ENVIRONMENTAL PARAMETERS RELATED TO WINTER MORTALITY OF THE RUSSIAN WHEAT APHID (HOMOPTERA: APHIDIDAE): BASIS FOR PREDICTING MORTALITY

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Environmental Parameters Related to Winter Mortality of the Russian Wheat Aphid (Homoptera: Aphididae): Basis for Predicting Mortality

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ABSTRACT Relationships between winter environment and mortality of the Russian wheat aphids *Diuraphis noxia* (Mordvilko), infesting winter wheat, *Triticum aestivum* (L.), were investigated. Russian wheat aphid densities from 0.3 m drill row of 'TAM 107' (dependent variable), accumulated subzero temperatures, soil moisture, snow amounts, snow cover duration, and solar radiation (independent variables) were measured in 2 differing winter environments in 1989, 1990, and 1991. Multiple regression analysis for best-fit relationships indicated that Russian wheat aphid winter mortality was highly correlated with the accumulation of freeze-hours <0°C. A 2nd relationship was established by regressing aphid densities against the accumulation of freeze-degrees <0°C. The hour accumulation resulted in stronger relationships with declining aphid densities compared with degree accumulations, especially in 1991–1992 when there was 87 d of snow cover. Freeze degrees accumulate faster the greater the soil surface temperature drops below 0°C, but are limited under insulating snow. Average daily snow cover was the 2nd most important independent variable in relation to aphid decline when the duration (>40 d) and depths (> 1 cm) were dominant winter factors. Neither soil moisture nor solar radiation were statistically significant components in our models. Complete Russian wheat aphid mortality occurred within 3,000 freeze-hours or −12,000 freeze-degrees when data for all 3 yr were included. The 2 climatic events that resulted in 100% mortality were a sudden drop (-29.6°C) in soil surface temperature and an extended (>40 d) period of snow cover.

KEY WORDS *Diuraphis noxia,* winter mortality, snow cover, freeze-degrees, freeze-hours

THE DISTRIBUTION AND economic loss caused by the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), infesting winter wheat, *Triticum aestivum* (L.), in the United States has been well documented (Stoetzel 1987, Morrison et al. 1988, Kieckhefer and Elliott 1989, Michels and Behle 1989, Archer and Bynum 1992, Burd and Burton 1992, Legg et al. 1993). If Russian wheat aphids are successful in overwintering on established, fall-seeded winter wheat, subsequent spring densities will increase rapidly. This may lead to increased control costs and decreases in yield if infestations go untreated. If Russian wheat aphids fail to overwinter, economic infestations occur later in the spring, reducing the need for the application of insecticides. This scenario is similar to that of the greenbug, *Schizaphis graminum* Rodani (Lowe 1952, Painter et al. 1954), although the Russian wheat aphid is more cold-tolerant (Harvey and Martin 1988) and reaches more northern latitudes (e.g., Lethbridge, Alberta, Canada; Butts 1992).

Aphid eggs from holocyclic reproduction are more cold-tolerant than anholocyclic nymphs or adults (Strathdee et al. 1995), and this increases their chance for winter survival. Russian wheat aphids in Northeastern Colorado have only been found in the anholocyclic form and have the potential to increase much faster in the spring compared to holocyclic aphids. Holocyclic aphids must complete 1 to 2 generations on a primary host before moving to cereal crops in the spring (Powell 1974, Bale et al. 1988).

Comparisons of the relationships between overwintering Russian wheat aphid populations and environmental data that cause significant mortality could be used in the management of this pest. Previous research on the overwintering mortality of the green peach aphid *Myzus persicae* (Sulzer), on cereal crops indicated that temperature data alone (i.e., daily mean temperature) was not useful as a predictor of aphid mortality (Harrington and Cheng 1984). This insignificant relationship of declining aphid densities with daily temperatures could be a result of not accounting for the combined effects of subzero temperature with duration of exposure (Casagrande and Haynes 1976). These combined factors proved to be related to Russian wheat aphid cold tolerance in laboratory studies.

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Life expectancy decreased with decreasing temperature and increasing exposure time (R. A. Butts, Agriculture Canada, Lethbridge, Alberta; unpublished data).

