Yield Response and Categories of Resistance to Russian Wheat Aphid in Four *Dn*4 Hard Red Winter Wheat Cultivars

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ABSTRACT A field experiment was conducted to determine whether resistance to Russian wheat aphid, *Diuraphis noxia* (Mordvilko), conferred by the *Dn*4 gene is affected by genetic background. This was done by comparing the yield responses to Russian wheat aphid-resistant wheat containing *Dn*4, derived through the backcross method, to those of the corresponding recurrent parents. Infested resistant cultivars had fewer Russian wheat aphids per tiller than infested susceptible cultivars at the Lamar and Fort Collins, CO sites but not at the Akron, CO site. At the Lamar site, resistant cultivars yielded more than the susceptible cultivars. 'Prairie Red' and 'Yumar' were more resistant than 'Prowers', especially at the higher infestation level. Resistance in these cultivars was categorized in a laboratory experiment to confirm this differential expression of resistance. Resistance in Prairie Red, 'Halt', 'Prowers 99', and Yumar was categorized at three plant growth stages. Antibiosis was expressed as reductions in maximum number of nymphs produced per 24 h and intrinsic rate of increase. The maximum number of nymphs produced per 24 h was reduced in Halt and 'Lamar'. Averaged over cultivars, the intrinsic rate of increase was less at jointing than at the seedling or tillering growth stages. Tolerance was expressed in the resistant cultivars as reduced chlorosis and leaf rolling. Growth reductions in infested Prowers 99 plants was less than the other cultivars. This study confirms that some cultivars containing *Dn*4 may express antibiosis and tolerance, whereas others may not show the same categories. Thus, expression is affected by genetic background.

KEY WORDS *Diuraphis noxia*, wheat, categories of resistance

RUSSIAN WHEAT APHID, *Diuraphis noxia* (Mordvilko), is a serious pest of wheat, *Triticum aestivum* L., and barley, *Hordeum vulgare* L., in the western United States. Current management practices for winter wheat include the use of resistant cultivars. Sources of resistance have been identified, and resistance genes have been characterized as part of the effort to develop additional resistant wheat (du Toit 1987, Webster et al. 1987, Nkongolo et al. 1989, Harvey and Martin 1990, Zemetra et al. 1990, Smith et al. 1991, Souza et al. 1991, Baker et al. 1992, Formusoh et al. 1992, Souza 1998, Liu et al. 2001). In the United States, winter wheat resistance to the Russian wheat aphid was first identified in 1987 in PI 372129 (Quick et al. 1991). Inheritance of this resistance was governed by a single dominant gene, *Dn*4 (Nkongolo et al. 1991, Saidi and Quick 1996). The first North American Russian wheat aphid-resistant hard red winter wheat cultivar, 'Halt', contained *Dn*4 and was released to growers by the Colorado Agricultural Experiment Station in 1994 (Quick et al. 1996). Since the release of Halt, other cultivars containing *Dn*4 have been released and are currently available to growers (Quick et al. 2000a, b, c, d; Haley et al. 2004). Roughly 25% of Colorado wheat acreage is planted to these Russian wheat aphid resistant wheat (CASS 2003).

Many researchers have categorized resistance in Russian wheat aphid-resistant wheat and have found varying degrees of antibiosis, antixenosis, and tolerance (du Toit 1989, Smith et al. 1991, Formusoh et al. 1994, Budak et al. 1999, Hawley et al. 2003, Miller et al. 2003). Hawley et al. (2003) and Miller et al. (2003) reported that wheat containing *Dn*4 exhibited antixenosis, antibiosis, and tolerance.

We conducted field and laboratory experiments to determine the influence of genetic background on the expression of *Dn*4-based resistance to Russian wheat aphid. The objective of the field experiment was to determine whether differences in resistance expression existed among resistant wheat containing *Dn*4 in three different locations in Colorado. The objective of the laboratory experiment was to better define the differential expression of resistance observed in the field study.

