

AN ABSTRACT OF THE THESIS OF

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Russian wheat aphid (RWA), Diuraphis noxia (Mordvilko), is a widely distributed species in western north America, and a major economic pest of wheat (Triticum aestivum L.) and barley (Hordeum vulgare L.). The objectives of this study were to : 1) determine the inheritance of seedling and adult plant resistances in a wheat line PI 294994 ; 2) establish whether greenhouse and field resistances were related ; 3) determine the effect of RWA infestation on the dry matter, grain yield, and harvest index in the crosses Moro/PI 294994 and Hyak/PI 294994 ; 4) determine whether there was a difference in the three traits between different genotypes due to RWA infestation ; and, 5) assess the degree of protection genetic resistance provided in the two crosses.

The club wheat cultivars 'Moro' and 'Hyak' were crossed with PI 294994. Progenies from these two crosses were artificially infested with RWA in the field and the

crosses were compared for their dry matter, grain yield, and harvest index. Plant reactions of F_2 seedlings, F_2 adult plants, and F_3 seedlings indicated that both seedling and adult plant resistances are controlled by two genes with dominant and recessive mode of inheritance and that plant reactions in the field were the same as those in the greenhouse. Comparison of mean values of dry matter, grain yield, and harvest index showed that the three traits were affected by RWA infestation and genotype in both crosses. Resistant genotypes and noninfested population were comparable with respect to the three traits in Moro/PI 294994 but they were not in Hyak/PI 294994.

Genetic Studies with Russian Wheat Aphid (Diuraphis noxia
Mordvilko) in PI 294994 Bread Wheat (Triticum aestivum L.)

by

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Typed by researcher for Ahmed A. Elsiddig

DEDICATED TO:

my parents

my brother,

Elsiddig

my wife,

Magda

and

my daughter

Ro'a

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Genetic Studies with Russian Wheat Aphid (Diuraphis
noxia, Mordvilko) in PI 294994 Wheat
(Triticum aestivum L.)

CHAPTER 1

Inheritance of Resistance to Russian Wheat Aphid in Bread
Wheat Line PI 294994

ABSTRACT

Russian wheat aphid (RWA), Diuraphis noxia (Mordvilko), has become a serious pest of wheat (Triticum aestivum L.), in the western United States. The objectives of this study were to: 1) determine the number of genes conferring resistance at the seedling and adult growth stages in the line PI 294994 which was previously determined to be resistant to RWA; and, 2) establish whether greenhouse and field resistances were related. The resistant line was crossed with the club wheat cultivars 'Moro' and 'Hyak'. Plant reactions of F_2 seedlings, F_2 adult plants, and F_3 seedlings showed that both seedling and adult plant resistances in the line PI 294994 are controlled by two genes with dominant and recessive mode of inheritance. Plant reactions to RWA infestation in the field were the same as those in the greenhouse.

INTRODUCTION

It has been almost six years since the introduction of RWA into the United States and the insect continues to thrive as an economic pest of wheat, barley, and certain forage grasses. By 1989, damage estimates for the western states exceeded \$200 million. More than 65% of wheat and barley is currently threatened by the aphid.

Sources of resistance to RWA have been reported in wheat and other related species by many researchers and have been intensively used in several breeding programs. Six wheat lines, PI 137739, PI 262660, PI 294994, PI 372129, PI 262605, and PI 243781 have been reported as sources of RWA resistance in common wheat. Greenhouse tests indicated that resistance in PI 137739, PI 262660, and PI 372129 is controlled by different independent dominant genes. The genetics of resistance in PI 294994 is still uncertain, but is probably under the control of two genes. The genetics of resistance in PI 262605 and PI 243781 have not yet been determined since their resistance was only recently discovered.

To make the most effective use of available resistant germplasm, plant breeders must determine the inheritance of RWA resistance of outstanding wheat lines and genetic relationships among various sources of resistance. The line PI 294994 represents a valuable source of resistance

to RWA for breeding programs. The objectives of this study, which was conducted in 1991, were to determine the genetics of resistance to RWA in seedlings and adult plants of PI 294994 and establish whether the field resistance to RWA in adult plants of PI 294994 correspond to greenhouse resistance in seedlings.

LITERATURE REVIEW

Distribution

Russian wheat aphid (RWA) was first detected in the Mediterranean region and south Russia in 1900 (Grossheim, 1914). It became recognized as a serious pest of wheat (Triticum aestivum L.) in South Africa in 1978, and until recently most of the information and research on RWA comes from South Africa (Walters et al., 1980). Russian wheat aphid was found in Mexico for the first time in 1980 (Gilchrist et al., 1984) and was subsequently discovered in the United States in 1986 in Bailey County, Texas (Webster et al., 1987), and in Canada in 1988 (Morrison, 1988). Since its discovery in Texas, the RWA has spread north and west, and by 1990 it occurred in seventeen western states and three Canadian provinces (Burton, 1989).

Major host plants

In addition to wheat, economically important host plants of RWA include barley (Hordeum vulgare L.) and triticale (* Triticosecale Wittmack). Oats (Avena sativa L.) and rye (Secale cereale L.), are the small grains least preferred by the aphid (Walters et al., 1980).

Damage symptoms

RWA feeding causes characteristic longitudinal leaf chlorosis and leaf rolling (Hewitt et al., 1984). Some purple coloration on the leaves, which may be caused by cold temperature or day length (Hewitt et al., 1984), has also been reported. Under severe infestations, plants may be stunted and spikes deformed (Gilchrist et al., 1984). In South Africa, Russian wheat aphid has been implicated as a plant disease vector by spreading barley yellow dwarf, brome mosaic, barley stripe mosaic, and viruses vectored by Rhopalosiphum padi (Rybicki and von Wechmar, 1984). In the United States and Mexico, researchers were unable to confirm any transmission of cereal viruses by RWA.

Control

Currently, the principal management strategies for this new pest in the United States include the use of systemic insecticides, delayed plantings, and growth of nonhost crops (Pike, 1988, Anonymous, 1989). The less expensive contact aphicides are not as effective as the systemics because RWA secludes itself within the rolled leaves. Classical biological control methods should aid in the management of this economically important pest of

small grains and could be effectively used in conjunction with other management techniques, such as host plant resistance (Reed et al., 1992). The use of resistant cultivars represent an ideal management option for RWA. Butts and Pakendorf (1984b) and Du Toit and van Niekerk (1985) demonstrated that potential RWA resistance exists in the ancestral wheat species Triticum monococcum, T. timopheevi, T. dicoccoides, and Aegilops squarrosa.

Amphiploids of T. monococcum/T. durum crosses were also resistant to the aphid (Du Toit and van Niekerk, 1985), but this resistance proved difficult to transfer to bread wheat. The highest levels of antibiosis, antixenosis, and tolerance have been found in triticale and oats (Webster et al., 1987; Frank et al., 1989). Du Toit (1987) and Du Toit and van Niekerk (1985) also reported a high level of resistance in T. monococcum.

Genetic resistance to RWA in bread wheat was first discovered in 1986 (Du Toit, 1987). Two wheat lines, PI 137739, a hard white spring wheat from Iran, and PI 262660, a hard white winter wheat from Bulgaria, showed high resistance in greenhouse tests. The high level of resistance exhibited by PI 262660 was not expressed when tested using RWA isolates collected in the United States (Nkongolo et al., 1989). In 1987, a third resistant bread wheat line, PI 294994, a hard red winter wheat from Bulgaria, was also identified (Du Toit, 1988). Resistance

of PI 137739 and PI 262660 was controlled by single, dominant, independently inherited genes (Dn1 and Dn2) (Du Toit, 1989a). Resistance was attributed to antibiosis, but PI 262660 also had tolerance (Du Toit, 1989b). The genetics of resistance in PI 294994 is uncertain, but it is probably under the control of more than one gene (F. Du Toit, unpublished work). Resistance in PI 294994 was attributed to antibiosis (Du Toit, 1989). Resistance to the North American RWA colonies has been found in four wheat cultivars, PI 294994, from Hungary, PI 372129, from Russia, PI 262605, from Russia, and PI 243781, from Iran (Quick, 1989). Nkongolo et al. (1991) reported that a single dominant gene conditions resistance in PI 372129 and data describing the mechanism of resistance indicate that the gene is probably different from Dn1 and Dn2. Nkongolo et al. (1991) also reported that Triticum tauschii SQ24 possesses a single recessive resistance gene (Dn3). Seedlings have been screened for resistance to RWA in the laboratory and greenhouse (Du Toit and Van Niekerk, 1985; Du Toit, 1987; Webster et al., 1987; Bush et al., 1989; Nkongolo et al., 1990; Scott et al., 1991), but reports of field screening for RWA resistance are scarce (Souza and Halbert, 1988). Conditions in a greenhouse or growth chamber rarely approximate the conditions or range of conditions that are experienced in the field, thus, the expression of resistance observed in indoor screening

trials may not be the same as expression in the field.

