EFFECT OF TEMPERATURE AND PHOTOPHASE ON BARLEY RESISTANCE TO GREENBUG BIOTYPES C AND E

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CHAPTER I

INTRODUCTION

For several decades the greenbug, Schizaphis graminum (Rondani), has been considered one of the most destructive pests of small grains in production areas around the world. Dahms (1957) reported losses in 1955 of more than 50 million bushels of small grains in the United States.

Greenbugs become active on small grains in the late fall and early spring. Later in the season, different kinds of sorghum become the preferred host. The greenbug can reproduce at much lower temperatures than its parasitoids and predators. For that reason natural and/or biological control is not always feasible.

Chemical control is an expensive way of reducing the aphid population as multiple applications are often required. Greenbugs are capable of multiplying to enormous numbers parthenogenetically within a short period of time, leading to problems with pest resurgence after insecticide usage. Development of resistance to the insecticide disulfoton by biotype "D" of the greenbug has added new questions about the continued effectiveness of chemical control (Teetes et al., 1975). Pesticide application can also be hazardous both for the applicators and for the environment. In spite of these problems, pesticides are still the most common weapon that the producers have in their struggle against the greenbug.

The above mentioned problems can be reduced by the use of resistant

crop varieties, which also diminish the production costs by avoiding insecticide applications. These resistant varieties appear to be an ideal method of insect control and have an important role in modern integrated pest management programs. Several greenbug resistant small grain and sorghum cultivars have been developed, and some of these were released for commercial use (Wood et al., 1974; Sebesta and Wood, 1977; Jackson et al., 1964). Selection for greenbug biotypes seems to be a real problem in the use of resistant cultivars in the Great Plains. The latest biotype identified ("E") was found in 1980 when previously resistant wheat lines became susceptible (Daniels and Chedester, 1981).

The purpose of this study was to provide additional information on the life span and fecundity of greenbug biotypes "C" and E, especially, in regard to behavior at different temperatures and light conditions when reared on "Will" and "Akyurek-100", varieties of barley (Hordeum vulgare L.). Resistance of the two varieties was compared; and influence of temperature and/or photophase on the resistance expression shown by the varieties Will and Akyurek-100 were determined.

CHAPTER II

REVIEW OF LITERATURE

The Greenbug as a Problem

First Appearance and World Occurence

The first description of this aphid was made by C. Rondani, who found the greenbug on grasses in Italy in 1847 (Hunter, 1909). More than 30 years later, in 1882, it was described in Virginia, U.S.A. (Webster and Phillips, 1912). Since these early descriptions, this cosmopolitan species has been found in all the continents except Antartica. To mention a few of the reports, it was found in Argentina in 1914 where its first outbreak occurred in 1937 (Griot, 1940). It was reported in the Philippines on wheat (Triticum aestivium L.) (Baltazar, 1962), in Australia (Hughes et al., 1964), and in Africa on small grains (Brown, 1971).

Outbreaks

Early outbreaks of the pest in the U.S. were in 1901 in northern Texas; in 1907 in Texas, Oklahoma and Kansas; and in 1916 in Oklahoma, Kansas and New Mexico. During these years, oat (Avena sativa L.) and wheat were the most frequently attacked crops. Infestations almost invariably resulted in death of oat and wheat plants, after which there was a migration of the winged aphids to other crops (Kelly, 1917).

During these years, the greenbug occasionally injured Sudan grass (Sorghum sudanese Stapf.) and other varieties of sorghum as well. In 1916, in Kansas, the species did considerable damage to sorghum, causing infested plants to become chlorotic and die (Hayes, 1922). Areas of Minnesota, which had been supposed to lie too far north for development of damaging greenbug populations, were the scene of damage during the spring and summer of 1926. Oats suffered more than other crops from this attack (Ainslie, 1926).

During the spring of 1939 a severe outbreak occurred in northeastern Oklahoma. In this case winter barley, wheat and spring oats were most severely damaged, and appearance of the parasitoid Lysiphlebus testaceipes (Cresson) occurred too late to save crops from greenbug damage (Fenton and Fisher, 1940). The 1950 outbreak was without doubt the most serious on record. It differed from all other previous ones in that farmers had new organic insecticides which proved very effective against the insect. They were also able to afford the expense financially and had the necessary equipment to apply insecticides. Development of modern organic insecticides began a new era in the struggle against the greenbug (Fenton and Dahms, 1951).

Losses Due to the Greenbug

The damage caused during the 1907 outbreak was conservatively estimated at $15,000,000 (Ainslie, 1926). An estimate of the 1939 outbreak in Oklahoma showed that 23,000 hectares of oats, 10,000 of barley and 9,500 of wheat were destroyed with estimated losses of more than $500,000 (Fenton and Fisher, 1940).

In 1947, near Stillwater, Oklahoma, work was carried out to find

the best of the new organic insecticides to control the aphid. In this case several insecticides were tested on seedling oat plants. The yield was 1000 kg/hectare for the untreated check and 1330 for the best treatment. This damage was done by a population of more than 100 aphids per 30 cm of drill row (Dahms, 1948a).

During the 1950 outbreak in Oklahoma, 21% of the wheat surface was abandoned and the yield in the infested areas dropped from 1800 kg. to 1300 kg/hectare. Similar losses accurred on the other host crops. The total estimation of loss was 790,000 metric tons of wheat, 72,000 metric tons of oats and 24,000 metric tons of barley. The loss in the wheat alone was more than $42,000,000 (Fenton and Dahms, 1951).

During 1956 research showed that an average infestation of 100 greenbug 0.3 meter of row caused a reduction from 0.4 to 1.0 kg. of wheat per ha. per day of infestation. In the case of oats, there was great variability in losses depending on the variety grown. In barley, the reduction was more than 0.22 kg./ha. per day, even with light infestations (Dahms, 1957). One of the latest investigations of economic losses due to greenbug was carried out in South Dakota with artificially colonized greenbugs on caged wheat plants (Kieckhefer and Kantack, 1980). Several yield components were measured at harvest. The most severe damage resulted when 25 to 30 aphids/stem fed during the seedling stage, and caused a 60% reduction in yield.

