seen moving and feeding when conditions permit (S.C.M., unpublished data). Because *D. noxia* reproduce parthenogenitically, using a telescoping generation strategy, population growth can be exceptionally rapid (Burd et al. 1998). Stress on aphids, such as caused by decreased host quality, leads to the production of alate *D. noxia* forms and results in increased dispersal (Baugh and Phillips 1991). One peak in *D. noxia* movement occurs in the spring, which allows dispersal to areas where *D. noxia* populations were absent. However, by the time of most spring flights (which generally start in April), wheat is typically at a late growth stage (F.B.P., unpublished data). When *D. noxia* infest later growth stages they do substantially less crop damage compared with infestations occurring on early growth stages (Peairs et al. 2006). Therefore, reduction of early season *D. noxia* densities should prove more beneficial than controls undertaken at a later date.

Some pest management strategies, such as shifting planting date (Hammon et al. 1996), have been shown to help reduce infestation levels, but most do not adequately protect yield (Randolph et al. 2002, Lee et al. 2005). Resistant wheat cultivars historically provided excellent crop protection, but with the advent of numerous new *D. noxia* biotypes (e.g., Haley et al. 2004) all commercially available winter wheat culti-

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vars are currently susceptible to *D. noxia* feeding damage and associated yield losses. Due to the development of these biotypes, insecticides have once again become the key management tactic in use on Colorado wheat. However, a single pesticide application generally costs ≈$25/ha. (Webster et al. 1994; F.B.P., unpublished data), which significantly reduces profit margins in dryland winter wheat. Typically, whole fields are treated with pesticides as a single unit based on aphid density, which has a variety of associated costs, including the indirect cost of leaving no within-crop refuges for natural enemies. Spraying pesticides across an entire field would be most beneficial if aphid densities were homogeneous. However, spatial homogeneity in aphid populations is atypical (Taylor 1984). Thus, there are benefits to precision targeting of control efforts.

Precision agriculture can be highly beneficial in agroecosystems that are not homogeneous because delineated areas can be managed differently, depending upon management goals. The most common application of precision agriculture is the development of yield maps, which enable practices such as precision fertilization or varying seeding rates within the field (Blackmore 1994). Precision agriculture concepts are also used for insect management. Precision pest management systems, which are currently being underused, are the combined use of directed scouting and site specific management. For example, in Pennsylvania, treating only the infested portions of potato fields reduced the amount of pesticide needed to control the Colorado potato beetle by 30–40% (Weisz et al. 1996). A spatially explicit model of *D. noxia* densities would greatly facilitate the development of tactics such as directed scouting and site specific management of *D. noxia.*

Numerous variables may be correlated with *D. noxia* overwintering mortality and therefore be correlated with the spatial heterogeneity observed in the density of *D. noxia* in the spring. Remotely sensed imagery has successfully been used to detect *D. noxi*a presence. For example, in a greenhouse experiment Riedell and Blackmer (1999) found excellent correlation between remotely sensed wavelengths and *D. noxia* feeding. Elliott et al. (2007) used a hyperspectral ground spectrometer to remotely sense *D. noxia* stress and incidence. And Dvorak et al. (2004) used aircraft based remotely sensed data to create vegetation indices, which were correlated with the presence of *D. noxia* in field plots.

Topographic variables such as aspect and slope have been found to influence *D. noxia* population dynamics. For example, Hammon and Peairs (1992) found that the south side of east–west facing irrigation beds accumulated more degree-days than the north side of the irrigation bed or either side of the north–south facing irrigation beds and consequently the south facing side had higher infestations of *D. noxia* in the spring. Moreover, they found that fields with irrigation beds with steep slopes had higher infestations than fields with irrigation furrows with more gradual slopes.

The interaction between overwintering aphid mortality and soil properties is an area that has seen limited, if any, research. However, it seems likely that soil properties play an important role in overwintering mortality. For example, aphid dispersal is affected by soil color (Loebenstein and Raccah 1980, Gibson and Rice 1989, Doring et al. 2004) and soil texture likely affects moisture availability and aphid desiccation.

Our goal was to develop a spatially explicit *D. noxia* density model to delineate *D. noxia* densities within the winter wheat agroecosystem. Such a model could be applied to generate risk assessment maps predicting areas of high *D. noxia* densities during the early spring. We hypothesized that some of the within-field variation in overwintering success is predictable based on remotely sensed satellite imagery, topography, and soil characteristics.