We sampled overwintering densities of the Russian wheat aphid (dependent variable) for 3 consecutive winters (1989–1991) and used cumulative subzero temperatures, soil moisture, solar radiation, snowfall depth, and snowfall duration (independent variables) in multiple regression models to explain and predict Russian wheat aphid winter mortality. Subzero temperature accumulation was conducted under the assumption that the lower threshold for Russian wheat aphid development approximates 0°C (Aalbersberg et al. 1987, Kieckhefer and Elliott 1989, Girma and Wilde 1990) and that mortality would occur below 0°C (Butts 1992).

Materials and Methods

Field Plot Preparation and Design for 1989, 1990, and 1991. Field studies of overwintering Russian wheat aphids were conducted from fall to spring with 'TAM 107' winter wheat on the Central Great Plains Research Station, Akron, CO. An 0.8-ha area was planted with a wheat drill calibrated to deliver 35 kg seeds per hectare on a 30.5-cm row spacing. The plots were planted in a north–south row direction on 11 September 1989, 19 September 1990, and 9 September 1991. The soil was classified as a fine, montmorillonite, mesic pachic Argiustoll.

After wheat emergence, a protective wall barrier (1 m high, 70.8 m long) running east–west was constructed in the middle of the 0.8-ha area to provide a protected environment (on the immediate south side of the wall), as opposed to a flat, open field which characterizes most of the wheat production in the Great Plains. The wall was constructed of metal sheeting (Strongbarn Metal, Pittsburgh, PA) secured with metal fence posts. The protective wall formed 2 overwintering environments termed unprotected (15 m north of the wall) and protected (directly adjacent to the south-facing side of the wall) for a contrast in snow amounts, snow distribution, and temperature. Within the 2 environments, a series of 90 different sections of 0.3-m wheat row, running perpendicular to the wall barrier were used for infesting and sampling during the winter.

Russian Wheat Aphid Infesting and Sampling Procedures. Thirty apterous Russian wheat aphids were transferred to each 0.3-m row with a camel's-hair brush when the wheat reached Feekes growth stage 2 (Cook and Veseth 1991), usually the 1st wk of October. The aphids used for infesting were collected from volunteer winter wheat on the Central Great Plains Research Station. Aphid densities were sampled by removing plants from 8 random sections (0.3 m of row) from each environment every other week. The plants were removed by chiseling if the soil was frozen, or by shovel if wet, and placed in large aluminum trays. The numbers of Russian wheat aphids and plants from each section were counted.

Environmental Measurements. The soil surface temperature (2.0 cm above soil surface) was measured at 5 locations in each environment with 30-gauge copper-constan thermocouple wire (Thermo-Electric, Saddle Brook, NJ) connected to a 21× micrologger (Campbell Scientific, Logan, UT). The sensing ends of the thermocouples were covered with a teflon rod (1.5 cm long, 0.95 cm diameter) to prevent electrical interference in the presence of moisture. The micrologger was programmed to record the temperature every 60 s and average to 24 h of a day and to record the daily maximum and minimum temperatures. Data were transferred from micrologger memory to a personal computer spreadsheet (Quattro Pro version 3.0; Borland International, Scotts Valley, CA) using a cassette tape recorder and Campbell Scientific 201 software.

Soil surface moisture was measured weekly to a 5.0-cm depth from 4 locations in each environment with a soil probe (3.7 cm diameter). Soil cores from the soil probe were weighed, placed in a drying oven at 52°C for 48 h, then weighed again to obtain percentage gravimetric moisture.

Average daily snow cover was measured from 12 stakes marked from 0.0 to 30.0 cm in both overwintering sites. Snow depth was measured after each snow event until the average depth was <1 cm.

Solar radiation was measured in each environment in megajoules/m^2/d with Li-Cor pyranometers (Li-Cor, Lincoln, NE) connected to the same micrologger that measured soil surface temperature. Both pyranometers were calibrated for each year of the study before being placed in the field.

Statistical Modeling Procedures. Two different methods of subzero temperature accumulation were calculated by spreadsheet after temperature data were committed to memory. The 1st method, termed accumulated freeze-degrees, was calculated by summing the average temperature of each hour below 0.0°C. For example, if on a given day the average hourly temperatures were −2.0°C at 0800 hours, −6.0°C at 0900 hours, −10.0°C at 0100 hours, and >0.0°C for the other 21 h of the day, the subzero degree accumulations for that day would sum to −8.0°C. The 2nd method, termed accumulated freeze-hours, was calculated by summing the number of hours the average hourly temperature was <0.0 °C.

