STUDIES OF GREENBUG (HOMOPTERA: APHIDIDAE) RESISTANCE IN RYE

By

RODOLFO OSCAR CURVETTO

Ingeniero Agronomo

Universidad Nacional del Sur

Bahia Blanca, Argentina

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STUDIES OF GREENBUG (HOMOPTERA: APHIDIDAE) RESISTANCE IN RYE

Thesis Approved:

James A. Webster
Thesis Adviser

W Scott Fargo

Alexander B. Filonow

Norman N. Durham
Dean of the Graduate College

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CHAPTER I

INTRODUCTION

The greenbug, Schizaphis graminum (Rondani) (Homoptera: Aphididae), is a major pest of small grains and sorghum in the Great Plains region of the United States and areas of the world where small grains are grown. It has been a major pest of U.S. wheat and other small grains since 1890. In 1976, the Oklahoma Agricultural Extension Service estimated that damage and control of the greenbug and army cutworm cost wheat producers about $ 80 million and 55% percent of that loss was due to greenbugs (D.C. Arnold, unpublished). Dahms et al. (1954) estimated that in outbreak years losses exceed 50 million bushels of small grains. The greenbug transmits the viruses that cause barley yellow dwarf and maize dwarf mosaic. A relatively small number of greenbugs can cause more damage than a much larger number of other species of aphids (Starks & Burton 1977).

Plant resistance to insects is considered one of the most important components in an integrated pest management system. Some level of greenbug resistance may prevent or delay the occurrence of economic damage, reducing the pesticide load in the agroecosystem (Van Emden & Wearing 1965).

Many examples of resistance involve of antibiosis (Painter 1951) where the host plant adversely affects the development and reproduction of the aphid. Non-preference or antixenosis (Kogan & Ortman 1978) occurs when aphids quickly reject the host as a food source. Antixenosis is an important type of plant resistance and is well suited to investigation using the electronic feeding monitor technique (Tarn & Adams 1982). The third resistance mechanism is tolerance on which the plant shows the ability to grow in spite of supporting a population that can damaging a susceptible host. These three mechanisms may interact with each other but may also operate independently (Painter 1951). Biotypes that overcome greenbug resistance in wheat have been a serious problem in wheat breeding programs and new sources of greenbug resistance are continually being sought.

Recently, Tyler et al. (1988) identified rye genotypes resistant to biotypes B, C, E, and F. They did not study the components of resistance, but reported that resistance to biotypes B and/or E in P.I. 240675 is correlated with resistance to biotypes C and F. The purpose of this research was to select biotype F resistant seedlings of P.I. 240675 and to compare the components of resistance and feeding behavior of biotype F on PI 240675 with those of 'Insave F.A.' rye and 'Century' wheat. An additional purpose was to evaluate PI 240675 for damage that may be caused by any new biotypes discovered during the study.

CHAPTER II

LITERATURE REVIEW

Biotypes of Greenbugs and Sources of Resistance in Wheat

Atkins & Dahms (1945) observed field tolerance to severe greenbug infestations in a number a wheat varieties in Denton, Texas and Lawton, Oklahoma in 1942. Dahms et al. (1955) found that 'Dickinson Selection 28 A' (DS 28 A, CI 13833) which is a hexaploid selected from a durum wheat line 'Dickinson 485' (CI 3707), was resistant to the "original" greenbug (biotype A). Daniels & Porter (1958) found that the resistance was controlled by a single recessive gene with a modifier gene. Resistance to the greenbug found in 'Dickinson 28 A' appeared to provide a permanent alternative method of control but in 1958 a new biotype designated as B, overcame the Dickinson single recessive gene for resistance and this biotype became dominant in the field (Wood 1961, Starks & Merkle 1977). Biotype C was discovered during the summer of 1968 in a widespread attack on sorghum. Since this time it has largely replaced B on small grain in much of the Great Plains. Biotype C was able to reproduce better at constant extreme temperatures than A and B (Wood & Starks 1972).

Biotype C then, is capable of attacking small grain during the winter and sorghum in the summer.

Biotype D gives the same reaction on plants as biotype C but is organophosphate-resistant (Peters et al. 1975). It was first reported on sorghum in west Texas in the summer of 1974. In 1975, it was reported in Texas, Oklahoma, Kansas, Nebraska and South Dakota (Starks & Burton 1977).

In 1974, Wood et al. reported resistance to biotype C in an octoploid triticale 'Gaucho' developed from a cross between 'Chinese Spring' wheat, Triticum aestivum L. and 'Insave FA' rye, Secale cereale L. (resistant). This resistance was transferred to wheat using an X-ray technique resulting in 'Amigo' (C.I. 17609) wheat (Sebesta & Wood 1978). 'Amigo' was resistant to all known biotypes (A, B & C).

However, Porter et al. (1982) detected a new biotype designated as E that overcame the 'Amigo' resistance. This biotype was first identified from a collection made from biotype C resistant 'Amigo' wheat near Amarillo, TX in December 1979. Biotype E was first identified in Kansas and Nebraska by T.L. Harvey from a collection in sorghum in August 1980. 'Amigo' was found to be susceptible to biotype F by Kindler & Spomer (1986).

Thus, two sources of greenbug resistance in wheat germplasm, 'DS 28A' and 'Amigo', were documented prior to 1980. Since this date, three additional sources of resistance have been identified and numerical designations

have been assigned to the five distinct sources of resistance as follows: Gb1 ('Dickinson Sel 28 A'), Gb2 ('Amigo'), Gb3 ('Largo'), Gb4 (C.I. 17959) and Gb5 (C.I. 17882) (Tyler et al. 1987).

'Amigo' has a single dominant gene located on chromosome 1A derived from 'Insave F.A.' rye which provides resistance to biotypes A, B, C but not to E (Hollenhorst & Joppa 1983). Resistance to biotype C and E derived from Triticum tauschii (Coss.) ('Largo' (C.I 17895)), and C.I. 17959 amphiploidies of T. turgidum/tauschii have been identified. Later, 'Largo' was found to be susceptible to biotype B by Webster et al. (1986) and to biotype F by Puterka & Peters (1988). The resistance of 'Largo' to greenbug biotypes C and E is inherited as a single dominant gene located on the 7D chromosome (Joppa et al. 1980). In CI 17882 resistance is inherited as a single dominant gene (Tyler et al. 1987).

Rye provides greenbug resistance to many biotypes. Livers & Harvey (1969) evaluated twenty cultivars to biotype B greenbug and found that 17 had at least one resistant plant. The 17 entries ranged between 1 to 48 % resistant plants. Arriaga (1954) developed the Argentine resistant rye 'Insave F. A.' which, as mentioned previously, is the source of greenbug resistance in 'Amigo'. Arriaga & Re (1963) reported that the greenbug resistance in 'Insave F.A.' is controlled by a single dominant gene. 'Insave F.A.' is resistant to biotypes B, C & E. It was found resistant to biotype F by Kindler & Spomer (1986) but found

susceptible to the same biotype by Tyler et al. (1988).

Lukaszewsky & Gustafson (1983) pointed out that large numbers of wheat/rye translocations could be derived from triticale (x Triticosecale Wittmack) x wheat crosses without use of irradiation. Several generations of four triticale x wheat populations were analyzed plant by plant using the C-banding technique. They found that out of 785 karyotyped plants cytologically analyzed plant by plant, 195 were wheat/rye and 64 were rye/rye translocated chromosomes and 15 were rye chromosomes that were modified by deletion. Most of the translocations involved complete chromosome arms. Out of 39 identified wheat/rye translocations, 10 ocurred in homoeologous and 29 in non-homoeologous chromosomes. They stated that wheat/rye translocations "can be produced in sufficient numbers to allow the use of this method for the introduction of alien variation into wheat research programs". Wild and cultivated relatives of wheat like rye provide vast germplasm pools to improve desirable characteristics and resistance to pests, diseases and adverse environmental conditions in wheat breeding and cytogenetic research programs.

Webster & Inayatullah (1984) evaluated 264 new introductions of triticale. Seven lines with rye parents from CIMMYT Program were found to be highly resistant to biotype E.

Tyler et al. (1988) testing eleven rye accessions of diverse origin found that P.I. 240675 rye segregated for

resistance to biotypes B, C, E and F greenbugs. P.I. 240675 had 3 F greenbug resistant plants out of 41. This rye originated in Uruguay ('Centeno de La Estanzuela'). This resistance may be also transferred to wheat, rye and triticale as outlined by Lukaszewsky & Gustafson (1983).

Resistance Components

After resistance is detected, it is important to learn about the components of resistance and to compare the feeding behavior of greenbugs on resistant and susceptible plants.

Many workers have described and studied resistance components, including Dahms et al. (1955), Starks et al. (1972), Teetes et al. (1974), Starks & Merkle (1977), Starks & Weibel (1981), Webster & Starks (1984) and Webster & Inayatullah (1984). Painter (1951) proposed that plant resistance could be explained by three fundamental mechanisms: nonpreference, antibiosis and tolerance. Painter (1951) and other workers explained that these mechanisms are most frequently interrelated although they may also operate independently. Painter (1941) stated that preference or nonpreference "denotes the group of plant characters and insect responses that led to or away from the use of a particular plant or variety, for oviposition, for food, or for shelter, or for combinations of the three". Because non-preference is not a property of the plant but it is a response of an insect, Kogan & Ortman (1978), proposed

the term antixenosis which means "to keep the guest away". The term antibiosis was proposed by Painter (1941) as "those adverse effects on the insect life history which result when the insect uses a resistant host-plant variety for food". Antibiosis clearly defines those plant properties that adversely affect the metabolism of an animal feeding on a plant and it is further defined as "the allelopathic relationships that encompass all adverse physiological effects of a temporary or a permanent nature resulting from the ingestion of a plant by an insect" (Kogan & Ortman 1978).