Lowe et al. (1985) have reported differences between field and greenhouse expression of resistance to Sitobion avenae (Fabricius) in wheat.

MATERIALS AND METHODS

Greenhouse Experiments

The resistant line PI 294994 was crossed with the susceptible club wheat cultivars 'Moro' and 'Hyak'. In February 1991, 281 F_2 seedlings from the Moro/PI 294994 and 453 F_2 seedlings from the Hyak/PI 294994 crosses were tested for their reaction to the RWA. During August 1991, because of shortage of F_2 seeds, only 80 and 203 F_2 seedlings from the same crosses were tested. In a second experiment, 32 selected F_3 families from each cross generated from individual F_2 plants with determined field reactions to RWA, were tested in the greenhouse to establish whether resistance or susceptibility in the field were the same in the seedling stage. The 32 F_3 families consisted of 10 randomly selected families from each of the reaction types 2, 3, and 4. Because most plants with reaction type 5 did not produce seeds, only 2 families were included. No family from reaction type 6 was included because no plant produced seeds. In a third experiment, 70 F_3 families from each cross, generated from a noninfested F_2 population, were randomly selected and tested for their reactions to RWA. Each F_3 family was planted in 2 rows of 10 plants each. For each of the two crosses, the parents, F_2 and F_3 populations, as well as

oats used as a resistant check and barley as a susceptible check, were planted in a standardized greenhouse soil mixture in wooden flats of 12 rows each. Nutrient concentrations in the soil mixture were adequate for normal plant growth. Each flat contained 10 rows of segregating F_2 population or F_3 families, half-a row of each parent, oats, and barley. Each row contained 12 to 17 plants in February and 8 plants in August, with 4-cm spacing between rows. Flats were uniformly watered throughout the experiments. The seedlings were grown under a 12 h photoperiod at 21\10 C day\night.

Seedlings were infested at the one to two-leaf stage (approximately 8-10 days after planting) with three to five RWA placed at the base of each plant by use of a "bazooka" insect applicator (Mihm, 1982). Aphids were mixed with cream of wheat as a carrier in such a way that 3-5 aphids were discharged per plant. In February, seedlings were scored for their reactions to RWA by using the one to nine damage rating scale described by Quick et al. (1991) and Webster et al. (1987). In this scale:

- 1 = Plants appear healthy; may have small isolated chlorotic spots
- 2 = Chlorotic spots become more noticeable
- 3 = Chlorotic spots become larger; up to 15 % of total leaf area
- 4 = Up to 25 % of total leaf area is chlorotic

- 5 = Chlorotic spots coalesced; up to 40 % of total leaf area is chlorotic
- 6 = Up to 55 % of total leaf area is chlorotic
- 7 = Up to 70 % of leaf area is chlorotic
- 8 = Extensive chlorosis and necrosis; up to 85 % of leaf area is chlorotic
- 9 = Dead plants or no recovery possible

In August, the one to six scale described by Du Toit (1987) was used instead of the one to nine damage rating scale because it was easier to separate reaction types into resistant and susceptible with the one to six damage rating scale. In this scale:

- 1 = Small isolated chlorotic spots on the leaves, highly resistant;
- 2 = Larger isolated chlorotic spots on the leaves, resistant;
- 3 = Chlorotic spots tending to become streaky, moderately resistant;
- 4 = Mild streaks visible and leaves tending to roll lengthwise, moderately susceptible;
- 5 = Prominent white/yellow streaks present and leaves tightly rolled, susceptible;
- 6 = Severe white/yellow streaks, leaves tightly rolled and starting to die from the tips, highly susceptible;

Histograms were used to reflect the frequency distributions of different reaction types in the two damage rating scales for both crosses. Resistant and susceptible F_2 seedlings and segregating and nonsegregating F_3 families were counted 25-30 days after infestation and when the susceptible cultivars showed severe streaking and tightly rolled leaves (scores of 8-9 in February and 5-6 in August). Plants with a rating of 1 through 4 were recorded as resistant, and those with 5 through 9 were recorded as susceptible in February. Plants with a rating of 1 through 3 were recorded as resistant and those with 4 through 6 were recorded as susceptible in August. Chi square tests were used to compare plant and family ratios for resistant and susceptible seedlings.

Field Experiment

F_2 seeds from crosses described above were sown at Pendleton, OR, in 8 November 1990, in 1.5 m wide by 6.1 m long plots of 5 rows each. Plots were caged with 1.4 m tall by 6.4 m long by 1.8 m wide propylene material. The structure that supported the caging material was made of 3.8 cm PVC pipe. The field sown Plants were infested when the seedlings were in the 5 leaf stage, just as the plants began to joint, Zadoks 15, as above. A group of three

plants received 60 to 80 greenhouse-reared aphids of various instars. At the post heading stage, Zadoks 59 to 65, 146 and 149 individual adult F_2 plants from both crosses were rated based on their reaction to RWA, using a one to six scale, where:

- 1 = flat leaves with little or no chlorosis;
- 2 = flat leaves with some chlorotic areas;
- 3 = some leaf rolling with some heads trapped inside rolled leaves but most heads are normal;
- 4 = most leaves are rolled and most heads are trapped with few heads sterile;
- 5 = all heads trapped inside rolled leaves and most are sterile; and
- 6 = dead plants.

Plants with scores 1 through 3 were considered resistant and those with 4 through 6 were considered susceptible. Chi square tests were used as above.

RESULTS AND DISCUSSION

All Moro, Hyak, and barley plants were susceptible, and all PI 294994 and oat plants were resistant (Table 1). The counts of resistant and susceptible seedlings were recorded 3-4 weeks after infestation when the susceptible parent and check showed severe streaking and tightly rolled leaves. Frequency distributions of F_2 plants for Moro/PI 294994 and Hyak/PI 294994 showed that plants separated into two distinct classes of resistant and susceptible when using the 1 to 9 and the 1 to 6 damage rating scales (Appendix Figures 1, 2, 3, and 4).

Different hypotheses on segregation ratios were tested including a 15 resistant:1 susceptible (duplicate dominant genes) and a 9 resistant:7 susceptible (duplicate recessive genes). However they were rejected. F_2 seedlings and F_2 adult plants from both crosses segregated in a 13:3 ratio of resistant to susceptible plants (Tables 1 and 2). This ratio agreed with the hypothesis of two resistance genes with a dominant and recessive mode of inheritance in the resistant line PI 294994. Previous studies indicate that the resistance in PI 294994 is probably under the control of two genes and that these resistance genes are probably different from the genes Dn1 and Dn2 identified in PI 137739 and PI 262660, respectively (Du Toit, 1989). Resistance of PI 372129 is

controlled by a single, dominant gene that is probably different from Dn1 and Dn2 but no gene symbol is assigned yet (Nkongolo et al., 1991). No significant difference in RWA damage ratings was found between the wheat lines PI 294994 and PI 372129 in greenhouse tests (Nkongolo et al., 1989; Quick, 1989).

