THE EFFECT OF HOST PLANT GENOTYPES AND DROUGHT STRESS ON THE INTERACTION OF GREENBUG (*SCHIZAPHIS GRAMINUM*, RONDANI) BIOTYPE *E* AND WHEAT (*TRITICUM AESTIVUM* L.)

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CHAPTER I

INTRODUCTION

Wheat (Triticum aestivum L.) is one of the major crops grown in the Great Plains of the United States for domestic and foreign export. In the State of Oklahoma alone, 1983 total acreage of wheat under rainfed and irrigation was 7,800,000 and 195,000 acres, respectively (Craig and Legate, 1983). Drought and greenbug (Schizaphis graminum, Rondani) stress are two of the major limiting factors in wheat production. Long-term average rainfall in Oklahoma ranges from 40 cm to 86.4 cm annually but rainfall amounts vary widely from year to year (Cuperus and Johnston, 1983). The greenbug occurs in most wheat growing areas and can cause severe damage in the southern and central Great Plains (Joppa et al., 1980).

The greenbug was first reported in the United States in Virginia in 1882 on sorghum (Sorghum bicolor L.) but was not a serious pest until 1968 (Harvey and Hecherott, 1969). In 1976, crop damage and control costs on wheat in Oklahoma alone exceeded 80 million dollars (Starks and Burton, 1977). Rogers et al. (1972) also reported that there have been 15 major outbreaks on wheat in Oklahoma since the insect was reported.

Chemical control is the main greenbug control method. However, it does not give satisfactory solution to the problem because of the rapid buildup of greenbug populations under favorable conditions, and

considerable damage often occurs before the problem is recognized (Joppa et al., 1980). Greenbug resistant varieties of sorghum and small grains have been developed and released. However, the occurrence of new greenbug biotypes has reduced the usefulness of newly developed resistant varieties. Five biotypes (A, B, C, D, E) of greenbug have occurred in the Great Plains of the United States. Greenbug biotype A (GBA) was proceeded by biotype B, which is virulent to the wheat cultivar Dickson Sel. 28-A (Starks et al., 1983). Biotype B was dominant during the early 1960's but was replaced by biotype C in 1968 (Porter et al., 1975). Biotype D occurred being resistant to organophosphate insecticides (Porter et al., 1982). Later, in 1980, a new biotype, biotype E, appeared and was able to attack the GBC resistant variety, Amigo (Porter et al., 1982). These repeated occurrences of greenbug biotypes have drawn the attention of many researchers and some research has been conducted on the feeding behavior of greenbugs using electronic monitors (Campbell et al., 1982, Montllor et al., 1983). However, most of these monitoring studies were completed on sorghum and little if any studies have been attempted on wheat.

Drought stress is also a major problem in wheat production in the Great Plains and it is known that great yield losses occur as a result of drought. Although the drought stress is often coupled with greenbug stress (Ortman and Painter, 1960), it has not been incorporated in many greenbug studies.

Intensive studies on various aspects of host, pest, and environment interactions are needed. Thus this research focuses on greenbug, wheat, and drought interactions. Experiment one deals with

greenbug growth and development, experiment two with greenbug feeding behavior, and experiment three with honeydew production and chlorophyll damage.

The objectives of this research are:

1. To determine how wheat genotypes and drought stress affect the growth, development, honeydew production, and feeding behavior of greenbug biotype E.
2. To determine the chlorophyll damage due to greenbugs and drought stress.

CHAPTER II

LITERATURE REVIEW

Greenbugs Growth and Development

Greenbugs (Shizaphis graminum, Rondani), order Homoptera and family Aphididae, reproduce parthenogenetically (mainly) and viviparously. The optimum temperature for greenbugs reproduction and development is approximately 24°C. A study by Wadley (1936) indicated that at an average temperature of 27.7°C greenbugs produced 69.3 offspring within a mean of 19.3 days of reproductive life and lived for 20.3 days. The average number of offspring produced per day was 3.58. A recent experiment by Summer et al. (In press) also showed that greenbug biotype C on winter wheat cultivar Sturdy variety had 40 days longetivity, 20 days reproductive period, and 3 offspring per reproductive day. Rapid greenbug development and their parthenogenic reproduction has apparently contributed to the development of new greenbug biotypes (Kennth et al., 1983). Five greenbug biotypes are distinctively described and biotype 'E' is the most damaging currently. Greenbug biotype 'E' was first recognized in the collections made at Bushland, Texas, in 1980 (Porter et al., 1982).

Campbell et al. (1982) have studied greenbug growth and development by putting 2nd instar nymphs of greenbugs (biotype C) on 5

week old sorghum plants and allowing them to feed for 15 days. In this experiment the rate of greenbugs population growth was significantly greater on susceptible lines of sorghum than on resistant lines. A similar experiment done by Montllor et al. (1983) showed that greenbug biotype E (GBE) reproduced at twice the rate of biotype C (GBC) on a sorghum cultivar resistant to GBC but susceptible to GBE.

Aphid Feeding

Greenbugs with their piercing and sucking mouth parts, remove plant sap and have a phytotoxic effect on plant tissue during the feeding process (Chatter and Shlehuber, 1951). While probing, aphids lower their head, protract their rostrum, and extend and vibrate their antennae. During feeding aphids secrete saliva (salivary sheath and watery saliva) which helps them to disrupt plant tissue and insert their stylet bundle (Miles, 1972). The sheath material is secreted continuously along the stylet penetration to form stylet sheath. The watery saliva which contains pectinase and cellulase is released to aid in the penetration of plant tissue.

Ingestion occurs mostly from sieve tubes and sometimes from sub-epidermal tissue, mesophyll parenchyma, phloem parenchyma (Pollard, 1973; Chatters and Shlehuber, 1951) and xylem (McLean and Kinsey, 1967). Entry of stylet bundle is predominantly intercellular (Chatter and Schlehuber, 1951). A study by Pennington (1985) indicated that in greenbug biotype E the path of saliva sheath through mesophyll tissue was intercellular. There seems to be a correlation between feeding behavior and digestive enzymes of aphids. Aphids

producing pectinase protrude their stylets between cells at the middle lamella layer or penetrate both intercellularly and through cells, whereas aphids without pectinase penetrate directly through cells (McAllen and Adams 1961). Vascular feeders secrete carbohydrase while mesophyll feeders produce proteinases (Pollard, 1973).