The tolerance mechanism is more or less independent of the effect on the insect. It was defined as a "basis of resistance on which the plant shows an ability to grow and reproduce itself or to repair injury to a marked degree in spite of supporting a population approximately equal to that damaging a susceptible host" (Painter 1951). Thus, tolerance is an adaptative mechanism for survival of a plant against the herbivore response and is independent of the herbivore response (Kogan & Ortman 1978).

The percent chlorophyll loss have been used as a variable to measuring tolerance. Greenbug damaged and non-damaged plants can be compared by measuring the percent chlorophyll loss in infested plants. Different techniques described by MacKinney (1941), Arnon (1949) and modifications of bothhave been used. The absorption of light by a chlorophyll solution can be measured as

absorbance with an ELISA reader, as there is a high correlation between absorbance readings and pigment content (El-Nashaar 1988, personal communication).

These resistance mechanisms, or components of resistance have been studied individually, but there had not been a model to quantify the overall resistance in a host plant until the Host Plant Resistance Index (HPRI) was reported by Ullah (1985) and Webster et al. (1985). The HPRI integrates the values of all three of the resistance components into a single value or index and is easier to understand than the independent interpretation of each resistant component. Plant breeders and entomologists can make final germplasm selections on the basis of the HPRI.

Electronic Feeding Monitor in Aphids

McLean & Kinsey (1964) developed a technique for recording aphid feeding and salivation. They noted that when an appropriate current was applied to an aphid when the stylet was filled with saliva or liquid substrate, an electric circuit was completed. Variations in the strength of the current could be monitored on an oscilloscope. Production of a stylet sheath was found to be related to change in voltage and these data were recorded on a chart. Aphid feeding behaviors have different wave patterns which can be recorded, interpreted and analyzed. Alteration in durations or in the order of these patterns help indicated where and for how long the aphid is feeding on susceptible

or resistant cultivars.

Wave forms are associated with the aphid's stylet-tip location in the plant. When a waveform sequence S-X-I (S= salivation, X= phloem penetration and I= phloem ingestion) is recorded, the stylet-tips are invariably located in the phloem tissue. Whenever waveform sequences of S-I, S-X-S, I or any sequence when an X wave does not immediately precede the I wave, stylet tips are usually located either in the mesophyl parenchyma or vascular sheath cells, but never in epidermal cells. With greenbugs feeding on sorghum, probing either resistant or susceptible plants usually produces one X wave and rarely 2 or 3 prior to phloem ingestion. The most pronounced difference in the feeding behavior of greenbugs on susceptible and resistant sorghum plants is in the duration of phloem ingestion. Mean duration of salivation is shorter for aphids feeding on susceptible plants than on resistant plants (Campbell et al. 1982).

Niassy (1986) studying susceptible and resistant wheat for both biotypes B and E, found that the duration of phloem ingestion was longer on the susceptible compared to resistant genotypes. Also, the same author found that biotype E, during the first four hours of monitoring, showed slightly more salivation time, and extensively more phloem ingestion on 'TAM 105' than on 'Largo' x 'TAM 105'. 'Largo' is resistant to biotype E.

Biotype B in the first four hours showed slightly more salivation duration, but shorter phloem ingestion on 'TAM

105' compared to 'TAM 107' or 'LARGO' X 'TAM 105' (Niassy 1986). 'TAM 107' has the 'Amigo' gene and is therefore resistant to biotype B, but Largo is susceptible to biotype B.

In plant resistance to aphids, the major difference as detected by feeding monitors between resistant and susceptible lines of the same crop plant is the length of probing time by the aphid in reaching the phloem. The electronic monitoring technique used to measure aphid probing shows that initially, the length of probing time required to reach the phloem is at least twice as long on resistant entries as on related suceptible lines (Dreyer & Campbell 1987). Also the amount of time that aphids spend ingesting from the phloem is much shorter on resistant lines where difficulty in locating the phloem is encountered during probing (Campbell et al. 1982).

CHAPTER III

MATERIALS AND METHODS

A biotype F culture was provided by Dr. S.D. Kindler, USDA-ARS, from a culture in Lincoln, NE. The biotype F culture was maintained on 'Wintermalt' barley in growth chambers and in a greenhouse at Stillwater, OK since January 1986. Techniques used for culturing greenbugs and evaluating plants for resistance were similar to those described by Starks & Burton (1977).

The resistance components of P.I. 240675 and 'Insave F.A.' rye and 'Century' wheat to biotype F greenbug were examined in this study in independent tests of antibiosis, antixenosis and tolerance. Each of these tests measures a different parameter associated with resistance.

Selection of P.I. 240675 Resistant Plants

Unlike other small grains, rye is cross pollinated. Thus, many of the rye accessions are heterozygous for a given trait unless they have been subjected to controlled pollination for several generations. This is the case with P.I. 240675 from the ARS National Small Grain Collection.

Tyler et al. (1988) reported that only a portion of the plants from this accession were resistant to biotype F

greenbug. Therefore, biotype F resistant plants had to be isolated from a large number of P.I. 240675 seedlings before initiating the antibiosis test. To obtain a sufficient number of resistant seedlings for this test, over 90 seeds of P.I. 240675 were planted in rows in a greenhouse flat (36 x 54 x 18 cm) containing standard soil. After 5-7 days seedlings (less than 5 cm high) were infested in the one leaf stage with 20 biotype F greenbugs per plant. The flat was isolated, caged and placed in a growth chamber at 21 ^{o}C and 14:10 (L:D) hours photoperiod. Seedlings of P.I. 240675 were examined daily for signs of resistance. Approximately three weeks were required to identify the resistant plants. Resistant plants retained the normal green color and showed little feeding damage while susceptible plants were either dying or chlorotic and stunted. The biotype F resistant plants were then transplanted individually to 7.6 cm-diameter pots. Similarly, seeds of 'Century' and 'Insave F.A.' were also planted in flats, caged, and placed in the growth chamber, but they were not infested with aphids since they are susceptible. Individual seedlings of 'Century' and `Insave F.A.' were transplanted from the flats to 7.6 cm-diameter pots at the same time the biotype F resistant P.I. 240675 seedlings were transplanted.

Antibiosis Test

The reproductive capacity of the biotype F greenbugs was used to measure antibiosis of the three cultivars.

The test was performed with 14 replications in each treatment. Individual plants were infested by placing three adult laboratory-reared greenbugs on each plant with a fine moistened brush. Each plant was covered with a 6 cm diameter by 30 cm high plastic cage with cloth-covered ventilation holes. When at least one of the adults began to reproduce they were removed, leaving three nymphs on each plant. These nymphs were allowed to mature and when one of these began reproducing all but one were removed. The total number of progeny produced by one female on an individual plant was determined by removing, counting and recording newborn nymphs every other day until the female stopped reproduction.

The test was conducted in a growth chamber at a constant temperature of 22 °C and 14:10 (L:D) hours photoperiod. Plants were clipped periodically to facilitate handling and watered as needed.

A completely randomized design was used. An analysis of variance (PROC ANOVA, SAS Institute, 1985) of the data was performed and the mean number of total progeny produced in each treatment were separated using Duncan's (1955) multiple range test at $P = 0.05$.

Tolerance Test

This test measured the effect of greenbug feeding on seedlings of the three test entries. Tolerance was evaluated in three different ways. First, infested plants were visually rated for damage by using a scale of 0= no damage to 9= plant death. Second, the height of the two sets of plants (infested and uninfested) was measured and compared at the beginning and end of the test. The third method involved determining the chlorophyll loss of infested plants.

Damage Ratings and Reduction in Plant Growth

Ninety seeds of P.I. 240675 and 30 seeds each of 'Insave F.A.' and 'Century' were planted in individual 7.6 cm pots. Seedlings were heavily infested at the one leaf stage (within 48 h after germination and 5-7 cm high) with 15 greenbug adult aphids per plant. Another set of 20 plants at the same age for each entry was left without aphids as an uninfested check. Before infestation, the plant height from the soil surface to the tip of the longest leaf was measured on all seedlings (infested and uninfested). Resistant plants of P.I. 240675 were selected during the test. Plants of P.I. 240675 which proved to be susceptible were removed. After infestation the same initial number of aphids (15 per plant) were maintained daily until 'Century' showed clear signs of damage (complete chlorosis and dead plants). Every 24 hours newborn nymphs were

counted, removed and recorded. Also, the number of missing adults and a visual damage score were recorded daily for each plant. Pots, cages, methods of infestation and growth chamber conditions were the same as those described in the antibiosis test. Pots were randomized daily and there was one plant per replication and 12 replications in a completely randomized design. Growth (final plant height - initial plant height) of infested and uninfested plants of the same entry was determined and mean growth was calculated. The damage score, number of adults added, and number of nymphs removed daily were analyzed. Analysis of variance was performed and Duncan's multiple range test (P= 0.05) was used to separate treatment means.