The ratio of 7:8:1 resistant\segregating\susceptible obtained in both crosses (Table 3), agreed very well with the F_2 segregation data and provided strong evidence that PI 294994 has two resistance genes with dominant and recessive mode of inheritance. Within segregating F_3 families, a fit to a 2:1:1 ratio of 13 resistant : 3 susceptible, 3 resistant : 1 susceptible, and 3 susceptible : 1 resistant from both crosses was significant ($P = 0.77$ and 0.86 for Moro/PI 294994 and Hyak/PI 294994 respectively) (Table 4). F_3 seeds taken from susceptible adult plants gave either susceptible seedlings or seedlings that segregated in a ratio of 3 susceptible : 1 resistant. All F_3 seeds taken from resistant adult plants, except from one family, gave either resistant seedlings or seedlings that segregated in ratios of 13 resistant : 3 susceptible and 3 resistant : 1 susceptible. The only F_3 family taken from a resistant adult plant (score of 3), gave seedlings that did not segregate in either 13 resistant : 3 susceptible or 3 resistant : 1 susceptible ratios and this might be a

result of an insufficient number of plants tested due to space limitations. Du Toit (1989), testing for a single dominant gene, did not obtain a significant fit for a 3 resistant : 1 susceptible ratio for plants within the segregating F_3 families from the cross SA 2199 / Tugela and he attributed that to an insufficient number of F_3 families available for the experiment. Two genes one dominant and one recessive were identified in both the seedling and adult plant stages. These data indicate that resistance to RWA in PI 294994 is controlled in a similar fashion in both growth stages. At present, different biotypes of RWA are not known to occur in the Pacific Northwest. The occurrence of different biotypes within the aphididae is not uncommon and has been reported in the corn leaf aphid, Rhopalosiphum maidis (Fitch) (Painter, 1958), and the spotted alfalfa aphid, Therioaphis maculata (Buckton) (Nielson and Lehman 1980). Five different dominant genes with differing reactions to four greenbug, Schizaphis graminum (Rondani), biotypes have been reported (Tyler et al., 1987). The release of different varieties in the United States may lead to the development of new RWA biotypes. Thus the development of RWA biotypes able to overcome varietal resistance is of great concern. PI 372129 is tolerant to RWA (Meyer et al., 1989). Varieties incorporating this type of resistance may be less likely to provoke the development of RWA biotypes than would

antibiotic or antixenotic varieties. Another approach to biotype avoidance being considered is the development of varieties incorporating a combination of resistance types or mechanisms. Therefore, availability of different resistance genes should be carefully exploited in a breeding program to delay any possible development of a new RWA biotype able to attack newly released resistant cultivars. The backcrossing technique is suggested to incorporate the PI 294994 resistance genes into adapted wheats. The genes symbols for the RWA resistance genes in PI 294994 will be assigned when confirmed by allelism tests with PI 137739, PI 262660, and PI 372129 resistance genes.

Table 1. Reactions of parents, barley and oats checks to the Russian wheat aphid. Chi square and P values test fit to a 13:3 ratio in F₂ progeny in February and August 1991.

Entries	<u>Number of plants</u>		X ²	P
	Res. ¹	Susc. ²		
<u>February 1991</u>				
PI 294994	40	0	-	-
Moro	0	21	-	-
Hyak	0	22	-	-
Barley	0	38	-	-
Oats	36	0	-	-
F2				
- Moro/PI294994	237	44	1.76	0.18
- Hyak/PI294994	363	90	0.37	0.54

¹ Res. = Resistant
² Susc. = Susceptible

Table 1. (continued) Reactions of parents, barley and oats checks to the Russian wheat aphid. Chi square and P values test fit to a 13:3 ratio in F₂ progeny in February and August 1991.

Entries	<u>Number of plants</u>		X ²	P
	Res.	Susc.		
<u>August 1991</u>				
PI 294994	16	0	-	-
Moro	0	4	-	-
Hyak	0	11	-	-
Barley	0	13	-	-
Oats	14	0	-	-
F2				
- Moro/PI294994	67	13	0.33	0.57
- Hyak/PI294994	165	38	0.0001	0.99

Table 2. Reactions of adult F₂ plants to the Russian wheat aphid with Chi square and P values test fit to a 13:3 ratio in 1991.

Cross	<u>Number of plants</u>		X ²	P
	Res.	Susc.		
- Moro/PI 294994	111	35	2.61	0.11
- Hyak/PI 294994	117	32	0.73	0.39

Table 3. Reactions of F3 families derived from randomly selected F₂ seeds to the Russian wheat aphid with Chi square and P values test fit to a 7:8:1 ratio in January-March 1992.

Cross	<u>Number of plants</u>			X ²	P
	Res.	Seg. ³	Susc.		
- Moro/PI 294994	31	33	6	0.72	0.7
- Hyak/PI 294994	28	37	5	0.43	0.8

³ Seg. = Segregating

Table 4. Segregation pattern within segregating F₃ families with Chi square and P values test fit to a 2:1:1 ratio.

Cross	<u>Number of F₃ families segregating*</u>			X ²	P
	13 R:3 S	3 R:1 S	3 S:1 R		
- Moro/PI 294994	15	10	8	0.52	0.77
- Hyak/PI 294994	20	9	8	0.30	0.86

*
R = Resistant
S = Susceptible

SUMMARY AND CONCLUSIONS

The objectives of this study were: 1) to determine the number of genes conferring resistance at the seedling stage, 2) to determine the number of genes conferring resistance at the adult plant stage, and 3) to establish whether greenhouse and field resistances were related.

To obtain such information, the resistant line PI 294994 was crossed with the club wheat cultivars 'Moro' and 'Hyak'. Resistance reactions of F_2 seedlings, F_2 adult plants, and F_3 seedlings were recorded. Chi square tests were used to compare plant and family ratios for resistant and susceptible seedlings.

The following conclusions were drawn based on the results of this study.

1. Seedling resistance in PI 294994 is controlled by two genes with dominant\recessive mode of inheritance.

2. Adult plant resistance in PI 294994 is controlled by two genes with the same mode of inheritance.

3. Resistance\susceptibility reactions of PI 294994 to RWA were the same in the field and the greenhouse.

4. The two damage rating scales, the one to nine and the one to six scales, yielded similar results, however the one to six damage rating scale was easier to use in genetic studies.

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CHAPTER 2

Effect of Russian Wheat Aphid on Dry Matter, Grain Yield,
and Harvest Index in Two Wheat Populations Segregating
for Susceptible and Resistant RWA Reactions

ABSTRACT

The Russian wheat aphid (RWA), Diuraphis noxia (Mordvilko), has caused significant economic loss in the western United States. Genetic resistance to RWA in wheat offers an avenue to reduce yield loss. The objectives of this study were to assess the effect of RWA infestation on dry matter, grain yield, and harvest index in two crosses between susceptible club wheat cultivars ('Moro' and 'Hyak') and the resistant common wheat line (PI 294994). Resistant and susceptible genotypes in the infested populations were compared with noninfested populations to determine the degree of protection genetic tolerance provided in the club wheat background. Dry matter, grain yield, and harvest index were significantly reduced in the RWA infested populations. The resistant genotypes in Moro/PI 294994 were not different from the noninfested group for dry matter, grain yield, and harvest index. However, resistant genotypes in Hyak/PI 294994 were significantly different from the noninfested group for the three traits. Susceptible genotypes were significantly

different from the resistant genotypes and the noninfested populations in both crosses.

INTRODUCTION

The Russian wheat aphid Diuraphis noxia (Mordvilko), was first reported from the United States near Muleshoe, Texas in March, 1986 (Morrison, 1989). The movement of this pest has been rapid to the north and west and slow to the east. It has now been found in all the states west of Texas, as well as in the Canadian provinces of Alberta, British Columbia, and Saskatchewan.

RWA causes serious yield loss in wheat and barley in many parts of the world particularly in dry areas. In the United States, researchers estimated the total losses for the years 1987 through 1990 to be \$325.2 million for direct loss (control cost, yield loss, and grazing loss) and \$357.7 million for indirect loss, for a total loss of \$657.9 million (Massey, 1991).

The Pacific Northwest has experienced some of the highest RWA populations ever documented (Pike et al., 1989). Researchers are conducting extensive investigations of the pest because of the aphid's adverse impact in cereal agriculture coupled with its expanding regional, national, and global occurrence. The following research was conducted to determine the effect of RWA infestation on the dry matter, grain yield, and harvest index in two crosses involving the club wheat cultivars 'Moro' and 'Hyak' and

the RWA resistant bread wheat line PI 294994. The research also addressed the effectiveness of the genetic resistance by comparing resistant to susceptible genotypes in the infested populations as well as to the noninfested populations.

