

Quantifying Russian Wheat Aphid Pest Intensity Across the Great Plains

SCOTT C. MERRILL¹ AND FRANK B. PEAIRS²

Environ. Entomol. 41(6): 1505–1515 (2012); DOI: <http://dx.doi.org/10.1603/EN12172>

ABSTRACT Wheat, the most important cereal crop in the Northern Hemisphere, is at-risk for an approximate 10% reduction in worldwide production because of animal pests. The potential economic impact of cereal crop pests has resulted in substantial research efforts into the understanding of pest agroecosystems and development of pest management strategy. Management strategy is informed frequently by models that describe the population dynamics of important crop pests and because of the economic impact of these pests, many models have been developed. Yet, limited effort has ensued to compare and contrast models for their strategic applicability and quality. One of the most damaging pests of wheat in North America is the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov). Eighteen *D. noxia* population dynamic models were developed from the literature to describe pest intensity. The strongest models quantified the negative effects of fall and spring precipitation on aphid intensity, and the positive effects associated with alternate food source availability. Population dynamic models were transformed into spatially explicit models and combined to form a spatially explicit, model-averaged result. Our findings were used to delineate pest intensity on winter wheat across much of the Great Plains and will help improve *D. noxia* management strategy.

KEY WORDS spatial model, pest, agriculture, *Diuraphis noxia*, Russian wheat aphid

Human nutrition worldwide is generated primarily from cereal crops (Tilman 1999). One of the most important of these cereal crops is wheat, with over two thirds of a billion tons produced in 2009 across the planet (FAO 2011). Pests cause billions of dollars of damage to wheat crops annually, with production loss from animal pests roughly estimated to be 7.9% (Oerke 2006). However, pest intensity varies substantially from year to year, and damage can range from indiscernible to complete crop loss (Morrison and Peairs 1998). Substantial monetary and research resources have been dedicated to studying agroecosystems to help predict when and where economically damaging pest infestations will occur. Yet there has been little advance in the science of predicting interannual variability in pest intensity. One measure of pest intensity is aphid days, which quantifies the accumulated number of aphids per tiller per day (Ruppel 1983). For example, five aphids spending 7 d on a tiller of wheat would result in the accumulation of 35 aphid days.

Our goal was to use aphid days to delineate conditions that may lead to pest outbreaks, in this case with the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Hemiptera: Aphididae). Within this overarching goal, we sought to resolve the importance of en-

vironmental factors and seasonal effects on pest intensity, largely from a mechanistic perspective.

From a trophic standpoint, pest intensity may be controlled largely by food availability or quality (Girma et al. 1990, Bale et al. 2002). Moreover, predation and parasitism may greatly reduce pest density (Brewer and Elliott 2004, Lee et al. 2005). Pest intensity should decrease with food limitations and with increasing risk of mortality from natural enemies. The complexity of explicit inclusion of trophic interactions on pest intensity is vast. Therefore, we directed our efforts primarily toward quantifying pest intensity explicitly though pest phenological and physiological factors, which will implicitly include many trophic interactions. Because insect pests are primarily ectothermic, phenological and physiological factors are largely dependent upon environmental conditions (Deutsch et al. 2008). Pests use a variety of strategies to optimize survival during adverse seasonal periods (e.g., overwintering dormancy strategies). The success of these strategies largely depends upon the severity of environmental conditions (Tauber et al. 1986, Leather et al. 1995). Models seeking to forecast pest intensity frequently rely on quantifying the effect of environmental conditions on pest populations (Luedeling et al. 2011).

A rich literature exists describing the influence of the environment on small grain aphids, including a substantial body of work on *D. noxia* (Quisenberry and Peairs 1998). This aphid pest has caused in excess of one billion dollars in damage to small grains, princi-

¹ Corresponding author: S. C. Merrill, Department of Plant and Soil Science, University of Vermont, Burlington, VT 05405-0082 (e-mail: scott.c.merrill@uvm.edu).

² Department of Bioagricultural Sciences and Pest Management, Colorado State University, Fort Collins, CO 80523-1177.

pally wheat, since its introduction into North America in the mid-1980s (Morrison and Peairs 1998). *Diuraphis noxia* is a phloem feeding pest that relies primarily on year round parthenogenic reproduction within the United States (Fouche et al. 1984, Halbert and Stoetzel 1998). Seasonality of *D. noxia* populations can be described by using four phases: 1) Spring population growth, which is characterized by peak annual abundance and damage. 2) The overwintering phase, which describes the period from crop senescence and harvest through emergence in the fall of the winter wheat crop. This phase typically extends from approximately July through September. During this phase *D. noxia* primarily rely on noncultivated grasses, which are often poor hosts relative to wheat and barley, and are frequently heat or drought stressed. 3) Fall infestation, which describes the phase during which emerged winter wheat is potentially infested by *D. noxia* immigrants. And 4) the overwintering phase, which commonly features population reductions caused by adverse weather conditions. Overwintering aphids can be found on numerous grass hosts but are less of a concern on noncultivated hosts because of the reproductive delay necessitated by emigration to crops.

Models seeking to predict *D. noxia* density and damage frequently attempt to quantify the effect of one or more of these phases. Arguments exist as to the importance of each of these phases and predictive quality of each of the population dynamic models (Merrill et al. 2010). We sought to clarify the ability of existing aphid population dynamic models to predict *D. noxia* intensity. Moreover, attempts were made to create additional aphid population models to quantify the hypothesized effects of seasonal environmental conditions. For example, the relationship between temperature and population growth has been described with optimal fecundity occurring when average temperatures are $\approx 18^{\circ}\text{C}$ (Merrill et al. 2009). Thus, regional average temperatures during the spring likely influence *D. noxia* density mediated through physiological changes in insect metabolic growth rates such as measures of fecundity and intrinsic rate of increase (Merrill et al. 2009).

Many models exist to explicitly describe population dynamics of *D. noxia*. More exist when one considers that environmental factors that impact one small grain aphid species likely have a similar effect on other small grain aphid species (e.g., the relationship between cold temperatures and *D. noxia*'s population growth rate is similar to that of *S. avenae* [Merrill et al. 2009]). Aphid population dynamic models generally describe the relative fitness of a population or factors that modulate mortality.

Aphid populations are expected to increase during the spring phase and factors that dampen or strengthen growth are used frequently to model population size. For example, Legg and Brewer (1995) used heat units and rainfall to predict *D. noxia* population growth, with cumulative heat positively affecting growth and rainfall negatively affecting population growth. Negative relationships between rainfall and aphid populations exist, possibly because aphid feeding

is physically disrupted by precipitation (e.g., aphids may be knocked off the crop) or because nearby rain-induced disturbance triggers a defensive dropping (predator avoidance) behavior by the aphid (e.g., resulting in reduced time on their food source and increased risk of attack by ground predators) (Legg and Brewer 1995, Mann et al. 1995, Kerzicnik et al. 2010).

