Natural Enemy Impact on the Russian Wheat Aphid in Southeastern Colorado

J. H. LEE,[1] N. C. ELLIOTT,[2,3] S. D. KINDLER,[2] B. W. FRENCH,[4] C. B. WALKER,[5] AND R. D. EIKENBARY[6]

Environ. Entomol. 34(1): 115–123 (2005)

ABSTRACT The effectiveness of predators and parasitoids of the Russian wheat aphid was experimentally evaluated using mechanical exclusion in production winter wheat, *Triticum aestivum* L., fields at four locations in southeastern Colorado. Three types of enclosure were used: complete exclusion enclosures, partial exclusion enclosures that permitted entry by parasitic Hymenoptera, and environmental exclusion enclosures that reduced the effects of wind and rain on Russian wheat aphids and trapped emigrating alate Russian wheat aphids so that they could not return to plants within the enclosure. Russian wheat aphids in nonenclosed plots were also studied. Russian wheat aphid density varied among treatments in the following order: complete exclusion ≥ partial exclusion > environmental exclusion > nonenclosed plots. The trapping of alatae within enclosures and reduced adverse stresses such as rain and wind within enclosures were partially responsible for the greater Russian wheat aphid density in complete and partial exclusion enclosures compared with environmental exclusion enclosures and nonenclosed plots. The aphidophagous coccinellid, *Hippodamia convergens* Guèrin-Mèneville, and the generalist *Nabis* spp. were the most abundant predators during the increasing phase of Russian wheat aphid population development, but they did not substantially reduce Russian wheat aphid numbers. *H. convergens*, *Coccinella septempuntata* L., and *H. sinuata* Mulsant were the most abundant predators during the declining phase of Russian wheat aphid population growth. The dominant parasitoid was *Lysiphlebus testaceipes* (Cresson), but parasitism rates were very low. Canonical correspondence analysis showed close associations between the abundance of predators and Russian wheat aphid density, Russian wheat aphid density and wind during the increasing phase of Russian wheat aphid population development, and Russian wheat aphid density and rainfall late in the growing season.

KEY WORDS *Diuraphis noxia*, mechanical exclusion, biological control, predatory insect, parasitoid

THE RUSSIAN WHEAT APHID, *Diuraphis noxia* (Mordvilko), was first detected in the United States in Texas in 1986 (Stoetzel 1987). It spread rapidly throughout the western cereal growing regions of the United States and Canada (Jones et al. 1989), and by 1990, it was found in 16 western states and three Canadian provinces. Host plants of the Russian wheat aphid include wheat, *Triticum aestivum* L., barley, *Hordeum vulgare* L., and several species of noncultivated Graminae (Kindler and Springer 1989).

Studies of the impact of aphidophagous parasitoids and predators on Russian wheat aphid populations soon after invasion by the pest indicated that native natural enemies were ineffective at controlling the Russian wheat aphid (Rice and Wilde 1991, Wraight et al. 1993). In contrast, Hopper et al. (1995) observed that natural enemies played a significant role in suppressing Russian wheat aphid populations in Europe, where presumably the Russian wheat aphid is native. These and similar observations prompted initiation of a classical biological control program against the Russian wheat aphid. Greater than 15 million predator (Coleoptera: Coccinellidae; Diptera: Chamaemyiidae and Syrphidae) and parasitoid (Hymenoptera: Aphelinidae and Braconidae: Aphidiinae) individuals were released in 18 U.S. states for nearly 10 yr beginning in 1987 (Pike et al. 1997, Prokrym et al. 1998).

Exclusion methods have previously been used to evaluate the impact of natural enemies on aphids in cereals, including the Russian wheat aphid (e.g., Kring et al. 1985, Rice and Wilde 1988, Hopper et al. 1995, Nechols and Harvey 1998, Michels et al. 2001). Therefore, we decided to use mechanical exclusion by enclosures to study the impact of both endemic and exotic natural enemies on Russian wheat aphid pop-

[1] Current address: Research Institute for Natural Science, Dongguk University, 26, 3ga, Pil-dong, Seoul, ROK 100–715.
[2] USDA–ARS, SPA, Plant Science Research Laboratory, 1301 N. Western St., Stillwater, OK 74075.
[3] Corresponding author, e-mail: norman.elliott@ars.usda.gov.
[4] Current address: USDA–ARS-NGIRL, 2923 Medary Ave., Brookings, SD 57006.
[5] Department of Bioagricultural Sciences and Pest Management, Colorado State University, Prowers County Cooperative Extension Office, 1001 S. Main Street, Lamar, CO 81052.
[6] Department of Entomology and Plant Pathology, Oklahoma State University, Stillwater, OK 74078.

ulations in southeastern Colorado, where numerous releases of natural enemies had occurred during the Russian wheat aphid classical biological control program and where establishment of some species had been observed (Elliott et al. 1995). Simultaneously, we monitored the population of Russian wheat aphids in the wheat fields in which the enclosure studies were conducted. We also measured meteorological variables during the study in an attempt to determine the effects of abiotic environmental variables on the Russian wheat aphid and natural enemies. Canonical correspondence analysis (CCA) was used in data analysis because of its use for quantifying relationships between species abundance and environmental variables (Palmer 1993). If such associations can be determined in the open field, it could help in understanding the effects of those variables on Russian wheat aphid population changes in the enclosures. Our objectives were to (1) determine whether natural enemies had an effect on Russian wheat aphid population change using natural enemy exclusion techniques and (2) estimate potential impact of various natural enemies and the abiotic environment on Russian wheat aphid population change by measuring these factors in the open field simultaneously with exclusion studies.