LITERATURE REVIEW

Description

Diuraphis noxia is a small (< 2.3mm), spindle-shaped aphid, pale yellow-green to grey-green in color with a dusting of fine mealy wax (Stoetzel, 1987). The antennae are short and the cornicles are vestigial. A supracaudal process on the eighth abdominal tergite in combination with the cauda gives apterae a characteristic "forked tail" appearance when viewed from the side (Stoetzel, 1987).

RWA is probably the most easily identifiable aphid in small grains because of its unique shape as well as the symptoms it produces on the plants. Scouting for plant damage symptoms is the easiest method to detect RWA in the field. Damage appears as white to reddish streaks running the length of the leaves, which may be tightly rolled. Plants usually are stunted. The aphid most easily confused with RWA is the greenbug, Schizaphis graminum (Rondani). This species is similar in color to RWA, but has cornicles present and may have a dark green stripe running the length of its back. However, this characteristic is lacking in some biotypes of the greenbug. Greenbug damage appears as generalized red or yellow areas on the leaf where its feeding has destroyed the chlorophyll. Greenbug tends to

feed on the upper surface of the leaf, anywhere along its length, and do not cause leaf rolling, where as RWA tend to feed at the base of the youngest leaf or within curled leaves prior to heading. On the other hand the western wheat aphid, Diuraphis tritici (Gillette), which is closely related to RWA, gives the characteristic white to red stripes and curling of leaves but it can be separated from RWA easily in the field because it appears grey in color due to accumulated waxes on the surface of the aphid.

Diuraphis noxia is monoecious on grasses and the North American population is apparently solely parthenogenetic and viviparous.

Host Plant Range

Wheat, barley and triticale are the preferred small-grain hosts (Walters et al., 1980). Kindler and Springer (1989), found that jointed goatgrass (Triticum cylindricum (Host) Ces.) was the most suitable host, followed by barley, European dunegrass (Elymus arenarius L.) and little barley (Hordeum pusillum Nutt.). Webster et al. (1987) found that Russian wheat aphids could damage other cereal grains including oats (Avena sativa L.) and rye (Secale cereale L.) as well as Kentucky bluegrass (Poa pratensis L.) and perennial ryegrass (Lolium perenne L.). They also

reported that Russian wheat aphids caused little damage to corn (Zea mays L.), sorghum (Sorghum bicolor (L.) Moench), pearl millet (Pennisetum americanum (K.) K. Schum), "Kentucky 31" tall fescue (Festuca arundinacea Schreber), and bermuda grass (Cynodon dactylon (L.) Pers.).

Damage and Economic Importance

Diuraphis noxia is devastating because of its direct injury to cereal plants and the effect of the phytotoxin it injects during feeding. The phytotoxin of D. noxia causes breakdown of chloroplasts (Fouche et al., 1984). Researchers at the plant science research laboratory at Stillwater, OK were unable to identify a toxin and thus they questioned the toxin concept with RWA. However, they mentioned that the rolled leaves could result from the not expanding bulliform cells (Personal Communications). A reduction of the chlorophyll in infested leaves of up to 85% (Kruger and Hewitt, 1984) results in yield reductions of 25-50%. If feeding occurs in the flag leaf, a contorted grain head interfering with head extension and self-pollination results. The physiological effects of RWA feeding in many ways mimic drought stress, even in the presence of ample soil moisture, and limit the ability of plants to adjust to soil moisture deficit (Riedell, 1989).

Miller and Haile (1988) reported a 41 to 71% yield loss in barley and a 68% yield loss in wheat from small plots in Ethiopia. Yield losses between 35 and 60% have been recorded in South African wheat tests (Du Toit and Walters, 1984). Hewitt (1989) reported a 21 to 92% yield loss from wheat in South Africa. In 1988, wheat production losses in the United States due to D. noxia damage were \$130 million (Anonymous, 1989). By 1989, economic losses from the RWA in the United States were more than \$200 million (Burton, 1989). In the U.S., the cumulative economic loss from 1987 through 1990 attributed to RWA exceeds \$657 million, with over \$70 million being spent on control, \$250 million in lost production, and \$325 million in additional lost economic activity to local communities (Massey et al., 1991).

Host plant resistance offers one of the few economical control methods, particularly in the semiarid, lower-yielding environments where RWA tend to thrive (Kriel et al., 1984). Screening for RWA resistance relies primarily on the classification of genotypes based on differential expression of typical RWA feeding symptoms such as longitudinal chlorosis in leaves and leaf rolling (Du Toit, 1987; Webster et al., 1987). However, it is not known to what extent expression of these visual foliar symptoms relates to yield loss under field conditions. Visual

symptoms of barley yellow dwarf, for example, often do not indicate the extent of damage that is ultimately expressed in lower yield (Qualset, 1990).

MATERIALS AND METHODS

F₂ seeds from Moro/PI 294994 and Hyak/PI 294994 crosses were sown at Pendleton, OR, on 8 November 1990. Each cross was grown in two plots of five rows each and one plot was caged with a propylene material. One plot was used for each cross and treatment because the study was originally part of the club wheat breeding program. The number of plants evaluated for Moro/PI 294994 was 146 for the infested population and 146 for the noninfested population. The number of plants evaluated for Hyak/PI 294994 was 147 for the infested population and 128 for the noninfested population.

Plants inside the caged plot were infested at the 5 leaf stage, Zadoks 15, with 60-80 Russian wheat aphids for a group of three plants with the bazooka insect applicator while plants in the other plot were not infested.

Individual F₂ plants within the infested populations were scored at the post heading growth stage, Zadoks 59 to 65, using the one to six damage rating scale as described in chapter 1 and labelled for their reaction to RWA. Plants with scores of 1 to 3 were recorded as resistant and those with scores of 4 to 6 were recorded as susceptible to the RWA.

Individual F_2 plants from infested and noninfested populations were pulled on 6 August 1991 and wrapped in numbered paper bags to avoid loss of seeds and dry matter. Roots were cut in the lab and the above ground dry matter weight for each F_2 plant was determined. Heads were then threshed and the grain yield for each F_2 plant was determined. The harvest index was calculated for each F_2 plant by dividing the grain yield by the dry matter weight and multiplying by 100. Bartlett's test was used to check the homogeneity of variances between infested and noninfested populations of both crosses. The variances were homogeneous for the three traits. The dry matter weight (DM), grain yield (GY), and the harvest index (HI) were statistically compared between infested and noninfested populations. The (DM), (GY), and (HI) were also statistically compared between resistant and susceptible classes within the infested population by using analysis of variance (ANOVA) and graphical representation. LSD was used to separate means of different data.

RESULTS AND DISCUSSION

Effect of RWA Infestation

1 - Dry Matter

RWA infestation reduced DM production in both crosses (Table 5). Dry matter weight in Moro/PI 294994 was 34.69 g and 41.43 g for the infested and noninfested populations, respectively (Fig. 1). The comparison of the mean values between infested and noninfested populations showed the two groups were statistically different (Table 6). Dry matter production for the infested and noninfested populations of Hyak/PI 294994 was 36.81 g and 52.08 g, respectively (Fig. 2). Tables 5 and 6 confirm the differences were statistically significant.

RWA infestation reduced DM production in both crosses, however, the club backgrounds appeared to react differently in DM reduction. Although the control population for Hyak/PI 294994 produced more DM than Moro/PI 294994 (Figures 1 and 2), the infested populations produced similarly. Thus the infested population for Moro/PI 294994 produced 84% of the control DM, whereas Hyak/PI 294994 produced only 71% of the control DM.

2 - Grain Yield

Mean GY from infested and noninfested populations of

Moro/PI 294994 was 11.46 g and 13.52 g respectively (Fig. 1). Mean GY for infested and noninfested populations of Hyak/PI 294994 was 11.57 g and 19.52 g respectively (Fig. 2). Analysis of data indicated significant ($P = 0.048$ and $P < 0.01$ for Moro/PI 294994 and Hyak/PI 294994 respectively) effects on GY due to RWA infestation (Table 5).

Russian wheat aphid infestation reduced GY in both crosses but the two club backgrounds reacted differently in GY reduction. Although the control population for Hyak/PI 294994 produced more GY than Moro/PI 294994 (Figures 1 and 2), the infested populations produced similarly. The infested populations of Moro/PI 294994 and Hyak/PI 294994 produced 85% and 60% of their control respectively.

