Wheat Genotype, Early Plant Growth Stage and Infestation Density Effects on Russian Wheat Aphid (Homoptera: Aphididae) Population Increase and Plant Damage[1]

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Abstract Population increase of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), and its effect on early plant growth and damage were studied under laboratory conditions on two winter wheat genotypes, susceptible 'Stephens' and resistant 10085-5. Three early plant growth stages (one-, two-, and three-leaf stage), and three insect densities (0, 5 and 20 aphids per plant) were compared. Insect counts, plant damage assessments, plant height, leaf number and dry weight measurements were made. *Diuraphis noxia* population increase was greater on 'Stephens' than on 10085-5, but this was highly influenced by plant growth stage at time of infestation and initial aphid density. Host quality of 'Stephens' decreased rapidly when plants were infested at the 1-left stage, especially with the high initial density (20 aphids), resulting in low aphid population increase. For all plant developmental stages and genotypes, *D. noxia* per capita population increase was lower at initial densities of 20 compared to 5 aphids per plant, probably due to a density-dependent reduction in reproductive rate associated with a reduction in host-plant quality and/or crowding. *Diuraphis noxia* significantly affected plant growth, but the magnitude of the effect was influenced by genotype. In general, susceptible 'Stephens' had significantly more damage and a greater reduction in growth than resistant 10085-5.

Key Words Plant resistance, antibiosis, tolerance, plant growth, insect-plant interactions, *Diuraphis noxia, Triticum aestivum*

The Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), is a serious pest of cereals, especially wheat and barley. Following its accidental introduction into Mexico, it entered the United States in 1986 and spread rapidly northward across the western half of the country. By 1993, total losses attributed to *D. noxia* in the U.S., including cumulative crop losses and control costs, were estimated to exceed $893 million, with over 100 million bushels of grain lost in the western U.S. (Morrison and Peairs 1998). Although in most of the U.S. *D. noxia* is sporadic, when outbreaks occur yield losses in winter wheat can reach 60% (Archer and Bynum 1992). During feeding, aphids inject toxic saliva into the plants that appears to destroy chloroplasts (Kruger and Hewitt 1984), resulting in leaf chlorosis and reduction in photosynthetic capacity. In susceptible varieties, damaged leaves tend to roll longi-

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tudinally, and as a result emergence of new leaves is obstructed. For these plants, when new leaves are able to emerge they often appear folded and deformed.

Host plant resistance is an important control tactic for this pest. Sources of *D. noxia* resistance have been identified (Du Toit 1987, Nkongolo et al. 1989, Zemetra et al. 1990, Smith et al. 1991) and resistant varieties and advanced breeding lines have been developed in the U.S. (Quick et al. 1996, Souza et al. 1997a, b) and South Africa (Anonymous 1997, Tolmay et al. 1997).

Plant introduction (PI) line 294994 has been reported to contain one or two genes that confer resistance to *D. noxia*. More recently, it was determined that variation exists within PI 294994, and four sub-accessions were created based on their resistance to *D. noxia* (Zhang et al. 1998). The advanced breeding line 10085-5, results from a cross of ‘Stephens’ and the resistant source PI 294994, followed by two backcrosses to the parental line ‘Stephens’ and selection for *D. noxia* resistance at each generation.

Understanding interactions between resistant host plants and aphid population dynamics is critical for the effective utilization of plant resistance as part of a management strategy. *Diuraphis noxia* population increase had been studied on some of the PI lines used as sources of resistance (Smith et al. 1992, Quisenberry and Schotzko 1994). Following the advances in breeding for resistance to this pest, it is important to include resistant breeding lines in aphid-plant interaction studies. Experiments were conducted to assess the effects of plant resistance, plant growth stage at the time of infestation and initial aphid infestation density on population increase of *D. noxia* and the aphid effect on plant growth and damage levels.

Materials and Methods

Experiments were conducted at the University of Idaho Manis Entomological Laboratory, Moscow, ID. Environmental conditions were set at 21 ± 2°C and a 16:8 (L:D) photoperiod. A *D. noxia* colony was established from aphids collected on spring wheat near Asotin, WA in August 1988 and re-inoculated with aphids collected near Moscow, ID each year since that time. Insect colonies were maintained in environmental chambers as described by Quisenberry and Schotzko (1994). Prior to experimental use, insects were pre-conditioned on Stephens wheat for one generation as described by Schotzko and Smith (1991). This provided a cohort of insects of similar age and physiological state that was used to infest experimental plants.

