

# *Diuraphis noxia* Reproduction and Development With a Comparison of Intrinsic Rates of Increase to Other Important Small Grain Aphids: A Meta-Analysis

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**ABSTRACT** The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov), is a significant pest of small grains in the United States and worldwide. There is an increasing need for quality population dynamic models to aid in development of integrated pest management strategies. Unfortunately, there exists high variability in published data regarding basic life history traits that frequently direct model parameterization. Metadata were analyzed to develop relationships between temperature and reproductive and developmental traits of *D. noxia*. Specifically, functions were developed between temperature and the following traits: lifespan, fecundity, fecundity rate, pre-nymphpositional period, reproductive period, and intrinsic rate of increase. Lower and upper temperature reproductive thresholds were calculated as 0.6 and 36.9°C, respectively. The lower temperature developmental threshold was calculated as -0.69°C. Modeled longevity reached its maximum at ≈80 d. Meta-analysis indicates maximum fecundity at ≈18.5°C, with a maximum fecundity rate of ≈2.1 nymphs per day over the nymphpositional period. The calculated maximum total fecundity was ≈55 nymphs per female. The maximum reproductive period was calculated to be 29.9 d. Compared with other aphid species, as temperature increased, the intrinsic rate of increase of *D. noxia* increased more slowly relative to *Schizaphis graminum* (Rondani) and *Rhopalosiphum padi* L., but at a similar rate to *Sitobian avenae* (F.).

**KEY WORDS** Russian wheat aphid, reproduction, development, intrinsic rate of increase, meta-analysis

Aphid phenology and population growth rates are largely dictated by climate and weather variables. For example, temperature has been correlated with spring migration flight date in cereal aphids (Turl 1980, Walters and Dewar 1986). The severity of winter weather has been directly related to aphid overwintering success (Dewar and Carter 1984, Messina 1993, Armstrong and Peairs 1996). Many species have mechanisms that mitigate population mortality during periods of harsh climatic conditions. For example, the egg-laying stage of holocyclic aphid species is more resistant to stressful conditions and thus enables a relatively robust strategy for survival during harsh overwinter or oversummer periods. However, some species rely largely on an anholocyclic strategy, which can give them the advantage of early and rapid population growth during mild conditions but does not protect them from increased mortality resulting from exposure to extreme conditions by life stages that are ill-equipped to deal with them.

An important pest species with an anholocyclic life-cycle within North America is the Russian wheat

aphid, *Diuraphis noxia* (Kurdjumov) (no male *D. noxia* have been found to date in North America). Since its introduction into the United States in the mid-1980s, this aphid has caused losses of more than one billion dollars to the small grain industry, prompting efforts to develop an effective integrated pest management (IPM) strategy (Webster et al. 1994, Morrison and Peairs 1998). Localized overwintering success has been linked to increased crop losses. That is, *D. noxia* populations that survive the overwinter period in a given field typically cause significantly more damage than populations that build up after migration from outside sources (Peairs et al. 2006). Population mortality has been found to be correlated with snow, precipitation, and temperature variables (Armstrong and Peairs 1996), with temperature variables having the largest impact (Merrill and Holtzer unpublished work). Variables that drive population dynamics (e.g., temperature) must be robustly quantified if we are to develop accurate population dynamic prediction models (e.g., outbreak prediction models and risk assessment models for use in IPM). Prediction models frequently rely on accurate boundary conditions as well as rate and stage functions quan-

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tifying aphid development and reproduction. However, results from studies examining the influence of temperature on development and reproduction of *D. noxia* are highly variable. For example, Nowierski et al. (1995) found a reproductive period of  $\approx 41$  d for *D. noxia* at 19.5°C, whereas Girma et al. (1990) found a reproductive period of 9 d at 19.7°C.