3 - Harvest Index

Analysis of HI data for both Moro/PI 294994 and Hyak/PI 294994, indicated highly significant ($P < 0.01$) effects due to RWA infestation (Table 5). Mean HI for infested populations of Moro/PI 294994 and Hyak/PI 294994, was 27.04% and 28.77% respectively (Table 6). Mean HI for the noninfested populations was 32.33% and 36.14% for the two crosses respectively (Figures 1 and 2).

Harvest index was significantly reduced due to RWA infestation in both crosses. While the infested populations produced similarly as in the case of the other

two traits, the control population of Hyak/PI 294994 produced slightly higher HI than the control population of Moro/PI 294994 (Figures 1 and 2). The infested populations produced 84% and 80% of the control HI for Moro/PI 294994 and Hyak/PI 294994 respectively.

Dry matter production was reduced by RWA infestation in both crosses. Calhoun et al. (1991) found that RWA significantly reduced the straw yield of barley. Grain yield was also significantly reduced in the two populations. Calhoun et al. (1991) found that grain yield was not significantly reduced by RWA infestation 40 days after planting (DAP) in 1989. The RWA resistance expressed at this early stage carried with it little or no penalty in terms of GY. Grain yield was not a good predictor of RWA resistance in 1989. However, in 1990, they obtained a significant correlation between GY and RWA symptoms at 40 and 70 DAP.

Effect of Genotype and RWA Infestation

1 - Dry Matter

Mean DM for susceptible and resistant genotypes within the infested population of Moro/PI 294994 was 8.83 g, 42.84 g, respectively (Table 7 and Fig. 3). The susceptible and resistant genotypes produced 21% and 103% of the control DM

respectively. Mean DM for Hyak/PI 294994 was 13.99 g, 43.16 g for susceptible and resistant genotypes respectively (Table 7 and Fig. 4). The susceptible and resistant genotypes produced 27% and 83% of the control respectively. Analysis of DM data indicated significant ($P < 0.01$) effects due to RWA infestation and genotype in both crosses (Table 8). Mean DM production of resistant and noninfested populations of Moro\PI 294994 was comparable but it was not comparable in the two populations of Hyak\PI 294994.

2 - Grain Yield

Mean GY in Moro/PI 294994 was 1.27 g, 14.69 g for susceptible and resistant genotypes respectively (Table 7 and Fig. 3), susceptible and resistant genotypes produced 9% and 108% of the control GY respectively. In Hyak\PI 294994, mean GY was 3.53 g, 13.81 g for the susceptible and resistant genotypes respectively (Table 7 and Fig. 4). Susceptible and resistant genotypes produced 18% and 71% of the control respectively. Significant ($P < 0.01$) effects on GY due to RWA infestation and genotype were found in a similar fashion as DM in both crosses (Table 8).

3 - Harvest Index

Analysis of HI data indicated highly significant ($P < 0.01$) effects due to RWA infestation and genotype in both

crosses (Table 8). The mean HI for Moro/PI 294994 was 8.08% for the susceptible class and 33.03% for the resistant class (Table 7 and Fig. 3). The susceptible and resistant genotypes produced 25% and 102% of the control HI respectively. The mean HI for Hyak/PI 294994 was 19.27% for the susceptible class and 31.41% for the resistant class (Table 7 and Fig. 4). The susceptible and resistant genotypes produced 53% and 87% of the control HI, respectively.

The two club backgrounds appeared to react differently with respect to the difference between the resistant genotypes and the noninfested populations. Although the resistant and noninfested populations of Moro/PI 294994 were comparable in their DM production, GY, and HI, the three traits were not comparable between resistant and noninfested populations of Hyak/PI 294994. Natural infestation of the noninfested population of Moro/PI 294994 may have contributed to a reduction in the three traits. Genetic background in 'Hyak' and 'Moro' also appeared to play a role in the differing resistant reactions.

The infested and noninfested populations of the two crosses included in this study differed significantly in their dry matter production, grain yield, and harvest index when exposed to artificial infestation with 60-80 RWA at the 5 leaf stage. Resistant genotypes and the noninfested

F2 populations in Moro/PI 294994 reacted differently from those of Hyak/PI 294994 for the three traits. Gray et al. (1990) reported that RWA infestation at the tiller and boot stages of plant development significantly reduced the weight of heads per plant, the number of seeds produced per plant, and the seed weight per plant in spring wheat. The traits were not significantly reduced when RWA was introduced at the seedling stage. The aphids were allowed to feed for two weeks in both growth stages. The plants were then fumigated and allowed to mature for harvest. They concluded that plants in later stages of development are most susceptible to yield reductions caused by RWA infestation.

In the genetic study conducted, it was found that both seedling and adult plant resistance in PI 294994 were controlled by two genes with a dominant and recessive mode of inheritance. The effectiveness of the resistance appeared to differ when crossed into the 'Hyak' and 'Moro' backgrounds. The incorporation of these resistance genes in superior commercial wheat cultivars will help reduce yield losses due to the feeding of Russian wheat aphid on wheat.

Table 5. Observed mean squares and coefficient of variation of three traits for RWA infested and noninfested F₂ populations of Moro/PI 294994 and Hyak/PI 294994 grown at Pendleton 1990-1991.

Source of Variations	d.f	Dry Matter - g -	Grain Yield - g -	Harvest Index - % -
<u>MORO/PI294994</u>				
Total	291	-	-	-
Between groups	1	3317.29 ¹ *	308.22 *	0.20 **
Within groups	290	588.73	78.20	0.01
C.V. (%)	-	63.75 ²	70.80	33.68
<u>HYAK/PI294994</u>				
Total	274	-	-	-
Between groups	1	15944.08 **	4316.01 **	0.37 **
Within groups	273	991.48	144.51	0.008
C.V. (%)	-	71.69	78.72	27.78

1 * , ** Significant at the 0.05 and 0.01 probability levels, respectively

2 based on plants within plot variability.

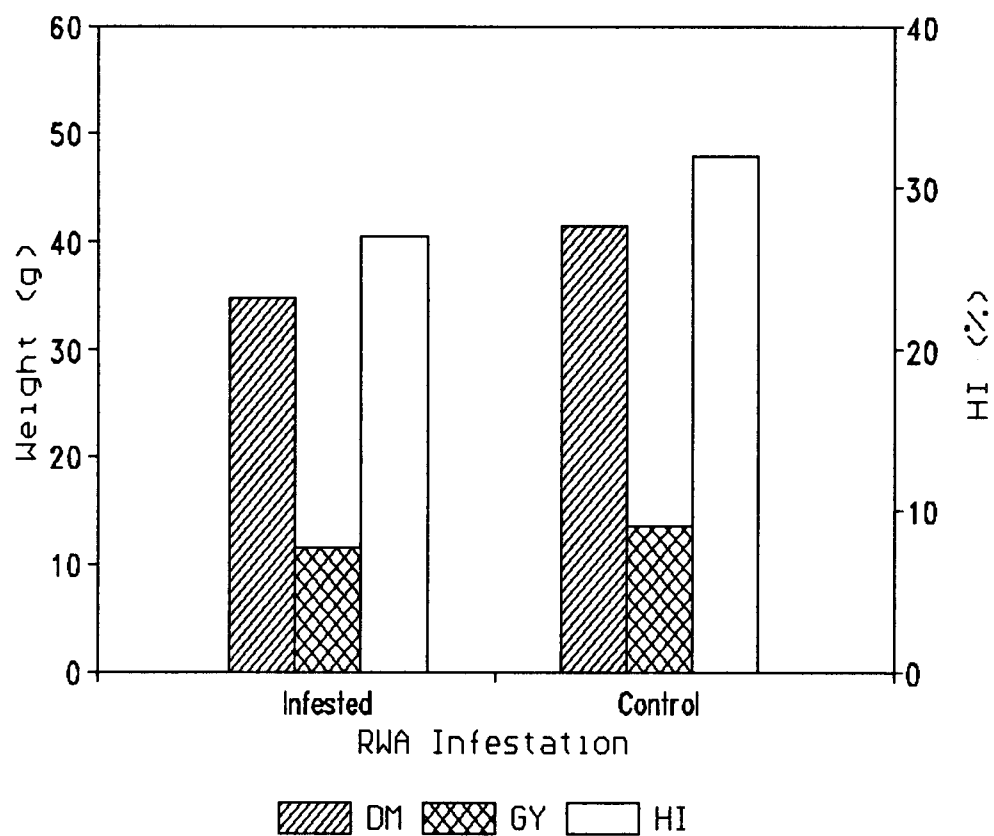


Figure 1. Effect of RWA on the DM, GY, and HI of Moro/PI 294994

Table 6. Comparison of the mean values of three traits for RWA infested and noninfested F₂ populations of Moro/PI 294994 and Hyak/PI 2949942 grown at Pendleton, 1990-1991.