The total number of aphid samples (eight 0.3-m sections) from each environment and sample date was transformed [ln(total+1)] before analysis because of high variability in aphid numbers within samples. The linear relationship of transformed aphid numbers with the independent variables was investigated using the PROC CORR procedure (PC SAS, SAS Institute 1988) for all sample dates (winters 1989, 1990, and 1991) and for both pro-

Table 1. Accumulations of subzero temperature and snowfall recorded in protected and unprotected overwintering test sites when Russian wheat aphid populations reached lowest population densities, Central Great Plains Research Station, Akron, CO

Date of lowest aphid population density	Lowest aphid density[a]	AFD	AFH	Snow days[b]	Accumulated snow, cm
		Protected site			
20 Mar. 1990	13	−7,271	1,975	40	447.2
6 Feb. 1991	0	−9,591	1,519	24	130.8
27 Mar. 1992	0	−2,944	2,535	87	1,183.3
		Unprotected site			
20 Mar. 1990	4	−6,387	1,786	51	406.6
19 Feb. 1991	0	−11,133	1,651	31	102.8
3 April 1992	0	−6,053	2,428	77	949.8

AFD, accumulated freeze-degrees <0°C; AFH, accumulated freeze-hours <0°C.
[a] Actual (untransformed) numbers of aphids from 2.4-m row of winter wheat.
[b] Number of days with average snow cover >1 cm.

tected and unprotected environments. Multiple regression models were calculated using PROC REG procedure followed by the SELECTION=MAXR, CP, and MSE statements. We also used Mallows Cp Weisburg 1985) and MSE (mean square error) statistics to compare and select the subset of models that best described aphid mortality. Subzero degree and hour accumulation models were developed for each environment (protected and unprotected) and year (1989, 1990, and 1991), then constructed to include both environments and all 3 yr.

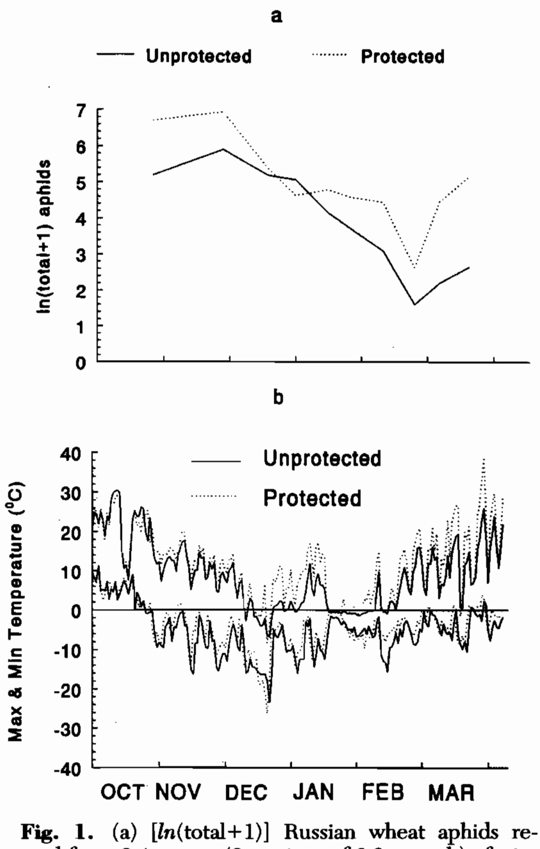

Fig. 1. (a) [*ln*(total+1)] Russian wheat aphids removed from 2.4-m row (8 sections of 0.3 m each) of winter wheat grown in protected and unprotected winter environments. (b) Daily maximum and minimum soil surface temperatures for protected and unprotected Russian wheat aphid test plots, winter 1989–1990, Central Great Plains Research Station, Akron, CO.