Materials and Methods

Experimental Fields. Experiments were conducted during 1994 in four production winter wheat fields, two located near Prichett and two located near Walsh, in southeastern Colorado. The pair-wise distance between fields ranged from ≈7.5 to 45 km. The two fields near Prichett were designated P1 and P2, and the two fields near Walsh were designated W1 and W2. All fields were planted to winter wheat and maintained using cultural methods determined by the grower. A 100 by 100-m plot was established in each field, within which the studies were conducted. Two complementary studies were undertaken in the study plot within each of the four fields. In the first study, natural enemy exclusion methods were used to investigate natural enemy impact on Russian wheat aphid population change. Similar exclusion techniques have been used to evaluate the impact of predators and parasitoids on aphids in cereal crops (Kring et al. 1985, Hopper et al. 1995, Nechols and Harvey 1998, Michels et al. 2001). In the second study, populations of Russian wheat aphids and natural enemies in the open field surrounding the exclusion study were intensively sampled to characterize population change over time using a variety of methods.

Natural Enemy Exclusion Study. Enclosures used in the experiments were constructed of mesh material sewn in the form of a tube of ≈0.3 m diameter and 1 m length. The tube was fitted over a frame constructed from two pieces of 0.95-cm-diameter rebar bent into u-shapes. The u-shaped pieces of rebar were pushed into the ground facing in perpendicular directions to create a rectangular frame ≈0.75 m high over which the mesh tube was fitted. The upper end of the tube was tied in a knot, and the lower end was buried in the ground to seal the enclosure. Four treatments were used in the experiment: (1) a fine mesh enclosure made of polyester organza with ≈2,500 cells/cm^2, which was a small enough cell size to prevent all insects from entering the enclosure (complete exclusion); (2) a coarse mesh enclosure made of Lumite screening with 64 cells/cm^2, which was coarse enough to permit entry of parasitic Hymenoptera but not predaceous coccinellids or other aphid predators typically found in wheat fields (partial exclusion); (3) a 0.3 by 0.3-m area of wheat marked with a plot flag, which allowed complete exposure to natural enemies and environmental conditions (nonenclosed plots); and (4) a fine mesh enclosure as in treatment 1 but with the lower end of the enclosure left raised ≈10 cm above ground level and the inside surface of the top of the enclosure treated with Tanglefoot (Tanglefoot, Grand Rapids, MI). This type of enclosure was intended to provide access by predators and parasitoids and to trap dispersing winged Russian wheat aphids in the Tanglefoot-coated surface so they could not return to the plants within the enclosure and to protect the Russian wheat aphids from adverse environmental conditions, such as rain, and were designated as environmental exclusion enclosures.

Fifty replicates each of treatments 1, 2, and 3 and 10 replicates of treatment 4 were positioned randomly within 10 rows in fields P1, P2, and W1 for a total of 160 experimental units in each field. Forty replicates each of treatments 1, 2, and 3 and eight replicates of treatment 4 were positioned randomly in eight rows in field W2, for a total of 128 experimental units. Experimental units were positioned ≈5 m apart within rows, with ≈5 m separating the rows. Immediately after experimental units were established in the field, the wheat plants in each unit were treated with insecticide chlorpyrifos (1.12 kg/ha AI, Lorsban) to kill any insects that were present. Two weeks after insecticide application and 2 wk before the first sampling date, each experimental unit was infested with four adult greenhouse-reared Russian wheat aphids by carefully placing each Russian wheat aphid on a leaf of a wheat plant within the experimental unit.

Enclosures were sampled biweekly from 22 April to 7 June for a total of five samplings. Because wheat plants in each experimental unit were sampled destructively, a particular experimental unit was sampled only once during the experiment. On each sampling date, 10 tillers were cut from within each of 10 complete exclusion enclosures, partial exclusion enclosures, and nonenclosed plots selected randomly without replacement from among the 50 replicates of each treatment. At W2, eight replicates of each treatment were sampled. The cut tillers from each replicate were placed quickly and carefully into a resealable plastic bag, labeled, and placed in an ice chest for transport to the laboratory. The 10 environmental exclusion enclosures at each site (8 at W2) were sampled only once on calendar date 152, which approximately coincided with the peak of Russian wheat aphid population density in each field.

At the laboratory, the numbers of alate and apterous Russian wheat aphids and mummified aphids were determined for each sample. All mummies encountered in each sample were collected and placed individually in gelatin capsules. The gelatin capsules from each sample were placed in a petri dish labeled with location, enclosure type, replicate, and sampling date. Mummies were stored at room temperature for emergence of adult parasitoids, which were identified to species.

The rate of population increase for the aphids for each treatment was calculated using the following equation: $A_n = A_0q^n$, where A_n = number of aphids on day n, A_0 = initial maternal population, and q = daily rate of increase. The value of q was computed from the equation $q = \exp[(\ln A_n/A_0)/n]$ (Tamaki et al. 1974).

Russian Wheat Aphid and Natural Enemy Populations in the Open Field. Russian wheat aphids and natural enemies were sampled from the open field within a 100 by 100-m plot containing the exclusion experiment in each field. The plot was divided into 16 25 by 25-m subplots within which sampling was undertaken. Russian wheat aphids were sampled weekly by cutting a single wheat tiller at ground level from eight arbitrary locations in each subplot (total of 128 tillers) and counting the number of Russian wheat aphid, other aphids, mummified Russian wheat aphids, and mummified other aphids on each tiller. When the Russian wheat aphid population was at high density, 4 tillers were sampled from each subplot (total of 64 tillers), and aphids and mummies were counted as described above. Wheat plant growth stage (Zadoks et al. 1974) was measured for each field on a weekly basis.

Predators were sampled weekly using a sweep net. A sample of four 75 pendular sweep samples with a sweep net (38 cm diameter) were taken from the 100 by 100-m plot in each field. Each 75-sweep sample was taken along a transect through a row of four subplots, so that sweeps were taken from each subplot. Each 75-sweep sample was placed in a plastic bag, labeled, and returned to the laboratory in an ice chest. At the laboratory, the samples were placed in a freezer until they could be sorted and identified.