Materials and Methods

Sampling Design. Sites were established near Last Chance, CO (39° 44′ N 103° 48′ W, approximately an hour east of Denver, CO) and near Lamar, CO (37° 58′ N 102° 30′ W, near the southeastern corner of CO), which had disparate topographic and climatic variables and representative of the Colorado wheat production environments. Each year ≈80 plots were established at each field site, which were georeferenced using a Garmin GPSmap76S or a Garmin GPS 12 Map (Garmin International, Olathe, KS). For the first two overwintering seasons (2001–2002 and 2002–2003), plots were selected based on a stratified random grid design. The third season (2003–2004) was stratified across soil type because early analysis indicated that soil type was an important variable. Plots consisted of three consecutive rows (subplots) of dryland winter wheat. Wheat planted by the farmer was removed with a hoe. The winter wheat 'TAM 107' was planted at a rate of 2.45 g/m row. Water was added (at a rate of 1 liter per subplot) to offset soil disturbance and to increase wheat emergence. Because of the extremely dry conditions that occurred during this study, subplot length was reduced from one meter in the first overwintering season to 0.30 m in the second and third seasons to maximize the logistically available water applied per subplot.

Subplots were infested in late fall with *D. noxia* from the *D. noxia* biotype 1 colony at Colorado State University. All subplots were infested with ≈150 *D. noxia* per subplot, by using a Davis Inoculator (Davis and Oswalt 1979). The sample design was intended to obtain samples over 3 yr at two sites. Data were collected over two sampling periods per site per year allowing us to observe variation in the spatial distribution of *D. noxia* during the spring while maximizing the available sampling resources. Data for one of two sampling periods was not obtained in our second season at the Lamar field site because of equipment failure, leaving 11 sampling sets (SS). To determine *D. noxia* densities, tillers were removed from subplots on two sample dates per site per spring, with the exception of the second season at the Lamar field site (i.e.,

only one sample set was obtained from Lamar in spring 2003). Sample design was for tillers to be removed at a rate of six tillers per subplot. If tiller density was low (e.g., from poor crop emergence), tillers were removed to maximize the number of tillers obtained in each sample period. For example, if only eight tillers existed on a subplot during the first sample period, half of the tillers were removed allowing the second set of four tillers to remain for sampling during the second sample period. Tillers were clipped, placed into ziplock bags, and transported to Colorado State University's Agricultural Research Development and Education Center (ARDEC, Fort Collins, CO). Tillers were then removed from the ziplock bags and placed into Berlese funnels for ≈24 h to extract the aphids for counting under a dissecting microscope. *D. noxia* densities were calculated per tiller. Subplot densities were averaged to obtain a plot average (aphid density per tiller). Plot densities were normalized using the log + 0.1 method. The Last Chance field site sampling numbers and sampling dates were as follows: 158 subplot samples were obtained on 23 March 2002, 175 subplot samples were obtained on 6 April 2002, 190 subplot samples were obtained on 30 March 2003, 119 subplot samples were obtained on 25 April 2003, 173 subplot samples were obtained on 19 March 2004, and 153 subplot samples were obtained on 13 April 2004. The Lamar field site sample numbers and sampling dates were as follows: 187 subplot samples were obtained on 23 February 2002, 175 subplot samples were obtained on 12 April 2002, 183 subplot samples were obtained on 11 April 2003, 140 subplot samples were obtained on 25 March 2004, and 114 subplot samples were obtained on 25 April 2004. Subplot measurements were averaged to obtain a whole plot average. If any of the three subplot measurements per plot were missing, data were averaged over the remaining subplots. Over 3 yr at the two sites, subplot averaged measurements yielded *D. noxia* densities at 641 plots.

This research made use of geographic information systems (GIS), remote sensing, global positioning systems (GPS), and spatial statistical analysis. Three types of predictor variables were used to determine *D. noxia* densities: Landsat satellite imagery, topographic variables, and soil characteristics.

Two sets of Landsat seven ETM+ images per year at each site were obtained, one in the spring between sampling periods and one in the late fall or early winter (e.g., typically ≈15 December). Image date was variable due to the frequency of the satellite overpass timing and the necessity of cloud-free imagery over the field site. Landsat ETM+ 7 bands from the spring are denoted with an (S), whereas bands obtained during fall/winter are denoted with a (W). To examine vegetation, we developed a Normalized Difference Vegetation Index (NDVI) for each set of satellite images. NDVI was calculated as a function of Landsat Band 3 and Band 4: NDVI = [Band 4-Band 3]/[Bands 3 + 4]). The scan line corrector for the Landsat seven satellite failure that occurred in the spring of 2003 did not dramatically affect our project. In our study, the failure only affected some of the data from the thermal

bands (Bands 6.1 and 6.2). That is, <7% of plot level data during the last field season from these bands were affected. These missing data were treated as conventional missing data during the analysis.