Results and Discussion

Winter, 1989–1990. On 6 December 1989, untransformed aphid numbers from 2.4 m of wheat row were 1,024 for the protected environment and 367 for the unprotected environment; these numbers were reduced to 4 and 13, respectively, by 20 March 1990 (Table 1; Fig 1a). The freeze-degree and freeze-hour accumulations for the lowest seasonal aphid density of 20 March were −7,271 and 1,975, respectively, for the protected environment, and −6,387 and 1,786, respectively, for the unprotected environment. Snow melt occurred at a faster rate in the protected environment because of radiant heat reflecting from the wall barrier. This resulted in fewer snow cover days (Table 1) that allowed for colder minimum temperatures and higher freeze-degree and freeze-hour accumulations. Snow cover insulates the soil surface temperature based on its depth (Marchant 1982). There were 11 fewer snow cover days and 41.4 cm more of accumulated snow in the protected environment than in the unprotected environment. The longest period of continuous snow cover for the unprotected environment was 30 d (14 January to 12 February). The protected environment was uncovered for 6 d between these dates.

The coldest soil surface temperature for the 1989–1990 winter occurred on 22 December, reaching lows of −26.3 and −23.4°C for the protected and unprotected environments, respectively. Russian wheat aphid densities increased by 4 April 1990 in both environments because of warm day and mild night temperatures.

Winter, 1990–1991. Russian wheat aphid densities increased throughout November to the

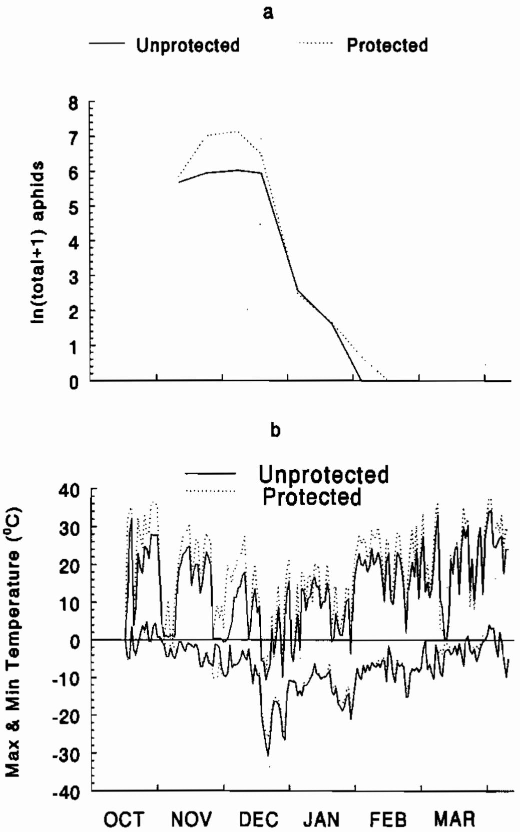

Fig. 2. (a) [*ln*(total+1)] Russian wheat aphids removed from 2.4-m row (8 sections of 0.3 m each) of winter wheat grown in protected and unprotected winter environments. (b) Daily maximum and minimum soil surface temperatures for protected and unprotected Russian wheat aphid test plots, winter 1990–1991, Central Great Plains Research Station, Akron, CO.

1st wk in December for both environments (Fig. 2a). On 10 December 1990 there were 1,249 Russian wheat aphids from 2.4 m of wheat row in the protected and 410 in the unprotected environment. Soil surface temperatures remained mild throughout October, November, and the first 15 d of December (Fig. 2b). The temperature in the protected environment reached −26.0°C on 22 December 1990, whereas the unprotected environment was slightly lower at −29.8°C. This was the 2nd consecutive year that the lowest minimum temperatures occurred on 22 December. The protected environment had 2.5 cm of snow compared with 1.2 cm for the unprotected. Minimum temperatures dropped again on 29 December to −25.3°C for the protected and −26.7°C for the unprotected site. These temperatures occurred in the absence of snow cover and were followed by sharp declines in aphid densities for both environments. The result of the 2 successive cold fronts was 100% mortality in the Russian wheat aphid population. Freeze-degree accumulations increased from −2,986 on 21 December to −7,202 on 7 January for the protected site, and from −2,704 to −6,092 during the same period in the unprotected site. This was the greatest accumulation of freeze-degrees recorded for all 3 yr of this study. Total Russian wheat aphid densities dropped sharply between 21 December and 7 January for the protected and unprotected environments. One hundred percent mortality occurred in the protected environment by 6 February, whereas the unprotected environment reached 100% mortality by 19 February.

