STUDIES OF INSECT-PLANT INTERACTIONS: GREENBUGS (HOMOPTERA: APHIDIDAE), HOST-PLANT RESISTANCE, AND DROUGHT STRESS IN WINTER WHEAT

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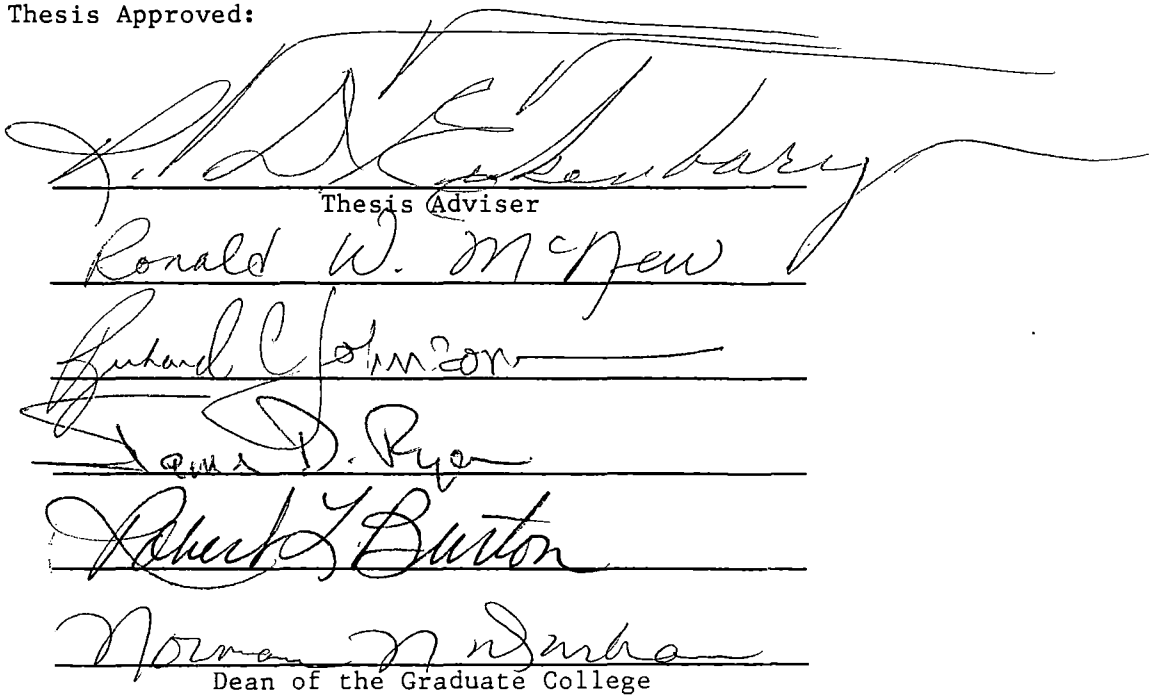

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PART III

INTRODUCTION

Each part of this thesis is a separate and complete manuscript for publication. Part I has been published in Environmental Entomology (15: 118-121). Parts II and III will also be published in journals as yet unchosen.

PART I

INSECT-PLANT INTERACTIONS: GREENBUGS (HOMOPTERA: APHIDIDAE) DISRUPT ACCLIMATION OF WINTER WHEAT TO DROUGHT STRESS

ABSTRACT

This growth-chamber study was designed to investigate the effect of greenbug, Schizaphis graminum (Rondani), feeding on physiological responses of wheat, Triticum aestivum L., associated with drought stress, to determine how drought stress affects greenbug density, and to determine how drought and greenbug-resistant cultivars alter these responses. The cultivars chosen were 'Amigo' (relatively resistant to biotype C greenbugs), 'Sturdy' (comparatively drought and greenbug susceptible), and "TAM W-101" (comparatively drought resistant and greenbug susceptible). Greenbugs altered two potentially adaptive responses of wheat to drought; they virtually negated an increase in cell membrane stability associated with wheat conditioned to drought stress, and solute potential was reduced less in greenbug plus drought stress treatments than in drought stress-only treatments; water potential, however, was not altered by greenbug infestations. The lowered turgor pressure that resulted for infested plants suggests that osmotic adjustment (the maintenance of turgor through the accumulation of solutes in plants under drought stress) was also reduced by greenbugs. In addition, greenbug density (number of greenbugs per mg shoot dry weight) was greater on drought-stressed plants. These data provide physical and physiological evidence supporting field observations that greenbug infestations are potentially more damaging when wheat is subjected to drought than when rainfall is sufficient.

INTRODUCTION

Periodic Drought and infestations of the greenbug, Schizaphis graminum (Rondani), are important stresses commonly associated with the production of winter wheat, Triticum aestivum L., in the Great Plains of the United States. Yet the interactions of these stresses with wheat physiology and the effect of water deficits on greenbug biology have remained relatively unstudied. This is true despite field observations that greenbug infestations are potentially more damaging in conjunction with drought than when rainfall is adequate (Kelly 1917).

Greenbugs feeding on a greenbug-susceptible wheat cultivar that was drought-stressed using polyethylene glycol showed a sharp decline in fecundity, longevity, reproductive period, and progeny produced per reproductive day with increasing stress levels (Sumner et al. 1983). This suggests that greenbugs are detrimentally affected by drought stress. Indeed, greenbug outbreaks have been associated with normal to above-normal rainfall in central Oklahoma (Rogers et al. 1972). There is, however, evidence indicating that periods of drought can promote greenbug outbreaks (Wadley 1931, Walker 1954), and greenbugs have greatly reduced the yield of severely drought-stressed grain sorghum in the field (Kindler and Staples 1981).

Although susceptible genotypes sustain greater damage, greenbugs are known to damage or alter the cell walls and membranes of both susceptible (Chatters and Schlehuber 1951, Al-Mousawi et al. 1983) and resistant (Al-Mousawi et al. 1983) wheat genotypes. The implications of

damage of this type to potentially adaptive drought-response mechanisms in wheat have not been investigated.

The objectives of our study were to investigate the effects of greenbug infestations on physiological plant responses associated with drought stress, to determine how drought stress affects greenbug density, and to determine how drought- and greenbug-resistant cultivars of winter wheat influence these responses.

MATERIALS AND METHODS

Wheat cultivars were chosen to represent a range of host plant reactions to both greenbug and drought stress. 'Amigo' was used because of its resistance to biotype C greenbugs (GBC), 'Sturdy' because it is comparatively susceptible to both drought and GBC, and 'TAM W-101' because it is comparatively drought-resistant, but susceptible to GBC (Johnson et al. 1984). Seeds of these cultivars were vernalized in petri dishes on moist filter paper at 4°C for 6 weeks and then transplanted in sand in pots (20 by 20 cm, 4 liters capacity) and placed in growth chambers. The growth chambers were maintained at 20°C, 50-60% RH, and 16:8 (L:D) photoperiod averaging 650 $mol \cdot m^{-2} \cdot s^{-1}$ photon flux density. The experiment was randomized in seven complete blocks over two tests with cultivars, water level (stressed or not stressed), and greenbugs (infested or not infested) as experimental factors. All data were subjected to analysis of variance after averaging over blocks. The sources of variation were test, cultivar, water level, cultivar x water level, greenbug, cultivar x greenbug, water level x greenbug, and cultivar x water level x greenbug, with the residual used as the error term.

Before starting the stress treatments, plants were grown unstressed for 32 days, after which time most were in the boot-growth stage.

Greenbug treatments then received an initial infestation of one apterous adult GBC for every 5 cm^2 leaf area. Leaf areas of the test plants were estimated using a leaf-area meter and determined as the average of six other plants of each cultivar growing in the same chamber. Drought stress was initiated by withholding water until considerable leaf rolling and wilting were observed. Then, to prevent plant death and maintain stress, all drought-stressed plants received ca. 50 ml of 10% Hoagland's solution every other day. Plants not drought stressed required about 100 ml of solution daily to maintain moist conditions.

The drought/greenbug stress period lasted 3 weeks, after which greenbugs were removed and counted. This allowed adequate time for the plants to become conditioned to the drought stress and, therefore, exhibit adaptive responses. Living tillers per plant were counted before and after the stress treatments began. From this, proportional tiller survival was calculated. The last fully emerged living leaf of a given tiller was taken for both free amino acid and proline analysis, and a similar leaf from another tiller was taken for membrane stability tests. For infested plants, membrane stability was examined using leaves that had been fed up upon. Free amino acids and proline were extracted by grinding the leaf with a mortar and pestle in 10 ml of a 3% sulfosalicylic acid solution and then filtering through Whatman No. 2 filter paper (Tan and Halloran 1982). A 1-ml amount of the filtrate was assayed for free amino acids (excluding proline) by the ninhydrin method (Yemm and Cocking 1955) using a glycine standard. Absorbance was read on a spectrophotometer (Bausch and Lomb 2000) at 570 nm. Another 1-ml amount of the filtrate was assayed for free proline using the acid ninhydrin method (Bates et al. 1973) with absorbance read at 520 nm. Membrane stability was investigated using the methods of Blum and Ebercon (1981). This procedure

utilizes the measurement of electroconductivity of aqueous media containing sets of matched leaf disks from a single leaf. One set of leaf disks was osmotically stressed by incubation in a solution of 40% wt/vol polyethylene glycol while the other set remained unstressed by incubation in distilled water. In this manner, the amount of solute leakage from cells in response to the osmotic stress is measured and, in general, less leakage is observed after plants have been conditioned to drought stress.