Chlorophyll Extraction and Measurement.

The same experimental plants used in the previous test were used to measure absorbance which is an indirect measure of chlorophyll content. The chlorophyll extraction method and the absorbance reading procedure was devised by Dr. El-Nashaar (1988, personal communication). Immediately after the data from the previous test were recorded the two basal leaves of individual plants were removed and stored in a refrigerator at 6 °C until chlorophyll extraction was conducted. Leaves were weighed using a balance Mettler (G A 24) before chlorophyll content extraction. Samples from every experimental unit were placed in (1 cm dia. x 7.5 cm) vials containing 95% ethanol. Leaves were

ground with an electric grinder (Tekmar Tissumizer) for 3 minutes. Later, the solution was filtered through Whatman # 1 filter paper. Before reading, the solutions were compensated for evaporation to the same volume (10 ml) with 95% ethanol. Samples of each entry then were placed with a micropipette in three adjoining wells of a rectangular microplate containing 96 (12 x 8) wells. Absorbance was measured with a micro ELISA reader (Microplate reader. Biotech Instruments EL 308) utilizing filter # 490. The three absorbance readings from each sample were averaged and standardized to 1 milligram leaf weight. Data were expressed as percent loss (PL) in total chlorophyll using the formula:

$$PL = \frac{C - D}{C} \times 100$$

where C= Total chlorophyll content/per milligram in normal leaves.

D= Total chlorophyll content/per milligram in infested leaves.

Data were analyzed with analysis of variance and means were separated using Duncan's multiple range test at P = 0.05.

Antixenosis Test

The 1987 antixenosis test was conducted in a plant growth chamber at 22 °C and 14:10 (L:D) hr photoperiod. The three entries were randomized and planted (2 seeds for each cultivar) in a circular pattern ca 3 cm from the edge of a 12 cm-diameter pot with 10 replications (pots). When the seedlings were between 7 and 9 cm tall they where thinned to one for each entry. Then 10 adult greenbugs per plant were released in the center of each pot. Greenbugs were allowed to select plants and the numbers of aphids on each plant were recorded after 24 and 48 h.

In 1988, a second antixenosis test was performed in the same conditions but using P.I. 240675 resistant plants which came from the antibiosis test. Pots of the same age (3 months) of the three entries were placed in flats (36x54x18 cm) and covered with soil and randomized in a circular pattern with 14 replications.

Data were analyzed as a randomized complete block design and Duncan's multiple range test (P= 0.05) to separate treatment means was used.

Electronic Monitoring of Greenbug Feeding

Aphid feeding monitors modified by Brown and Holbrock (1976) and built by Kendow Technologies, Perry, Oklahoma were used in this study.

Individual plants of P.I. 240675 rye, 'Insave F.A'. rye and 'Century' wheat were monitored in a completely randomized design with 10 replicates. In each treatment the dorsum of a selected young adult greenbug was attached to a 10 micron x 5 cm gold wire with colloidal silver cement and placed on the terminal leaf of the plant. When an aphid feeds an electric circuit is completed and the current moves through the plant-aphid system. The signal is amplified and recorded as voltage fluctuations on a strip chart recorder. The following wave forms were recorded from different phases of feeding:

1: Baseline: when the aphid is not feeding.

2: Probe: insertion of the stylet into the leaf.

3: Salivation: formation and injection of sheath material.

4: Non-phloem ingestion: an ingestion wave different from phloem ingestion.

5: X-wave: penetration of the sieve element in the phloem.

6: Phloem ingestion: ingestion from the phloem sieve tube.

Total duration and frequency of feeding over a 6 h period, total probes, number, percentage of phloem ingestion and time of first phloem contact were conducted in a completely randomized design experiment and the variance in differents feeding events was analyzed.

Host Plant Resitance Index

After values for the three resistance components had been obtained, antibiosis, tolerance, and antixenosis indices were determined for P.I. 240675, 'Insave F.A.' and 'Century'. Because the components were measured in different scales; ie, nymphs per plant, plant damage ratings, and aphids per plant, respectively, the data for each component were first normalized to a common scale because they were measured in different scales. This was done by dividing each value of an individual resistance component by the highest value that occurred for that resistance component. The resulting values were designated as component indices. The HPRI was then calculated for each entry using the following equation: 1/(XYZ), were X = the antibiosis index, Y = the antixenosis index, and Z = the tolerance index (Ullah 1985 & Webster et al. 1985).

Reaction to Other Biotypes

While the biotype F studies were in progress biotypes G and H were discovered (Puterka et al. 1988). Thus, additional tests were conducted to determine the reaction of the three cultivars to biotype G. Biotype H was not tested since its virulence to wheat resistance was the same as biotype E and biotype H`s virulence to resitance in rye was the same as F (Puterka, personal communication).

The leaf cage technique (Puterka & Peters 1988) utilizes clip-on cages for quickly determining greenbug resistance in small grains. Entries were exposed to biotype G greenbugs to evaluate the feeding damage characterized by brown necrotic lesions on susceptible cultivars after 72 hours. The clip-on cages were constructed from clear plastic drinking straws, hair curl clips, and white felt.

Resistant plants of P.I. 240675, 'Insave F.A.' rye and 'Century' wheat of the same age were tested with ten replications. Two clip-on cages were placed on a young leaf of each plant. Later, two adult females were placed in each cage. Plants were placed in a controlled growth chamber at 21-22 °C and 14:10 (L:D) h photoperiod. After 72 hours the greenbugs were removed and signs of lesions were recorded as follows:

a) without signs: resistant,

b) few noticeable signs: low resistance and

c) necrotic lesions: susceptible.

Seed Production of P.I 240675 Resistant Plants

Resistant plants of P.I. 240675 rye were vernalized in a cold room at temperatures below 5 °C for more than 40 days to ensure seed production. Plants of P.I. 240675 resistant to biotype F were then grown to maturity in a separate greenhouse from other ryes to prevent outcrossing. The progeny of these plants will be used in future cytological studies and in greenbug plant resistance breeding programs.

CHAPTER IV

RESULTS AND DISCUSSION

Antibiosis Test

In the antibiosis test significantly fewer nymphs were produced per female on 'Insave F.A.' and P.I. 240675 ryes compared with 'Century' wheat. The number of nymphs produced on the two ryes were almost equal and not significantly different from each other (Table I).

TABLE I

GREENBUG NYMPHS PER ADULT IN ANTIBIOSIS TEST

ENTRY	MEAN	
'CENTURY'	70.2	a
'INSAVE F.A.'	43.0	b
P.I. 240675	43.4	b

Means followed by the same letter in a column are not significantly different (P > 0.05; Duncan's [1955] multiple range test). C V = 18.6 %

The reproductive period was 29 days for greenbug adults on 'Century' and 27 days for those on 'Insave F.A.' and P.I. 240675. Smaller nymphs were observed on the two ryes than on 'Century' wheat. Adults feeding on 'Century' usually did not change feeding sites but adults on 'Insave F.A.' often moved to different feeding sites. Nymphs on 'Century' stayed near the adult and did not change feeding sites.

Figure 1 shows the distribution of nymphs every other day on the three entries. Figure 2 represents the same data but expressed as cumulative nymphs/day.

The average number of nymphs was 39 % lower on P.I. 240675 and 'Insave' compared with 'Century' wheat.

Tolerance

1 Damage rating

Damage ratings were recorded daily and the final scores were analyzed when the susceptible check ('Century' wheat) showed clear signs of damage. This ocurred after maintaining a constant number of 15 greenbug adults on each plant for 12 days. Highly significant differences were found in the analysis of variance ($P < 0.01$).

PI 240675 was significantly more tolerant to biotype F greenbug than 'Insave F.A.' and 'Century' wheat. 'Century' was the most severely damaged cultivar. The final damage scores thus indicated that P.I. 240675 was resistant to biotype F and that 'Century' was susceptible to this greenbug biotype. Although the mean separations indicated

that 'Insave F.A.' was classified in a separate group from the two other cultivars the damage score was almost within the 7-9 susceptible range. Results are shown in Table II.

TABLE II

FINAL SCORES OF DAMAGE RATING IN TOLERANCE TEST OF THREE GENOTYPES

ENTRY	MEAN FINAL SCORE[1]/	
'Century'	8.1	a
'Insave F.A.'	6.9	b
P.I. 240675	3.4	c

Means followed by the same letter in a column are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test). C V = 10.1 % . [1]/ : 0 = healthy plant, 9 dead plant.

2. Plant Growth

Plant height measurements were taken at infestation and at the end of the test and plant growth was then calculated from these measurements. Since there was a significant interaction of plant entries and infestation (plant genotype x treatment) it can be stated that biotype F greenbug affects height depending on the plant entry. The LSD test

was used to compare means from interaction. Data for means are shown in Table III.