Turgor pressure and host plant water content are essential to feeding aphids (Wearing, 1967, 1968; Wearing & Van Emden, 1969) and they may affect population growth (Kennedy et al., 1958). Under drought stress, plants may lose their turgor and it becomes harder for the insects to acquire plant sap. Kennedy (1958) also noted that aphids moving from flaccid leaves may be due to a repellent increase resulting from the change of water content. The frequency of probing may be increased by starvation of aphids (Nault and Gyrisco, 1966) or wilting of the plant (Mittler, 1957). Mittler and Dadd (1964) noted that food uptake is markedly affected by nutrients. For example, Myzus persicae shows greater preference for a mixture of sucrose and amino acides than for either alone.

Greenbug infestations can occur at different stages of host plant development and it has been found that the most marked loss occurs in seedling and minimum loss occurs in boot stage of the plant (Kieckefer and Kantack, 1980). Damage by aphids varies on different host plants. A study by Al Mousarwi et al. (1983) indicated that greenbugs feeding on the susceptible winter wheat cultivar Tam W-101 caused macroscopic lesions, necrotic sites circled by chlorotic halos within 4 days after feeding. However, resistant cultivars did not show any macroscopic symptom even after 10 days.

Electronic Monitoring of Greenbug Feeding

A technique to record the feeding behavior of aphids was reported by Mclean and Kinsey in 1964. Since then, the technique has been instrumental in developing new information on aphid feeding behavior. However, modifications have been made as described by Mclean and Kinsey (1967), Mclean and Weight (1968), and Brown and Holbrook (1976). A study by McLean and Kinsey (1967), Brown and Holbrook (1976) and others indicated that in a feeding monitor system, the aphid is connected to the electrical circuit with a fine wire attached to its dorsum. When the aphid starts probing the leaf, the circuit becomes complete and the chart recorder will start recording different wave forms corresponding to the different feeding activities. Using this technique much research has been done on aphids. Some feeding monitor studies were done by Zettler and Wilson (1960) with green peach aphid, Nielson and Don (1974) with spotted alfalfa aphids, Campbell et al. (1982) and Montllor et al. (1983) with greenbugs. These previous works on greenbug feeding behavior were all on sorghum and there was no study on wheat.

There are five distinct wave forms identified corresponding to the different feeding activities (probing, salivation, non-phloem ingestion, stylet penetration of sieve elements and phloem ingestion) of aphids (McLean and Kinsey, 1967; Campbell et al., 1982). These wave forms were correlated with the different feeding activities by locating the salivary sheath and stylet tips of the aphids in the plant through leaf sectioning.

Probing is the first physical contact of aphid stylet to the host plant. Aphids make test probes before starting ingestion and an

increased number of separate probes and increased duration of non-probing were observed on aphids feeding on resistant lines (Campbell et al., 1982).

Initial probing is usually followed by a salivation event, which is the formation of sheath material from the time of initial probing to the location of vascular bundles. The total duration of salivation by aphids feeding on a resistant variety is longer compared to aphids feeding on susceptible variaties (Nielson and Don, 1974). However, according to Campbell et al. (1982), there was no significant difference on mean duration of salivation between resistant and susceptible varieties.

Aphids sometimes feed on non-phloem tissues such as mesophyll and parenchyma cells and differences in the mean durations of non-phloem ingestion by greenbugs were not definitively correlated to resistance in sorghum (Campbell, 1982).

A combination of salivation wave forms, x-wave forms, and ingestion wave forms are usually observed while aphids feed (Mclean & Weight, 1986; Nielson and Don, 1974; Campbell et al., 1982). X-wave forms are formed when a stylet penetrates the sieve elements in the phloem and they always precede an ingestion wave form (Campbell et al., 1982; McLean and Kinsey, 1967). The ingestion wave form indicates withdrawal of sap from the sieve element. The duration of phloem ingestion by aphids is longer on susceptible hosts than on resistant hosts (Campbell et al., 1982; Montllor et al., 1983). The reduction of phloem ingestion by aphids on resistant hosts is not clearly known whether to be due to lack of a stimulant or the presence of feeding deterrent (Campbell et al., 1982).

Drought Stress

A water deficit (drought stress) usually causes loss of cell turgor in the plant. This loss of turgor is disadvantageous to the feeding aphid because sap pressure assists in food uptake (Wearing et al., 1967). This study also showed that the lowering of phloem turgor pressure may have greater effect on the reduction of the duration and/or frequency of feeding than reducing the rate of ingestion of sap.

The reproduction of aphids is influenced by water deficits in the host plant; both increases and decreases have been reported. The increases in reproduction has been explained by the hydrolysis of protein under water stress, which enrichs the phloem sap with soluble nitrogen favorable to aphids (Wearing et al., 1967).

Maxwell & Painter (1959) showed that reduction of moisture content in the host plant significantly affects the rate of honeydew deposition by the greenbug.

There is evidence showing promotion of greenbug outbreaks during periods of drought (Walker, 1954). Greenbugs can greatly reduced the yield of drought-stressed sorghum (Kindler and Staples, 1981). Greenbugs can also alter potentially adaptive responses of wheat to drought stress. For example, Dorschner et al. (1986) found greenbugs reduced cell membrane stability and osmotic adjustment in drought stressed wheat.

Host-Plant Resistance

Studies by Al-Mousawi et al. (1983) suggest that resistance in wheat is physiological and biochemical, and wheat plants may contain

greenbug inhibitor compounds or cell wall materials that contain components which are unaffected by insect enzymes.

A recent study by Dreyer & Campbell (1984) concluded that irregular feeding behavior of greenbugs was associated with the degree of methylation of pectin in the plant intercellular matrix. The enzyme pectinase, present in the greenbug biotype C, could not readily hydrolyze pectins of the resistant variety of sorghum 'IS 809'. However, a newer biotype E (GBE) was able to feed on the GBC resistant variety of sorghum because of its more active pectin methylestrase. This indicates that the methylated pectins inside the leaf may be broken down by the pectinase of biotype E.