Individually calibrated leaf-cutter psychrometers (J. R. D. Merrill Specialisty Equipment, Logan, Utah) were used to estimate water potential (ψ), solute potential (ψ_s), and turgor pressure (ψ_p), of leaf tissue as described by Johnson et al. (1984). Leaf disks (0.24 cm^2) were taken from living, fully expanded leaves and ψ measured after the psychrometers had equilibrated for 2 h in a 30°C water bath. Estimates of ψ_p were made as $\psi_p = \psi - \psi_s$, which assumes the matric potential to be near zero.

Shoot and root dry weights were also determined. Sand was washed from the roots and all plant parts were dried at 70°C for 48 h. After the dry weights were determined, the roots were rubbed on a threshing board to remove sand that could not be washed off. The sand was separated from the root material with the careful use of a seed blower. The clean sand was then weighed and the weight subtracted from the original weight to obtain actual root dry weight.

RESULTS AND DISCUSSION

Several effects were induced by water deficits alone, without significant cultivar or greenbug effects or interactions. These included reductions in root dry weight (d.w.) ($F = 7.62$; $df = 1,11$; $P < 0.05$), shoot d.w. ($F = 16.92$; $df = 1.11$; $P < 0.05$), and tiller survival

($F = 12.06$; $df = 1,11$; $P < 0.05$), as well as increases in free amino acids ($F = 27.5$; $df = 1,66$; $P < 0.05$), free proline ($F = 41.14$; $df = 1,66$; $P < 0.05$), and root-to-shoot ratio ($F = 4.31$; $df = 1,11$; $P = 0.05$) (Table 1). All of these responses have been traditionally associated with drought stress in plants (Levitt 1980).

Other responses, however, contained significant greenbug effects. Membrane stability tests revealed that the feeding activities of greenbugs caused increased membrane injury in winter wheat ($F = 12.99$; $df = 1,66$; $P < 0.05$). We also found that all cultivars had equally reduced membrane injury after drought stress compared with unstressed plants ($F = 23.21$; $df = 1,66$; $P < 0.05$), but this adjustment was negated by the presence of greenbugs (Table 2). Under drought stress without greenbugs, membrane damage was very low, indicating that cell membrane adjustment had occurred. On plants subjected to both greenbugs and drought stress, however, percent membrane damage was much greater, and similar to that of plants receiving neither stress. Blum and Ebercon (1981) showed that a high degree of membrane stability is an attribute of drought-tolerant wheat cultivars as well as drought-tolerant plant species in general. They also found that drought-stressed wheat apparently adapts in such a way as to make its membranes more resistant to solute leakage when subjected to an osmotic stress, and this is apparently an important adaptive response of plants exposed to drought. Thus, the apparent adaptive response of decreased membrane injury in response to drought stress in winter wheat was virtually eliminated when greenbug infestations were present. Plant water relations were changed by drought stress or by greenbug infestations, or both, but no significant cultivar effects or interactions with cultivars were found. Drought stress alone affected water potential, ψ ($F = 56.53$; $df = 1,66$; $P < 0.05$), which was

lowered as expected. But solute potential (ψ_s) was affected by the interaction of greenbug and drought stress ($F = 3.88$; $df = 1,66$; $P = 0.05$) (Table 2).

As anticipated, ψ_s became lower (more negative) in response to drought stress as dehydration concentrated solutes. In addition, wheat tends to accumulate solutes under drought stress and can maintain higher turgor pressure (ψ_p) through osmotic adjustment than if no osmotic adjustment occurred (Johnson et al. 1984). On plants subjected to greenbugs and drought stress, greenbugs caused increased (less negative) ψ_s compared with plants subjected to drought stress alone (Table 2). Thus, greenbugs prevented ψ_s from declining as far as it would have if greenbugs had been absent from drought-stressed plants. Because ψ was not altered by greenbugs at these drought stress levels, the increase in ψ_s caused by greenbugs translated into a decrease in ψ_p for infested plants ($F = 25.11$; $df = 1,66$; $P < 0.05$) (Table 2).

The reason for these results is not clear, but may be related to our findings on membrane stability. As discussed earlier, greenbugs prevented the full acclimation of cell membranes to drought stress. The increased membrane damage of drought-stressed plants caused by greenbugs may interfere with the plant's ability to liberate and accumulate solutes, which act to lower ψ_s and thereby maintain ψ_p. Alternatively, the lowered concentrations of solutes associated with greenbug feeding could decrease the plant cells' ability to lower membrane damage, as compatible solutes may play an important role in drought-stress tolerance by stabilizing macromolecular structure and function (Yancey et al. 1982). The solutes affected are apparently not free amino acids or free proline, as the concentrations of these compounds in plant leaves were not significantly

altered by greenbugs. This is consistent with the findings of Miles et al. (1982) concerning Brevicoryne brassicae (L.) on drought-stressed rape plants. It is also possible that greenbugs destroyed chloroplasts (Al-Mousawi et al. 1983), which would result in lowered photosynthesis for infested plants. This effect combined with removal of assimilate through greenbug feeding could have increased ψ_s.

Even though there were many more greenbugs on unstressed than drought-stressed plants at the end of the experiment (9,487 versus 5,412; $F = 5.21$; $df = 1,30$; $P < 0.05$), greenbug density (number of greenbugs per mg shoot d.w.) was greater on plants that were drought stressed (1.39 versus 1.04; $F = 4.15$; $df = 1,30$; $P = 0.05$). Thus, plant growth was apparently more detrimentally affected than greenbug population growth during drought stress.

We found no cultivar x greenbug interactions for any of the physiological plant parameters measured in this experiment, indicating that all cultivars responded similarly to the greenbug stress. This may be because the greenbugs were allowed to feed and reproduce for 3 weeks, essentially overwhelming even the relatively resistant 'Amigo', and causing it to respond no differently than 'TAM W-101' or 'Sturdy'. It may, therefore, be that the resistance of 'Amigo' to GBC is only discernible under light to moderate feeding pressure as used by Al-Mousawi et al. (1983). They have shown that a selection from the cross 'TAM W-101' x 'Amigo' (a GBC-resistant genotype) remained largely unaffected by a single biotype C greenbug that had fed for 1 h. The GBC-susceptible genotype 'TAM W-101' sustained much greater damage after the same period of greenbug feeding. It is not clear, however, that the greenbug was actually in the process of feeding on the resistant selection because

greenbugs may show more probing behavior on such genotypes (Starks and Burton 1977, Campbell et al. 1982) and the greenbug may require more time to reach the phloem of resistant plants, as reported for sorghum by Dreyer and Campbell (1984).

Although the treatment means were in a direction indicating greenbug damage, we found that root and shoot d.w. were unaffected by greenbug infestations. Perhaps this is because the greenbug infestations were begun in the boot-growth stage, when much of the plant's vegetative growth (both root and shoot) was nearly complete. The initial infestations were also rather small, which allowed the plants additional time to develop without severe feeding pressure. In cotnrast, drought stress was readily apparent after 6 days of withholding water and did affect root and shoot d.w. and root-to-shoot ratios.

In conclusion, this research provides evidence that supports field observations considering greenbug infestations potentially more damaging in wheat subjected to drought as compared with wheat receiving adequate moisture. Part of the increased greenbug damage with drought is likely related to the frequency of high-intensity rainfall events, which appear to adversely affect greenbug survival. But we have found that greenbugs may also interfere with the ability of the wheat plants to adapt to drought stress. Regardless of cultivar, greenbugs were shown to decrease adaptive cell membrane hardening in response to drought stress, as well as possibly inhibiting the adaptive process of osmotic adjustment. The density of greenbugs was also greater on drought-stressed plants as compared with nonstressed plants. Although nonstressed plants supported more greenbugs, the infestations appeared more severe on plants that had been drought stressed. As far as we know, this is the first report of an insect altering plant adaptive responses to drought stress.

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TABLE I

RESPONSES OF WINTER WHEAT PLANTS TO DROUGHT STRESS

(n = 42 FOR EACH MEAN)

Treatment	Root d.w./ plant (g)	Shoot d.w./ plant (g)	Root: shoot ratio	Tiller survi- val/ plant	Free amino acids (μmol/g f.w.)	Free proline (μmol/g f.w.)
Drought stressed	2.67	4.59	0.58	0.83	61.11	27.40
Not drought stressed	4.90	11.06	0.44	1.88	20.21	2.40
SE	0.57	1.11	0.07	0.21	4.37	2.18

d.w., dry weight; f.w., fresh weight.

