FEEDING BEHAVIOR AND DEVELOPMENT OF BIOTYPES E, G, AND H OF SCHIZAPHIS GRAMINUM (HOMOPTERA: APHIDIDAE) ON 'WINTERMALT' AND 'POST' BARLEY, AND THE EVALUATION OF RESISTANCE SOURCES IN SORGHUM TO SEVERAL GREENBUG CLONES

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CHAPTER I

INTRODUCTION

The greenbug, (Schizaphis graminum (Rondani), is an economically important pest of small grain cereals and sorghum, (Sorghum bicolor (L.) Moench, in the U.S.A. and most parts of the world. The occurrence of greenbug biotypes is well documented (Woods 1961, Harvey and Hackerott 1969a, Peters et al. 1975, Porter et al. 1982, Kindler and Spomer 1986, and Puterka et al. 1988).

New biotypes are characterized mainly by their ability to damage host plants previously resistant to greenbug populations (Puterka et al. 1988). Puterka et al. (1988) characterized new greenbug biotypes G and H using major plant sources of greenbug resistance. Greenbug biotype G was found to damage all known sources of greenbug resistance in wheat, Triticum aestivum L., but did not damage 'Wintermalt' barley, Hordeum vulgare L., a variety previously reported to be susceptible to all greenbug biotypes. In the same study biotype H was reported to be avirulent on all sorghum varieties but severely damaged 'Post' a barley variety supposedly resistant to all previously described biotypes. High levels of resistance to greenbugs among barley cultivars were reported in 1945 by Atkins and Dahms, but biotype H was the first to overcome a resistant barley cultivar.

The occurrence of greenbug biotype C on sorghum in 1968 (Harvey and Hackerott 1969b) led to a concerted effort to screen germplasm for resistance,

explain the mechanisms of resistance and its inheritance, and transfer this resistance to elite germplasm (Schuster and Starks 1973, Teetes et al. 1974a, b). In 1980 biotype E developed and was capable of injuring the majority of sorghum genotypes resistant to biotype C (Porter et al. 1982). Only four sources of resistance to biotype C were resistant to biotype E (Johnson et al. 1981, Porter et al. 1982, Starks et al. 1983).

A critical prerequisite to resistance management is anticipation of development of insect resistance before control actually fails. This involves field monitoring and laboratory tests of the field collected samples, which in some situations is done when it is already too late for new resistant plant genotypes to be deployed.

There are several techniques used for characterizing greenbug biotypes. Among such techniques, the electronic monitoring of feeding behavior has been very useful in defining possible differences among greenbug biotypes on wheat (Niassy et al. 1987), sorghum (Campbell et al. 1982), and barley cultivars (Peters et al. 1988).

Puterka and Slosser (1986) reported on techniques to induce greenbugs into sexual cycle and achieve egg hatching and therefore making it possible to cross different greenbug biotypes in the laboratory. Breeding greenbug biotypes has produced recombinants that have a broader range of virulence than their parents (Puterka and Peters 1989a, b). Through the laboratory production of highly virulent types, it is now possible to screen potential sources not yet recognized in the field.

My research at OSU had two somewhat different objectives. They were:

Determine, by use of the electronic feeding monitor, any differential response in feeding behavior by biotypes E, G, and H on resistant 'Post' and susceptible 'Wintermalt' barley and also to determine the possible relationships with development and fecundity; and to evaluate some of the available resistance sources in sorghum to determine potential durability of their resistance to the laboratory clones of greenbug biotypes and crosses.

CHAPTER II

LITERATURE REVIEW

Greenbug Biotype

History of Biotypes

The greenbug, Schizaphis graminum (Rondani) (Homoptera: Aphididae), is a major pest of small grain cereals and sorghum in the Great Plains of the United States and other parts of the world. This aphid was first described in Italy (Rondani 1852). The first greenbug infestation in the United States was reported on oat in Virginia as early as 1882 (Webster and Phillips 1912).

Greenbug populations are comprised of distinct races that differ in the ability to damage the different resistance sources. These races are commonly referred to as 'biotypes' and each biotype is a phenotypic expression of an indefinite number of genotypes (Puterka et al. 1988). The first greenbug resistant wheat, Dickinson Selection 28A (DS 28A), was reported by Dahms et al. (1955). However, DS 28A was found to be susceptible to the greenbug population in 1959 while this source was being incorporated into wheat varieties. The race that had the ability to damage DS 28A was designated biotype B (Wood 1961). This marked the beginning of biotype history of greenbugs. The identification of resistant DS 28A made possible the beginning of biotype classification. By using DS 28A wheat as a differential variety, Wood (1961) was able to distinguish two

biotypes. Biotype B survived on DS 28A but biotype A did not. In 1968, biotype C developed and extended the host range of the greenbug to include sorghum (Harvey and Hackerott 1969a).

Wood and Starks (1972) reported that a major genetic change in the aphid population increased its importance as a pest of sorghum. Biotype C had increased adaptation and fecundity at extremely high temperatures compared with biotype B. Biotype C also could be distinguished from biotype B by morphological differences (Harvey and Hackerott 1969a).

Harvey and Hackerott (1969b) reported that 'Insave F.A.' rye and Dicktoo barley were resistant to both biotype B and the sorghum greenbug. 'Piper' sudangrass was found to be resistant in the seedling stage to biotype B but not to the greenbug found in sorghum. They concluded that the difference between biotype B from wheat and the greenbug found on sorghum was sufficient to designate the sorghum greenbug biotype C. Wood et al. (1969) also differentiated biotypes A, B and C on the basis of differences due to morphological change in the greenbug and to preferred feeding sites in the leaves. Biotype C predominated the biotype complex in wheat and sorghum up to the mid 1980's (Puterka et al. 1982, Kindler et al. 1984). Biotype D, an insecticide resistant race was first reported on sorghum in west Texas in 1974. Biotype D gives the same reaction on plants as biotype C but is resistant to organophosphorous insecticides (Teetes et al. 1975). In 1975, it was reported in Texas, Oklahoma, Kansas, Nebraska and South Dakota (Peters et al. 1975, Starks and Burton 1977a).

Porter et al. (1982) reported the collection of a new greenbug biotype E on

previously resistant wheat and sorghum. Hackerott et al. (1983) concluded that by 1981 this new biotype had largely replaced biotype C in the Great Plains States. It is still the predominant biotype in the Great Plains (Kindler et al. 1984, Bush et al. 1987, Kerns et al. 1987). Kindler and Spomer (1986) identified biotype F which had the ability to damage 'Amigo', but not DS 28A, and was later determined to be virulent to 'Largo' wheat (Puterka and Peters 1988).

Biotype surveys initiated in Oklahoma (Kerns et al. 1987) and Texas (Bush et al. 1987) detected two greenbug isolates that were designated biotypes G and H, respectively (Puterka et al. 1988). Biotype G was virulent to all known sources of resistance in wheat, but was relatively avirulent to sorghum and barley. Biotype H shared the same host relationship as biotype E on wheat, but was relatively avirulent to sorghum and was the first biotype reported to be virulent to greenbug resistant 'Post' barley. The biotypic diversity in greenbugs is far greater than first imagined and it is evident that there are many new biotypes to be discovered.

Biotype Concept

Eastop (1973) defined biotypes as those individuals of an insect species able to feed and grow significantly better on a resistant crop variety than other genotypes of the same species. Genetic variations in the herbivore pest population, gene for gene concept, and host parasitic compatibility and competence were some of the factors considered in biotype development (Maxwell and Jennings 1980). Biotypes are pest variants capable of overcoming the specific resistance of a cultivar, and for their success they must be compatible

with that specific cultivar and be competent. The variants may have arisen from chance mutation or through recombination, or existing polymorphism may have been favored through selection pressure from introduced resistant plant cultivars which disrupt the genetic balance in the population. Thus with the introduction of resistant cultivars, selection tends to proceed in the direction of fitness in pest population and individuals with high parasitic compatibility and competence establish and increase.