The harsh overwintering phase is marked by factors that will increase mortality, such as a lack of food or temperatures that are above optimal reproductive thresholds. For example, *D. noxia* feed solely on C3 grasses (Armstrong et al. 1991). Because *D. noxia* rely on noncultivated grasses during the overwintering phase, availability of C3 grasses should influence aphid population mortality. Therefore, we can use environmental conditions associated with high C3 plant productivity as a measure of aphid mortality and consequently pest intensity in the next season. Substantial research suggests that increased time spent above high temperature thresholds decreases aphid reproductive rates (Ma and Bechinski 2008). Moreover, Archer and Bynum (1993) noted that *D. noxia* abundance during the fall in Texas was low and alate forms were common. They postulated that low aphid abundance was a result of the long period between crop harvest and emergence combined with high temperatures during this period.

Relatively little is known about the effects of environmental conditions on aphid population dynamics during the fall phase. Anecdotally, warm and dry fall conditions are suspected to benefit infestation of the winter wheat crop and subsequent aphid population growth.

Models describing the overwintering phase of aphid population dynamics frequently rely on the duration or intensity of cold temperatures (e.g., decrease in reproductive success caused by chill damage (Knight et al. 1986) or by decreased physiological growth rates [Merrill et al. 2009]). In addition, winter precipitation has been correlated with overwintering success because snow cover appears to insulate *D. noxia* from colder air temperatures (Armstrong and Peairs 1996). However, extended snow cover does not allow for reproduction and is suggested to result in localized population extinction after ≈ 40 d of continuous cover (Armstrong and Peairs 1996). Therefore, snow cover is expected to have a nonlinear relationship with aphid survival. Moreover, the influence of rainfall during winter months is unclear, but likely would affect aphid populations differently than snow cover given the same quantity of precipitation.

We found many different lower temperature thresholds reported in the literature (Legg and Brewer (1995) use 4.1°C and Armstrong and Peairs (1996) use 0°C). Development thresholds are difficult to quantify primarily because high aphid mortality occurs in these marginal temperature regions. Thus, most studies extrapolate data to find upper and lower temperature thresholds, often using different methodologies and resulting in different threshold values.

As noted, numerous models exist that could be used to explain *D. noxia* population dynamics. That is, there are a lot of models and anecdotal "evidence," each

advocating the virtues of their approach for predicting aphid population dynamics (Merrill and Holtzer 2010). However, there seems to be a dearth of validation of these models and arguments. Thus, we used an independently obtained database of *D. noxia* densities collected over multiple growing seasons to test the relative quality of each of these models for predicting *D. noxia* intensity. Moreover, we sought to combine the good models to increase our ability to understand and predict *D. noxia* growing season infestations.

Methods

We obtained *D. noxia* density data across a broad spatial extent, observed over the course of multiple winter wheat growing seasons. Samples were taken during the course of the USDA-ARS Areawide Pest Management of Russian Wheat Aphid and Greenbug project. Specifically, *D. noxia* density samples were obtained at 21 winter wheat field sites across Texas, Oklahoma, Colorado, Nebraska, and Wyoming. Our design sought for 25 plots sampled at each site, multiple times per year over four growing seasons (2002–2006). Sample design called for 100 tillers to be removed from each plot. Tillers were clipped, placed into ziplock bags, and transported to the laboratory. Tillers then were removed from the ziplock bags and placed into Berlese funnels for ≈ 24 h to extract the aphids for counting under a dissecting microscope. Plot measurements were averaged to obtain a within-site, within-sample date average aphid density. Four hundred and forty-nine measurements of within-site, within-sample date average aphid density were obtained.

Aphid days were calculated for each site for each growing season (Ruppel 1983). Aphid days were calculated by averaging the aphid density measurements between sample dates multiplied by the number of days between sampling dates, repeated for each intrasampling period, and then summed (Ruppel 1983). Seventy-seven measures of aphid day accumulations were calculated (seven measures were not calculated because of missing data). Because aphid day data were skewed, the natural log of aphid days per site per year were treated as the response variable and tested against the predictor models (Archer and Bynum 1993). Aphid days have been correlated with yield loss and thus can be considered a measure of pest intensity (Archer and Bynum 1992).

Aphid population dynamic models were tested to determine their relative strength for determining the patterns in aphid day accumulations. Eighteen population dynamics models (PDMs) were developed and tested against aphid days as detailed starting with the models quantifying dynamics during the spring phase:

Models describing aphid populations during the spring frequently examine relationships between population growth and temperature, and aphid population mortality associated with increased rainfall. Our first PDM was an index of a population growth model developed by Legg and Brewer (1995). They used cumulative *D. noxia* aphid days regressed against heat

units and rainfall (accumulation starting when the first aphid was detected) to predict population growth:

$$\hat{Y} = 0.2608 * \text{CHU}^{0.3} - 0.000012666 * \text{CRF}^{1.9}$$

$$\text{Aphid Days} = (\hat{Y})^{12.658}$$

where CHU are cumulative heat units (Degree days above 4.1°C, accumulation starting at first detection) and CRF are cumulative rainfall units (millimeters, accumulated starting at first detection).

If \hat{Y} was negative, it was considered locally extinct, and thus, transformed to zero.

Because first aphid detection was not a reasonable measurement in this data set (e.g., aphids were detected at some sites in the fall and had continued low level rates through the winter), we used accumulated degree-days and rainfall units during the months of April and May as inputs into the Legg and Brewer (1995) model to serve as an index of *D. noxia* intensity (PDM 1).

In addition, Legg and Brewer (1995) found a negative relationship between spring rainfall and *D. noxia* populations. Thus, our second model used precipitation from 1 April to 31 May as an index of population mortality (PDM 2).

Models describing the effects of the harsh overwintering period typically seek to quantify mortality caused by high temperatures and low food resources. *Diuraphis noxia* are obligate feeders on C3 grasses, and thus, quantification of C3 plant availability could be a good index of aphid mortality. Epstein et al. (1997) quantified C3 plant productivity across the Great Plains region by using mean annual temperature and mean annual precipitation.

C3 Productivity Index (PDM 3)

$$= \text{MAT} * (-11.240) + \text{MAP} * 0.322 + 178.6$$

where MAT is mean annual temperature in Celsius, MAP is mean annual precipitation in centimeters (PDM 3).

Degree days above 28°C in July (i.e., the hottest month in the year throughout the Great Plains) were used as an index (PDM 4) of the severity of overwinter conditions with increasing time spent above the high temperature threshold hypothesized to decrease reproductive rates.

As noted previously, little research exists to quantify the effects of environmental conditions during the fall. However, anecdotally, the effects of warm and dry fall conditions are expected to increase aphid populations. These two factors were quantified individually using precipitation and average temperature from 1 October to 30 November (PDMs 5 and 6).

Overwintering models typically quantify the negative effects of winter severity on aphid populations. Population dynamic model 7 was developed using the research of Dewar and Carter (1984) predicting the size of the aphid spring flight from winter severity data. They quantified overwintering severity as the time spent below 0°C from October through April. The number of degree-days below 0°C from 1 October to 30 April was used as an overwintering severity index (PDM 7).