The Greenbug and the Natural Factors, Temperature and Light

Temperature

Early research was related to the variation of the reproduction rate of greenbug with changing temperatures (Sanderson, 1910). Nymphal births were verified at 7°C daily mean, with a regular increase up to 20°C, from which the rate of reproduction gradually decreased until ceasing at 37° to 40°C.

A statistical analysis was made of the rate of development of S. graminum, in relation to temperature (Wadley, 1936). Several curves were fitted by regression analysis and it was found that a straight line showed a better expression of temperature vs. development correlation than curvilinear models. The effect of low temperatures was tested, to find limits where the greenbug can successfully reproduce (Daniels, 1963). The maximum number of offspring was obtained at 22° - 24°C. There was a decrease down to 10°C, when reproduction practically stopped. Similar work was conducted with two greenbug biotypes, "A" and "B" (Singh and Wood, 1963). In this case the maximum number of offspring were obtained with biotype B at 21° - 25°C on "Dickinson Selection 28 A" wheat. With biotype A on the same host, maximum nymphal production occurred at 16°C and at 18° - 21°C on "Ward" barley. In all cases there was no reproduction at 2° and 38°C. In a study by Daniels (1967), normal development of the greenbug ceased between 31° and 35°C, since at the former temperature the average offspring was 48 nymphs/female and the total days of life was ca. 44 days; and at 35°C the number of nymphs produced was reduced to fewer than six/female in

ca. 17 days of life.

Influence of temperature on flight behavior of the greenbug was studied by Berry (1969). The work was carried out during 2 years, and suction traps were used to monitor flight of the aphids. In both years, flight activity increased after temperatures reached 20°C and it was reduced above 40°C. It was not entirely inhibited at 42°C, the maximum temperature recorded. The instrument sensors for temperature were placed at levels similar to crop height in barley, to evaluate conditions nearest the aphid habitat. Results by Dry and Taylor (1970) were similar, in that flights were recorded between 17° and 41°C, with the greatest increases in flight activity above 20°C.

In 1970, the influence of the interaction between temperatures and two barley varieties on the biology of three greenbug biotypes was studied (Wood and Starks, 1972). The test cultivars were "Will" (resistant) and "Rogers" (susceptible) and the temperatures varied from 10° to 32.9°C. Optimum reproduction occurred between 21.9° and 23.9°C, however, production of nymphs was observed at either extreme of temperature. The fecundity of greenbug was much lower on resistant than on susceptible plants and biotype C was better adapted than A or B to either temperature extreme.

Temperature also influences appearance of alate forms (Mayo and Starks, 1972). Depending upon the immediate temperatures to which greenbug were exposed and on temperatures at which their parents and other generations were reared, the largest number of alates was obtained in nymphs from aphids reared at 4°C which were exposed to 27°C.

The temperature influence on resistance expression was the subject of a work with biotype C (Schweissing and Wilde, 1978). Resistance was

associated with optimum temperatures for plant growth, i.e., greater resistance in cool season crops (barley, oat, and rye) under cooler temperatures and greater resistance in the warm season crop (sorghum) under warm temperatures.

Determination of the influence of cold temperatures on greenbug was conducted over 26 year period (Daniels and Chedester, 1980). This study indicated that, in the Texas Panhandle, when the minimum mean was below -6°C for a consecutive period of at least a week, more than 95% of the greenbug population was killed. One of the latest observations in the area of cold temperature influences was also carried out in fields of Oklahoma (Arnold, 1981). Temperatures under -12°C for one night with temperatures rising no higher than 0°C the next day caused slight population reductions. When temperatures remained under -12°C during 3 days followed by 2 days under 0°C, the greenbug population was reduced 75%.

Light

Light intensity greatly influences insect behavior. The most important characteristic of sunlight is its periodicity or day length, which regulates many functions in lives of insects. Little is known about the relation of photoperiod to S. graminum biology. One of the first research projects in this area showed that as light intensity increases, the flight responses in the alienicola greenbug also increases (Halgren and Taylor, 1968). The maximum light tested was 2000 ft-candles, but studies suggested that brighter light might have slightly increased the response. Another related study was carried out in natural conditions to measure the influence of the light in the

greenbug flight (Berry, 1969). The work was based on continuous daily collections, during June and July in 1966 and 1967. In the first year maximum flight occurred between 100 and 1000 ft-candles. However, in 1967 the largest average percent flight frequency was between 1000 and 10000 ft-candles. A similar experiment, but in laboratory conditions, was made with the greenbug and five other aphids (Dry and Taylor, 1970). S. graminum required the maximum given light (1350 ft-candles) for full takeoff.

The influence of temperature and photoperiod on the occurrence of sexual forms of the greenbug was studied in Romania (Barbulescu, 1973). Temperatures of not more than 22°C and photophase of not more than 12 hours favored the appearance of sexual forms.

The Greenbug and Resistant Barley Varieties

From 1940 to 1944, before organochlorine insecticides were available, other means of reducing greenbug population were sought, including the development of resistant varieties. Tests had shown considerable differences among barley varieties in resistance to greenbug injury (Walton, 1944). This research was conducted under field conditions, with natural infestations which reached maximum levels during the first week of April, 1940. Although definite conclusions were not reached, some varieties showed a degree of resistance, mainly based on the vigor of the plants.

A comprehensive study was begun on greenbug resistance in barley during the severe attack of 1942 in central Texas and Oklahoma (Atkins and Dahms, 1945). This research indicated that a considerable number of barley varieties, mostly from the Orient, were highly resistant and

survived to produce grain when the surrounding strains were killed. Several other cultivars that originated from crosses on Oriental barleys also showed good resistance, suggesting that the resistance can be transferred to adapted varieties by crossing.