Biotype Identification

I prefer to recognize biotypes on the basis of differential response in feeding activities, growth and reproduction on selected resistant crop varieties (Puterka et al. 1988), but other indicators have been reported. Inayatullah et al. (1987) and Fargo et al. (1986) found that alate and apterous greenbug biotypes formed morphometrically distinct groups when multivariate analysis was applied to a large number of morphological measurements.

Abid et al. (1989), reported observation of differences in isozyme patterns among aphid species and some greenbug isolates. Mayo et al. (1988) have observed differences in chromosome measurements between biotypes C/E group and B/F group, but no significant differences between the biotypes within a group. Comparisons of the mitochondrial DNA digested by restriction enzymes have found restriction fragment length polymorphism between biotypes B, C, E, and F (Powers et al. 1989).

Greenbug Reproduction

The greenbug has two principle life modes in the United States. The monoecious anholocyclic mode occurs in the southern region while the holocycle may be found in the northern parts of the United States (Webster and Phillips 1912). The greenbug matures in six to eight days and then reproduces by parthenogenesis for 20 to 30 days giving birth to 50-60 nymphs. Greenbugs have five instars from birth to maturity (Wood and Starks 1975).

Greenbug sexuals have been reported in laboratory colonies (Mayo and Starks 1972). The greenbug holocycle provides a mechanism for genetic recombination during the sexual phase and is likely to produce many different combinations of virulence to any number of the resistance sources (Puterka and Peters 1990).

Greenbug Feeding Behavior and The Electronic Monitor

The feeding behavior of greenbugs is typical of that of other aphids. As aphids probe their hosts, they lower their heads and protract their antennae (Dixon et al. 1990b). During feeding aphids secrete saliva (salivary sheath and watery saliva) which helps them to disrupt plant tissues and insert their stylet into the vascular bundles (Miles 1972). Ingestion occurs mainly from sieve elements of the phloem which is the preferred feeding site but ingestion can also occur in epidermal tissues, mesophyll parenchyma (Pollard 1973, Chatters and Schlehuber 1951), and xylem (McLean and Kinsey 1967). McLean and Kinsey (1964) developed a technique for monitoring and recording aphid feeding and salivation.

Aphid feeding behaviors have different wave patterns which can be recorded by a strip chart recorder or other system, and these can later be interpreted and analyzed statistically. Distinct sequences in wave forms are uniquely associated with salivation and/or ingestion in specific plant tissues (McLean and Kinsey 1967, Campbell et al. 1982). Brown and Holbrook (1976) reported on an improved version of this technique. A small electric current is passed across the greenbug while feeding on the potted plant and a complete circuit is made comprising the aphid, plant and the soil. A full description of the feeding monitor and the distinct feeding behaviors (baseline, probe, salivation, non-phloem ingestion, x-wave and phloem ingestion) is provided by Niassy et al. (1987).

In plant resistance to aphids, the major differences between resistant and susceptible entries of the same crop have been in length of time taken by the aphids in reaching the phloem which was usually longer on resistant than on susceptible plants (Dreyer and Campbell 1984). Also the amount of time that aphids spend ingesting from the phloem was much shorter when the aphids feed on resistant entries and they had more difficulty in locating the phloem (Campbell et al. 1982, McLean and Kinsey 1968). Niassy et al. (1987) studied susceptible and resistant wheat using greenbug biotypes B and E, and found that phloem ingestion was longer on susceptible compared to resistant genotypes. Also the same authors 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. Biotype B in the first four hours showed slightly more salivation duration, but shorter phloem ingestion on

TAM 105 compared to the resistant 'TAM 107' or Largo x TAM 105 (Niassy et al. 1987). Peters et al. (1988) found differences in feeding behavior among biotypes B, C, and E using susceptible Wintermalt and resistant Post barley. There is a relationship between the reproductive capacity of the greenbug with the ability to ingest from the phloem. Greenbug fecundity (Kindler and Spomer 1986, Niassy et al. 1987) and intrinsic rate of increase (Kerns et al. 1989) of biotypes B, C, and E appears to be strongly correlated with the greenbug resistance in wheat varieties, 'Amigo', TAM 107 and Largo. Fecundity and intrinsic rate of increase of biotype F and G did not increase significantly on wheat varieties to which they were virulent compared with varieties to which they were avirulent (Kerns et al. 1989).

Greenbug Damage and Crop Loss

Plant damage from greenbug feeding occurs as a response to an unknown substance in the saliva which the aphid injects while feeding. The salivary product (assumed to determined by the virulence genes) interacts with the complementary gene products in the host plant to begin a cascade of physiological reactions in the plant that ultimately results in plant damage (Puterka and Peters 1990). The same authors reported that in sorghum, the phytotoxic damage manifests itself in quite a different manner. Greenbug damage on susceptible sorghum is exhibited as chlorosis, anthocyanosis, and necrosis which is a typical phytotoxic reaction. Methylated intercellular pectins have been implicated as one of the biochemical factors responsible for sorghum resistance to the greenbug saliva (Dreyer and Campbell 1984, Campbell and

Dreyer 1985).

After the outbreak of biotype C on sorghum in 1968, greenbugs have been recognized as one of the key destructive insect pests of sorghum, and have caused substantial losses to sorghum producers (Harvey and Hackerott 1969a, Starks and Burton 1977b). Coppock (1969) estimated that 7.5 million acres (3,037,500 ha) were damaged in 1968 in the United States at a cost to the sorghum producers of sixty-eight million dollars. In 1976, greenbug damage and control costs exceeded eighty million dollars (Starks and Burton 1977b).

Greenbug Control

Control Alternatives

Insecticide applications proved successful in controlling greenbugs after the outbreak in 1968. However, apart from the huge cost and environmental hazards involved with this control method, insecticides do not give long term solution to the problem because of the rapid build up of greenbug populations under favorable conditions (Dixon 1990a). Biological control although ecologically sound, tends to be less predictable and sometimes less reliable than chemical control. The use of natural enemies in the control of greenbug had been suggested (Walker et al. 1973), and attempts were made to import and establish the natural enemies and parasitoids (Eikenbary and Rogers 1973) but effective utilization is still debatable (Starks et al. 1974). Natural enemies may not keep abreast of the rapid build up of greenbug populations, thus economic damage may occur before parasite and predator populations build up (Bynum and Archer

1981).

The third option of controlling greenbugs is host plant resistance, which has several advantages: It is economical, specific to the target species, leaves no harmful residue in foods or the environment and is usually compatible with biological, chemical and other control methods. Painter (1958) defined three basic types of host plant resistance mechanisms: Tolerance- Plants produce relatively good yield in spite of infestations. Non-Preference (Antixenosis- of Kogan and Ortman 1978) Plants are avoided by the insect for oviposition, food or shelter. Antibiosis- An adverse effect by plant on the survival and reproduction of the insect. Resistance to insect pests is usually the result of more than one mechanism. The primary goal of host plant resistance is to breed resistance that is durable in the field. Satisfactory success in breeding durable greenbug resistant grain sorghum was achieved by breeders despite the biotype shifts (Puterka and Peters 1990). Biotype C resistant sorghum, available in 1975 (Starks et al. 1983) had a durability of about 10 years. Approximately 38% of the sorghum seed sold in 1986 was biotype E resistant (Kerns et al. 1987); therefore, greenbug resistance continues to be feasible in sorghum.

Sources and Mechanism of Resistance

Atkins and Dahms (1945) observed tolerance to severe infestations of greenbugs in the field in a number of wheat varieties in Denton, Texas and Lawton, Oklahoma in 1942. The same authors reported high level of resistance in barley cultivars.

