STUDIES ON GREENBUG, *SCHIZAPHIS GRAMINUM* (RONDANI) (HOMOPTERA:APHIDIDAE), IN KENYA, WITH SPECIAL REFERENCE TO HOST-PLANT RESISTANCE

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by

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JOSEPH KIMANI WANJAMA

A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

Dedicated to my wife Esther Wangari

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June, 1986. Studies on Greenbug, *Schizaphis graminum* (Rondani) (Homoptera:Aphididae), in Kenya, with Special Reference to Host-Plant Resistance.

Major Professor: N.J. Holliday

ABSTRACT

Frequent greenbug, *Schizaphis graminum* (Rondani), outbreaks occur in Kenya and cause extensive damage to cereal crops especially wheat. Due to a lack of information on greenbug concerning its biology, ecology and host-plant interactions no integrated control has been possible with a consequence that insecticidal use is the only method of control available. Studies were initiated to identify wheat cultivars that are likely to resist greenbug attack and to investigate some factors that may have led to the economic importance of this pest.

A total of 50 wheat entries were included in initial tests for host-plant resistance against the greenbug, *S. graminum* in 1982. Antibiosis of host-plants was determined by the capacity for increase (r_c) which was considered to be a better estimate of the reproductive performance than the net reproductive rate, R_o, (fecundity). Although there were no significant differences among the entries tested, retesting with six entries (four highest and two lowest in r_c) in 1983, and 1985 showed significant differences. Tolerance in 1982 was determined by the ability of the greenbug-damaged plants to recover and produce grain. In addition to grain yield, seedling dry weight was found to be a good indicator of the impact of greenbug feeding in 1983 and 1985. Antixenosis was

determined by counting the greenbugs that settled on the various wheat entries. Both alatae and apterae were used in the greenhouse. In the field, antixenosis was determined by the number of immigrants that landed on the wheat entries. Most entries were susceptible but Kenya Fahari exhibited some resistance by all the mechanisms.

Yellow water traps were found to be completely ineffective in catching *S. graminum* while clear sticky traps caught this aphid species at 1.5, 3.0, 4.5 and 6.0 m above ground. Two flight periods were distinguished each year; the first one occurred from June to September when catches were frequent with a peak in July or August; in the second one, from October to February low numbers of greenbugs were caught. No greenbugs were caught from March to May. Population build up after initial infestation was adversely affected by heavy precipitation. As a result of these studies, it is recommended that wheat in the area of Njoro should be planted early, in April, to avoid synchronizing the susceptible early seedling stage with the time of greenbug invasion.

Paedogenesis was found to occur among both alate and apterous greenbugs in the fourth instar and was influenced by temperature; the incidence of paedogenesis was 0, 0.46 and 3.93% at 15, 21 and 25^{o}C respectively among alatae and occurred only at 25^{o}C among apterae with 0.93% reproducing paedogenetically. Twelve percent of alate greenbugs produced alate offspring when crowded as fourth instars followed by a second crowding soon after the last moult. The two phenomena were thought to be adaptations enabling greenbugs to exploit ephemeral habitats.

The amount of heterogeneity in greenbug populations varies from one year to another, and may be reduced by possible selection during the dry years. It is suggested that factors increasing heterogeneity are genetic mutation and immigration of individuals from areas where sexual reproduction may take place.

CHAPTER I

INTRODUCTION

1.1 The Greenbug Problem

The greenbug, *Schizaphis graminum* (Rondani) (Homoptera:Aphididae), is a widely distributed aphid occurring in the United States of America and Canada, some parts of South America, Europe, USSR, India, East and South Africa (Hill, 1975). Its major host is wheat, *Triticum aestivum* L., but it also attacks other cereal crops e.g. barley, *Hordeum vulgare* L.; oats, *Avena sativa* L.; sorghum, *Sorghum bicolor* L.; millet, *Eleusine coracana* L; rye *Secale cereale* L. and is also reported on many other species of grasses (Dahms et al., 1954; Starks et al., 1975).

Injury to the plants is caused through direct sucking of the plant juices, and injection of toxic saliva that damages plant tissues and causes them to die (Starks and Burton, 1977). Wheat is most susceptible to greenbug attack when in the seedling stage, particularly the two leaf stage (Starks et al., 1975). The ability of greenbug to transmit barley yellow dwarf virus (BYDV) to both wheat and barley (Gill, 1967) further explains the seriousness of this pest.

In Kenya, greenbug outbreaks are frequent and result in extensive damage to crops (Wanjama, 1979). The control is entirely by use of insecticides because there are no resistant wheat varieties grown in Kenya. Elswhere greenbug has developed resistance to insecticides (Teetes et al., 1975) and reliance on insecticides is not an adequate long term solution to the problem.

Wheat ranks second to maize in importance in Kenya, among food crops (Anon., 1982), with a fluctuating annual production that has been below self sufficiency, except in 1976 (Anon., 1976). Therefore any factors that further reduce the production indirectly dictate an increase in wheat importation. The greenbug is one such factor, and hence there is a need to conduct studies aimed at reducing the losses it causes.

1.2 Objectives

The studies were approached with the following objectives:

i. To investigate whether resistance to *S. graminum* is found among the wheat germplasm available in Kenya.

ii. To determine the pattern of the flight periods of the greenbug in Kenya.

iii. To find out the extent of variation between greenbug populations from several wheat fields in Kenya.

iv. To examine some biological aspects of *S. graminum* that are likely to influence its rate of increase.

v. To determine whether resistance to *S. graminum* varies in different cereal crop species.

1.3 Thesis Organization

This thesis is a report of research work carried out in controlled environments, greenhouses and the field at the National Plant Breeding Station at Njoro, Kenya, in 1982, 1983 and 1985.

Chapter II is a review of pertinent literature. Chapter III presents the detailed report of the research in five parts, each written in a scientific paper style suitable for publication. It is anticipated that Part I will be submitted to the Bulletin of Entomological Research, Parts II and III to Insect Science and Application, and Part IV to Environmental Entomology. Part V may not be submitted to a journal, but is written in the style of the Bulletin of Entomological Research. Chapter IV contains a general discussion.

CHAPTER II

2. LITERATURE REVIEW

2.1 The Biology of the Greenbug

2.1.1 Description

The greenbug, *Schizaphis graminum* (Rondani), has four distinguishable forms; the winged (alate) and wingless (apterous) females, alate males and apterous oviparae (females producing fertilized eggs). The forms that are usually seen are the apterous viviparous (bearing live nymphs) and alate viviparous females and the parthenogenetically produced young (Starks et al., 1975). Adults of these forms are about 1.3-2.1 mm long (Mayo and Starks, 1972; Blackman and Eastop, 1984). Adult males are always winged and slightly smaller than the alate females, averaging about 1.4 mm long (Washburn, 1908; Mayo and Starks, 1972). The oviparae are distinguished by ova that are visible through the abdominal wall. They are about 2 mm long and resemble the apterous viviparous females except their hind tibiae appear swollen (Washburn, 1908).

2.1.2 Life History

Most of the work on life history of greenbug was done in the United States. The apterous viviparous female is the most abundant form appearing on infested cereal crops, on which they may produce three or four generations a month (Pfadt, 1978). Reproduction takes place between 10 and 33^{o}C with an optimum between 22-24^{o}C (Wood and Starks, 1972). The

young pass through four nymphal instars in about a week (Pfadt, 1978). Adults start reproducing a few hours after the last moult; young adults bear three to four offspring per day and older adults up to 10 per day (Pfadt, 1978). The reproductive period is about 20 days and up to 100 offspring per female may be produced. The lifespan is about one month (Schuster and Starks, 1975).

Most progeny of apterous parthenogenetic females are apterae but some alatae are also produced especially when females are crowded. The alate females emigrate, assisted by wind, and colonize new crops and establish new colonies parthenogenetically (Starks et al., 1975).

In the higher latitudes sexual forms are produced in the fall. The oviparae lay eggs in the field, especially on Kentucky bluegrass, *Poa pratensis* L. (Niemczyk, 1980; Niemczyk and Power, 1982; Blackman and Eastop, 1984). In the lower latitudes the apterous viviparous females overwinter and their progeny migrate northwards in summer (Starks et al., 1975). It is probable that in the tropics the species undergoes constant parthenogenesis and goes through the dry months in patches of green vegetation (Eastop, 1983).

2.1.3 Sexual Reproduction

The significance of sexual reproduction in the greenbug is not clear. Greenbug eggs have been obtained in the insectary (Washburn, 1908) although the author did not find either eggs or sexuales in the field. Washburn described the sexuales (males and gamic females) in the insectary: winged males are smaller than viviparous females and

have a larger number of secondary sensoria on their antennae. Oviparae differ from the viviparae in having swollen hind tibiae, eggs that can be seen through the abdominal wall, and circular sensoria on the antennae. The first report of possible greenbug eggs south of 35°N was given by Daniels (1956), who was not sure whether these were actually eggs or aborted embryos. In the greenhouse, the percentage of males among the alate population may be as high as 17% and oviparae may be 15-25% of the apterous population (Mayo and Starks, 1974).

