Population Dynamics of Aphids (Aphididae: Homoptera) on Different Wheat Cultivars and Response of Cultivars to Aphids in Respect of Yield and Yield Related Parameters

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Abstract.- To see the population dynamics and to evaluate the resistance ability of seven wheat cultivars (Inqilab-91, Fakhar-e-Sarhad, Bakhtawar-92, Nowshera-96, Khyber-87, Suleman-96 and Tatara) against aphid, an experiment was conducted at Agriculture Research Institute, Tarnab, Peshawar. The aphid attack started in mid January on the wheat cultivars and increased gradually with the growth of plant. The highest aphid population 8.2 aphids tiller⁻¹) was recorded on Khyber-87 which was significantly more than the other tested cultivars. Tatara with 6.85 aphids tiller⁻¹, although, had significantly low number of aphids than Suleman-96 and Khyber-87 was statistically similar in aphid population with any other tested cultivar. In cultivar Tatara, the spiklet spike⁻¹ were significantly more than Inqilab-91 which may be because of its resistance to this insect pest. Khyber-87 and Nowshera-96 had significantly more number of seed spike⁻¹ as compared to the other tested wheat cultivars. The length of spike tiller⁻¹ and the height of tiller plant⁻¹ in all seven wheat cultivars were not affected by aphids. The weight of 1000 grain of seed and overall yield was statistically similar among these wheat cultivars.

Keywords: Aphid, wheat varieties, host plant resistance.

INTRODUCTION

Wheat (Triticum aestivum L.) is a convenient nutritious and economical source of food. It provides about 20% of the world's food calories and is a food for nearly 40% of the world's population. In many countries more wheat is consumed per capita than other foods (Wiese, 1987). In 2001, the leading wheat producing countries were India, China, Russian Federation, U.S.A., Australia, Canada, Turkey, and Pakistan (Anonymous, 2001). In Pakistan, wheat is the most important single crop. Although, in Pakistan wheat is grown on a fair percentage of the total cultivated area, it is still struggling hard to become selfsufficient in wheat production. Numerous factors are responsible for the low yield of wheat in Pakistan. Beside, the lack of modern agronomic practices, insect pests play important role in reducing the yield/hectare. Most of these pests belong to eight major orders Orthoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, and

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Hymenoptera in the class Insecta and mites in the class Arachinda (Hatchett and Webster, 1987). Among the sap sucking arthropods, aphids are the most widely distributed group. Aphids pierce and suck sap from leaves, stems, and less frequently the developing kernels of wheat. Some inject toxic substances that destroy plant tissue while some are vectors of viruses that may cause widespread losses exceeding those attributed to the direct feeding damage (Gair et al., 1983). Several control methods have been evolved for the control of aphids. These include cultural, physical, mechanical, biological, chemical, and host plant resistance. Mostly aphid's population is kept below the economic injury level by the combination of naturally occurring population regulating factors. But some times, the aphids can be extremely injurious if present in large number and chemicals have to be used for control (Hatchett and Webster, 1987).

In order to combat with the increasing resistance development in the aphid against pesticides and also to reduce the pesticides load on the environment, adoption of Integrated Pest Management (IPM) strategies are needed. Host plant resistance is an important part of IPM for aphids. A population of *Sitobion avenae* on wheat is often effectively controlled by natural enemies in Europe and with positive interaction between natural enemies and host plant resistance. In resistant wheat cultivars, dihydroxy phenols are associated with feeding deterrence to the *Rhopalosiphum padi* and *S. avenae* (Leszcynski, 1985).

The present studies were therefore, undertaken to know the response of different wheat cultivars with respect to aphid attack.