Cross	Dry Matter - g -	Grain Yield - g -	Harvest Index - % -
<u>MORO / PI 294994</u>			
Infested	34.69 ¹ a	11.46 c	27.04 ² e
Noninfested	41.43 b	13.52 d	32.33 f
LSD (0.05)	5.59	2.05	2.00
<u>HYAK / PI 294994</u>			
Infested	36.81 g	11.57 i	28.77 k
Noninfested	52.08 h	19.52 j	36.14 l
LSD (0.05)	7.51	2.86	2.00

- ¹ Rows with the same letter within each column are not significantly different based on Fisher's protected least significant difference (LSD) at the 0.05 probability level.
- ² Calculated on an individual plant basis.

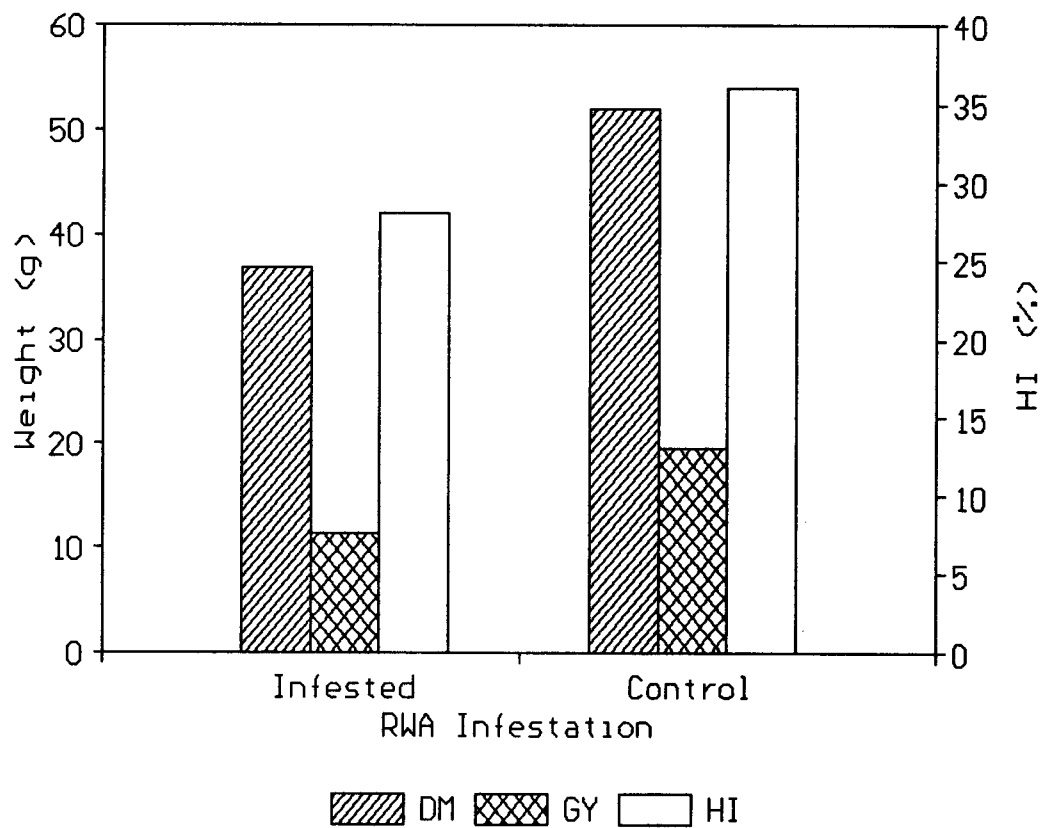


Figure 2. Effect of RWA on the DM, GY, and HI of Hyak/PI 294994

Table 7. Comparison of the mean values of three traits for resistant and susceptible genotypes within infested F₂ populations of Moro/PI 294994 and Hyak/PI 294994 grown at Pendleton, 1990-1991.

Cross	Dry Matter - g -	Grain Yield - g -	Harvest Index - (%) -
<u>MORO/PI 294994</u>			
Susceptible	8.83 ¹ a	01.27 c	08.08 ² e
Resistant	42.84 b	14.69 d	33.03 f
LSD (0.01)	(8.65)	(3.49)	(4.51)
<u>HYAK/PI 294994</u>			
Susceptible	13.99 g	03.53 j	19.27 m
Resistant	43.16 h	13.81 k	31.41 n
LSD (0.01)	(13.36)	(4.63)	(4.92)

- ¹ Rows with the same letter within each column are not significantly different based on Fisher's protected least significant difference (LSD) at the 0.01 probability level.
- ² Calculated on an individual plant basis.