Parasitism of Russian wheat aphids and fecundity of adult Russian wheat aphids in the field were estimated by rearing field-collected Russian wheat aphids. A single tiller infested with Russian wheat aphids was collected from each of five arbitrarily chosen locations in each of the 16 subplots in a field, placed in a plastic bag, and returned to the laboratory in an ice chest. At the laboratory, the Russian wheat aphids in the sample were removed from the tillers into a white pan. To estimate parasitism, 100 fourth-instar nymphs were selected arbitrarily from among those in the pan. The nymphs were placed on seedling wheat plants (20 nymphs/plant) growing individually in 10-cm-diameter plastic pots. The plant in each pot was covered with a clear plastic vented cylindrical cage (7.5 cm diameter by 30 cm height). The plants were kept for 48 h in the environmental chamber maintained at 20 ± 0.5°C and 16 D:8 L photoperiod. After 48 h, the number of mummies that formed on each plant was determined. Mummies were placed individually in gelatin capsules to await emergence of adult parasitoids, which were identified to species. To estimate fecundity of Russian wheat aphids, 20 adult Russian wheat aphids were selected arbitrarily from among those in the pan. The 20 adults were placed individually on a seedling wheat plant (cultivar 'Lamar') growing in a 10-cm-diameter plastic pot covered with a clear plastic cylindrical cage. The plants were placed in the environmental chamber at 20 ± 0.5°C and 16 D:8 L for 24 h, after which the number of nymphs produced by each aphid were counted and recorded.

Meteorological Measurements. Meteorological variables, air temperature, relative humidity, rainfall, and wind speed were monitored continuously with CR-10 microloggers (Campbell Scientific, Logan, UT) located at P1 and at the Plainsman Research Station near Walsh, CO. The Plainsman Research Station was located ≈4 km south of W1 and 3 km north of W2. The CR-10 at P1 was located ≈10 km east of P2. Meteorological data from the Plainsman Research Station were used for both W1 and W2, and data from P1 were used for P1 and P2.

At P1, temperature was measured in a single cage of each type over the duration of the study using shaded SM-192 temperature sensors attached to the CR-10 micrologger located at the site. The sensors were positioned in the center of the cage at mid-canopy height. Sensors were rotated among cages biweekly to reduce the chance that bias among sensors would affect estimates of mean temperature in cages. The height of each sensor was adjusted when it was rotated to maintain it at midcanopy level.

Data Analysis. Analyses of variance (ANOVAs) were calculated using PROC GLM with means for predetermined comparisons tested for equality statistically using *t*-tests, which were calculated using the LSMEANS statement (SAS Institute 1990). One ANOVA was calculated with the number of Russian wheat aphids per tiller as the response variable for data from the three treatments that were sampled on the five sampling dates in each of the four fields. The experimental design was a factorial with fields, sampling dates, interaction between fields and sampling dates, and enclosure type nested within fields and sampling date included as factors in the model. A second ANOVA was calculated with the number of Russian wheat aphids per tiller as the response variable for data from the four enclosure types sampled on calendar date 152. The design for this ANOVA had fields and enclosure types nested within fields as factors. A third ANOVA was calculated with the proportion of alate Russian wheat aphids for data from the three enclosure types and nonenclosed plots sampled on calendar date 152 as the response variable, with fields and enclosure type nested within fields as factors.

CCA (ter Braak 1987) was used to simultaneously examine the strength of associations between biotic and abiotic variables and the abundance of predatory insects in the four fields. Data from open field sampling for each field were used in constructing the

Table 1. No. Russian wheat aphids per wheat tiller in three types of enclosure and nonenclosed plots in four winter wheat fields in southeastern Colorado

Location[a]	Sample date	Mean ± SE no. RWA/tiller[b]			
		Complete exclusion	Partial exclusion	Environmental exclusion	Nonenclosed plots
P1	112	0.1 ± 0.1a	1.4 ± 0.9a		0.2 ± 0.1a
	125	0.2 ± 0.2a	0.7 ± 0.3a		0.3 ± 0.2a
	137	3.8 ± 1.6ab	11.2 ± 4.1a		0.6 ± 0.3b
	152	52.0 ± 19.6a	54.1 ± 15.4a	13.3 ± 3.3b	6.1 ± 1.4b
	158	42.3 ± 28.3a	40.6 ± 7.8a		5.3 ± 2.6a
P2	112	2.7 ± 1.0a	4.5 ± 1.5a		2.4 ± 0.5a
	125	13.8 ± 2.7a	9.7 ± 2.0a		1.9 ± 0.6b
	137	22.5 ± 5.1a	50.3 ± 8.7b		3.0 ± 1.0c
	152	193.5 ± 42.7a	152.0 ± 28.0a	27.1 ± 6.3b	12.8 ± 3.8b
	158	146.1 ± 22.8a	29.1 ± 12.6b		13.7 ± 2.8b
W1	112	1.7 ± 1.0a	1.8 ± 0.6a		0.2 ± 0.7a
	125	4.7 ± 1.1a	2.8 ± 0.7a		0.2 ± 0.1b
	137	34.0 ± 20.4a	28.4 ± 21.8a		0.2 ± 0.1a
	152	286.8 ± 63.4a	98.7 ± 51.2b	26.9 ± 2.3b	14.5 ± 3.9b
	158	27.0 ± 5.8a	16.4 ± 3.7a		3.3 ± 1.4b
W2	112	2.9 ± 1.0a	2.4 ± 0.8a		1.3 ± 0.6a
	125	28.0 ± 5.1a	16.3 ± 3.5b		1.8 ± 1.0c
	137	118.0 ± 22.2a	25.7 ± 5.1b		2.5 ± 1.2b
	152	238.1 ± 73.9a	236.9 ± 45.8a	50.2 ± 11.1b	22.5 ± 2.4b
	158	35.9 ± 10.3a	38.4 ± 12.6a		7.4 ± 1.5b

[a] Two fields near Prichett were designated P1 and P2; two fields near Walsh were designated W1 and W2.
[b] Means in a row followed by the same letter are not significantly different ($P < 0.05$) based on a test of least significant difference.