MATERIALS AND METHODS

Population dynamics of aphids on different wheat cultivars

In order to evaluate different wheat varieties for their resistance against aphids, an experiment was conducted at Agricultural Research Institute Peshawar. Seven commercial wheat Tarnab. varieties (Ingilab-91, Khyber-87, Baktawar-92, Nowshera-96, Sulaiman-96, Fakhar-e-Sarhad and Tatara) were used in this study. The seed of the mentioned cultivars were obtained from CCRI. Pirsabak, Nowshera and were sown on November 16. 2003. The experiment was laid out in Randomized Complete Block Design. Each treatment was replicated three times and distance between replicates was kept 1.5 m. Each variety was sown in plot measuring 5x6 m (30 sq m). There were 16 rows in each plot and row to row distance was kept 36 cm. A uniform agronomic practices were applied to each plot. Each plot was divided in to two sub-plots. One sub-plot in each plot and each replicate was sprayed with Supracide @ of 1.5 ml 1 lit⁻¹ of water and or Methamedophos @ 2 ml 1 lit⁻¹ of water at the interval of 15 days, in order to ensure the complete control of aphids throughout the crop season. The other subs-plot was left untreated (control) for the comparison of yield and other yield related parameters (spikelets spike⁻¹, number of seed spikeler⁻¹, number of tillers plant⁻¹, 1,000 grains weight etc.). The spray was made with 10 ltrs. capacity hand operated knap sack sprayer. Wooden slices were used during spray to avoid the insecticidal drift to the untreated plot. The data was recorded fortnightly beginning with 4rth week of germination of the crop till the maturity of crop. Four plants in each untreated plots were randomly selected and aphids were counted on one tiller plant⁻¹. The data was recorded at weekly interval. The data was analyzed with analysis of Variance (ANOVA) and means separated with Least Significant Difference Test (LSD).

Effect of aphids on the yield and yield related parameters

Yield and other yield related parameters *i.e.*, height of plants, number of spikes plant⁻¹, number of spikelets spike⁻¹, length of tiller plant⁻¹ and 1000 grain weight etc were recorded at the end of the experiments in both treated and untreated plots. In this regard 5 tillers per plant were randomly selected and the mean of the 5 selected plants was taken. To see the difference between treated and untreated plots, the data taken on the above parameters were statistically analyzed and the means separated with Least Significance Difference Test.

RESULTS

Varietal resistance of wheat cultivars against aphid

The attack of aphids on different wheat varieties started on 17-01-2002. The aphid population increased gradually with the growth of plants. It is obvious, that aphid multiplication rate was slower during vegetative growth stage (Table I). However, a continuous increase in the population was observed. The overall mean aphid density tiller⁻¹ on different wheat varieties indicated that highest population of 8.42 aphids tiller⁻¹ was recorded on variety Khyber-87 which were significantly more than the aphid population tiller⁻¹ in Suleman-96, Nowshera-96, Bakhtawar, Fakhar-e-Sarhad, Ingilab-91, and Tatara with 6.85, 6.28, 6.08, 5.83, 5.15, and 5.01 aphids tiller⁻¹, respectively. The aphid density tiller⁻¹ in Ingilab-91, Tartara, Fakhar-e-Sarhad, Nowshera-96, and Bakhtawar-92 were statistically similar to each other. Tatara with 5.01 aphid tiller⁻¹ were significantly different at $\alpha = 0.05$ to the 6.85 aphids tiller⁻¹ in wheat variety Suleman-96.

Spikelets spike⁻¹ *assessment*

The cultivar Tatara showed maximum number (19.80 and 19.27) spikelets spike⁻¹ both in Table I. Arbids negative filter¹ cleart¹ or various who the treated and untreated plots, respectively. The

 Table I. Aphids population tiller⁻¹ plant⁻¹ on various wheat cultivars at different time intervals.

Varieties	Aphids density on different dates						Means							
	17/1	24/1	1/2	8/2	17/2	23/2	1/3	8/3	15/3	23/3	30/3	6/4	15/4	
Inqilab-91 Fakhar-e- Sarhad Bakhtawar- 92 Nowshera- 96 Khyber-87 Suleman-	1. 58 1. 42 0.75 1. 50 2.00 0.92	24/1 2.00 4.00 1.50 2.67 2.33 2.42		8/2 4.08 4.50 5.00 4.58 10.50 4.42	6.92 6.17 9.92 11.75 9.25 9.92	9.50 10.42 13.83 17.33 13.75 12.92	1/3 16.17 15.67 18.08 16.83 14.67 18.33	8/3 10.00 18.92 13.50 14.17 25.08 20.17	8.50 6.92 8.17 5.15 20.92 10.58	23/3 225 2.50 2.67 2.25 4.00 3.83	1. 08 1. 08 1. 08 1. 08 0.92 1. 42 1.17	0.17 0.25 0.17 0.25 0.17 0.25 0.17 0.25	15/4 0.00 0.00 0.17 0.25 0.17 0.17	5.15c 5.83bc 6.08bc 6.28bc 8.42a 6.85b
Tatara	1.58	2.58	3.08	3.67	6.92	8.67	18.33	13.00	4.00	1.83	1.17	0.33	0.00	5.01c