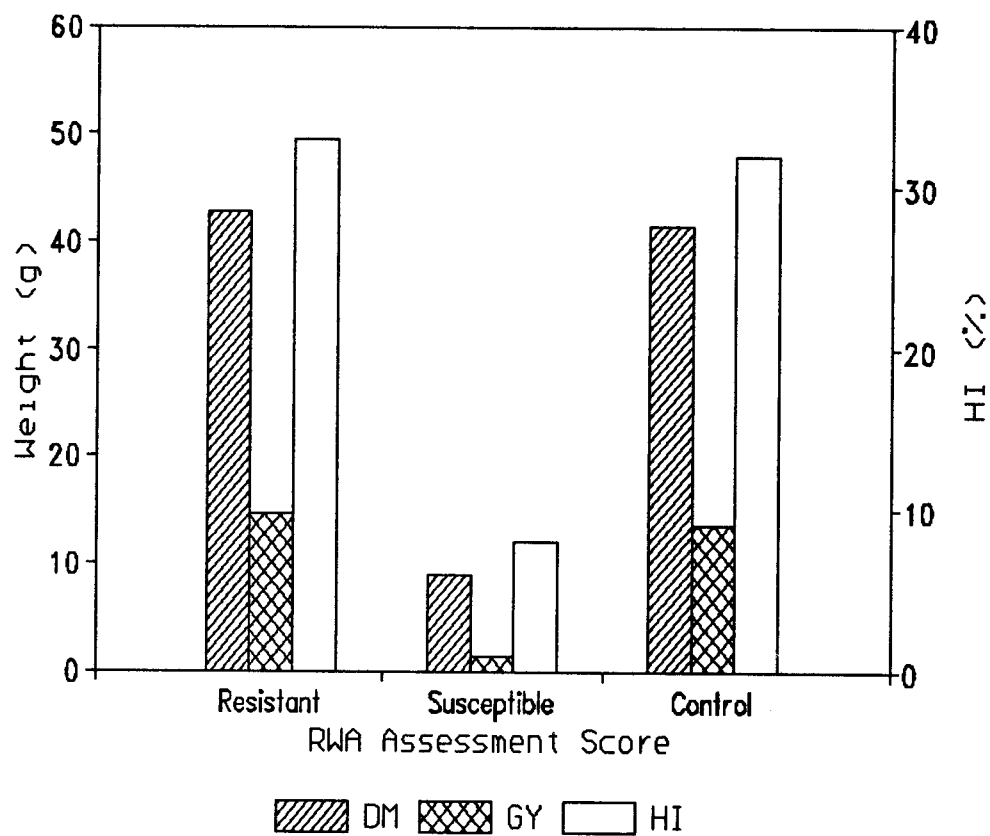


Figure 3. Effect of RWA on the DM, GY, and HI of Moro/PI 294994

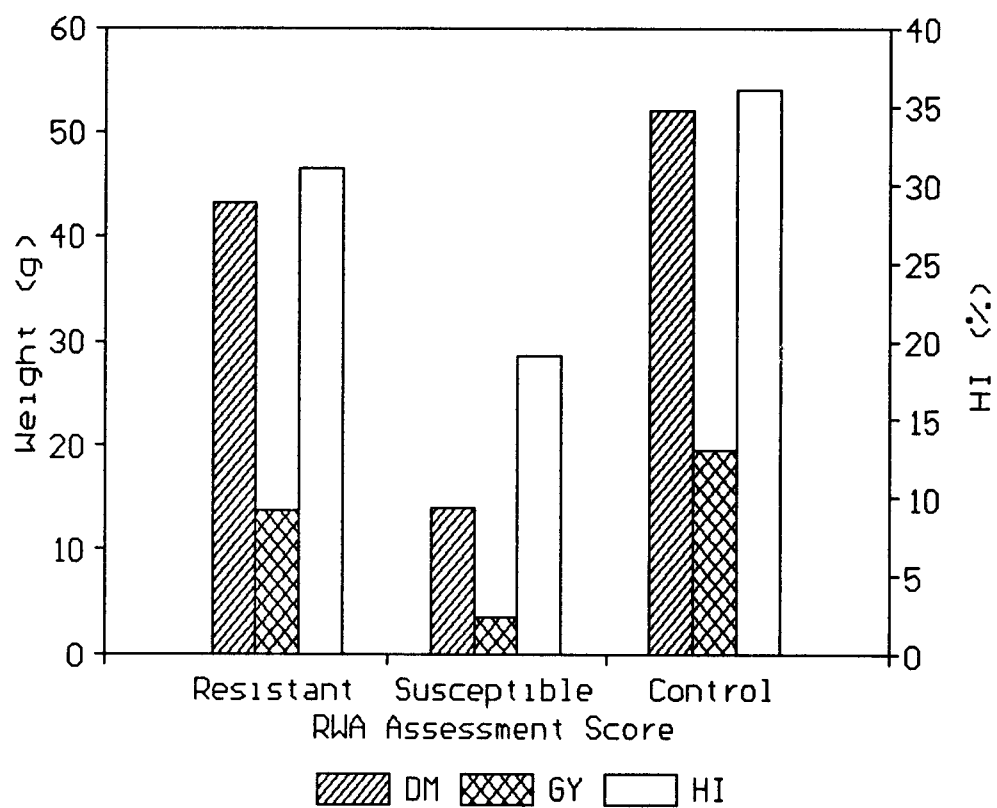


Figure 4. Effect of RWA on the DM, GY, and HI of Hyak/PI 294994

Table 8. Observed mean squares and coefficient of variation of three traits for resistant and susceptible genotypes within infested F₂ populations of Moro/PI 294994 and Hyak/PI 294994 grown at Pendleton 1990-1991.

Source of Variations	d.f	Dry Matter - g -	Grain Yield - g -	Harvest Index - % -
<u>MORO/PI294994</u>				
Total	145	-	-	-
Between groups	1	30775.54 ¹ **	4748.05 **	1.66 **
Within groups	144	294.63	47.95	0.008
C.V. (%)	-	49.47 ²	60.73	34.40

¹ ** Significant at the 0.01 probability level

² based on plants within plot variability

Table 8. (Continued) observed mean squares and coefficient of variation of three traits for resistant and susceptible genotypes within infested F₂ populations of Moro/PI - 294994 and Hyak/PI 294994 grown at Pendleton 1990-1991.

Source of Variations	d.f	Dry Matter - g -	Grain Yield - g -	Harvest Index - % -
<u>HYAK/PI 294994</u>				
Total	146	-	-	-
Between groups	1	21305.33 **	2643.97 **	0.37 **
Within groups	145	663.59	79.78	0.009
C.V. (%)	-	69.81	77.00	33.88

¹ ** Significant at the 0.01 probability level
² based on plants within plot variability

SUMMARY AND CONCLUSIONS

The objectives of this study were : 1) to determine the effect of RWA infestation on the dry matter, grain yield, and harvest index, and 2) to determine the effect of RWA infestation and genotype on the same three traits.

To obtain such information, the three traits were compared between infested and noninfested F_2 populations of Moro/PI 294994 and Hyak/PI 294994 using ANOVA and LSD. The infested population in the two crosses was divided into RWA resistant and RWA susceptible classes and these were compared with the noninfested population for the same three traits using the same statistical procedures.

Based on the results of this study, the following conclusions were drawn.

1. RWA infestation has a highly significant effect on the dry matter, grain yield, and harvest index in both crosses.

2. Resistant and susceptible genotypes produced significantly different dry matter, grain yield, and harvest index due to RWA infestation in both crosses.

3. Resistant genotypes and the noninfested population of Moro/PI 294994 produced similar dry matter, grain yield, and harvest index, however, the noninfested population outyielded the resistant genotypes in Hyak/PI 294994.

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APPENDIX

APPENDIX TABLE 1

Selected weather data collected at Columbia Basin Agric. Research Center, Pendleton, Oregon for the crop year 1990-1991.

Month	Air Temp. (F)		Soil Temp. (F)		Precipitation (cm)	Evaporation (cm)
	Max.	Min.	(4 in.) Max.	Min.		
November	55	35	43	34	1.73	- ¹
December	35	15	31	27	1.18	-
January	40	23	31	28	1.15	-
February	55	34	46	37	0.86	-
March	53	31	49	35	1.71	3.45
April	62	36	61	43	1.01	5.13
May	66	42	67	48	4.73	5.49
June	73	46	77	55	2.22	7.70
July	89	51	91	65	0.15	12.09
August	91	53	91	67	0.24	11.88