CHAPTER III

MATERIALS AND METHODS

Greenbug Growth and Development Studies

Four hexaploid wheat genotypes, Largo, OK-80268, Tam W-101, and Sturdy were used. Largo has a greenbug biotype C and E resistant gene derived from Triticum tauschii; OK-80268 has the 'Amigo' source of biotype C resistance derived from Secale cereale and is susceptible to biotype E; and Tam W-101 and Sturdy are susceptible to both biotype E and C. Tam W-101 is relatively drought resistant as compared to Sturdy (Johnson et al., 1984). Plants were grown in 10 cm diameter pots, in a growth chamber at 21°C, 14 hours photophase (250 μ mol quanta m^{-2} s^{-1}) and 65-70% relative humidity for four weeks. Nutrients were supplied with 25% Hoagland's solution every two days. Greenbugs were cultured on a susceptible barley (Hordeum vulgar L.) variety (wintermalt) and maintained in a growth chamber.

The experiments were designed in randomized complete blocks with four wheat genotypes and two water levels. There were a total of eight treatment combinations per block and three blocks per experiment. The experiment was repeated two times.

Prior to infestation with greenbugs, water potential (WP), solute potential (SP) and turgor pressure (TP) of last fully expanded leaf were taken using leaf cutter psychrometers as described by Johnson et

al. (1984). Each plant was then infested with two 2-day old biotype E nymphs and these nymphs were confined in cylindrical polyethylene cages to limit migration of greenbugs from one treatment to the other. Host plants in the wet treatments were watered every day but plants in the dry treatment were watered once after seven days. After seven days without water the seedlings were severely drought stressed and greenbugs started leaving the plant. Greenbugs were grown for 15 days in the growth chamber. Leaf water potential readings were taken at the end of the experiments to determine the level of plant stress. At the end of the experiment, greenbugs were collected from each plant and their fresh weight, total number, number of adult, juveniles, and alates were recorded.

Electronic Monitoring of Greenbug Feeding

Aphid feeding monitors designed by Brown and Holobrook (1976) and modified at Oklahoma State University were used. In this feeding monitor system, a 25 hz and 200 microvolt alternating current is passed into the plant and greenbug. In each treatment, the dorsum of a greenbug was attached to a 10 micron diameter 2 cm long gold wire with collodial silver cement. The greenbugs were placed on the adaxial surface of the last fully expanded leaf of the plant. When a greenbug feeds and makes electrical contact with the plant, a small current passes through the aphid and plant system. A strip chart recorder, attached to the system, records wave forms as voltage fluctuations resulting from different phases of feeding.

Wheat genotypes OK-80268, Largo, and Sturdy, which were used in the greenbug growth and development study, were also used in this

study. Greenbugs were cultured on the greenbug susceptible wheat cultivar Tam W-101. These plants were infested with several one-day old greenbug nymphs and were allowed to grow until they reached adulthood. By this method, equal aged adult greenbugs were obtained for the monitoring experiment.

Germinated seeds were planted in 7.62 cm diameter plastic pots filled with 270 gm pre-dried and weighed soil. Each pot was watered with 25% Hoagland's solution up to near its water holding capacity (50 ml.) and placed in a growth chamber. The growth chamber was set at 19-21°C, 12 hour photophase (650μ mol quanta m^{-2} sec^{-1}) and 60-75% relative humidity. Weighing and re-watering of pots was done every two days to maintain the initial water level in the soil. Usually about 40 mls of water was lost from a pot over the two day period.

Fifteen day old plants with fully emerged leaves were used in the experiment. Before starting the monitoring, leaves of dry treatments were stressed to an average level of -2.0 MPa after two days without water. The wet treatments were maintained well watered and unstressed. At the beginning of greenbug monitoring leaf samples from control plants were taken to determine leaf water potential as described above. Leaf samples were also taken from the test plant at the end of the 24 hour monitoring period.

The experiment layout was a split plot experiment. The main units are the days in which monitoring is done and the factors are water treatment. There were a total of six treatment combinations (Largo wet, Largo dry, Sturdy wet, Sturdy dry, OK-80268 wet, and OK-80268 dry). Three treatment combinations were monitored in the first day and the remaining three treatments in the second day. All dry

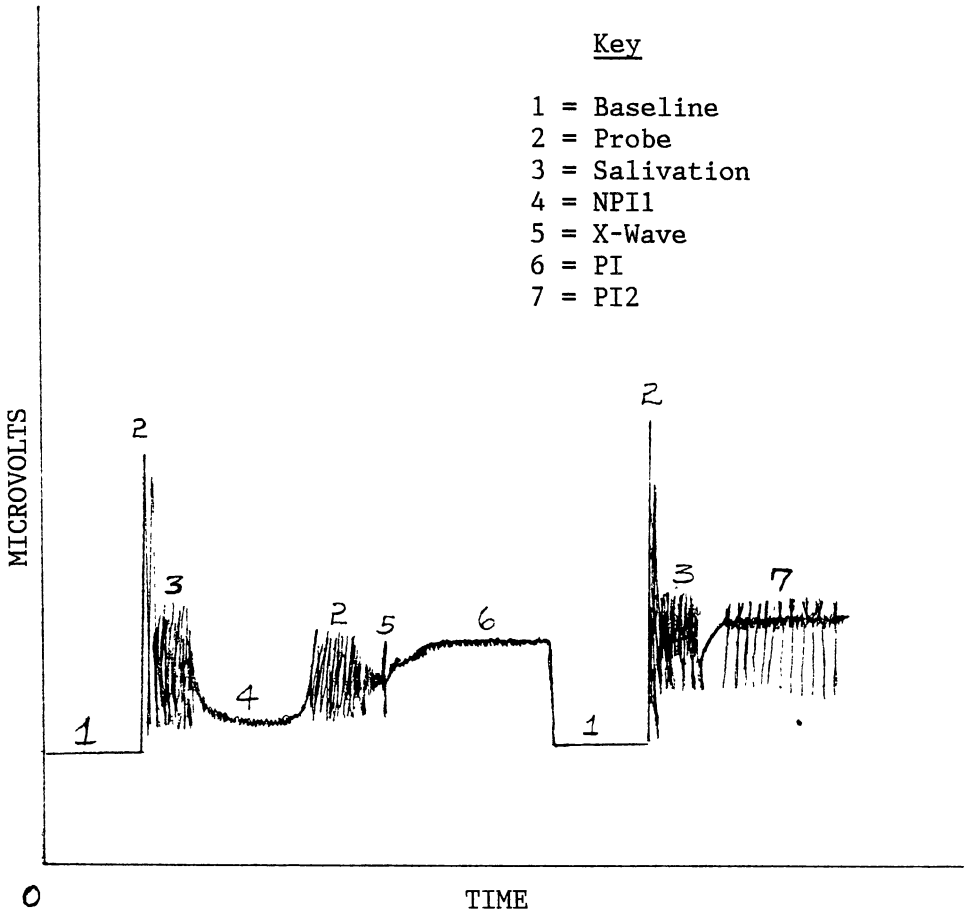
treatments were monitored at one time in order to maintain similar stress levels and reduce variation in stress levels of dry treatments, which might occur from separate monitoring days. Treatments in each block were randomized over the three feeding monitors used. During monitoring, plants were under these conditions: 21-24°C, 55-65% relative humidity, and a 12 hour photophase.