Knight et al. (1986) suggested chill damage occurs with increased time under -8.1°C . The number of accumulated degree-days under -8.1°C in January (the coldest month in the Great Plains region) was used as a measure of winter severity (PDM 8).

Armstrong and Peairs (1996) correlated decreasing overwintering success of *D. noxia* populations with increasing time spent below 0°C . Accumulated degree-days from 1 December to 28 February were used to quantify this winter severity model (PDM 9).

Merrill and Holtzer (2010) argued that *D. noxia* populations during the winter are reproduction limited as contrasted with cold damaged. Thus, a combination of increasing precipitation and increasing degree-days above 0°C equate to increasing *D. noxia* population (PDM 10).

No spatially-explicit, winter precipitation models were found that incorporated the predominately positive effects of snow cover, and predominantly negative effects of winter rainfall. Because of the complex threshold dynamics associated with snow cover, snow cover duration, and rainfall (Armstrong and Peairs 1996), we did not include a winter precipitation model in this analysis.

In addition to models seeking to describe aphid population structure within a season (e.g., spring population-density models), population growth rate parameters can be quantified for each season throughout the year. Merrill et al. (2009), using a meta-analysis approach, developed nonlinear curves describing the relationship between temperature and lifetime average fecundity. Using this relationship, population growth models were calculated for each season based on the average temperature during that season. Specifically, PDMs 11–14 are indices of population growth by using average temperatures from the spring, summer, fall, and winter:

Lifetime average fecundity

$$= 55.34 * e^{-((\text{Temperature} - 18.40)^2)/92.46}$$

Additional population growth models were calculated for each season by using the intrinsic rate of increase approximation of Wyatt and White (1977) with temperature and the life history trait inputs; pre-nymphositional period, and daily fecundity rate (Merrill et al. 2009) (PDMs 15–18):

$$\text{Daily Fcnd} = 2.1 * e^{-((\text{Temperature} - 20.6)^2)/131.0}$$

$$\text{Prenymph} = 353.61 * \text{Temperature}^{-1.14}$$

Intrinsic rate of increase (r_m)

$$= 0.74 * \ln(\text{Prenymph} * \text{Daily Fcnd}) / \text{Prenymph}$$

where Prenymph is the pre-nymphositional period and Daily Fcnd is the Daily Fecundity. Informed by spatially explicit temperatures averages, we used intrinsic rate of increase calculations and average lifetime fecundity calculations to create temperature-specific population increase models for each of the four seasonal phases resulting in eight models (e.g., Spring Fecundity, Spring Intrinsic Rate of Increase,

Summer Fecundity, and others) with spring defined as 21 March–20 June, summer (21 June–20 September), fall (21 September–20 December), and winter (21 December–20 March).

Each of the aforementioned predictor models (e.g., PDM 7; Dewar and Carter (1984) fall and winter severity model) could be used to derive a measure of aphid population success. Each of the predictor models (PDMs) was transformed into a geographic information system (GIS) layer. Specifically, because each PDM was derived using environmental covariates (e.g., precipitation) approximations of environmental covariates at each site for each year could be used to generate predictions for each PDM. Although each PDM is derived from environmental covariates, covariates are different between PDMs. For example, the overwintering models all use temperature during the winter but measure the effects or duration of those temperature data differently (e.g., time spent under -8.1°C as a measure of chill damage versus time spent above 0°C , which is likely related to reproduction).

Unfortunately, measures of heat accumulation and cold accumulation (e.g., degree-days below 0°C) were not readily available at resolutions applicable to *D. noxia* physiology or phenology. That is, spatially explicit weather data were available on a monthly basis and spatially implicit data (e.g., weather station data) were available on a daily basis, but daily spatially-explicit data were unavailable. One solution to this problem was to synthesize multiple sources of weather data for each site for each year using spatially-explicit, but temporally coarse, weather data and spatially-implicit daily weather data (S.C.M. and F.B.P., unpublished data). The PRISM climate group (PRISM 2004) provided monthly total precipitation, average maximum temperature, and average minimum temperature data on a 4-km² gridded surface for the entire United States. Extending spatially-explicit monthly data to daily data required quantification of the distribution of daily average temperatures within a month. S.C.M. and F.B.P. (unpublished data) developed a measure of within-month, daily temperature variation (i.e., standard deviation) using daily temperature data collected from weather stations over a 30-yr time period (1971–2000). Moreover, because we used temperature developmental thresholds, we quantified the number of days in a given month that were likely to fall above or below these thresholds and calculated the mean value of temperatures for each of those days. Using these temperature distributions, we were able to create an estimate of the number of degree-days accumulated on any given day.

With spatially and temporally explicit degree-day layers, used in concert with other environmental GIS layers (e.g., precipitation layers obtained from the PRISM climate group [PRISM 2004]), we were able to transform many spatially-implicit insect PDMs into spatially-explicit models. For example, Dewar and Carter (1984) suggest that the size of the aphid flight in the spring would decrease as degree-days below 0°C accumulate from October to April (PDM 7). Therefore, using the aforementioned spatially-explicit de-

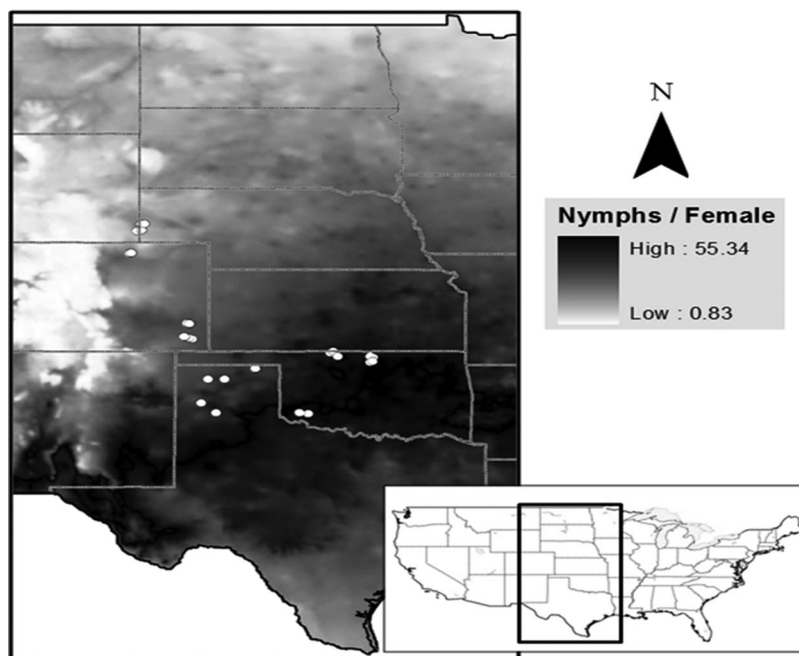


Fig. 1. Spring Fecundity modeled using weather conditions observed in the spring of 2005. Spatially explicit models quantifying the relationship between observed spring average temperature and estimated aphid fecundity were developed from formulas in Merrill et al. (2009). White circles indicate field site locations. Lower right inset depicts the portion of the United States modeled.

gree-day methodology, degree-days below 0°C were calculated for each grid cell across the Great Plains from October to April and used to create a fall and winter severity GIS layer. Geographic Information System layers for each PDM were developed for use as predictor variables. Specifically, values were extracted from each PDM layer in conjunction with the observed aphid day accumulation values. For example, Fig. 1 depicts the Spring Fecundity GIS layer (PDM 15) derived using 2005 spring weather conditions. Once spring fecundity was quantified in a GIS format, values were extracted from the layer at each site-specific location (i.e., values were extracted from the 2005 Spring Fecundity (PDM 15) layer at each of the white circles depicted on Fig. 1).