TABLE III

AVERAGE GROWTH (cm) OF THREE PLANT ENTRIES

Treatment	'Century'	'Insave F.A.'	P.I. 240675
uninfested	24.0	22.8	27.4
greenbug infested	3.8	4.2	13.6

LSD 0.05 = 3.26; C V = 25.1 %

Comparisons between uninfested and infested plants within every cultivar were significantly different. There were no significant differences between 'Century' wheat and 'Insave F.A.' rye infested plants. But when P.I. 240675 infested plants were compared with either 'Century' or 'Insave F.A.' the differences were significant at P = 0.05 These results explain the tolerance of PI 240675 and the susceptibility of 'Insave F.A.'.

The same data expressed as percent reduction of height were 84.2 % reduction with 'Century', 81.3 % with 'Insave

F.A.' and 51.4 % with PI 240675.

3. Absorbance

In this test the values expressed as absorbance readings per 1 mg of fresh leaf weight were taken as a measure of chlorophyll damage between a set of infested and uninfested plants within each cultivar. The interaction of cultivar and infestation was significant at 0.06 level of probability. Averages of treatments are illustrated in Table IV.

TABLE IV

AVERAGE ABSORBANCE PER MILLIGRAM OF FRESH LEAVES OF THREE PLANT ENTRIES

Treatment	'Century'	'Insave F.A.'	PI 240675
uninfested	3.66	2.93	4.28
infested	1.96	2.08	3.18
PL	46.5 %	29.0 %	25.7 %

LSD = 0.465 for 12 replications- 0.475 for 11 replications.
C V = 19.0 %

The treatment 'Century'-uninfested had a missing value so there were only 11 replications.

More chlorophyll damage in 'Insave F.A.' was expected but the 29% loss in chlorophyll content could be explained by the behavior of the aphids to change feeding sites often on this cultivar. This observation was consistent with Wood et al. (1974) who observed the number of probing areas of biotype C in the leaf tissue of 'Insave F.A.' and 'Gaucho' triticale and found that biotype C changed feeding sites often on these genotypes compared with the susceptible cultivar 'Chinese Spring'. Since samples were taken from the two basal leaves to compare losses in chlorophyll content, the values obtained from these samples may have underestimated the whole plant value of the 'Insave F.A.' infested set of plants as a result of the greenbug's behavior of moving to, and probing other parts of the plant.

4. Tolerance test: Adults added

In order to maintain an infestation level of 15 adults per plant during the tolerance test, the adults were counted daily and missing or dead adults were replaced with new adults from the stock culture. The number of new adults added per plant were recorded and data were analyzed as total adults added per plant during the 12 days of the test. Means for cultivars are illustrated in Table V.

TABLE V

GREENBUG ADULTS ADDED IN THE TOLERANCE TEST

ENTRY	ADULTS/PLANT (MEAN)	
PI 240675	35.8	a
'Insave F.A.'	25.8	b
'Century'	10.2	c

Means followed by the same letter in a column are not significantly different ($P > 0.05$; Duncan's multiple range test). C V = 37.3 %.

The analysis of variance was highly significant ($P < 0.01$) but the C V was 37.3 %. When data were transformed by the square root transformation to stabilize the variance the C V changed to 17.8 % but the mean separation was the same as shown in Table V.

The average number of aphids added per day per plant was 0.85 for 'Century', 2.2 for 'Insave F.A.' and 3.0 for P.I. 240675 (Figure 3). These results suggest that the tolerance test can be utilized to learn more about antibiosis and antixenosis effects of the test plant.

Regression analysis was performed on the data of average adults (added/plant per) day against time in days. The adjusted models were as follows :

'Century' wheat: $y = 0.0136 + 0.152 x - 0.0025 x^2$

$R^2 = 0.61$

'Insave F.A.' : $y = 0.427 + 0.575 x - 0.037 x^2$

$R^2 = 0.36$

P.I. 240675 : $y = 4.230 - 0.191 x$

$R^2 = 0.48$

where x = days and y = number of adult added

These functions are illustrated in Figure 4.

The susceptible check 'Century' was preferred by the adults as a source of food. With P.I. 240675, the aphids rejected the plant as a source of food and died, indicating an antibiosis effect or an extreme antixenosis effect.

The difference between 'Century' and 'Insave F.A.' in this variable (adults added/plant) suggests that both antibiosis and antixenosis are components of the final effect.

5.Tolerance test: Nymphs removed

The number of nymphs removed from each plant in the tolerance test were recorded daily during the 12 days of the test. The total nymphs produced were analyzed and the differences were highly significant. ($P < 0.01$). Mean separations are shown in Table VI.

Mean numbers of nymphs removed per plant/day for the first forth days are illustrated in Figure 5.

TABLE VI

GREENBUG NYMPHS REMOVED IN THE TOLERANCE TEST

ENTRY	NYMPHS/PLANT (MEAN)	
'Century'	152.2	a
'Insave F.A.'	126.4	b
P.I. 240675	115.7	b

Means followed by the same letter in a column are not significantly different ($P > 0.05$; Duncan's multiple range test). C V = 15.6 %

These results suggest differential antibiotic effects between 'Century' wheat and the two ryes. The average number of nymphs removed from 'Century' wheat was not much greater than the other entries probably because after the seventh day the nutrient components in 'Century' were unable to support an increasing aphid population (Figures 6 and 7). This observation is consistent when is compared with the damage score in 'Century' wheat which at the seventh day was 7 in the susceptible range (Figure 8).

Regression analysis performed with the data from nymphs removed/plant per day during the test, gave the following equations:

'Century' : $y = 2.891 + 3.512\ x - 0.252\ x^2$

$R^2 = 0.87$

'Insave F.A.': $y = 3.153 + 3.428\ x - 0.478\ x^2 + 0.021\ x^3$

$R^2 = 0.76$

P.I. 240675 : $y = 3.212 + 0.897\ x$

$R^2 = 0.94$

where x = days and y = number of nymphs removed

These regressions are illustrated in Figure 6.

Regression models were also applied to the variable average damage score/day per plant. The following expression were obtained:

'Century' : $y = -0.127 + 1.572\ x - 0.077\ x^2$

$R^2 = 0.98$

'Insave F.A.': $y = 0.531 + 1.074\ x - 0.0457\ x^2$

$R^2 = 0.99$

P.I. 240675 : $y = 0.338 + 0.284\ x$

$R^2 = 0.93$

where x = days and y = damage score

Graphic representation of this regressions are shown in Figure 7. Means score of damage per day in the first half of the test is shown in Figure 8.

The results of the tolerance test show that differences in growth, and damage scores of infested and uninfested plants are the best way to classify resistant and susceptible plants for this specific component of resistance.

Although the chlorophyll reduction test showed some differences between cultivars it appeared not to clearly separate plant entries where the means were narrow.

Conducting the classical tolerance test in the usual manner, but recording the adults added, nymphs removed and damage score daily or every other day, adds more information about the plant-aphid interaction to the other two components of resistance. More important is the fact that this information can be used to measure expressions of antibiosis or/and antixenosis effects on an individual plant. Another advantage of this additional information is that resistant plants can be selected in the tolerance test within the limitations of the number of plants which can be handled daily.

Antixenosis

Two different antixenosis tests were conducted, one in 1987 and the other in 1988. In the first test, seedlings of P.I. 240675 without selection to biotype F were used. The number of greenbugs were recorded 24 h after release but no significant differences among the entries were found. A second count was made 48 h after release. At the 48 h count, the number of greenbugs on the 'Century' plants ranged from 2 to 17, whereas those on 'Insave F.A.' and P.I. 240675 ranged from 2 to 14 and 1 to 7, respectively. The variances of 'Century', 'Insave F.A.' and P.I. 240675 were 20.7, 19.4 and 5.4, respectively. Data were therefore

transformed by the square root transformation trying to stabilize the variance. After the transformation the data were analyzed by PROC ANOVA using a randomized complete block design. Significant differences were found at $P < 0.077$. Means were separated using Duncan's multiple range test. The results are shown in Table VII.

TABLE VII

GREENBUG ANTIXENOSIS TEST - 48 HOURS (1987)

ENTRY	No. GREENBUGS/PLANT	
	MEAN	MEAN SQUARE ROOT TRANSF.
'Insave F.A.'	6.9	2.49 a
'Century'	6.0	2.32 a b
P.I. 240675	2.9	1.52 b

Means followed by the same letter in a column are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test). C V = 44.9 %

In the second antixenosis test (1988) three month old plants were used. The P.I. 240675 plants in the test were previously selected as resistant to biotype F. The data were also transformed as in the first test and highly significant differences were found ($P < 0.01$). The results at 48 h after release are shown in Table VIII.

TABLE VIII

GREENBUG ANTIXENOSIS TEST - 48 HOURS (1988)

ENTRY	No. GREENBUGS/PLANT		
	MEAN	MEAN SQUARE ROOT TRANSF.	
'Insave F.A.'	12.6	3.3	a
'Century'	7.6	2.6	a b
P.I. 240675	4.6	1.9	b

Means followed by the same letter in a column are not significantly different (P > 0.05; Duncan's [1955] multiple range test). C V = 41.9 %

The separation of means were consistent in the two antixenosis tests in that 'Insave F.A.' was significantly different from P.I. 240675.

Host Plant Resistance Index (HPRI)

After values were obtained for the three resistance components, normalized indices for antibiosis, tolerance, and antixenosis were determined as well as the HPRI for the three entries (Table IX). The HPRI data clearly show the lack of biotype F resistance in 'Insave F.A.' and the superior resistance of PI 240675.