In 1947 a series of tolerance tests were made with two greenbug populations from Oklahoma and Mississippi (Dahms, 1948b). No difference was found in terms of damage caused. From these studies the varieties "Mignon" and "Omugi" were developed with a high degree of resistance when compared to other varieties. They survived greenbug attack for 30 to 60 days, which was 2-3 times the survival time for the susceptibles. Fecundity and longevity of greenbugs was also studied on these varieties. These studies also showed the good resistance of both varieties to the greenbug. This work was followed by others, with the same objective of develop adapted resistant varieties (Dahms et al., 1955). With few exceptions, resistance appeared to be governed by two or more dominant genes. Further studies of the inheritance of resistance factor present in the varieties Omugi, "Derbent", and "Kearney", indicated that the three varieties derived their resistance from the same gene or closely linked genes (Gardenhire and Chada, 1961). The theory of the common single dominant gene for resistance was confirmed later (Smith et al., 1962), but this time for the varieties Omugi, "Dobaku", Kearney, and an experimental strain C.I. 5087.

Inheritance and chromosomal linkage relationships of resistant Omugi were studied (Gardenhire, 1965). Again, the single dominant gene controlling the resistance was confirmed, but no associations were found between this gene and the genes conditioning diseases resistance.

Breeding programs to transfer resistance to adapted varieities were

initiated, based on those which were resistant during greenbug outbreaks (Chada et al., 1961). As a result from one of these programs, the variety Will was released in 1961 (Jackson et al., 1964). This variety resulted from a cross between Rogers and Kearney, and the agronomic characteristics added to the greenbug tolerance made Will an important step in the struggle against this insect. A study that included this variety and others concluded that small grains cause greenbugs show increased rate of movement on resistant plants, which could reduce feeding and lessening plant injury (Starks and Burton, 1977). Another conclusion was that the greenbugs congregated on upper portions of resistant plants, where there may be less protection from environmental hazards.

The gene for greenbug resistance in Will was found to be on linkage group 1 and on the centromere bearing segment of chromosome 1 in the TI-6a translocation (Gardenhire et al., 1973). This was determined by using primary and tertiary homozygous translocations.

The Greenbug Biotypes

The development of new strains of insects constitutes an important feature of the environment that may modify the expression of resistance. In the fall of 1958, resistant Dickinson Sel. 28 A and other previously resistant wheat lines were severely injured by the greenbug (Wood, 1961). Investigations with this variety and "Ward" barley indicated that a new greenbug strain had developed in the greenbug culture when compared with those collected from the field. Later, this strain was called biotype B.

Biotype C was found when "Piper" sorghum, a biotype B resistant variety, was severely damaged by this new greenbug (Harvey and

Hackerott, 1969). Differences in greenbug reaction or plant injury caused by the two biotypes were also recorded for wheat, rye, oat and barley. "Dicktoo" barley and "Insave F.A." rye were the only cultivars resistant to both biotypes (Harvey and Hackerott, 1969).

The biology of the three biotypes was studied in relation to different temperatures and varieties (Wood and Starks, 1972). Host plants included greenbug resistant and susceptible barley and sorghum, and it was found that biotype C was better adapted than A or B to high or low temperatures extremes.

Since 1968, the greenbug, in some areas of the Texas High Plains, had been subjected to multiple applications of the organophosphate insecticide disulfoton. During the fall of 1973, there were reports, from this area, of poor control in wheat. This failure was repeated, again in 1974. Laboratory test confirmed the finding of resistance to disulfoton and demonstrated a decrease in insecticide induced mortality of ca. 30 fold. The organophosphate resistant greenbugs were designated as biotype D (Teetes et al., 1975).

In December 1979 greenbugs destroyed the formerly resistant wheat "Amigo" near Bushland, Texas. This new population was called biotype E. The new biotype, morphologically similar to the C, was found to begin reproduction earlier under higher temperatures than biotype C. However, biotype C seemed to be better adapted than E to high temperatures, since its life span was longer (Daniels and Chedester, 1980).

The barley cultivar "Akyurek-100", originating from Turkey, was used in this study because it had shown resistance to biotype E in a preliminary screening test in the greenhouse (K. Starks, 1981, unpublished).

CHAPTER III

MATERIALS AND METHODS

Experiments were conducted to study the three components of resistance (non-preference, antibiosis and tolerance) described by Painter (1951).

Each experiment had all combinations of two temperatures, 20° and 27°C, with two photophase levels, 10 and 14 hours daylight. Two biotypes, C and E, were studied at the above mentioned conditions, on each of two barley cultivars, Will and Akyurek-100. Four similar growth chambers made by Western Environmental Inc., Napa, California, were used, one for each temperature-photophase setting, and several pots for each biotype-variety combination were used in each chamber.

Due to lack of time and facilities it was not feasible to replicate the temperature and photophase setting. In order to get an indication of temperature and photophase influences, data from the four chambers were combined in the statistical analysis. The error near square term is expected to be small for testing temperature, photophase and their interactions; however, in order to reduce the variability, the four chambers were checked and adjusted before each experiment with the same hygrothermograph, which was alternately placed in each chamber during the experiment to check the temperature. The light control mechanism in each chamber was also checked and adjusted before each experiment

started, as well as along the study days. No malfunction of either temperature or photophase control systems was detected.

Non-preference Test

There were two temperatures; 19° and 27°C and two photophases; 10 and 14 hours in these studies. Four chambers were used to obtain all combinations of temperature and photophase. Only one trial of each combination was used in the experiment. The relative humidity within the chambers was between 50 and 60%.

Four seeds of each of Will (biotype C barley resistant cultivar) and Akyurek-100 (Ak) (biotype E barley resistant cultivar) were planted at random in a circle around the edge of each 15cm diameter plastic pot. When plants were 4-5cm tall, 50 adult apterous aphids of either biotype C or biotype E from laboratory cultures were released on the soil surface in the center of each pot. Pots were then covered with plastic cages with cloth covered ventilation holes. There were four pots for each biotype within a chamber. This gives a split-plot design for each temperature-photophase setting in which the main plots were greenbug biotypes and the varieties were subplots. The main plots were in a completely randomized design.