There is not much information on factors that bring about the production of sexual morphs. Purteka and Slosser (1983) have suggested that photoperiod may be the major factor inducing sexual morph production, while temperature affects the percentage of the morph produced. Oviparae appear during the second generation at 22.1°C, L:D 11:13 and 18.7°C cycled to 12.9°C L:D 11:13. Under the first set of conditions males appear in the 4th generation, and in the 3rd generation under the second set of conditions. Cold treatment (2°C for 2h, 24h apart) causes a slight increase in the production of oviparae and males.

In the field, the shiny black eggs of the greenbug may be numerous in the fall and spring (Starks et al., 1975) on gramineous plants (Eastop, 1983). However, despite the occurrence of the greenbug eggs in the greenhouse, growth chambers and field, it has been difficult to determine whether they hatch (Mayo and Starks, 1972; Starks et al., 1975; Purteka and Slosser, 1983). Niemczyk (1980) and Niemczyk and Power (1982) have, however, indicated that the greenbugs could be overwintering on Kentucky blue lawn grass in Ohio. In the first report (Niemczyk, 1980), egg-

producing females were found from October to December 1970, and greenbug nymphs were collected from some of these lawns in April of the following year, 1980. Later, greenbug eggs were collected from lawns during March, and placed in the greenhouse at about 24^{o}C or in the laboratory; in both cases eggs hatched within 2 days of being placed in these warm environments (Niemczyk and Power, 1982).

2.1.4 Parthenogenesis

Parthenogenesis refers to reproduction occurring through development of unfertilized eggs (Suomalainen, 1950). It is a frequent occurrence in many insects e.g. cockroaches (Hagan, 1939; Roth and Willis, 1956), locusts (Hamilton, 1955), phasmids and lepidopterans (Wigglesworth, 1972), scale insects (Hughes-Schrader, 1930), dipterans and hymenopterans (Suomalainen, 1962), coleopterans (Crowson, 1981) and is commonest among the aphids (Wigglesworth, 1972; Dixon, 1973; Blackman, 1979; Eastop, 1983). It may occur in a species that also reproduces sexually (sporadic parthenogenesis) or it may constitute the only mode of reproduction (constant parthenogenesis) with intermediate degrees between these extremes (Wigglesworth, 1972; Dixon, 1985a). The unfertilized eggs may give rise to females only (thelytokous parthenogenesis) or to males only (arrhenotokous parthenogenesis) or to both sexes (amphitokous parthenogenesis) (Suomalainen, 1950; Lees, 1966; Hille Ris Lambers, 1966).

Parthenogenesis is further complicated by the occurrence of paedogenesis. The latter refers to reproduction by immature stages (Wyatt, 1961) and is confined to individuals that reproduce parthenogenetically

(Dixon, 1985b). Paedogenesis has most frequently been reported among gall midges especially *Heteropeza pygmaea* Winnertz (Cecidomyiidae) (Went, 1971), and in *Micromalthus* (Coleoptera) (Suomalainen, 1950).

Among the aphids, the first suggestion of the occurrence of paedogenesis was made by Uichanco (1924). However, what Uichanco considered as paedogenesis was the development of embryos within immature stages but with larviposition occurring only after the last moult. Bodenheimer and Swirski (1957) supported Uichanco's report on the basis of a lack of a haploid phase in development of such embryos. The report of Wood and Starks (1975) seems to be the only one where larviposition was observed to occur among the immature stages. Their observations were made on alate 4th instars of *S. graminum*. Paedogenesis as observed by Wood and Starks is thus distinct from neotonous reproduction (retention of youthful characteristics in the adult) because in the latter case the individuals showing these youthful characteristics are sexually mature (Wigglesworth, 1972). However, Wood and Starks did not observe paedogenesis in apterae and their experiments were done in uncontrolled conditions in a greenhouse where contamination of test plants before and in the process of introducing greenbugs could not be ruled out.

In temperate regions aphid reproduction is mainly by cyclical parthenogenesis (Dixon, 1973, 1985b), although this may not be true for the greenbug (Mayo and Starks, 1972), but in the tropics aphids probably exhibit constant parthenogenesis (Blackman, 1979; Eastop, 1983). The first offspring of the sexuales, from overwintering eggs, are apterous fundatrices (Hille Ris Lambers, 1966) but parthenogenetically

produced offspring may exhibit alary polymorphism. Alate aphids disperse or migrate readily (Taylor, 1975).

In parthenogenetic reproduction, there is no genetic recombination and aphid populations therefore are comprised of many different clones, each clone originating from a single female of a new genotype (Blackman, 1979; Dixon, 1985b). The variation between clones, alary polymorphism, and dispersal and migration are treated separately below.

2.1.5 Variation Between Clones

In aphids that undergo cyclical parthenogenesis, different genotypes are produced every year when sexual reproduction takes place, and these genotypes give rise to new clones (Dixon, 1985b). Each clone may rapidly become numerous as a result of parthenogenesis, and eventually may become widespread. Competition between clones for resources is occasionally likely to be intense. This, together with variation in the ability of clones to locate and feed on certain plants, avoid death from natural enemies, and withstand periods of stress, determines which genotypes survive (Dixon, 1985a).

Where aphids reproduce by constant parthenogenesis, variation among genotypes may be expected to be low due to the lack of genetic recombination that normally occurs in sexual reproduction, and to the effects of selection discussed above. Cognetti (1961) claimed that genetic recombination occurs during parthenogenesis and provides a significant and continued source of variation. He called this process "endomeiosis". But Blackman (1979) found no evidence of genetic recombination during parthenogenesis of *Myzus persicae* (Sulzer) or *Acyrthosiphon pisum* (Harris), and concluded that aphid parthenogenesis

should be regarded as of an ameiotic or apomictic type. Mutations that result in a marked change of fitness (e.g. those conferring resistance to an insecticide or ability to colonize another host plant) are likely to occur as frequently in parthenogenetically as in sexually producing populations (Dixon, 1985b). Recombination could be a disadvantage in such circumstances, by diluting the effect of the mutant allele and delaying its establishment in the population (Blackman, 1979).

If two favourable mutations occur in different individuals reproducing by constant parthenogenesis, it is not possible to incorporate them in the same individual in the population. In sexual reproduction this is possible and therefore sexually reproducing populations will evolve rapidly while parthenogenesis limits the rate of evolution (Smith, 1971). But an expected consequence, then, in a constant parthenogenetic aphid population is an increasing degree of heterozygosity (Suomalainen, 1962). This according to Suomalainen may provide the basis for the great adaptiveness and dispersal ability of such parthenogenetic forms. In large competing populations of aphids however, selection pressure operates favouring the survival of fittest individuals which may reduce the number of clones.

The term "biotype", as used in entomological literature, refers to individuals or a population of a species that is normally distinguished by criteria other than morphology, for example parasitic ability (Gallun and Khush, 1980). So far, five greenbug biotypes have been described in the United States as being economically important on cereal crops. Biotype A was probably preceded by others, but no attempt was

made to separate biotypes until after Dickinson selection 28-A (DS 28-A) wheat was found to be resistant to greenbugs (Dahms et al., 1955).

The resistance of DS 28-A was overcome by a biotype that was designated biotype B by Wood (1961). Biotype C differs from A and B in its ability to attack sorghum, and the first extensive and severe damage to sorghum occurred in 1968 (Harvey and Hackerrot, 1969). Biotypes A, B and C are all susceptible to insecticides (Starks and Burton, 1977) and the appearance of insecticide-resistant greenbugs led to the description of biotype D which is resistant to organophosphate insecticides (Teetes et al., 1975). "Amigo" wheat is resistant to biotypes A, B and C (Sebesta and Wood, 1978), but Porter et al., (1982) have reported susceptibility of this wheat and its derivatives, to a new biotype and designated this biotype, E. The distribution of this biotype is now similar to that of biotype C in Kansas, Nebraska, Oklahoma and northern Texas (Kindler et al., 1984).

Despite the elaborate description of greenbug biotypes by the various workers, there is no agreement regarding the "biotype concept". Eastop (1973) described "biotype" as a concept used by non-taxonomists to refer to individuals of equal genotypes. This idea is reflected in the definition of biotype; individual or population of a species that is differentiated by criteria other than morphology, for example parasitic ability (Gibson and Plumb, 1977; Gallun and Khush, 1980). It may be impossible for natural populations, reproducing sexually, as do greenbugs (Niemczyk, 1980), to consist of genetically identical individuals (Claridge and Den Hollander, 1983); different greenbug biotypes have

been shown to exist in the same geographical areas (Kindler et al., 1983). As the term biotype is commonly used, an individual or population may belong to more than one biotype (Eastop, 1973) and the progeny of a single female (*A. pisum*) may contain individuals of more than one biotype (Subasinghe, 1983). Variation within the progeny of a single parthenogenetic female (clone) may be caused by genetic mutation (Blackman, 1979). Therefore the concept is rather confusing and in these studies clones from field populations are used without differentiating such field populations into biotypes.