TABLE II

RESPONSES OF WINTER WHEAT TO THE FOUR TREATMENT COMBINATIONS OF DROUGHT STRESS AND GREENBUG INFESTATION (n = 21 FOR EACH MEAN)

Treatment combination	Membrane damage[ab] (%)	Water potential[b] (MPa)	Solute potential[c] (MPa)	Turgor pressure[a] (MPa)
Drought stressed, infested	38.27	-1.60	-2.10	0.51
Drought stressed, not infested	22.55	-1.79	-2.88	1.09
Not drought stressed, infested	48.71	-0.72	-1.39	0.66
Not drought stressed, not infested	42.04	-0.62	-1.67	1.05
SE	1.75	0.77	0.71	0.54

[a] Difference between greenbug infested and not infested treatments significant without a significant interaction with cultivar.

[b] Difference between drought-stressed and not drought-stressed treatments significant without a significant interaction with cultivar.

[c] Because of a significant greenbug x drought stress interaction not involving cultivar, the difference between infested and not-infested treatments under drought stress is not equal to the difference between infested and not-infested treatments without drought stress.

PART II

YIELD AND GROWTH REDUCTIONS CAUSED BY GREENBUG (HOMOPTERA:APHIDIDAE) AND DROUGHT STRESS DURING DIFFERENT WINTER WHEAT GROWTH STAGES

ABSTRACT

The effects of drought stress and greenbug (Schizaphis graminum [Rond.], biotype E) infestations on winter wheat (Triticum aestivum L. cvs. 'Sturdy' and 'TAM W-101') were studied during different plant growth stages in the field and greenhouse. Field grown wheat was most severely stressed from booting to 50% anthesis (approximate growth stages 46 to 65, Zadoks et al. 1974). Stresses were applied in the greenhouse during three growth intervals (approximate growth stages 23 to 29, 30 to 47, and 47 to 66. After receiving a treatment combination, all plants were maintained drought and greenbug free until maturity.

Drought stress reduced yield per plant only during post-vernalization growth intervals. Drought stress during growth stages 30 to 47 reduced total spikelets per head, fertile spikelets per head and kernels per head whereas during growth stages 47 to 66 drought stress reduced fertile spikelets per head, heads per plant and kernels per head but also increased mean kernel weight. Although plants that were drought stressed before vernalization (growth stages 23 to 29) suffered reductions in both root and shoot dry weights, yield was not affected because the plants were able to partition more dry weight production into grain as evidenced by an increase in the harvest index (the proportion of plant dry weight composed of grain). Post-vernalization drought stress decreased the harvest index.

Greenbug infestations reduced yield per plant during all growth intervals examined but the reductions were more severe when stress

occurred post vernalization. Yield per plant was significantly reduced by greenbug stress from growth stages 23 to 29, however, no individual component of yield was significantly lowered. Greenbug stress from growth stages 30 to 47 reduced mean kernel weight, kernels per head and fertile spikelets per head whereas from growth stages 47 to 66 heads per plant, mean kernel weight and kernels per head were reduced. Post-vernalization greenbug stress had a residual effect on photosynthesis because mean kernel weight was reduced despite the termination of all infestations prior to grain filling. Greenbug infestations during all growth intervals lowered root and shoot dry weights even though the plants were maintained stress free after the stress interaction periods until maturity. The permanent reduction in root d.w. suggests that winter wheat severely infested for a brief period in the fall would have a stunted root system and be less able to tolerate a subsequent stress (especially drought) later in the season.

Reductions in yield per plant were correlated to bugdays per tiller, a new aphid index assuming logarithmic population growth between sampling periods. One bugday per tiller reduced yield per plant by similar amounts regardless of wheat cultivar or growth interval infested. But the rate of yield reduction was greater on well-watered when compared to drought-stressed plants probably because drought-stressed plants yielded much less. Greenbugs may have reduced yields more on well-watered plants simply because there was more potential for yield loss.

INTRODUCTION

The yield of winter wheat, Triticum aestivum L., is commonly limited by both the greenbug, Schizaphis graminum (Rondani), and drought. In the southern Great Plains these stresses may be concurrent at any time of the growing season. For practical purposes, therefore, it is desirable to specify the effects of drought stresses and greenbug infestations of equal severity when they occur during different growth stage intervals in winter wheat. Such information would be valuable for determining under which conditions control of the greenbug is economically justified.

Kolbe and Linke (1974) stated that aphid stress on cereals most strongly affects certain yield components depending upon the plants stage of growth at the time of infestation. For Rhopalosiphum padi, Sitobion avenae, and Metopholophium dirhodum, heads per plant is most affected when aphid stress occurs from seedling emergence to stem extension. Kernels per head is most affected from stem extension to grain formation and mean kernel weight during ripening. Whether greenbug effects follow this pattern is unknown.

Kieckhefer and Kantack (1980) noted the effect of cereal aphid populations (the greenbug included) of equal initial size on the yield of spring wheat when infested during different growth stages. In general, the aphid infestations were more damaging to younger plants. This is probably because the infestations were of equal size for each growth stage and not proportional to the size of the plants. The younger plants with very small tillers were subjected to a more severe infestation than the more mature plants with larger tillers.

Apablaza and Robinson (1967) also examined the effects of the greenbug and other cereal aphids when infested at different stages of

plant growth. Their infestations began with one aphid and continued until plant death or harvest. The earlier their infestations began, the larger they became and larger infestations cause more plant damage. This does not suggest that young plants are more susceptible to aphid infestations for any reasons other than plant size and potential duration of infestation. It does show that, if given time, a very small infestation can grow large and indeed can kill plants in the absence of biotic and abiotic forces which normally limit aphid population growth.

Burton et al. (1985) observed the effects of a fall infestation (began from growth stages 10 to 11, Zadoks et al. 1974) versus a spring infestation (began from growth stages 22 to 29) of greenbugs on resistant and susceptible winter wheat cultivars in the field. In general, for a given infestation level these researchers found more yield loss associated with fall infestations compared to spring. However, this may have been due to a plant size differential; at equal infestation levels, the smaller plants infested in the fall sustained, on the average, a higher damage rating that the larger spring-infested plants. When only the most severe infestations are examined (60 and 80 greenbugs per plant in the fall and spring, respectively) the damage ratings were similar as were the yields per plant and seeds per plant. This suggests that early fall to early spring infestations that are adjusted to plant size may cause equivalent yield reductions. The relative magnitude of yield losses due to greenbug infestations occurring near and during anthesis, however, still need to be quantified.

Many studies have shown that cereals are more susceptible to aphid (although not necessarily greenbug) damage during flowering than afterwards (Ba-Angood and Stewart 1980, George and Gair 1979, Wratten and

Lee 1979, Lee et al. 1981a, 1981b, and Rautapaa 1966). In addition, using treatments which overlapped at anthesis, Watt and Wratten (1984) observed much more damage in the treatment which had the most aphid stress during flowering. Still others have found cereal aphids more damaging during flowering than when occurring earlier (George 1974 and Lowe 1974). Holt, et al. (1984) observed no damage when M. dirhodum infestations occurred before anthesis and that winter wheat seemed especially sensitive to aphid feeding late in flowering. Also, Wood (1965) observed a pre-anthesis infestation of S. avenae that did not reduce the yield of field grown winter wheat. Taken together, these studies indicate a sensitivity of cereals to aphid infestations that peak during anthesis (growth stages 60 to 69).

Although not a pest of cereals, one aphid has been shown to cause more damage when host plants are subjected to early infestations and then maintained aphid-free until maturity. Petit and Smilowitz (1982), using a constant infestation rate based upon plant size, found that early infestations of Myzus persicae reduced both the yield and growth of potato plants compared to equally severe infestations that occurred later in plant development. This represents a loss of growth (or yield) potential for plants which had an early infestation of limited duration. Whether the greenbug, with it's toxic effect on plant tissue, has this effect when infestations are proportional to plant size is unknown.

The effect of drought stress also varies depending upon the plant growth stage in which it occurs. In general, the stage most sensitive to drought stress in winter wheat occurs around the last 15 days before anthesis and kernels per head is the yield component most affected (Fischer 1973). This is apparently associated with meiosis in pollen

mother cells (Bingham 1966, Skazkin and Lukomskaya 1962). But Day and Intalap (1970) found the critical period was during jointing and resulted in fewer kernels per head plus fewer heads per plant. Drought stress during earlier stages is generally less damaging (Lehane and Staple 1962) although Langer and Ampong (1970) found more damage in plants drought stressed from floral initiation to spikelet formation than in plants stressed later. At any rate, these references indicate that once seedlings are established drought stress seems to be most detrimental to yield when it occurs after wheat plants have initiated floral development.

The interaction of greenbug and drought stress on wheat yield has not been adequately studied. Daniels (1972) could not increase the yield of dry land sorghum through adequate insecticidal controls even though infestations were heavy, whereas yield was increased by spraying irrigated sorghum. Kindler and Staples (1981), on the other hand, showed large increases in yield when severely drought stressed sorghum was sprayed for greenbugs. Dorschner et al. (1986) indicated that the greenbug may be interfering in some potentially adaptive plant responses to drought stress in winter wheat. Whether the effects of greenbug stress on yield are exacerbated when infested wheat plants are drought stressed is unknown, as no study has yet examined wheat yield in relation to concurrent drought and greenbug stress, even during a single growth stage.

The objectives of this study were then to:

1) determine the effect on yield and yield components when winter wheat is subjected to equally severe drought and greenbug stress during different growth stages,

2) determine the effect that a drought resistant cultivar has on these responses, and

3) develop a cumulative index of aphid infestations assuming logarithmic population growth between sampling periods and correlate this with the yield of infested plants.