Topography layers were developed from a United States Geological Survey 30-m digital elevation map (DEM). All topography data layers were generated with a 30-m grid resolution. Topography layers tested are as follows: relative elevation, the measure of the elevational distance (in meters) from the mean elevation at the field site. A Slope layer was developed (measured in degrees) from the USGS 30-m DEM by using the ArcGIS 9.1 (ESRI 1995–2007) slope tool. An Aspect layer (measured in degrees from 0° to 360°) was derived from the USGS 30-m DEM by using the ArcGIS 9.1 (ESRI 1995–2007) aspect tool. A north–south Aspect data layer was derived from the Aspect data layer using the Raster Calculator function in ArcGIS 9.1 (ESRI 1995–2007) with the function: Float(Abs(180 − [Aspect])). This creates a continuous variable from 0 to 180 with 0 directly north and 180 directly south. A Landshape data layer was created by the ArcGIS 9.1 (ESRI 1995–2007) Raster Calculator function: Focalmean ([DEM],Circle,3,nodata) − [DEM]. This function calculates the mean elevation value (i.e., from the DEM) in a circle with a three-cell (90-m) radius around the georeferenced plot, then subtracts that value from the elevation at the plot. The resulting value describes the relative elevation of the georeferenced plot to its surroundings.

Soil data were obtained from Colorado county soil survey paper copies (USDA–NRCS 2007) and digitized into a GIS for each site. Developing soil characteristic variables was difficult due to the scale of variability seen in the field. Therefore, soil series or types based on the soil Musyms (i.e., map unit symbol) were used as categorical surface grid layers. The following soil series (USDA–NRCS 2007) were used in this study: Wiley Series (≈5000 acres on sites), Weld Series (≈300 acres on sites), Shingle Series (≈500 acres on sites), Samsil Series (≈1000 acres on sites), Colby Series (≈300 acres on sites), Baca Series (≈400 acres on sites), Arvada Series (≈200 acres on sites), Adena Series (≈900 acres on sites), Soil Type: Gullied Land (≈124 acres on sites), Soil Type: Loamy Alluvial Land (≈660 acres on sites), and Soil Type: Alluvial Land Complex (≈39 acres on sites).

Upon generation of the complete data set, there were 36 predictor variables: landshape, slope, relative elevation, aspect, north-south aspect, imagery from spring and winter Landsat 7 ETM+ imagery [Landsat 7 ETM+ Bands and indices: Band 1 (450–515 nm), Band 2 (525–605 nm), Band 3 (630–690 nm), Band 4 (750–900 nm), Band 5 (1500–1750 nm), Thermal Bands 6.1 and 6.2 (10400–12500 nm), Band 7 (2090–2950 nm), Panchromatic Band 8 (520–900 nm), and the vegetation indices NDVI (S), NDVI (W)], and the soil types (Shingle, Arvada, Samsil, LAL, Colby, Baca, Weld, Wiley, Break, Gullied, and Adena). All GIS data layers were projected to NAD 84 (North American Datum of 1984).

Model Development. The spatial location of each *D. noxia* sample was used to identify and extract predictor variables from the soil, topography, and satellite data layers. GIS layers were normalized using the standard formula $(X_i - \text{Minimum}(X)/(\text{MaximumX} - \text{MinimumX}))$ for all data points *i*. All GIS layers were normalized to values between 0 and 1. Normalization allows for comparisons of the magnitude of the effect size between predictor variables. All Landsat imagery was normalized within image capture date (i.e., within ETM+ acquisition package) to observe relatively high and low reflectance data within-field instead of between fields.

Because within-field, small extent knowledge was our goal, each SS was treated as a data set to examine within-field differences in aphid densities (i.e., using SS as a categorical variable standardizes the differences between the mean densities across SS.) The SS categorical variable was included in every model in the candidate model set. All subsets of the predictor variables were linearly regressed against the dependent variable (ln (aphid density) + 0.1).

Data Analysis. We used an information theoretic approach to compare multiple hypotheses or models. Examining multiple competing models reduces model selection bias (Burnham and Anderson 2002) compared with null model testing. Models and predictor variables were evaluated based on the strength of evidence in the data using the following statistical tools: Akaike's Information Criterion with a correction for small sample sizes (AIC_c), ΔAIC_{cr} values (i.e., the difference between the AIC_c value of the best model and the AIC_c value of model *r*), and Akaike weights (w_r) (Burnham and Anderson 2002, 2004). AIC_c is the appropriate information criterion when sample size is small relative to the number of parameters (Burnham and Anderson 2002) and produces more conservative estimates of strength of evidence in high dimensional models (Twombly et al. 2007).

We used a model averaging approach (i.e., multimodel inference) because it is considered superior to making model predictions and inferences about variable importance based only on one best approximating model when alternate models are nearly as well supported as the best approximating model (Burnham and Anderson 2004). Models with a $\Delta\text{AIC}_c < 7$ were selected for model averaging because they are considered to have some support of evidence for being the best approximating model (Burnham and Anderson 2002).