The greenbug resistant strain of DS 28A was used by Painter and Peters

(1956) to investigate the inheritance of resistance to greenbugs. In 1959 the resistance was broken by biotype B (Wood 1961). Within the small grains, Amigo is resistant to biotype B and C, but is susceptible to biotype E (Porter et al. 1982) and F (Kindler and Spomer 1986). DS 28A and 'CI 9058' are resistant to biotype F, but susceptible to biotype B, C, and E (Kindler and Spomer 1986). Largo is resistant to biotypes C and E (Porter et al. 1982), but is susceptible to biotype B (Webster et al. 1986).

Biotype G is virulent to these resistance sources in wheat but avirulent to 'Wintermalt' (WM) barley, whereas biotype H exhibits most of the host plant reactions of biotype E but is virulent to Post barley (Puterka et al. 1988). In sorghum, the rise of new greenbug biotype C led to concerted efforts to screen sorghum germplasm for resistance and to transfer this resistance to adapted germplasm. A total of 9 sources of sorghum resistant to greenbug biotype C were reported for the seedling and the adult plant stages, (Teetes et al. 1974a, b). By 1980 at least 90% of the sorghum acreage in the U.S.A. was planted to resistant hybrids. These hybrids were derived mainly from SA 7536-1 and KS 30. Both of these sources were thought to derive their resistance from the Sorghum virgatum (Hack) Staph. (Starks et al. 1983). Only 4 sources of resistance to biotype C maintained their resistance when attacked by biotype E. These were PI 264453, PI 220248, PI 229828, and Capbam (Sarvasi) (Johnson et al. 1981, Porter et al. 1982, Hackerott et al. 1983, Starks et al. 1983). The results of comparative screening (Starks et al. 1983) for resistance to biotype E in 9 sources of resistance to biotype C indicated that Capbam and PI 264453 maintained their resistance at about the same level to the new biotype, but that the resistance of PI 220248 was

reduced. Peterson (1985) reported that sorghum lines resistant to biotype C are not necessarily resistant to biotype E; however, all known sources of resistance to biotype E are also resistant to biotype C. Hackerott et al. (1983) reported on efforts to screen 9,000 additional germplasm accessions for resistance to biotype E. Greenbug biotypes F and the new biotypes G and H were less virulent to sorghum (Puterka et al. 1988).

Schuster and Starks (1973) studied the components of host plant resistance to greenbug biotype C using eleven sorghum entries including 'BOK 8' as the susceptible check. They concluded that PI 229828, PI 302178, PI 226096, IS-809 and SA 7536-1 possessed high degrees of all three mechanisms of resistance. Tolerance was the main component of resistance in PI 264453, but PI 302231 and PI 220248 showed relatively low levels of tolerance. Teetes et al. (1974a) in a similar study found that PI 264453, SA 7536-1 and KS-30 also showed non-preference and antibiosis. Hackerott et al. (1969) reported that tolerance was the major component of resistance in accessions of S. virgatum, although antibiosis and/or non-preference were also important in confinement tests. Dixon (1990a), reported that out of the twelve varieties tested for biotype E resistance, PI 229828 had the highest level of tolerance and the least tolerant was PI 302136, with all other remaining entries showing intermediate tolerance. Teetes et al. (1974b), and Schuster and Starks (1973) concluded that tolerance was the most desirable and enduring mechanism because: 1) It reduced the selection pressure on the insect, which would delay evolution of new biotypes; 2) it would be less disruptive of the ecosystem since aphid and parasite populations would be maintained at adequate levels, and 3) it could easily be integrated with other natural controls.

Schuster and Starks (1973) concluded further that the antibiosis and non-preference components of resistance would remain effective unless mutations in the physiological composition of the greenbug were to occur.

Resistance of lines derived from S. virgatum was reported to be conferred by dominant genes at more than one locus (Hackerott et al. 1969). Several studies (Dixon et al. 1990 a) indicate that biotype C resistance derived from IS-809, SA 7536-1, PI 220248, and PI 302236 is incompletely dominant and simply inherited. Resistance to biotype E derived from PI 220248, Capbam, and TAM BK42, a derivative of PI 264453, is not inherited as a recessive characteristic.

Screening Techniques and Greenbug Laboratory Breeding

The rise of greenbug biotype C on sorghum led to a concerted effort to develop screening techniques to evaluate sorghum germplasm for resistance to greenbugs (Starks and Burton 1977a), transfer this resistance to adapted germplasm, and elucidate the mechanism of resistance and its inheritance (Dixon 1990a). Screening methods to separate mechanisms of resistance have been described (Schuster and Starks 1973). The greenhouse visual ratings for resistance and seedling survival measured the confounded effects of all the three mechanisms of resistance, but tolerance was emphasized (Starks and Burton 1977a). Visual damage ratings in the greenhouse have been shown to have a high positive correlation with adult plant resistance under natural field conditions (Teetes et al. 1974a, b).

CHAPTER III

FEEDING BEHAVIOR AND DEVELOPMENT OF BIOTYPES E, G, AND H ON 'POST' AND 'WINTERMALT' BARLEY

Introduction

The occurrence of greenbug, Schizaphis graminum (Rondani), biotypes is well documented. New biotypes are characterized mainly by their ability to damage host plants previously resistant to greenbug populations (Puterka & Peters 1990).

Kindler & Spomer's (1986) study on development and damage by greenbug biotypes and three isolates on resistance sources of small grains, sorghum, and blue grass provides a summary of greenbug biotypes in the United States. Puterka et al. (1988) using major plant sources of greenbug resistance, characterized an Oklahoma isolate and a Texas isolate and designated these as new biotypes 'G' and 'H', respectively. Biotype G (GBG) was found to damage all known sources of greenbug resistance in wheat, Triticum aestium L., but did relatively little damage to 'Wintermalt' (WM) barley, Hordeum vulgare L., a variety previously reported to be susceptible to all greenbug biotypes. Biotype H (GBH) was relatively avirulent on the sorghum, Sorghum bicolor (L.) Moench, varieties tested but severely damaged 'Post', reported to be a resistant barley variety to all previously described biotypes (Puterka et al. 1988).

High levels of resistance to greenbugs have been reported among several barley cultivars (Atkins & Dahms 1945). Greenbug resistance in barley has not been broken in more than 40 yrs by any of the biotypes which have prevented the cultivation of resistant wheat (Wood 1961, Porter et al. 1982).

The electronic monitoring of greenbug feeding behavior on wheat has been useful in defining possible differences among greenbug biotypes and wheat cultivars (Niassy et al. 1987). Monitoring studies using barley have also been carried out to differentiate feeding responses of biotypes B, C, and E (Peters et al. 1988), but none have been carried out on feeding behavior of biotypes G and H.

The electronic monitoring of aphid feeding behavior developed by McLean & Kinsey (1967) provides information on time to initiation, duration, and termination of a series of aphid feeding activities, and it also provides information on the sequence of these activities (Peters et al. 1988).

Phloem has been considered the optimum feeding site of greenbugs (Chatters & Schlehuber 1951). Niassy et al. (1987) monitored feeding behavior of GBB and GBE on wheat and found that the time to beginning of ingestion from the phloem was greater on resistant than on susceptible wheat, and the duration of phloem ingestion was shorter. Peters et al. (1988) monitored feeding behavior of GBB, GBC, and GBE on susceptible and resistant barley and found that the greenbug resistant Post caused significantly greater frequencies of probing, salivation, and nonphloem ingestion events in GBC and GBE compared with the susceptible cultivar WM, but the differences observed on GBB were not significant.

My objective was to determine whether, by using electronic monitors to study feeding behavior, there would be any differential response by biotypes E, G, and H on resistant Post and susceptible WM barley and to determine the possible relationships with development and fecundity. My hypothesis was that GBG was not compatible with either of the two cultivars while GBE would thrive on WM only. GBH was supposed to be compatible with both cultivars.