2.1.6 Alary Polymorphism

There is extensive literature concerning alary polymorphism in aphids and the phenomenon is complex such that few generalizations can be applied to all aphids. Crowding seems to be the major stimulus resulting in production of alate offspring as demonstrated for the vetch aphid, *Megoura viceae* Buckton (Lees, 1966, 1967), pea aphid, *A. pisum* (Sutherland, 1969a; MacKay, 1977), and green peach aphid, *M. persicae* (Blackman, 1979). Other factors too may influence the extent to which alate offspring are produced when the crowding stimulus is administered. These include host plant type (Sutherland, 1969b); host plant condition, which may indirectly intensify the crowding stimulus since aphids on a poor host will be more unsettled than those on one that is providing satisfactory food (Lees, 1966); photoperiod (Schaefers and Judge, 1971); and temperature (Mayo and Starks, 1974).

The method commonly used to stimulate aphids to produce alate offspring by crowding is described by Lees (1966). Aphids are placed in a 5x2.5 cm glass vial closed with a plug of cotton wool and left for 24h with a photoperiod of 16h at 15°C. A plastic vial of similar size yields comparable results (MacKay, 1977). The number of individuals required to stimulate production of alatae varies depending on the crowding sensitivity of the clone (and probably species) being tested (Sutherland, 1969a). Two individuals of the pink strain of *A. pisum* will respond strongly when confined in the 5x2.5 cm vial, but the green strain of the same species requires 19 individuals for a similar response.

There is no information on the number of greenbugs/vial that would give a strong crowding response resulting in alatae production. Higher percentages of alate greenbugs were produced when the progeny of a single apterous greenbug on a single plant were allowed to continue reproduction at 27°C than at lower temperatures (4, 21 and 24°C), L:D 14:10 and RH ranging from 30-60% (Mayo and Starks, 1974).

The capacity to develop alatae differs for the various greenbug biotypes described in the United States with biotype C being considerably more prolific in production of alatae than biotypes A, B and D (Kvenberg and Jones, 1974). Under field conditions production of alatae by biotype C greenbug starts abruptly after a short period of immigration by alatae on sorghum in June and July in Texas, and progressively increases to peak intensity during the period of maximum population decline (late August to mid-September) (Summy and Gilstrap, 1983).

The intrinsic factors that determine the development of alate and apterous forms in aphids were earlier attributed to a mechanism termed an

"interval timer" (Lees, 1960). This concept assumed that these factors were time dependent and that the new morph could be produced only after a fixed passage of time. MacKay (1977) and MacKay and Wellington (1977) have, however, shown that "maternal age effects" determine the production of alata producers in *A. pisum*. These authors found the firstborn progeny of apterae respond more strongly to a crowding stimulus than do later born progeny. It may be assumed that maternal age effects operate also in greenbug in the absence of similar data for this species. Therefore in order to determine sensitivity of greenbug to a crowding stimulus firstborn progeny of individuals subjected to crowding should be observed for wing development.

2.2 Dispersal and Migration

2.2.1 Take-off

Directed aphid flights occur below the boundary layer (Taylor and Palmer, 1972). The boundary layer is the height at which an insect's flight speed is exceeded by the wind speed (Southwood, 1978) and for most aphids this ranges between 0.9 and 1.2 m (Broadbent, 1948). In contrast, in long-distance migratory flights, aphids are above the boundary layer and are carried by the wind (Johnson, 1969). Both types of aphid flights start with the aphid taking off from its host plant; take-off does not occur below minimum levels of temperature and light (Taylor, 1963).

S. graminum takes off mostly between 20 and 35^{o}C (Halgren, 1970) and, in the field, maximum take-off of *S. graminum* occurs during the morning, once threshold temperatures are reached; then there is a gradual

decline until midday, and a small increase in the evening (Berry, 1969). For most aphids, newly flight-mature aphids accumulate overnight and await dawn before taking off because their flight is inhibited by low light intensity even when nocturnal temperatures are suitable for flight (Johnson and Taylor, 1957; Dry and Taylor, 1970).

High winds may delay, but do not inhibit, take-off (Halgren and Taylor, 1968; Walters and Dixon, 1984), apparently because aphids adjust to new thresholds (Dixon, 1985b). Although the effects of relative humidity on the take-off by greenbugs are not clear, Broadbent (1949) found the green peach aphid, *M. persicae* and the cabbage aphid, *Brevicoryne brassicae* (L.) take off readily within the range 50-100% R.H.

2.2.2 Flight

Flights by aphids may range from a few metres to hundreds of kilometres, and marking aphids to determine the distance over which they fly has not been successful (Taylor and Palmer, 1972). The tendency of aphids to disperse has been measured in terms of the proportion of a population that develops into alatae (Lamb and MacKay, 1979) and by comparing the proportion of alate nymphs to that of subsequent alate adults (Summy and Gilstrap, 1983). In very still conditions close to the vegetation, aphids may fly within sight of vegetation and alight at short intervals without flying very far (Dixon, 1985b). Aphids that fly upwards and out of the boundary layer are likely to be carried long distances down wind (Johnson, 1969) and probably fly down-wind within the air mass (Berry and Taylor, 1968).

S. graminum is known for its long distance mass flight (Johnson, 1969), and its attacks on cereal crops in the North Central United States since the late 19th century (Kelley, 1917; Fenton and Fisher, 1940; Fenton and Halms, 1951; Rogers et al., 1972) have been attributed to immigration from the South Central States (Taylor and Palmer, 1972). Infestations in Manitoba are attributed to similar immigration (Robinson and Hsu, 1963).

The distance covered in such migrations is great and it is estimated to take about 36h in low-level jet streams blowing at heights of 500-1,000 m (Taylor and Palmer, 1972; Kieckhefer et al., 1974). Sampling with aircraft has shown that the greenbug may be found at heights of about 600 m, both during the day and at night (Berry and Taylor, 1968) in low-level jet streams. No work however reports on greenbug movements in Africa although this pest is known to occur in East and South Africa.

2.2.3 Monitoring Aphids

Various types of traps used in monitoring aphids in the air are described by Taylor and Palmer (1972). Suction traps such as Johnson's suction trap (Johnson, 1950; Taylor, 1951), and the Rothamsted Insect Survey Trap which samples insects at a height of 12.2 m (Taylor and French, 1970), sample insects in the air by filtering a given volume of air per unit time. Since the insects are not attracted to such traps (Johnson, 1950; Taylor and Palmer, 1972) these are particularly suitable for estimating aerial populations of aphids (Johnson, 1950).

Prior to the development of the Rothamsted Insect Survey Trap,

sticky traps had been used for many years (Broadbent, 1948; Broadbent and Heathcote, 1961; Heathcote, 1966). Sticky traps are usually about 1 m above the ground and are smeared with a sticky substance and are yellow, as many aphid species are attracted more to yellow than to other colours.

Yellow pans (Moericke Traps) attract aphids and are more effective when placed against a bare background than against a crop background (Gonzalez and Rawlins, 1968). The yellow pans attract more aphids than white pans which attract even less than those caught on black sticky traps (Zettler et al., 1967).

Although it has been pointed out that the greenbug is not attracted to yellow (Taylor and Palmer, 1972), Roach and Agee (1972) and Harvey et al. (1982) reported that greenbugs are attracted to yellow sticky traps. But it has also been reported that white sticky traps catch more aphids than black ones (Broadbent, 1948) and that white water pans catch fewer aphids than black sticky traps (Zettler et al., 1967). The latter reports suggest that the catches on the sticky trap may largely be due to aphids' impaction on the sticky substance on the coloured traps rather than to attraction to the colour by directed flight.

Background colour influences trap catches as the greenbugs land. Fewer greenbugs are caught on sticky traps on ground covered by green crops (Harvey et al., 1982). Different tillage implements turn the soil and cover plant residues to varying degrees. Increased soil cover (with unturned plant residues) decreases trap catches of the greenbug with the lowest number being caught on traps in zero tillage plots (Burton and Krenzer, 1985).

2.3 Host Plant Resistance

2.3.1 Definitions

Painter (1951) described resistance as "the relative amount of the heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect. In practical agriculture, resistance represents the ability of a certain variety to produce a larger crop of good quality than do ordinary varieties at the same level of insect population". The definition by Beck (1965) narrows plant resistance to "the collective heritable characteristics by which a plant species, race, clone or individual may reduce the probability that an insect species, race, biotype or individual successfully uses the plant as a host". The latter definition is less informative and that of Painter will therefore be reviewed further.