MATERIALS AND METHODS

Investigations were conducted in the field and greenhouse. In both environments the cultivars used were the drought susceptible 'Sturdy' and the comparatively drought resistant 'TAM W-101' and the infestations were of biotype E greenbugs. The field experiment consisted of stress during one interval of plant growth whereas the greenhouse work included the same interval but also two earlier ones.

Plexiglass chambers were used for all treatments in the field to exclude precipitation. These chambers were constructed similar to those described by Sij et al. (1972) and Johnson and Kanemasu (1983) and covered 1.8 m^2 of soil surface. Continuously running fans attached to the north side of each chamber provided ventilation to help minimize heat build up during the day (temperatures averaged 5 to 10°C higher within these chambers) and also helped to dry drought stressed treatments by removing evapotranspired water. Trenches were dug 0.6 meters deep immediately to the inside of the areas to be covered by each chamber. Plastic covered plywood was buried in these trenches and served as barriers to lateral water movement into the chambers.

A 1.5 m row of each of the test cultivars were planted with 30 cm row spacing in the areas to be covered by the chambers. To the outside of these north-south rows, but still within the chambers, were border rows of 'TAM W-105'. Smaller cages composed of lexan and a fine mesh material were used to separate infested from not-infested plots (0.5 m long) within the rows of test cultivars. The treatments were factorial and the experiment was designed as a split-split plot with water level (drought stressed or well watered) as main units, cultivar ('TAM W-101'

or 'Sturdy') as subunits and greenbugs (infested or not infested) as sub-sub units. From between 5 to 8 plants were used in each sub-sub plot.

The field was planted 31 October 1983, fertilized (60 lb. N/acre as urea) on 12 March, and the field chambers installed 21 March. Drought stress was then initiated by not watering the plots receiving dry treatments. The chambers containing well watered treatments received 2.5 cm of water applied weekly with watering cans. The drought stressed treatments were allowed to dry and on 6 April the greenbug infestations began.

The infestation level of each infested sub-sub plot was based on leaf area and leaf areas of the test cultivars were determined with a leaf area meter by taking the average of extra plants of the same cultivar growing outside the main plots. The infestation rate was 0.5 greenbug/cm^2 leaf area and, at the time of infestation, both cultivars had recently initiated floral development (growth stages 31 to 32). The infestations and drought stress were allowed to progress until 7 May when anthesis of at least 50% of all heads was 50% complete (growth stage 65).

The chambers were removed and water relations determined with leaf-cutter psychrometers (Johnson et al. 1984). Greenbugs were also removed and counted. From then until harvest on 18 June all areas were kept well-watered and greenbug free. It was apparent in this portion of the study that neither stress had built up to appreciable levels until late in the stress interaction period. The plants were, therefore, most stressed from booting (growth stage 46) to 50% anthesis.

Greenbug and drought stress were studied in the greenhouse during

three growth intervals. The first growth interval (GI1) was before vernalization (stress from growth stages 23 to 29). The second growth interval (GI2) was stressed from just after floral initiation (growth stage 30) to booting (growth stage 47). Booting (growth stage 47) to 50% anthesis (growth stage 66) comprised the third growth interval examined (GI3).

Seeds of the test cultivars were planted 6 January in eight inch azalea pots (2 liters capacity) filled with a 1:1 mixture of sand and top soil and fertilized weekly with 100 ml Hoaglands nutrient solution for the duration of the study. As in the field, the drought stress was initiated by cessation of watering but after about one week, dry treatments required 50 ml of water daily in order to maintain stress without killing the plants.

The greenbug infestations were also based on plant size with leaf areas determined from extra plants of the same cultivars growing in the same greenhouse. All plants were caged during the stress interaction period in which they were involved. Cylindrical cages were made of lexan with two large offset ventilation holes and the top covered with a fine mesh material.

The stress interaction periods were allowed to continue until it was judged that each growth stage had received an equivalent amount of stress and this was determined by observation of greenbug behavior. When densities are high, greenbugs appear restless. As soon as this behavior was noted on any infested plant, the stresses were terminated, the greenbugs were collected and counted and water relations determined with leaf-cutter psychrometers. From then until maturity the plants were maintained stress free.

The initial infestation for GI1 was 0.5 greenbug/cm^2 leaf area and the stress interaction period was from 6 February to 23 February. All plants were then vernalized in a cold frame from 25 February to 17 April and returned to the greenhouse for tests involving post-vernalization growth intervals. For GI2, the same infestation rate was used as for GI1 but the interaction period was shorter, from 26 April to 10 May. At this point the plants were developing very rapidly. The infestation rate for GI3 was, therefore, increased to 2.0 greenbugs/cm^2 leaf area to assure a severe stress by 50% anthesis and the interaction period was shorter; from 12 May to 22 May. As the plants became larger, they also extracted water from the soil at increasing rates. Less time was needed in later growth intervals to achieve an equivalent amount of drought stress compared to the early growth interval and, as in the field, more stress was experienced by the plants late in the growth intervals. The greenhouse study was in four randomized complete blocks with cultivar ('Sturdy' or 'TAM W-101'), drought stress (well-watered or drought-stressed), greenbug (infested or not infested), and growth interval (GI1, GI2, or GI3) in a factorial treatment design.

The data collected in both the field and greenhouse studies were similar and included heads per plant, yield per plant, kernels per head, average kernel weight, total spikelets per head, and fertile spikelets per head (spikelets containing at least one kernel). In addition, the shoot dry weights (d.w.) and harvest indexes (the proportion of total shoot d.w. which consists of grain) were determined. In the greenhouse, roots were also collected and root d.w. determined as by Dorschner et al. (1986). Root to shoot ratios were then calculated. All data from both studies were subjected to analysis of variance procedures and Duncan's

multiple range test when interactions were detected at the $\alpha = 0.05$ level.

The following cumulative aphid infestation index based upon logarithmic population growth between initial and final population levels was used for infested plants:

$$\text{Bugdays} = \frac{t_o\ (N_1 - N_o)}{\ln N_1 - \ln N_o}$$

where N_o is the population at time $t = 0$ (initial infestation), N_1 is the population at the time $t = t_o$ (final greenbug count), and t_o is the number of days from time $t = 0$ to $t = t_o$.

This provides a measure of the magnitude of the greenbug stress in terms of bugdays where one bugday represents the feeding of one greenbug on a wheat plant for one day. Bugdays per plant was then placed on a per living tiller basis in order to compensate for varying plant sizes at the end of a stress interaction period.

RESULTS AND DISCUSSION

Drought Stress Effects

The degree of drought as measured by water potential was relatively even between growth stages in the greenhouse and in each case water potential, osmotic potential, and turgor pressure were significantly different between wet and dry treatments (Table I). But in the field we did not develop a drought stress as severe (Table I) and differences in water potential were not observed, although measurements with a porometer (Li-Cor LI-1600 Steady State Porometer, Lincoln, NB) indicated significant differences ($P < 0.05$) between stressed and not stressed treatments for diffusive conductance of leaves to water vapor (0.19 vs. 0.32 $cm \cdot s^{-1}$) and leaf transpiration (3.69 vs. 5.55 $\mu g\ H_2O\ cm^{-2} \cdot s^{-1}$). The only yield component reduced by drought in the field was fertile spikelets per head (11.37 vs. 12.59, $P < 0.05$). Total spikelets per head, however, was not significantly reduced (15.01 vs. 15.43, $P > 0.05$) because of the failure to provide a drought stress during spikelet formation. There were no significant cultivar x drought stress interaction in any of the variables measured in the field indicating that both cultivars responded similarly to the mild drought stress.

Drought stress reduced yield significantly in the greenhouse only when plants were stressed post-vernalization (GI2 and GI3) (Table II). Yield was reduced during GI2 by fewer kernels per head, which resulted from a reduction in both total spikelets per head and fertile spikelets per head (Table II). This was expected because GI2 included initial floral development and thus spikelet formation. Fertile spikelets per head were fewer because there were fewer spikelets to begin with, but

probably also through an interference with pollination because the proportion of fertile spikelets was also reduced (Table II).

Drought stress during GI3 reduced yield per plant by equivalent amounts as stress during GI2, but through different mechanisms (Table II). Kernels per head was reduced similarly as in GI2 but total spikelets per head was not significantly reduced because spikelets were already developed prior to stress initiation. Drought stress during GI3 inhibited pollination as almost half of the spikelets per head were infertile. Wheat plants appeared to be able to compensate for drought stress during GI3 by increasing mean kernel weight after the stress period relative to well-watered plants. This is in agreement with Wardlaw (1971) who noted that a reduction in seed set in response to drought stress was associated with an initially greater development of the existing kernels. So although heads per plant was reduced during GI3 and not during GI2, the yield reduction caused by drought was similar. The reduction in heads per plant during GI3 was due to a failure of the heads to extrude from the boot.