Materials and Methods

The tests were conducted in the Controlled Environment Research Laboratory at Oklahoma State University, and the United States Department of Agriculture, ARS, Plant Science Research and Water Conservation Laboratory, Stillwater, Oklahoma. Temperature in the feeding monitoring room was 27℃ and the relative humidity was 34% with continuous photophase throughout monitoring time. Greenbug biotypes obtained from confirmed cultures were maintained on 'Triumph 64' wheat under laboratory conditions.

Plexiglass ring cages were used to rear even aged adults of the respective biotypes (Niassy et al. 1987). The greenbug resistant barley cultivar Post and susceptible WM used had known backgrounds (Peters et al. 1988). A total of 48 plastic pots (8 cm dia X 10 cm high) were filled with sandy soil to a weight of 270 gms and later planted with the barley seeds. A staggered planting of eight pots per day was performed and pots were watered with half-strength Hoagland's solution to a weight of 300 gm (field capacity) every other day. The plants were kept in a growth chamber with 13:11 L:D photophase, 600 μmol quanta m^{-2} s^{-1} (LI-COR, LI-190 SB held at top of plants), and temperature of 20℃. After

three weeks plants with a fully formed third leaf were chosen for the experiments.

The electronic feeding monitors and recording system were similar to those described by Niassy et al. (1987). A 9-volt power supply (Oklahoma Engineering and Technical Services, 111 Noble Street, Perry, OK 73077) replaced the 9-volt batteries and provided a more consistent power flow. Six feeding monitors were used per monitoring session. Combinations of host cultivars and three greenbug biotypes were selected at random within the block (monitoring session) and were randomly assigned to monitors. Feeding was monitored for eight hours. Each monitoring session represented a replication and the sessions continue until there were six replications per treatment.

Feeding behaviors, as described for greenbugs on barley by Peters et al. (1988), were coded from the chart recorder. Each feeding event was listed and duration in minutes was tabulated and evaluated. The feeding behaviors observed and recorded were: nonfeeding (baseline), probing, salivation, X-wave (a wave form diagnostic of phloem penetration), phloem ingestion, and non-phloem ingestion as described by Niassy et al. (1987). Greenbugs produce what is recorded as a power surge of approximately 60 sec duration when they first penetrate the plant which may be followed by reduced flow and waveforms typical of either salivation or nonphloem ingestion. This effort at initiating feeding was referred to as probing, although in a broad sense some authors may refer to the entire sequence as probing.

It was assumed that greater frequencies of probes, or withdrawals from the phloem and more time in nonfeeding activities were indications of plant resistance or of the greenbugs' inability to feed efficiently on the resistant plant

(Peters et al. 1988).

After each greenbug was monitored electronically, part of the third leaf on the plant was caged to observe greenbug growth and reproduction using nymphs produced by the adults during the feeding monitoring session. Daily observations were made to determine developmental time and progenies counted for the equivalent period as described by Peters et al. (1988).

Data were analyzed by a general linear model procedure for analysis of variance and tests of genotype/biotype combinations were compared using the "t" test at the 5% level for significance (SAS Institute 1985).

Results and Discussion

Feeding Monitoring

Frequencies (Table I) of nonfeeding (baseline), probes, and salivation events pooled for the three greenbug biotypes were significantly greater on Post compared to WM barley. Differences in frequencies among the biotypes were nonsignificant on WM. On Post, GBE had significantly greater frequencies of these events than H; however, biotype G was intermediate between biotypes E and H. Frequencies of X-waves and phloem ingestion events were not significantly different among biotypes or between cultivars.

Mean duration time (Table II) spent not penetrating plant tissues (baseline) by greenbugs was significantly greater on Post for GBE and GBG than for GBH or than the three biotypes on WM. GBG spent significantly more time per salivation event on WM than did GBE and GBH. When mean duration times for

the biotypes were pooled, there was no statistically significant difference between the cultivars for salivation and nonphloem ingestion event. There were no significant differences among biotypes or between cultivars in mean duration of nonphloem ingestion or X-wave events. Mean duration of phloem ingestion for all biotypes was significantly more on WM than on Post. There was no statistically significant differences in duration of phloem ingestion among the biotypes although GBG spent less time feeding within phloem on WM compared to GBE and GBH.

Total duration of feeding activities (Table III) for greenbugs provides an overall analysis on the apportionment of the 480 minutes into respective feeding events. Time spent in non-phloem ingestion and during X-wave activity showed no significant differences. Total duration of baseline was significantly greater for both GBE and GBG on Post than on WM; this was not the case for GBH which had a significantly shorter baseline time on Post than the other two biotypes. GBG spent significantly more time salivating and less total time feeding within the phloem than did GBE and GBH on WM. Thus indicating GBG was less successful feeding on WM and conforms with the results by other authors (Purteka et al., 1988).

Development and Reproduction

The fitness of a biotype is determined by its ability to feed and grow on host plants, and its rate of reproduction. The number of nymphs produced will depend on the host plant (resistant/susceptible) which should also influence the developmental time (the length of time it takes a nymph to develop into an adult

and produce its first nymph). Aphids with short developmental times have a potentially higher rate of population increase according to Wyatt and White (1977), and they proposed that the effective fecundity can be regarded to be the number of nymphs produced in a time span equal to the developmental time. However, Wyatt and White (1977) cautioned that the assumption is only valid if the patterns of reproduction are similar. The number of nymphs produced during the period should be half the total fecundity, but they are produced in less than half of the adult reproductive period. This approach should give a better estimate of population increase potential than would be true for fecundity counts for a fixed time interval (Peters et al. 1988).

GBG took significantly longer to reach first reproduction than did GBE and GBH, if results for the cultivars were pooled (Table IV). The relative times for GBE and GBH on WM vs Post switched rankings. When all biotypes were pooled, time to initiation of first reproduction on Post barley was significantly longer than on WM.

GBE produced significantly more nymphs on WM than did GBG and GBH, but on Post GBH produced significantly more nymphs than GBE and GBG. Overall more nymphs were produced on WM than on Post. The estimated r_m (intrinsic rate of increase) for the biotypes when calculated on the mean values for WM and Post in Table 4 respectively were: GBE, 0.446 and 0.302; GBG, 0.339 and 0.264; and GBH, 0.411 and 0.364. I concluded that GBG was less successful in feeding and reproducing on barley when compared to GBE and GBH which confirms the findings of Puterka et al. (1988). GBH feeding and reproduction on Post was significantly better than GBE and GBG.

CHAPTER IV

A STUDY OF GREENBUG CLONES ON SORGHUM SOURCES OF GREENBUG RESISTANCE

Introduction

The greenbug, Schizaphis graminum (Rondani), has been a major insect pest of sorghum, Sorghum bicolor (L.) Moench, in the United States since 1968 when biotype C (GBC) developed (Harvey & Hackerott 1969b, Wood & Starks (1972). Dixon et al. (1990a) have given an excellent review of the efforts to screen germplasm for greenbug resistance, transfer this resistance to adapted germplasm, explain the mechanisms of resistance, and characterize the inheritance of resistance in sorghum to the greenbug biotypes. Several authors (Schuster & Starks 1973, Teetes et al. 1974a, b) found that the level and mechanisms of resistance varied among all sources studied, and they concluded that tolerance was the most desirable and enduring mechanism because the reduced selection pressure on the insect should delay the evolution of new biotypes.