TABLE IX

HOST PLANT RESISTANCE INDEX

ENTRY	RAW SCORES			NORMALIZED INDICES			HPRI
	AXI	ABI	TRI	AXI	ABI	TRI	
Cent.	7.60	70.20	8.10	0.60	1.00	1.00	1.66
Insav.	12.60	43.00	6.90	1.00	0.61	0.85	1.92
P.I.	4.60	43.40	3.40	0.37	0.62	0.42	10.56

AXI= antixenosis index, ABI= antibiosis index, TRI= tolerance index, HPRI= host plant resistance index. Greater values, or resistance units, indicate superior resistance levels.

Feeding Behavior - Electronic Feeding Monitor

The frequency, total duration, and mean duration of baseline (BC = 1), probing (BC = 2), salivation (BC = 3), non-phloem ingestion (BC = 4), X-wave (BC = 5) and phloem-ingestion (BC =6) in the three entries were analyzed. The data for frequency, mean duration, and total duration in 360 minutes for baseline, salivation, phloem ingestion and non-phloem ingestion are shown in Tables X, XI and XII.

Though in many feeding events there are large differences in mean frequency, mean duration, and total duration among the three entries, no significant differences ($P < 0.05$ level) were found due to the large variation. However, significant differences were found in total salivation duration ($P < 0.05$) (Table XII). Total

salivation duration is one of the feeding events considered to separate resistant genotypes with the electronic feeding monitor. According to Niassy (1986) the key events which characterize resistant genotypes in wheat are: increased frequency of probes, higher total salivation duration, and shorter phloem ingestion. Probing frequency for P.I. 240675 was 12.3 times, for 'Insave F.A.', 11.8 times and, for 'Century', 7.5 times, but no significant differences were found (C V = 84.4 %). Also, no significant differences was found for total time in phloem ingestion. Previous tests have established that 'Century' wheat is susceptible to biotype F greenbug, but when 'Century' was compared with the two ryes, it appeared as a resistant entry. Therefore, it may be concluded that it is not valid to compare entries of different species with the feeding monitoring technique in plant resistance tests. A more valid comparison would be to consider the data from total salivation duration of the two ryes, P.I. 240675 and 'Insave F.A.'. Total salivation duration of greenbugs on P.I. 240675 was significantly greater than on 'Insave F.A.', with 181.4 and 116.5 minutes respectively (Table XII). This difference may help explain why P.I. 240675 is more resistant than 'Insave F.A.' to biotype F greenbug. These results also agree with the results from antixenosis tests and the statement that "the feeding behavior studies were essentially host preference studies" (Niassy 1986, Tarn & Adams 1982).

TABLE X

FREQUENCY OF BEHAVIORAL ACTIVITIES FOR 360 MINUTES OF BIOTYPE F GREENBUG ON THREE ENTRIES

	FREQUENCY (MEAN)			
Entry	Baseline	Salivation	Phloem Ingestion	Nonphloem Ingestion
'Century'	7.4 a	10.4 a	2.5 a	1.8 a
'Insave F.A.'	11.8 a	12.8 a	2.5 a	1.7 a
P.I. 240675	12.4 a	13.9 a	3.3 a	1.3 a
C V %	82.7	66.2	73.8	70.0

Mean followed by the same letter in a column are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).

TABLE XI

MEAN DURATION OF BEHAVIORAL ACTIVITIES FOR 360 MINUTES OF BIOTYPE F GREENBUG ON THREE ENTRIES

Entry	TIME IN MINUTES (MEAN)			
	Baseline	Salivation[1]/	Phloem Ingestion	Nonphloem Ingestion
'Century'	1.5 a	26.6 a	24.9 a	7.8 a
'Insave F.A.'	3.0 a	13.2 b	90.2 a	10.3 a
PI 240675	2.6 a	16.6 b	59.6 a	2.8 a
C V %	63.6	46.7	174.4	109.5

Mean followed by the same letter in a column are not significantly different (P > 0.05; Duncan's [1955] multiple range test). [1]/ Significant at 0.057 alpha level.

TABLE XII

TOTAL DURATION OF BEHAVIORAL ACTIVITIES FOR 360 MINUTES OF BIOTYPE F GREENBUG ON THREE ENTRIES

	TIME IN MINUTES (MEAN)			
Entry	Baseline	Salivation	Phloem Ingestion	Nonphloem Ingestion
'Century'	12.0 a	261.2 a	63.2 a	16.2 a
'Insave F.A.'	40.1 a	116.5 c	167.5 a	27.0 a
P.I. 240675	31.7 a	181.8 b	127.4 a	7.6 a
C V %	114.4	31.7	68.7	186.7

Mean followed by the same letter in a column are not significantly different (P > 0.05; Duncan's [1955] multiple range test).

Reaction to biotype G

Two biotypes were discovered after the study began. The three entries were tested to reaction to biotype G using two clip-on cages for plant in 10 replicates. Three adults per cage were placed in each cage. After 72 hours signs for reaction to G biotype were evaluated. Both ryes presented resistance to biotype G greenbug. 'Century' wheat was susceptible to this biotype.

Seed Production of P.I. 240675 Resistant Plants

After the tests finished resistant plants to biotype F greenbug of P.I. 240675 rye were vernalized. More than 50 resistant plants were grown to maturity in a separate greenhouse. Seed from these plants were harversted and preserved at 6 °C in a refrigerator for future studies.

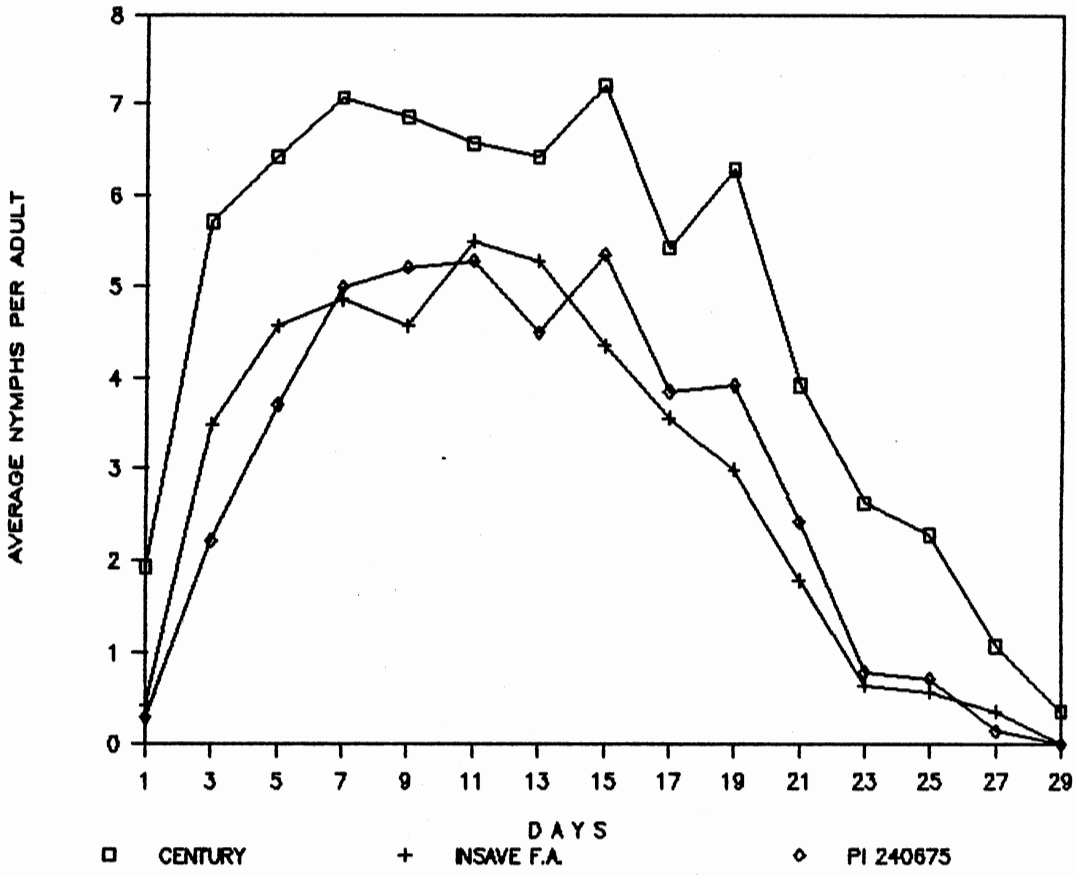

Figure 1. Antibiosis test: Distribution of nymphs per adult every other day of greenbug biotype F.