AIC_c weights were used to assess the relative importance of each predictor variable in explaining variation in aphid density (Adair 2005). Variable relative importance weight $w_{+(i)}$ is the sum of the AIC_c weights for predictor variable *i* over all models in which predictor variable *i* occurs (Burnham and Anderson 2004). The resulting $w_{+(i)}$ can range from 0 to 1. The more important predictor variables have weights with higher values (e.g., given this data set, variables that are more likely to correctly predict aphid density will have weights close to 1). Because $w_{+(i)}$s are derived from AIC_c weights, $w_{+(i)}$ can be interpreted as the likelihood of predictor variable *i* being an important predictor variable for understanding variation in *D. noxia* density. That is, variable weights provide insight as to which variables are most likely to be correlated with aphid densities.

Weighted average parameter estimates ($\beta_{+(i)}$) are calculated by using AICc w_rs in conjunction with parameter estimates from each model in the model selection set:

Formula 1: $\beta_{+(i)}$

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

where w_r is the AICc weight for model *r* and $\beta_{r(i)}$ is the parameter estimate for variable *i* in model *r*. In a similar manner to determining a weighted parameter estimate, upper and lower confidence limits were developed. That is, upper and lower confidence limits were developed for each variable in each candidate model. Confidence limit values were weighted and summed based on AIC_c weights. These weighted confidence limits create unconditional confidence intervals as described by Burnham and Anderson (2002).

Model Selection. To reduce the number of candidate models to a reasonable level (i.e., an all-subsets approach would include a set of ≈69 billion models), we followed a criterion-based, forward selection procedure for model selection (Faraway 2005, Twombly et al. 2007). SS categorical variables were included in every model because elucidation of within-field variance was the goal. Variance inflation factors (VIFs) and Pearson's pairwise correlation coefficients were calculated for all predictor variables to test for colinearity (i.e., test for independence) (Proc Corr, SAS 2002–2003). During the forward selection procedure, no variable was considered for inclusion if it was highly correlated to a variable already included in the model. Correlation can be measured by Pearson's pairwise correlation coefficients. Therefore, potential variables to be added during the forward selection procedure were limited to those without substantial colinearity (i.e., models including any variables with a Pearson's pairwise correlation coefficient >0.6 were discarded).

A criterion based, forward selection procedure was used for model selection (Twombly et al. 2007). Specifically, each of the 36 variables was added to the null model (i.e., the model with only the SS categorical variables) to build 36 single-variable models. These were fit to measured field density data using SAS 9.1, Proc GLM (SAS 2002–2003), and AIC_c values were computed for each single-variable model. If the ΔAIC_c value of the single-variable models was greater than 2.0 compared with the null model, model selection was finished. Otherwise, all models with $\Delta\text{AIC}_c < 2.0$ were selected as the best single-variable model(s) (BSVM). Then each of the remaining 35 variables was iteratively added to the BSVM(s) to build 35 two-variable models for each BSVM model, excluding any variables with high colinearity. If the ΔAIC_c value of the two-variable models was greater than 2.0 compared with the BSVM, model selection was finished. Otherwise,

all candidate models with a ΔAIC_c <2.0 were selected as the BTVM(s). Selection proceeded by iteratively adding each of the remaining 34 variables to the BTVM(s) to build candidate three-variable models. This process was repeated to build four-variable models, five-variable models, etc., by adding any of the remaining variables until ΔAIC_c values were >2.0 compared with the candidate model with the lowest overall AIC_c. After which, candidate model selection was finished. All models selected as candidate models during the forward selection procedure were considered in the candidate model set.

After candidate models were selected, each model was examined for exclusion from the candidate model set based on the following criterion: removal of a candidate model from consideration was based on the confidence intervals (CIs) of parameterized variables in each of the models. If any variable was parameterized with 0 included in its 95% CI, the model was discarded. That is, candidate models were removed if they included a variable parameterized such that the direction of its effect was in question (i.e., if the parameter value associated with a variable included both positive and negative values in its 95% CI, then its effect on *D. noxia* density could either be positive or negative). Candidate models with a ΔAIC_c <7 were selected for model averaging, That is, models with an ΔAIC_c >7 have a very low probability of being selected as the best approximating model given a similar data set (Burnham and Anderson 2002) and were therefore discarded.

Validation Using Site Specific Pesticide Applications. Precision agriculture assumes that cropping systems are not homogenous; therefore, there are benefits to developing management units within which important management factors are similar. Site specific management units may be based upon a number of factors, including expected yield or expected pest densities. Pest management tactics could be focused on site specific management zones predicted to have high pest densities, and eliminated from areas of the field predicted to have low pest densities. This approach could reduce pesticide application by reducing the areas sprayed, resulting in all of the benefits associated with pesticide reduction (such as the creation of refuges for natural enemies). Observed densities were divided into three management zones: high risk, medium, risk and low risk for aphid damage. Model results were validated by simulated spraying of sites predicted by the model to have high aphid densities and determining the correlation between sprayed sites and observed *D. noxia* densities.