Porter et al. (1982) reported on the collection of a new greenbug biotype in a wheat field near Bushland, Texas in 1979. Hackerott et al. (1983) reported that by 1981, biotype E (GBE) had largely replaced GBC in the Great Plains. Only four sources of resistance to GBC were resistant to GBE. These were PI 264453, PI 229828, PI 220248, and 'Capbam' (Johnson et al. 1981, Porter et al. 1982,

Hackerott et al. 1983, Starks et al. 1983). The results of the comparative screening (Starks et al. 1983) for resistance to GBE in nine sources of resistance to GBC indicated that Capbam and PI 264453 maintained their resistance at about the same level to the new biotype, but that the resistance of PI 220248 was reduced. None of these three sources was as resistant, based upon average damage scores, as were two thirds of the nine sources when infested with GBC.

Biotype F (GBF) was reported to have varying potential to damage sorghum (Puterka et al. 1988), while biotypes G (GBG) and H (GBH) were relatively avirulent to sorghum. Puterka & Slosser (1986) reported on techniques to induce greenbugs into the sexual cycle and to achieve egg hatching; thereby making it possible to cross different greenbug biotypes in the laboratory. Breeding greenbug biotypes has produced recombinants that have a broader range of virulence than their parents (Puterka & Peters 1989a, b). Through the laboratory production of highly virulent types, it is now possible to screen potential virulent sources not yet recognized in the field.

Therefore, the objective of this study was to evaluate some of the available resistance sources in sorghum to determine the stability of their resistance to aphid genetic stocks, field collections, and greenbug biotypes. This should give sorghum breeders a head start to incorporate new resistance sources within the sorghum germplasm before the new biotypes develop. This is a kind of insurance to continuous use of host plant resistance in greenbug management.

Materials and Method

Greenbug clones and crosses from biotypes C, E, and F retained from the

genetic studies reported by Puterka and Peters (1990) were maintained as parthenogenetically reproducing clones (137 clones) on caged pots of susceptible 'Triumph 64' wheat in a growth chamber (14:10 L:D, 17°C). An additional 18 field collections and biotype G sib-matings made a total of 155 clones used to evaluate sorghum breeding lines containing resistance sources PI 229828, PI 220248, Capbam, and KS-30. Hereafter "clones" will be used to designate any of the greenbug genetic stocks tested. All clones were parthenogenetic progeny of a selected single individual. 'Pioneer 8300' sorghum and Triumph 64 wheat were included as susceptible checks, since a differential response was expected to the crop species among the clones tested (Puterka et al. 1988).

The six crop entries were planted in a 15 cm diam. pot containing sandy soil. Each entry was planted in a radial star arrangement with 4 or more seeds per row and kept in the growth chamber at (13:11 L:D) photophase with cycling temperatures of 25°C:22°C. The pots were caged before plant emergence to eliminate any possible infestation. The plants in each pot were infested with 150-250 aphids from a clone when the seedlings were 5-6 d old, and then caged to evaluate the damage. The heavy infestation was to ensure that tolerance was manifested and the confounding effects of plant antibiosis and antixenosis should be reduced (Puterka et al. 1988). If the synchrony between clone multiplication and plant emergence broke down, as few as 75 aphids were used to infest the 5-6 d old plants rather than delay infestation and allow plant age to become a factor in the comparisons.

All of the plants in the pot were evaluated when one of the susceptible cultivars showed clear signs of severe damage (complete chlorosis or dead plants).

Plant damage was scored by a 1 to 6 damage scale (1=no damage to 6=dead plant) as described by Puterka et al. (1988). The data was analyzed using PROC GLM and the mean damage ratings of cultivars were compared using Duncan's Multiple Range Test ($P \geq 0.05$) (SAS Institute 1985).

Resistance classification criteria were based on:

Resistant= mean damage rating less than or equal to 3.0

Intermediate= mean damage rating above 3.0 but less than 4.8

Susceptible= mean damage rating of 4.8 or above.

Results and Discussion

At the seedling stage in the growth chamber, almost all the cultivar entries differed significantly for the level of tolerance as measured by the average damage rating score per cultivar caused by the various greenbug clones (Table V). The clones are arranged alphabetically / numerically in Table V by parent-progeny groups. Since the clones represent varying levels of selection for reaction to another series of cultivars tested by Puterka (1988), no attempt was made to determine the possible nature of inheritance among the sorghum/biotype sources, but the emphasis was on extending our knowledge of potential utility of these resistance sources and to determine the applicability of the "star pot" technique.

The following greenbug clones were noteworthy, since they were observed to be highly damaging to all of the sorghum resistance sources: CV61, EC55, EE134, EF48, EF106, FE33, FE234 and K4. The least virulent clones to these sorghum genotypes were: BD48, CE4, CF81, CY1, FC103, FF4, FF272, FYO3, F, G, I, SS85, and XX50. The rest of the clones damaged one or more of the

sorghum genotypes or at least caused an intermediate rating.

The responses of the susceptible checks to the clonal groups was of interest in that 3 of 8 clones of GBC sib-matings caused significantly more damage to Triumph 64 than to Pioneer 8300; whereas, the GBE crosses often caused more damage to Pioneer 8300, but 11 of 22 crosses involving GBE by GBC, CC77 or CC81 caused significantly more damage to Triumph 64. GBF and GBG and their progeny caused relatively more damage to the Triumph 64 wheat than to Pioneer 8300 sorghum as would be expected (Puterka et al. 1988). PI 229828 had the highest level of tolerance to most greenbug clones, but it gave a susceptible response to 10% of the clones tested. While GBC, GBE and GBF on PI 229828 caused damage ratings of 2.0, 2.3, and 2.0 respectively, sib-matings and crosses involving these biotypes and their progeny had 16 susceptible, 16 intermediate, and 102 resistant ratings. PI 220248 was the next best with 28 susceptible, 41 intermediate, and 65 resistant responses. The responses on Capbam were: 48 susceptible, 27 intermediate and 57 resistant. On KS 30 the responses were 73 susceptible, 38 intermediate and only 22 resistant. All 10 of the field collected isolates (ALA-A to TM3) caused a susceptible response on KS 30 which further eliminates any use for this entry as a resistance source.

From the study, we can conclude that the potential resistance level of Capbam and PI 220248 are moderate while that of PI 229828 is still high, but KS 30 is of no further value in greenbug resistance breeding. This is particularly alarming since Dixon et al. (1990) reported that the greater percentage of the sorghum hybrids planted commercially in the USA are derivatives of either KS 30 or SA 7536-1.

The large number of intermediate responses observed deserves further attention since these tests were not designed to determine the genetic bases for these resistance sources. Within row variation in damage ratings was generally small but the raw rating scores for KS 30 and PI 220248 appeared most variable which suggests more intensive evaluations should be made.

Crosses between greenbug biotypes C, E, and F were observed to produce recombinants, varying in the degree of virulence to sorghum genotypes. Crosses between greenbug biotypes E / F and C / E had recombinants which were virulent or damaging to many sorghum genotypes. This confirms the report by (Puterka and Peters 1989a), that biotypes C, E, and F were heterozygous for many virulence loci and that crosses between them resulted in a tremendous amount of variability due to the expression of the hidden mutations accumulated during parthenogenesis. They further suggested this would explain the greenbugs ability to respond to selection pressure and a broad range of hosts. Selection among these recombinants can be utilized for future sorghum improvement for hybrid production.

CHAPTER V

SUMMARY AND CONCLUSIONS

Feeding monitor studies were carried out on greenbug biotypes E, G, and H to determine any differential response in feeding behavior on susceptible WM and resistant 'Post' barley. All biotype-cultivar combinations were also tested for differences in developmental time and fecundity. Post caused significantly greater frequencies of non feeding, probes, and salivation for GBE and GBG than GBH. GBG spent significantly more mean and total duration time salivating and less time feeding within the phloem on WM. It also took a significantly longer time to begin reproduction and produced fewer progenies than did GBE and GBH on WM barley. This indicates GBG is less successful in feeding on WM and confirms previous reports about its inability to feed successfully on WM. Both GBE and GBH were relatively more successful in feeding within the phloem on WM but GBE was less successful on Post.