We hypothesized that a combination of multiple PDM layers likely would predict aphid days better than any single PDM layer (e.g., conditions during the winter plus conditions during the spring would likely predict better than spring conditions alone). Unfortunately, this creates a confusing syntax. The population dynamic models (PDMs), which were turned into PDM layers, will be referred to as predictor variables. Models that regressed individual or combinations of predictor variables against aphid days are labeled candidate models (i.e., candidates for being the best model for predicting aphid days). We used an information-theoretic approach for candidate model selection and multimodel inference (Burnham and Anderson 2001, 2002, 2004). We linearly regressed all subsets of the predictor variables against the log of aphid days

by using the GLMulti function in R (GLMulti package, R Development Core Team 2008). That is, all subsets of candidate models of the following form were created and tested for model fit:

$$\ln(\text{aphid days} + 0.1) = \text{intercept} + \beta_1 * (\text{predictor variable}_1) + \beta_2 * (\text{predictor variable}_2) \dots$$

Akaike's Information Criterion adjusted for small sample sizes (AICc) was used to quantify goodness-of-fit (Burnham and Anderson 2002, 2004). For each candidate model, we calculated values for AICc; ΔAICc (ΔAICc measures the distance between the best AICc candidate model and the candidate model of interest); AICc L (which quantifies the likelihood that the candidate model is the best candidate model given the data); and AICc weight (AICc w_i , provides a measure of the probability that the selected candidate model is the best model within the selected candidate model set, given the data) (Burnham and Anderson 2002, 2004). Models were removed from the candidate model set if they were parameterized such that values were beyond a biologically meaningful range or were biologically illogical. For example, if a candidate model was parameterized to suggest that aphid populations increased with increased accumulation of degree-days below -8.1°C , the model was removed from the candidate model set. Remaining candidate models with strong likelihoods of being the best approximating model (AICc $L > 0.05$) were selected and used for multimodel inference.

Variable relative importance weight is the sum of the AICc w_r s over all candidate models in which a predictor variable occurs. For example, if the predictor variable Spring Precipitation occurs in three of the selected candidate models, with AICc w_r s of 0.4, 0.2, and 0.1, then the Spring Precipitation predictor variable's relative importance weight would equal 0.7 and would be compared with the relative importance weight of the other tested variables (Burnham and Anderson 2002, 2004). The resulting variable relative importance weights can range from 0 to 1. The more important predictor variables have weights with higher values. Because a variable's relative importance weight is derived from AICc w_r s, they could be interpreted as the probability of the predictor variable being an important predictor variable for understanding variation in aphid days.

Multimodel averaging was used to create a model-averaged result (Burnham and Anderson 2002, 2004). The model-averaged result was calculated using a weighted average of the selected candidate models, weighted with their associated AICc w_r s:

$$\ln(\text{aphid days} + 0.1) = \sum w_r * \text{model}_r \text{ for all} \\ \text{selected candidate models } r$$

For each growing season, GIS surfaces of the model-averaged aphid day result were created using the raster calculator function in ArcMap 9.3 (ESRI 1999–2008).

Additional to methodology described above, simple interpolated surfaces were developed using accumulated aphid day data to examine how the spatial structure of the data changed over the course of the growing season. Surfaces quantifying the natural log of aphid day accumulations were created using ordinary kriging (Cressie 1993) in ArcMap 9.3 (ESRI 1999–2008) for the full season and for aphid day accumulations accrued by the middle of the spring (6 May). Using ordinary kriging without removing variation associated with important covariates can lead to misleading results. However, for purposes of quantification of within-season change, these interpolated surfaces provide increased insight into the within-season changes in the spatial structure of these data.

Results and Discussion

Measurements of aphid days ranged from no observed *D. noxia* (zero aphid days, observed 20 times) to 54,389 aphid days observed in 2004 in western Nebraska (latitude 41.688, longitude -104.003). The median aphid day measurement was 262 aphid days, which would be considered a relatively low infestation and would likely not receive a recommendation for a pesticide application.

Of the predictor variables (PDMs), the best was C3 plant productivity (AIC $w_r = 0.989$, $P < 0.001$, F-stat = 77.54, DF = 75, Adj $R^2 = 0.50$). Fall Precipitation and Spring Fecundity came in a distant second and third, respectively.

However, no single predictor variable (PDM) captured the variability of aphid days as well as candidate models with a combination of predictor variables. Of the tested candidate models, 30 were selected as being good candidate models (Table 1). Adjusted R^2 values ranged between 0.68 and 0.71. All 30 candidate models included two predictor variables: C3 plant productivity and fall (October and November) precipitation. Thus, these two predictor variables had relative importance weights of one (Table 2) and were highly correlated with aphid days. Increased summer C3 plant productivity and decreased fall precipitation were associated with increased aphid populations. Spring Precipitation was included in all of the top 21 selected candidate models with a strong variable relative importance weight of 0.8. Thus, increasing spring rainfall was associated tightly with decreasing aphid days. Three overwintering variables (July Intrinsic Rate of Increase: variable importance weight = 0.33, July Degree Days above 28°C: variable importance weight = 0.33, and July Fecundity: variable importance weight = 0.30) each had approximately a one-thirds probability of being correlated with overwintering aphid population dynamics, and thus, aphid days in the next season. These relatively low variable importance weights indicate marginal value in delineating aphid days. However, some measure of the overwintering effect (in addition to C3 plant productivity) was included in 21 of the 30 selected candidate models. Spring Fecundity also has a relatively low variable importance weight of 0.30 (selected in nine of the 30 models). Increased spring fecundity was parameterized to increase the number of aphid days. Three additional variables were found to have low variable importance weights: Fall temperature had a variable importance weight of 0.20 (selected in six of the 30 models). The index (PDM 1) created from Legg and Brewer's (1995) research was an important variable in three of the candidate models with a variable relative importance weight of 0.10. The winter severity index (PDM 7) developed from Dewar and Carter (1984) received a variable relative importance weight of 0.10 (selected in three of 30 models). While these weights are low, they can be interpreted as the probability that, given a similar data set obtained under similar conditions, ≈10–20% of the time, each would be chosen as a component variable in the best AICc selected model. That is, even though these three variables have relatively low value compared with other selected variables, there is some probability that they could each be an important variable for delineating variation in aphid days. The following eight predictor variables were not selected in any of the top 30 candidate models: Knight et al. (1986) chill damage model (PDM 8), Armstrong and Peairs (1996) overwintering model (PDM 9), Merrill and Holtzer (2010) overwintering model (PDM 10), Fall Fecundity (PDM 13), Winter Fecundity (PDM 14), Spring Intrinsic Rate of Increase (PDM 15), Fall Intrinsic rate of increase (PDM 17), and Winter Intrinsic Rate of Increase (PDM 18).