Tests were conducted with two wheat genotypes, Stephens (susceptible to *D. noxia*) and 10085-5 (resistant to *D. noxia*). Seeds from each genotype were planted in 10.2-cm plastic pots filled with soil mixture [6:1 ratio of Sunshine mix # 1 (Sun Gro Horticulture, Bellevue, WA) and sand]. All treatments were planted simultaneously. Plants were infested at one of three early growth stages: 1-leaf, corresponding to Zadoks scale 11 (6 d post-planting), 2-leaf (Zadoks 12) (9 d post-planting), and 3-leaf stage (Zadoks 13) (14 d post-planting) (Zadoks et al. 1974). When plants reached the appropriate growth stage they were infested with either 0, 5 or 20 aphids each. Infestation of plants was accomplished by transferring the appropriate number of adult aphids with a camel-hair brush and placing them on filter paper surrounding the base of the plant. Plants infested with no aphids were used as checks. All plants were individually covered with glass cages (8.5 cm diam × 31.2 cm tall) at the time of infestation of the first treatment and kept covered for the duration of the experiment. Three replications were arranged in a randomized complete block design. Each replication contained 2 plants of each treatment. The experiment was repeated twice, for a total of 6 replicates and 12 plants per treatment.

Plants were destructively sampled 14 d after infestation of the last treatment, and insects were counted and plant measurements made. Because different treatments were exposed to aphids for varied lengths of time, population increase was expressed as number of aphids per day. Additionally, because aphid infestation density was a variable in the experiments, per capita population increase was calculated and expressed as number of aphids per female per day, where per capita population increase = [final aphid density—initial aphid density / initial aphid density] / number of days. Measurements of plant height were taken at the beginning and end of the experiment. *Diuraphis noxia* feeding damage assessments were made by counting total number of leaves, number of rolled leaves, number of folded leaves and number of chlorotic leaves (Smith et al. 1991). Percentages of damaged leaves were then calculated. The aerial portion of plants (i.e., shoot) was cut at the surface of the soil, dried in an oven at 80°C for 72 h and weighed. Soil was washed from the roots, roots dried as described above and weighed.

Data were analyzed using SAS PROC UNIVAR, PROC CORR and PROG GLM, and mean differences were tested using Ryanís Q test (SAS Institute 1990). Data were analyzed as a randomized complete block design, except insect count data which were treated as a factorial design. The insect and plant measurements between the two experiments were not significantly different ($P > 0.05$) and thus, were pooled for further statistical analysis. Orthogonal contrasts were used to compare specific treatments where appropriate. The significance level was set at $P < 0.05$. Only significant interactions are discussed.

Results

Overall population increase. *Diuraphis noxia* population increase was significantly affected by the growth stage of plants at the time of infestation and the initial infestation density (Tables 1, 2). Population increase of *D. noxia* on plants infested at the 3-leaf stage was significantly greater than on those infested at the 2-leaf stage, which was significantly greater than on those infested at the 1-leaf stage (Tables 1, 2). Irrespective of genotype or growth stage, plants infested with 20 *D. noxia* had greater population increase than those infested with 5 (Table 1). *Diuraphis noxia* population increase was not significantly affected by wheat genotype when comparisons were made across growth stage and infestation density (Table 2). There was no significant interaction between genotype and infestation density.

The genotype by plant growth stage interaction was significant; that is, genotypes did not have similar responses in relation to the growth stage when infested. Population increase of *D. noxia* on 10085-5 was significantly greater on plants infested at the 2-leaf stage compared to the 1-leaf stage, but there was no significant difference between plants infested at the 2-leaf and 3-leaf stage. On 'Stephens' plants infested at the 2-leaf stage, population increase of *D. noxia* was significantly greater than on plants infested at the 1-leaf stage. Population increase also was significantly greater on 'Stephens' plants infested at the 3-leaf stage compared to the 2-leaf stage (Tables 1, 2).