Each value is a mean of 3 replications. Means followed by similar letters are not significantly different with each other at $\alpha = 0.05$. LSD = 1.394.

Table II	Effect of aphids on	the number of s	spikelets spike ⁻¹

Cultivora	Spik	elets spike ⁻¹	Spikelets pike ⁻¹ loss	Percent spikelets spike ⁻¹	
Cultivars	Treated	Untreated		difference	
Inqilab-91	18.30ABC	17.33C	0.97	5.30	
Fakhar-e-Sarhad	18.70ABC	17.77BC	0.93	4.98	
Bakhtawar-92	19.40AB	18.33ABC	1.07	5.52	
Nowshera-96	19.53AB	18.87ABC	0.68	3.48	
Khyber-87	19.33AB	18.30ABC	1.03	5.33	
Suleman-96	19.00ABC	18.27ABC	0.73	3.84	
Tatara	19.80A	19.27AB	0.53	2.68	
Means	19.151	18.306	0.85	4.375	

Each value is a mean of 3 replications Mean followed by the same letters are not significantly different at $\alpha = 0.05$

spikelets spike⁻¹ in the treated plot of Tatara were statistically similar to the lowest number (18.30) spikelets spike⁻¹ in Inqilab-91. However, the 19.27 spikelets spike⁻¹ in the untreated plot of Tatara cultivar were significantly different from 17.33 spikelets spike⁻¹ in the untreated plot of Inqilab-91. This significant difference may be because of the test insect (Table II).The number of spikelets spike⁻¹ in the treated and untreated plots of all the other cultivars were statistically similar. The number of spikelets spike⁻¹ loss and Percent spikelets spike⁻¹ loss in the rest of the test cultivars were not significantly different from each other.

Number of seeds spike⁻¹ assessment

The number of seed spike¹ in each tested variety were statistically similar in treated and

untreated plots. In the untreated plots, Khyber-87, and Nowshera with 52.53 seed spike⁻¹ and 48.93 seed spike⁻¹, respectively, although, statistically similar to each other, they were significantly better in the number of seed spike⁻¹ to the rest of the tested varieties (Table III). The 0.027 percent seed spike⁻¹ loss in variety Suleman-96 indicated its resistance to the test insect. The significant difference in the number of seed spike'! among the cultivars may be because of their genetic make up which remained in the untreated plot also.

Length of spike tiller⁻¹ (*cm*) *assessment*

The maximum length (15.92 cm) of spike tiller⁻¹ was recorded in variety Suleman-96 and the minimum length (14.67cm) of spike tiller⁻¹ was recorded in Tatara. The untreated cultivar Suleman-

96 showed a difference of 1.19 cm due to aphid attack indicating 7.47% decrease in length of spike tiller⁻¹. Maximum decrease of 1.42 cm (9.68%) in Table III.- Effect of aphids on the number of seeds spike⁻¹.

length of spike tiller-1 was recorded in Tatara

Cultivora	Number	of seeds spike ⁻¹	Seeds spike ⁻¹ loss	Percent seeds spike ⁻¹ difference
Cultivals	Treated	Untreated		
Inqilab-91	35.27C	35.00C	0.27	0.77
Fakhar-e-Sarhad	37.80 BC	37.07BC	0.73	1.93
Bakhtawar-92	39.97 A	39.23BC	0.74	1.851
Nowshera-96	49.83A	48.93A	0.9	1.836
Khyber-87	53.20A	52.53A	0.8	1.503
Suleman-96	36.08 BC	36.07C	0.01	0.027
Tatara	42.23B	41.90B	0.33	0.781
Means	42.054	41.37	0.54	1.242