ordinations. Data from calendar date 99 to calendar date 152, during which Russian wheat aphid populations were increasing in the exclusion study plots but not in open field, were used in the CCA ordinations. Using CCA, predator species abundance scores were plotted simultaneously in ordination biplots against scores for biotic and abiotic environmental variables. Environmental variables were represented by vectors in the biplots, and predator species abundance scores were represented by symbols. Biotic environmental variables were Russian wheat aphid rate of population increase, alate rate of increase, mean number of Russian wheat aphids per tiller, Russian wheat aphid fecundity, and wheat plant growth stage. Abiotic environmental variables were average temperature, rainfall, and wind speed. Average temperature for a particular sampling date was calculated as the mean over all days for the interval from that date to the previous sampling date. Wind speed was calculated as the maximum hourly wind speed recorded per day averaged over each day in the sampling interval. Rainfall was the average of daily rainfall over all days in the sampling interval. Preliminary CCA ordinations showed that average temperature was highly correlated with plant growth stage, so only plant growth stage was included in the final CCA.

Results

Natural Enemy Exclusion Study. Mean numbers of Russian wheat aphids per tiller for each type of enclosure and for nonenclosed plots are listed in Table 1. The number of Russian wheat aphid per tiller in enclosures and nonenclosed plots differed significantly among fields ($F = 14.9$; df = 3,511; $P < 0.0001$) and dates ($F = 83.4$; df = 4,511; $P < 0.0001$). There was a significant field by date interaction ($F = 5.64$; df = 12,511; $P < 0.001$), reflecting the observation that Russian wheat aphid numbers changed at different rates in the four fields (Table 1). The number of Russian wheat aphids per tiller differed significantly among enclosure types within fields and dates ($F = 9.13$; df = 40,511; $P < 0.0001$). Differences among enclosure types were more frequently significant for later sampling dates than for early dates (Table 1). The number of Russian wheat aphid per tiller was frequently lower in partial exclusion enclosures than in full exclusion enclosures, but the difference was usually not significant. The number of Russian wheat aphids per tiller was usually significantly lower in nonenclosed plots than in partial or full exclusion enclosures. For calendar date 152, when environmental exclusion enclosures as well as full and partial exclusion enclosures and nonenclosed plots were sampled, there was a significant difference in the number of Russian wheat aphids per tiller among fields ($F = 8.16$, df = 3,136; $P < 0.001$) and among enclosure types within fields ($F = 9.81$; df = 12,136; $P < 0.001$). The number of Russian wheat aphids per tiller was lower in partial exclusion than in complete exclusion enclosures in three of the four fields, but the difference was usually small and was significant only at W1 (Table 1). The number of Russian wheat aphids per tiller was four to seven times lower in environmental exclusion enclosures than in complete or partial exclusion enclosures, and this difference was significant for three of the four fields. The number of Russian wheat aphids per tiller in environmental exclusion enclosures was intermediate between partial exclusion enclosures and nonenclosed plots. The difference in the number of Russian wheat aphids per tiller in environmental exclusion enclosures compared with nonenclosed

Table 2. Rate of population increase for Russian wheat aphids in three types of enclosures and in nonenclosed plots in four winter wheat fields in southeastern Colorado

Location[a]	Population phase	Date	Growth stage	Rate of population increase		
				Complete exclusion	Partial exclusion	Nonenclosed plots
P1	Increasing	112	2			
		125	4	1.05	0.948	1.032
		137	5	1.28	1.26	1.059
		152	7.9	1.19	1.111	1.167
		112–152	2–7.9	1.17	1.096	1.089
	Decreasing	158	8	0.97	0.953	0.977
P2	Increasing	112	2			
		125	3	1.13	1.061	0.982
		137	4	1.04	1.147	1.039
		152	7	1.15	1.077	1.102
		112–152	2–7	1.11	1.092	1.063
	Decreasing	158	8	0.95	0.759	1.011
W1	Increasing	112	2.3			
		125	4	1.08	1.035	1.001
		137	5	1.18	1.213	1.004
		152	8	1.15	1.087	1.322
		112–152	2.3–8	1.14	1.105	1.113
	Decreasing	158	9	0.71	0.774	0.809
W2	Increasing	112	2.4			
		125	4	1.19	1.159	1.025
		137	5	1.13	1.074	1.028
		152	8	1.05	1.129	1.158
		112–152	2.4–8	1.12	1.12	1.074
	Decreasing	158	9	0.76	0.771	0.853

[a] Two fields near Prichett were designated P1 and P2; two fields near Walsh were designated W1 and W2.

plots was not significant for any of the four fields (Table 1).

Two phases of Russian wheat aphid population development were observed in the open field: an increasing phase was observed generally through early grain filling (Zadoks' growth stage 7), followed by a decreasing phase during later stages of wheat plant development (Zadoks' growth stages 8–9; Table 2). Russian wheat aphid abundance increased over time in all types of enclosures and nonenclosed plots until the last sampling date, calendar date 158, when abundance decreased at both the Walsh and Prichett fields. The more dramatic decrease in population growth rate in the Walsh fields was probably the result of the more advanced growth stage of wheat at Walsh compared with Prichett, which is ≈200 m higher elevation than Walsh, with correspondingly lower average temperatures. Russian wheat aphid population growth rates in the four fields ranged from 1.11 to 1.17 in complete exclusion enclosures, 1.09 to 1.13 in partial exclusion enclosures, and 1.06 to 1.11 in nonenclosed plots. During the increasing phase, the highest rate of increase occurred in complete exclusion enclosures and the lowest rate occurred in nonenclosed plots for three of the four fields. At W1, the Russian wheat aphid population growth rate was greatest in complete exclusion enclosures and lowest in partial exclusion enclosures during the increasing phase of population growth.