The number of aphids on each plant was recorded one and two days after the infestation to determine possible variated preference between barley varieties. Thus, there were two analyses, one for each count.

In the statistical analysis the variation among pots within temperature-photophase-biotype combination was used to test the temperature, photophase, biotype and their interactions and the variation among pots x varieties within temperature-photophase-biotype

combination was used to test the varieties and its interactions.

Treatment effects were tested by the "F" test. The distinction between pairs of means were checked by Least Significant Difference (LSD), at 5% level. The description and discussion of the results were based on those means which were significantly different.

Antibiosis Test

For this test the same conditions in the same chambers as described in Non-preference Test were used, with the same temperature, photophase and relative humidity conditions. Single barley seeds were planted in 7.6cm diameter plastic pots. The varieties Will and Akyurek-100 were tested in this experiment with greenbug biotypes C and E. Each variety x biotype combination had 10 pots. This makes a 2 x 2 factorial experiment in a completely randomized design for each temperature-photophase combination, with a total of 40 pots per chamber.

When the plants were ca. 5cm tall, two adult apterous greenbugs were placed on each pot, and pots were covered with plastic cages with cloth covered ventilation holes. When the first newly born nymph appeared, the adults were removed and the nymph was allowed to grow. Nymphal and adult life spans were recorded for these aphids as well as fecundity of adults.

In the statistical analysis the data from the four chambers were also combined. The variation among pots within temperature, photophase, biotype and varieties combinations were used to make all the tests.

Treatment effects were tested by the "F" test. The distinction between pairs of means were checked by Least Significant Difference (LSD), at 5% level. The description and discussion of the results was

based on those means which were significantly different.

Tolerance Test

Environmental conditions for this test were the same as described for previous two tests. Two barley seeds for the same variety were planted in 7.6cm diameter plastic pots. When the plants were ca. 10cm tall, 20 adult apterous greenbugs were placed on the pot, which were covered with plastic cages with ventilation holes. The average size of the two plants in each pot was recorded before infestation and after the 12th infestation day, to estimate the growth. The aphid population was kept constant along the 12 days by removing the nymphs.

There were two varieties, Will and Akyurek-100, and three infestations, namely biotype C, biotype E and no infestation (check). Five pots for each variety-biotype combination were used, giving a total of 30 pots per chamber. This makes a 2 x 3 factorial experiment in a completely randomized design for each temperature-photophase combination as described in the antibiosis test.

The data from the four chambers were combined for statistical analysis.

The effects on growth during the 12 infestation days were tested by using subplot means (size before infestation and after the 12 infestation days). The error term for making this test was pot x growth within temperature, photophase, biotype and variety combinations.

Treatment effects in the analysis for tolerance test were calculated by the "F" test. The distinction between pairs of means were checked by Least Significant Difference (LSD), at 5% level.

The description and discussion of the results was based on those means which resulted significantly different.

CHAPTER IV

RESULTS AND DISCUSSION

Non-preference Test

Significant effects ($P<5\%$) were found for readings taken 24 to 48 hours after infestation, between varieties, and in the variety x photophase and variety x photophase x biotype interactions (Table I).

The varietal choice by the aphids was influenced by photophase and biotype being tested. Of these, photophase appeared to be the more important. At both 24 and 48h reading in the 14h photophase, Akyurek-100 was significantly less preferred than Will. At the 10h photophase the result was the opposite with Will having fewer aphids per plant, though the results were not significantly different after 24h. This indicated that if both greenbug biotypes are considered together, a strong non-preference is particularly evident in favor of Akyurek-100 in the 14h light period. At the shorter photophase Will was less preferred.

The differences in preference between biotypes depended on photophase and variety. The greatest differences were found with biotype C at 14h photophase, with Akyurek-100 strongly non-preferred; by contrast, Will was less preferred in 10h photophase by the same biotype. This biotype influence was repeated in both readings, which indicated a slight influence of this factor. Again, photophase played an important role in terms of preference of biotypes for varieties.

TABLE I

NUMBER OF BIOTYPE C AND E GREENBUGS PREFERRING TWO VARIETIES OF BARLEY WITH TWO PHOTOPHASES

Variety	Photo Phase (h)	24 hours Biotype[1] C	24 hours Biotype[1] E	24 hours Avg. for biotypes[2]	24 hours Avg. for varieties[3]	48 hours Biotype[4] C	48 hours Biotype[4] E	48 hours Avg. for biotypes[5]	48 hours Avg. for varieties[6]
	10	8.90	7.84	8.37		8.34	7.12	7.73	
Ak					6.86				6.49
	14	4.37	6.34	5.35		4.56	5.96	5.26	
	10	6.53	8.31	7.42		4.93	7.09	6.01	
Will					8.18				7.59
	14	9.59	8.31	8.95		9.81	8.56	9.18	

[1] LSD 0.05 = 2.39 for biotypes

[2] LSD 0.05 = 1.69 for biotypes averages

[3] LSD 0.05 = 1.19 for varieties

[4] LSD 0.05 = 1.46 for biotypes

[5] LSD 0.05 = 1.03 for biotypes averages

[6] LSD 0.05 = 0.73 for varieties

The analysis of variance and means for 24 and 48 accounts for this test are presented in the Appendix, Tables XIII, XIV, XV and XVI respectively.

Antibiosis Test

Life Span

Temperature, photophase and variety influenced greenbugs longevity. No difference was found between biotypes.

Both temperature and photophase considered independently and in combination influenced the greenbug life span. The greatest longevity occurred at 19°C and 14h photophase, in this case the greenbugs lived an average of 49.5 days. The opposite conditions, 27°C and 10h photophase, permited the shortest aphid survival, with an average of 34.4 days (Table II).