Each value is a mean of 3 replications. Means sharing common characters between rows are non-significant at $\alpha = 0.05$. LSD = 5.358

Table IV Effect of aphids on the length of spike tiller ⁻¹ (cm	Table IV	Effect of aphids on the length of spike tiller ⁻¹ (cm).
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Cultivers	Length of seeds	s spike tiller ⁻¹ (cm)	Spike tiller ⁻¹ (cm)	Percent seeds spike tiller ⁻¹	
Cultivals	Treated	Untreated	loss	difference	
Inqilab-91	15.47AB	14.42ABC	1.05	6.78	
Fakhar-e-Sarhad	14.75ABC	13.90BC	0.85	5.76	
Bakhtawar-92	15.08ABC	13.68C	1.4	9.28	
Nowshera-96	14.83ABC	14.33BC	0.5	3.37	
Khyber-87	15.02ABC	14.33BC	0.69	4.59	
Suleman-96	15.92A	14.73ABC	1.19	7.47	
Tatara	14.67ABC	13.25C	1.42	9.68	
Means	15.105	14.091	1.01	6.70	

Each value is a means of 3 replications. Means sharing common characters are not significantly different at $\alpha = 0.05$. LSD = 1.515

Table V.- Effect of aphids on the height of tillers plant⁻¹.

Cultivana	Height tiller	plant ⁻¹ (cm)	Tiller plant ⁻¹ (cm)	Percent seeds tiller plant ⁻¹	
Cultivars	Treated	Untreated	loss	difference	
Inqilab-91	91.33A	90.00ABC	1.33	1.456	
Fakhar-e-Sarhad	88.75ABC	87.33C	1.42	1.6	
Bakhtawar-92	89.10ABC	88.33BC	0.77	0.86	
Nowshera-96	89.37ABC	87.33BC	1.17	1.307	
Khyber-87	88.37BC	87.33BC	1.04	1.176	
Suleman-96	90.67AB	89.17ABC	1.5	1.65	
Tatara	90.17AB	89.67ABC	0.5	0.555	
Means	89.698	88.59	1.104	1.229	

Each value is a means of 3 replications. Means sharing common characters are not significantly different at $\alpha = 0.05$. LSD = 2.799

followed by 1.4 cm (9.28%), 1.19 cm (7.47%), 1.05 cm (6.78%), 0.85 cm (5.762%), and 0.69 cm (4.59%) in Bakhtawar-92 Suleman-96, Inqilab-91, Fakhar-e-Sarhad, and Khyber-87, respectively (Table IV). Overall results showed 6.704\% mean

decrease in the length of spike tiller⁻¹ in all entries, where the means were not significantly different with one another at a = 0.05.

Height of tiller plant⁻¹ *loss assessment*

The maximum 91.33 cm height of tiller plant⁻¹

was recorded in variety Inqilab-91 and the minimum 88.37 cm height of tiller planr1 was found in variety Khyber-87. However, the untreated variety Inqilab-91 showed a difference of 1.33 cm due to aphid Table VI.- Effect of aphids on 1000 grains weight (gm).

attack indicating 1.46 % decrease in the height of tiller plant⁻¹. Maximum decrease in height of tiller

Cultivora	1000 gr	ain weight (gm)	1000 grain weight	Percent 1000 grain weight	
Cultivars	Treated	Untreated	(gm)	difference	
Inqilab-91	39.13 A	38.03A	1.1	2.81	
Fakhar-e-Sarhad	39.26A	38.74A	0.52	1.325	
Bakhtawar-92	38.28A	37.98A	0.3	0.78	
Nowshera-96	38.44 A	37.98A	0.46	1.197	
Khyber-87	37.14A	36.81A	0.33	0.88	
Suleman-96	39.23A	38.36A	0.87	2.22	
Tatara	38.08A	37.70A	0.38	0.99	
Means	38.508	37.94	0.565	1.457	

Each value is a means of 3 replications. Means sharing common characters are not significantly different at $\alpha = 0.05$. LSD = 3.752