Table 1. Candidate models selected for multimodel inference

Rank	Predictor variables: ^a in (aphid days + 0.1) =	AICc	ΔAICc	AICc L	AICc w _r
1	Fall PPT, Spr PPT, C3 Prod	363.258	0.000	1.000	0.141
2	Fall PPT, Spr PPT, C3 Prod, July Fecd	364.477	1.219	0.544	0.077
3	Fall PPT, Spr PPT, C3 Prod, July DD > 28C	364.499	1.242	0.538	0.076
4	Fall PPT, Spr PPT, C3 Prod, Spr Fecd	364.703	1.445	0.486	0.069
5	Fall PPT, Spr PPT, C3 Prod, July r _m	364.984	1.726	0.422	0.060
6	Fall PPT, Spr PPT, C3 Prod, Fall T	365.224	1.966	0.374	0.053
7	Fall PPT, Spr PPT, C3 Prod, Spr Fecd, July Fecd	365.351	2.093	0.351	0.050
8	Fall PPT, Spr PPT, C3 Prod, DC Index	365.555	2.297	0.317	0.045
9	Fall PPT, Spr PPT, C3 Prod, LB Index	365.610	2.352	0.309	0.044
10	Fall PPT, Spr PPT, C3 Prod, Spr Fecd, July DD > 28C	365.860	2.602	0.272	0.038
11	Fall PPT, Spr PPT, C3 Prod, July Fecd, July r _m	366.106	2.849	0.241	0.034
12	Fall PPT, Spr PPT, C3 Prod, July Fecd, July DD > 28C	366.800	3.542	0.170	0.024
13	Fall PPT, Spr PPT, C3 Prod, July Fecd, Fall T	366.802	3.544	0.170	0.024
14	Fall PPT, Spr PPT, C3 Prod, July r _m , July DD > 28C	366.806	3.548	0.170	0.024
15	Fall PPT, Spr PPT, C3 Prod, Spr Fecd, July r _m	366.883	3.625	0.163	0.023
16	Fall PPT, Spr PPT, C3 Prod, July DD > 28C, Fall T	366.893	3.635	0.162	0.023
17	Fall PPT, Spr PPT, C3 Prod, Spr Fecd, Fall T	367.080	3.822	0.148	0.021
18	Fall PPT, Spr PPT, C3 Prod, Spr Fecd, LB Index	367.110	3.852	0.146	0.021
19	Fall PPT, Spr PPT, C3 Prod, July r _m , Fall T	367.266	4.008	0.135	0.019
20	Fall PPT, Spr PPT, C3 Prod, July r _m , DC Index	367.358	4.100	0.129	0.018
21	Fall PPT, Spr PPT, C3 Prod, Spr Fecd, July Fecd, July r _m	367.593	4.335	0.114	0.016
22	Fall PPT, C3 Prod, July DD > 28C	367.693	4.435	0.109	0.015
23	Fall PPT, Spr PPT, C3 Prod, Spr Fecd, July Fecd, July DD > 28C	367.844	4.586	0.101	0.014
24	Fall PPT, C3 Prod, July r _m	367.886	4.628	0.099	0.014
25	Fall PPT, Spr PPT, C3 Prod, LB Index, DC Index	367.977	4.719	0.094	0.013
26	Fall PPT, C3 Prod, July Fecd, July r _m	368.200	4.943	0.084	0.012
27	Fall PPT, C3 Prod, Spr Fecd, July DD > 28C	368.708	5.450	0.066	0.009
28	Fall PPT, C3 Prod, July r _m , July DD > 28C	369.040	5.782	0.056	0.008
29	Fall PPT, C3 Prod	369.130	5.872	0.053	0.008
30	Fall PPT, Spr PPT, C3 Prod, July Fecd, Fall T, July DD > 28C	369.249	5.991	0.050	0.007

^a Where Spr is spring, PPT is precipitation, Prod is productivity, Fcnd is fecundity, DD is degree days, LB Index refers to an index developed from the population dynamic model of Legg and Brewer (1995), DC Index refers to an index of the population dynamic model developed from Dewar and Carter (1984), T is temperature, and r_m denotes the intrinsic rate of increase.

The only selected predictor variable associated with winter conditions was PDM 7 developed from Dewar and Carter (1984), which had a low variable relative importance weight. On the surface, this would argue that winter severity (with a summed variable importance weight of 0.1) is less important than variables associated with spring conditions (with summed variable importance weights of 1.2), summer conditions (with summed variable importance weights of 0.96 not including C3 productivity) or fall (with summed vari-

able importance weight of 1.00). However, we should note that these variables are not causal and may be associated with other patterns. For example, the C3 plant productivity (PDM 3) is calculated using a function of mean annual temperature and mean annual precipitation. Patterns created by C3 productivity likely relate to environmental factors additional to plant productivity, possibly inclusive of aphid population reductions during the winter. That is, areas with lower mean annual temperature typically observe more severe winters. Therefore, it is reasonable to say that C3 productivity is highly correlated with *D. noxia* intensity but unreasonable to assume (from this analysis) a causal or definitive relationship between plant community composition and *D. noxia* intensity.

The 30 candidate models selected were averaged together using their model specific AICc weights (w_s) resulting in the following model-averaged formula:

$$\ln(\text{aphid days} + 0.1) = -1.683 + 0.024 * \text{Fall T} \\ - 0.28 * \text{Fall PPT} - 0.00016 * \text{DC} - 0.028 * \\ \text{Spring PPT} + 0.019 * \text{Spring Fecd} + 0.093 * \\ \text{C3 Prod} - 0.16 * \text{DD}28^{\circ}\text{C} + 9.45 * \text{July } r_m \\ + 0.012 * \text{July Fecd} + 0.0000011 * \text{LB}$$

where T is temperature, PPT is precipitation, DC refers to the PDM seven developed from Dewar and Carter (1984), Fcnd is fecundity, Prod is productivity,

Table 2. Variable relative importance weight

Variable rank	Predictor variable (model) ^a	Variable relative importance wt	Parameter value	Effect direction
1	Fall precipitation	1.00	-0.281	-
1	C3 productivity	1.00	0.0927	+
3	Spring precipitation	0.80	-0.0281	-
4	July r _m	0.33	9.452	+
4	July degree days > 28°C	0.33	-0.163	-
6	July fecundity	0.30	0.0124	+
6	Spring fecundity	0.30	0.0191	+
7	Fall temperature	0.20	0.0239	+
9	Legg and Brewer index	0.10	0.00000111	+
9	Dewar and Carter index	0.10	-0.000163	-
X	Intercept	N/A	-0.811	-

^a Where r_m denotes the intrinsic rate of increase.