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Materials and Methods

Yield Response to Russian Wheat Aphid Infestation. Field experiments were conducted during the 1996–1997 growing season at three eastern Colorado locations: Akron, Fort Collins, and Lamar. At each site there were eight replications and three infestation levels (0×, 1×, and 10×). 'TAM 107' (Porter et al. 1987), 'Lamar', and 'Yuma', which are susceptible to the Russian wheat aphid, and 'Prairie Red' (Quick et al. 2002c), 'Prowers' (Quick et al. 2000a), and 'Yumar' (Quick et al. 2002d), which are corresponding backcross-derived cultivars containing *Dn*4, were used. Resistant cultivars and their corresponding susceptible recurrent parents were paired within each infestation level. Plots were 1.8 by 1.8 m with six rows and were planted in Lamar on 12 September 1996, in Akron on 23 September 1996, and in Fort Collins on 10 September 1996. Winter barley was planted as a buffer between plots. Seed for the 0× infestation plots was treated with imidacloprid (5.2 ml of product Gaucho 480 per kilogram of seed) (Gustafson, Plano, TX). The 1 and 10× plots were artificially infested with greenhouse-reared Russian wheat aphid biotype 1 at spring regrowth. Two, 1-m rows in the center of each of the 1 and 10× plots were infested with ≈100 and 1000 Russian wheat aphids in Lamar, 23 and 106 Russian wheat aphids in Akron, and 110 and 1,030 Russian wheat aphids in Fort Collins, respectively. One infested row was sampled destructively to determine aphid densities, and the other row was harvested for yield estimation. To ensure that the 0× plots remained aphid free, they were treated with disulfoton (1.2 kg [AI]/ha Di-Syston 15G) (Bayer Crop Protection, Kansas City, MO) on 22 April 1997 in Fort Collins and with chlorpyrifos (0.58 kg [AI]/ha Lorsban 4E-SG) (Dow Agrosciences, Indianapolis, IN) on 13 March 1997 in Lamar. There was no additional insecticide treatment in Akron.

Infestation levels for each plot were evaluated by collecting all tillers from one-half of the row designated for destructive sampling from each plot at stem elongation (Zadoks 31) and again at boot (Zadoks 45) (Zadoks et al. 1974). The tillers were placed in Berlese funnels for 24 h to extract the aphids for counting. Yield was estimated from the other infested row. Spikes were harvested, counted and threshed with a mechanical thresher. Total seed weight, kernel weight, and total number of spikes were recorded.

The study was a three-factor design analyzed as a split-split plot. The whole plot treatment was infestation level, the subplot treatment was cultivar, and the sub-subplot treatment was resistance. Because the aphids remained on the plants for the duration of the experiment and were found to be more evenly distributed and more numerous at the boot stage (Zadoks 45), aphid data collected at this growth stage was used for the analyses presented here. Aphid counts were transformed before analysis by the $\log(x + 0.5)$ method, but original means are presented. Data were analyzed for effects of infestation level, cultivar, resistance, and their interactions by using PROC MIXED (SAS Institute 2001). When significant effects were observed, means were separated using pairwise *t*-tests. Linear regression analysis was used to describe the relationship of Russian wheat aphid per tiller to wheat yield (kilograms per hectare), 1000 seed weight (grams), and number of seeds per spike (SAS Institute 2001). Percentage yield or seed weight loss per Russian wheat aphid per tiller was calculated by dividing the slope estimate by the intercept estimate and multiplying by 100.

Categorization of Resistance. Four Russian wheat aphid-resistant cultivars containing *Dn*4, Prairie Red, Halt (Quick et al. 1996), Prowers 99 (Quick et al. 2000b), and Yumar, were used in this study. These were compared with susceptible TAM 107. Resistance was categorized at three different growth stages: seedling (Zadoks 10), tillering (Zadoks 20), and jointing (Zadoks 30) (Zadoks et al. 1974). For the seedling stage, two seeds of a cultivar were sown into a 10-cm pot containing a three parts soil, two parts perlite, and one part peat moss potting soil mixture. After the plants reached the two leaf stage, they were thinned to one seedling per pot. Vernalized seedlings were used for the tillering and jointing stages and were prepared and planted in the same manner as in Miller et al. 2003. Due to space constraints, each experiment at each growth stage was performed separately. However, temperature (25°C daytime and 20°C nighttime) and lighting (photoperiod of 16:8 [L:D]) conditions were kept constant during the experiment. The Russian wheat aphids were from the same colony used by Miller et al. 2003. To control for maternal effects, aphids used in the antibiosis experiment had been reared for at least five generations on the cultivar to be tested (Schotzko and Smith 1991).