Painter (1951) separated the various mechanisms of resistance as follows: 1. antibiosis - all adverse effects exerted by the plant on the insect's biology e.g. survival, development and reproduction, 2. tolerance - includes all plant responses resulting in the ability to withstand infestation and to support insect populations that would severely damage susceptible plants, and 3. nonpreference - the insects response to plants that lack the characteristics to serve as hosts, resulting in negative reactions or total avoidance during search for food, oviposition or shelter. Nonpreference is thus defined as a response of insects rather than of plants, as is the case for antibiosis and tolerance (particularly when the adjectives from these terms, antibiotic and tolerant, are used) and Kogan and Ortman (1978) have suggested the term

"antixenosis" for this mechanism of resistance. The new term with a Greek root *Xenos* meaning "guest", conveys the idea that the plant is a bad host.

2.3.2 Resistance of Wheat to Insects

The Hessian fly *Mayetiola destructor* (Say) is a serious pest of wheat in the United States and is controlled mainly by the use of resistant varieties (Painter, 1951; Maxwell et al., 1972; Pfadt, 1978; Everson and Gallun, 1980). Varieties resistant to the wheat stem sawfly, *Cephus cinctus* Norton, have also been developed (O'Keeffe et al., 1960; Pfadt, 1978; Everson and Gallun, 1980); stem solidness is associated with resistance (O'Keeffe et al., 1960). But Maxwell et al. (1972) pointed out that stem solidness is also associated with low yields and therefore resistant varieties are not universally grown in the stem sawfly area. Aphids too are serious pests of wheat and although the use of insecticides is the main control measure (Everson and Gallun, 1980) sources of resistance against some aphid species have been sought. Leaf pubescence of the wheat cultivar "Vel" contributes to the resistance of this cultivar to the bird cherry oat aphid, *Rhopalosiphum padi* (L.) (Roberts and Foster, 1983). Lowe (1984, 1985) has screened several wheat cultivars in Britain for resistance to the English grain aphid *Sitobion avenae* (F.) and found a few that could be used as sources of resistance. Much of effort, especially in the United States, has been devoted to searching for sources of resistance against the greenbug; more information on this is presented below.

2.3.3 Need for Greenbug Resistant Varieties

During years of high greenbug infestations, insecticides may be applied to thousands of hectares of cereal crops to reduce losses inflicted by this pest (Wood, 1965). The most widely used insecticides are organophosphates. Starks et al. (1975) have given the details of effective insecticides and rates of application for various cereal crops that are attacked by the greenbug. The rate of application for an insecticide may be varied so that lower rates that kill the greenbugs while sparing their natural enemies are used (Cate et al., 1973; Smith et al., 1985). However, the greenbug has the capacity to develop resistance to the organophosphate insecticides, and the appearance of the greenbug biotype D was associated with an increase in resistance to disulfoton (Teetes et al., 1975). Highest levels of resistance are found in greenbug colonies from locations of high insecticide usage (Chang et al., 1980). A control method that combines natural enemies, insecticides and resistant varieties is likely to be more effective against insect pests (Adkisson and Dyck, 1980) including the greenbug. Development of wheat varieties resistant to greenbug in Kenya will reduce the prophylactic control and hence decrease the hazards posed by insecticides to the natural enemies of this pest.

2.3.4 Search for Greenbug Resistance

Sources of resistance to greenbug seem to be rare in cultivated cereals. From a total of 4,343 oat selections from the United States Department of Agriculture (USDA) only 31 were found to possess resistance

against greenbug (Daniels, 1978) while several sorghum hybrids and selections are known to be resistant (DePew and Witt, 1979). Several lines of barley (Webster and Starks, 1984) and triticale (Webster and Inayatullah, 1984) are also resistant.

Starks and Merkle (1977) found six wheat cultivars that they screened for greenbug resistance to have low resistance, while the resistant triticale entry, "Gaucho" - a cross between a greenbug susceptible "Chinese Spring" common wheat and resistant rye, Insave F.A. (Wood et al., 1974) continued to show high resistance. The solution to the development of resistant wheat varieties therefore will depend on either interspecific crosses (Harvey et al., 1980) or on screening vast numbers of wheat cultivars as has been done for oats (Daniels, 1978). This search should include locally adapted cultivars and exotic germplasm of wheat and its closely related species (Ortman and Peters, 1980).

The greenbug-resistant wheats that have been available in the United States include "Dickinson Selection 28A" (DS 28A), Amigo, and Largo. DS 28A is a hexaploid selection from a durum (*Triticum turgidum* var *durum*) cultivar Dickinson No. 485' CI 3707 (Curtis et al., 1960) resistant to greenbug biotype A (Dahms et al., 1955). Amigo has a single dominant gene for greenbug resistance, from a triticale parent, "Gaucho" (Sebesta and Wood, 1978), and is resistant to biotype C. It was released in 1977. Largo (CI 17895) was selected from a cross between "Langdon" durum and a plant introduction PI 268210 (*Triticum tauschii* (Coss.) Schmal) (Joppa and Williams, 1982). It is resistant to biotypes C and E (Porter et al., 1982).

Elsewhere development of cereal cultivars resistant to greenbug is not as advanced as in the United States. In South America, varieties developed in the United States are grown (e.g. DS 28A, Amigo (wheat) and Gaucho (triticale) and are more resistant to the greenbug than the local varieties (Arriaga et al., 1980). In Eastern Africa, attempts have not been made to develop varieties resistant to the greenbug and control is therefore entirely by use of insecticides (Hill, 1975; Wanjama, 1979).

2.3.5 Testing for Antibiosis

Reproduction of greenbugs on test crop cultivars is used to test for antibiosis (Webster and Inayatullah, 1984) and such tests may be carried out in the greenhouse (Starks and Burton, 1977), in controlled environments (Schuster and Starks, 1973), or in the field (Teetes et al., 1974). In the greenhouse and controlled environments test cultivars are planted individually in plant pots. About one week after emergence, 5-10 adult greenbugs are placed on each seedling, caged and left for 24h. Caging may be done by covering the whole plant (Schuster and Starks, 1973) or by confining the greenbugs on a portion of intact leaf with a clip cage (Harvey et al., 1980). The adult greenbugs are removed from the plants after 24h leaving the nymphs, all of them within 24h of the same age. The nymphs are reduced to one per plant after 4 days and the remaining nymphs observed as they mature and begin to reproduce. Their offspring are counted and removed every two days until reproduction ceases (Wilson et al., 1978). The data obtained are used to determine the level of antibiosis of the test cultivars by comparing the mean

fecundity on the various cultivars (Wood and Starks, 1972c; Schuster and Starks, 1973). However the use of mean fecundity does not provide information on the period over which reproduction took place or on how the population is likely to increase.

An alternative method for assessing antibiotic resistance to the greenbug is described by Schuster and Starks (1973). Test cultivars are planted and infested with greenbugs as in the method outlined above. The adults too are removed after 24h as before. Five nymphs of uniform age are left on each plant. When the nymphs are five days old they are removed and weighed immediately. The mean weights of nymphs on different cultivars are compared and differences attributed to the effects of plants. Although it has been argued that large aphids are more fecund than small ones (Dixon and Dharma, 1980) this method too does not indicate how the greenbugs are expected to increase in subsequent generations. Although these methods yield useful results, a method that evaluates antibiosis of different cultivars by taking into account not only the mean fecundity, but also the generation time and the rate of increase of greenbug populations, provides more information on the effects of host-plant on the greenbugs feeding on it.

2.3.6 Testing for Tolerance

The tolerance of crop cultivars is measured by the ability of the plants to grow in the presence of greenbugs (Wilson et al., 1978). This has been done by comparing damage ratings and heights of test cultivars at the end of a given time period, or by comparing the functional plant loss index (FLPI). For the damage rating method, a constant number of

adult greenbugs is maintained by frequently removing the nymphs and replacing dead adults for 10 days. The plants are then rated for damage (Schuster and Starks, 1973; Wilson et al., 1978; Peiretti et al., 1980). The FLPI is determined by infesting caged plants with adult or 4th instar greenbugs when seedlings are about 4 cm high. They are left for 2, 4, 6 or 8 days and at the end of each time period, plant leaf area is measured and plants rated for damage on leaves. The FLPI is given by:

$$FLPI = 1 - \frac{LC-LI}{LC} \quad (1-DR) \times 100,$$

where LC is the mean leaf area of control plants, LI the mean leaf area of infested plants and DR the mean damage rating. The FLPI method is described by Morgan et al. (1980).

Damage rating and seedling height at the end of a given time period as suggested for these two methods may be useful for reflecting the impact of the greenbugs on seedlings. However, tolerance also includes the ability to repair tissues and recover from an attack (Johansen, 1978). A method that adequately determines the level of tolerance should, besides measuring the impact of greenbugs on seedlings, assess the ability of the plants to recover and produce a normal yield.