Trend Surface Models. The Raster Calculator function in ArcGIS 9.1 (ESRI 1995–2007) was used to create trend surface models spatially delineating *D. noxia* densities at the site level, using model-averaged results.

Results

As expected, variance in observed *D. noxia* densities was large between sites, between years, and between plots within sites. Variance between sites and between years was controlled using the SS terms in the model, allowing for parameterization of within site, between plot differences. Densities ranged from a maximum of 49.5 aphids per tiller in April of 2004 at a plot in the Lamar field site to a frequently observed measurement of zero aphids per tiller. 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). The 2001–2002 winter produced an average across both sites of 1.4 aphids per tiller, 2002–2003 produced $\approx$1.0 aphid per tiller, and 2003–2004 produced the high of $\approx$3.3 aphids per tiller. A substantial proportion of the overall 2003–2004 high can be attributed to the Lamar field site (5.7 aphids per tiller on average during the 2003–2004 winter).

The three overwintering seasons saw relatively dry conditions with temperatures within the normal range. Winter temperatures ranged from a high of an average daily temperature of $\approx$4°C for the Lamar field site from December 2003 to April 2004 to a 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. Precipitation ranged from a low of 2 cm in Last Chance during the 2001–2002 winter to $\approx$14 cm in Lamar during the 2003–2004 winter $\approx$10 cm of which fell during one storm in late April. Snow cover did not persist for over 40 d at either of the sites during the study.

Model Selection and model Averaging. Eleven models (Table 1) had ΔAIC_c values <7. There were several distinctive features associated with these models based on the inclusion of important variables. None of the models had <18 parameterized values. Therefore, each would be considered relatively complex with a potential for large errors. However, given the structure of the model averaging method (i.e., using weighted results from all quality models), results become more conservative. All 11 of the quality models were averaged resulting in the final model-averaged formula: ln (*D. noxia* + 0.1) = −0.850 * SS1−1.348 * SS2−0.477 * SS3−1.374 * SS4−0.501 * SS5−0.42 * SS6−1.401 * SS7 + 0.285 * SS8−0.00 * SS9−0.691 * SS10−0.282 * SS11 + 1.502 * NDVI(S) + 0.708 * Band3 (S) + 0.278 * Band8(W) + 0.019 * Band2(W) − 0.019 * Band5(W) + 0.204 * Band3(W) + 0.797 * Baca + 0.51 * LAL + 1.312* Slope − 0.597 * R_Elevation −1.159, where SS$_n$ is the categorical variable associated with the *n*th sampling date per site per year, and R_Elevation is the relative elevation. Interpretation of the above model-averaged formula is synonymous with interpretation of any linear regression equation.

Variable Importance Results. Variable $w_{+(i)}$s are indicative of the predictor variable's importance in determining aphid density, with higher variable $w_{+(i)}$s indicative of a strong likelihood for the variable explaining variation in aphid abundance. Because all of the variables were normalized between zero and one, they can be used to compare the relative magnitude of the effect size of each predictor variable (Table 2).

Table 1. Models included in the Model Averaging Procedure, where SS is the categorical variable sampling date per site per year

Model	Variables	AIC$_c$[a]	ΔAIC$_c$	L (g$_r$/data)[b]	AIC$_c$ w$_r$ normalized[a]
1	SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Baca, Band 8 (W)	341.86	0.0000	1.0000	0.340
2	SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Baca, Band 3 (W)	342.08	0.2186	0.8964	0.304
3	SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Baca	343.92	2.0577	0.3574	0.121
4	SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Band 8 (W)	345.4	3.5449	0.1699	0.058
5	SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Band 3 (W)	346.26	4.4023	0.1107	0.038
6	SS, NDVI (S), Band 3 (S), Slope, Band 8 (W), Band 5 (W), LAL	346.44	4.5793	0.1013	0.034
7	SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Band 2 (W)	346.54	4.6832	0.0962	0.033
8	SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, Baca	347.28	5.4270	0.0663	0.023
9	SS, NDVI (S), Band 3 (S), Slope, Baca, LAL	347.42	5.5598	0.0620	0.021
10	SS, NDVI (S), Band 3 (S), Slope, Band 8 (W), LAL	347.91	6.0519	0.0485	0.016
11	SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL	348.53	6.6730	0.0356	0.012

[a] Akaike's Information Criterion for small sample sizes (AIC$_c$) and AIC$_c$ weights (w$_r$) quantify support in the data for each of the models (Burnham and Anderson 2002).
[b] L(g$_r$/data) is the likelihood of the model (g$_r$).