The experiment was repeated ten times and in each experiment greenbugs were monitored for 24 hours for each treatment. During monitoring, wave forms corresponding to different greenbug feeding events were recorded for each treatment. Interpretation of wave forms corresponding to the different feeding events was done using studies done by Mclean and Kinsey (1964) and Nielson and Don (1974). Figure 1 illustrates wave forms formed by feeding aphids and wave forms were described by the previous studies (1-6) as follows:

1. Baseline - when the greenbug is not probing.
2. Probe - insertion of stylet into the plant.
3. Salivation - formation of sheath material from the time of initial probe to location of the vascular bundle.
4. Non-phloem ingestion 1 (NPI 1) - ingestion wave form different from wave form due to ingestion from phloem tissue.
5. X-wave - penetration of the sieve element in the phloem.
6. Phloem ingestion (PI) - ingestion from the phloem sieve tube.
7. Non-phloem ingestion 2 (NPI 2) - undescribed (new) ingestion wave form.

Using the recorded data the following parameters were analyzed:

1. Total duration and frequency of feeding behaviors over 24 hours feeding period.
2. Total duration and frequency of feeding behaviors over four hours time intervals.



The sequence of wave forms are not necessarily the same as the ones shown above.

Figure 1. Illustration of Wave Forms Corresponding to Different Greenbug Feeding Events

3. Total probes, the number and percentage of phloem ingestion and time to the 1st phloem contact and ultimate phloem acceptance.

4. Total probes, the number and percentage of phloem ingestion and time to the 1st phloem contact of greenbugs feeding on water stressed wheat plants.

Honeydew Production and Chlorophyll Damage

Experimental plants used for the feeding monitor study were also used for honeydew and chlorophyll studies. Right after the monitoring experiment, the test plants were arranged in a randomized complete block design. The experimental factors were wheat genotypes and water levels. On each plant the last fully expanded leaf was selected and placed flat on a foam stage covered with aluminum foil. Two plexiglass cages were placed on each leaf and two adult greenbugs were put into each cage. For each block, control plants were used to determine the cage effects. The experimental plants were kept under the same conditions (temperature, humidity, photoperiod, light intensity and water application) as was in the previous monitoring experiment. After 5 days the cages were removed and aphids brushed off the leaf. Greenbugs were counted and their fresh and dry weight determined. The honeydew deposited on the cages and aluminum foil were collected and stored. The honeydew and infested leaf parts were used for honeydew and chlorophyll analysis.

Honeydew Extraction Method

Five milliliters of hot water was poured into a preweighed foil cup kept on a hot plate. Cages and foil were washed in the cup with hot water to remove honeydew. The cup with dissolved honeydew was put

in an oven at 70°C to evaporate the water. The difference in the cup weight before and after drying was the honeydew dry weight.

Chlorophyll Extraction Method

The extraction method described by Arnon (1949) and Mackiney (1941) was used. Leaf weight and leaf area measurements were taken before analyzing for chlorophyll loss. Leaves from each experimental plant were then ground until complete maceration with mortar and pestle. Eighty-five percent acetone was used to wash the mortar. The solution was stirred until all chlorophyll had been extracted and filtered through Whatman #1 filter paper into a volumetric flask. After the filteration process the volume of solution was brought to 25 ml. with 80% acetone and flask was capped and kept in darkness. Absorbance readings were taken at 645 nm and 663 nm and chlorophyll was calculated using the formula:

$$\text{Total Chlorophyll} = \frac{(20.2\ D_{645} + 8.02\ D_{663})\ V}{cm^2}$$

where:

D_{645} = absorbance at 645 nm

D_{663} = absorbance at 663 nm

cm^2 = leaf area

V = total volume of volumetric in cm^3

Total Chlorophyll = microgram/cm^2

CHAPTER IV

RESULTS AND DISCUSSION

Greenbug Growth and Development

Greenbug biotype E was found to grow and develop better on susceptible wheat genotypes Sturdy, OK-80268, and Tam W-101 than on the resistant Largo. There was no interaction between water level and genotypes. Thus, means in Table I are averages of unstressed and stressed plants. Table I shows the mean number and fresh weight of greenbugs recovered from plants four weeks after infestation of two 2-day-old nymphs per plant. The total number of greenbugs, adults, and juveniles on Largo were significantly fewer than on Tam W-101, Sturdy, or OK-80268. The percentage of adult on Largo and Tam W-101 was higher than on OK-80268. But the percentage of juveniles was smaller on Largo and Tam W-101 than OK-80268 and Sturdy. These results, which showed the reduction of greenbug reproduction, suggest antibiosis effect of Largo. It was also observed that the total weight of greenbugs on Largo was significantly smaller than on OK-80268, Sturdy, and Tam W-101. This shows that greenbugs did not feed as well on Largo compared to the other genotypes which might be due to feeding deterrent compounds in Largo tissue.