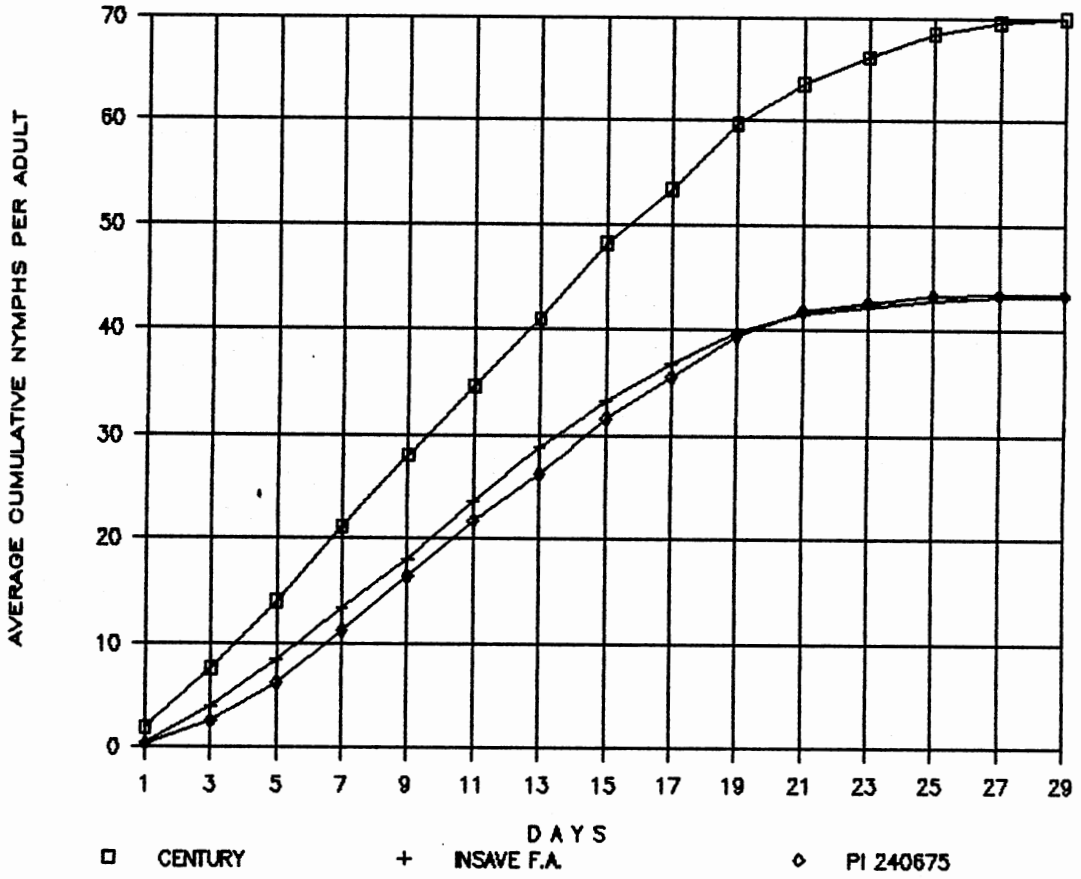

Figure 2. Antibiosis test: Cumulative nymphs every other day of greenbug biotype F in three entries.

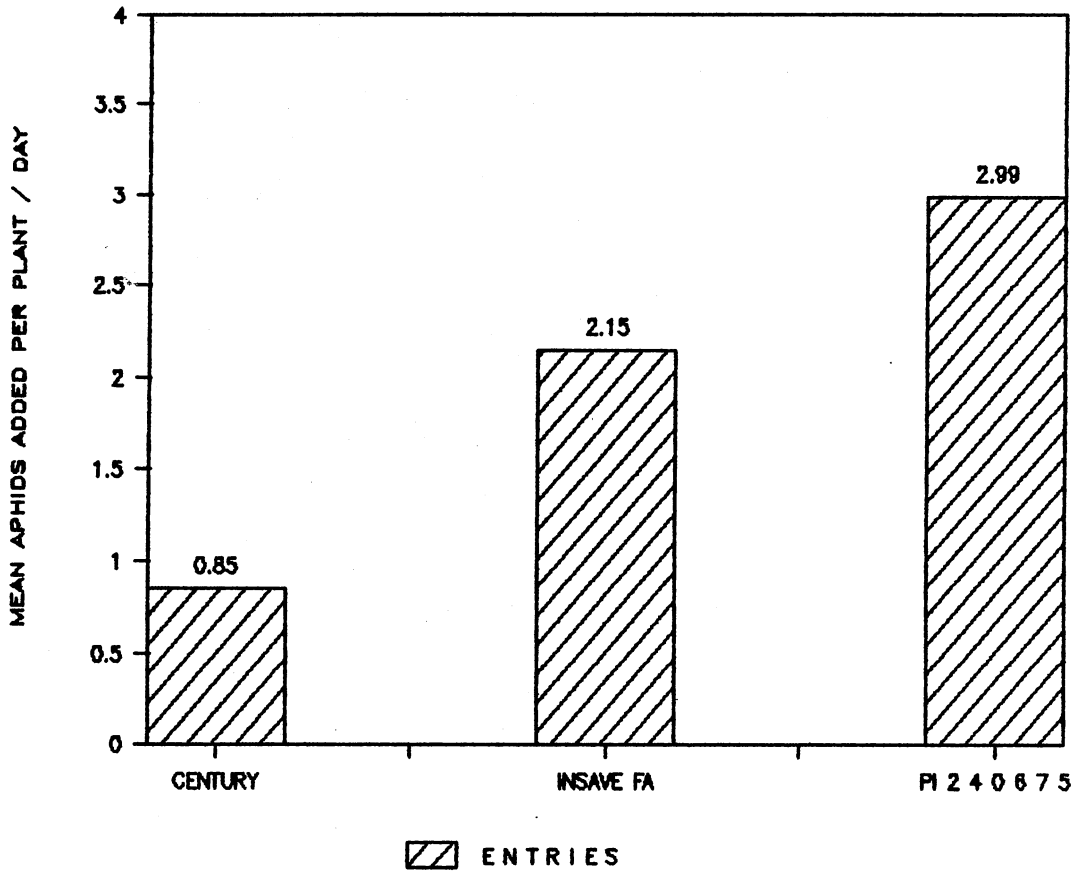

Figure 3. Tolerance test: Mean aphids added per plant per day.

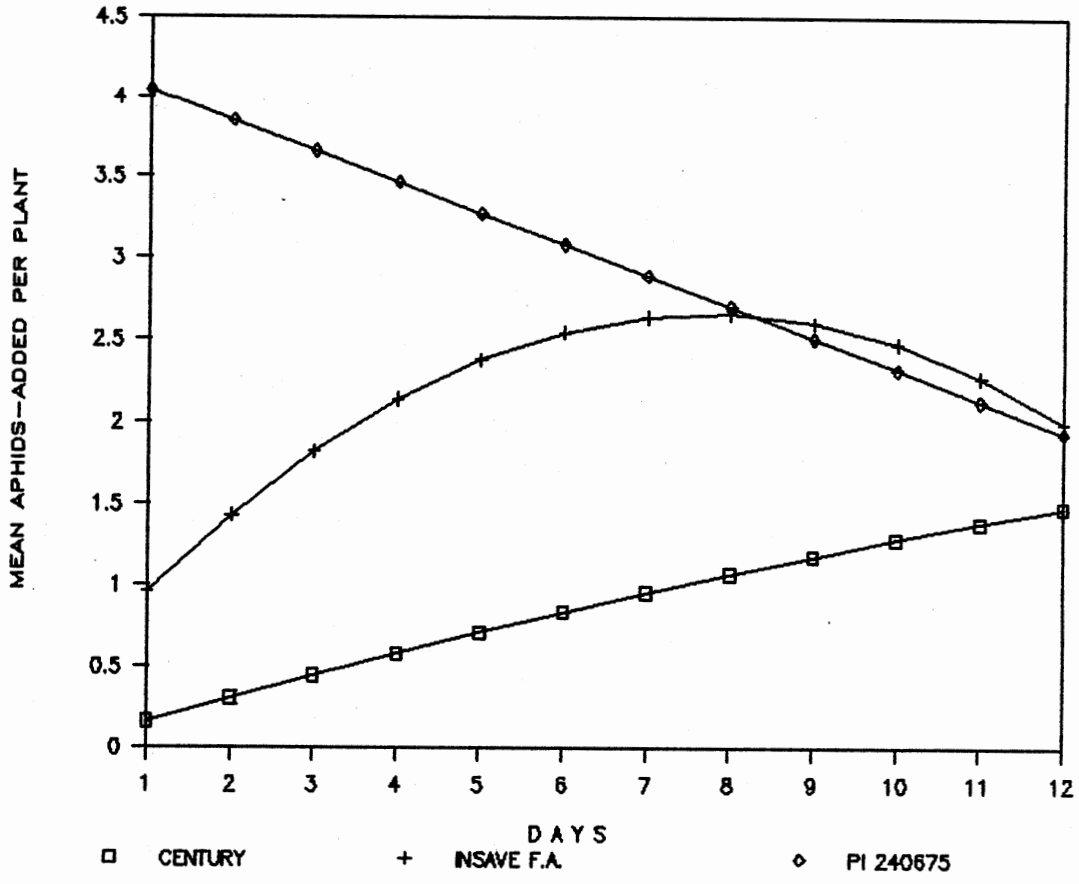

Figure 4. Tolerance test: Regression Analysis aphids added per plant per day.