Drought stress reduced shoot d.w. per plant in all growth stages. However, the reduction was less severe for an early stress (GI1) as compared to stress post-vernalization (GI2 and GI3) (Table III). Root d.w. per plant, on the other hand, was reduced by similar amounts regardless of the growth interval in which the plants were drought stressed (Table III). An early drought stress did not significantly alter root to shoot ratios but drought stress post-vernalization increased them as is the conventional effect of this stress (Table III).

Drought stress during GI1 resulted in a significant increase in the harvest index (Table III). This suggests that plants stressed while

young are able to compensate by partitioning more dry weight production into grain at the expense of vegetative growth. It must be remembered, however, that these plants were maintained stress free from after the stress interaction period until maturity. If a second drought stress had been applied to the plants later in their development, perhaps the reduced root systems of pre-stressed plants would have resulted in them being unable to extract sufficient moisture and nutrients from the soil and therefore yield as much as plants which had not been stressed. Plants could not compensate as thoroughly for the drought stress during the post-vernalization growth intervals as the harvest indexes were decreased (Table III).

The comparatively drought resistant cultivar 'TAM W-101' did not perform better under drought stress than 'Sturdy' perhaps because of the nature of its resistance mechanisms. 'TAM W-101' tends to develop a steeper water potential gradient from the leaves to the soil than does 'Sturdy' (Johnson et al. 1984). As a result, 'TAM W-101' may withdraw moisture from the soil more effectively under drought conditions and because the plants in this experiment were grown in pots, they were greatly restricted in the volume of soil that was available to extract water from. 'TAM W-101' may have "wasted" available water resulting in drought stress becoming more severe earlier. Thus, the benefit 'TAM W-101' has over 'Sturdy' in drought resistance may have been nullified in this experiment.

Effects of Greenbug Infestations

Greenbug infestations (Table IV) significantly reduced the yield of greenhouse grown wheat regardless of the interval of growth in which

the infestations occurred, but the reductions were more severe in the post-vernalization growth intervals (Table V). The small yield reduction during GI1 occurred although no individual component of yield was significantly reduced. Infestations reduced yield per plant during GI2 by affecting all components of yield except total spikelets per head (Table V). Unlike drought stress, greenbugs did not inhibit spikelet formation, perhaps because spikelet formation occurred early in GI2 before sufficient bugdays had accumulated. In contrast, floret development or pollen mother cell meiosis appeared to be greatly affected as fertile spikelets per head, the proportion of spikelets which were fertile, and kernels per head were all significantly decreased (Table V).

Infestations decreased yield during GI3 by severe reductions in heads per plant, mean kernel weight and kernels per head, but unlike infestations during GI2, fertile spikelets per head and the proportion of total spikelets which were fertile were not significantly lowered (Table V). As with drought stress during GI3, the reduction in heads per plant was due to a failure of the heads to extrude from the boot. Mean kernel weight was reduced more by greenbugs during GI3 as compared to GI2. Because of the severe greenbug infestations used in this study, greenbugs infested during GI3 were observed to be feeding and causing damage to the heads and head photosynthesis accounts for a large portion of the assimilates used in grain development (Evans and Rawson 1970). Plants infested during GI3, therefore, could not fill their kernels properly because of damage to both heads and flag leaves whereas during GI2 the heads were not emerged and greenbugs were only able to feed upon the flag leaves. Because the infestations were removed prior to grain filling, greenbugs appear to have a strong residual effect on

kernel-filling capacity. This effect could be caused by accelerated senescence of photosynthetic tissues caused by aphid feeding in general (Lee et al. 1981b) and, in particular, by the toxic effects of greenbug feeding (Chatters and Schlehuber 1951, Al-Mousawi et al. 1983). Honeydew accumulation has also been shown to have a residual effect on photosynthesis (Rabbinge et al. 1981).

Infestations during any growth interval lowered both the root and shoot d.w. of wheat plants upon maturity (Table VI). These findings are different from those of Ortman and Painter (1960), Daniels (1965) and Havlickova (1984) because in those studies root and shoot d.w. were determined immediately following the infestations. In this study, the infestations were removed and the plants maintained greenbug free until harvest. The reductions in root and shoot dry weights observed represent an inability of the plants to recover after a single severe infestation of limited duration, even if the plants were quite young when damaged. Wheat plants infested before vernalization had significantly lower root to shoot ratios compared to plants infested during post-vernalization growth intervals (Table VI). This suggests that wheat plants greenbug stressed in the fall would be less able to tolerate a drought stress later in the season. Indeed, Matthew (1953) found that a fall greenbug infestation of limited duration on winter wheat reduced grain yields significantly perhaps because precipitation during the winter months was much below normal and rainfall during the month of harvest was almost nonexistent.

The ability of wheat to partition dry matter production into grain as measured by the harvest index was not altered by greenbug infestations during GI1 (Table VI). Post-vernalization infestations, however,

decreased the harvest index, especially during GI3. As with other cereal aphids, greenbugs appear to be most damaging when severe infestations peak near and during anthesis as opposed to before.

Plants greenbug stressed post-vernalization in the field responded similarly to plants stressed during GI2 and GI3 in the greenhouse. Reductions in yield per plant, heads per plant, mean kernel weight, kernels per head, fertile spikelets per head, and the proportion of fertile spikelets were all observed (Table VII). As in the greenhouse during GI2, total spikelets per head was not altered by greenbugs because infestations were not severe during spikelet formation. Shoot d.w. per plant and the harvest index were also lowered.

Greenbug infestations did not reduce yield per plant in the greenhouse as drastically when infested pre-vernalization (during GI1) as compared to post-vernalization (during GI2 and GI3) (Table VI) even though infestations appeared equally severe between growth intervals. Regression analysis, on the other hand, indicated that yield was equally affected by a single bugday/tiller regardless of the growth interval infested (Table VIII). Yield per plant was less affected by pre-vernalization infestations simply because of plant size. Small, young plants could not have supported the large greenbug populations that more mature plants could and still remain living. So although the infestations appeared equally severe, yield was reduced less with young plants because there were fewer greenbugs present (Table IV). Regression analysis also revealed that the rate of yield loss in response to a single bugday per tiller was greater with well-watered as compared to drought-stressed plants in the greenhouse. In this environment the drought-stress became very severe and resulted in large yield reductions.

Greenbugs probably caused more damage with well-watered plants because the potential for yield reductions in these plants was greater. In the field, where potential yields per plant were much greater, one bugday per tiller reduced yields far more than in the greenhouse (Table VIII).

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TABLE I

WATER RELATIONS OF DROUGHT STRESSED AND WELL WATERED WINTER WHEAT IN THE GREENHOUSE AND FIELD

Location (growth interval)	Water level[a]	Water potential[b] (MPa)[c]	Solute potential[b] (MPa)	Turgor pressure[b] (MPa)
Greenhouse	D	-2.84	-2.93	0.093
(GI1)	W	-1.06	-1.53	0.468
Greenhouse	D	-2.58	-2.60	0.023
(GI2)	W	-1.17	-1.61	0.437
Greenhouse	D	-2.75	-2.60	0.000
(GI3)	W	-1.16	-1.40	0.249
Field	D	-1.16	-2.29	1.13
	W	-1.16	-2.20	1.04

[a] D, drought stressed; W, well watered.

[b] Differences between drought stressed and well watered treatments significant ($P < 0.05$) for greenhouse grown wheat but not for field grown wheat ($P > 0.05$).

[c] MPa, Megapascals.

TABLE II

EFFECTS OF DROUGHT STRESS ON YIELD COMPONENTS IN GREENHOUSE GROWN WINTER WHEAT STRESSED AT DIFFERENT GROWTH INTERVALS

Growth interval	Water level[a]	Yield/ plant (g)[b]	Heads/ plant[b]	Weight (mg)/ kernel[b]	Kernels/ head[b]	Total spikelets/ head[b]	Fertile spikelets/ head[b]	Proportion of fertile spikelets/ head[b]
GI1	D	3.55 a	5.06 a	33.24 a	21.37 a	13.03 a	9.95 a	0.76 a
	W	3.66 a	5.06 a	34.03 a	22.08 a	13.16 a	10.23 a	0.77 a
GI2	D	1.84 c	4.50 a	33.37 a	12.54 b	12.15 b	7.80 b	0.65 b
	W	3.05 b	4.69 a	33.17 a	19.79 a	13.39 a	9.85 a	0.74 a
GI3	D	1.61 c	3.50 b	33.65 a	13.42 b	13.33 a	7.16 b	0.54 c
	W	2.94 b	4.69 a	31.91 b	19.47 a	13.53 a	10.40 a	0.77 a

[a] D, drought stressed; W, well watered.

[b] Significant drought stress X growth interval interaction ($P < 0.05$) without interactions with cultivar or greenbug. Means in a column followed by the same letter are not significantly different at the $\alpha = 0.05$ level (Duncan's MRT).

TABLE III

EFFECTS OF DROUGHT STRESS APPLIED DURING DIFFERENT GROWTH INTERVALS OF GREENHOUSE GROWN WINTER WHEAT

Growth interval	Water level[a]	Shoot d.w./ plant (g)[b]	Root d.w./ plant (g)[c]	Root:shoot[b]	Harvest index[b]
GI1	D	7.77 b	2.26	0.29 d	0.46 a
	W	8.95 a	3.04	0.34 c,d	0.41 b
GI2	D	5.22 c	2.28	0.44 a,b	0.35 c
	W	8.02 b	3.02	0.38 b,c	0.38 b,c
GI3	D	5.10 c	2.34	0.47 a	0.31 d
	W	7.73 b	2.66	0.35 c,d	0.37 b,c

[a] D, drought stressed; W, well-watered.