On date 152, the proportion of alate Russian wheat aphid was usually greater in complete and partial exclusion enclosures than in environmental exclusion enclosures and nonenclosed plots in all fields (Table 3). The proportions of alate Russian wheat aphids in environmental exclusion and nonenclosed plots were similar in all fields, as were the proportions of alatae in full and partial exclusion enclosures. The proportion of alatae on calendar date 152 differed significantly among enclosure types at W1 and W2 ($F = 6.14$; df = 9,135; $P < 0.001$), with the proportion of alatae being significantly greater in complete and partial exclusion enclosures than in environmental exclusion enclosures and nonenclosed plots. The proportion of alatae was greater in complete and partial exclusion enclosures than in environmental exclusion enclosures and nonenclosed plots at P1 on date 152, but not significantly so.

Russian Wheat Aphids and Natural Enemy Populations in the Open Field. Coccinellidae, Nabidae (*Nabis* spp.), Chrysopidae, Hemerobiidae, Syrphidae, and spiders were collected in sweepnet samples from the open field surrounding the exclusion study (Table 4). Voucher specimens were deposited in the entomological collection, Department of Entomology and Plant Pathology, Oklahoma State University. Among these predators, coccinellids and nabids were most abundant (Table 5). *Hippodamia convergens* Guèrin-Mèneville and *Nabis* spp. exhibited the highest abundance during the increasing phase of Russian wheat aphid population growth, and *H. convergens*, *H. sinuata* Mulsant, and *Coccinella septempunctata* L. exhibited highest abundance during the decreasing phase. The exotic parasitoid *Aphelinus asychis* Walker, and three native parasitoids, *Lysiphlebus testaceipes* (Cresson), *Diaeretiella rapae* (M'Intosh), and *Trioxys* spp., were reared from field-collected Russian wheat aphids. Parasitism rates were very low throughout the study, averaging <0.5% of 1,250 Russian wheat aphids reared from P1 and P2 and 0% from 1,141 Russian

Table 3. Proportion of Russian wheat aphid alatae in three types of enclosures and in nonenclosed plots in four winter wheat fields in southeastern Colorado

Location[a]	Sample date	Mean proportion ± SE of alatae/tiller[b]			
		Complete exclusion	Partial exclusion	Environmental exclusion	Nonenclosed plots
P1	112	0.00 ± 0.00	0.00 ± 0.00a		0.00 ± 0.00
	125	0.00 ± 0.00	0.02 ± 0.02		0.00 ± 0.00
	137	0.00 ± 0.00	0.01 ± 0.00		0.07 ± 0.06
	152	0.06 ± 0.01a	0.08 ± 0.02a	0.04 ± 0.02a	0.03 ± 0.03a
	158	0.30 ± 0.07	0.56 ± 0.23		0.15 ± 0.04
P2	112	0.00 ± 0.00	0.00 ± 0.00		0.00 ± 0.00
	125	0.00 ± 0.00	0.00 ± 0.00		0.06 ± 0.05
	137	0.00 ± 0.00	0.00 ± 0.00		0.15 ± 0.11
	152	0.02 ± 0.00a	0.02 ± 0.01a	0.01 ± 0.00a	0.02 ± 0.01a
	158	0.25 ± 0.08	0.39 ± 0.12		0.08 ± 0.02
W1	112	0.00 ± 0.00	0.00 ± 0.00		0.00 ± 0.00
	125	0.00 ± 0.00	0.04 ± 0.02		0.00 ± 0.00
	137	0.00 ± 0.00	0.00 ± 0.00		0.00 ± 0.00
	152	0.15 ± 0.04a	0.17 ± 0.03a	0.05 ± 0.02b	0.02 ± 0.00b
	158	0.19 ± 0.06	0.21 ± 0.07		0.87 ± 0.22
W2	112	0.00 ± 0.00	0.00 ± 0.00		0.00 ± 0.00
	125	0.02 ± 0.01	0.00 ± 0.00		0.02 ± 0.02
	137	0.01 ± 0.00	0.02 ± 0.01		0.03 ± 0.02
	152	0.32 ± 0.06a	0.21 ± 0.02a	0.05 ± 0.01b	0.07 ± 0.01b
	158	0.45 ± 0.11	0.37 ± 0.09		0.15 ± 0.03

[a] Two fields near Prichett were designated P1 and P2; two fields near Walsh were designated W1 and W2.
[b] Means in a row followed by the same letter are not significantly different ($P > 0.05$) based on a test of least significant difference.

wheat aphid reared from W1 and W2. Most parasitoids reared were *L. testaceipes.*

CCA analysis was conducted to assess the degree of association between the abundance of various predator species, Russian wheat aphid population density and growth rate, and the meteorological variables (Fig. 1). The eigenvalues for CCA axes 1–4 were 0.650, 0.138, 0.071, and 0.044, respectively, from combined open field sampling data from the four fields. These values represent the proportion of the variation in species abundance explained by the respective axis, and therefore, by the environmental variables (ter Braak 1987). The cumulative percentage variance in abundance explained by the four axes was 95.5%. Axis 1 separated natural enemy species by sampling date. Species present late in the growing season had negative scores on axis 1, whereas early season predators had positive scores. Predators usually fell near the origin in CCA biplots with scores from 0.1 to −0.2 on axis 1.

Table 4. Natural enemies of the RWA collected by sweep net sampling in four wheat fields in southeastern Colorado during 1994 and abbreviations used for selected natural enemies in the CCA biplot

Taxa	Abbreviation
Coleoptera	
Coccinellidae	
Coleomegilla maculata (DeGeer)	CM
Coccinella septempuntata L.	CS
Hippodamia convergens Guerin-meneville	HC
Hippodamia parenthesis (Say)	HP
Hippodamia sinuata Mulsant	HS
Chrysopidae	CH
Hemerobiidae	HE
Nabidae	
Nabis spp.	NA
Syrphidae	SY
Spider	SP
Unidentified larvae	UNID
Parasitic wasps	PA

The positions of predator species in Fig. 1 relative to vectors for explanatory variables give an indication of the level of association of their abundance with the particular variable. The length of each vector indicates the relative importance of the particular environmental variable. The location of species abundance scores for predators relative to the vectors indicates the strength of the correlation between the abundance of the particular species and the environmental variable. Abundance of most predators was associated with plant growth stage and Russian wheat aphid abundance. Predator abundance exhibited a weak association with the rate of Russian wheat aphid population increase, rainfall, and wind. The ordination indicates that predator abundance was only weakly associated with the rate of Russian wheat aphid population growth during the increasing phase of Russian wheat aphid population development, suggesting that, during most of the spring growing season of winter wheat, mortality caused by predators was not an important factor limiting Russian wheat aphid population growth.