The antixenosis experiments were conducted on 17 April 2002 for the seedling stage, 21 August 2001 for the tillering stage, and 15 August 2001 for the jointing stage. The arenas used and methods performed for the antixenosis experiments were similar to those described by Webster et al. (1994) for the antixenosis tests on the yellow sugarcane aphid, *Sipha flava* (Forbes), except that the leaves used in the arenas were not excised from the plants. One plant of each cultivar was arranged around an arena with the youngest unfurled leaf used in the arena. Fifty apterous Russian wheat aphids were released into the center of each arena. Each arena was one replication. The number of adult aphids was counted on each entry 24 h after the aphids were released. The percentage of aphids that chose each cultivar at each growth stage was calculated.

The antibiosis experiments were conducted from 22 April 2002 to 31 May 2002 for the seedling stage, from 7 November 2001 to 5 January 2002 for the tillering stage, and from 5 February to 11 April 2002 for the jointing stage. The clip cages and methods used for the antibiosis experiments were similar to those described by Hawley et al. (2003). Birth date, death date, number of nymphs produced each day, and the beginning and end of reproduction were recorded for each mother. Each cultivar containing a clip cage (main

plots) was one replication. Nymphipositional period, longevity, number of nymphs produced per day of nymphipositional period, number of nymph production days, and maximum number of nymphs produced in a 24-h period were calculated as described by Hawley et al. (2003). Intrinsic rate of increase was calculated as described in Wyatt and White (1977).

The tolerance experiments were conducted from 25 November 2002 to 20 December 2002 for the seedling stage and from 24 August 2001 to 17 September 2001 for the tillering and the jointing stages. The methods for the tolerance experiments are similar to those described by Miller et al. (2003). Plants of each growth stage were paired according to similar height and tiller number so that there were six pairs for each growth stage. The initial height of the main tiller and tiller number were recorded for each plant. Plants were infested for a total of 21 d. At the end of the experiment, each plant was examined and rated for chlorosis on a 1–9 scale (Webster et al. 1987) and leaf rolling on a 1–3 scale (Burd et al. 1993). Plants were then remeasured for height of the main tiller, the number of tillers were counted, and dry weights of the entire plant excised above the soil level were obtained. Plant growth was determined from the differences between plant height at the beginning and end of the experiment (Webster 1990). Percentage of differences between infested and uninfested plants in growth, number of tillers produced, and fresh and dry weights were calculated.

There were six replications for each growth stage for the antixenosis, antibiosis, and tolerance experiments. The data for the antixenosis experiment were analyzed as a randomized complete block. The data for the antibiosis experiments were analyzed as a split-plot design with growth stages as the whole plot treatment and cultivar as the subplot treatment. The tolerance experiment was a three-factor design analyzed as a split-split plot design. The whole plot treatment was growth stage analyzed as if they were completely randomized. The subplot treatment was cultivar, and the sub-subplot treatment was infestation assigned to paired pots. Although the antibiosis and tolerance experiments for each growth stage were run separately, results were analyzed as a single experiment in which pots were assigned randomly to growth stages. Data for the antixenosis experiment were analyzed for effects of wheat cultivar by using PROC GLM. Data for the antibiosis and tolerance experiments were analyzed for effects of cultivar, growth stage, and their interaction by using PROC MIXED (SAS Institute 2001) and when significant effects were observed, LSMeans were separated using pairwise *t*-tests. The SAS estimate statement was used to show differences between resistant wheat and the susceptible check for the antixenosis experiment and chlorosis and leaf rolling for the tolerance experiment.