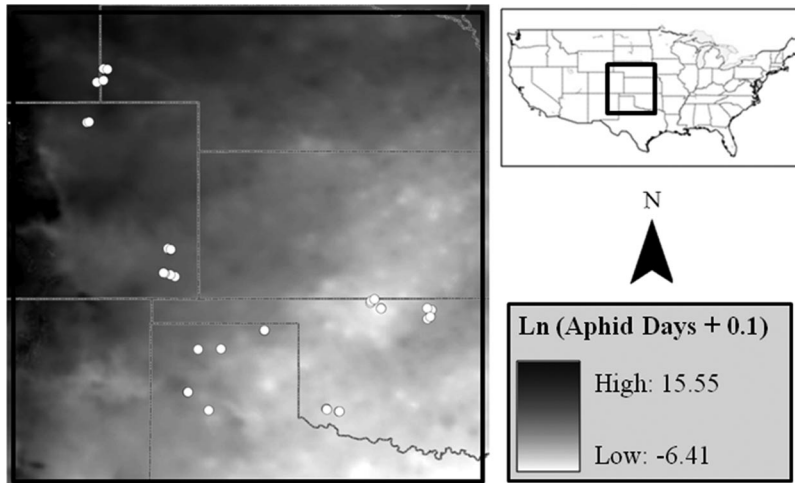


Fig. 2. Model-averaged results depicting the log of the accumulated *D. noxia* aphid days (i.e., $\text{Ln}[\text{aphid days} + 0.1]$) calculated using environmental conditions observed from July 2002 to June 2003. The area modeled is in the Great Plains from ≈ 33 to 43° latitude and from 96 to 106° longitude. White circles indicate field sites.

$\text{DD}_{28^\circ\text{C}}$ is PDM four quantifying the number of degree-days accumulated above a 28°C threshold in July, r_m denotes the intrinsic rate of increase, and LB refers to PDM one developed from Legg and Brewer (1995).

The model-averaged result was calculated as a GIS surface using the raster calculator function in ArcMap 9.3 (ESRI 1999–2008). For example, Fig. 2 depicts aphid day accumulations for the 2002–2003 growing season. This figure suggests aphid intensity decreasing in high precipitation regions and regions where high temperature regimes marginalized aphid survival. The high adjusted R^2 values (i.e., ≈ 0.7) associated with all selected candidate models argues that a real signal in the aphid day data are being detected. We suggest that modeling results should be viewed with limited confidence in regions where input variable values are well beyond observed values at the field sites (e.g., C3 plant productivity, precipitation and temperature values found in mountainous regions or regions well north of our northernmost sites).

The general pattern created by our results does not correlate well with areas of suggested high yield loss (Archer et al. 1998, Elliott et al. 1998). Previous research suggested yield loss caused by aphid feeding damage was high in relatively southern climatic zones within the Great Plains (e.g., southeastern Colorado and Texas) and, contrasting with our aphid intensity results, showed decreasing yield loss values in increasingly northern climatic zones (e.g., Wyoming and Montana). The discrepancy between areas with high yield loss and areas depicted by Fig. 2 to have high *D. noxia* intensity causes some concern. Model results, which show a dearth of the effects of winter severity, depict increasing aphid days with increasingly northern latitudes. This result, at some point, must be incorrect. Further consideration of model parameterization highlights one factor that was not considered during the analysis. That is, length of growing season was not included in the model parameterization and

may have dramatic effects on aphid day accumulations. Harvest date and crop growth stage are both related to growing degree-days, which in turn is tightly correlated to latitude. Because later harvest dates can be correlated with increasingly northern latitudes, aphid populations have increased time to accumulate as latitude increases. Aphid day accumulations should increase with lengthening seasons and with northern sites. Moreover, plant-herbivore interactions, including resources allocated toward resistance and tolerance, change over ontology. Boege and Marquis (2005) found that these changes typically result in more feeding damage occurring at intermediate plant growth stages. More specifically, relationships between crop growth stage and yield loss from *D. noxia* feeding damage have been quantified, with more damage occurring during intermediate crop growth stages such as jointing (i.e., Zadoks growth stages Z30–Z39) (Girma et al. 1993). When crops are infested at later, more tolerant wheat growth stages, less yield loss is expected. Thus, aphid population will result in increased yield loss if found on an intermediate growth stage as compared with an equivalent aphid population size that occurs at late growth stages (this analogy assumes that both populations were limited in their time spent on wheat and that the earlier population was extirpated from the wheat after an equivalent time interval).

To confirm the possibility that aphid days may be a good indicator of yield loss if crop growth stage was considered, we created ordinary kriged surfaces to examine aphid day accumulations under two scenarios; 1) aphid days truncated on 6 May, which is the calendar middle of the spring and 2) aphid days through the full season (Fig. 3). On 6 May (scenario 1), the peak of aphid day accumulations is near southeastern Colorado, whereas aphid days accumulated over the full season (scenario 2) depicts high values toward the northern latitudes. That is, aphid popula-

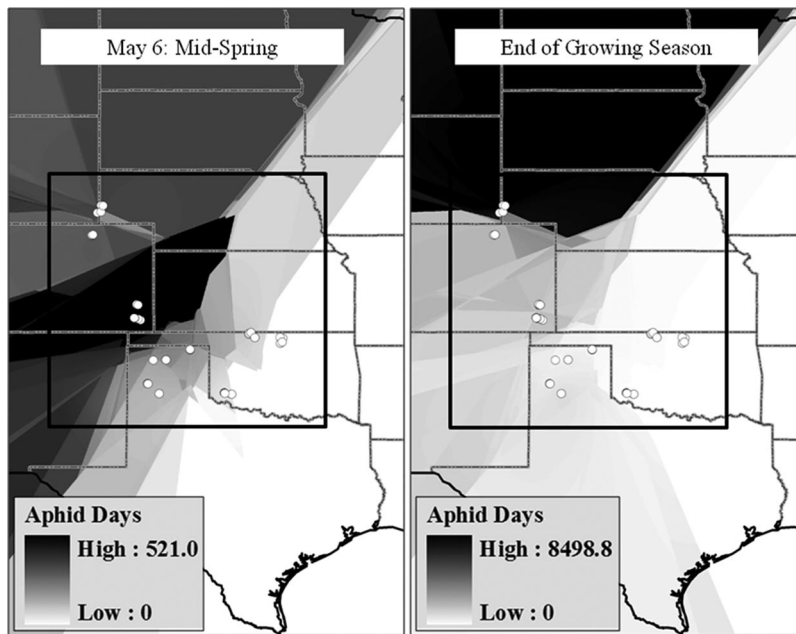


Fig. 3. Ordinary Kriged surfaces (interpolated surfaces) depicting an accumulated aphid day surface on 6 May (left, mid-spring) and an accumulated aphid day surface at the end of the growing season (right, full season). High to low aphid day accumulations are depicted from dark to light. The scale on the two images is different, with the high aphid accumulation regions on 6 May having much lower values than the high aphid day accumulations at season's end. White circles indicate field sites.

tions appear to start increasing in the north (e.g., Wyoming with harvest dates possibly in August) later in the growing season as contrasted with areas such as Texas, where harvest may have occurred by the first of June.