Discussion

The higher proportion of alate Russian wheat aphid in exclusion enclosures compared with nonenclosed plots suggests that alate Russian wheat aphids trapped inside the former type of enclosures contributed to the density of Russian wheat aphids in the enclosures through their presence and probably also through reproduction. The increased density would exaggerate the effect of natural enemies on Russian wheat aphid density based on comparison of densities in

Table 5. Russian wheat aphid natural enemy abundance from sweep net samples in four winter wheat fields in southeastern Colorado during 1994

Location[a]	Sample date	Mean no. of natural enemies/75 sweeps[b]			
		Coccinellids	Other predators (including Nabidae)	Nabidae	All predators
P1	112	0.0	10.7 ± 1.8	0.0	10.7 ± 1.8
	125	3.0 ± 0.9	0.0	0.0	3.0 ± 0.9
	137	4.0 ± 1.2	0.8 ± 0.5	0.0	4.8 ± 0.9
	152	0.8 ± 0.5 (15.0)	0.8 ± 0.8 (16.3)	0.0 (10)	1.5 ± 1.2 (31.3)
	158	114.5 ± 29.2	29.0 ± 4.4	23 ± 4.0	143.5 ± 33.5
P2	112	0.0	0.0	0.0	0.0
	125	0.3 ± 0.3	0.0	0.0	0.3 ± 0.3
	137	2.0 ± 0.7	0.0	0.0	2.0 ± 0.7
	152	2.3 ± 0.8 (23.0)	2.0 ± 0.3 (2.8)	0.0 (2)	4.4 ± 1.3 (25.3)
	158	64.3 ± 6.1	4.0 ± 1.4	3.0 ± 1.4	68.3 ± 7.5
W1	112	0.0	13.7 ± 5.5	0.0	13.7 ± 5.5
	125	2.3 ± 0.5	2.8 ± 0.3	2.3 ± 0.5	5.1 ± 0.4
	137	1.0 ± 0.4	1.0 ± 0.4	0.0	2.0 ± 0.7
	152	15.8 ± 4.2	60.0 ± 8.8	56 ± 8.4	75.8 ± 12.5
	158	40.0 ± 4.1	5.5 ± 1.2	4.3 ± 0.5	45.5 ± 4.8
W2	112	0.0	4.4 ± 3.3	0.3 ± 0.3	4.7 ± 3.7
	125	12.3 ± 5.8	2.8 ± 0.8	1.0 ± 0.4	15.1 ± 6.3
	137	3.0 ± 0.8	1.3 ± 0.3	0.0	4.3 ± 0.6
	152	2.3 ± 1.9 (20.0)	1.1 ± 0.7 (8.5)	0.3 ± 0.3 (4)	3.3 ± 2.2 (28.5)
	158	70.5 ± 4.7	4.0 ± 0.7	2.3 ± 0.5	74.5 ± 4.3

[a] Two fields near Prichett were designated P1 and P2; two fields near Walsh were designated W1 and W2.
[b] The values in parentheses for fields P1, P2, and W2 on calendar date 152 are averages from data from the two neighboring sample dates (144 and 158, the estimation was not done if data values at 144 were 0) because hail hampered sampling and abnormally low means were obtained for those fields on that date.

complete and partial exclusion enclosures compared nonenclosed plots.

In complete and partial exclusion enclosures, Russian wheat aphids were at least partially protected from the adverse effects of both wind and rain compared with nonenclosed plots and environmental exclusion enclosures, which probably contributed to the higher densities in those types of enclosures. Nechols and Harvey (1998) speculated that differences in microclimatic factors such as wind contributed to differences they observed in Russian wheat aphid densities among open and closed cages. Meteorological variables are known to be important sources of mortality on aphids (Sanderson et al. 1994, Maudsley et al. 1996), which are often dislodged from plants by rain and wind (Hodek et al. 1972, Trumble 1982). Eight measurements made on a single day with a hand-held anemometer indicated that wind velocity in partial and complete exclusion enclosures was about one-half that in the open field (4.2 ± 0.9 km/h in partial ex-

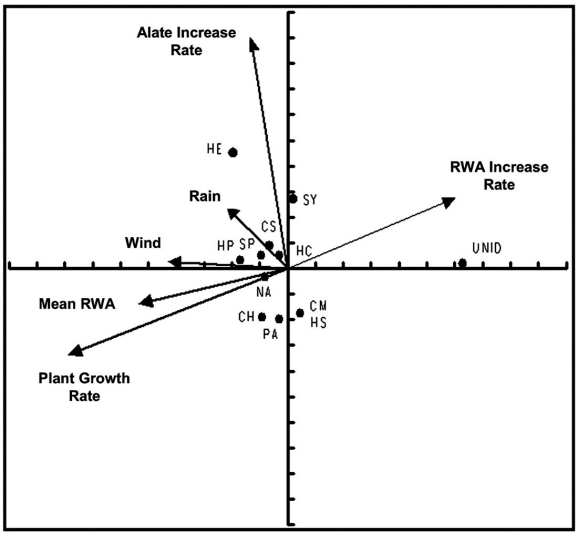

Fig. 1. Biplot of species scores and environmental variables obtained from CCA for the increasing phase of Russian wheat aphid population growth in four wheat fields in southeastern Colorado. Natural enemies are indicated by closed circles (abbreviations for names are listed in Table 4), and environmental variables are indicated by vectors.

clusion enclosures and 5.1 km/h ± 1.3 in the complete exclusion enclosures compared with 10.0 ± 2.2 km/h in the open field). Wind speeds in excess of 40 km/h were often recorded at Pritchett and Walsh during March and April of 1994. Wind speeds that high probably dislodged some Russian wheat aphid from plants, resulting in mortality, especially to early instar nymphs. Moran et al. (1987) found that rain caused aphid mortality directly by killing small or immobile insects and indirectly by altering the foraging behavior of predators. Hill et al. (1993) reported that gorse spider mites, *Tetranychus lintearius* (Dufour), that were protected from direct rainfall had greater survival than unprotected colonies.