Results

Yield Response to Russian Wheat Aphid Infestation. Site differences interacted with the main effects and variance was high between the sites, so sites were analyzed separately. There were infestation level by wheat cultivar by resistance level interaction effects on Russian wheat aphids per tiller at Lamar ($F = 4.54$; df = 4, 63; $P = 0.0028$) and Fort Collins ($F = 2.68$; df = 4, 63; $P = 0.0396$) but not at Akron (Table 1). At Lamar, the 1 and 10× infested resistant cultivars had fewer Russian wheat aphids per tiller than their susceptible counterparts, and the 1 and 10× infested 'Prairie Red' and 'Yumar' had fewer Russian wheat aphids per tiller than the other infested cultivars. At Fort Collins, the number of Russian wheat aphids per tiller was less on the 1× infested 'Prowers' and 'Yumar' than on their susceptible counterparts and 10× infested Yumar had less Russian wheat aphids per tiller than the other infested cultivars. At both sites, the number of Russian wheat aphids per tiller increased with increasing infestation levels. Although there were no infestation level by wheat cultivar by resistance level interaction effects at Akron, there was an infestation level by resistance interaction ($F = 8.81$; df = 2, 69; $P = 0.0004$). The 1 and 10× infested susceptible cultivars had more Russian wheat aphids per tiller (1× = 13.5 and 10× = 31.5 Russian wheat aphid per tiller) than the resistant 1 and 10× infested cultivars (1× = 10.6 and 10× = 12.6 Russian wheat aphid per tiller) and the number of aphids increased with infestation level.

There was an infestation level by wheat cultivar by resistance level interaction for yield at both Lamar ($F = 3.68$; df = 4, 63; $P = 0.0094$) and Akron ($F = 2.56$; df = 4, 63; $P = 0.0472$) but not at Fort Collins (Table 2). At Lamar, Prowers had the lowest yield at the 1 and 10× infestation levels. At the 10× infestation level, Prairie Red and Yumar had the highest yields. Overall, Yumar yields were not reduced by Russian

Table 1. Mean Russian wheat aphid per tiller for the susceptible and resistant winter wheat at three infestation levels at Lamar and Fort Collins, CO, 1997

Site	Entry	Russian wheat aphid per tillerat three infestation levels[a,b]		
		0×	1×	10×
Lamar	'TAM 107' (S)	0.0Ca	1.7Bb	3.5Ab
	'Prairie Red' (R)	0.0Ca	0.7Bc	1.7Ac
	'Lamar' (S)	0.0Ba	4.4Aa	5.8Aa
	'Prowers' (R)	0.0Ca	1.3Bb	2.9Ab
	'Yuma' (S)	0.0Ca	1.5Bb	4.9Aa
	'Yumar' (R)	0.0Ca	0.3Bd	1.2Ac
Fort Collins	'TAM 107' (S)	2.1Ca	8.8Ba	17.2Aa
	'Prairie Red' (R)	0.2Cb	5.5Bab	12.1Aa
	'Lamar' (S)	1.5Bab	9.4Aa	18.2Aa
	'Prowers' (R)	0.2Cb	4.5Bbc	13.7Aa
	'Yuma' (S)	0.1Bb	8.7Aa	16.7Aa
	'Yumar' (R)	0.3Cab	3.0Bc	5.6Ab

[a] Results of an infestation level by cultivar by resistance level interaction. Means in the same row followed by the same uppercase letter(s) are not statistically different and means in the same column within location followed by the same lowercase letter are not statistically different, LSMeans ($\alpha = 0.05$).

[b] Infestation levels are the number of aphids applied at spring regrowth. The number of aphids per one application is ×. The 1 and 10× plots were infested with ≈100 and 1000 Russian wheat aphids in Lamar, 23 and 106 Russian wheat aphids in Akron, and 110 and 1030 Russian wheat aphids in Fort Collins, respectively.

Table 2. Yield for the susceptible and resistant winter wheat at three infestation levels at Lamar and Fort Collins, CO, 1997