2.3.7 Testing for Antixenosis

To evaluate the antixenotic (nonpreference) effects of cereal cultivars to the greenbug the entries (various test cultivars) are planted in a random arrangement in a free choice arena into which the greenbugs are introduced to settle on plants of their choice (Painter,

1951). Round plant pots have been used with entries randomly arranged in a circle close to the edge of the pot. Adult apterous greenbugs are then released in the middle of the pots at the rate of about five greenbugs per plant and are left for 2 to 4 days. Then the number of greenbugs on each plant is recorded (Starks et al., 1972; Schuster and Starks, 1973; Wilson et al., 1978; Peiretti et al., 1980; Starks et al., 1983). Starks and Burton (1977) described a second method involving wooden flats (wooden trays). The test cultivars are all planted in each flat and infested with greenbugs about two days after emergence. The greenbugs are introduced onto the flats by brushing them off infested plants or by placing infested leaves in between rows of seedlings in the flats. They are allowed about 4 days to settle after which the greenbugs on each plant are counted.

Morgan et al. (1980) have described a method for evaluating antixenosis under field conditions. Field plots are planted with various entries, and observations are made on landing greenbugs from the time of crop emergence. Five randomly selected plants from each plot are examined for alate greenbugs. The mean numbers of alatae per plant are compared for the various entries.

The alate greenbugs are the migrant morph and are therefore the colonizers of new crop and the procedure of Morgan et al. is therefore a realistic one. Selection of plants by apterae in the greenhouse, as described above, is disimilar to host plant selection as it happens in the field. Therefore more field-applicable results may be obtained if alatae are used in greenhouse tests.

2.4 Culturing Greenbug

In order that a uniform culture of the greenbug be obtained, a single female from a mixed population is placed on an aphid-free caged plant and its progeny allowed to multiply as a new culture clone (Halgren and Taylor, 1968). The culture plants are caged to exclude extraneous insects. The cages may be made to fit plant pots of varying sizes (Starks and Burton, 1977) or may be constructed to contain a few plant pots for larger cultures (Halgren and Taylor, 1968). If actively flying greenbugs are required, the latter type of cage is convenient because alatae fly to the top of the cage and can be collected easily.

Barley is the preferred culture plant for rapid build up of greenbug cultures, but is quickly killed by feeding greenbugs and its rate of growth is reduced above 26^{o}C and so alternatively, susceptible cultivars of seedling sorghum may be used (Starks and Burton, 1977). Resistant varieties should be avoided as culture plants because of the preconditioning effects which may obscure the true response of test plant material in subsequent screening for greenbug resistance (Starks and Schuster, 1976; Wilson and Starks, 1981). There are little preconditioning effects after a short culturing period (e.g. 2 months) (Wilson and Starks, 1981), but the effects are stronger if greenbug is continuously cultured for 2 years (Starks and Schuster, 1976). Continued greenhouse culturing can lead to the development of a new greenbug biotype (Wood, 1961).

Sexuales in greenhouse cultures have been observed (Washburn, 1908; Mayo and Starks, 1972) at certain times of the year; males then may comprise about 17% of the alate greenbug population and oviparae

about 25% of the apterous population (Mayo and Starks, 1972; Starks and Burton, 1977). Increasing the day length with light from 250 W tungsten filament lamps discourages production of the sexual forms (Halgren and Taylor, 1968).

CHAPTER III

Part I

Resistance of Wheat to *Schizaphis graminum* (Homoptera:Aphididae) in Kenya

by

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Resistance of wheat to *Schizaphis graminum* (Homoptera:Aphididae) in Kenya

ABSTRACT

Fifty Kenyan and exotic wheat entries were evaluated for resistance to greenbug, *Schizaphis graminum* (Rondani); separate tests were run to detect antibiosis, tolerance and antixenosis. Life tables were constructed and the capacity for increase (r_c) used to evaluate wheat for resistance by antibiosis. Apterae were used in initial tests but both apterae and alatae were used in subsequent tests for antibiosis. Seedling dry weight and grain yield provided useful information on tolerance of seedling wheat and the ability of attacked plants to recover but seedling height and number of tillers were not useful for assessing tolerance. Tests for antixenosis of wheat entries to greenbug suggested a similar order of host preference of alatae and apterae in the greenhouse, and this order was consistent with that in the field trials.

Entries that ranked high in one mechanism were often low in others. However, Kenya Fahari ranked high in all three mechanisms. This is a commercial variety and could be incorporated into an integrated pest control programme and could also be used in the development of future greenbug-resistant wheat varieties.

INTRODUCTION

The greenbug (also wheat aphid, Hill, 1975), *Schizaphis graminum* (Rondani), is a serious pest of cereal crops and occurs in many parts of the world (Hill, 1975). Although sorghum has recently been attacked (Harvey and Hackerott, 1969), the major host is wheat (Wadley, 1931). Field infestations of greenbug in wheat may start soon after seedling emergence; the two leaf stage is the most susceptible stage (Starks et al., 1975).

Wheat in Kenya is grown mainly in areas over 1,800m above sea level (a.s.l.) with an annual rainfall of about 1,000 mm (Harder, 1974). Frequent greenbug outbreaks occur in the wheat growing areas resulting in extensive use of insecticides (Wanjama, 1979). The wheat breeding programme in the country is well established (Harder, 1974), but has not addressed the development of varieties resistant to greenbug. The extent to which existing varieties are resistant is not known.

The mechanisms of resistance as defined by Painter (1951) are antibiosis, tolerance and nonpreference (= antixenosis; Kogan and Ortman, 1978). However resistance of cereals to greenbug resulting from any of these mechanisms appears to be a rare characteristic. Consequently the amount of germplasm screened before positive results are obtained can be enormous (Daniels, 1978), and all results may be negative if only a few entries (cultivars tested) are evaluated (Starks and Merkle, 1977). Although cultivated hexaploid wheat varieties are generally lacking in high resistance to this pest (Harvey et al., 1980), some resistant varieties have been developed. For example, in the United States

Dickinson Selection 28A is resistant to greenbug biotype A (Wood, 1961), "Amigo" wheat to biotype A, B and C (Joppa and Williams, 1982) and "Largo" to biotypes C and E (Joppa et al., 1980).

This work was initiated to investigate whether wheat germplasm available in Kenya is resistant to greenbug, and to identify the mechanism of such resistance. A resistant entry would be useful in the development of new resistant varieties and if such an entry were a commercial variety, it could be recommended to wheat growers to reduce losses from greenbug attacks.

MATERIALS AND METHODS

Initially 50 wheat entries were obtained. These included commercial varieties and breeder's lines from Kenya, three greenbug-resistant selections from the United States and several exotic lines. In 1982 all the entries were tested for antibiosis and 46 for tolerance. In 1985 most of these were tested for antixenosis. The decline in the number of entries tested was due to reduced seed viability following storage. Based on the initial testing, more intensive tests were carried out for each mechanism of resistance. For each mechanism the four most and two least resistant entries were selected for this intensive testing.

Three greenbug clones were raised from three samples collected in 1982 from Njoro (about 180 km NW of Nairobi and 2,100m a.s.l.), Eldoret (at similar elevation but about 180 km NW of Njoro) and Mau Narok (about 2,700m a.s.l. and approximately 40 km to the S of Njoro). Each clone was the progeny of a single parthenogenetic female. The clones were maintained on wheat (cv. Kenya Kifaru) in the greenhouse in plexiglass cages 45x45x60 cm. Nylon netting (about 20 meshes/cm) at the front and top of the cage allowed aeration but prevented greenbugs from escaping. The three clones were used in 1982. The Njoro clone alone was maintained in the greenhouse and used in 1983 and 1985 tests.

Antibiosis

In the greenhouse, wheat seeds were planted in pots 8.25 cm square and 9.5 cm deep which were individually caged before seedling emergence. Cages were of nylon netting supported on two crossed U-shaped wires with

their ends pushed into the soil. The top of the cage was 30 cm above the soil and the netting extended about 2.5 cm down the outside of the pot where it was secured by an elastic band. At growth stage 12 (GS 12) (Zadoks et al., 1974; Tottman and Makepeace, 1979) the seedlings were thinned to one per pot, and two gravid (female with unborn embryos) apterous adult greenbugs were placed on each plant and removed after 24h. The resulting nymphs were reduced to one per plant after four days. The remaining nymph was observed daily until first reproduction and then once every two or three days until no further reproduction was observed. All offspring of test greenbugs were counted and removed at each sampling day.

In 1982, each of the 50 wheat entries were tested, using the three greenbug clones, in four replicates. In 1983, six entries selected on the basis of overall performance in 1982, were tested using only the Njoro clone; treatments were replicated ten times. In 1985, only the Njoro clone was used, and six entries were selected on the basis of antibiosis in the 1982 studies. In 1985, both apterae and alatae were tested in separate trials, and 24 replicates were used in each trial.