TABLE II

LIFE SPAN (DAYS) OF GREENBUGS WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

	Photophase (h)[1/]		
Temp. (°C)	10	14	Avg.[2/]
19	42.1	49.5	45.8
27	34.4	37.6	36

[1/] LSD 0.05 = 2.51 for photophase

[2/] LSD 0.05 = 1.78 for temperature average

The differences in aphids life span between varieties depended on temperature and photophase. At the highest temperature (27°C), greenbugs lived longer on Will than an Akyurek-100; this difference was larger at 10h than at 14h photophase. At 19°C, the aphid's life span was shorter on Will than on Akyurek-100, so this result was just the opposite as the one obtained at 27°C. The photophase showed its influence by making the difference between aphids life span significant at 10h light period. (Table III).

TABLE III

LIFE SPAN (DAYS) OF GREENBUGS ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

Var.	Temp. (°C)	Photophase (h)[1/] 10	14	Avg. for Temperature[2/]
Ak	19	45.1	50.5	47.8
	27	32.1	37.3	34.7
Will	19	39.1	48.5	43.8
	27	36.7	38.0	37.3
Average[3/]		38.2	43.5	

[1/] LSD 0.05 = 3.56 for photophase

[2/] LSD 0.05 = 2.52 for temperature average

[3/] LSD 0.05 = 1.78 for photophase average

Although variety and photophase had a slight influence on the

greenbugs life span, temperature was the most important factor in determining longevity. The analysis of variance and means for aphids lifespan are presented in the Appendix, Tables XVII and XVIII respectively.

Total Number of Nymphs per Female

All four factors studied, temperature, photophase, variety and biotype, influenced greenbug fecundity. Temperature and photophase influenced independently (Table IV) and together (Table V) on the two varieties. In the above cases, the reproductive rates were greater on Akyurek-100 than on Will. The greatest difference was at 19°C, where the females produced an average of 22.1 nymphs on Will and 51.1 nymphs on Akyurek-100. This difference was similar at both photophases. At 27°C and 10h light period (Table V) there was an average of 43.5 nymphs and will 35.8 nymphs per female on Akyurek-100. This difference was also significant.

TABLE IV

AVERAGE NYMPHAL PRODUCTION PER FEMALE ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

	Temps. (°C)		Photophase (h)	
Var.	19	27	10	14
Ak	51.1	52.2	45.9	57.4
Will	22.1	37.2	27.9	31.4

LSD 0.05 = 4.56

TABLE V

AVERAGE NYMPHAL PRODUCTION PER FEMALE ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

Temp. (°C)	Var.	Photophase (h)[1] 10	Photophase (h)[1] 14	Avg. for Temperature[2]
19	Ak	48.3	53.8	36.5
	Will	19.9	24.2	
27	Ak	43.5	60.9	44.7
	Will	35.8	38.7	
Average (2)		36.9	44.4	

[1] LSD 0.05 = 6.44 for photophase

[2] LSD 0.05 = 3.22 for temperature average

The significant difference between biotypes was confounded with temperature and variety (Table VI). The largest difference was at 27°C on Will, where reproduction of biotype E was greater than that of C (42.7 vs. 31.8 nymphs).

All four factors were important in aphid fecundity, but the varietal influences were the greatest, with the lowest reproduction on Will (29.6 nymphs per female).

The analysis of variance and means for the total offspring per female are presented in the Appendix, Table XIX and XX respectively.

TABLE VI

AVERAGE NYMPHAL PRODUCTION PER FEMALE OF GREENBUG BIOTYPES C AND E ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE CONDITIONS

Biotypes	Temp. (°C)	Varieties[1/] Ak	Will	Avg. for Biotypes[2/]
C	19	47.8	19.0	37.9
	27	53.1	31.8	
E	19	54.4	25.1	43.4
	27	51.3	42.7	
Average (2)		51.6	29.6	

[1/] LSD 0.05 = 6.44 for varieties

[2/] LSD 0.05 = 3.22 for biotypes averages

Average of Nymphs per Day per Female

Temperature, varieties and biotypes either independently or combined in different interactions were the factors that regulated the average of nymphs produced per female per day. Biotype E had a higher average of nymphs per day on Will compared with biotype C. But both were more prolific on Ak. (Table VII).

Temperature also influenced this biological parameter, since on Will at 27°C the difference in favor of biotype E (more nymphs per day) was significant when compared with biotype C. There were no difference at 19°C. (Table VIII).

TABLE VII

AVERAGE NYMPHAL PRODUCTION PER FEMALE PER DAY OF GREENBUG BIOTYPES C AND E ON TWO BARLEY VARIETIES

Biotypes	Varieties[1]		Average for Biotypes[2]
	Ak	Will	
C	1.31	0.63	0.97
E	1.28	0.87	1.07
Average (2)	1.29	0.75	

[1] LSD 0.05 = 0.11 for varieties

[2] LSD 0.05 = 0.08 for biotypes average

Temperature was also important in determining the nymphs produced per female per day, since the average for both biotypes was 0.79 nymphs at 19°C and 1.25 nymphs at 27°C. There was antibiosis for both biotypes exhibited by Will.

The analysis of variance and means for average of nymphs per female per day are presented in the Appendix, Tables XXI and XXII, respectively.

TABLE VIII

AVERAGE NYMPHAL PRODUCTION PER FEMALE PER DAY OF GREENBUG BIOTYPES C AND E ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE CONDITIONS

Biotype	Var.	Temperature (°C)[1] 19	27
C	Ak	1.05	1.57
	Will	0.44	0.82
E	Ak	1.11	1.45
	Will	0.56	1.17
Average for Temperature[2]		0.79	1.25

[1] LSD 0.05 = 0.16 for temperature

[2] LSD 0.05 = 0.08 for temperature average

Nymphal Developmental Period

The difference between the two varieties was highly significant (P = 0.01%), with the nymphal stage lasting 6.42 days on Akyurek-100 and 9.98 days on Will.

The environmental factors, light and temperature, had a strong influence in the nymphal length period. This period was longer at the lower photophase and temperature values (Table IX). No difference was found between biotypes when compared at the same temperature or photophase condition.