Site	Entry	Kilograms/hectare at three infestation levels[a,b]		
		0×	1×	10×
Lamar	'TAM 107' (S)	2700.3Aab	2096.6Ba	1620.5Cb
	'Prairie Red' (R)	2757.6Aa	1865.3Ba	1981.8Ba
	'Lamar' (S)	2536.7Aabc	1492.9Bb	1021.0Cc
	'Prowers' (R)	2290.4Ac	1815.8Ba	1401.6Cb
	'Yuma' (S)	2434.3Aabc	1764.4Bab	1321.9Cbc
	'Yumar' (R)	2361.6Abc	2053.5Aa	2285.3Aa
Akron	'TAM 107' (S)	2677.9Aab	2225.4Aa	2277.6Aa
	'Prairie Red' (R)	2175.7Ac	2415.7Aa	2466.2Aa
	'Lamar' (S)	3070.4Aa	2563.6ABa	2299.4Ba
	'Prowers' (R)	2609.7Abc	2594.9Aa	2362.3Aa
	'Yuma' (S)	3058.9Aab	2602.7Aa	1705.5Bb
	'Yumar' (R)	2919.1Aab	2346.2Ba	2416.9ABa

[a] Results of an infestation level by cultivar by resistance interaction. Means in the same row followed by the same uppercase letter(s) are not statistically different and means within each column within location followed by the same lowercase letter are not statistically different, LSMeans ($\alpha = 0.05$).

[b] Infestation levels are the no. of aphids applied at spring regrowth. The number of aphids per one application is ×. The 1 and 10× plots were infested with ≈100 and 1000 Russian wheat aphids in Lamar, 23 and 106 Russian wheat aphids in Akron, and 110 and 1,030 Russian wheat aphids in Fort Collins, respectively.

wheat aphid infestations. At Akron, Yuma had the lowest yield at the 10× infestation level. There were no differences among yields for infested and noninfested Prairie Red and Prowers. Averaged over wheat cultivar, an infestation level by resistance level interaction was observed at Fort Collins ($F = 6.62$; df = 2, 127; $P = 0.0018$). In general, susceptible cultivars yielded more than resistant cultivars when not infested (susceptible, 4,526.5 kg/ha; resistant, 3,998.9 kg/ha), but infested resistant cultivars yielded higher (1×, 3448.6 kg/ha; 10×, 3,160.0 kg/ha) than infested susceptible cultivars (1×, 3,420.2 kg/ha; 10×, 2,474.0 kg/ha). Also, averaging over infestation levels, a wheat cultivar by resistance level interaction was found at Fort Collins ($F = 6.62$; df = 2, 127; $P = 0.0018$). The highest yielding cultivar was TAM 107, at 4,310.0 kg/ha, whereas the lowest yielding cultivars were Lamar at 2,952.9 kg and Yuma at 3,158.8 kg/ha.

Relationships between wheat yield (kilograms per hectare) and Russian wheat aphid per tiller were similar at Fort Collins and Lamar (Table 3). Russian wheat aphid per tiller was negatively related to yield for TAM 107, Lamar, Yuma, and Prowers but not for Prairie Red or Yumar. The percentage of yield loss per unit was greater at Lamar than Fort Collins. At Akron, significant negative yield responses to Russian wheat aphid per tiller were observed for Yuma and Yumar. Russian wheat aphid per tiller had a negative effect on kernel weight with nearly all wheat at each site (Table 4) with the exception of Yumar at Lamar and Fort Collins and Prairie Red at Akron. Yumar kernel weight was least affected by Russian wheat aphid per tiller. There were more yield loss relationships between kernel weight and Russian wheat aphid per tiller than Russian wheat aphid per tiller and yield which may be explained by a higher variability in yield than in seed weights. Significant R^2 values were not observed for the regression analyses of Russian wheat aphid per tiller versus number of seeds per spike. Thus, results for number of seeds per spike are not included.

Categories of Resistance. There were no differences in aphid preference among wheat for each growth stage for the antixenosis choice experiment. Also, there were no differences in antixenosis when comparing all four resistant cultivars to the susceptible check.

There was no growth stage or growth stage by cultivar interaction for the maximum number of nymphs produced per 24 h. However, there were cultivar effects ($F = 4.25$, df = 4, 50, $P = 0.0048$). The maximum number of nymphs produced per mother in 24 h was

Table 3. Relationship between wheat yield (kilograms per hectare) and Russian wheat aphid per tiller at Lamar, Akron, and Fort Collins, Colorado, 1997