Because of high variability observed between studies (stemming from differences in sampling techniques to sampling conditions), individual experiments may have limited value if they cannot be generalized to address the overall questions of interest (Gurevitch and Hedges 1993). Combining results from multiple experiments typically allows for greater generalization than the use of a single experiment. Of the available methods for combining results from independent experiments, meta-analyses are encouraged because they provide statistically defensible quantification of the analysis results, in contrast to a number of other methods currently used (Gurevitch et al. 1992, Gurevitch and Hedges 1993). For example, one potentially misleading method for synthesizing results from independent studies is called “vote counting.” Vote counting is frequently used to determine whether an effect is significant by first categorizing multiple studies where the effect has been studied by whether the effect was found to be significant or not significant. Vote counting results (significant or not) are determined simply by declaring the category that received the most votes the winner. Unfortunately, vote counting and other similar methods can be misleading because significance varies based on both effect and sample sizes (Gurevitch et al. 1992). The meta-analysis we conducted enables a useful synthesis of research from numerous studies, resulting in a more robust understanding of the relationships between temperature and life history traits of *D. noxia* compared with the use of results from a single data set.

The influence of weather and climate (particularly temperature) on *D. noxia* biology has been extensively studied (Webster and Starks 1987). Temperature seems to be a dominant factor influencing reproductive and development rates (Aalbersberg et al. 1987). However, many other variables play strong roles. Examples of factors influencing reproductive and developmental rates include host plant growth stage (Girma et al. 1990), host quality (Merrill et al. 2008), aphid biotype (Randolph et al. 2008), population density (Michaud et al. 2006), and feeding site on the plant (Stary 1999). Much more of the variation associated with reproduction and development could be explained if all these covariates were included in a meta-analysis. However, our analysis was restricted because of inconsistencies among studies (e.g., different protocols), inadequately reported data, or data were considered too variable to be included (e.g., unexplained variation resulting from cultivar effects). Rather, we concentrated on temperature effects and ignored the variability associated with other covariates.

Our goal was to provide robust quantification of the relationships between temperature and life history traits of *D. noxia*. Quantified relationships provided by

**Table 1.** List of metadata sources

Citation	F	RR	TDT	L	NP	PNP	$r_m$
Aalbersberg et al. (1987)	x	x	x	x	x	x	
Behle and Michels (1990)	x	x	x	x	x	x	x
Girma et al. (1990)	x	x	x	x	x	x	x
Hawley et al. (2003)	x	x					x
Kieckhefer and Elliott (1989)	x		x			x	x
Merrill et al. (2008)	x	x	x	x	x	x	x
Michels and Behle (1988)	x	x	x	x	x	x	
Michels and Behle (1989)	x			x	x		x
Miller et al. (2003)	x	x		x	x		x
Nowierski et al. (1995)		x		x	x		x
Randolph et al. (2007)	x	x		x	x		x
Webster and Starks (1987)	x	x	x		x		
Webster et al. (1993)	x					x	

The x indicates that metadata were obtained from the source for each category. Metadata either were extracted directly from text or calculated from data provide in the source.

F, fecundity; RR, reproductive rate; TDT, temperature developmental threshold; L, longevity; NP, nymphpositional period; PNP, pre-nymphpositional period;  $r_m$ , intrinsic rate of increase.

this meta-analysis can be used to improve *D. noxia* model parameterization and in the development of IPM strategies.

## Materials and Methods

We used the following references as *D. noxia* metadata sources: Aalbersberg et al. (1987), Webster and Starks (1987), Michels and Behle (1988, 1989), Kieckhefer and Elliott (1989), Behle and Michels (1990), Girma et al. (1990), Webster et al. (1993), Nowierski et al. (1995), Hawley et al. (2003), Miller et al. (2003), Randolph et al. (2008), and Merrill et al. (2008). Table 1 indicates which metadata (e.g., fecundity or longevity metadata) were provided by each reference.

Parameters for development and reproduction variables were extracted from each of the aforementioned research papers. Parameterized variables of interest were longevity, total fecundity, daily fecundity rate, reproductive period (or nymphpositional period), pre-nymphpositional period (i.e., the period from birth to the production of the aphid's first offspring), and intrinsic rate of increase. Ideally, measures of variance would be reported across studies, which would allow for temperature data to be weighted based on a measure of their variance (e.g., the SE). Unfortunately, central tendency measurements were not uniformly reported. However, sample number was uniformly reported and can be related to the SE, which is equal to the SD of the sample population divided by the square root of the number of samples. Therefore, because an increased sample size reduces the SE, metadata were weighted by the square root of the sample size. Specifically, the higher the number of samples used to obtain a data point, the more weight was conferred on that data point. If multiple temperatures were studied within a single research paper, each temperature was considered a data point and was weighted by the sample size used to develop the temperature-specific data.