There was a significant interaction between infestation density and plant growth stage at the time of infestation (Table 2). *Diuraphis noxia* population increase on plants infested at the 1-leaf stage with 5 aphids each, was significantly lower than on

Table 1. Effect of wheat genotype, *D. noxia* initial infestation density, plant growth stage, and their interactions on aphid population increase

Contrast	Population increase (aphids/day)	PPI* (aphids/female/day)
Genotype		
10085-5	39.2	4.7
Stephens	42.1	5.1
Infestation density		
5 aphids	38.1	7.6
20 aphids	43.3	2.2
Plant growth stage		
1-leaf	19.2	2.9
2-leaf	43.1	5.7
3-leaf	59.6	6.1
Genotype by infestation density		
10085-5		
5 aphids	36.6	7.3
20 aphids	41.7	2.1
Stephens		
5 aphids	39.5	7.9
20 aphids	44.8	2.2
Genotype by plant growth stage		
10085-5		
1-leaf	27.5	3.8
2-leaf	43.4	5.5
3-leaf	46.7	4.8
Stephens		
1-leaf	10.9	1.9
2-leaf	42.9	5.9
3-leaf	72.6	7.4
Infestation density by plant growth stage		
5 aphids		
1-leaf	25.4	5.1
2-leaf	47.7	9.5
3-leaf	41.1	8.2

Table 1. Continued.

20 aphids		
1-leaf	13.1	0.7
2-leaf	38.6	1.9
3-leaf	78.2	3.9

* PPI = per capita population increase

those infested at the 2-leaf stage. However, population increase in plants infested at the 2-leaf stage was not significantly different from those infested at the 3-leaf stage (Tables 1, 2). Plants infested at the 2-leaf stage with 20 *D. noxia* had a significant, three-fold increase in aphid population compared to those infested at the 1-leaf stage. Similarly, *D. noxia* population showed a two-fold increase on plants infested at the 3-leaf stage compared to those infested at the 2-leaf stage (Tables 1, 2).

Analysis of the 3-way interaction revealed significant variation between genotypes within the different growth stages and densities (Table 3). 10085-5 plants infested with either 5 or 20 *D. noxia* at the 1-leaf stage had a significantly greater aphid population increase than similarly infested 'Stephens.' There was no significant difference between the genotypes when infested with 5 or 20 *D. noxia* at the 2-leaf stage. However, when plants were infested at the 3-leaf stage at either density, aphid population increase on 'Stephens' was significantly greater (one-and-a-half times higher) than on 10085-5 (Table 3).

Per capita population increase. *Diuraphis noxia* per capita population increase was significantly affected by initial aphid infestation density and plant growth stage at infestation (Tables 1, 2). On plants infested with 5 *D. noxia,* per capita population increase was significantly higher (over three times more) than on plants infested with 20. While per capita population increase was not significantly different between plants infested at the 3-leaf and 2-leaf stage, it was significantly lower (approximately half) on plants infested at the 1-leaf stage. Per capita population increase was not significantly affected by wheat genotype, when comparisons were made across growth stage and infestation density. No significant interaction between infestation density and genotype was detected.

A significant genotype by plant growth stage interaction was detected for per capita population increase of *D. noxia* (Table 2). When comparisons were made within a genotype, per capita population increase was significantly greater on 'Stephens' plants infested at the 2-leaf stage than on those infested at the 1-leaf stage, but significantly smaller compared to plants infested at the 3-leaf stage. On 10085-5, per capita population increase was significantly lower on plants infested at the 1-leaf stage compared to those infested at the 2-leaf stage. There was no significant difference in *D. noxia* per capita population increase between 10085-5 plants infested at the 2-leaf stage compared to those infested at the 3-leaf stage (Table 2).

A significant interaction between *D. noxia* infestation density and plant growth stage at the time of infestation was found (Table 2). Per capita population increase of *D. noxia* was significantly lower on plants infested at the 1-leaf stage with 5 aphids, than on those infested at the 2-leaf stage. On plants infested with 20 *D. noxia,* there was a progressive increment in per capita population increase with plant growth

Table 2. *F* and *P* values for the significance of wheat genotype, *D. noxia* initial infestation density, plant growth stage, and their interactions on aphid population increase

	Population increase		PPI*	
Contrast	*F*	*P*	*F*	*P*
Genotype				
10085-5 vs Stephens	1.96	0.192	1.16	0.306
Infestation density				
5 aphids vs 20 aphids	6.13	0.033	266.31	<0.001
Plant growth stage	123.69	<0.001	37.11	<0.001
1-leaf vs 2-leaf**	74.13	<0.001	37.53	<0.001
2-leaf vs 3-leaf**	35.28	<0.001	0.49	0.487
Genotype by infestation density	0.00	0.960	0.38	0.550
10085-5				
5 aphids vs 20 aphids**	2.78	0.103	109.04	<0.001
Stephens				
5 aphids vs 20 aphids**	2.53	0.119	93.70	<0.001
Genotype by plant growth stage	34.54	<0.001	14.99	0.001
10085.5				
1-leaf vs 2-leaf**	16.19	0.001	6.74	0.013
2-leaf vs 3-leaf**	0.71	0.403	1.31	0.259
Stephens				
1-leaf vs 2-leaf**	66.47	<0.001	36.82	<0.001
2-leaf vs 3-leaf**	57.08	<0.001	4.55	0.038
Infestation density by plant growth stage	57.28	<0.001	10.55	0.003
5 aphids				
1-leaf vs 2-leaf**	32.33	<0.001	45.43	<0.001
2-leaf vs 3-leaf**	2.84	0.099	3.99	0.052
20 aphids				
1-leaf vs 2-leaf**	42.13	<0.001	3.70	0.061
2-leaf vs 3-leaf**	101.73	<0.001	4.93	0.033