In this experiment drought stress did not significantly affect greenbug growth and development at 5% probability level (Table II).

TABLE I

MEANS OF GREENBUG BIOTYPE E GROWTH AND DEVELOPMENT ON WHEAT GENOTYPES[1]

	Wheat Genotypes			
	Largo	OK-80268	Sturdy	Tam W-101
Total greenbugs	27[b]	148[a]	157[a]	107[a]
Adults	7[b]	23[a]	27[a]	25[a]
% adults	29[ab]	19[b]	20[b]	33[a]
Juveniles	19[b]	124[a]	128[a]	80[a]
% Juveniles	69[b]	80[a]	79[a]	65[b]
Alate	1[a]	1[a]	1[a]	1[a]
% alate	1[a]	1[a]	1[a]	2[a]
Total greenbug fresh weight (mg.)	5.6[b]	23.3[a]	25.4[a]	21.6[a]
Fresh weight/greenbug (mg.)	0.30[a]	0.24[a]	0.20[a]	0.38[a]

[1]Means followed by different letters within rows are significantly different ($p = 0.05$) by t-test. Means are averages of unstressed and stressed plants.

TABLE II

MEANS OF GREENBUG BIOTYPE E GROWTH AND DEVELOPMENT ON WHEAT GENOTYPES WITH DROUGHT STRESSED AND UNSTRESSED CONDITIONS[1]

	Water Status	
	Stressed -3.7 MPa[2]	Unstressed -0.9 MPa[2]
Total greenbugs	96[a]	124[a]
Adults	19[a]	22[a]
% adults	26[a]	24[a]
Juveniles	75[a]	101[a]
% juveniles	72[a]	74[a]
Alate	2[a]	1[a]
% alate	1[a]	1[a]
Total greenbug fresh weight (mg.)	18[a]	21[a]
Fresh weight/greenbug (mg.)	0.29[a]	0.27[a]

[1]Means are averages over wheat genotypes (Largo, Sturdy, Tam W-101, and OK-80268). Means followed by different letters within rows are significantly different ($p = 0.05$) by t-test.

[2]Leaf water potential at the end of the experiment as megapascals (MPa).

Honeydew Production and Chlorophyll Reduction

Honeydew production by greenbug biotype E was not significantly affected by the wheat genotypes (Table III). Within error, equal amounts of honeydew accumulated by greenbugs feeding on Largo, Sturdy, and OK-80268. Also the amount of honeydew produced per greenbug was similar for all the genotypes.

Drought stress, however, reduced greenbug reproduction, weight gain and honeydew production (Table IV). The lesser amount of honeydew production under drought stress by greenbugs might be due to reduced sap flow as a result of reduced turgor pressure of the plant. The higher proportion of weight gain by greenbug per unit honeydew excreted on stressed plant than on unstressed plant may be due to the improvement of sap quality through the hydrolysis of protein and enrichment of phloem sap with soluble nitrogen (Wearing et al., 1967). Comparing Tables III and IV, greenbug reproduction and honeydew production were not significantly affected by wheat genotypes (Table III), but they were reduced by drought stress (Table IV). Greenbug weight gain was reduced by both drought stress and resistant genotypes. Drought stress affected greenbug growth and development in this experiment as opposed to the previous experiment. The reason for these different results is not clear, but may be associated with higher variance in the first experiment.

Visual observation of greenbug feeding sites indicated that there was higher tissue damage (necrotic followed by chlorotic areas) on Sturdy and OK-80268 than on Largo. Largo showed a less sensitive visual reaction to greenbug feeding, indicating its higher tolerance as compared to the other two genotypes. Chlorophyll analysis was done

TABLE III

MEANS OF REPRODUCTION, BIOMASS ACCUMULATION AND HONEYDEW PRODUCTION OF GREENBUG BIOTYPE E ON WHEAT GENOTYPES UNDER WET CONDITIONS[1]

	Wheat Genotypes		
	Largo	OK-80268	Sturdy
Total greenbugs	75[a]	77[a]	80[a]
Total greenbug dry weight (mg.)	3.1[b]	3.8[a]	4.0[a]
Dry wt./greenbug (mg.)	0.042[b]	0.048[a]	0.049[a]
Total honeydew dry wt. (mg.)	4.4[a]	4.9[a]	4.9[a]
Honeydew dry wt./greenbug (mg.)	0.058[a]	0.064[a]	0.062[a]
Greenbug dry wt./honeydew dry wt.	0.78[a]	0.96[a]	0.86[a]

[1]Means followed by different letters within rows are significantly different ($p = 0.05$) by t-test.

TABLE IV

MEANS OF REPRODUCTION, BIOMASS ACCUMULATION, AND HONEYDEW PRODUCTION OF GREENBUG BIOTYPE E ON WHEAT GENOTYPES WITH WATER STRESSED AND UNSTRESSED CONDITIONS[1]

	Wheat Genotypes					
	Largo		OK-80268		Sturdy	
	Stressed[2]	Unstressed[3]	Stressed	Unstressed	Stressed	Unstressed
Total greenbugs	51[b]	75[a]	65[b]	77[a]	69[b]	80[a]
Total greenbug dry wt. (mg.)	1.49[a]	3.13[b]	2.67[a]	3.68[b]	3.08[a]	3.94[b]
Dry weight/greenbug (mg.)	0.029[a]	0.042[b]	0.042[a]	0.048[b]	0.045[a]	0.049[b]
Total honeydew dry wt. (mg.)	1.88[a]	4.41[b]	2.59[a]	4.86[b]	2.86[a]	4.94[b]
Honeydew dry wt./greenbug (mg.)	0.038[a]	0.058[b]	0.038[a]	0.064[b]	0.039[a]	0.062[b]
Greenbug dry wt./honeydew dry wt.	1.22[a]	0.78[a]	1.44[a]	0.96[a]	1.39[a]	0.86[a]

[1]Means followed by different letters within rows for each wheat genotypes are significantly different ($p = 0.05$) by t-test.