The 1990–1991 winter was characterized by several storm systems that produced small amounts of snow. The protected environment had 24 d with >1.0 cm of snow cover and 130.8 cm of total accumulated snow. The unprotected environment had 31 d with >1.0 cm and 102.8 cm of total accumulated snow (Table 1). This was, as previously mentioned for 1989–1990, a result of radiant heat from the protective barrier causing a faster rate of snow melt.

Winter, 1991–1992. Cold temperatures in late November early October kept artificially infested wheat plants in both environments from having high numbers of Russian wheat aphids (Fig. 3 a and b). Highest aphid densities for the year were on the 1st sample date (16 November), where there were 223 live aphids in the protected environment and 194 in the unprotected environment.

A cold front moved across northeastern Colorado on 29 October 1991, causing the temperature to decrease from 25.0°C to −14.9°C within 24 h. The storm produced an average of 11.2 cm of snow on the protected environment. The soil surface temperature reached −8.0°C. The unprotected environment received 2.2 cm of snow and a minimum soil surface temperature of −16.0°C. The maximum soil surface temperature stayed below 0.0°C for the next 5 d, dropping to −4.0°C (9.2 cm snow) in the protected environment and −18.0°C (2.8 cm of snow) in the unprotected environment. The 6.8 cm greater snow cover in the protected environment resulted in a 14.0°C higher soil surface temperature. The largest accumulation of freeze-degrees and freeze-hours for both environments occurred between 16 November and 18 December, followed by a consistent snow cover.

Russian wheat aphid densities declined in a linear fashion during the 1991–1992 winter. The protected environment reached 100% mortality on 27 March and the unprotected environment reached 100% mortality on 3 April.

The most significant environmental influence in both environments was the extended period of snow cover (Table 1). Snow cover stabilized the soil surface temperature below zero where freeze-degree accumulations were minimal but freeze-hour accumulation continued. The insulating factor of the extended snow cover can be seen clearly in the protected environment by comparing accumulated freeze-degrees with freeze-hours at the

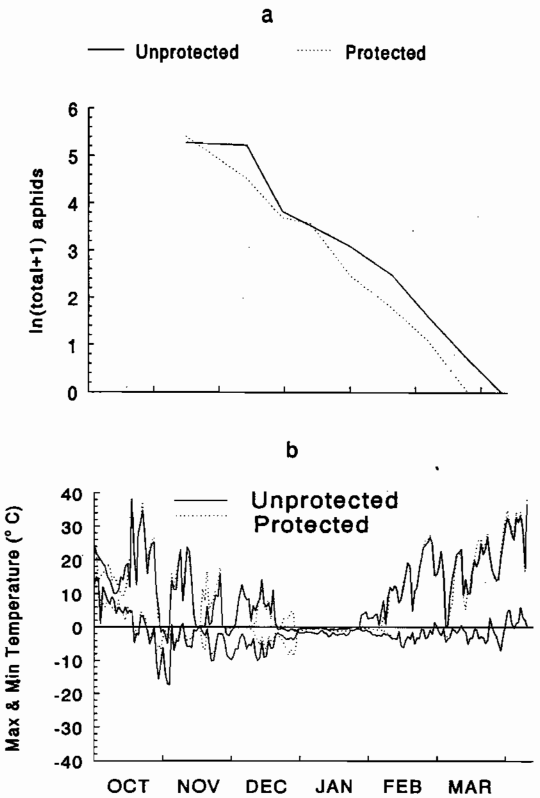

Fig. 3. (a) [*ln*(total+1)] Russian wheat aphids removed from 2.4-m row (8 sections of 0.3 m each) of winter wheat grown in protected and unprotected winter environments. (b) Daily maximum and minimum soil surface temperatures for protected and unprotected Russian wheat aphid test plots, winter 1991–1992, Central Great Plains Research Station, Akron, CO.