* PPI = per capita population increase
** *F* and *P* values from orthogonal contrasts

Table 3. Effect of plant growth stage, *D. noxia* initial infestation density, and wheat genotype on aphid population increase and per capita population increase

Plant stage at infestation	Initial density (aphids/plant)	Genotype	Population increase (aphids/day)	F*	P	PPI** (aphids/female/day)	F	P
1-leaf	5	Stephens	18.3			3.7		
		10085-5	32.5	6.54	0.014	6.5	9.20	0.004
	20	Stephens	3.5			0.2		
		10085-5	22.6	11.80	0.001	1.1	1.04	0.314
2-leaf	5	Stephens	50.5			10.1		
		10085-5	44.9	1.04	0.314	9.0	1.46	0.234
	20	Stephens	35.3			1.8		
		10085-5	41.8	1.37	0.248	2.1	1.12	0.730
3-leaf	5	Stephens	49.6			9.9		
		10085-5	32.6	9.42	0.004	6.5	13.24	<0.001
	20	Stephens	95.6			4.8		
		10085-5	60.8	39.29	<0.001	3.0	3.45	0.070
Check	0	Stephens	0.0			0.0		
		10085-5	0.0			0.0		

* F and P values from orthogonal contrasts

** PPI = per capita population increase

stage, with per capita population increase over 5 times greater on plants infested at the 3-leaf stage compared to 1-leaf stage plants. The difference between plants infested at the 1-leaf stage compared to the 2-leaf stage was not significant, however there was a significant difference between plants infested at the 2-leaf stage compared to those infested at the 3-leaf stage.

Examination of the 3-way interaction demonstrated significant variation between the genotypes within the different growth stages and densities (Table 3). Per capita population increase was significantly greater on 10085-5 plants infested with 5 *D. noxia* at the 1-leaf stage, than on similarly infested 'Stephens.' There was no significant difference in the per capita population increase of *D. noxia* between plants of the two genotypes infested with 5 aphids at the 2-leaf stage. On plants infested at the 3-leaf stage with 5 *D. noxia* each, per capita population increase was significantly higher on 'Stephens' (1.5× greater) than on 10085-5. There was no significant difference in the per capita population increase of *D. noxia* on plants of the two genotypes infested with 20 aphids at any of the growth stages (Table 3).

Plant measurements. There was no significant variation in the height of plants at the initiation of experiments, thus, differences at the end of experiments were due to the effect of *D. noxia* feeding on plants. Because all plants were the same age at the time biomass measurements were made, comparisons across treatments are appropriate. There were no significant differences between the genotypes for dry shoot weight ($F = 1.20$, $P = 0.28$), dry root weight ($F = 3.49$, $P = 0.07$), plant height ($F = 0.05$, $P = 0.82$), or number of leaves ($F = 0.68$, $P = 0.41$) when plants were not subjected to insect infestation.

Diuraphis noxia infestation significantly affected all the plant variables measured, including dry shoot weight, dry root weight, ending plant height, and number of leaves (Tables 4, 5). Irrespective of growth stage, *D. noxia* infestation density, or genotype, plants infested with *D. noxia* had significant reductions in all the plant parameters measured compared to uninfested plants of the same genotype.

Genotype had a significant effect on shoot weight with resistant 10085-5 weighing more following *D. noxia* infestation than 'Stephens' (Table 4). Initial *D. noxia* infestation density also had a significant effect on plant weight. At the time experiments were terminated, plants originally infested with 5 *D. noxia* were significantly heavier than those infested with 20, irrespective of genotype or plant growth stage at infestation (Table 4).

The plant growth stage at the time of infestation had a significant effect on the relative impact of *D. noxia* on plant weight with plants infested at the 3-leaf stage significantly heavier (both shoot and root weight) at the end of the experiment than those infested at the 2-leaf stage. Plants infested at the 1-leaf stage weighed significantly less at the end of the experiment than those infested at the 2-leaf stage (Table 4).