Life tables were constructed by recording the proportion of surviving adults (l_x) and the age specific reproduction (m_x) at each sampling date (Birch, 1948). In 1985 the replicates/entry were grouped into four cohorts of six for this purpose. From the life tables, net reproductive rate (R_o), cohort generation time (T_c) and daily capacity for increase (r_c) were calculated for greenbugs on each entry. Where $R_o = \Sigma l_x m_x$, T_c is the age in days at which 50% of the offspring are

produced, and

$$r_c = \frac{\log_e R_o}{T_c} \qquad \text{(Laughlin, 1965)}$$

The values for R_o, T_c and r_c were subjected to analysis of variance and tested for significance at ($P \leq 0.05$) using Tukey's multiple comparison test (Sokal and Rohlf, 1981).

Tolerance

In the greenhouse, entries were planted in pots, caged as described for the antibiosis experiment, and seedlings thinned to one per pot at GS 12. Two apterous adults were placed on each infested seedling. After 10 days all the greenbugs on each seedling were counted. Feeding was allowed to continue for another four days, then the seedlings were uncovered and the greenbugs killed by spraying malathion (6.25 g a.i./ℓ). When the plants were uncovered, their height was measured to the tip of the largest leaf. Plants were then allowed to grow to maturity, when the number of tillers and grain yield was recorded.

In 1982, 46 entries were tested. Each entry was planted in 16 pots. Four randomly selected seedlings were infested with each of the three greenbug clones; the remaining four plants were uninfested controls. In 1983, six entries were selected on the basis of overall performance in 1982, and tested using the Njoro clone only with eight replicates. The plants, including the uninfested controls, were washed out of the pots, separately wrapped in aluminum foil and oven dried to constant weight.

In 1985 the procedure was repeated but eight replicates were weighed as in 1983 and an additional eight were grown to maturity and the yield recorded.

The data were subjected to analysis of variance. Means of infested plants were adjusted for the number of greenbugs (counted after 10 days) by analysis of covariance and adjusted means were contrasted with the means of respective controls using one tailed t-test of contrasts (Sokal and Rohlf, 1981).

Antixenosis

The 35 entries still viable (from the initial number of 50 entries used in 1982) in 1985 were tested. The entries were planted in wooden flats 45x60 cm. A 60 cm-high wood-framed cage of nylon netting was placed on the soil in each flat enclosing the entries in an arena 41x56 cm. Twelve wooden flats were marked with 35 planting positions (five rows of seven plants each) and in each flat, four seeds of each entry were planted in a randomly selected position. In each flat, planting positions were randomized separately. The flats were then individually caged and at GS 12, seedlings were thinned to one per planting position.

Alate greenbugs were introduced in six cages and apterae were introduced in the remaining six. Alatae were introduced by placing 200/flat in a glass vial covered with black plastic and inserted horizontally in a hole in the top bar of the cage frame. The greenbugs crawled to the edge of the vial and flew into the cage. After four days the cage was removed and alatae on each plant counted. In the remaining six

cages apterae and nymphs were introduced on infested wheat leaves placed on the soil between plant rows (Starks and Burton, 1977). After 4 days the plants were uncovered and the apterae and nymphs on each plant counted.

From the results of the above experiments, six entries were selected and retested in the greenhouse and in the field. In the greenhouse, a 10-plant-row of each of the six entries was planted in each of 12 flats. The positions of rows of each entry were randomized separately for each flat. Alate greenbugs were introduced into six cages and apterae and nymphs into the remainder; introduction and counting procedures were as described above.

In the field, the six entries were planted in 1.5x6 m plots in a randomized complete block design with six replicates. Each replicate (block) was 14x41 m; a 1 m path surrounded each plot. A low seed rate of 25 g/plot was used so that plants could be singled out easily and searched for greenbugs. The seedlings were observed for the first appearance of immigrant greenbugs and then sampled weekly by randomly selecting five plants/plot and examining them for greenbugs in situ. Alatae and apterae plus nymphs were counted separately.

A transformation of $\sqrt{X + 0.5}$ was used for both greenhouse and field data of alatae while $X^{0.2}$ was used for data on apterae and nymphs. These transformations stabilized the variance. Analysis of variance was performed on the transformed data and tested for significance at $P = 0.05$ using Tukey's multiple comparison test.

RESULTS

Antibiosis

In 1982, there were no significant differences in the net reproductive rate (R_o), the cohort generation time (T_c) or the daily capacity for increase (r_c) between the three greenbug clones, nor were there significant interactions between the clones and entries for any of these variables (Appendix 1). The data for the three clones were therefore pooled for each entry and subjected to one way analysis of variance. No significant differences were found in R_o, T_c or r_c for greenbugs on all the 50 wheat entries tested in 1982 (Table I).

In 1983, the entries could be divided into two groups on the basis of r_c (Table II, Test 1). One entry (K7002-13) overlapped the two groups. Kenya Fahari, Kenya Kiboko, Africa Mayo and R306 were significantly more resistant than Kenya Kifaru. The entries tested in 1985 could also be divided into two overlapping groups on the basis of r_c (Table II, Tests 2 and 3).

There were differences in estimates of the life table parameters. The overall means R_o for apterae and alatae in 1985 (39.0 and 39.5 respectively) were not significantly different, but the two morphs had a mean T_c of 15.0 and 13.2 days respectively and this difference was significant. The mean r_c for the two morphs were 0.241 and 0.267 respectively, and this difference was also significant (paired t-test, $P<0.05$).

Tolerance

The means for the seedling height 14 days after infestation, number of tillers and grain yield at harvest for the 46 entries tested, with the three greenbug clones, are given in appendices 2-5. Analysis of variance revealed no significant variation due to differences among the three clones in any of these variables. Also there were no significant interactions between clones and wheat entries, and so the data for the three clones were pooled for each entry and tested against their respective controls. The results of this analysis are summarised in Table III. For each entry, control (uninfested) plants were taller than greenbug infested plants, although the height difference was significant only for one entry, Trophy. Some infested entries produced more, and some fewer, tillers than their control plants, while some showed no change. Only plants of three entries produced a significantly different number of tillers when infested plants were compared with controls. In seven entries grain yield was significantly reduced by greenbugs (Table III).

In 1983 and 1985, seedling dry weight 14 days after infestation was used to assess the impact of greenbugs feeding on wheat seedlings. In all entries, greenbug feeding for two weeks resulted in a reduction in seedling weight compared with the respective controls (Table IV). In 1983, R306, Africa Mayo and K7002-13 did not suffer significant seedling weight reduction, while in 1985 only Kenya Fahari did not have a significant reduction in seedling dry weight. Inconsistencies in weight reduction of Kenya Fahari, Africa Mayo and K7002-13 seedlings between the two years may have been due to uncontrolled conditions in the

greenhouse affecting the growth of the plants and feeding activity of the greenbugs.

Grain yield reduction in 1985 was not significant for Kenya Fahari and Africa Mayo (Table IV); but the % yield reduction for Africa Mayo (31.7%) was similar to that of K7002-13 (31.9%). This indicates that Kenya Fahari may be the only entry that is tolerant.

Antixenosis

Greenhouse: There were no significant differences between the number of alate or apterous greenbugs that settled on the 35 entries tested (Table V). However there was a significant correlation between the number of alate and apterous greenbugs that settled on the same entries ($r = 0.68$, 33 df, $P<0.05$).

The number of alatae that settled on the six selected entries did not differ significantly, but the highest numbers settled on Leopard wheat (Table VI). Bounty and Leopard had been selected from the previous test (Table V) because they were the least antixenotic entries. Apterae showed some significant differences in their choice of host plants (Table VI). Significantly fewer greenbugs settled on Kenya Kuro than Bounty or Leopard.

Field: The alate greenbugs on plots increased in number from the first week (July 16) of their appearance to the second week and then declined to the fourth week (August 6th) (Table VII). Numbers of apterae increased from the first week to the fourth week. The alatae were immigrants that colonized the crop and their decline indicates that the

period of high immigration was between the first and second week, after which the rate of death exceeded that of immigration and alatae production. The apterae were the progeny of the alate immigrants.

The pattern of abundance of alatae on entries in the field was similar to that in greenhouse antixenosis trials. The ranks for the field (at peak density) and greenhouse tests with alatae were positively, but not significantly correlated (Spearman's rank correlation coefficient, $r_s = 0.37$, 4 df, $P>0.05$) (Sokal and Rohlf, 1981). Leopard again had the highest numbers of alatae (Table VIII) but there were no significant differences between numbers found on the different entries. There was a significant positive correlation between the alatae at peak density (second week) and their progeny in the same week ($r = 0.92$, 4 df, $P<0.05$), but the peak density of alatae was negatively correlated to the progeny in the fourth week ($r = -0.17$, 4 df, $P>0.05$).