[2]Average leaf water potential = -2.0 MPa.

[3]Average leaf water potential = -0.5 MPa.

with the objective of determining the chlorophyll damage on the infested leaf by greenbug feeding. The result indicated that susceptible genotypes lost significantly more chlorophyll than the resistant Largo did (Table V). Chlorophyll reductions due to greenbug infestations were significantly higher on stressed than on unstressed greenbug susceptible genotypes. This indicates that on susceptible wheat genotypes, drought stress and greenbug stress had a synergistic effect on chlorophyll loss.

Feeding Monitor

The total duration of non-phloem ingestion, probing, salivation and phloem ingestion differed for greenbugs feeding on Largo than either Sturdy or OK-80268 (Table VI). On Largo greenbugs spent less time with stylet contact on the leaf (baseline), more time probing and more time salivating, compared to Sturdy and OK-80268. Greenbugs spent less time, however, ingesting on Largo compared to the other wheat genotypes for the 24 hour feeding period. The increased duration of salivation on Largo implied a physical barrier to greenbug stylet movement toward the phloem. A study by Dreyer and Compbell (1984) indicated this stylet barrier to be intercellular pectin in the plant. They also concluded that irregular feeding behavior of greenbugs on resistant plants was associated with the degree of methyletion of pectin in the intercellular matrix.

The frequency of different greenbug feeding behavior patterns over a 24 hour feeding period was also analyzed. The analysis indicated that greenbugs feeding on Largo performed more frequent probing, salivation, x-waves, and phloem ingestion events than on

TABLE V

MEANS OF CHLOROPHYLL DAMAGE BY GREENBUG BIOTYPE E ON WHEAT GENOTYPES WITH DROUGHT STRESSED AND UNSTRESSED CONDITIONS[1]

Wheat Genotype	Water Status[2]	Greenbug Infestation	Chlorophyll μ g./cm^2	Chlorophyll Lost (μ g.)	Percent Chlorophyll Reduction
Largo	Unstressed	NIF	54.4		
	Unstressed	IF	46.9	8.7^{c}	15.0^{c}
	Stressed	NIF	55.6		
	Stressed	IF	46.2	8.2^{c}	14.8^{c}
OK-80268	Unstressed	NIF	55.6		
	Unstressed	IF	41.0	14.9^{bc}	25.5^{c}
	Stressed	NIF	54.4		
	Stressed	IF	25.1	29.1^{a}	53.2^{a}
Sturdy	Unstressed	NIF	50.4		
	Unstressed	IF	38.0	12.3^{c}	23.8^{c}
	Stressed	NIF	50.6		
	Stressed	IF	30.4	20.1^{b}	39.9^{b}

[1]Means followed by different letters within columns are significantly different (p = 0.05) by t-test.

[2]Leaf water potentials for unstressed and stressed are -0.5 MPa and -2.0 MPa respectively.

TABLE VI

TOTAL DURATION AND FREQUENCY OF DIFFERENT FEEDING BEHAVIORS OF GREENBUG BIOTYPE E OVER A TWENTY-FOUR HOUR MONITORING PERIOD[1]

		Wheat Genotype		
		Largo	OK-80286	Sturdy
Baseline	Frequency	27^{a}	8^{c}	14^{b}
	Duration (min.)	74^{a}	19^{b}	45^{b}
Probe	Frequency	27^{a}	8^{c}	14^{b}
	Duration (min.)	14^{a}	4^{b}	7^{b}
Salivation	Frequency	31^{a}	7^{c}	13^{b}
	Duration (min.)	345^{a}	100^{b}	114^{b}
Non-phloem ingestion 1	Frequency	2^{a}	2^{a}	1^{a}
	Duration (min.)	67^{a}	9^{a}	4^{a}
X-wave	Frequency	8^{a}	3^{b}	4^{b}
	Duration (min.)	7^{a}	2^{b}	4^{b}
Phloem ingestion	Frequency	8^{a}	3^{b}	4^{b}
	Duration (min.)	902^{b}	1241^{a}	1247^{a}
Non-phloem ingestion 2	Frequency	3^{a}	3^{a}	2^{a}
	Duration (min.)	67^{a}	84^{a}	20^{b}

[1]Means followed by different letters within rows are significantly different ($p = 0.05$) by t-test.

Sturdy and OK-80268 (Table VI). An increased number of separate probes by greenbugs biotype C feeding on a resistant sorghum variety has been reported by Campbell et al. (1982) and Montllor et al. (1983). More frequent probes and shorter duration of phloem ingestion on Largo might be due to greenbugs non-preference to plant phloem sap.

The feeding behavior of greenbugs was also compared at four hour time intervals during the 24 hour assay period (Tables VII and VIII). In the first twelve hours of feeding there were significant differences between Largo and Sturdy and OK-80268 for the important feeding events like probing, salivation, and phloem ingestion. Later during the day these differences become smaller and smaller for most of the feeding events. The reason for the disappearance of differences after 12 hours was not clear. Studies by Montller et al. (1983) show that, after a long period of probing, greenbug biotype C (GBC) will ingest from the phloem of resistant sorghum IS 809 for long periods. They speculated that GBC can adjust to the presence of feeding deterrent or the absence of feeding stimulant in resistant host-plants.