The effect of *D. noxia* on plant height was influenced by wheat genotype, with 'Stephens' significantly taller than 10085-5 (Table 5). The number of leaves was significantly affected by genotype, with 10085-5 having greater number of leaves following *D. noxia* infestation, than 'Stephens' (Table 5).

Initial *D. noxia* infestation density significantly influenced plant height with plants infested with 5 *D. noxia* significantly taller at the end of the experiment than those infested with 20 (Table 5). The number of leaves was also significantly greater on plants infested with 5 *D. noxia* compared to those infested with 20.

Plant growth stage at the time of infestation had a significant effect on plant height.

Table 4. Effect of genotype, *D. noxia* initial infestation density, and plant growth stage on plant weight

Contrast	Shoot dry weight (mg)	*F**	*P*	Root dry weight (mg)	*F*	*P*
Genotype						
10085-5	126			25		
Stephens	104	10.76	0.001	25	0.0	0.99
Infestation density						
5 aphids	108			25		
20 aphids	73	21.98	<0.001	17	21.82	<0.001
Plant growth stage						
1-leaf	45			15		
2-leaf	73			17		
3-leaf	153			30		
1-leaf vs 2-leaf		10.10	0.002		0.89	0.349
2-leaf vs 3-leaf		78.71	<0.001		36.26	<0.001
Checks						
10085-5	252			56		
Stephens	272	1.20	0.277	47	3.49	0.066

* *F* and *P* values from orthogonal contrasts

Plants infested at the 2-leaf stage were significantly taller at the end of the experiment than those infested at the 1-leaf stage, while those infested at the 2-leaf stage were significantly shorter than plants infested at the 3-leaf stage (Table 5). Plants infested at early stages had significantly fewer leaves at the end of the experiment than those infested at later stages.

The genotype by infestation density and plant growth stage interaction was not significant and did not have any variation which provides insights into the aphid-plant interaction.

Plant damage. Genotype was a significant factor determining the degree to which plants were damaged by *D. noxia.* Susceptible 'Stephens' had a significantly greater percentage of leaves rolled, folded or chlorotic than 10085-5 (Tables 6, 7).

Initial *D. noxia* infestation density also influenced levels of damage. Irrespective of genotype or growth stage, plants infested with 5 *D. noxia* had a significantly lower percentage of chlorotic leaves than plants infested with 20 *D. noxia* (Table 7). However, the percentage of leaves folded was significantly greater on plants infested with 5 *D. noxia,* than on those infested with 20.

The plant growth stage at the time of infestation also had a significant effect on the level of damage caused by *D. noxia.* At the end of the experimental period, plants infested at the 2-leaf stage had a significantly lower percentage of leaves rolled or chlorotic than those infested at the 1-leaf stage. Similarly, plants infested at the 3-leaf

Table 5. Effect of genotype, *D. noxia* initial infestation density, and plant growth stage on plant height and number of leaves

Contrast	Height (mm)	*F**	*P*	No. leaves	*F*	*P*
Genotype						
10085-5	369			3.9		
Stephens	387	5.87	0.018	3.4	16.25	<0.001
Infestation density						
5 aphids	370			3.7		
20 aphids	323	35.61	<0.001	3.2	16.13	<0.001
Plant growth stage						
1-leaf	263			2.7		
2-leaf	331			3.4		
3-leaf	445			4.3		
1-leaf vs 2-leaf		48.46	<0.001		18.27	<0.001
2-leaf vs 3-leaf		138.16	<0.001		33.54	<0.001
Checks						
10085-5	567			5.0		
Stephens	571	0.05	0.825	4.8	0.68	0.411

* *F* and *P* values from orthogonal contrasts

stage had a significantly lower percentage of leaves rolled or chlorotic than those infested at the 2-leaf stage (Table 7). There was no significant difference in leaf folding between the plant growth stages.

The percentage of leaves with chlorosis was significantly lower on 10085-5 plants infested with 5 *D. noxia* compared to 20 *D. noxia.* However, on 'Stephens' there was no significant difference between plants infested at either density (Table 7).