[b] Significant growth intervalx drought stress interaction ($P < 0.05$) without interaction with cultivar or greenbug. Means in a column followed by the same letter are not significantly different at the $\alpha = 0.05$ level (Duncan's MRT).

[c] Significant drought stress effect ($P < 0.05$) without interactions with growth interval, cultivar, or greenbug.

TABLE IV

GREENBUG INFESTATIONS IN THE GREENHOUSE AND FIELD FOR EACH TEST CULTIVAR

Location (growth interval)	Cultivar[a]	Initial leaf area per plant (cm^2)	Initial infestation (greenbug per plant)	Infestation length (days)	Bugdays per plant[b,d]	Bugdays per tiller per plant[c,d]
Greenhouse	S	30	15	17	1,815	346
(GI1)	T	22	11		1,680	412
Greenhouse	S	160	80	15	14,346	2,744
(GI2)	T	132	66		11,625	3,236
Greenhouse	S	233	466	10	16,785	5,700
(GI3)	T	193	386		12,164	3,071
Field	S	196	98	28	23,826	2,813
	T	144	72		18,497	3,628

[a] S = 'Sturdy', T = 'TAM W-101'.

[b] Significant cultivar and growth interval effect ($P < 0.05$) for greenhouse grown wheat.

[c] Significant cultivar X growth interval interaction ($P < 0.05$) for greenhouse grown wheat.

[d] Difference between cultivars not significant ($P > 0.05$) in field grown wheat.

TABLE V

EFFECTS OF GREENBUG ON GREENHOUSE GROWN WINTER WHEAT YIELD METRICS WHEN INFESTED DURING DIFFERENT INTERVALS OF PLANT GROWTH

Growth interval	infestation	Yield/ plant (g)[a]	Heads/ plant[a]	Weight (mg)/ kernel[a]	Kernels/ head[a]	Total spikelets/ head[b]	Fertile spikelets/ head[a]	Proportion of fertile spikelets/ head[a]
GI1	infested	3.39 b	4.81 a,b	33.75 b	21.50 a	13.15	10.19 a	0.77 a
	not infested	3.82 a	5.31 a	33.53 b	21.95 a	13.04	9.98 a	0.76 a
GI2	infested	1.95 d	4.50 b	32.30 c	13.97 c	12.86	7.74 c	0.60 c
	not infested	2.93 c	4.69 b	34.24 a,b	18.36 b	12.68	9.91 a	0.78 a
GI3	infested	1.64 d	3.56 c	30.28 d	14.96 c	13.65	8.63 b	0.63 b,c
	not infested	2.90 c	4.63 b	35.27 a	17.92 b	13.22	8.94 b	0.68 b

[a] Significant greenbug x growth interval effect ($P < 0.05$) without interactions with cultivar or drought stress. Means in a column followed by the same letter are not significantly different at the $\alpha = 0.05$ level (Duncan's MRT).

[b] No significant differences ($P > 0.05$).

TABLE VI

RESPONSES OF GREENHOUSE GROWN WINTER WHEAT WHEN INFESTED WITH GREENBUG DURING DIFFERENT GROWTH STAGE INTERVALS

Growth interval	infestation	Root d.w./ plant (g)[a]	Shoot d.w./ plant (g)[a]	Root:shoot[b]	Harvest index[b]
GI1	infested	2.30	7.95	0.29 c	0.43 a
	not infested	2.99	8.78	0.34 b	0.44 a
GI2	infested	2.46	5.73	0.43 a	0.34 c
	not infested	2.84	7.51	0.39 a,b	0.39 b
GI3	infested	2.26	5.52	0.43 a	0.29 d
	not infested	2.74	7.30	0.39 a,b	0.39 b

[a] Significant greenbug effect ($P < 0.05$) without interactions with drought stress, growth interval, or cultivar.

[b] Significant greenbug x growthinterval interaction ($P < 0.05$) without interactions with cultivar or drought stress. Means in a column followed by the same letter are not significantly different at the $\alpha = 0.05$ level (Duncan's MRT.).

TABLE VII

EFFECT ON YIELD METRICS OF FIELD GROWN WINTER WHEAT TO INFESTATIONS OF GREENBUG

Infestation	Yield/ plant (g)[a]	Heads/ plant[a]	Weight/ kernel[a] (mg)	Kernels/ head[a]	Total spikelets/ head[b]	Fertile spikelets/ head[a]	Proportion fertile spikelets[a]	Shoot d.w./ plant (g)[a]	Harvest index[a]
infested	6.84	7.9	35.8	22.0	14.94	10.83	0.72	17.48	0.36
not infested	10.73	9.2	38.8	30.4	15.49	13.13	0.85	24.43	0.44

[a] Significant greenbug effect ($P < 0.05$) without interactions with cultivar or drought stress.

[b] Infested and not infested treatments are not significatnly different ($P > 0.05$).

TABLE VIII

YIELD PER PLANT REGRESSED AGAINST BUGDAYS PER TILLER IN THE GREENHOUSE AND FIELD EXPERIMENTS

Location (Growth Interval)	Water Level[a]	b_o[b]	b_1B[c]	b_2B^2[d]	R^2
Greenhouse (GI1)	D	3,605	-0.303	0.0000186	
	W	3,767	-0.494		
Greenhouse (GI2)	D	2,185	-0.303	0.0000186	0.97
	W	3,730	-0.494		
Greenhouse (GI3)	D	2,049	-0.303	0.0000186	
	W	3,792	-0.494		
Field	Pooled (D+W)	10,526	-1.081	NS	0.51

[a] D, drought-stressed; W, well-watered.

[b] b_o, intercept (yield per plant in mg).

[c] Significant bugdays per tiller x water level interaction ($P < 0.05$) in greenhouse grown wheat without interactions with cultivar or growth interval. Significant linear effect ($P < 0.05$) for field grown wheat without interactions with cultivar or water level.

[d] Significant quadratic effect ($P < 0.05$) for greenhouse grown wheat without interactions with cultivar, water level or growth interval. NS, effect in field grown wheat not significant ($P > 0.05$).

PART III

PROBING BEHAVIOR OF VIRULENT AND AVIRULENT BIOTYPES OF *SCHIZAPHIS GRAMINUM* (RONDANI) ON AMIGO-TYPE WINTER WHEAT AND THE EFFECTS OF SENESCENCE-LIKE FEEDING DAMAGE ON APHID PERFORMANCE

ABSTRACT

Probing behavior and population growth of biotype C greenbugs (GBC), Schiziphis graminum (Rondani), was compared to biotype E greenbugs (GBE) on a winter wheat selection with Amigo resistance (resistant to GBC, susceptible to GBE). GBC probing behavior was detrimentally affected by the resistance but only during the first 12 h following initial plant contact. Superior population growth of GBE compared to GBC is related to senescence-like feeding damage and proposed subsequent enrichment of the phloem sap. GBC, when feeding upon tissue damaged previously by GBE, reproduced and grew as if it were feeding from a susceptible host. Probing behavior, however, was not altered dramatically by prior infestation. The significance of these findings in relation to biotype evolution, diversity, and host-plant resistance in winter wheat is discussed.

INTRODUCTION

During investigations of greenbug, Schizaphis graminum (Rondani), resistance in wheat, Triticum aestivum L., we observed that, at least for 'Amigo'- and 'Largo'-type resistances, high levels of antibiosis were associated with high levels of tolerance. Susceptible biotype/plant genotype combinations were always typified by small necrotic lesions at the feeding sites each surrounded by a chlorotic halo, an effect macroscopically similar to senescence. Biotypes damaging plants in this manner reproduced rapidly. Resistant biotype/plant combinations never displayed these symptoms, even when infestations became very heavy feeding damage was light and reproduction slow. We hypothesized that biotypes severly injurous to their host-plants may have a selective advantage over biotypes that are not. Perhaps by causing symptoms similar to senescence, the greenbug is improving the quality of its host as a food source. This seemed to us reasonable given the general increase of aphid growth and reproductive performance when feeding on senescing plant tissue (Dixon 1971, MacKinnon 1961, Van Emden 1972). Biotypes incapable of inducing senescence-like feeding injury would perform poorly and the wheat genotype would be considered by entomologists to be both antibiotic and tolerant. The objective of this study was, therefore, to determine the degree to which Amigo-type antibiosis is dependent upon tolerance mechanisms.

MATERIALS AND METHODS

Biotype C (GBC) and biotype E (GBE) greenbugs were maintained on susceptible 'Truimph 64' winter wheat until required. Only even-aged, apterous, virginoparous greenbugs were used in these studies. Several adults of each biotype were removed from the cultures and caged on uninfested 'Triumph 64'. They were removed the next day leaving only first instar nymphs less than 24 h old. Upon maturity these aphids were used in the experiments, usually about 8 to 10 days old and activity reproducing.