Greenbug clones and crosses from biotypes C, E, and F retained from the genetic studies reported by Puterka and Peters (1990) and an additional 18 field collections and GBG sib-matings were used to evaluate sorghum resistance sources PI 229828, PI 220248, Capbam, and KS-30 plus Pioneer 8300 sorghum and Triumph 64 wheat. The six crop entries were planted in a 6-inch diameter pot in a radial star arrangement with 4 or more seeds per row and kept in the growth chamber. Plant damage was scored by a 1 to 6 damage scale (1=no

damage to 6=dead plant).

The sorghum cultivars differed significantly in the level of resistance to greenbug clone damage. PI229828 had the highest level of resistance, while PI220248 and Capbam had moderate levels of resistance. KS30 had a very reduced level of resistance compared to the other cultivars.

The following greenbug clones were observed to be highly damaging to all of the sorghum resistance sources: CV 61, EC 55, EE 134, EF 48, EF 106, FE 33, FE 234, and K4. These could be utilized in further screening of sorghum resistance sources.

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APPENDIX

TABLES

TABLE I

FREQUENCIES ($\bar{X}$±SE) OF FEEDING BEHAVIORAL EVENTS OBSERVED IN 480 MIN FOR GREENBUG BIOTYPES E, G, AND H ON WM AND 'POST' BARLEY.

Cultivar	Biotype	No. obs	Baseline	Probes	Salivation	Nonphloem ingestion	X-wave	Phloem ingestion
	E	6	10.0±3.8a	10.0±3.8ab	8.8±3.4a	1.0±0.8a	3.0±1.1a	3.0±1.1a
WM (S)	G	6	8.8±3.8a	8.7±3.8ab	12.3±3.4ab	1.3±0.8a	4.2±1.1a	4.0±1.1a
	H	6	8.3±3.8a	8.3±3.8a	9.0±3.4a	1.3±0.8a	3.2±1.1a	3.2±1.1a
	E	6	36.7±3.8c	36.2±3.8d	30.7±3.4c	2.2±0.8a	2.2±1.1a	2.2±1.1a
Post (R)	G	5	24.8±4.2b	24.6±4.2c	22.2±3.8bc	2.0±0.9a	2.4±1.2a	2.2±1.2a
	H	6	19.2±3.8ab	19.5±3.8bc	19.5±3.4b	1.3±0.8a	4.0±1.1a	3.8±1.1a
WM	All	18	9.0±2.2a	9.0±2.2a	10.1±2.0a	1.2±0.5a	3.4±0.7a	3.4±0.6a
Post	All	17	26.8±2.3b	26.7±2.3b	24.1±2.1b	1.8±0.5a	2.8±0.7a	2.7±0.7a
Both	E	12	23.3±2.7b	23.0±2.7b	19.8±2.4a	1.6±0.6a	2.6±0.8a	2.6±0.8a
Both	G	11	16.8±2.8ab	16.6±2.8ab	17.3±2.5a	1.7±0.6a	3.3±0.8a	3.1±0.8a
Both	H	12	13.8±2.7a	13.9±2.7a	14.3±2.4a	1.3±0.6a	3.6±0.8a	3.5±0.8a

Values with same letter in each column are not significantly different (t test, $P < 0.05$)

TABLE II

MEAN DURATION (MINUTES±SE) OF FEEDING BEHAVIORAL EVENTS OBSERVED IN 480 MIN FOR GREENBUG BIOTYPES E, G, AND H ON WM AND 'POST' BARLEY.

Cultivar	Biotype	No. obs	Baseline	Probes	Salivation	Nonphloem ingestion	X-wave	Phloem ingestion
	E	6	1.7±0.7a	0.4±0.04a	13.3±7.7a	13.0±10.1a	1.0±0.1a	187±41c
WM (S)	G	6	2.2±0.7a	0.4±0.04a	37.8±7.7b	34.5±10.1a	0.9±0.1a	98±41abc
	H	6	1.8±0.7a	0.4±0.04a	14.6±7.7a	9.1±10.1a	0.8±0.1a	147±41bc
	E	6	4.3±0.7b	0.4±0.04a	14.0±7.7a	12.4±10.1a	0.9±0.1a	1±41a
Post (R)	G	5	4.8±0.8b	0.5±0.04a	16.2±8.5ab	19.7±11.1a	0.7±0.1a	6±45a
	H	6	1.8±0.7a	0.5±0.04a	17.7±7.7ab	7.0±10.1a	0.8±0.1a	36±41ab
WM	All	18	1.9±0.4a	0.4±0.02a	21.9±4.5a	18.8±6.0a	0.9±0.1a	144±24a
Post	All	17	3.6±0.4b	0.4±0.02a	16.0±4.6a	13.0±6.0a	0.8±0.1a	14±24b
Both	E	12	3.0±0.5ab	0.4±0.03a	13.6±5.5a	12.7±7.2a	0.9±0.1a	94±29a
Both	G	11	3.5±0.5b	0.5±0.03a	27.0±5.7a	27.1±7.5a	0.8±0.1a	52±30b
Both	H	12	1.8±0.5a	0.4±0.03a	16.2±5.5a	8.0±7.2a	0.8±0.1a	91±29a

Values with same letter in each column are not significantly different (t test, $P < 0.05$)

TABLE III

TOTAL DURATION (MINUTES±SE) OF FEEDING BEHAVIORAL EVENTS OBSERVED IN 480 MIN FOR GREENBUG BIOTYPES E, G, AND H ON WM AND 'POST' BARLEY.

Cultivar	Biotype	No. obs	Baseline	Probes	Salivation	Nonphloem ingestion	X-wave	Phloem ingestion
	E	6	20±11a	4±2a	103±28a	20±17a	3±1a	330±31c
WM (S)	G	6	18±11a	4±2a	232±28b	55±17a	4±1a	166±31b
	H	6	15±11a	3±2a	137±28a	20±17a	3±1a	302±31c
	E	6	117±11b	15±2c	299±28bc	42±17a	2±1a	5±31a
Post (R)	G	5	118±12b	12±2bc	289±31bc	37±19a	2±1a	23±34a
	H	6	35±11a	9±2b	321±28c	19±17a	4±1a	92±31ab
WM	All	18	18±6a	4±1a	157±16a	32±10a	3±1a	266±18b
Post	All	17	90±6b	12±1b	303±17b	33±10a	3±1a	40±19a
Both	E	12	69±8b	9±1a	201±20a	31±12a	3±1a	167±22b
Both	G	11	68±8b	7±1a	260±21a	46±13a	3±1a	94±23a
Both	H	12	25±8a	6±1a	229±20a	20±12a	3±1a	197±22b

Values with same letter in each column group are not significantly different (t test, $P < 0.05$)

TABLE IV

DEVELOPMENT, REPRODUCTION AND GROWTH OF GREENBUG BIOTYPES E, G, AND H ON 'POST' AND WM BARLEY.

Cultivar	Biotype	No. Obs.	Time to begin reproduction (HRS)	Progeny produced
	E	12	142.0±5.4a	35.5±1.6a
WM (S)	G	12	160.0±5.4bc	21.3±1.6cd
	H	12	146.0±5.4ab	29.4±1.6b
	E	10	170.7±5.8cd	18.2±1.7de
Post (R)	G	10	184.0±6.6d	15.4±1.9e
	H	12	156.0±5.4abc	24.5±1.6c
WM	All	36	149.5±3.1a	28.7±0.9a
Post	All	32	170.0±3.4b	19.3±1.0b
Both	E	22	156.4±3.9a	27.0±1.2a
Both	G	22	172.0±4.2b	18.3±1.3b
Both	H	24	151.0±3.8a	27.0±1.1a

Values with the same letter in each column section are not significantly different (t test $P < 0.05$).