Temperature probably also contributed to differences in Russian wheat aphid density in complete and partial exclusion enclosures compared with environmental exclusion and open enclosures. There was an ≈1°C difference in mean temperature in complete exclusion enclosures compared with the nonenclosed plots (15.4 versus 14.6°C). Thus, Russian wheat aphids in complete exclusion enclosures accumulated more heat units than those in nonenclosed plots, which would be expected to contribute to greater densities in the enclosures because Russian wheat aphid population growth is strongly dependent on temperature (Kieckhefer and Elliott 1989). The enclosures may have affected Russian wheat aphid population growth in other unknown ways, for example, by altering light intensity and humidity compared with the open field.

Parasitism accounted for <0.5% mortality in the study. Aphelinids, but not braconids, can cause mortality by host feeding, which would not have been detected in our measurements of parasitism. However, considering the extremely low parasitism rate, mostly by the braconid *L. testaceipes,* it is unlikely that host feeding by aphelinids caused significant mortality. The low mortality led us to conclude that parasitoids were unimportant sources of mortality on Russian wheat aphid during the study. Michels et al. (2001) found similarly low parasitism levels on Russian wheat aphid in a 2-yr study in the Texas Panhandle, where exotic Russian wheat aphid natural enemies had established. The Texas Panhandle is climatically similar to southeastern Colorado. However, Brewer et al. (1998) found parasitism to be a more important mortality factor on the Russian wheat aphid in southeastern Wyoming than in our study or that of Michels et al. (2001).

The exclusion study indicates that protection provided by enclosures exaggerated the effects of natural enemies on Russian wheat aphid population growth. Trapping of winged aphids that otherwise would have dispersed from enclosures also increased Russian wheat aphid density inside enclosures. Abundance of predators was weakly associated with the rate of Russian wheat aphid population growth during the increasing phase of Russian wheat aphid population development, suggesting that, during most of the spring growing season of winter wheat, mortality caused by predators was not the main factor limiting Russian wheat aphid population growth. Late in the growing season, predator abundance was more strongly associated with Russian wheat aphid population growth rate. Thus, the mortality caused by predators may be more important for determining Russian wheat aphid numbers on oversummering hosts than for reducing damage to wheat plants during the growing season.

Despite the presence of such cage effects, the exclusion study indicated that natural enemies, mainly predators, did restrain Russian wheat aphid population growth, although probably not enough to curtail economic injury to wheat plants, which occurs at densities far below those achieved in the four fields (Archer and Bynum 1992). Ordination by CCA indicated that a complex of predators dominated by native nabids, the native coccinellids, *H. convergens* and *H. sinuata,* and the exotic coccinellid, *C. septempunctata,* were primarily responsible for the mortality inflicted by natural enemies on Russian wheat aphid in wheat fields in southeastern Colorado.

This study was conducted shortly after verification of establishment by the exotic parasitoids *Aphelinus asychis* and *A. albipodus* Hayat and Fatima in the southern High Plains (Michels and Whitaker-Deerberg 1993, Michels et al. 1994, Elliott et al. 1995). Our results are similar to those obtained by Michels et al. (2001), who studied natural enemies of the Russian wheat aphids in wheat during roughly the same time period (1993–1995). In our study and in theirs, native and exotic predators were the most abundant aphidophagous species in wheat and were primarily responsible for levels of suppression caused by natural enemies. Parasitoids had minimal impact on Russian wheat aphid populations. Results of both studies are similar to those reported by Nechols and Harvey (1998), who observed limited suppression of Russian wheat aphid infestations by natural enemies, mostly resulting from predation by coccinellids and other predators. Their study was conducted in 1991, before establishment of natural enemies released during the Russian wheat aphid classical biological control program. Studies conducted from 1993 to 1994 in southeastern Wyoming (Brewer et al. 1998), after establishment of *A. asychis* and *A. albipodus,* documented high levels of parasitism of the Russian wheat aphid by these parasitoids, especially *A. albipodus.* Thus, there may be regional differences in the importance of parasitoids in biological control of the Russian wheat aphid. However, the current status of parasitoids as biocontrol agents of the Russian wheat aphid in the southern High Plains is unknown, and it is possible that they have gained a stronger foothold since our study and the study of Michels et al. (2001) were conducted.

Acknowledgments

We thank J. Burd, K. Jackson, T. Johnson, B. Jones, and P. Shelby for assistance with the project. We also thank J. Gould and D. Prokrym for providing exclusion cages and encouragement. The research was partially supported by a cooperative agreement with USDA-APHIS Biological Con-

trol Laboratory, Niles, MI. Mention of trade names or commercial products in this article is solely for providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

References Cited

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

Brewer, M. J., J. M. Struttman, and D. W. Mornhinweg. 1998. *Aphelinus albipodus* (Hymenoptera: Aphelinidae) and *Diaeretiella rapae* (Hymemoptera: Braconidae) parasitism on *Diuraphis noxia* (Homoptera: Aphididae) infesting barley plant differing in plant resistance to aphids. Biol. Control. 11: 255–261.