TABLE IX

NYMPHAL DEVELOPMENTAL PERIOD (DAYS) OF GREENBUG BIOTYPES C AND E WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

	Temperature (°C)[1/]		Photophase (h)[1/]	
Biotype	19	27	10	14
C	9.55	6.85	8.90	7.50
E	10.32	6.10	8.30	8.12
Averages[2/]	9.93	6.47	8.60	7.81

[1/] LSD 0.05 = 0.81 for temperature and photophase

[2/] LSD 0.05 = 0.57 for photophase and temperature averages

Both greenbug biotypes developed slowly on Will compared with Akyurek-100. Temperature was also an important factor in the juvenile stage length. The nymphal aphid developmental time was 6.47 and 9.93 days at 27° and 19°C, respectively.

The analysis of variance and means for nymphal developmental period are presented in the Appendix, Tables XXIII and XXIV, respectively.

Tolerance Test

The four studied factors influenced plant growth. The differences between varieties in greenbug tolerance depended on which biotype caused the damage. Both varieties did not tolerate biotype C, Akyurek-100 had a higher tolerance to biotype E than Will (Table X).

TABLE X

PLANT GROWTH (cm) OF TWO BARLEY VARIETIES AT TWO PHOTOPHASE CONDITIONS AND INFESTED BY TWO GREENBUG BIOTYPES

Var.	Time of height measurement	Photophase (h)[1]		Biotypes[2]			Avg. for Var.[3]
		10	14	C	E	K[4]	
Will	at inf.	10.44	11.01	11.17	10.19	10.82	10.73
	12 days after inf.	13.94	17.19	13.29	14.17	19.23	15.56
Ak	at inf.	11.52	11.79	11.62	12.16	11.19	11.66
	12 days after inf.	14.98	19.59	13.39	16.94	21.52	17.28

[1] LSD 0.05 = 0.78 for photophase

[2] LSD 0.05 = 0.96 for biotypes

[3] LSD 0.05 = 0.55 for varieties averages

[4] K = uninfested check

Photophase was also a regulator of plant growth, since at 14h both varieties developed better than at 10h photophase (Table X). Photophase also influenced greenbug biotypes behavior; at 10h the differences in plant growth were minimum and at 14h biotype E permited more growth than C (Table XI).

TABLE XI

PLANT GROWTH (cm) OF BARLEY VARIETIES UNDER TWO PHOTOPHASE CONDITIONS INFESTED BY TWO GREENBUG BIOTYPES

Biotypes	Time of height measurement	Photophase (h)[1]		Avg. for Biotypes[2]
		10	14	
C	at inf.	11.40	11.39	11.39
	12 days after inf.	12.70	13.97	13.34
E	at inf.	11.10	11.25	11.18
	12 days after inf.	13.03	18.08	15.56
Uninfested	at inf.	10.45	11.56	11.00
	12 days after inf.	17.63	23.11	20.37

[1] LSD 0.05 = 0.96 for photophase

[2] LSD 0.05 = 0.68 for biotypes average

Photophase was confounded with temperature. At the lower photophase, both barley varieties grew better at 19°C. At 14h photophase the better grown was observed at 27°C. (Table XII).

TABLE XII

PLANT GROWTH (cm) OF BARLEY VARIETIES AT TWO TEMPERATURE AND PHOTOPHASE CONDITIONS

Photophase	Time of height measurement	Temperature[1] 19	27	Avg. for Photophase[2]
10	at inf.	10.85	11.12	10.98
	12 days after inf.	14.67	14.25	14.46
14	at inf.	11.45	11.35	11.40
	12 days after inf.	17.59	19.18	18.39

[1] LSD 0.05 = 0.78 for temperature

[2] LSD 0.05 = 0.55 for photophase average

Although related to other factors, photophase (Table XII) and biotypes (Table XI) were the most important plant growth regulators. Biotype C inhibited plant development to a greater extent than biotype E; and both varieties grew better at 14h photophase.

The analysis of variance and means for tolerance test are presented in the Appendix, Tables XXV and XXVI, respectively.

CHAPTER V

SUMMARY AND CONCLUSIONS

The research was conducted at four different combination of two temperatures (19 and 27°C) and two photophase periods (10 and 14 light hours), to compare the resistance of Will and Akyurek-100 barley varieties when attacked by biotypes C and E of the greenbug; and to determine if the temperature and photophase conditions influenced on the resistance expression by the two varieties.

The work followed the three resistance mechanisms described by Painter (1951). In the non-preference study the photoperiod played an important role, since it regulated the highly significant difference in favor of Akyurek-100 at 14 photophase. The differences in preference between the biotypes were not significant.

Four parameters were measured in the antibiosis test: aphid life span, number of days spent as nymph, total offspring per aphid and average offspring per day per aphid. Both, temperature and photoperiod had a strong influence on life span, the best combination for a long survival being 14 hour light period at 19°C. No difference was found between biotypes. Temperature, photophase and varieties were the most important factors in determining the nymphal stage length of the aphids. Both biotypes spent more time as nymph when reared on Will than on Akyurek-100. They also needed more time at the lower temperature and shorter photophase. The total number of nymphs per aphid depend on:

temperature, with the most offspring at 27°C; photophase, with more nymphs per aphid at 14 hour light period; biotypes, with E more prolific than C; and on varieties, since Akyurek-100 permitted more reproduction than Will. Finally, the temperature had a strong influence on the average number of nymphs per aphid per day; the higher the temperature, the higher the reproduction rate. Biotype E had more nymphs per day, and the reproduction was higher on Akyurek-100 than Will, for both biotypes.

In the tolerance test a highly significant difference was found between biotypes. Biotype C was more effective in keeping both varieties from growing. In this test the photoperiod again showed its influence in determining plant tolerance. At 14 light period the difference between biotypes was larger than at 10h light period.

The photophase was an important regulator of the aphids preference between the two barley varieties studied.

Antibiosis was found in the variety Will when compared with Akyurek-100 in most of the aphids biological parameters checked. Temperature also appeared as an important factor in the greenbug life.

Biotype C was more harmful than E in the tolerance test.