Wheat with Amigo-type resistance ('OK 80268', unreleased breeding line, Okla. Agric. Exp. Stn., Stillwater), resistant to GBC but susceptible to GBE, was grown in an environmental chamber (16L:8D photoperiod, 25°C, 60% RH) in 7.5 cm plastic pots filled with 280 g sifted sandy loam. The plants were watered every other day with approximately 50 ml Hoaglands nutrient solution. The plants used for experimentation were about three weeks old and were beginning to tiller. The plants were subjected to two separate infestations. The primary infestation involved both biotypes with each plant receiving either GBC or GBE. The secondary infestation was of GBC only and was restricted to the leaf area that had been fed upon during the primary infestation. The effect of GBE's feeding damage on food quality and probing behavior of GBC was then deduced.

Before the experiments began, the plants were removed from the growth chamber and placed under artificial lighting in the laboratory. The photoperiod was set to 16L:8D and room temperatures and humidities were between 25-30°C and 50-70% RH. For the primary infestations, half the plants received GBC while the other half received GBE. The infestations were confined to the last fully expanded leaf of the largest

tiller of each plant with two plexyglas ring cages (inside diameter 1.9 cm). Each plant was initially infested with 2 greenbugs/cage (4 greenbugs/plant). A styrofoam stage wrapped in aluminum foil supported the ring cages. The infestations were terminated after 5 days to ensure that only the progeny of the original greenbugs were present. The greenbugs were removed and counted and their honeydew collected by rinsing the cages and aluminum foil with 5ml 70°C distilled H_2O. Greenbug and honeydew dry weights (d.w.) were determined after drying for 24 h in a 70°C oven. From these data, d.w. per greenbug, honeydew eliminated per greenbug, and honeydew eliminated per unit greenbug d.w. accumulated were calculated.

Only GBC were used for the secondary infestation and they were confined to the same area which had previously been fed upon by either GBC or GBE during the primary infestation. The infestation rate, length of infestation, and data collected were identical to the primary infestation.

Electronic feeding monitors (Kendow Technologies, Perry, OK) were used to monitor the probing behavior of unstarved greenbugs during a 24 h period. These monitors were modified after Brown and Holbrook (1976) to provide a 25 Hz AC voltage and the voltage applied to the test plants via the soil was limited to 200 mV. Probing activities of the greenbugs were recorded with a chart speed of 0.5 cm/min. Both GBC and GBE were monitored on 'OK 80268' in order to establish the probing behavior of a virulent (GBE) and avirulent (GBC) biotype. Later, GBC was monitored on the leaf tissue previously damaged by GBC or GBE during the primary infestation. This is to determine whether the probing behavior of an avirulent biotype is affected by prior infestation of a

virulent biotype. The parameters of aphid probing behavior measured were total number of separate probes, total number of probes in which phloem contact was observed (successful probes), total number of probes in which committed phloem sap injestion occurred (continuous ingestion for longer than 15 min. as coined by Montllor et al. 1983), time to first phloem contact, total number of phloem contacts observed, duration of salivation, duration of phloem sap ingestion, duration of ingestion from non-phloem tissues and duration of non-probing (aphid stylets not in electrical contact with the plant). The proportion of successful probes was determined (probes with phloem contact per total probes) as was the proportion of successful probes with committed phloem sap ingestion (probes with committed ingestion from the phloem per successful probes). Also, the number of phloem contacts per successful probe was calculated. This provided a measure of phloem sap acceptance within individual probes.

The experiments were in completely randomized designs with 16 replications and all data was subjected to analysis of variance procedures. Significant differences were declared at the $\alpha = 0.05$ level.

RESULTS AND DISCUSSION

The penetration graphs generated by greenbugs when probing winter wheat are identical to those observed by Campbell et al. (1982) for greenbugs probing sorghum and, in general, the penetration graphs closely resemble those observed for other aphids on their host-plants.

The Amigo-type resistance of 'OK 80268' affected GBC probing behavior dramatically and was characterized by increases in the duration of non-probing, total number of separate probes, duration of salivation and the total number of phloem contacts relative to GBE on undamaged 'OK 80268' (Table I). A reduction in the duration of phloem sap ingestion was also associated with GBC probing this resistant genotype. These responses are typical of greenbugs and other aphids probing resistant host-plants (Campbell et al. 1982, Tarn and Adams 1982). However, other perhaps atypical responces were observed. Although the time to first committed phloem sap ingestion was increased by plant resistance (Table II), as was observed for greenbugs on sorghum by Montllor et al. (1983), the time to first phloem contact was not significantly different between GBC and GBE (Table II). This is in contrast to GBC probing a resistant sorghum (Dreyer and Campbell 1984). In addition, Amigo-type resistance did not decrease the probability of a probe leading to phloem contact (successful probe) as has been shown in resistant muskmelon with Aphis gossypii Glover (Kennedy et al. 1978) nor did it increase the amount of ingestion from non-phloem tissues as was observed by Campbell et al. (1982) in sorghum. Resistance instead greatly decreased the probability of committed phloem sap ingestion after a sieve element had been contacted (Table II). This is similar

to the results of Kennedy et al. (1978) who found that resistance resulted in fewer phloem contacts leading to ingestion. GBC initiating a probe on resistant wheat with Amigo-type resistance can apparently find the phloem just as often and in the same amount of time as GBE. But once a sieve element has been contacted, GBC cannot commit as often to phloem sap ingestion and, because the number of phloem contacts per successful probe was not significantly different (Table II), GBC will exit the phloem and, if unable to depart, will begin an entirely new probe. Resistance is, therefore, initially characterized by repeated probing in which rapid phloem contact is made; but with only short periods of sap ingestion followed by loss of electrical contact with the plant. Over time, however, GBC ingests longer from the phloem and after 12 h spends as much time in phloem sap ingestion on 'OK 80268' as does GBE (Table III). This may be the result of acclimation of GBC to the resistant host-plant over time as noted by Montllor et al. (1983). At any rate, in agreement with Adams and Wade (1976), host discrimination occurred shortly after probing activities were initiated.

Greenbug population growth during the primary infestation (GBC or GBE on undamaged 'OK 80268') revealed that GBE out-performed GBC in total number of progeny produced, average individual d.w., and the amount of honeydew eliminated per unit d.w. accumulated (we have found that a low value is always associated with greenbug biotypes feeding on susceptible host-plants) (Table IV). The amount of honeydew eliminated per greenbug, however, did not differ significantly between biotypes (Table IV). This was unexpected considering that GBE ingested significantly longer from the phloem during an entire 24 h period on 'OK 80268' than did GBC (Table I). But, as discussed above, analysis of

probing behavior over time showed that GBE differed from GBC in the duration of phloem sap ingestion only during the first 12 h (Table III). Afterwards GBC is equivalent to GBE in terms of duration of phloem sap ingestion. It is also possible, however, that GBE was responding to increased sap quality by ingesting more slowly from the phloem compared to GBC (Mittler 1958). These effects may have occurred over the 5-day infestation period and resulted in GBC eliminating about the same amount of honeydew per individual as GBE. But GBE was able to gain more benefit from sap ingested from 'OK 80268' than GBC. For every μg d.w. accumulated by GBC, 1.78 μg honeydew was eliminated (Table IV). GBE, on the other hand, eliminated only 1.36 μg honeydew in order to accumulate 1 μg of d.w. Because GBC ingested from the phloem just as much as GBE after 12 h, it appeared that the sap GBE ingested from 'OK 80268' was enriched by the senescence-like feeding damage and was, therefore, more capable of supporting greenbug growth than the sap GBC was ingesting. But it was also possible that there was a feeding deterrent in the phloem sap of 'OK 80268' that only GBC was sensitive to.

The results of the secondary infestation support the enriched sap hypothesis, however. GBC reared on leaves of 'OK 80268' that had previously been damaged by GBE performed similar to GBE in all respects (Table IV). Compared to GBC on GBC-damaged tissue GBC on GBE-damaged tissue produced more progeny, averaged greater individual d.w., and less honeydew was required to be eliminated in order to gain a unit of d.w. It appeared that Amigo-type antibiosis could be completely overcome by avirulent biotypes providing that a previous infestation of a virulent biotype had occurred. On the other hand, probing behavior was not altered by prior infestation and, in general, the behavior noted was

similar to GBC on undamaged 'OK 80268' (a resistant response) (Tables I, II and III). This indicates that the differences noted in population growth between GBC on GBC-damaged tissue and GBC on GBE-damaged tissue is associated with the senescence-like damage induced by GBE and not due to a modification of the leaves by GBE making the phloem differentially more accessible to GBC on GBE-damaged plants. In support of this, MacKinnon (1961) found that the senescing leaves of a resistant host may be just as acceptable to aphids as mature leaves from a prefered host.

Senescence could increase phloem sap food quality by increasing the amount, or changing the balance, of amino acids through protein hydrolysis. Membrane damage also occurs during senescence and leads to the leakage of many other potentially beneficial cytoplasmic solutes (Thimann 1980). Dixon (1963, 1970) demonstrated that when soluble nitrogen is high in plant tissue, aphids reproduce more rapidly and grow larger. In a previous study we could not detect a significant difference between infested and not-infested wheat in the total amount of free amino acids present (Dorschner et al. 1986). But the balance of particular amino acids may be important (Van Emden 1972) and, consistent with the effects of natural senescence, we did note an increase in membrane damage and solute leakage associated with infested plants.