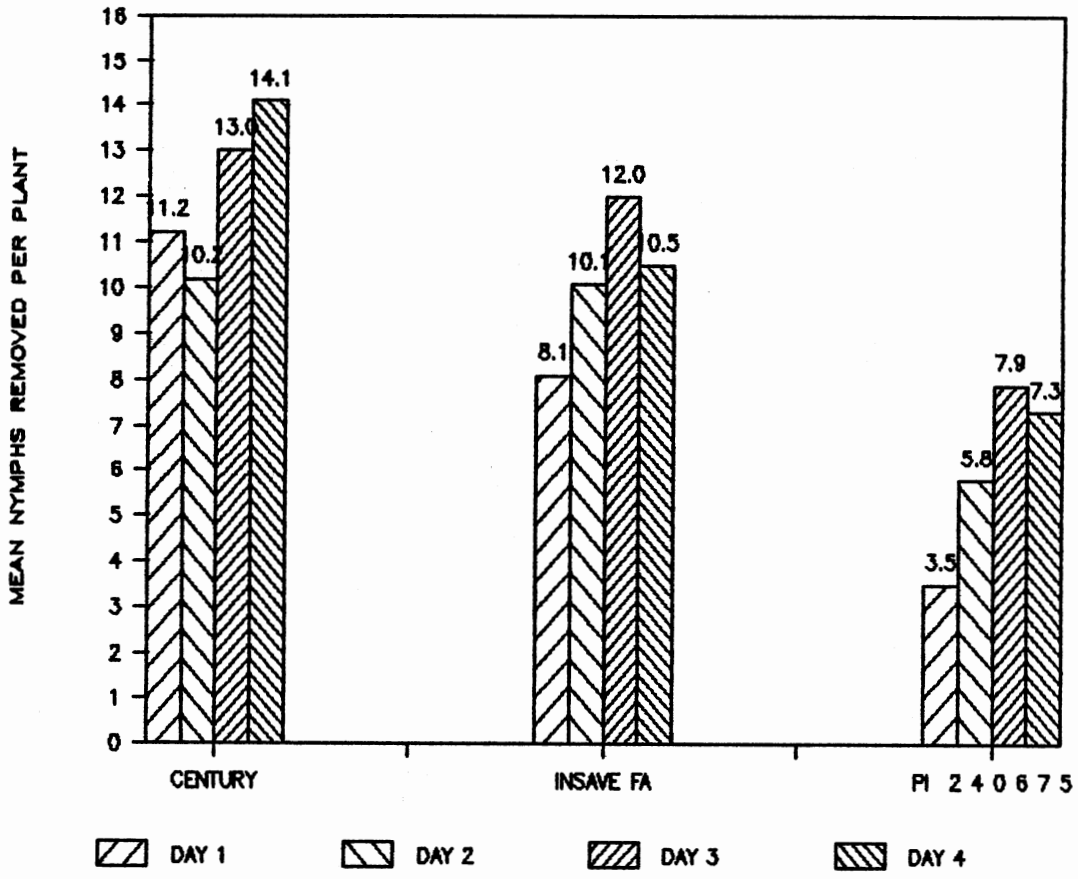

Figure 5. Tolerance Test: Mean nymphs removed per plant per day in the forth first days.

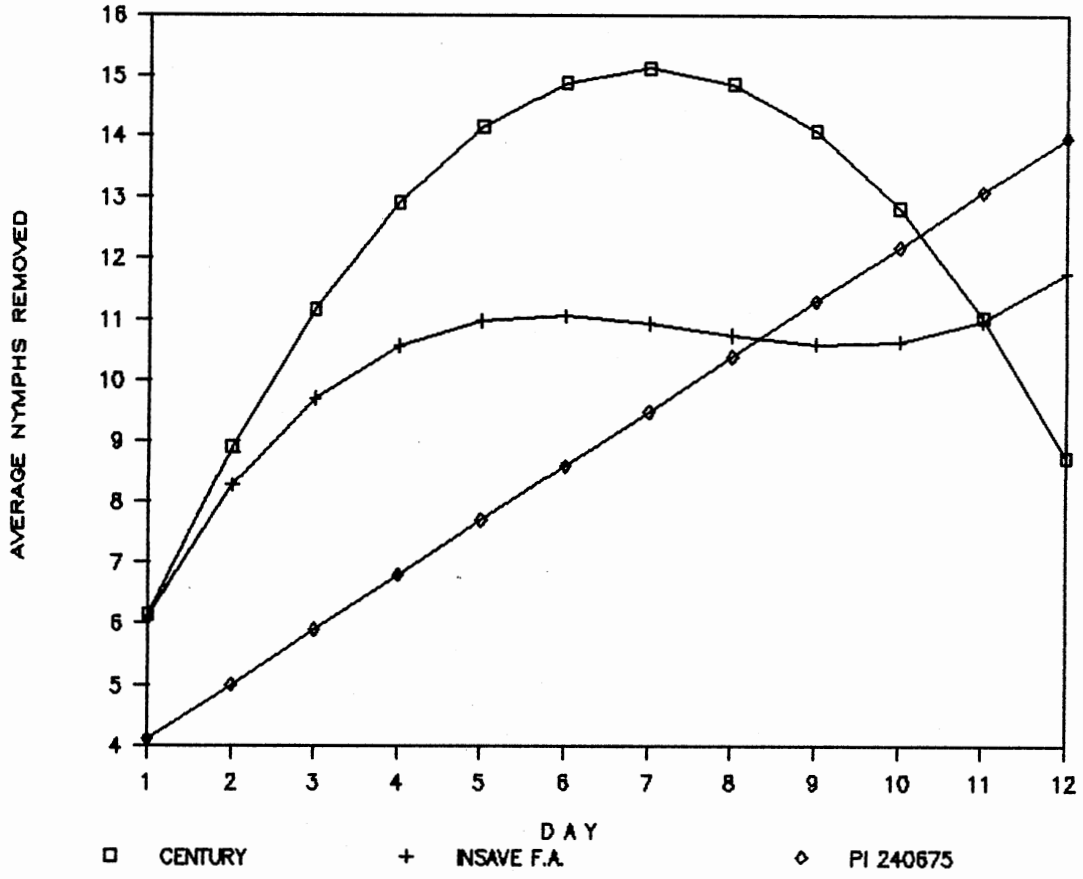

Figure 6. Tolerance test; Regression Analysis Average nymphs removed per plant per day.

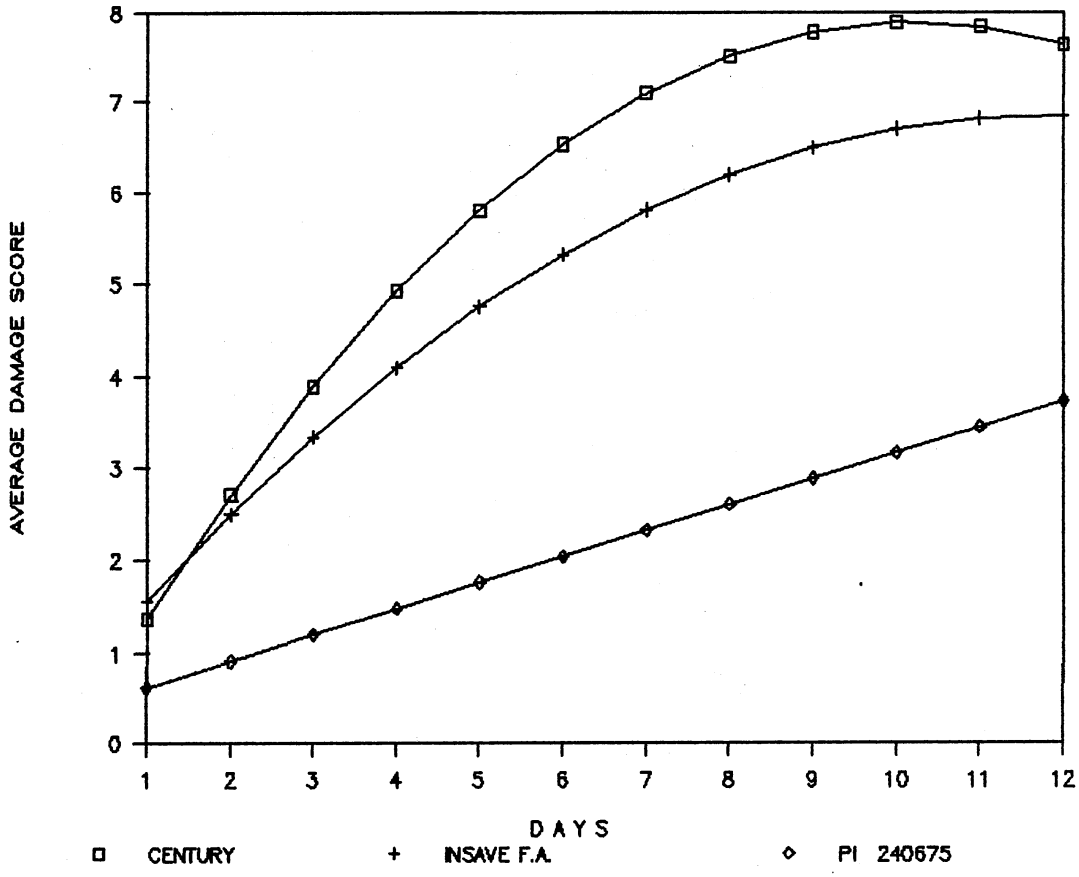

Figure 7. Regression Analysis Average Damage Score per Plant per day.