Elliott, N. C., J. D. Burd, J. S. Armstrong, C. B. Walker, D. K. Reed, and F. B. Peairs. 1995. Release and recovery of imported parasitoids of the Russian wheat aphid in eastern Colorado. Southwest. Entomol. 20: 125–129.

Hill, R. L., A. H. Gourlay, and C. J. Winks. 1993. Choosing gorse spider mite strains to improve establishment in different climates, pp. 377–383. *In* R. A. Prestidge (ed.), Proceedings, the Sixth Australasian Conference on Grasslands Invertebrate Ecology. AgResearch, Ruakura Agricultural Centre, Hamilton, New Zealand.

Hodek, I., K. S. Hagen, and H. F. van Emden. 1972. Methods for studying effectiveness of natural enemies, pp. 147–188. *In* H. F. van Emden (ed.), Aphid technology. Academic Press, New York.

Hopper, K. R., S. Aidara, S. Agret, J. Cabal, D. Coutinot, R. Dabire, C. Lesieux, G. Kirk, S. Reichert, F. Tronchetti, and J. Vidal. 1995. Natural enemy impact on the abundance of *Diuraphis noxia* (Homoptera: Aphididae) in wheat in southern France. Environ. Entomol. 24: 402–408.

Jones, J. W., J. R. Byers, R. A. Butts, and J. L. Harris. 1989. A new pest in Canada: Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae). Can. Entomol. 121: 623–624.

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.

Kindler, S. D., and T. L. Springer. 1989. Alternate hosts of Russian wheat aphid (Homoptera: Aphididae). J. Econ. Entomol. 82: 1358–1362.

Kring, T. J., F. E. Gilstrap, and G. J. Michels, Jr. 1985. Role of indigenous coccinellids in regulating greenbugs (Hommoptera: Aphididae) on Texas grain sorghum. J. Econ. Entomol. 78: 269–273.

Maudsley, M. J., A. MacKenzie, J. I. Thacker, and A.F.G. Dixon. 1996. Density dependence in cereal aphid populations. Ann. Appl. Biol. 128: 453–463.

Michels, G. J., and R. L. Whitaker-Deerberg. 1993. Recovery of *Aphelinus asychis,* an imported parasitoid of Russian wheat aphid, in the Texas Panhandle. Southwest. Entomol. 18: 11–17.

Michels, G. J., Jr., R. L. Whitaker-Deerberg, F. E. Gilstrap, and L. K. McKinnon. 1994. Release of exotic parasitoids and predators of the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov), in the Texas Panhandle, 1987–1993. Texas Agric. Exp. Bull. B-1720.

Michels, G. J., N. C. Elliott, R. A. Romero, D. A. Owings, and J. B. Bible. 2001. Impact of indigenous coccinellids on Russian wheat aphids and greenbugs (Homoptera: Aphididae) infesting winter wheat in the Texas Panhandle. Southwest. Entomol. 26: 97–114.

Moran, V. C., J. H. Hoffman, and N.C.J. Basson. 1987. The effects of simulated rainfall on cochineal insects (Homoptera: Dactylopidiiae): colony composition and survival on *Cactus cladodes.* Ecol. Entomol. 12: 51–60.

Nechols, J. R., and T. L. Harvey. 1998. Evaluation of a mechanical exclusion method to assess the impact of Russian wheat aphid (Homoptera: Aphididae) natural enemies, pp. 270–279. *In* S. S. Quisenberry and F. B. Peairs (eds.), Response model for an introduced pest—the Russian wheat aphid. Thomas Say Publishers, Lanham, MD.

Palmer, M. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology. 74: 2215–2230.

Pike, K. S., P. Stary, T. Miller, D. Allison, and L. Boydston. 1997. Small-grain aphid parasitoids (Hymenoptera: Aphelinidae and Aphidiidae) of Washington: distribution, relative abundance, seasonal occurrence, and key to known North American species. Environ. Entomol. 26: 1299–1311.

Prokrym D. R., K. S. Pike, and D. J. Nelson. 1998. Biological control of *Diuraphis noxia* (Homoptera: Aphididae): implementation and evaluation of natural enemies, pp. 183–208. *In* S. S. Quisenberry and F. B. Peairs (eds.), Response model for an introduced pest—the Russian wheat aphid. Thomas Say Publishers, Lanham, MD.

Rice, M. E., and G. E. Wilde. 1988. Experimental evaluation of predators and parasitoids in suppressing greenbugs (Homoptera: Aphididae) in sorghum and wheat. Environ. Entomol. 17: 836–841.

Rice, M. E., and G. E. Wilde. 1991. Aphid predators associated with conventional—and conservation—tillage winter wheat. J. Kans. Entomol. Soc. 64: 245–250.

SAS Institute. 1990. SAS/STAT user's guide. Version 6.12. SAS Institute, Cary, NC.

Sanderson, T. A., M. J. Maudsley, and A.F.G. Dixon. 1994. The relative role of natural enemies and weather in determining cereal aphid abundance. Aspects Appl. Biol. 31: 1–11.

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.

Tamaki, G., J. U. Mcguire, and J. E. Turner. 1974. Predator power and efficacy: a model to evaluate their impact. Environ. Entomol. 3: 625–630.

ter Braak, C.J.F. 1987. CANOCO, version 2.1. Institute of Applied Computer Science, Wageningen, The Netherlands.

Trumble, J. T. 1982. Temporal occurrence, sampling, and within-field distribution of aphids on broccoli in coastal California. J. Econ. Entomol. 75: 378–382.

Wraight, S. P., T. J. Poprawski, W. L. Meyer, and F. B. Peairs. 1993. Natural enemies of Russian wheat aphid (Homoptera: Aphididae) and associated cereal aphid species in spring-related wheat and barley in Colorado. Environ. Entomol. 22: 1383–1391.

Zadoks, J. C., T. T. Chang, and C. F. Konzak. 1974. A decimal code for the growth stages of cereals. Weed Res. 14: 415–421.

Received 31 March 2004; accepted 25 October 2004.