The percentage of leaves rolled on 10085-5 was significantly lower on plants infested at the 2-leaf stage compared to the 1-leaf stage, but there was no significant difference between plants of this genotype infested at the 2-leaf and 3-leaf stage. In contrast, on 'Stephens' plants infested at the 2-leaf stage, the percentage of leaves rolled was significantly greater than on plants infested at the 3-leaf stage (Table 7). While on 10085-5 the percentage of leaves with chlorosis was significantly lower on plants infested at the 2-leaf stage compared to the 1-leaf stage, on 'Stephens' there was no significant difference between plants infested at the 1-leaf and 2-leaf stage (Table 7).

The percentage of leaves with chlorosis was significantly lower on plants infested with 5 *D. noxia* at the 2-leaf stage compared to the 1-leaf stage. In contrast, on plants infested with 20 *D. noxia,* there were no significant differences between plants infested at either growth stage (Table 7).

10085-5 plants infested with 5 *D. noxia* at the 1-leaf stage had a significantly lower

Table 6. Effect of wheat genotype, *D. noxia* initial infestation density, plant growth stage, and their interactions on leaf damage levels

	Percentage of leaves with damage		
Contrast	Rolled	Folded	Chlorotic
Genotype			
10085-5	18.8	1.9	74.4
Stephens	46.0	10.2	89.0
Infestation density			
5 aphids	32.3	8.9	78.4
20 aphids	32.3	3.2	85.0
Plant growth stage			
1-leaf	43.4	2.8	94.3
2-leaf	31.3	6.4	84.2
3-leaf	22.3	9.0	66.6
Genotype by infestation density			
10085-5			
5 aphids	19.6	3.2	68.7
20 aphids	18.0	0.7	80.0
Stephens			
5 aphids	45.0	14.5	88.2
20 aphids	46.7	5.8	89.9
Genotype by plant growth stage			
10085-5			
1-leaf	34.5	0.0	93.8
2-leaf	14.3	3.1	71.9
3-leaf	7.6	2.8	57.4
Stephens			
1-leaf	52.3	5.6	94.8
2-leaf	48.3	9.7	96.5
3-leaf	37.0	15.2	73.8
Infestation density by plant growth stage			
5 aphids			
1-leaf	41.9	5.6	94.1
2-leaf	31.3	10.0	79.6
3-leaf	23.8	11.0	61.6

Table 6. Continued.

20 aphids			
1-leaf	44.9	0.0	94.4
2-leaf	31.2	2.8	88.9
3-leaf	20.8	5.9	71.5

percentage of leaves rolled or folded than similarly infested 'Stephens,' while there was no significant difference in the percentage of leaves with chlorosis on these plants (Table 8). 'Stephens' plants infested with 5 *D. noxia* at the 2-leaf stage had a significantly higher percentage of leaves with chlorosis and rolling than similarly infested 10085-5, with no significant difference in the percentage of leaves folded. When plants were infested at the 3-leaf stage with 5 *D. noxia,* the percentages of leaves rolled, folded or chlorotic were significantly greater on 'Stephens' than on 10085-5 (Table 8).

For plants infested with 20 *D. noxia* at the 1-leaf stage, 10085-5 had a significantly lower percentage of leaves rolled than 'Stephens,' but there was no significant difference between the genotypes in the percentage of leaves folded or chlorotic (Table 8). There were significant differences between the genotypes when infested with 20 *D. noxia* at the 2-leaf stage. Both the percentage of rolled leaves and of chlorotic leaves were significantly greater on 'Stephens' than on 10085-5, while there was no significant difference in the percentage of leaves folded. When 3-leaf stage plants were infested with 20 *D. noxia,* there were significantly greater percentages of leaves rolled or folded in 'Stephens' than on 10085-5 (Table 8).

Discussion

Diuraphis noxia population increase was greater on plants of the susceptible genotype 'Stephens' than on resistant 10085-5, but this was influenced by plant stage at the time of infestation and initial aphid density. 'Stephens' plants infested at the 1-leaf and 2-leaf stage with the high insect density (20 aphids), had a rapid decrease in host quality and as a consequence they were unable to support large aphid populations. Plants infested with the low insect density (5 aphids), supported greater *D. noxia* population increase during the duration of the study. On the resistant genotype, aphid feeding resulted in less differential reduction in host quality, and plants infested at the 1-leaf stage with 20 aphids were able to support greater aphid densities than the susceptible genotype. On resistant plants infested at the 2-leaf stage, initial aphid infestation level had little effect on final aphid density. Plant quality was more negatively affected at the high initial density, and this offset the greater initial aphid density. Plants of both genotypes infested at 3-leaf stage were able to support aphid population increase within the temporal scale of this experiment. On both genotypes, initial infestation with 20 *D. noxia* resulted in a final aphid density approximately double that of plants infested with 5 *D. noxia.* However, final aphid density was 1.5× greater on 'Stephens' than 10085-5. This negative effect of 10085-5 on the life history of *D. noxia* relative to 'Stephens,' is an indication of antibiosis.