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TABLE XIII

ANOVA FOR THE PREFERENCE OF TWO GREENBUG BIOTYPES FOR TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS AFTER 24 HOURS INFESTATION

SOURCE	DF	MEAN SQUARE	F VALUE	PROB > F
Temp	1	0.00	0.00	.9838
Light	1	35.25	2.70	.1099
Temp*Phot	1	46.41	3.55	.0684
Bio	1	7.91	0.60	.5502
Temp*Bio	1	12.69	0.97	.6647
Phot*Bio	1	0.00	0.00	.9838
Temp*Phot*Bio	1	9.37	0.71	.5904
Error A	24	13.05		
Var	1	111.56	5.18	.0303
Temp*Var	1	4.25	0.19	.6644
Phot*Var	1	330.78	15.36	.0009
Temp*Phot*Var	1	20.81	0.96	.6633
Bio*Var	1	0.66	0.03	.8566
Temp*Bio*Var	1	6.56	0.30	.5921
Phot*Bio*Var	1	148.53	6.89	.0141
Temp*Phot*Bio*Var	1	4.78	0.22	.6462
Error B	24	21.52		

TABLE XIV

MEANS FOR THE PREFERENCE OF TWO GREENBUG BIOTYPES FOR TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS AFTER 24 HOURS INFESTATION

		Temperature			
		19		27	
		Phot.		Phot.	
Bio.	Var.	10	14	10	14
C	W	6.93	9.06	6.12	10.12
	Ak	10.18	4.12	7.62	4.62
E	W	7.93	8.31	8.68	8.31
	Ak	8.25	5.43	7.43	7.25

TABLE XV

ANOVA FOR THE PREFERENCE OF TWO GREENBUG BIOTYPES FOR TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS AFTER 48 HOURS INFESTATION

SOURCE	DF	MEAN SQUARE	F VALUE	PROB > F
Temp	1	2.06	0.20	.6566
Phot	1	7.91	0.79	.6152
Temp*Phot	1	69.09	6.95	.0138
Bio	1	4.78	0.48	.5010
Temp*Bio	1	0.09	0.00	.9187
Phot*Bio	1	2.44	0.24	.6299
Temp*Phot*Bio	1	0.09	0.00	.9187
Error A	24	9.93		
Var	1	77.66	9.65	.0049
Temp*Var	1	6.56	0.81	.6215
Phot*Var	1	509.06	63.31	.0001
Temp*Phot*Var	1	2.06	0.25	.6223
Bio*Var	1	2.06	0.25	.6223
Temp*Bio*Var	1	9.37	1.16	.2910
Phot*Bio*Var	1	145.50	18.09	.0005
Temp*Phot*Bio*Var	1	5.34	0.66	.5720
Error B	24	8.04		

TABLE XVI

MEANS FOR THE PREFERENCE OF TWO GREENBUG BIOTYPES FOR TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND PHOTOPHASE CONDITIONS AFTER 48 HOUR INFESTATION

		Temperature			
		19		27	
Bio.	Var.	10	14	10	14
C	Will	5.25	8.93	4.62	10.68
	Ak	9.25	4.50	7.43	4.62
E	Will	7.50	8.43	6.68	8.68
	Ak	7.93	5.31	6.31	6.62

TABLE XVII

ANOVA FOR GREENBUG BIOTYPES C AND E LIFE SPAN ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

SOURCE	DF	MEAN SQUARE	F VALUE	PR > F
Temp	1	3822.02	116.57	0.0001
Phot	1	1134.22	34.59	0.0001
Temp*Phot	1	172.22	5.25	0.0234
Bio	1	34.22	1.04	0.3086
Temp*Bio	1	55.22	1.68	0.1964
Phot*Bio	1	93.02	2.84	0.0943
Temp*Phot*Bio	1	55.22	1.68	0.1964
Var	1	18.22	0.56	0.4571
Temp*Var	1	442.22	13.49	0.0003
Phot*Var	1	0.02	0.00	0.9780
Temp*Phot*Var	1	156.02	4.76	0.0308
Bio*Var	1	30.62	0.93	0.3354
Temp*Bio*Var	1	5.62	0.17	0.6793
Phot*Bio*Var	1	0.62	0.02	0.8904
Temp*Phot*Bio*Var	1	2.02	0.06	0.8041
Error	144	32.78		

TABLE XVIII

MEANS FOR GREENBUG BIOTYPES C AND E LIFE SPAN (DAYS) ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

		Temperature			
		19		27	
		Photophase		Photophase	
Bio.	Var.	10	14	10	14
C	Will	39.60	46.40	37.80	38.40
	Ak	45.20	47.80	31.60	36.80
E	Will	38.60	50.60	35.60	37.60
	Ak	45.00	53.20	32.60	37.80

TABLE XIX

ANOVA FOR TWO GREENBUG BIOTYPES TOTAL OFFSPRING ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

SOURCE	DF	MEAN SQUARE	F VALUE	PR > F
Temp	1	2665.05	24.86	0.0001
Phot	1	2257.50	21.06	0.0001
Temp*Phot	1	273.00	2.55	0.1127
Bio	1	1193.56	11.13	0.0011
Temp*Bio	1	31.50	0.29	0.5888
Phot*Bio	1	3.90	0.04	0.8489
Temp*Phot*Bio	1	23.25	0.22	0.6421
Var	1	19338.00	180.40	0.0001
Temp*Var	1	1967.00	18.85	0.0001
Phot*Var	1	620.15	5.79	0.0174
Temp*Phot*Var	1	445.55	4.16	0.0433
Bio*Var	1	375.15	3.50	0.0634
Temp*Bio*Var	1	438.90	4.09	0.0449
Phot*Bio*Var	1	3.90	0.04	0.8489
Temp*Phot*Bio*Var	1	94.55	0.88	0.3492
Error	144	107.19		

TABLE XX

MEANS FOR TWO GREENBUG BIOTYPES TOTAL OFFSPRING ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

		Temperature			
		19		27	
		Photophase		Photophase	
Bio.	Var.	10	14	10	14
C	Will	17.60	20.50	30.30	33.30
	Ak	43.90	51.70	45.60	60.70
E	Will	22.30	28.00	41.40	44.10
	Ak	52.80	56.00	41.50	61.20