Table 2 provides the variable weight, parameter estimates (effect size), and the upper and lower confidence limits for all predictor variables. Five variables had large variable weights (w$_{+(i)}$) and positive effects on *D. noxia* density: NDVI (S) (w$_{+(NDVI\_S)}$ = 1), Band 3 (S) (w$_{+(Band3S)}$ = 1), slope (w$_{+(Slope)}$ = 1), and the soil types LAL (w$_{+(LAL)}$ = 0.977) and Baca (w$_{+(Baca)}$ = 0.809). Relative elevation (w$_{+(R\_Elevation)}$ = 0.928) had a negative effect. That is, areas of the field that are relatively high (e.g., ridge tops) supported lower *D. noxia* densities. Band 8 (W) (w$_{+(Band8W)}$ = 0.448) and Band 3 (W) (w$_{+(Band3W)}$ = 0.342) both had small relative weights with a positive effect on *D. noxia* densities. Band 5 (W) (w$_{+(Band5W)}$ = 0.034) and Band 2 (W) (w$_{+(Band2W)}$ = 0.033) had very low relative weights, making their effects negligible. The six variables with the highest variable w$_{+(i)}$ values [i.e., NDVI (S), slope, Band 3 (S), Relative elevation, and the soil types LAL and Baca] were included in most or all of the models with larger model weights, indicative of a strong likelihood for explaining variation in *D. noxia* density given similar conditions. Band 8 (W) and Band 3 (W) were included in a couple of the models with larger model weights, and two variables (i.e., Band 5 (W) and Band 2 (W)) were each included in only one low weight model.

Table 2. Variable importance and parameterization

Variable	AIC$_c$ variable wt (w$_{+(i)}$)	Parameter estimate (95% CI)
NDVI (S)	1.000	1.502 (0.937, 2.067)
Band 3 (S)	1.000	0.708 (0.176, 1.240)
Slope	1.000	1.312 (0.712, 1.912)
LAL	0.977	0.510 (0.152, 0.868)
Relative Elevation	0.928	−0.597 (−1.054, −0.141)
Baca	0.809	0.797 (0.199, 1.395)
Band 8 (W)	0.448	0.278 (0.045, 0.510)
Band 3 (W)	0.342	0.204 (0.021, 0.387)
Band 5 (W)	0.034	−0.019 (−0.037, −0.001)
Band 2 (W)	0.033	0.019 (0.002, 0.036)
Intercept		−1.159 (−1.796, −0.522)

Because variables have been normalized, parameter estimates yield the magnitude of the variable's effect size and the direction of its effect. Also included are the upper and lower confidence limits for the parameter estimates.

Generating *D. noxia* Density Trend Surface Models from Model-Averaged Results. The model-averaged results for each sampling period were entered into the Raster Calculator Function (ArcGIS 9.1, ESRI 1995–2007) to create *D. noxia* density trend surface models by using GIS layers associated with the important predictor variables. *D. noxia* density trend surface models can be depicted in a variety of ways. For example, Fig. 1 depicts a continuous *D. noxia* density surfaces for the Last Chance field site based on data from 25 April 2003. In addition, *D. noxia* density surfaces can be used to develop risk assessment maps, which are maps that indicate areas that are at high, medium, and low risk for aphid population expansions with associated yield damages. Figure 2 is a risk assessment map based on data from the 19 March 2004 sampling date at the Last Chance field site.

Validation Using Simulated Site-Specific Pesticide Application. The model averaged result has an R^2 value of 0.35. Although the model explains a limited proportion of the variance, it has substantial value in using site-specific pesticide applications. Plot density data were partitioned into three management zones: high, medium, and low predicted *D. noxia* density. Simulated spraying of all of the plots predicted by the model to be at risk for having high aphid densities (i.e., spraying 33.3% of the plots) resulted in 64% of the observed high *D. noxia* plots sprayed. If the model-predicted highest 50% of the plots were sprayed, the proportion of observed high density plots being sprayed was 79%, and if 70% of the plots were sprayed >90% of the plots in the high *D. noxia* density management zone would be sprayed. These results show that simulated site specific pesticide application using model results would greatly reduce pesticide inputs yet result in a large reduction in risk of crop loss from aphid damage.