Site	Entry[a]	Regression equation	F value	$Pr > F$	R^2	% loss/unit[b]
Lamar	'TAM 107' (S)	$Y = 2506.3 - 210.5X$	17.98	0.0003	0.45	8.40
	'Prairie Red' (R)	$Y = 2380.5 - 224.5X$	2.75	0.1115	0.11	
	'Lamar' (S)	$Y = 2329.8 - 188.9X$	28.34	0.0001	0.56	8.11
	'Prowers 99' (R)	$Y = 2168.9 - 238.5X$	18.98	0.0003	0.46	11.00
	'Yuma' (S)	$Y = 2266.1 - 204.2X$	20.53	0.0002	0.48	9.01
	'Yumar' (R)	$Y = 2240.5 - 14.7X$	0.01	0.9174	0.00	
Akron	'TAM 107' (S)	$Y = 2520.9 - 8.6X$	3.10	0.0924	0.12	
	'Prairie Red' (R)	$Y = 2407.4 - 5.2X$	0.77	0.3900	0.03	
	'Lamar' (S)	$Y = 2924.3 - 22.28X$	3.09	0.0928	0.12	
	'Prowers 99' (R)	$Y = 2722.8 - 26.0X$	3.88	0.0616	0.15	
	'Yuma' (S)	$Y = 2753.1 - 16.6X$	6.00	0.0228	0.21	0.60
	'Yumar' (R)	$Y = 2723.4 - 30.7X$	4.54	0.0446	0.17	1.13
Ft. Collins	'TAM 107' (S)	$Y = 4749.1 - 46.8X$	3.97	0.0589	0.15	
	'Prairie Red' (R)	$Y = 3850.4 + 4.6X$	0.02	0.9007	0.00	
	'Lamar' (S)	$Y = 3563.6 - 62.9X$	11.58	0.0026	0.34	1.77
	'Prowers' 99 (R)	$Y = 3616.3 - 46.1X$	5.90	0.0238	0.21	1.27
	'Yuma' (S)	$Y = 3675.2 - 61.0X$	9.16	0.0062	0.29	1.66
	'Yumar' (R)	$Y = 3537.0 + 54.0X$	1.76	0.1984	0.07	

[a] S, susceptible cultivar; R, resistant cultivar.

[b] % Loss/unit is the percentage of yield loss per unit of aphid per tiller. The percentage of loss per unit was not calculated when significance was not found ($Pr > F$).

Table 4. Relationship between 1000 seed weight (grams) and Russian wheat aphid per tiller at Lamar, Akron, and Fort Collins, CO 1997

Site	Entry[a]	Regression equation	*F* value	*Pr* > *F*	R^2	% loss/unit[b]
Lamar	'TAM 107' (S)	$Y = 25.5 - 1.4X$	25.1	0.0001	0.53	5.49
	'Prairie Red' (R)	$Y = 24.2 - 1.8X$	7.23	0.0134	0.25	7.44
	'Lamar' (S)	$Y = 20.9 - 1.0X$	20.75	0.0002	0.49	4.78
	'Prowers 99' (R)	$Y = 22.7 - 1.4X$	7.72	0.0110	0.26	6.17
	'Yuma' (S)	$Y = 22.7 - 1.8X$	42.79	0.0001	0.66	7.93
	'Yumar' (R)	$Y = 23.6 - 0.5X$	0.58	0.4549	0.03	
Akron	'TAM 107' (S)	$Y = 33.4 - 0.1X$	4.40	0.0476	0.17	0.30
	'Prairie Red' (R)	$Y = 32.5 - 0.0X$	3.55	0.0727	0.14	
	'Lamar' (S)	$Y = 30.0 - 0.2X$	23.93	0.0001	0.52	0.67
	'Prowers 99' (R)	$Y = 30.9 - 0.2X$	15.41	0.0007	0.41	0.65
	'Yuma' (S)	$Y = 29.3 - 0.1X$	19.84	0.0002	0.47	0.34
	'Yumar' (R)	$Y = 29.1 - 0.1X$	16.21	0.0006	0.42	0.34
Ft. Collins	'TAM 107' (S)	$Y = 35.2 - 0.4X$	8.37	0.0084	0.28	1.14
	'Prairie Red' (R)	$Y = 32.3 - 0.3X$	7.86	0.0103	0.26	0.93
	'Lamar' (S)	$Y = 26.8 - 0.3X$	22.04	0.0001	0.50	1.12
	'Prowers 99' (R)	$Y = 29.6 - 0.4X$	4.22	0.0521	0.16	
	'Yuma' (S)	$Y = 25.3 - 0.2X$	10.46	0.0038	0.32	0.79
	'Yumar' (R)	$Y = 26.7 - 0.1X$	0.50	0.4869	0.02	