Per capita population increase was greatly influenced by initial aphid infestation

Table 7. *F* and *P* values* for the significance of wheat genotype, *D. noxia* initial infestation density, plant growth stage, and their interactions on leaf damage levels

	% Rolled		% Folded		% Chlorotic	
Contrast	*F*	*P*	*F*	*P*	*F*	*P*
Genotype						
10085-5 vs Stephens	122.68	<0.001	22.75	<0.001	28.01	<0.001
Infestation density						
5 aphids vs 20 aphids	0.00	0.99	10.66	0.001	5.54	0.022
Plant growth stage						
1-leaf vs 2-leaf	16.38	<0.001	2.93	0.092	8.73	0.004
2-leaf vs 3-leaf	9.02	0.004	1.52	0.222	27.08	<0.001
Genotype by infestation density						
10085-5						
5 aphids vs 20 aphids	0.25	0.622	1.05	0.309	8.30	0.005
Stephens						
5 aphids vs 20 aphids	0.25	0.619	12.90	<0.001	0.20	0.655
Genotype by plant growth stage						
10085-5						
1-leaf vs 2-leaf	22.73	<0.001	1.05	0.309	20.61	<0.001
2-leaf vs 3-leaf	2.53	0.117	0.01	0.926	9.22	0.003
Stephens						
1-leaf vs 2-leaf	0.92	0.342	1.95	0.167	0.13	0.718
2-leaf vs 3-leaf	7.06	0.010	3.38	0.071	18.69	<0.001
Infestation density by plant growth stage						
5 aphids						
1-leaf vs 2-leaf	6.24	0.015	2.22	0.141	9.13	0.004
2-leaf vs 3-leaf	3.20	0.079	0.12	0.728	14.02	<0.001
20 aphids						
1-leaf vs 2-leaf	10.40	0.002	0.87	0.355	1.34	0.252
2-leaf vs 3-leaf	6.05	0.017	1.95	0.167	13.06	<0.001

* *F* and *P* values from orthogonal contrasts

density. For all plant growth stages and genotypes, per capita population increase was diminished at initial aphid densities of 20 compared to 5. This was probably due to a density-dependent reduction in reproductive rate associated with a decrease in host-plant quality and/or crowding. On the susceptible genotype, the differential effect

Table 8. Mean percentage of leaves with damage as influenced by plant growth stage, *D. noxia* initial infestation density, and wheat genotype

Plant stage at infestation	Initial density (aphids/plant)	Genotype	Percentage of leaves with damage								
			Rolled	*F**	*P*	Folded	*F*	*P*	Chlorotic	*F*	*P*
1-leaf	5	Stephens	50			11			98		
		10085-5	34	7.32	0.009	0	6.93	0.011	90	1.26	0.265
	20	Stephens	55			0			92		
		10085-5	35	10.54	0.002	0	—**	—**	97	0.67	0.416
2-leaf	5	Stephens	45			14			93		
		10085-5	18	21.31	<0.001	6	3.40	0.069	66	15.73	<0.001
	20	Stephens	51			6			100		
		10085-5	11	45.25	<0.001	0	1.73	0.193	78	10.70	0.002
3-leaf	5	Stephens	40			19			74		
		10085-5	8	28.96	<0.001	4	12.87	<0.001	50	12.22	0.001
	20	Stephens	34			12			78		
		10085-5	8	19.83	<0.001	2	5.31	0.024	65	3.69	0.059
Check	0	Stephens	0	—**	—**	0	—**	—**	0	—**	—**
		10085-5	0	—**	—**	0	—**	—**	0	—**	—**

* *F* and *P* values from orthogonal contrasts
** No leaves damaged

between the high and low initial aphid density was more pronounced when plants were infested at the 1-leaf stage compared to later plant stages with an aphid per capita population increase 18.5× greater when the initial density was 5 compared to 20. In contrast, on the resistant genotype the per capita population increase was 6× greater when the initial density was 5 compared to 20. Overall, per capita population increase of *D. noxia* was lower on the susceptible genotype when plants were infested at the 1-leaf stage compared to the resistant one, due in part, to host quality decreasing rapidly when plants were infested at an early stage. Compared to 10085-5, per capita population increase of *D. noxia* was greater on 'Stephens' plants infested at the 3-leaf stage, once again illustrating antibiosis on the resistant genotype.