Spatial Autocorrelation. Residuals were examined for spatial autocorrelation using Moran's i. The Moran's i value was found to be significant (Moran's i = 0.165, $P = 0.0009$) in the residuals indicative of an additional signal in the data that has not been explained by the examined variables. That is, residuals
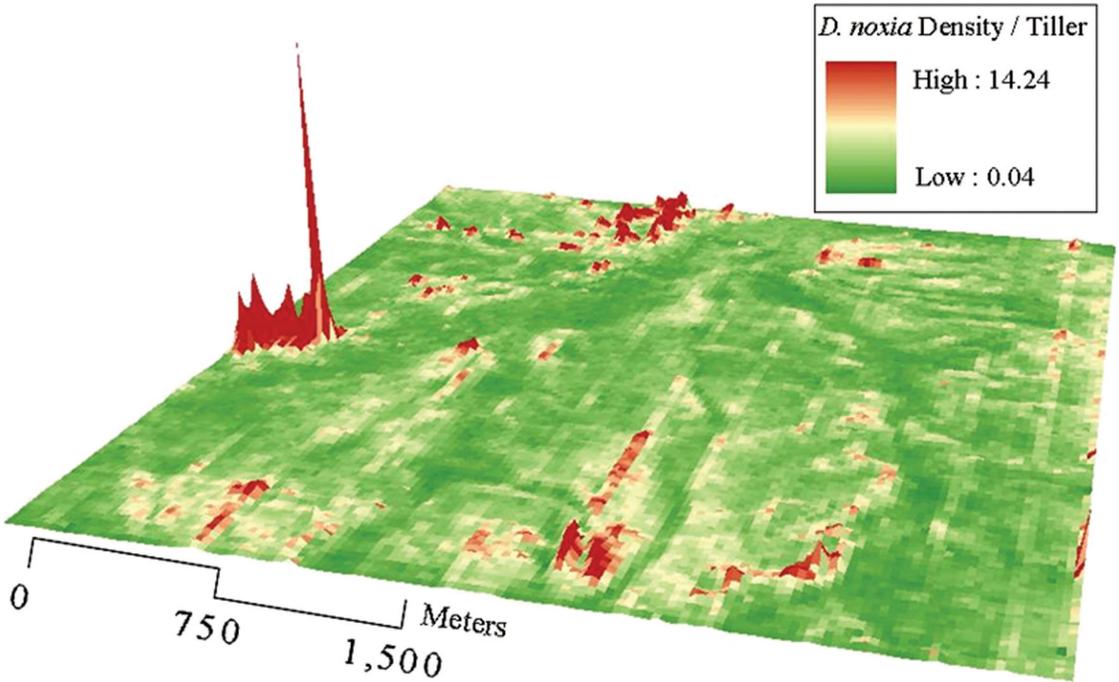
Fig. 1. The modeled *D. noxia* density trend surface model for the Last Chance Field Site, 25 April 2003 sampling date.

from the model are not spatially independent (this could lead to elevated confidence in traditional hypothesis testing were that being used). Although explained aphid density variance could be improved by including this information (e.g., with a kriged layer), the black box nature of inclusive use of spatial autocorrelation in the residuals was deemed ill-advised for a predictive model. However, this additional signal provides promise for further refinement of this model. That is, understanding that additional spatial autocorrelation exists, future examination of alternative variables or examined variables at alternate scales may lead to more accurate predictions.

Discussion and Conclusions

Application of a spatially explicit *D. noxia* density model would have numerous benefits to the agroecosystem and to the producer, including 1) reducing pesticide inputs and associated costs, 2) reducing environmental contamination, 3) improving pesticide resistance management, 4) reducing exposure to agricultural researchers, and 5) preserving refuges for natural enemies. Moreover, an increased understanding of variables that influence *D. noxia* density will increase our management opportunities.

Variables with $w_{+(i)}$ values close to 1 can be considered good predictors of *D. noxia* density and can be used to delineate areas of differential *D. noxia* population densities. Six variables have large $w_{+(i)}$ and are likely to elucidate variation in *D. noxia* densities: slope, Band 3 (S), NDVI (S), relative elevation, and the soil types LAL and Baca. Other variables have limited support in the data.

Increasing the slope was observed to decrease aphid mortality. This finding is consistent with work by Hammon and Peairs (1992) who found that fields with higher, steeper sloped irrigation beds had higher infestations than fields with lower or more shallow sloped beds. Both NDVI (S) and Band 3 (S) detect aspects of vegetation. Band 3 (S) may be detecting
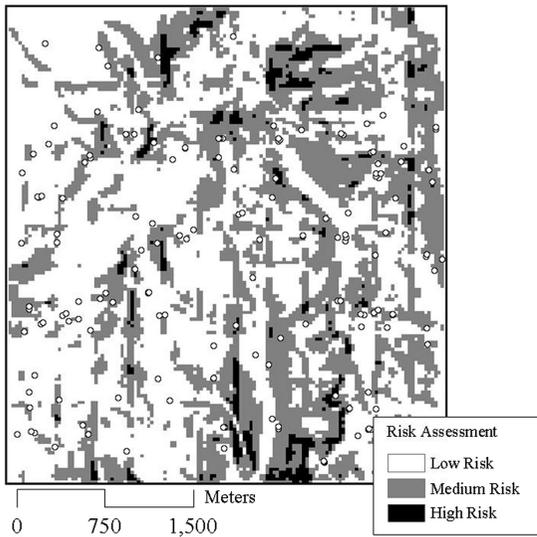
Fig. 2. A risk assessment map based on the *D. noxia* density trend surface model for the Last Chance Field Site, 19 March 2004 sampling date. White circles represent plot locations.