Our findings highlight the complexity of prediction of yield damage using pest intensity. That is, aphid day accumulations do not appear to be good indicators of yield loss if the length of season and the growth stage of the wheat are not considered or are not relatively uniform across the region of interest. Because growth stage and harvest date are correlated with latitude, creating an estimated yield loss map from our aphid day accumulation map would likely be fraught with errors. In essence, aphid day accumulations accurately describe population dynamics on a crop and, on a regional scale, are likely highly correlated with yield loss (because regional growth stage is relatively homogenized, yield loss differences by growth stage are minimal). For example, Archer et al. (1998) published aphid day relationships for different individual states. Thus, our aphid day model may have substantial value for looking at potential yield loss on a regional basis (with region defined by relatively uniform planting and harvesting dates). For example, if planting date and harvest date were relatively uniform (within approximately a week) across central Nebraska, eastern Nebraska should on average experience less yield loss caused by *D. noxia* feeding damage (primarily because of differences in precipitation). Moreover, understanding the relationship between environmental

components and aphid day accumulations may provide insight toward relative yield loss. That is, conditions that may portend economically damaging infestations of *D. noxia* are a cool summer with good C3 grass availability, and spring and fall conditions marked by low precipitation. While warm spring conditions are related to increased aphid day accumulations, increased heat units in the spring are also related to increased crop growth rate (McMaster and Wilhelm 2010), and thus, warm springs (with higher-than-average aphid day accumulations and advanced crop growth stages) may not correlate with higher yield losses. These factors should be considered when creating a pest management strategy. For example, restraint should be used in pesticide usage if the crop has experienced high rainfall.

Further examination of the complex interactions between weather components that influence crop growth stage and environmental components that influence aphid days may provide insight into the large interannual variability in yield loss. Conditions that augment crop growth such as increased precipitation and above-average temperatures (above-average growing degree-days) may allow for the crop to tolerate large aphid infestations without sustaining economically damaging yield losses. Conversely, relatively small aphid infestations could cause high yield loss if environmental conditions retarded plant growth during the crop's vulnerable growth stages.

Although much of the range of possible harvest dates has been captured by sites sampled during this

project, much of the observed habitat of *D. noxia* has not been sampled, including many suboptimal aphid habitats such as winter wheat fields in some of the Canadian provinces and many of the northern and eastern states in the U.S. Great Plains. Examination of environmental factors near boundary conditions could provide valuable insight. That is, parameterization, development, and testing of pest intensity models would be improved by increased sampling of areas that see limited to zero *D. noxia* infestations. In the northern reaches of the Great Plains, growth stage and harvest dates are constrained by growing season length. However, many environmental conditions become increasingly extreme (e.g., overwintering severity). Thus, aphid day data from these regions would provide a clearer picture of the influence of winter severity on aphid intensity. For example, in southern Alberta, Canada, fall infestations of *D. noxia* frequently occur. However, because of the severity of winter conditions, these populations rarely survive through to the spring (Butts 1992).

Predation and parasitism are implicit in these data, but unlike our focal aphid species, predator and parasitoid species assemblages vary across the region. Moreover, the effect of climate and weather will vary by natural enemy species. Thus, the effect of predation and parasitism on *D. noxia* will vary by species, species assemblage, and by the effect of weather and climate on those natural enemy species. Although some promise exists for developing general insect predation and consumption models (e.g., Deutsch et al. 2008, Tewksbury et al., unpublished data), until these models become spatially and temporally explicit, the effects of predators and parasitoids on *D. noxia* likely will remain difficult to quantify.

Of interest was the lack of support for population dynamic models that we considered likely to be selected as quality predictor variables (e.g., overwintering model, PDM 10; Merrill and Holtzer (2010)). This provides an important reminder that models that work well on a regional basis may lack support at different scales or may have value only under a limited set of conditions. This modeling framework provides excellent oversight and provides incentives to avoid attachments to specific models.

From a management perspective, quality predictor variables should be used as guides for indicating conditions that may promote high or low relative aphid intensity. For example, a year with relatively low spring precipitation might be expected to have higher pest intensity. In addition, these results can serve to direct further research, ideally to determine if causality can be attributed to any of these environmental components.

Our results provide modeled surfaces depicting aphid days and pest incidence for *D. noxia*. However, these aphid day surfaces do not seem to correlate with expected yield loss. This fascinating result leads us to believe that aphid days may not be the best indicator of yield loss, if crop growth stage is not considered. We conclude that pest intensity modeling should provide good indicators for predicting regional pest outbreaks.

Moreover, variables correlated with aphid days likely indicate conditions favorable for aphid outbreaks, such as dry spring conditions. These environmental cues should be used to inform management strategy. Further, our pest intensity models should provide increased food security by allowing for development of improved pest management strategies based on the risk of infestation.

Acknowledgments

We thank Norman Elliott, project director, for access to data from the USDA-ARS Area-wide Pest Management of Russian Wheat Aphid and Greenbug project. We thank Laurie Kerzicnik for reviewing an early manuscript draft. Research was supported by the Agriculture and Food Research Initiative of the USDA National Institute of Food and Agriculture, grant numbers COLO-2007-02967 and COLO-2009-02178.

References Cited

- Archer, T. L., and E. D. Bynum. 1992. Economic injury level for the Russian wheat aphid (Homoptera, Aphididae) on dryland winter-wheat. *J. Econ. Entomol.* 85: 987-992.
- Archer, T. L., and E. D. Bynum. 1993. Ecology of the Russian wheat aphid (Homoptera, Aphididae) on dryland winter-wheat in the southern United-States. *J. Kans. Entomol. Soc.* 66: 60-68.
- Archer, T. L., F. B. Peairs, K. S. Pike, G. D. Johnson, and M. Kroening. 1998. Economic injury levels for the Russian wheat aphid (Homoptera : Aphididae) on winter wheat in several climate zones. *J. Econ. Entomol.* 91: 741-747.
- Armstrong, J. S., and F. B. Peairs. 1996. Environmental parameters related to winter mortality of the Russian wheat aphid (Homoptera: Aphididae): basis for predicting mortality. *J. Econ. Entomol.* 89: 1281-1287.
- Armstrong, J. S., M. R. Porter, and F. B. Peairs. 1991. Alternate hosts of the Russian wheat aphid (Homoptera, Aphididae) in northeastern Colorado. *J. Econ. Entomol.* 84: 1691-1694.
- Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar, et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Chang. Biol.* 8: 1-16.
- Boege, K. and R. J. Marquis. 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology & Evolution* 20: 441-448.
- Brewer, M. J., and N. C. Elliott. 2004. Biological control of cereal aphids in North America and mediating effects of host plant and habitat manipulations. *Annu. Rev. Entomol.* 49: 219-242.
- Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildl. Res.* 28: 111-119.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: the practical information theoretic approach. Springer, New York.
- Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference - Understanding AIC and BIC in model selection. *Sociol. Methods Res.* 33: 261-304.
- Butts, R. A. 1992. Cold hardiness and its relationship to overwintering of the Russian wheat aphid (Homoptera, Aphididae) in southern Alberta. *J. Econ. Entomol.* 85: 1140-1145.