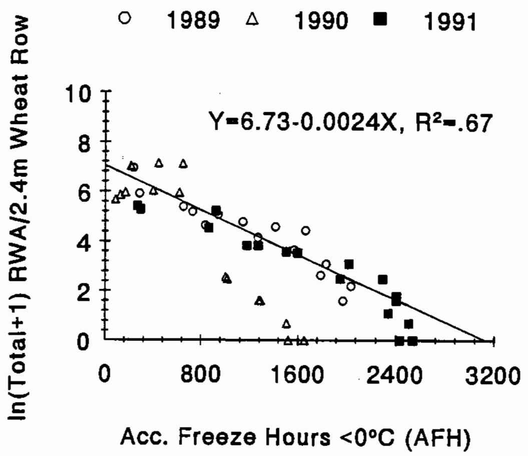

Fig. 4. Accumulated freeze-hours (AFH) where 1 subzero hour was accumulated for every hour the average soil surface temperature was <0°C (*x* axis) versus the [*ln*(total+1)] aphids removed from 2.4-m row (8 sections of 0.3 m each) of winter wheat grown in protected and unprotected winter environments, Central Great Plains Research Station, Akron, CO.

time 100% mortality occurred. On 27 March, freeze-degrees from the protected site were −2,944 compared with 2,535 freeze-hours. This is the smallest difference in the comparison of these 2 accumulations within an environment (Table 1).

Mortality Models, 1989–1991. In comparing the regression statistics for the additive effects of independent variables over the 3 yr, the freeze-hour accumulation alone resulted in the closest relationship with declining aphids ($R^2 = 0.67$, $P > F = 0.0001$; $n = 47$) compared with freeze-degrees ($R^2 = 0.50$; $P > F = 0.0001$; $n = 47$) (Table 2). These regression statistics indicate that freeze-hour accumulation was a more useful independent variable in the development of Russian wheat aphid mortality models, and 100% Russian wheat aphid mortality will occur before 3,000 freeze-hours (Fig. 4).

Aphid densities start to decline over a wide range of freeze-degrees (Fig. 5). Two distinct population declines can be observed within the aphid numbers versus freeze-degree accumulation. The 1st decline (protected environment, winter 1991–

Table 2. Best-fit linear regression models of Russian wheat aphids expressed as [ln(total + 1)] aphids per 2.4-m row of winter wheat (dependent variable *y*) versus independent variables from protected and unprotected environments, 1989–1992; Central Great Plains Research Station, Akron, CO

Best-fit model (n = 47)	R^{2a}	CP	F	MSE[b]
$y = 6.03 - 0.0054(\text{AFD})$	0.50	29.6	44.3	1.55
$y = 8.69 - 0.0062(\text{AFD}) - 0.17(\text{SM})$	0.63	12.0	37.8	1.34
$y = 8.56 - 0.0061(\text{AFD}) - 0.084(\text{ADSC}) - 0.13(\text{SM})$	0.67	7.9	29.7	1.26
$y = 8.81 - 0.0061(\text{AFD}) - 0.087(\text{ADSC}) - 0.11(\text{SM}) - 0.79(\text{SR})$	0.71	5.0	25.5	1.22
$y = 6.75 - 0.0024(\text{AFH})$	0.67	7.1	93.4	1.26
$y = 7.16 - 0.0023(\text{AFH}) - 0.067(\text{SR})$	0.70	5.1	51.5	1.22
$y = 7.18 - 0.0026(\text{AFH}) + 0.064(\text{ADSC}) - 0.067(\text{SR})$	0.72	3.8	37.3	1.18
$y = 6.82 - 0.0026(\text{AFH}) + 0.055(\text{ADSC}) + 0.036(\text{SM}) - 0.074(\text{SR})$	0.73	5.0	28.0	1.19

Models are statistically the best from all possible combinations of independent variables added stepwise from statement selection = maxr, and selection = rsquare MSE CP (SAS Institute 1988). AFD, accumulated freeze-degrees <0°C; ACH, accumulated freeze-hours <0°C; ADSC, average daily snow cover; SM, soil mixture; SR, solar radiation.

[a] All correlation coefficients significant at 0.05 and 0.01% levels.

[b] Square root of the mean square error or standard deviates of the fitted model.

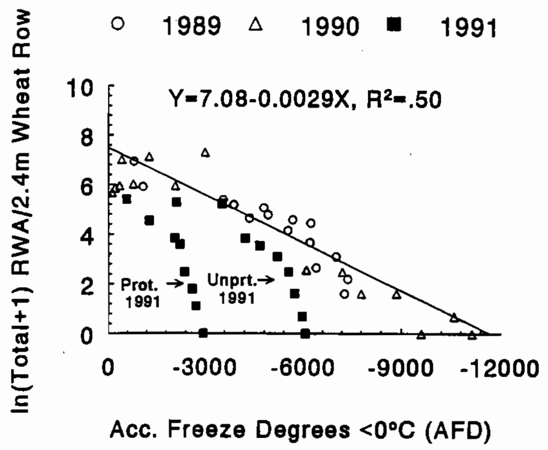

Fig. 5. Accumulated freeze-degrees (AFD) where the average hourly soil surface temperature <0°C is summed (x axis) versus the [ln(total+1)] aphids removed from 2.4-m row (8 sections of 0.3 m each) of winter wheat grown in protected and unprotected winter environments, Central Great Plains Research Station, Akron, CO.