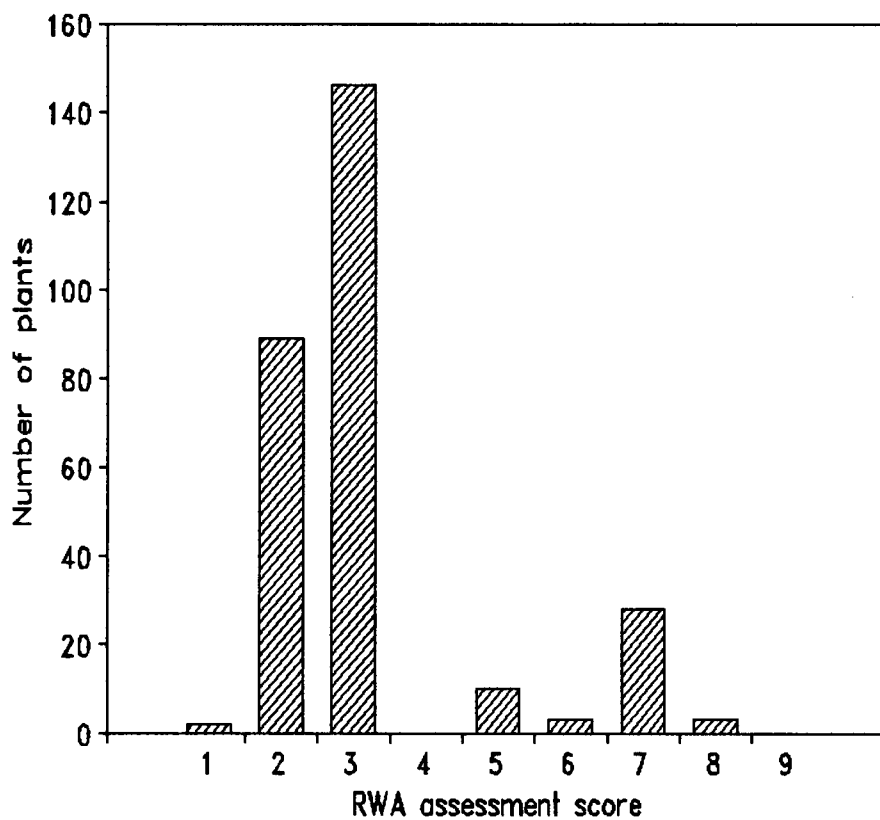
¹ - denotes missing data

APPENDIX TABLE 2

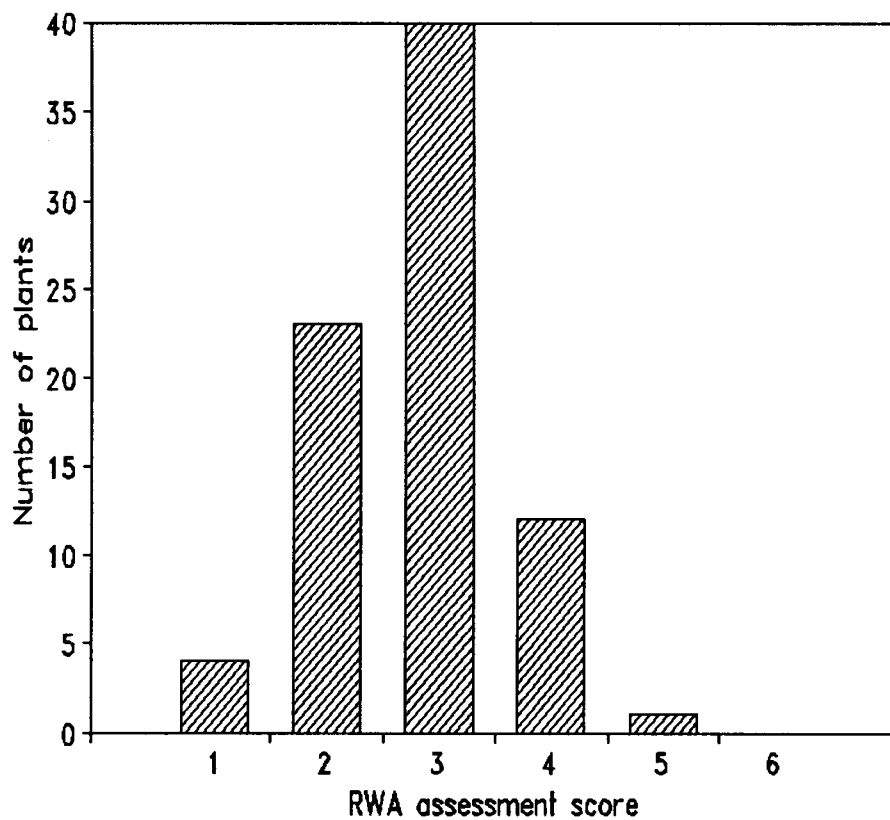
Parentage and some characteristics of the RWA susceptible club wheat cultivars 'Moro' and 'Hyak' and the RWA resistant wheat line PI 294994.

Cultivar or Line	Moro	Hyak	PI 294994
Parentage	PI 178383/2* Omar, 1721	VPM1/Moisson 421//2*Tyee	Strelinskaja mestnaja
First crop	1965	1984	- *
Origin	Oregon	Washington	Hungary
Class	Club	Club	Hard winter
Height (in.)	48	36	49
Test weight (lb/bu)	60	60	59
Seed color	White	White	Red
Glume color	Bronze	White	White

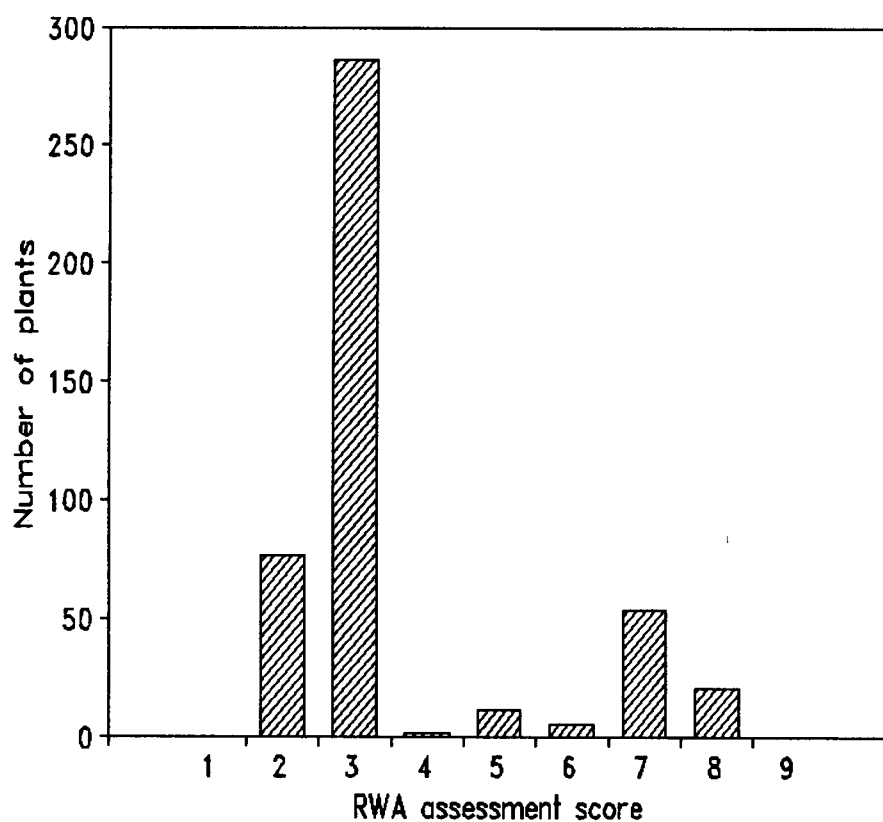
* denotes missing data
 Oat check = Appaloosa
 Barley check = Gus



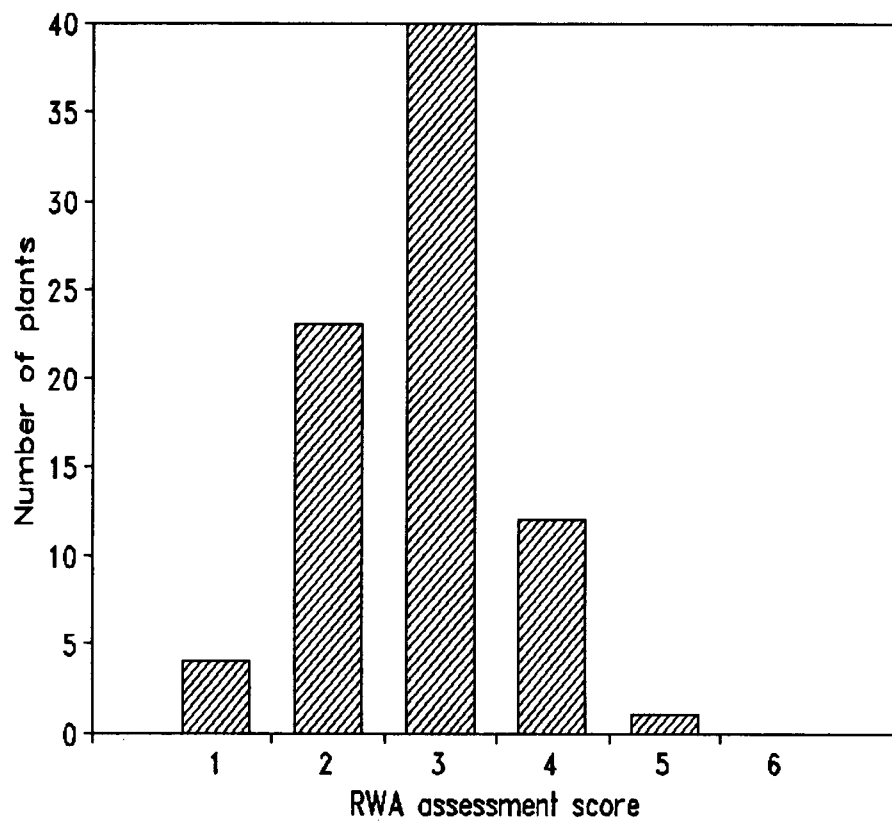
Appendix fig. 1. Frequency distribution of RWA assessment scores on one to nine scale of Moro/PI 294994



Appendix fig. 2. Frequency distribution of RWA assessment scores on one to six scale of Moro/PI 294994



Appendix fig. 3. Frequency distribution of RWA assessment scores on one to nine scale of Hyak/PI 294994



Appendix fig. 4. Frequency distribution of RWA assessment scores on one to six scale of Hyak/PI 294994