- Cressie, N.A.C. 1993. Statistics for spatial data. Wiley, New York.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. U.S.A.* 105: 6668–6672.
- Dewar, A. M., and N. Carter. 1984. Decision trees to assess the risk of cereal aphid (Hemiptera, Aphididae) outbreaks in summer in England. *Bull. Entomol. Res.* 74: 387–398.
- Elliott, N. C., G. L. Hein, M. R. Carter, J. D. Burd, T. O. Holtzer, J. S. Armstrong, and D. A. Waits. 1998. Russian wheat aphid (Homoptera: Aphididae) ecology and modeling in Great Plains agricultural landscapes, pp. 31–64. *In* S. S. Quisenberry and F. B. Peairs (eds.), Response model for an introduced pest—the Russian wheat aphid. Thomas Say Publications in Entomology, Lanham, MD.
- Epstein, H. E., W. K. Lauenroth, I. C. Burke, and D. P. Coffin. 1997. Productivity patterns of C-3 and C-4 functional types in the US Great Plains. *Ecology* 78: 722–731.
- ESRI 1999–2008. ArcGIS 9 computer program, version 9.3. ESRI, Redlands, CA.
- [FAO] Food and Agriculture Organization. 2011. Food and Agriculture Organization of the United Nations FAOstats. Chief, Publishing Policy and Support Branch, Office of Knowledge Exchange, Research and Extension, Rome, Italy. (<http://faostat.fao.org/site/291/default.aspx>).
- Fouche, A., R. L. Verhoeven, P. H. Hewitt, M. C. Walters, C. F. Kriel, and J. DeJager. 1984. Russian wheat aphid (*Diuraphis noxia*) feeding damage on wheat, related cereals, and a Bromus grass species, pp. 22–33. *In* M. C. Walters (ed.), Progress in Russian wheat aphid (*Diuraphis noxia* Mordv.) research in the Republic of South Africa. Department of Agriculture, Republic of South Africa.
- Girma, M., G. Wilde, and J. C. Reese. 1990. Influence of temperature and plant-growth stage on development, reproduction, life-span, and intrinsic rate of increase of the Russian wheat aphid (Homoptera, Aphididae). *Environ. Entomol.* 19: 1438–1442.
- Girma, M., G. E. Wilde, and T. L. Harvey. 1993. Russian wheat aphid (Homoptera, Aphididae) affects yield and quality of wheat. *J. Econ. Entomol.* 86: 594–601.
- Halbert, S. E., and M. B. Stoetzel. 1998. Historical overview of the Russian wheat aphid (Homoptera: Aphididae), pp. 12–30. *In* S. S. Quisenberry and F. B. Peairs (eds.), Proceedings, Response model for an introduced pest - The Russian wheat aphid. Thomas Say Publications in Entomology, Lanham, MD.
- Kerzicnik, L. M., F. B. Peairs, and J. D. Harwood. 2010. Implications of Russian wheat aphid, *Diuraphis noxia*, falling rates for biological control in resistant and susceptible winter wheat. *Arthropod Plant Interact.* 4: 129–138.
- Knight, J. D., J. S. Bale, F. Franks, S. F. Mathias, and J. G. Baust. 1986. Insect cold hardiness - supercooling points and prefreeze mortality. *Cryo Letters* 7: 194–203.
- Leather, S. R., K.F.A. Walters, and J. S. Bale. 1995. The ecology of insect overwintering. Cambridge University Press, New York.
- Legg, D. E., and M. J. Brewer. 1995. Relating within-season Russian wheat aphid (Homoptera, Aphididae) population-growth in dryland winter-wheat to heat units and rainfall. *J. Kans. Entomol. Soc.* 68: 149–158.
- Lee, J. H., N. C. Elliott, S. D. Kindler, B. W. French, C. B. Walker, and R. D. Eikenbary. 2005. Natural enemy impact on the Russian wheat aphid in southeastern Colorado. *Environ. Entomol.* 34: 115–123.
- Luedeling, E., K. P. Steinmann, M. H. Zhang, P. H. Brown, J. Grant, and E. H. Girvetz. 2011. Climate change effects on walnut pests in California. *Glob. Chang. Biol.* 17: 228–238.
- Ma, Z. S., and E. J. Bechinski. 2008. Developmental and phenological modeling of Russian wheat aphid (Hemiptera: Aphididae). *Ann. Entomol. Soc. Am.* 101: 351–361.
- Mann, J. A., G. M. Tatchell, M. J. Dupuch, R. Harrington, S. J. Clark, and H. A. McCartney. 1995. Movement of apterous *Sitobian-avenae* (Homoptera, aphididae) in response to leaf disturbances caused by wind and rain. *Ann. Appl. Biol.* 126: 417–427.
- McMaster, G. S., and W. W. Wilhelm. 2010. The wheat plant: development, growth and yield, pp. 7–16. *In* F. B. Peairs (ed.), Wheat production and pest management for the Great Plains region. Colorado State University, Fort Collins, CO.
- Merrill, S. C., and T. O. Holtzer. 2010. Using weather data to generate estimates of Russian wheat aphid overwintering success. Colorado State University Agricultural Experiment Station Technical Report TR10–14.
- Merrill, S. C., T. O. Holtzer, and F. B. Peairs. 2009. *Diuraphis noxia* reproduction and development with a comparison of intrinsic rates of increase to other important small grain aphids: a meta-analysis. *Environ. Entomol.* 38: 1061–1068.
- Merrill, S. C., T. O. Holtzer, and F. B. Peairs. 2010. Examining spatial correlation between fall and spring population densities of the Russian wheat aphid (Hemiptera: Aphididae). Colorado State University Agricultural Experiment Station Technical Report TR10–15.
- Morrison, W. P., and F. B. Peairs. 1998. Response model concept and economic impact, pp. 1–11. *In* S. S. Quisenberry and F. B. Peairs (eds.), Response model for an introduced pest—the Russian wheat aphid. Thomas Say Publications in Entomology, Lanham, MD.
- Oerke, E. C. 2006. Crop losses to pests. *J. Agric. Sci.* 144: 31–43.
- PRISM. 2004. PRISM Climate Group. Oregon State University. (<http://www.prismclimate.org/>).
- Quisenberry, S. S., and F. B. Peairs (eds). 1998. Response model for an introduced pest - The Russian wheat aphid. Entomological Society of America, Lanham, MD.
- R Development Core Team. 2008 R: a language and environment for statistical computing. R Foundation for Statistical Computing computer program, Vienna, Austria.
- Ruppel, R. F. 1983. Cumulative insect-days as an index of crop protection. *J. Econ. Entomol.* 76: 375–377.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. Seasonal adaptations of insects. Oxford University Press, New York.
- Tilman, D. 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. *Proc. Natl. Acad. Sci. U.S.A.* 96: 5995–6000.
- Wyatt, I. J., and P. F. White. 1977. Simple estimation of intrinsic increase rates for aphids and tetranychid mites. *J. Appl. Ecol.* 14: 757–766.

Received 8 June 2012; accepted 15 August 2012.