DISCUSSION

Antibiosis

The effects of antibiosis of a resistant host-plant take the form of reduced fecundity, decreased size, increased duration of development or increased mortality of the insect (Painter, 1951). The evaluation of crop plants for antibiosis against greenbugs has usually been measured by assessing mean fecundity (the net reproductive rate) and longevity (e.g. Wood and Starks, 1972; Schuster and Starks, 1973; Starks and Schuster, 1976; Teetes et al., 1974; Webster and Inayatullah, 1984). However the highest fecundity may not necessarily result in the largest population over time, because this also depends on the generation time. Leather and Dixon (1984) used reproduction over a period equivalent to the preoviposition period to determine the intrinsic rate of increase (r_m) of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.). However r_m relates to populations with stable age distribution (Southwood, 1978). Laughlin (1965) suggested that r_c is a useful statistic that indicates the expected population increase per unit time with no overlapping generations. This statistic is therefore more appropriate to apply to data on aphid reproduction where nymphs are removed at each sampling.

Population increase will be higher for greenbugs with high rather than low r_c for a given time period, hence entries with low r_c values exhibit greater antibiosis. The capacity for increase is r in the equation

$$N_t = N_o e^{rt}$$

where N_o and N_t are the number of individuals at time zero and any time t respectively (Southwood, 1978). Starting with one-day old alate greenbug nymphs on Kenya Kiboko (Table II, Test 3), after 10 days the population will have grown 11.2 times while the population on Kenya Kulungu (same test) will have grown 15.5 times. It is to be noted that R_o is higher for the former than the latter but T_c are the reverse (Table II, Test 3).

The mean R_o for apterae and alatae on all the six entries (Table II, Tests 2 and 3) are not significantly different but alatae have significantly shorter T_c than apterae and this results in r_c for apterae being lower than for alatae. The alate greenbugs colonize new crops and since this species attacks the seedling stage the ability to produce a large number of offspring in a short time may ensure a rapid population growth and hence effective exploitation of the ephemeral habitat. These results differ from those for other species: for example Dixon and Wratten (1971) and Wratten (1977) found that alatae of *Aphis fabae* Scopoli and *Metopolophium dirhodum* (Walker) and *Sitobion avenae* (F.) all have a lower fecundity than apterae of comparable weight up to 20 days. In our studies, R_o is the mean fecundity over the entire reproductive life of the test greenbugs.

Using r_c as the criterion, in the 1983 test Kenya Fahari, Kenya Kiboki, Africa Mayo and R306 are the most antibiotic entries tested while Kenya Kifaru is the least antibiotic entry. In previous reports mean fecundity (R_o) has been used to determine levels of antibiosis (Wood and Starks, 1972; Schuster and Starks, 1973; Teetes et al., 1974; Webster and Inayatullah, 1984). If R_o was used in this study, different

conclusions would have been reached, and these may have been erroneous in the context of the multiple generations greenbug goes through on wheat in Kenya.

Tolerance

Tolerance may result either from the ability of a plant to withstand insect damage (Wilson et al., 1978), or to recover following cessation of insect attack (Johansen, 1978). Ability of wheat to withstand greenbug damage can be determined after a 14 day feeding period when susceptible plants would be more stressed than resistant ones. However when greenbugs are confined on seedlings and allowed to feed and multiply, the seedlings will eventually die because the greenbugs cannot leave the host plant and are sheltered from environmental hazards such as severe weather and natural enemies. Therefore to allow the plants to continue to grow and produce grain, an application of insecticide is necessary. This is consistent with field practice where a heavy greenbug infestation on seedling wheat is controlled with insecticide.

Comparison of seedling height at the end of the feeding period and the number of tillers, for infested and control plants, do not appear to be good methods for detecting tolerance. Increased tillering of wheat after the feeding of Hessian fly, *Mayetiola destructor* (Say), at high temperatures is an important component of tolerance in compensating for temperature-induced loss of resistance (Cartwright et al., 1946; Tingey and Singh, 1980). Such a generalization on tillering of wheat after greenbug feeding does not seem possible because of the variations in

plant response.

Seedling dry weight seems to be a good measure of wheat tolerance to greenbug. Significant feeding effects are detected, and help to identify those entries that compensate most for seedling losses once greenbugs are removed. In 1985 Kenya Kifaru and Kenya Kiboko had been selected as the susceptible checks and the test confirmed their susceptibility and indicated that Kenya Fahari was the most tolerant entry.

Antixenosis

Apterous greenbugs have commonly been used in tests of antixenosis (e.g. Schuster and Starks, 1973; Starks and Burton, 1977; Peiretti et al., 1980), but alatae are the colonizers of new habitats. The correlation between the numbers of alate and apterous greenbugs suggests a low level of antixenosis operates in some entries and that both morphs select their host plants in the same way when plants of different entries are close together. The alatae however, colonize crops in the field and are therefore the best morph to use in tests of the antixenotic effects of wheat entries.

In the field, the alate immigrants increased rapidly to the second week and sharply decreased in the third week. It is apparent these immigrants reproduce rapidly after landing on the crop as was indicated by the antibiosis experiment. The peak density of alatae (in the second sampling week) were significantly correlated to their progeny during the second week ($r = 0.92$, 4 df ($P<0.05$) but negatively correlated to the progeny in the fourth week ($r = -0.17$) and not significantly so (Table

VIII). This may be largely due to the effects of antibiosis of the plants because the partial correlation was shown to be positive ($r = 0.14$ 3 df) when $e^{r}c$ (a component of population growth rate from antibiosis experiment, Table I) was held constant. Although the correlation is still not significant, it is noted that the r_c for alatae and apterae are different (Table II) and the two morphs contributed in the progeny.

CONCLUSIONS

Most of the entries tested which included most of the wheat germplasm available in Kenya, lacked high level resistance to the greenbug. However some entries possessed low levels of resistance by one mechanism or another. Some of the entries ranking high in one mechanism were very low in others, e.g. Kenya Kiboko ranked high in antibiosis but it was not tolerant of those greenbugs which did feed on it. Leopard ranked high in antibiosis but it was not antixenotic. Kenya Kifaru, which is a commercial variety, ranked low in resistance in most tests and was therefore considered a susceptible entry.

Overall, Kenya Fahari showed good performance for all mechanisms of resistance tested and further work may be focused on this entry. Kenya Fahari is a current commercial variety. This makes it easy for its incorporation into an integrated pest control programme. It has been shown that late planted wheat (late May-June) around Njoro has a high risk of suffering greenbug attack (Wanjama and Holliday, 1986b). Kenya Fahari matures in 125 days and so it is suitable for late planting as an alternative to the use of susceptible varieties which are more likely to need insecticidal treatment. This variety could also be used as sources of greenbug resistance in the development of new resistant wheat varieties.

Table I. Antibiosis of wheat entries to apterous greenbugs as measured by mean reproductive rate (R_o), cohort generation time (T_c) and capacity for increase (r_c) in 1982 experiment

Entry	Entry status[1]	R_o	T_c (Days)	r_c (Per day)
Kenya Kima	C	25.2[2]	18.2[2]	0.176[2]
Kenya Kiboko	R	27.6	18.2	0.178
Leopard	C	26.1	17.5	0.178
Kenya Kulungu	C	29.9	15.8	0.184
K7155-36	BL	22.3	16.5	0.187
R351	P1	38.5	19.1	0.188
Kenya Fahari	C	32.3	18.6	0.189
Kenya Popo	C	22.3	16.2	0.191
R301	P1	30.8	18.1	0.191
Kenya Mamba	C	41.3	18.3	0.191
Kenya Kongoni	C	21.0	15.8	0.192
Kenya Nyumbu	C	26.2	16.4	0.197
K6940-1	BL	36.6	18.6	0.197
Kenya Ngiri	C	39.3	18.5	0.198
K7207-1	BL	40.1	17.3	0.199
Kenya Nyangumi	C	41.7	18.5	0.200
Kenya Nungu	C	34.6	17.6	0.201
Hunter	R	31.6	15.5	0.203
Kenya Nyati	R	41.6	18.3	0.204
K7002-13	BL	42.1	18.2	0.204
R306	P1	46.3	18.7	0.204
Africa Mayo	C	31.3	16.6	0.206
GB5764	RS	34.1	17.2	0.206
K7000-1	BL	49.3	18.8	0.208
Bounty	C	25.6	14.3	0.211

Continued .....