Diuraphis noxia significantly affected plant growth as demonstrated by differences in dry plant weight between uninfested plants and aphid-infested plants. The magnitude of the effect was a function of genotype, plant developmental stage and initial infestation density. When subjected to an aphid infestation, dry shoot weight was significantly greater on 10085-5 than on 'Stephens,' demonstrating the resistance to *D. noxia* in this genotype. For both genotypes, infestations with the high aphid density resulted in lower dry plant weights than those with the low aphid density. Similarly, infestations at early stages resulted in significantly lower dry shoot weight than those at later stages.

Compared to the 0-aphid treatment, 'Stephens' plants infested with 20 *D. noxia* at the 1-leaf stage had a 91% reduction in dry matter accumulation over the duration of the experiment. Plants infested at the 2-leaf stage had an 83% reduction, while those infested at the 3-leaf stage suffered a 60% reduction in dry matter accumulation. A similar, but less pronounced, effect was observed on 'Stephens' plants infested with 5 *D. noxia*. Infestations at the 1-leaf stage resulted in an 82% reduction in dry matter accumulation, infestation at the 2-leaf stage in a 72% reduction, and at the 3-leaf stage in a 36% reduction. Although 10085-5 plants suffered reductions in dry matter accumulation as a result of *D. noxia* feeding, the magnitude of the effect was not as large as that observed for 'Stephens,' demonstrating the resistance of 10085-5 to *D. noxia*. Infestation of 10085-5 plants with 20 *D. noxia* at the 1-leaf stage caused a 78% reduction in dry matter accumulation, infestation at the 2-leaf stage a 69% reduction, and at 3-leaf stage a 45% reduction. 10085-5 plants infested with 5 *D. noxia* at the 1-leaf stage had a 72% reduction in dry matter accumulation, those at the 2-leaf stage a 59% reduction, and at the 3-leaf stage only a 23% reduction. Thus, the impact of *D. noxia* on plants was less pronounced as plants matured, within the temporal scale of these experiments.

As for other plant variables, the magnitude of variations in plant height was a function of initial aphid density, plant growth stage at infestation and genotype. For both genotypes, infestations at early stages resulted in smaller gains in height than those at later stages. Similarly, compared to the low density, infestations with the high aphid density resulted in smaller gains in height. The impact of *D. noxia* on plant height was more pronounced on the susceptible genotype. Height gain on 'Stephens' plants infested with 20 *D. noxia* at the 1-leaf stage was only 21% that of non-infested plants.

If a ratio of shoot weight over plant height is calculated for the different treatments, the ratios are consistently lower for 'Stephens' than 10085-5, except in the absence of aphids. Ratios for 'Stephens' ranged between 0.09 for plants infested with 20 *D. noxia* at the 1-leaf stage, to 0.35 for those infested with 5 *D. noxia* at the 3-leaf stage. Similarly infested 10085-5 had ratios of 0.20 and 0.44, respectively. The ability of

10085-5 to support greater growth than 'Stephens' under similar insect challenge is an indication of tolerance. Thus, this genotype combines tolerance and antibiosis to the Russian wheat aphid. PI 294994, the resistant parental line of 10085-5, was reported to exhibit tolerance to *D. noxia* by Smith et al. (1992).

Levels of plant damage were significantly affected by initial *D. noxia* density, but this was influenced by plant stage at time of infestation and varietal resistance. In general, plants exhibited less damage when infested at later growth stages. The impact of aphid feeding was less pronounced on the resistant genotype compared to the susceptible one. This was especially noticeable in the percentage of leaves rolled, which was over 1.5× greater on 'Stephens' than 10085-5. The ability of 10085-5 leaves to remain unrolled in the presence of *D. noxia* is an important factor for enhancing the efficacy of predators and parasites. *Diuraphis noxia* is easier for natural enemies to reach on open leaves than on rolled ones (Farid et al. 1997). The combination of tolerance, moderate antibiosis and a potential for enhanced natural enemy activity should prove valuable in the management of this important pest. Field studies are now underway to assess the impact of resistance to *D. noxia* on natural enemies.

Testing over a range of plant growth stages and insect densities allowed us to detect multiple categories of resistance. As discussed by Quisenberry and Schotzko (1994) and illustrated in this paper, pest population statistics examined independently of plant quality could be misleading, and use of appropriate temporal scales when measuring host plant resistance to an insect is critical for understanding the complex biological processes involved.

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