1992) occurs between 0 and (2,600) freeze-degrees and was a result of the protected environment (1991–1992) receiving 1,183.3 cm of total accumulated snow with 87 d of >1.0 cm. The 2nd decline (unprotected environment, winter 1991–1992) occurs between −3,900 and −6,065 freeze-degrees where aphids were exposed to less total accumulated snow (949.8 cm) and fewer (77) snow cover days of >1 cm.

Russian wheat aphid mortality at low freeze-degree and freeze-hour accumulation in both environments for the 1991–1992 winter is a direct result of snow cover. The soil surface temperature remained below 0.0°C for 42 d (29 December to 8 February) so that subzero temperature accumulation was minimal but aphid mortality continued. The effect of 42 d of subzero exposure on the Russian wheat aphid is also supported by comparing it with the lower threshold for development, which approximates 0°C (Aalbersberg et al. 1987, Kieckhefer and Elliott 1989, Girma and Wilde 1990).

The remaining data points (protected and unprotected environments, winters 1989–1990 and 1990–1991; Fig. 5) for aphids versus freeze-degrees do not show the same pattern of decline because they were from years with significantly less snow cover. Regression statistics (n = 30, R^2 = 0.82, F = 128.6, $P > F$ = 0.001) improve when the 1991–1992 data are excluded and 1989–1990 and 1990–1991 data are used in the simple model of aphids versus freeze-degrees. The combined analysis for all years shows that 100% Russian wheat aphid mortality occurred before 12,000 freeze-degrees.

Other independent variables (solar radiation, soil moisture, average daily snow cover) were beneficial in developing statistical models. Their stepwise addition always improved model statistics after the main effect of freeze-hours or freeze-degrees.

In the 3 winters that maximum and minimum soil surface temperatures were measured, there was at least 1 cold front that dropped the minimum temperature below −20.0°C. Snow cover during the coldest minimum temperatures significantly insulated soil surface temperatures and the Russian wheat aphid microenvironment. Extended periods of continuous snow cover (>40 d), in which the temperature stabilized between 0.0 and −4.0°C, was responsible for complete Russian wheat aphid mortality with no replacement natality. Snow distribution and soil temperatures were altered in the protected environment because of heat radiating from the wall barrier. Reflective (radiant) heat caused snow to melt at a faster rate, resulting in fewer days with insulating snow. Fewer days with insulating snow allowed for colder minimum soil temperatures and greater freeze-degrees and freeze-hour accumulations. In the first 2 yr of the study, Russian wheat aphid numbers from the protected site were 3–4 times those of the unprotected site. This is believed to be caused by warmer temperatures created from radiant heat reflected from the metal wall in the protected environment. Early fall temperatures for the final year of the study were exceptionally cold and cloudy. This did not create higher temperatures in the protected environment, and aphid densities from 2.4 m of row were similar (223 for the protected and 194 for the unprotected) on the 1st sample date of 1991.

This study has demonstrated that snow can be beneficial or detrimental to overwintering Russian wheat aphids. Snow was beneficial when it insulated the subnivean environment from extreme temperature drops caused by fast-moving cold fronts. An extended period of snow (>40 d) stabilized the subnivean temperature to <0.0°C and eventually eliminated the Russian wheat aphid population. Even though snow amounts and durations differed within the protected and unprotected environments, there was not a winter in which aphids survived in one environment and not the other.

Extreme drops in temperature did not always result in expected declines in overwintering Russian wheat aphid populations. This may have been the result of measuring soil surface temperature rather than the insulated environment within a curled wheat leaf. Although we did not measure the microenvironmental temperature of the Russian wheat aphid inside a curled wheat leaf, our data shows that the accumulation of subzero soil surface temperature can be used as the basis for predicting winter mortality. We believe that freeze-hours were the most accurate independent variable related to Russian wheat aphid winter mortality because they account for both the degree of coldness and the duration of exposure.