We modeled the relationships between temperature, reproduction, and development using simple mathematical relationships. Functions for describing arthropod temperature-dependent rates may fit a non-symmetric curve around an optimal value (Logan et al. 1976). For example, high temperatures may create a rapidly declining curve, possibly attributed to enzyme denaturation or desiccation, in many temperature-related functions (Logan et al. 1976). However, until aphid data collection is more uniform across studies, a parsimonious approach may be warranted: that is, assuming linearity or symmetry until variability in data collection across studies is reduced. Therefore, we modeled relationships between temperature, reproduction, and development using linear, Gaussian, Weibull, and power (as suggested by exponentially increasing population growth rates) functions based on reasonable biological expectations (e.g., fecundity rate was not expected to linearly increase with temperature, and therefore linear functions were not fit to the fecundity data). We used an information theoretic approach for model selection and, where necessary, model averaging (Burnham and Anderson 2002, 2004).

**Comparison of Intrinsic Rates of Increase Between Important Small Grain Aphids and *D. noxia*.** Metadata were assembled for three other important aphid pests of small grains on the Great Plains: *Rhopalosiphum padi* L. (Dean 1974, Michels and Behle 1989, Selhorst 1994, Sengonca et al. 1994, Asin and Pons 2001, Nyaanga et al. 2005); *Sitobion avenae* (F.) (Dean 1974, Acreman and Dixon 1989, Sengonca et al. 1994, Asin and Pons 2001); and *Schizaphis graminum* (Rondani) (Wadley 1936, Webster et al. 1987, Walgenbach et al. 1988, Michels and Behle 1989, Nyaanga et al. 2005). Reliable intrinsic rate of increase metadata could not be found for high temperatures (e.g., >30°C) for all aphid species. Therefore, the temperature-intrinsic rate of increase relationship could not be comparatively modeled when an increase in temperature correlated with a decrease in the aphid's intrinsic rates of increase. However, reliable data were found for relationships between temperature and intrinsic rate of increase for temperatures in a range where the intrinsic rate of increase was increasing with temperature from the lower temperature development threshold toward a hypothetical maximum intrinsic rate of increase. To limit the meta-analysis to metadata within these constraints, data were discarded if the intrinsic rate of increase was less than half of the maximum reported value at temperatures higher than the temperature at the maximum reported intrinsic rate of increase. As an example, Asin and Pons (2001) reported an intrinsic rate of 0.15 at 27.5°C for *S. avenae*. This data point is likely on the decreasing portion of the intrinsic rate of increase curve and was therefore discarded. Across all studies, each of the temperature by intrinsic rate of increase values was treated as a datum in the meta-analysis and weighted by the square root of the sample size. Although different methods of calculation of the intrinsic rate of increase (Birch 1948, Wyatt and White 1977) may result in

slightly different values, this component of variation was not included in our analysis.

## Results

**Fecundity and Temperature.** Temperature has a strong effect on lifetime fecundity, defined as the total number of nymphs produced over the lifetime of an aphid. Exceptionally high and low temperatures result in no reproduction. After a preanalysis, maximum fecundity was estimated to occur at ≈20°C with upper and lower thresholds occurring at ≈0 and ≈35°C. Given these assumptions, we assumed that the fecundity-temperature relationship could be fit by a Gaussian or Weibull function. The Gaussian function had a lower AIC value than the Weibull function (Gaussian function AIC = 358.95, Weibull function AIC = 360.16). These AIC values are very close, making model selection complex. That is, the Gaussian function had a likelihood of 0.65 and the Weibull function had a likelihood of 0.35, indicating strong likelihoods for each model being the best approximating model (Burnham and Anderson 2004). Figure 1 depicts modeled lifetime fecundity using both the Gaussian and Weibull functions versus temperature metadata. A Gaussian function was fit to the data using a weighted least mean squares error approach and is calculated as:

Gaussian function: nymphs/female = 55.3

$$\times e^{-(T-18.4)^2/92.5} \quad [1]$$

where T is the temperature. The Gaussian function calculates a maximum fecundity of ≈55.3 nymphs (at 18.4°C), well under the maximum reported average of 81.5 nymphs (at 17.25°C) (Aalbersberg et al. 1987). The Weibull function was fit to the data using a weighted least squares approach and is calculated as:

Weibull function: nymphs/female = 156.5

$$\times (T/18.5)^{3.0} \times e^{[-(T/18.5)^{3.0}] \quad [2]$$

where T is the temperature. The Weibull function calculates a maximum fecundity of ≈57.6 nymphs (at 18.5°C).