TABLE V

MEAN DAMAGE RATING OF FIVE SORGHUM GENOTYPES AND ONE SUSCEPTIBLE WHEAT AT SEEDLING STAGE, AFTER INFESTATION BY GREENBUG CLONES.

CROSS	CLONE	TRIUMPH	PIONEER 8300	KS30	PI 220248	PI 229828	CAPBAM
Parent	C	6.0A	4.0BC	5.3AB	4.3C	2.0D	3.8C
C X C	CCO3	5.3AB	5.0AB	6.0A	4.5B	3.0C	5.8A
	CC21	6.0A	3.0C	3.0C	3.0C	2.0C	4.5B
	CC31	6.0A	5.3AB	4.8B	5.8B	2.3C	6.0A
	CC32	6.0A	3.0C	6.0A	4.5B	2.0D	6.0A
	CC77	6.0A	6.0A	6.0A	6.0A	4.0B	6.0A
	CC79	6.0A	6.0A	5.7A	4.0B	2.0C	3.0BC
	CC81	6.0A	6.0A	4.0B	3.0C	2.0D	2.0D
	CC137	5.3A	4.0B	3.3B	5.8A	2.0C	5.5A
CC6@[1]	CX09	4.6A	4.8A	4.7A	3.7AB	2.0C	2.5BC
	CX62	3.6B	5.7A	5.8A	2.6C	2.0C	2.4C
CC3@	CY01	6.0A	5.3A	2.8B	2.0B	2.0B	3.3B
	CY02	6.0A	6.0A	5.3B	2.8C	2.0D	2.0D
	CY39	4.3A	5.0A	4.5A	5.3A	2.5B	5.3A
77 X 81	MP03	5.8A	5.8A	5.5A	5.7A	3.0B	3.3B
	MP17	4.8A	6.0A	6.0A	5.0A	2.8B	5.5A
	MP49	5.8A	6.0A	5.8A	2.5C	2.0C	4.0B
	MP61	5.0AB	5.5A	4.5B	3.0C	2.0D	2.0D
	MP110	5.3A	4.8AB	5.3A	3.8B	2.5C	2.5C
	MP111	5.0B	6.0A	6.0A	4.3B	2.3C	2.5C
	MP112	6.0A	5.5A	6.0A	3.0B	2.0C	2.0C
CC81@	XX02	4.3B	6.0A	4.3B	3.3C	2.0D	2.0D
	XX33	5.3A	4.5AB	4.0AB	4.7AB	2.0C	3.5B
	XX34	6.0A	5.5AB	3.0C	2.5C	5.8AB	5.0B
	XX36	5.3A	5.8A	6.0A	2.3B	2.0B	2.0B
	XX37	6.0A	6.0A	5.5A	2.8B	2.5B	2.3B
	XX38	4.0AB	5.3A	3.8AB	2.5B	2.3B	2.5B
	XX39	5.0A	5.0A	5.3A	3.0C	4.0B	4.0B
	XX41	6.0A	5.3A	6.0A	4.3B	2.5C	2.0C
	XX43	6.0A	4.8B	4.8B	2.5C	2.0C	5.5AB
	XX45	6.0A	6.0A	5.0B	2.3C	2.0C	2.3C
	XX48	5.0B	5.0B	5.0B	3.5C	4.8B	5.8A
	XX50	6.0A	2.0B	2.0B	2.0B	2.3B	2.3B
	XX60	5.5A	5.5A	6.0A	2.0B	-	2.0B
	XX61	6.0A	4.0B	4.0B	2.5C	2.3C	6.0A
	XX69	6.0A	2.3BC	2.5BC	3.0B	2.0C	5.5A
	XX71	6.0A	5.8A	4.0B	3.3B	2.0C	2.0C
81 X C	CV15	6.0A	2.3B	2.0B	2.3B	2.0B	6.0A
	CV27	5.3A	5.0A	5.0A	2.3B	2.0B	2.0B
	CV59	5.5A	5.5A	3.3B	2.8BC	2.3C	5.5A
	CV61	6.0A	5.0B	5.0B	6.0A	6.0A	6.0A
C X 81	BC07	5.0AB	5.5AB	6.0A	2.8C	2.0C	4.5B
	BC95	6.0A	2.5C	4.0B	2.3C	2.0C	5.0B

[1] Sib mated

TABLE V (continued)

CROSS	CLONE	TRIUMPH	PIONEER 8300	KS30	PI 220248	PI 229828	CAPBAM
77 X C	XC02	6.0A	4.0B	4.0B	4.5AB	2.0C	6.0A
	XC18	4.5A	4.8A	5.0A	2.3BC	2.0C	3.0B
	XC58	6.0A	4.5BC	3.0D	5.3AB	3.8CD	6.0A
C X E	CE04	5.3A	3.0B	3.0B	2.7B	2.0B	2.7B
	CE104	6.0A	5.0B	4.5C	2.0D	2.0D	2.3D
	CE482	4.0C	4.0C	5.3B	6.0A	2.0D	2.3D
	CE502	5.0A	2.0B	2.0B	3.3B	2.0B	5.0A
	CE503	5.0A	5.3A	5.7A	4.8A	2.3B	3.0B
E X C	EC55	6.0A	5.8A	6.0A	5.8A	6.0A	6.0A
	EC68	4.0AB	3.3BC	4.0AB	3.5BC	2.0C	5.5A
	EC100	5.5A	5.3A	3.3B	4.5AB	3.0B	6.0A
	EC172	6.0A	2.3C	5.0AB	2.0C	2.0C	3.7BC
	EC228	6.0A	5.5A	5.5A	5.5A	2.0B	6.0A
	EC244	6.0A	3.3B	6.0A	5.0A	2.5B	5.5A
	EC250	5.5A	5.3A	4.5A	5.5A	2.3B	5.7A
E X 81	BD11	4.5A	2.0B	2.5B	2.3B	2.3B	4.5A
	BD48	6.0A	2.0B	2.8B	3.0B	2.0B	2.3B
	BD60	5.6A	5.4A	5.4A	3.8B	2.1C	2.5C
81 X E	BX01	6.0A	6.0A	5.8A	4.0B	3.0C	3.0C
	BX02	5.0AB	6.0A	5.8AB	4.5B	2.8C	2.7C
	BX27	4.5A	2.5B	4.3A	3.0B	5.3A	5.0A
77 X E	XE03	4.0A	2.8BC	3.5AB	3.0BC	2.3C	4.0A
	XE67	6.0A	3.0BC	2.3C	2.0C	2.3C	4.3B
	XE68	6.0A	6.0A	6.0A	6.0A	3.5B	6.0A
	XE76	4.0B	6.0A	5.5A	5.5A	3.0C	6.0A
Parent	E	4.0B	5.7A	5.0AB	4.8AB	2.3C	2.5C
E X E	EE134	4.0A	5.5A	5.0A	5.3A	5.0A	5.3A
	EE188	3.8B	4.5AB	5.3A	5.3A	2.3C	3.3BC
	EE500	4.0B	3.8B	3.5B	3.8B	2.3C	5.8A
	EE501	4.3AB	4.0AB	4.0AB	3.3B	6.0A	4.0AB
188EE@	EX01	5.4AB	4.6B	6.0A	4.9B	2.1D	3.5C
	EX76	4.0B	6.0A	5.5A	5.5A	3.0C	6.0A
	EX103	3.0BC	5.8A	5.8A	4.0B	2.0C	4.0B
	EX111	6.0A	2.0C	4.0B	2.0C	2.0C	2.0C
E X F	EF06	5.4A	5.5A	5.6A	2.1B	2.4B	2.7B
	EF23	5.5A	4.5A	5.5A	3.0B	2.4B	3.2B
	EF33	5.0A	5.0A	6.0A	5.0A	2.0B	2.7B
	EF44	4.5AB	4.3AB	5.3A	3.3B	5.3A	4.0AB
	EF48	6.0A	6.0A	6.0A	5.8A	6.0A	6.0A
	EF63	5.6A	4.3B	5.8A	2.8C	3.3BC	3.6BC
	EF64	4.0BC	5.3AB	6.0A	4.3BC	3.5C	6.0A
	EF106	5.0B	6.0A	5.3B	5.3B	5.0B	6.0A
	EF107	4.8A	2.8BC	3.5B	3.3BC	2.5C	2.8BC