Table VII	Effect	of a	phids o	n the	yield	(kg l	1a ⁻¹)	١.
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Cultivora	Grain yie	ld (kg ha ⁻¹)	Grain yield loss	Percent yield difference
Cultivars	Treated Untreated		(kg)	
Inqilab-91	5688A	5532A	156	2.74
Fakhar-e-Sarhad	5164A	4889A	275	5.33
Bakhtawar-92	5689A	5533A	156	2.74
Nowshera-96	5155A	4973A	182	3.53
Khyber-87	5867A	5510A	357	6.08
Suleman-96	5332A	5155A	177	3.32
Tatara	5472A	5332A	140	2.56
Means	5480.19	5274.86	206.14	3.76

Each value is a means of 3 replications. Means sharing common characters are not significantly different at $\alpha = 0.05$. LSD = 1262

plant⁻¹ was recorded in Suleman-96 with 1.5 cm (1.65%), followed by Fakhar-e-Sarhad with 1.42 cm (1.6%), Inqilab-91 with 1.33 cm (1.456%) Nowshera-96 with 1.17 cm (1.307%), Bakhtawar-92 with 0.77 cm (0.86%) and Tatara with 0.5 cm (0.55%) (Table V). The overall mean decrease of 1.104 cm (1.229%) in height of tillers plant⁻¹ in all entries were not significantly different at $\alpha = 0.05$.

Assessment of 1000 grain weight and overall yield

The weight of 1000 grain between treated and untreated plots of each variety and among the all tested varieties were statistically similar at a = 0.05(Table VI). The small non-significant difference in the 1000 grain weight may be due to aphid attack but negligible. Yield of cultivars as affected by the attack of aphids

At the end of the season, the yield in the treated and untreated sub-plots of the same cultivar as well as the yield in the different cultivars was statistically similar at $\alpha = 0.05$ (Table VI). A negligible variation in the yield of cultivars may be due to their genetic make up. The mean percent yield difference of 5.33 and 6.08 in the treated and untreated plots of Fakhar-e-Sarhad and Khyber-87, respectively, seems to be because of the aphid attack but without any significant impact.

DISCUSSION

Many research workers have studied the resistant ability of plants against their insect pests. Published information reveals that aphids are

serious pests of wheat crop (EL Bouhssini et al., 2000). They have also been implicated in the disease of wheat transmission of BYDV (Capsicaneo and Gilet, 1996). In the present study, the increase in population was gradual from vegetative growth stage to inflorescence. Similar results were also observed by Hussein (1993). According to him a maximum abundance of each aphid species occurred at the beginning of flowering period, after which the population fell rapidly. Rustamani et al. (1999) observed that the infestation of aphids appeared during the 3rd week of December on all wheat varieties. The increase in population was gradual during vegetative growth stage but the aphids multiplied rapidly during the reproductive stage. The variation in the aphid density tiller⁻¹ in different varieties could be the resistance response of these varieties to aphids attack. Our results favor the findings of Xiang (1999) who found that wheat varieties did not obviously affect the mortality of nymphal aphids, but significantly affected the development duration of nymphal aphids and the longevity and fecundity of adults. Similarly Havlickova (1989) found significant differences in the number of nymphs produced by the alates on tested cultivars. The percent reduction in spikelets spike⁻¹ and seed spike⁻¹ in the present study were not significantly different at different levels of probability may be because of the use of different varieties in the experiment. In contrast to our results, Rustamani (1999) observed that the agronomical characteristics such as plant height, number of spikelets spike⁻¹ and number of grains spike⁻¹ were variable with the tested varieties. Our results also disagree the results of Elmali and Toros (1997) who recorded 10.16% average loss in 1000 grain weight; However, they found that some yield and morphological characteristics (fertile spikelets spike⁻¹, grain spike⁻¹, plant height and spike length) were not. affected. The 6.70% reduction in the length of spike tiller⁻¹ and 1.22% reduction in the length of tiller plant⁻¹ because of the aphid infestation were not significantly different among the tested cultivars. Elmali and Toros (1997) observed that due to aphid infestation in winter wheat, some yield and morphological characteristics (fertile spikelets spike⁻¹, grains spike⁻¹, plant height and length of spike tiller⁻¹ were not affected. Bakhait

et al. (1989) found that the cultivars with high vielding ability were susceptible to aphid infestation. The percent reduction in 1000 grains weight and yield in the present study due to aphid attack was statistically similar. Our results favor the findings of Khan (2000), Zeb (2001), and Imran (2001) who observed non-significant yield losses in different wheat cultivars because of the aphids attack in N.W.F. Province. Insecticide used in this experiment was only used to completely stop the attack of the aphids which could be very correctly compared with yield and yield related parameters as affected by the aphid attack in the untreated plot of the same cultivar as well as of the different cultivars, though, Usually in wheat against aphids hot water treatment is made. It is evident from the results that aphids have no significant impact on the tested seven wheat cultivars.