The temperature reproduction thresholds are defined as the upper and lower temperature limits of reproduction (i.e., temperatures at which reproduction per female is less than one nymph per female). Because both the Gaussian and Weibull functions had support in the data (i.e., strong likelihoods for being the best approximating model), a model-averaged approach was used to calculate the reproductive thresholds (Burnham and Anderson 2002, 2004). That is, upper and lower reproduction threshold values were calculated for both the Gaussian and Weibull functions, and the AIC weight (or in this case the likelihood) was used to average the values. The Gaussian lower and upper reproduction threshold values were -0.9 and 37.7°C, whereas the Weibull lower and upper threshold values were 3.4 and 35.4°C, respectively. The model-averaged lower and upper thresholds were 0.6 and 36.9°C, respectively.

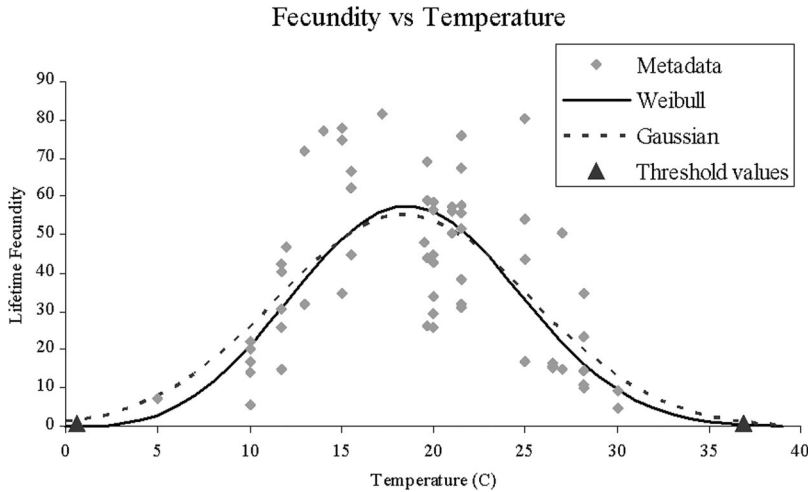


Fig. 1. Metadata and fitted Weibull and Gaussian functions for the average number of nymphs produced per female at temperatures from 5 to 30°C. Black triangles indicate the upper and lower reproductive threshold values.

Fecundity rate (Fig. 2), defined as the average number of nymphs per reproductive day, has a very similar relationship with temperature as average lifetime fecundity. However, unlike lifetime fecundity, the Gaussian function (AIC = -130.6, likelihood > 0.99) had a much lower AIC value than the Weibull function (AIC = -120.3, likelihood < 0.01). Therefore, only the Gaussian function was reported. Fecundity rate, modeled using a Gaussian function, was fit with a weighted least squares approach:

Gaussian function: fecundity rate

$$= 2.1 e^{-(T - 20.6)^2/131.0} \quad [3]$$

where T is the temperature. This function calculates a maximum of 2.1 nymphs per day (at 20.6°C) during the reproductive period. The maximum reported average nymphs per day was 6.0 at 26.5°C (Haile et al. 1999). However, when we considered this data point as an outlier, because it was approximately twice as large as the next highest value, and excluded it from the analysis, we obtained a maximum value of 3.1

nymphs per day at 20°C, which is similar to the value obtained by Behle and Michels (1990).

**Temperature Development Threshold.** The temperature development threshold, defined as the lowest temperature where development occurs, has been calculated for *D. noxia* in numerous studies: Aalbersberg et al. (1987) reported 0.54°C, Girma et al. (1990) reported a value of -1.57°C, and Kieckhefer and Elliott (1989) reported a lower developmental threshold limit of 4.1°C for development of immature *D. noxia*. Nowierski et al. (1995) reported 5.2°C on excised barley leaves. The average lower developmental threshold for these four studies was 2.06°C.