[a] S, susceptible cultivar; R, resistant cultivar.
[b] % loss/unit is the percentage of 1000 seed weight per unit of aphid per tiller. The percentage of loss per unit was not calculated when significance was not found (*Pr* > *F*).

reduced in Halt (3.9 nymphs) and Yumar (4.0 nymphs) relative to Prairie Red (5.8 nymphs) and susceptible TAM 107 (6.0 nymphs). There was no growth stage by cultivar interaction for intrinsic rate of increase. Intrinsic rate of increase was affected by growth stage ($F = 4.92$, df = 2, 15, $P = 0.0227$), but not by cultivar. The intrinsic rate of increase was lower at the jointing stage ($r_m = 0.21$) than at the seedling ($r_m = 0.26$) or tillering ($r_m = 0.25$) stages. No interaction or main effect differences were found for fecundity, nymphipositional period, number of days on which nymphs were produced, or longevity. No differences were found for any of the parameters among the four resistant cultivars and the susceptible check.

There was no growth stage by cultivar by infestation interaction, growth stage by infestation interaction, or growth stage by cultivar interaction for Russian wheat aphid chlorosis damage ratings. Also, there was no growth stage by cultivar by infestation interaction, growth stage by infestation interaction or growth stage by cultivar interaction for Russian wheat aphid leaf rolling damage ratings. Cultivar by infestation interaction differences were found for both chlorosis ($F = 71.38$; df = 4, 75; $P < 0.0001$) and leaf rolling ($F = 176.25$; df = 4, 75; $P < 0.0001$) (Table 5). Differences were found at each growth stage for both chlorosis and leaf rolling when the four resistant cultivars were compared with the susceptible check. The resistant cultivars combined had less chlorosis than TAM 107 at the seedling stage (estimate of resistant versus susceptible cultivars, 0.9167; $t = 3.14$, df = 150, $P = 0.0020$), the tillering stage (estimate of resistant versus susceptible cultivars, 1.4792; $t = 5.07$, df = 150, $P < 0.0001$), and the jointing stage (estimate of resistant versus susceptible cultivars, 1.0417; $t = 3.57$, df = 150, $P = 0.0005$). The resistant cultivars combined had less leaf rolling than TAM 107 at the seedling stage (estimate of resistant versus susceptible cultivars, 0.5833; $t = 6.75$, df = 150, $P < 0.0001$), the tillering stage (estimate of resistant versus susceptible cultivars, 0.5000; $t = 5.78$, df = 150, $P < 0.0001$), and the jointing stage (estimate of resistant versus susceptible cultivars, 0.4792; $t = 5.54$, df = 150, $P < 0.0001$). Growth stage by cultivar interaction differences were observed for percentage difference in plant height ($F = 2.11$, df = 8, 75, $P = 0.0451$) (Table 5). Plant height differences among infested and noninfested plants were greater for Halt in the seedling stage and TAM 107 in the tillering and jointing stages. Yumar and Prowers 99 had less aphid-induced plant height reductions than both TAM 107 and Prairie Red, especially at the jointing growth stage. The negative height differences may be due to infested plants compensating for the infestation. No interaction or main effect differences were found for percentage difference in tiller production or percentage of difference in dry weight.