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REFERENCES

- ANONYMOUS, 2001. Agricultural statistics of Pakistan. Ministry of Food, Agriculture and Livestock. Food, Agriculture and Livestock Division, Eco. Wing, Islamabad, Pakistan p. 4-5.
- BAKHAIT, B.R., MASSAD. M.G., EL-MORSHIDY, M.A. AND TAMAN, A.M., 1989. Correlation under normalfield and aphid infestation conditions and path analysis in durum wheat *Triticum turgidum* L. *Cereal Res. Commun.*, 17: 219-226.
- CAPSINCANEO, C. AND GILET. A., 1996. Viral Diseases of Cereals and their control measures. *Cultivar's Hors. Ser.*, **408**: 28-30.
- EL-BOUHSSINI, M, M., NACHIT, M., ROYO, C., FONZO. N. AND ARAUS, J. L., 2000. New sources of resistance in durum wheat and wild relatives of Russian wheat aphids. In: *Proceedings of a Seminar*. Zaragoza, Spain, April 12-14, 2000. Options-Mediterraneans,-Series, 40: 393-395.
- ELMALI, M. AND TOROS, S., 1997. Effect of Sitobion avenae (F.) Homoptera: Aphididae on wheat yield and quality. Turk. Ent. Derg., 21: 109-118.
- GAIR, R., E. JENKINS, E. AND LESTER, E., 1983. Cereal

pests and diseases. Farming Press Ltd., UK, pp. 54-80.

- HATCHETT, A. AND WEBSTER, H., 1987. Insect pests and mites of wheat. In: Wheat and wheat improvement (ed. E.G. Heyne), Madison. Wisconsin, USA, pp. 625-668.
- HAVLICKOVA, H., 1997. Differences in level of tolerance to cereal aphids in five winter wheat cultivars. *Rostlinna-Vyroba*, **43**: 596.
- HUSSEIN, I.A.A., 1993. Abundance dynamics of cereal aphids (Homoptera, Aphididae) and their natural antagonists on different wheat types in Deir Ezzor (Syrian Arab Rep.). Arch. Phytopath. Plant-Protect., **28**: 439-445.
- IMRAN, I., 2001. Screening of different wheat varieties against the resistance of aphids. M.Sc. theses, Department of Entomology, NWFP Agriculture University, Peshawar, pp. 60.
- KHAN, S.S., 2000. Impact of plant phonology of various wheat genotypes on aphid population and subsequent losses in wheat due to aphids. M.Sc. thesis, Department of Plant Protection, NWFP Agriculture University, Peshawar, pp. 51.

LESEZEZYNSKI, B., 1987. Use of plant resistance in insect

pest management systems. In: *Plant resistance to insect, a fundamental approach* (ed. C.M. Smith), pp. 243-268. John Wiley and Sons, New York.

- RUSTAMANI, M.A., SHEIKH, S.A., MEMON, N.M., LEGHARI, H. AND DHAUNROO, M.H., 1999. Impact of wheat plant phonology on the development of green-bug, *Schizaphis graminum* (Rondani). *Pakistan J. Zool.*, **31**: 245-248.
- WIESE, M.V., 1987. *Compedium of wheat disease*. The American Phytopathological Society, USA. pp. 21-91.
- XIANG, W. I., JIANG, J. H., CHENG, S. B. AND XIAOJI, S., 1999. Effect of wheat varieties on main life parameters of wheat aphids. *Chinese J. appl. Ecol.*, **10**: 447-451.
- ZEB, O., 2001. Population dynamics and biocontrol agents of wheat aphids. M.Sc. thesis, Department of Entomology, NWFP Agriculture University, Peshawar, pp. 46.

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