Using weighted metadata, the temperature development threshold (Fig. 3) was calculated as -0.69°C using a linear regression of the inverse of developmental time from birth to adult against temperature for all metadata (Aalbersberg et al. 1987, Kieckhefer and Elliott 1989, Girma et al. 1990).

**Longevity and Temperature.** Although many studies have indicated reduced longevity at subzero tem-

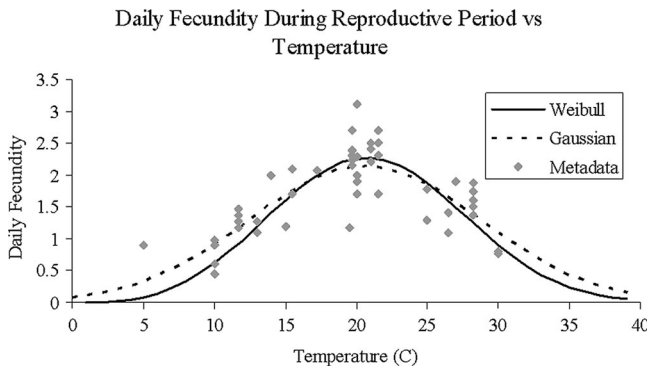


Fig. 2. Metadata and fitted Weibull and Gaussian functions for the average number of nymphs produced per female per day during the reproductive period at temperatures from 5 to 30°C.

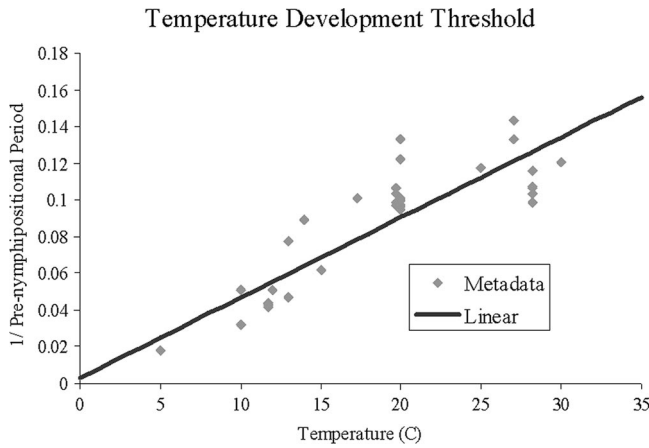


Fig. 3. Linear regression of the inverse of the pre-nymphositional time versus temperature metadata providing the temperature development threshold ( $-0.69^{\circ}\text{C}$ ).

peratures (Knight et al. 1986, Butts 1992), metadata for aphids born and held at temperatures under their developmental threshold do not (and arguable cannot) exist. We modeled longevity as linearly increasing as temperatures approached the lower temperature development threshold. Longevity was modeled as the following linear function of temperature using a weighted least squares approach (Fig. 4):

$$\text{Linear function: longevity} = -2.0 \times T + 79.6 \quad [4]$$

where  $T$  is the temperature. Modeled longevity reached its maximum at  $\approx 80$  d, with longevity increasing as temperature decreased toward the developmental threshold.

**Reproductive Period and Temperature.** Reproductive period (nymphositional period) is defined as the number of days from the first to last birth per mother aphid. These data (Fig. 5) are quite variable among studies and a pattern is not easily discerned. However, if we assume that the reproductive period

increases as temperatures decrease toward the reproduction threshold, these data can be modeled using either a linearly decreasing function or a power function. Alternatively Gaussian or Weibull function could be fit to the data if we assume that the aphid's reproductive period drops to zero when temperatures are under the reproductive threshold.

The Gaussian function generated the best fit with the lowest AIC and highest likelihood (AIC = 221.4, likelihood = 0.66) compared with the Weibull function (AIC = 223.2, likelihood = 0.27), linear function (AIC = 225.9, likelihood = 0.07), and the power function (AIC = 237.1, likelihood = 0.002). The Gaussian function (Fig. 5) for the reproductive period versus temperature relationship is given by the following equation:

$$\text{Gaussian function: reproductive period} = 29.9 e^{-(T - 12.0)^2/297.1} \quad [5]$$

where  $T$  is the temperature. Results indicate a maximum reproductive period of 29.9 d at  $\approx 12.0^{\circ}\text{C}$ . The