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References Cited

Aalbersberg, Y. K., M. C. VanDerWesthuizen, and P. H. Hewitt. 1987. Development rate, fecundity and lifespan of apterae of the Russian wheat aphid *Diuraphis noxia* under controlled conditions. Bull. Entomol. Res. 77: 629–635.

Archer, T., and E. D. Bynum. 1992. Economic injury level for Russian wheat aphid (Homoptera: Aphididae) on dryland winter wheat. J. Econ. Entomol. 85: 987–992.

Bale, J. S., R. Harrington, and M. S. Clough. 1988. Low temperature mortality of the peach-potato aphid *Myzus persicae*. Ecol. Entomol. 13: 121–129.

Burd, J. D., and R. L. Burton. 1992. Characterization of damage caused by Russian wheat aphid (Homoptera: Aphididae). J. Econ. Entomol. 85: 2017–2022.

Butts, R. A. 1992. Cold hardiness and its relationship to overwintering of Russian wheat aphid (Homoptera: Aphididae) in southern Alberta. J. Econ. Entomol. 85: 1140–1145.

Casagrande, R. A., and D. L. Haynes. 1976. A predictive model for cereal leaf beetle mortality from sub-zero temperatures. Environ. Entomol. 4: 761–769.

Cook, R. J., and R. J. Veseth. 1991. Wheat health management. American Phytopathological Society. APS, St. Paul, MN.

Girma, M., and G. E. Wilde. 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.

Harrington, R., and X. N. Cheng. 1984. Winter mortality, development and reproduction in a field population of *Myzus persicae* (Sulzer) in England. Bull. Entomol. Res. 74: 633–640.

Harvey, T. L., and T. J. Martin. 1988. Relative cold tolerance of Russian wheat aphid and biotype-E greenbug. J. Kans. Entomol. Soc. 61: 137–140.

Kieckhefer, R. W., and N. C. Elliott. 1989. Effect of fluctuating temperatures on development of immature Russian wheat aphid (Homoptera: Aphididae) and demographic statistics. J. Econ. Entomol. 82: 119–122.

Legg, D., S. Ammosson, L. Brooks, G. Hein, G. Johnson, W. Massey, W. P. Morrison, and F. Peairs. 1993. Economic impact of the Russian wheat aphid in the western United States: 1991–1992. Great Plains Agricultural Council Publication 147.

Lowe, A. E. 1952. Evidence of the overwintering of greenbugs in southwestern Kansas. J. Kans. Entomol. Soc. 25: 3–4.

Marchant, P. J. 1982. An index for evaluating the temperature stability of a subnivean environment. J. Wildl. Manage. 46: 518–520.

Michels, G. J., and R. W. Behle. 1989. Influence of temperature on reproduction, development, and intrinsic rate of increase of Russian wheat aphid (Homoptera: Aphididae). J. Econ. Entomol. 82: 439–444.

Morrison, W. P., F. Baxendale, L. Brooks, C. Burkhardt, J. Campbell, G. Johnson, W. Massey, D. McBride, F. Peairs, and J. Schultz. 1988. The Russian wheat aphid: a serious new pest of small grains in the Great Plains. Great Plains Agricultural Council Publication 124.

Painter, R. H., H. R. Bryson, and D. A. Wilbur. 1954. Insects that attack wheat in Kansas. Kans. Agric. Exp. Stn. Bull. 367.

Powell, W. 1974. Supercooling and low temperature survival of the green spruce aphid (*Elatobium abietinum*). Ann. Appl. Biol. 78: 27–37.

SAS Institute. 1988. SAS\STAT user's guide to personal computers: version 6.03. SAS Institute, Cary, NC.

Strathdee, A. T., G. G. Howling, and J. S. Bale. 1995. Cold hardiness of overwintering aphid eggs. J. Insect Physiol. 41: 653–657.

Stoetzel, M. B. 1987. Information on and identification of *Diuraphis noxia* (Homoptera: Aphididae) and other aphid species colonizing leaves of wheat and barley in the United States. J. Econ. Entomol. 80: 696–704.

Weisburg, S. 1985. Applied linear regression. Wiley, New York.

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