Discussion

At Lamar and Fort Collins, relationships between wheat yield or 1000 seed weight and Russian wheat

Table 5. Russian wheat aphid chlorosis and leaf rolling damage ratings and aphid-induced plant ht reductions at three growth stages of wheat cultivars

Cultivar	Chlorosis	Leaf Rolling	% difference in plant height[a]		
			Seedling	Tillering	Jointing
'TAM 107'	4.1Aa	2.1Aa	10.6Aab	10.9Aa	30.8Aa
'Prairie Red'	1.9Ab	1.0Ab	19.5Aab	6.6Aa	10.2Aa
'Halt'	1.9Ab	1.0Ab	27.1Aa	−3.5Bab	−14.7Bbc
'Prowers 99'	1.8Abc	1.1Ab	−0.7Ab	−22.7Ab	−5.9Ac
'Yumar'	1.6Ac	1.0Ab	−1.0Ab	5.4Aa	7.3Aabc

[a] Means of cultivar (within rows) followed by the same uppercase letter and means of growth stage (within columns) followed by the same lowercase letter are not significantly different, LSMeans ($\alpha = 0.05$).

aphid per tiller were not significant for Yumar, and yields were not reduced by the infestation levels as much as the other cultivars, thus making it the best choice of currently available cultivars for areas in eastern Colorado where Russian wheat aphid is a consistent problem. Although the level of resistance was not as high as Yumar, Prairie Red performed well in this study and also would be a good resistant cultivar choice for eastern Colorado. Prowers did not perform well in this study. Other field observations have shown that the resistance in Prowers was not uniform, so further reselection was done resulting in the release of Prowers 99 (Quick et al. 2000a) with more uniform resistance. Growers use a variety of criteria in addition to the level of Russian wheat aphid resistance when selecting wheat cultivars, so Halt and Prairie Red have dominated resistant wheat acreage in Colorado (CASS 2003).

The field experiment confirmed that infested wheat with *Dn*4 contained either antibiosis or antixenosis by supporting fewer Russian wheat aphids (Hawley et al. 2003, Miller et al. 2003). Although fewer aphids were observed on the resistant plants than the susceptible plants, Kieckhefer and Gellner (1992) found that low Russian wheat aphid infestations can reduce yield. Thus, tolerance also was confirmed with the wheat containing *Dn*4, with less reduced yields in infested resistant plants than their corresponding infested susceptible recurrent parent (Hawley et al. 2003, Miller et al. 2003). However, the level of resistance expression differed among resistant cultivars containing *Dn*4. Prowers showed less resistance potential than Prairie Red and Yumar by harboring more Russian wheat aphids and having declining yield as the infestation levels were increased. Prairie Red was less resistant than Yumar for the same reasons.

In our laboratory study, the antixenosis test indicated that there were no differences among cultivars containing *Dn*4 and the susceptible cultivar. This is different than previous studies where cultivars containing *Dn*4 were found to be preferred less than TAM 107 (Hawley et al. 2003, Miller et al. 2003). It is not clear why there were no differences in antixenosis in this experiment. A possible explanation could be that there were four cultivars containing *Dn*4 and only one check per arena, so the aphids may have chosen each cultivar equally because the choice difference was not as pronounced. Antibiosis, expressed as maximum number of nymphs produced in 24 h, was observed only in Halt and Yumar. Expression of antibiosis seemed to differ with genetic backgrounds. Also, measurements of intrinsic rate of increase indicate that plants become increasingly antibiotic with age, as noted by Hawley et al. (2003) and Miller et al. (2003). With respect to chlorosis and leaf rolling, all of the resistant cultivars had lower ratings than TAM 107, which confirms findings from other studies in which entries containing *Dn*4 were observed to be tolerant (Meyer et al. 1989, Hawley et al. 2003, Miller et al. 2003). However, with respect to aphid-induced plant height reductions, expression of tolerance varied among cultivars.

The results of the field and laboratory studies show that wheat containing *Dn*4 may express antibiosis and tolerance (Hawley et al. 2003, Miller et al. 2003), whereas other *Dn*4 cultivars may not express these resistant mechanisms. It is possible that unidentified modifier genes may affect the expression of the *Dn*4 resistance gene as suggested by Budak et al. (1999) for the *Dn*1, *Dn*2, and *Dn*5 resistance genes. In a breeding program for Russian wheat aphid resistance, routine screening based on whole plant response to Russian wheat aphid infestation should thus ensure success in identifying *Dn*4-carrying genotypes with optimum expression of resistance. Breeding for Russian wheat aphid resistance through the use of molecular markers linked to *Dn*4 (Ma et al. 1998, Liu et al. 2002) also should involve whole plant resistance screening to confirm maximum expression of resistance among selected progenies.

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