There were also significant differences in the frequency of feeding events (non-probing, probe, salivation, and phloem ingestion) between the resistant wheat genotype (Largo) and susceptible ones (Sturdy and OK-80268) for the first 12 hours. Significant differences were not observed, however, for the last 12 hours. It was also observed that the frequency of feeding events decreased from an interval to the next (Tables IX and X). This might be due to greenbugs making a lot of tasting before accepting the phloem in the early feeding period. Later the reduction in frequency of feeding

TABLE VII

TOTAL DURATION (MINUTES) OF FEEDING BEHAVIORS OF GREENBUG BIOTYPE E OVER FOUR HOURS TIME INTERVALS[1]

Time Interval	Wheat Genotype	Baseline	Probe	Salivation	NPI1	X-wave	PI	NPI2
0-4 hours	Largo	40[a]	8[a]	117[a]	6.9[a]	1.4[a]	45[b]	24[a]
	OK-80268	16[b]	3[b]	60[b]	--[2]	1.3[a]	134[a]	30[a]
	Sturdy	30[b]	6[b]	72[b]	1.7[a]	1.3[a]	118[a]	12[a]
4-8 hours	Largo	20[a]	3.3[a]	97[a]	18[a]	1.7[a]	101[b]	0.05[a]
	OK-80268	--	--	36[b]	--	1.5[a]	206[a]	--
	Sturdy	10[a]	0.4[b]	16[c]	3[b]	0.9[a]	212[a]	0.04[a]
8-12 hours	Largo	2[a]	0.5[a]	47[a]	3.6[a]	1.4[a]	182[b]	--
	OK-80268	--	--	--	--	--	226[a]	--
	Sturdy	0[a]	0.1[a]	0.4[b]	0.4[b]	0.2[b]	239[a]	--

[1]Means followed by different letters within columns for each time interval are significantly different ($p = 0.05$) by t-test.

[2]The feeding event did not appear on the indicated time interval.

TABLE VIII

TOTAL DURATION (MINUTES) OF FEEDING BEHAVIORS OF GREENBUG BIOTYPE E OVER FOUR HOURS TIME INTERVAL

Time Interval	Wheat Genotype	Baseline	Probe	Salivation	NPI1	X-wave	PI	NPI2
12-16 hours	Largo	3.2[a]	0.5[a]	19[a]	--	0.4[a]	198[a]	1.2[a]
	OK-80268	--[2]	--	--	--	--	228[a]	--
	Sturdy	1.8[a]	0.3[a]	8[a]	--	0.2[a]	217[a]	0.1[a]
16-20 hours	Largo	5.1[a]	0.5[a]	31.4[a]	14.0[a]	0.6[a]	190[a]	2.8[a]
	OK-80268	--	--	34.5[a]	--	2.0[a]	201[a]	9.9[a]
	Sturdy	3.0[a]	0.3[a]	10.0[a]	0.1[a]	0.1[a]	223[a]	1.6[a]
20-24 hours	Largo	3.2[a]	0.9[a]	35[a]	1.2[a]	1.0[a]	181[b]	10[a]
	OK-80268	--	--	--	--	--	238[a]	--
	Sturdy	0.1[b]	0.1[a]	9[a]	0.1[a]	0.6[a]	225[a]	2[a]

[1]Means followed by different letters within columns for each time interval are significantly different ($p = 0.05$) by t-test.

[2]The feeding event did not appear on the indicated time interval.

TABLE IX

FREQUENCY OF FEEDING BEHAVIORS OF GREENBUG BIOTYPE E OVER FOUR HOURS TIME INTERVALS[1]

Time Interval	Wheat Genotype	Baseline	Probe	Salivation	NPI1	X-wave	PI	NPI2
0-4 hours	Largo	16[a]	15[a]	14[a]	1[a]	2[a]	2[a]	1[b]
	OK-80268	6[b]	7[b]	5[c]	--[2]	2[a]	2[a]	3[a]
	Sturdy	12[b]	12[a]	8[b]	1[a]	2[a]	2[a]	1[b]
4-8 hours	Largo	7[a]	7[a]	9[a]	1[a]	3[a]	2[a]	1[a]
	OK-80268	--	--	4[b]	--	2[a]	1[b]	--
	Sturdy	2[b]	2[b]	3[b]	1[a]	2[a]	2[a]	1[a]
8-12 hours	Largo	2[a]	2[a]	4[a]	1[a]	3[a]	3[a]	--
	OK-80268	--	--	--	--	--	1[b]	--
	Sturdy	1[a]	1[a]	1[b]	1[a]	1[b]	1[b]	--

[1]Means followed by different letters within columns for each time interval are significantly different ($p = 0.05$) by t-test.

[2]The feeding event did not appear on the indicated time interval.

TABLE X

FREQUENCY OF FEEDING BEHAVIORS OF GREENBUG BIOTYPE E OVER FOUR HOURS TIME INTERVALS[1]

Time Interval	Wheat Genotype	Baseline	Probe	Salivation	NPI1	X-wave	PI	NPI2
12-16 hours	Largo	2[a]	2[a]	2[a]	1[a]	1[a]	1[a]	1[a]
	OK-80268	--[2]	--	--	--	--	1[a]	--
	Sturdy	1[a]	1[a]	2[a]	1[a]	1[a]	1[a]	1[a]
16-20 hours	Largo	2[a]	2[a]	3[a]	1[a]	2[a]	2[a]	1[a]
	OK-80268	--	--	5[b]	--	2[a]	1[a]	2[a]
	Sturdy	2[a]	1[a]	2[a]	1[a]	1[a]	1[a]	1[a]
20-24 hours	Largo	2[a]	2[a]	3[a]	1[a]	2[a]	2[a]	1[a]
	OK-80268	--	--	--	--	--	1[a]	--
	Sturdy	1[a]	1[a]	2[a]	1[a]	2[a]	2[a]	1[a]

[1]Means followed by different letters within columns for each time interval are significantly different ($p = 0.05$) by t-test.

[2]The feeding event did not appear on the indicated time interval.

events got could be as a result of greenbug adaptation to the chemical constituents in the host plants (Montllor et al., 1983) and continue feeding phloem sap for longer time.

The effect of wheat genotypes on greenbug probing frequency, percent of probes ending with phloem ingestion, and time taken to reach phloem were examined (Table XI). On Largo the total number of probes and number of probes with successful phloem contact were significantly higher than either in Sturdy or OK-80268. The percentage of probes with phloem ingestion is similar in Largo and Sturdy, showing that greenbugs have the same probability of getting into the phloem in resistant and susceptible wheat genotypes. The higher probability of phloem ingestion observed on OK-80268 compared to Largo was due to the significantly smaller number of probes in OK-80268. The percentage of probes with committed phloem ingestion was higher on OK-80268 and Sturdy than on Largo. The time spent by greenbugs to make the first phloem contact and ultimate phloem acceptance was longer on Largo. The longer time spent to accept the phloem and the lower percentage of probes with committed phloem ingestion suggest greenbug non-preference to phloem sap. This experiment verified that greenbugs get into the phloem of resistant or susceptible genotypes with equal probability but the probability of accepting the phloem is significantly lower in resistant than in susceptible genotype.