These findings may aid in the understanding of patterns of biotype abundance and diversity. They offer a mechanism for avirulent biotype survival even if vast acreages of resistant wheats are planted. Avirulent biotypes could persist as long as they occur in mixed colonies with virulent biotypes. Biotype diversity could be maintained or even increased under such conditions and this heightens the probability of

biotype evolution.

Our findings may offer a possible explanation for the evolution of GBE and the subsequent rapid loss of Amigo-type resistance in winter wheat. The greenbug has apparently evolved to be extremely virulent towards it's prefered host plants in order to gain an advantage in fitness through increased food quality for itself and its genetically similar offspring. If this is true, then greenbugs on newly developed tolerant (and, therefore, appearing also antibiotic) wheat genotypes would be under tremendous selection pressure to overcome the tolerance mechanism. This type of resistance might then be predictably short-lived.

Aspects of the nature of Amigo-type resistance may be deduced. This resistance did not significantly impede the processes involved in tissue penetration or phloem location. Instead, resistance was manifest by the apparent unacceptability of the phloem sap to GBC. This was evidenced by a tremendous reduction in the probability of committing to phloem sap ingestion after a sieve element had been penetrated and the overall delay of first committed phloem sap ingestion. However, this effect was largely overcome after only 12 h of probing by the avirulent biotype. The virulent biotype found the phloem sap immediately acceptable (first committed phloem sap ingestion after about 2 h of probing) perhaps because of senescence-like damage that is microscopically visible after only 1 h of probing (Al-Mousawi et al. 1983). Greenbugs feeding on resistant plants were also shown to cause damage but it was much less severe and did not seem to damage the phloem. It is interesting to note that GBC on 'OK 80268' previously damaged by either biotype committed more quickly to phloem sap ingestion than GBC on undamaged

tissue (Table II). This may indicate that even the feeding of an avirulent biotype can eventually enhance phloem sap acceptability to some degree. The ability of GBE to cause senescence-like damage on wheat with Amigo resistance may be related to it's complement of cell wall degrading enzymes (Dreyer and Campbell 1984) which may directly induce senescence-like damage or, alternatively, the enzymes of GBE may release a specific oligosaccharide from host cell walls which produces a hypersensitive response (Doares et al. 1985). Greenbugs may also be able to discriminate between the products of their cell wall degrading enzymes and assess their suitability while probing. This may explain the large number of total probes and phloem contacts observed for GBC on GBE-damaged leaves despite the apparent increase in sap quality (Table I). Other explanations are that the enzymes of GBE (or a toxin) may prevent the wound healing response in phloem tissue or GBE is capable of invading the plant without eliciting other plant defensive mechanisms such as phytoalexin production.

Lastly, in contrast to Campbell et al. (1982), Angandona et al. (1983), Montellor et al. (1983), and Nielson and Don (1974), no evidence was found indicating the presence of a specific feeding deterrent or other "odd substance" in the phloem sap of resistant plant genotypes which affects greenbug population growth. The avirulent biotype grew very well on resistant wheat provided the infestation sites were previously damaged by the virulent biotype. It is possible that the feeding damage of virulent biotypes may destroy the ability of the plant to produce a feeding deterrent. However, this seems unlikely because the infestations in these studies were confined to a small area on only one leaf and the remainder of the plant was undamaged

and apparently healthy. If a feeding deterrent is produced in less-damaged plant tissue then diffusion or transport into the infestation sites should be expected resulting in the inhibition of GBC population growth on GBE-damaged plants.

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TABLE I

RESULTS OF TWO EXPERIMENTS: PROBING BEHAVIOR OF GBC AND GBE ON UNDAMAGED AMIGO-TYPE WHEAT AND OF GBC ON GBC- AND GBE-DAMAGED AMIGO-TYPE WHEAT ($\bar{X}\pm SE$)

Biotype (plant condition)	Duration non-probing[a,b] (min)	Total probes[a,b]	Duration salivating[a,b] (min)	Total phloem contacts[a,b]	Duration ingesting from the phloem[a,b] (min)	Duration ingesting not from the phloem[b,c] (min)
GBC (undamaged)	52.1± 6.8	22.1±2.4	304.1±24.7	9.1±0.81	955.4±54.5	129.5±31.2
GBE (undamaged)	24.3± 6.5	9.7±2.2	98.2±23.4	2.7±0.76	1200.7±51.6	124.2±41.9
GBC (GBC-damaged)	89.6±18.4	24.7±3.7	321.3±41.1	7.3±1.2	898.9±82.3	69.0±13.3
GBC (GBE-damaged)	51.4±17.8	18.8±3.6	304.1±39.7	8.0±1.1	951.5±79.5	42.5±11.4

[a] Difference between biotype on undamaged plants significant ($P < 0.05$)

[b] Difference between GBC on GBC- and GBE-damaged plants not significant ($P > 0.05$).

[c] Difference between biotypes on undamaged plants not significant ($P > 0.05$).

TABLE II

RESULTS OF TWO EXPERIMENTS: PROBING BEHAVIOR OF GBC AND GBE ON UNDAMAGED AMIGO-TYPE WHEAT AND OF GBC ON GBC- AND GBE-DAMAGED AMIGO-TYPE WHEAT ($\bar{X}\pm SE$)

Biotype (plant condition)	Probability of a successful probe[a,d]	Probability that a successful probe will have CPI[b,c,d]	Number of phloem contacts per successful probe[a,d]	Time to first phloem contact[a,d] (min)	Time to first committed phloem sap ingestion[c,d] (min)
GBC (undamaged)	0.22±0.031	0.54±0.063	2.11±0.31	117.5±22.0	327.2±53.8
GBE (undamaged)	0.26±0.029	0.93±0.060	1.88±0.30	116.8±20.8	129.2±51.0
GBC (GBC-damaged)	0.17±0.022	0.66±0.067	2.40±0.37	102.8±13.0	155.3±41.3
GBC (GBE-damaged)	0.20±0.021	0.77±0.065	2.45±0.36	85.1±12.0	187.2±38.2

[a] Difference between biotypes on undamaged plants not significant ($P > 0.05$).

[b] CPI, committed phloem sap ingestion (continuous ingestion for > 15 min).

[c] Difference between biotypes on undamaged plants significant ($P < 0.05$).

[d] Difference between GBC on GBC- and GBE-damaged plants not significant ($P > 0.05$).

TABLE III

RESULTS OF TWO EXPERIMENTS: DURATION (MIN) OF PHLOEM SAP INGESTION OVER TIME FOR GBC AND GBE ON UNDAMAGED AMIGO-TYPE WHEAT AND FOR GBC ON GBC- AND GBE-DAMAGED AMIGO-TYPE WHEAT ($\bar{X}\pm SE$)

Biotype (plant condition)	Leaf Access Time (h)					
	0-4[a,b]	4-8[a,b]	8-12[a,b]	12-16[b,c]	16-20[b,c]	20-24[b,c]
GBC (undamaged)	66.7±15.6	133.1±18.3	135.4±19.3	204.1±10.9	206.1±18.0	210.1±17.0
GBE (undamaged)	119.2±14.8	220.1±17.4	232.2±18.2	231.3±10.3	197.2±17.0	220.7±16.1
GBC (GBC-damaged)	70.9±17.1	172.3±21.2	175.5±20.6	175.7±19.4	152.7±23.7	151.6±26.3
GBC (GBE-damaged)	78.4±16.6	152.6±20.4	164.8±19.9	168.7±18.8	198.3±22.9	188.8±25.4

[a] Difference between biotypes on undamaged plants significant ($P < 0.05$).

[b] Difference between GBC on GBC- and GBE-damaged plants not significant ($P > 0.05$).

[c] Difference between biotypes on undamaged plants not significant ($P > 0.05$).

TABLE IV

RESULTS OF TWO EXPERIMENTS: PERFORMANCE OF GBC AND GBE ON UNDAMAGED AMIGO-TYPE WHEAT AND OF GBC ON GBC- AND GBE-DAMAGED AMIGO-TYPE WHEAT ($\bar{X}\pm SE$)

Biotype (plant condition)	Total greenbugs[a,b]	dry weight/ greenbug[a,b] (µg)	Honeydew d.w./ greenbug[c,d] (µg)	Honeydew/ greenbug d.w.[a,b]
GBC (undamaged)	71±1.8	42.7±0.93	75.9±3.4	1.78±0.06
GBE (undamaged)	81±1.8	51.7±0.93	70.5±3.4	1.36±0.06
GBC (GBC-damaged)	68±2.1	35.6±0.75	70.2±3.7	1.97±0.09
GBC (GBE-damaged)	84±2.1	37.8±0.75	61.0±3.7	1.61±0.09

[a] Difference between biotypes on undamaged plants significant ($P < 0.05$).

[b] Difference between GBC on GBC- and GBE-damaged plants significant ($P < 0.05$).

[c] Difference between biotypes on undamaged plants not significant ($P > 0.05$).

[d] Difference between GBC on GBC- and GBE-damaged plants not significant ($P > 0.05$).

VITA

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