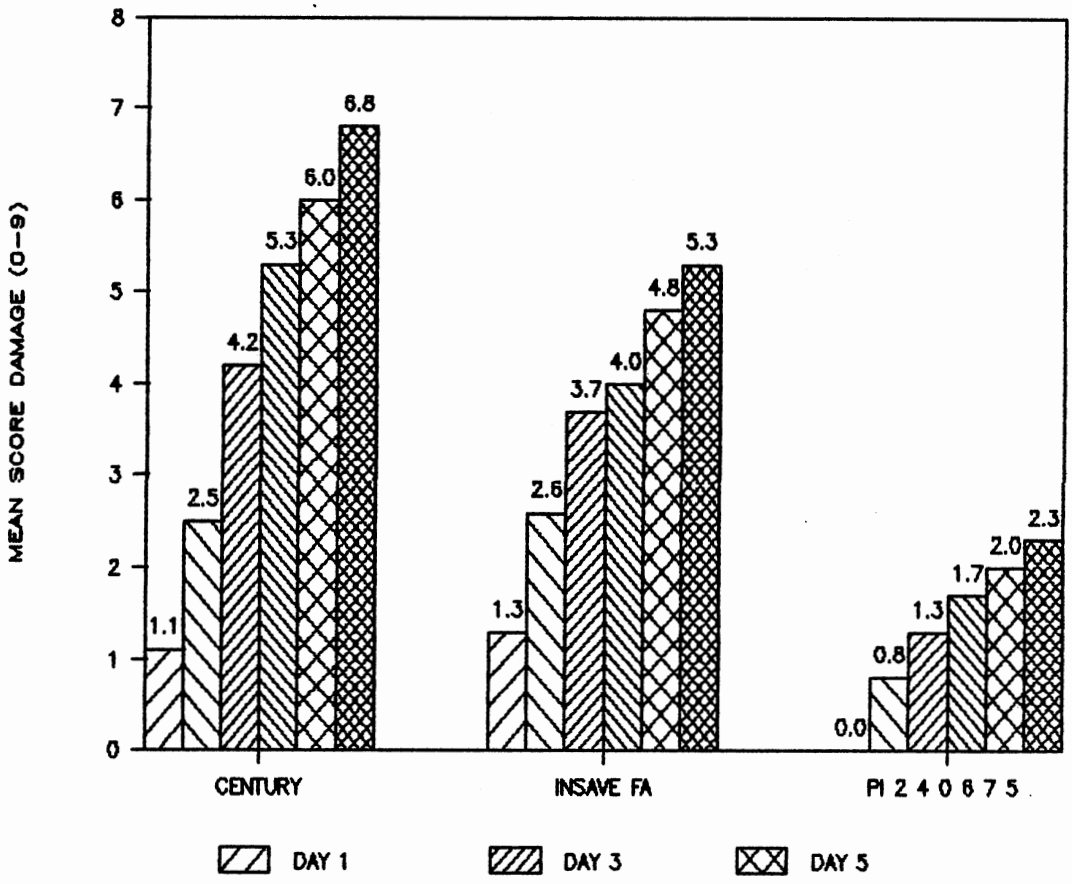

Figure 8. Tolerance Test: Mean Score of Damage per day in the Sixth First days after Infestation.

CHAPTER V

SUMMARY AND CONCLUSIONS

This research was conducted to determine the relative amount of the resistance components to biotype F greenbug Schizaphis graminum (Rondani) (Homoptera: Aphididae) in two ryes, P.I. 240675 and 'Insave F.A.' compared with 'Century' wheat as susceptible check.

The mechanisms of resistance were studied by Painter (1951). The three components of resistance: non-preference or antixenosis (Kogan & Ortman 1978), antibiosis, and tolerance are all important in plant resistance. Antibiosis and antixenosis involve plant-insect interactions while tolerance is a property of the plant and it is independent of the insect response.

Tyler et al. (1988) found that some plants of P.I. 240675 were resistant to biotypes B, C, E and F greenbugs, but they did not study the mechanisms of resistance of this line. In the same study, they also found that all 'Insave F.A' plants were susceptible to biotype F greenbugs. In another study, Kindler & Spomer (1986) stated that 'Insave F.A.' was highly resistant to all biotypes including biotype F.

Separate tests provide a more detailed characterization

of the mechanisms of resistance than those of the initial screening tests. Four separate tests were conducted to study the degree of resistance of the two ryes.

In the first test, P.I. 240675 and 'Insave F.A' showed the same levels of antibiosis and were significantly ($P < 0.05$) greater than those of 'Century'. The mean number of nymphs per adult produced on P.I. 240675 and 'Insave F.A.' were 43.3 and 43.0, respectively, compared with 70.2 on 'Century'.

The second test measured tolerance. When comparing means growth interaction for uninfested and infested plants, highly significant differences ($P < 0.01$) were found between P.I. 240675 (51.4 % reduction of growth), 'Insave F.A.' (81.3 %), and 'Century' (84.2%). In the same tolerance test, the differences in mean damage scores were also highly significant. Average means were 3.4 on P.I. 240675, 6.9 on 'Insave F.A.' and 8.1 on 'Century' (where 0 = a healthy plant and 9 = a dead plant). Measurements of absorbance with an ELISA reader were taken as an indirect measure of chlorophyll damage between infested and uninfested plants. Highly significant differences ($P < 0.01$) were found. Mean absorbance readings/1 mg of leaf weight were 3.18 for P.I. 240675, 2.08 for 'Insave F.A.' and 1.96 for 'Century'. In the same test the following variables were also determined from the individual plant data: number of aphids added per plant per day to maintain a constant number of 15 adults per plant, number of nymphs removed per plant per day, and daily

damage score of each plant. At the same time, resistant plants of P.I. 240675 were selected.

In the mean comparisons of the adults added per plant per day highly significant differences were found among the three entries. These results suggest that "aphids added" can be use to measure antibiosis and antixenosis on the plants in the tolerance test. The variable, "nymphs removed" in the test showed significant differences between 'Century' compared with the two ryes but no significant difference was found between the ryes. This variable can also be used to obtain information about antibiosis during the routine tolerance test.

In the third test, antixenosis (nonpreference) of the three entries was measured in two sets of plants. Seedlings which were unselected for resistance (segregating for resistance), and three month old P.I. 240675 plants resistant to biotype F greenbug were tested. In both tests, differences ($P < 0.077$) and ($P < 0.01$) were found between P.I. 240675 and 'Insave F.A.'. Data from these two antixenosis tests were consistent and indicated the lack of antixenosis in 'Insave F.A.' which, was not significantly different from the susceptible check.

Finally, a measure of resistance was attempted utilizing the electronic feeding monitoring technique for the three entries in the study. Data from the feeding events were analyzed, but significant differences were found only in total salivation duration in the 360 minute test.

Mean total salivation time for P.I. 240675 was 181.8 minutes, for 'Insave F.A.', 116.5 minutes and for 'Century' wheat, 261.2 minutes. Higher total salivation duration along with increased frequency of probes and shorter phloem ingestion are the feeding events which separate between resistant and susceptible genotypes (Niassy 1986). The results of the present test suggest greater resistance to biotype F greenbug on P.I. 240675 than on 'Insave F.A.'. Also the results suggest that it is incorrect to compare resistance between different species of plants with the feeding monitoring technique.

According to the results of all tests, it can be concluded that P.I. 240675 was significantly more tolerant than 'Insave F.A.', but the level of antibiosis of P.I. 240675 and 'Insave F.A.' were almost the same with no significant differences. Also P.I. 240675 showed a higher antixenosis level than 'Insave F.A.'. This difference was supported by the data from the electronic feeding monitoring test. Thus, on the basis of the results from all tests, P.I. 240675 exhibited the highest level of resistance of the three entries in the study, and had a relatively high degree of all three components of resistance.

The present tests showed that 'Insave F.A.' had only antibiosis which agrees with Kindler & Spomer (1986) but disagrees with the same authors who stated that 'Insave F.A.' is also tolerant.

Both P.I. 240675 and 'Insave F.A.' showed resistance to

biotype G using the clip-on cage technique (Puterka et al. 1988).

Although 'Insave F.A.' should not be considered as a susceptible genotype to biotype F greenbug, because of its very low tolerance and lack of antixenosis, it is not a good source of biotype F resistance for breeding purposes.

Thus, P.I. 240675 has resistance to all known greenbug biotypes (B, C, E, F, G and H) and can be used as a source of resistance with rye and species related to and crossable with rye.

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VITA

Rodolfo Oscar Curvetto

Candidate for the Degree of

Master of Science

Thesis: STUDIES OF GREENBUG (HOMOPTERA: APHIDIDAE) RESISTANCE IN RYE

Major Field: Entomology

Biographical:

Personal Data: Born in Bahia Blanca, Argentina, May 7 1945, the son of Alejandro and Maria Curvetto.

Education: Graduated from Colegio Nacional de Bahia Blanca, Bahia Blanca, Argentina, December, 1962; received Ingeniero Agronomo Degree from Universidad Nacional del Sur, Bahia Blanca, Argentina, December 1971; completed requirements for the Master of Science degree at Oklahoma State University, Stillwater, Oklahoma, May, 1989.

Professional Experience: Scholarships at Universidad Nacional del Sur, Argentina, from 1967 to 1971. Research entomologist at Instituto Nacional de Tecnologia Agropecuaria, Argentina, from 1972.