TABLE XXI

ANOVA FOR DAILY REPRODUCTION RATE OF TWO GREENBUG BIOTYPES ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

SOURCE	DF	MEAN SQUARE	F VALUE	PR > F
Temp	1	8.43	120.45	0.0001
Phot	1	0.26	3.80	0.0532
Temp*Phot	1	0.22	3.15	0.0779
Bio	1	0.43	6.21	0.0139
Temp*Bio	1	0.00	0.05	0.8294
Phot*Bio	1	0.03	0.48	0.4897
Temp*Phot*Bio	1	0.07	1.12	0.2922
Var	1	11.85	169.20	0.0001
Temp*Var	1	0.04	0.66	0.4175
Phot*Var	1	0.19	2.85	0.0933
Temp*Phot*Var	1	0.14	2.09	0.1506
Bio*Var	1	0.67	9.89	0.0022
Temp*Bio*Var	1	0.42	6.13	0.0145
Phot*Bio*Var	1	0.01	0.17	0.6849
Temp*Phot*Bio*Var	1	0.09	1.29	0.2587
Error	144	0.07		

TABLE XXII

MEANS FOR DAILY REPRODUCTION RATE OF TWO GREENBUG BIOTYPES ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

		Temperature			
		19		27	
		Photophase		Photophase	
Bio.	Var.	10	14	10	14
C	Will	0.44	0.44	0.80	0.84
	Ak	0.97	1.12	1.45	1.69
E	Will	0.57	0.56	1.16	1.17
	Ak	1.17	1.05	1.28	1.61

TABLE XXIII

ANOVA FOR NYMPHAL DEVELOPMENTAL PERIOD OF TWO GREENBUG BIOTYPES ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

SOURCE	DF	MEAN SQUARE	F VALUE	PR > F
Temp	1	479.55	139.87	0.0001
Phot	1	24.80	7.24	0.0080
Temp*Phot	1	12.65	3.69	0.0567
Bio	1	0.00	0.00	0.9660
Temp*Bio	1	23.25	6.78	0.0102
Phot*Bio	1	15.00	4.38	0.0382
Temp*Phot*Bio	1	0.15	0.05	0.8313
Var	1	507.65	148.07	0.0001
Temp*Var	1	6.80	1.99	0.1610
Phot*Var	1	4.55	1.33	0.2509
Temp*Phot*Var	1	6.80	1.99	0.1610
Bio*Var	1	0.75	0.22	0.6393
Temp*Bio*Var	1	1.80	0.53	0.4691
Phot*Bio*Var	1	5.25	1.53	0.2177
Temp*Phot*Bio*Var	1	1.40	0.41	0.5229
Error	144	3.42		

TABLE XXIV

MEANS FOR NYMPHAL DEVELOPMENTAL PERIOD (DAYS) OF TWO GREENBUG BIOTYPES ON TWO BARLEY VARIETIES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

		Temperature			
		19		27	
		Photophase		Photophase	
Bio.	Var.	10	14	10	14
C	Will	12.00	11.00	10.20	7.00
	Ak	8.00	7.20	5.40	4.80
E	Will	12.00	12.70	8.00	7.00
	Ak	8.20	8.40	5.00	4.40

TABLE XXV

ANOVA FOR PLANT GROWTH (TOLERANCE) OF TWO BARLEY VARIETIES DURING THE INFESTATION OF TWO GREENBUG BIOTYPES WITH TWO TEMPERATURE AND TWO PHOTOPHASE CONDITIONS

	DF	MEAN SQUARE	F VALUE	PROB > F
Growth	1	1641.43	774.59	.0001
Temp*Growth	1	3.81	1.79	.1797
Phot*Growth	1	185.06	87.33	.0001
Temp*Phot*Growth	2	21.33	10.06	.0024
Bio*Growth	2	286.40	135.15	.0001
Temp*Bio*Growth	2	1.18	0.55	.5797
Phot*Bio*Growth	2	19.00	8.96	.0005
Temp*Phot*Bio* Growth	2	3.95	1.86	.1585
Variety*Growth	1	9.30	4.38	.0364
Temp*Variety*Growth	1	0.11	0.05	.8147
Phot*Variety*Growth	1	10.31	4.86	.0280
Temp*Phot*Variety* Growth	1	0.03	0.01	.8952
Bio*Variety*Growth	2	6.54	3.08	.0488
Temp*Bio*Variety* Growth	2	3.88	1.80	.1673
Phot*Bio*Variety* Growth	2	4.22	1.99	.1400
Temp*Phot*Bio* Variety*Growth	2	2.29	1.08	.3439
Error	96	2.11		

TABLE XXVI

MEANS FOR PLANT GROWTH (cm) (TOLERANCE) OF TWO BARLEY VARIETIES DURING THE INFESTATION OF TWO GREENBUG BIOTYPES AND UNINFESTED CHECK WITH TWO TEMPERATURE AND PHOTOPHASE CONDITIONS

			Temperature			
			19		27	
		Time of height measure-	Photophase		Photophase	
Bio.	Var.	ment	10	14	10	14
	Will	at inf.	10.39	10.94	12.16	11.19
C		12 days after inf.	11.53	13.83	13.80	14.02
	Ak	at inf.	12.43	12.17	10.64	11.27
		12 days after inf.	13.36	13.33	12.14	14.27
	Will	at inf.	8.46	8.90	11.73	11.69
E		12 days after inf.	12.08	13.50	12.25	18.87
	Ak	at inf.	12.10	12.95	12.13	11.49
		12 days after inf.	14.47	19.99	13.35	19.98
	Will	at inf.	10.32	12.20	9.62	11.17
Uninfested Check		12 days after inf.	17.02	20.50	16.97	22.44
	Ak	at inf.	19.56	11.59	10.45	11.31
		12 days after inf.	19.56	24.43	17.00	25.09

VITA

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