differences in chlorophyll absorption directly relating to symptomatic changes caused by aphid feeding (e.g., streaking or chlorosis [e.g., Fouche et al. 1984]). Or Band 3 (S) and NDVI (S) may simply describe areas where aphid hosts are located and hence, could and conversely could not survive (e.g., winter wheat versus bare soil). Relative elevation was a strong predictor of *D. noxia* density, possibly because areas of low relative elevation may have increased snow accumulation, which has been correlated to overwintering success (Armstrong and Peairs 1996). Similarly soil types, with their associated differences in soil color and texture could affect snow accumulation (e.g., albedo affects), soil moisture availability, and temperature on a microclimatic scale.

Seven of the top 11 models included at least one of the Landsat 7 ETM+ winter bands. Most of these bands are highly correlated (i.e., the lowest Pearson's pairwise correlation of $r = 0.29$ is seen between Band 5 (W) and Band 8 (W), with a pairwise average between winter Bands 2, 3, 5, and 8 of $r = 0.57$). Of the included winter Landsat imagery, Band 5 (W) is the only emissive band with a negative effect. However, Band 5 (W) is only included in a single model, which also includes Band 8 (W). In this model, Band 8 (W) has a stronger positive effect than the negative effect of Band 5 (W). Band 2 (W), and Band 3 (W) both have positive effects on *D. noxia* density. Therefore, it seems that an increase in reflectance during the winter detected by many of the winter Landsat Imagery bands is indicative of a positive effect on *D. noxia* densities. Surprisingly, some of the predictor variables (e.g., aspect) that were thought to have the strongest support from previous research (e.g., Hammon and Peairs 1992) were not supported as quality predictors during this model selection process. Variables may not have been selected or have a low weight for a number of possible reasons: 1) The scale at which they were measured (i.e., aspect was measured at a 30-m grain size) did not correspond to the scale at which they affect the dependent variable; 2) the signal that related the predictor variable to *D. noxia* density was detected more strongly by another variable (using the model framework, this correlation may have removed one of the variables from the data set); 3) the predictor variable was not a good indicator of *D. noxia* densities; or 4) the data were biased, reducing the effect size of the variable. Although temperature and precipitation have been shown to be important variables in broad-scale patterns of overwintering success (Armstrong and Peairs 1996), many of the factors that could influence *D. noxia* abundance and density on a smaller scale (e.g., soil characteristics) had not been explored previously.

Important variables were used in conjunction with a GIS to build *D. noxia* density maps on a 30-m grid scale (e.g., Figs. 1 and 2). These maps could have a variety of functions such as tools for directed scouting. In combination with directed scouting, maps may be used to limit pesticide applications to areas of the agroecosystem delineated as having high *D. noxia* densities (above the economic threshold), thus reducing pesticide usage with all of the associated benefits.

Given the large variance associated with insect populations, a model that explains a major proportion of the variance ($R^2 = 0.35$) has value. However, this model includes variation that may be caused by differential effects of natural enemies across the landscape. Although biocontrol efforts have not been shown to be highly effective in Colorado (e.g., Randolph et al. 2002), it seems unlikely that natural enemies have uniform effects across the aphid's environment or at the same scale as studied here. Development of an additional model or GIS layer for *D. noxia* natural enemies might greatly increase the variability explained. That is, there may be areas of the field that are favorable for aphid predation and conversely favorable for predator avoidance by the aphids. Developing a spatially explicit predator prey model might greatly enhance our ability to spatially predict *D. noxia* densities, and provide information for more efficient placement of natural enemy refuges. Other variables, such as alternate vegetation indices (e.g., soil-adjusted vegetation index), may explain additional variation in aphid density. However, post hoc analysis of additional variables was deemed ill-advised for use in a predictive model. Data were collected from winter wheat fields that were heavily infested at a uniform rate. Different infestation rates (e.g., natural infestations), different crops, and environmental conditions outside of the range tested in this study may produce different results. However, the exceptional promise shown by the model's ability to predict aphid density could allow for drastic reduction in pesticide usage and thereby promote a more judicious integrated pest management strategy, which could provide all of the benefits associated with pesticide reduction. Moreover, increasing our understanding of the variables that are important to *D. noxia* overwintering success will lead to an increased ability to develop future aphid population dynamic models and hypotheses.

Acknowledgments

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