Drought stress had a significant effect on greenbug feeding behavior (Table XII). Fewer probes were observed on stressed than on unstressed plants. The number of probes with phloem ingestion was higher on stressed than on unstressed plants. Compared to unstressed

TABLE XI

EFFECT OF WHEAT GENOTYPES ON THE NUMBER OF PROBES, PERCENT OF PROBES WITH SUCCESSFUL PHLOEM CONTACT (X-WAVE) AND COMMITTED PHLOEM INGESTION (CPI) AND THE TIME TO FIRST X-WAVE AND CPI OF GREENBUG BIOTYPE E[1]

	Wheat Genotype		
	Largo	OK-80268	Sturdy
Number of probes	27[a]	7[b]	14[b]
Number of probes with successful phloem contact	3.23[a]	1.43[b]	1.95[b]
Percent of probe with phloem ingestion	14.78[b]	26.19[a]	17.68[b]
Percent of probe with committed phloem ingestion	60.10[b]	93.30[a]	84.00[a]
Time to the first phloem contact (min.)	190[a]	105[b]	117[b]
Time to the first committed phloem ingestion (min.)	320[a]	142[b]	129[b]

[1]Means followed by different letters within rows are significantly different ($p = 0.05$) by t-test.

TABLE XII

EFFECT OF WATER STRESS ON THE NUMBER OF PROBES, PERCENT OF PROBES WITH SUCCESSFUL PHLOEM CONTACT (X-WAVE) AND COMMITTED PHLOEM INGESTION (CPI) AND THE TIME TO THE FIRST X-WAVE AND CPI OF GREENBUG BIOTYPE E[1]

	Water Level	
	Stressed[2]	Unstressed
Number of probes	15.70[a]	17.13[a]
Number of probes with successful phloem contact	2.59[a]	1.81[b]
Percent of probes with phloem contact	23.80[a]	15.80[b]
Percent of probes with committed phloem ingestion	73.10[b]	85.20[a]
Time to the first phloem contact (min.)	116[b]	158[a]
Time to the first committed phloem ingestion (min.)	193[a]	203[a]

[1]Means followed by different letters within rows are significantly different (P = 0.05) by t-test. Means are averaged over wheat genotypes (Largo, Sturdy, OK-80268).

[2]Average water potential is -2.0 MPa.

plants, stressed plants had a higher percentage of probes that led to some phloem ingestion but a lower percentage of probes with committed phloem ingestion. This lower percentage of probes with committed phloem ingestion on stressed plants might be due to the decrease in plant turgor pressure under drought stress, which perhaps forces the greenbug to look for other feeding sites. It might also be due to the drought induced concentration of phloem sap constituents like feeding deterrent alkaloids. Greenbugs were observed getting into the phloem faster on stressed plants than on unstressed ones. This may be due to the presence of flaccid cells during drought.

The feeding monitor experiment showed significant difference in feeding behavior of greenbugs on resistant and susceptible and on stressed and unstressed wheat plants for the first 12 hours of monitoring. The feeding monitor experiment shows the total duration and frequency of feeding events but not the quantity of sap ingested by the greenbug. Thus, there could be significant differences in the amount of phloem sap ingested by greenbugs even though differences in total duration and frequency of feeding events disappear after 12 hours of feeding period.

This experiment helps to understand how greenbug feeding behavior is affected by host plants and environment (drought stress). Thus electronic feeding monitors are a useful adjunct to other methods of screening for resistance to greenbugs.

CHAPTER V

CONCLUSION

The greenbug growth and reproduction study indicated that greenbug growth and development were affected significantly by greenbug resistant wheat genotypes. Greenbugs grow and reproduce better on susceptible wheat genotypes (OK-80268, Tam W-101, and Sturdy) than on the resistant genotype Largo. This result could be related to greenbug feeding. Shorter duration of phloem ingestion and reduced weight gain and reproduction of greenbugs were associated with the resistant wheat genotype Largo.

The second experiment on greenbug feeding behavior showed variations of greenbug feeding behavior was influenced by wheat genotypes and drought stress. More frequent probes and salivation, longer duration of salivation, delayed phloem acceptance, and reduced ingestion were associated with greenbug feeding on the resistant wheat genotype Largo. The shorter duration and delayed commitment to phloem ingestion on Largo suggest non-preference of greenbugs to phloem sap. In this experiment, significant differences in feeding behavior events appear in the first 12 hours of feeding. Therefore, 12 hours feeding monitor will be enough to compare greenbug feeding behavior on different wheat genotypes.

The change of greenbug feeding under drought stress may be associated with plant turgor pressure. Under drought stress, the duration of phloem ingestion, weight gain, and fecundity of greenbugs were reduced. But drought stress apparently made it easier for greenbugs to find phloem tissue.

In the greenbug honeydew production and chlorophyll damage study, reduced growth and reproduction of greenbugs on the resistant wheat genotype Largo compared with OK-80268 and Sturdy was observed. But honeydew production was unaffected by wheat genotypes. Drought stress, however, altered greenbug reproduction and honeydew production significantly. Drought coupled with greenbug stress had a synergistic effect on chlorophyll damage.

The combination of the three experiments gives important information on host, insect and environment interaction in greenbug studies. Using these techniques wheat genotypes could be compared for their ability to resist or affect greenbug feeding behavior.

The biochemical and physiological nature of greenbug resistance should be further studied. The qualitative analysis of phloem fluid, honeydew and salivary gland fluid of greenbugs are important for a better understanding of the greenbug and host plant interaction. Analysis of honeydew and phloem fluid would give information on the nature of resistance of the host while analysis of the greenbug salivary gland may reveal the basis of greenbug virulence.

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