TABLE V (continued)

CROSS	CLONE	TRIUMPH	PIONEER 8300	KS30	PI 220248	PI 229828	CAPBAM
37FE@	FP185	4.5A	2.5AB	3.5AB	3.3AB	2.0B	4.5A
	FP207	6.0A	5.8A	5.5A	2.8B	3.3B	2.5B
	FP210	2.7B	5.0A	5.3A	2.7B	4.3AB	3.3B
	FP241	3.7BC	5.3A	3.0C	3.3BC	5.3A	4.0B
	FP242	5.3A	4.0B	4.0B	6.0A	2.0C	2.0C
	FP274	6.0A	5.5A	6.0A	2.3B	2.0B	2.3B
F X E	FE33	6.0A	6.0A	5.8A	6.0A	6.0A	6.0A
	FE42	5.0A	5.3A	4.5A	2.0C	2.0C	3.3B
	FE68	6.0A	6.0A	5.8A	2.0B	2.3B	2.3B
	FE74	5.0A	5.5A	5.7A	4.9A	2.0B	2.5B
	FE200	6.0A	6.0A	3.5B	2.0C	3.3B	5.0A
	FE215	6.0A	6.0A	5.3AB	2.0C	4.5B	3.0C
	FE234	5.8AB	5.9A	5.2BC	5.1C	5.5ABC	5.9A
	FE252	5.3B	5.8A	5.5AB	2.0C	2.0C	2.1C
	FE335	5.0B	6.0A	4.5B	2.3C	2.0C	2.3C
74FE@	FY01	5.7A	5.3A	6.0A	3.3B	5.3A	5.3A
	FY03	6.0A	3.3B	3.0B	2.0C	3.0B	2.8B
	FY05	6.0A	5.3A	5.8A	4.8AB	3.0BC	2.0C
200FE@	FA175	4.0B	6.0A	5.0A	2.3D	3.3C	3.0C
	FA227	3.8AB	5.0A	4.5AB	2.0C	2.0C	3.3BC
234FE@	FO31	5.5A	4.5BC	4.0C	3.7C	2.1D	5.3AB
	FO185	5.3A	5.5A	-	2.8B	6.0A	3.1B
C X F	CF4	5.0A	5.3A	4.5B	3.5B	3.3B	5.3A
	CF5	5.3B	6.0A	4.5C	2.0D	2.0D	2.0D
	CF64	5.7A	2.3C	2.0C	3.5B	2.0C	6.0A
	CF27	6.0A	4.0C	4.8ABC	4.3BC	2.0D	5.5AB
	CF36	6.0A	6.0A	2.7B	4.8A	2.0B	5.8A
	CF70	6.0A	5.0A	6.0A	3.5B	2.0C	3.3B
	CF81	6.0A	2.8B	2.8B	2.3BC	2.0C	2.3BC
	CF138	6.0A	5.3AB	4.3BC	4.0C	3.8C	5.7A
138CF@	JO57	5.0A	5.0A	5.0A	3.3C	5.3A	4.3B
	JO166	5.0A	5.0A	5.5A	2.0B	2.8B	2.0B
103FC@	JB36	5.8AB	4.8BC	4.0CD	3.3D	3.0D	6.0A
F X C	FC25	5.8A	4.1AB	3.0B	3.0B	2.8B	4.8A
	FC83	5.0A	5.0A	5.3A	2.5B	2.0B	2.0B
	FC87	6.0A	5.8A	6.0A	3.3B	3.5B	4.7AB
	FC103	5.5A	5.8A	2.8B	2.8B	2.0B	2.3B
	FC106	5.0AB	6.0A	5.3A	4.0BC	2.0D	3.3C
	FC114	5.8A	4.8B	5.8A	2.0D	3.3C	2.8C
	FC136	6.0A	3.0B	5.8A	2.3B	2.0B	2.8B
	FC138	6.0A	5.3A	3.0B	3.3B	3.8B	6.0A
	FC143	5.8A	4.5AB	4.7AB	3.0BC	2.5C	5.3A

TABLE V (continued)

CROSS	CLONE	TRIUMPH	PIONEER 8300	KS30	PI 220248	PI 229828	CAPBAM
Parent	F	5.8A	4.3B	2.0C	2.0C	2.0C	2.0C
F X F	FF4	6.0A	4.5B	2.8C	2.3C	2.3C	2.0C
	FF15	5.5A	4.8AB	4.0B	2.0C	2.5C	2.0C
	FF141	5.0A	5.5A	4.0B	2.5C	2.3C	2.8C
	FF161	6.0A	6.0A	6.0A	2.0B	2.0B	2.0B
	FF203	6.0A	6.0A	6.0A	2.0B	2.0B	2.0B
	FF272	5.0B	6.0A	2.3C	2.0C	2.0C	2.0C
15FF@	FX4	6.0A	3.5CD	4.0BC	2.8D	2.5D	4.8B
	FX161	4.8A	2.0B	4.0AB	4.0B	2.0B	2.0B
Parent	G	6.0A	2.8B	2.3B	2.3B	2.5B	2.3B
G X G	SS74	6.0A	6.0A	5.3A	2.3B	2.8B	-
	SS77	5.8A	3.0BC	3.7B	2.0C	3.0BC	4.0B
	SS85	6.0A	2.3B	2.0B	2.0B	2.3B	-
	SS102	6.0A	3.3B	3.5B	2.0C	2.3C	2.3C
Clone[2]	B	6.0A	5.0B	4.0C	2.5D	2.0D	2.0D
	H	6.0A	4.5B	5.5A	2.0C	3.8B	2.3C
	I	6.0A	4.5B	3.0C	2.0D	2.3CD	2.8CD
	ALA-A	6.0A	5.3B	6.0A	6.0A	2.0C	6.0A
	ALA-B	5.0A	4.0A	5.3A	5.0A	2.3B	5.0A
	GA-B	5.0A	5.8A	6.0A	3.5B	2.5C	5.7A
	K1	3.3C	4.5B	6.0A	2.0D	2.0D	2.0D
	K2	5.5A	5.3A	5.3A	3.8B	5.0A	5.3A
	K4	6.0A	5.8AB	5.3B	5.8AB	5.8AB	6.0A
	NPI	5.8A	5.0B	6.0A	5.8A	2.0D	3.0C
	P304	4.0B	5.0AB	6.0A	4.5B	2.0C	2.8C
	TM1	3.3B	5.0A	5.0A	2.0C	2.0C	2.3BC
	TM3	5.8A	6.0A	6.0A	6.0A	2.3B	5.0A

[2] Field Collected Clones from Various States

Means in each row followed by the same letter are not significantly different at, $P \geq 0.05$, Duncan's Multiple Range Test (SAS Institute 1985).

VITA

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Candidate for the Degree of

Master of Science

Thesis: FEEDING BEHAVIOR AND DEVELOPMENT OF BIOTYPES E, G, AND H OF SCHIZAPHIS GRAMINUM (HOMOPTERA: APHIDIDAE) ON 'WINTERMALT' AND 'POST' BARLEY, AND THE EVALUATION OF RESISTANCE SOURCES IN SORGHUM TO SEVERAL GREENBUG CLONES

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