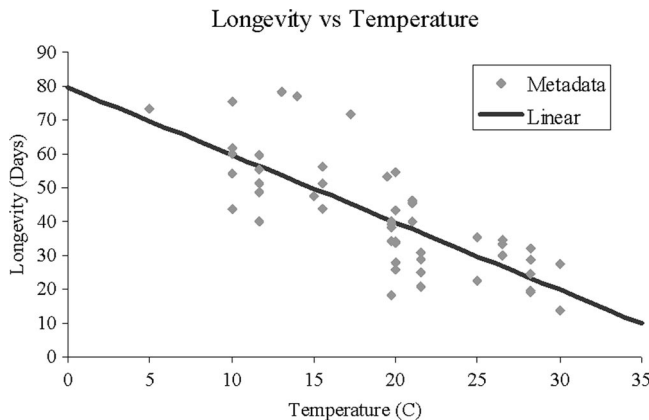


Fig. 4. Linear regression of the inverse of longevity versus temperature metadata providing the maximum longevity ( $\approx 80$  d).



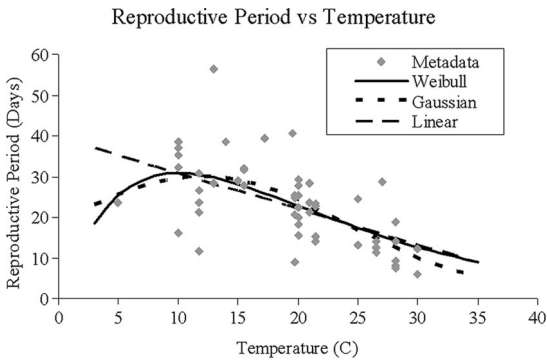


Fig. 5. Metadata and fitted Weibull, Gaussian, and linear functions for the length of the reproductive period in days versus temperature.

minimum reported average reproductive period reported in the original publications was 6 d by Michels and Behle (1988) at their highest temperature regimen (30°C). The maximum reproductive period reported was 56.44 d at 13°C (Aalbersberg et al. 1987).

**Pre-nymphipositional Period and Temperature.** Pre-nymphipositional period is defined as the number of days from birth of an aphid to the birth of its first offspring. Pre-nymphipositional period provides a necessary variable for calculating the intrinsic rate of increase. Specifically, the delay between birth and the potential for the newly born aphid to give birth is essential for calculating generation time. Data indicate that the number of days until first birth increases as temperature decreases toward the lower developmental threshold (Fig. 6). Pre-nymphipositional period was modeled using linear and power functions. The power function had a much better fit (AIC = 132.3, likelihood > 0.99) than the linear function (AIC = 233.2, likelihood < 0.01):

$$\text{Power function: pre-nymphipositional period} \\ = 353.6 \times T^{(-1.14)} \quad [6]$$

where T is the temperature.

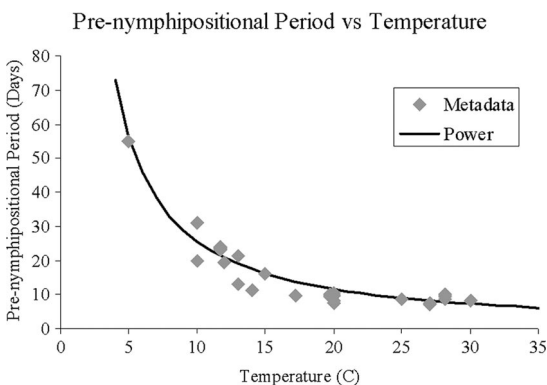


Fig. 6. Metadata and the fitted power function for pre-nymphipositional period versus temperature.

Interestingly, if one models pre-nymphipositional period as a power function (Fig. 6, Formula 6), a second estimate of the reproduction threshold can be obtained. The second estimate is based on the assumption that when the pre-nymphipositional period is equal to the maximum lifespan, no reproduction can occur. Substituting maximum lifespan (79.6 d as calculated using Formula 4) for the pre-nymphipositional period in Formula 6, the lower temperature reproduction threshold was calculated to be 3.7°C:

$$\text{Pre-nymphipositional period} = \text{max lifespan} \\ = 353.6 \times T^{(-1.14)} \quad [7]$$

**Comparison of Intrinsic Rates of Increase Between Important Small Grain Aphids and *D. noxia*.** Results indicate that the slope of the relationship between temperature and intrinsic rate of *D. noxia* was relatively low compared with *R. padi* ( $P = 0.0244$ ,  $t$ -value = 2.29) and *S. graminum* ( $P = 0.0854$ ,  $t$ -value = 1.74) but likely not different than *S. avenae* ( $P = 0.4176$ ,  $t$ -value = -0.81). The slope of the relationship between temperature and intrinsic rate of *R. padi* was higher than *S. avenae* ( $P = 0.0016$ ,  $t$ -value = -3.25) but not different than *S. graminum* ( $P = 0.8942$ ,  $t$ -value = -0.13). The slope of the relationship between temperature and the intrinsic rate of increase values was higher in *S. graminum* than *S. avenae* ( $P = 0.0148$ ,  $t$ -value = -2.48). In general, the aphid species *D. noxia* and *S. avenae* were similar to each other regarding changes to their intrinsic rates of increase in response to changes in temperature (Fig. 7). *R. padi* and *S. graminum* showed similar responses in their intrinsic rates of increase to changes in temperature.

## Discussion

This meta-analysis was designed to build a more comprehensive, more robust understanding of the interaction between life history traits of *D. noxia* and temperature. The relationships derived from this research have greater utility as guidelines for model parameterization and for informing IPM strategy than do individual data sets used alone or parameterization derived from simple averaging procedures. Our meta-analysis showed that the maximum lifespan of *D. noxia* is <3 mo, which indicates that aphid populations from the fall will not survive through to the spring unless reproduction occurs. Reproduction is unlikely below  $\approx 1^\circ\text{C}$  and above  $\approx 37^\circ\text{C}$ . *D. noxia* seems to have its highest fecundity occurring around 18.5°C. Longevity is increased as temperatures decrease toward the developmental threshold of approximately  $-1^\circ\text{C}$ , under which damage may occur to the aphid (e.g., chill coma; Knight et al. 1986). As longevity increases, a reproductive penalty is incurred. That is, fecundity decreases as longevity increases.

Although not quantified in this study, *D. noxia* reproductive and development rates seem to be optimal at lower temperatures compared with other important small grain aphid pests on the Great Plains. Therefore, typical conditions in the early spring

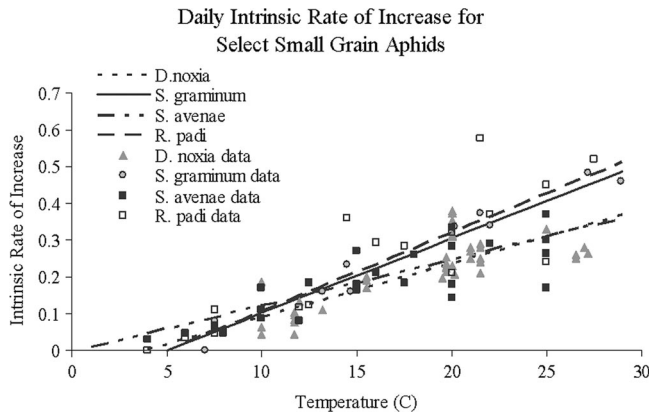


Fig. 7. Metadata and linear functions for the daily intrinsic rates of increase versus temperature for many important small grain aphids.

(cooler temperatures) should favor *D. noxia* population development over many other aphid pests. For example, Harvey and Martin (1988) studying aphids in Kansas found that *D. noxia* was more cold tolerant and better adapted to overwinter conditions than *S. graminum*.

Additional meta-analysis of important aphid pests of small grains on the Great Plains would be valuable for increasing our understanding of aphid population responses to different temperature regimens. Such meta-analysis would also have implications for pest forecasting and for predicting aphid response to climate change. Meta-analyses have a distinct advantage over decisions made using a selection of a single “best” study or a simple average of multiple studies in that they allow for mathematical and statistical formulation incorporating data from across a wider scope of conditions, which produces more robust results.

Our meta-analysis provides improved parameterization for *D. noxia* population dynamic models. For example, degree-day models would be enhanced by inclusion of derived temperature dependencies, and outbreak prediction models would be improved by more robust parameterization of the effects of temperature on aphids.

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