Table I continued

Entry	Entry status	R_o	T_c (Days)	r_c (Per day)
Kenya Swara	R	38.1	17.1	0.211
Kenya Bongo	C	54.5	18.6	0.211
K7207-19	BL	31.3	16.4	0.212
Trophy	R	32.8	16.2	0.214
Kenya Kuro	R	40.8	16.9	0.215
Kenya Tembo	C	44.2	17.3	0.215
R325	PI	39.7	17.1	0.216
Largo	RS	28.3	15.7	0.217
Kenya Kanga	R	41.8	17.0	0.217
Kenya Zabadi	C	27.2	14.9	0.218
K7186-1	BL	43.8	17.4	0.218
Fanfare	R	42.1	16.9	0.219
R235	PI	43.3	17.3	0.219
K7208-1	BL	42.0	17.1	0.220
K7000-6	BL	29.1	15.3	0.221
K6952-1	BL	38.4	16.6	0.221
GB5766	RS	48.5	17.6	0.221
Kenya Nyoka	R	50.4	17.2	0.221
Page	R	39.3	16.5	0.222
K7207-21	BL	40.3	16.2	0.228
R253	PI	46.1	16.7	0.228
Kenya Paa	C	46.3	16.6	0.229
Kenya Kudu	R	27.4	14.1	0.230
Kenya Paka	C	65.4	18.2	0.230
Kenya Kifaru	C	60.4	17.8	0.232

[1] Entry status: BL, Local Breeder's Line; C, Commercial variety; PI, Plant Introduction; R, Restricted variety; RS, Resistant selection from the United States.

[2] There were no significant differences between means in each column ($P>0.05$).

Table II. Antibiosis of selected wheat entries to apterous and alate greenbugs as measured by mean reproductive rate (R_o) cohort generation time (T_c) and capacity for increase (r_c

	R_o	T_c (Days)	r_c (Per day)
Test 1: 1983 Apterae			
Kenya Fahari	34.7ab	16.1a	0.220a
Kenya Kiboko	26.7a	14.4a	0.225a
Africa Mayo	29.3a	15.0a	0.225a
R306	32.8ab	14.8a	0.236a
K7002-13	40.2ab	15.1a	0.244ab
Kenya Kifaru	49.6b	14.1a	0.278b
Test 2: 1985 Apterae			
Kenya Kulungu	27.4c	15.0c	0.219c
Kenya Kiboko	33.9cd	14.7c	0.231cd
Kenya Paka	43.5cd	15.6c	0.242cd
Kenya Kifaru	48.3d	15.9c	0.246cd
Kenya Kima	42.3d	14.9c	0.251d
Leopard	38.7cd	14.1c	0.259d
Test 3: 1985 Alatae			
Kenya Kiboko	40.6ef	14.9g	0.242e
Kenya Kima	27.8e	11.4e	0.251ef
Leopard	34.8ef	13.0efg	0.264ef
Kenya Kulungu	36.0ef	12.8ef	0.274ef
Kenya Paka	49.2f	14.0fg	0.276ef
Kenya Kifaru	48.9f	13.3efg	0.293f

Within columns means followed by the same letter in the same test are not significantly different at P = 0.05 (Tukey's multiple comparison test).

Table III. Tolerance of wheat entries as determined by reduction in seedling height at the time of greenbug removal, tillers and grain yield at harvest, based on adjusted means in 1982 experiment

Entry	Mean % height reduction	Mean % tiller reduction	Mean yield g/plant control	Mean % yield loss
R306	2	2	2.25	-37
Kenya Fahari	16	24	2.51	-27
K7002-13	6	-10	3.49	-15
Kenya Nyumbu	14	-15	2.47	-13
K7155-36	13	4	2.54	-4
Kenya Paa	14	36	3.51	1
K6952-1	8	4	3.14	2
Africa Mayo	9	11	4.99	7
Kenya Paka	23	17	4.17	3
GB5764	14	18*	1.26	9
Kenya Kima	7	7	4.44	10
R351	8	33	3.63	15
K7186-1	15	14	4.15	6
Kenya Kulungu	2	-3	2.58	16
Kenya Nungu	1	14	5.43	13
Kenya Nyati	15	-1	4.24	5
Kenya Mamba	15	-31	5.02	10
Fanfare	18	-5	4.99	13
K7000-1	23	3	5.84	18
Kenya Swara	2	4	3.75	7
K7207-19	17	9	4.72	12
Kenya Ngiri	13	-11	6.01	16
Kenya Kongoni	2	10	4.20	17
Kenya Zabadi	8	2	3.85	18
Kenya Kanga	17	11	4.96	20

Continued .....

Table III continued

Entry	Mean % height reduction	Mean % tiller reduction	Mean yield g/plant control	Mean % yield loss
K7000-6	14	6	4.16	23
R253	9	-4	3.99	20
Kenya Popo	1	-10	4.06	22
R325	0	4	5.58	21
R235	21	-4	4.32	18
Leopard	4	-1	4.33	21
Kenya Kudu	5	-10	2.75	20
Kenya Kuro	2	-38	4.03	22
K6940-1	18	-10	6.41	24*
K7207-21	19	31*	4.34	25
Bounty	8	0	5.14	27*
K7208-1	14	4	4.95	26*
Kenya Kifaru	13	10	5.51	27*
Page	23	1	3.93	26
Trophy	24*	-6	4.10	27
Kenya Nyoka	19	8	4.50	27
Kenya Kiboko	21	8	3.55	23
R301	13	-7	5.76	31*
Kenya Tembo	5	15	4.31	33*
Hunter	14	-19	2.27	35
Kenya Bongo	18	-18*	2.54	50*

*Mean of infested plants was significantly reduced when compared to mean of respective control at P = 0.05 (one tailed t-test of contrast).

Table IV. Tolerance of selected wheat entries to greenbug as measured by seedling dry weight and grain yield. Means for infested plants are adjusted for population of greenbugs 10 days after infestation by analysis of covariance

	Seedling dry weight (mg)						Grain yield (g)		
	1983			1985			1985		
Entry	Infested	Control	% Reduction	Infested	Control	% Reduction	Infested	Control	% Reduction
R306	370	403	8.2	-	-	-	-	-	-
Africa Mayo	469	558	15.9	181*	425	57.4	1.55	2.27	31.7
Kenya Fahari	580*	748	22.5	259	265	2.3	3.16	2.62	-20.6
K7002-13	274	373	26.5	142*	275	48.4	2.48*	3.64	31.9
Kenya Kifaru	352*	518	32.0	199*	305	34.8	0.94*	3.52	73.3
Kenya Kiboko	330*	493	33.1	41*	260	84.2	0.19*	2.29	91.7

*Adjusted means of infested plants are significantly different from means of respective control at P = 0.05 (F - test of contrasts).

Table V. Antixenosis of wheat entries to the greenbug as shown by mean number/plant (± standard error) of alatae and apterae 4 days after infestation

Entry	Alatae	Apterae
Kenya Tembo	1.3±0.5	59.3±17.9
Kenya Nyati	1.8±0.9	63.0±16.8
Kenya Kuro	2.0±0.8	60.0±18.9
Kenya Kulungu	2.5±1.3	61.6±61.6
K7000-1	2.5±0.8	87.8±22.5
Kenya Bongo	2.6±0.8	87.8±32.6
Kenya Kongoni	2.5±1.0	67.7±21.3
Hunter	2.6±0.8	74.0±21.7
Kenya Fahari	2.8±1.9	133.3±46.6
Kenya Kiboko	2.8±0.7	66.0±21.5
R253	3.0±1.0	89.5±25.1
R301	3.0±1.6	77.0±38.1
Kenya Kifaru	3.0±0.9	95.8±29.9
Kenya Nyangumi	3.2±0.8	92.2±27.7
Kenya Zabadi	3.3±1.5	62.3±24.7
K7207-21	3.5±1.6	81.0±16.2
Kenya Nyoka	3.5±1.0	125.5±42.1
R235	3.8±1.8	87.0±35.2
Kenya Popo	4.0±1.3	80.2±20.7
Kenya Mamba	4.0±2.7	80.7±17.3
Africa Mayo	4.0±1.4	103.3±77.4
Kenya Ngiri	4.2±1.7	91.8±41.7
Kenya Paa	4.3±1.3	124.0±34.0
Page	4.7±2.4	95.0±32.6
Fanfare	4.7±1.2	104.0±33.1

Continued .....

Table V continued

Entry	Alatae	Apterae
Kenya Nungu	5.0±1.2	129.6±40.5
Kenya Paka	5.2±2.2	106.8±28.7
Kenya Nyumbu	5.3±3.7	79.3±14.5
Kenya Swara	5.5±1.9	137.3±14.9
Kenya Kima	5.6±0.9	110.3±47.6
Trophy	5.7±1.3	96.5±18.8
Kenya Kanga	5.8±1.4	111.5±43.1
Kenya Kudu	7.0±1.9	119.7±34.1
Leopard	7.0±2.2	133.3±46.6
Bounty	8.0±3.2	117.5±38.5

Means within each column are not significantly different at $P = 0.05$.

Correlation between means of alatae and apterae ($r = 0.68$, 33 df $P<0.05$).

Table VI. Antixenosis of selected wheat entries to the greenbug as measured by mean number of alatae and apterae per plant (± standard error) 4 days after infestation in independent experiments for the two morphs

Entry	Alatae	Apterae
Kenya Kuro	4.0±0.4a	37.0±3.3a
Kenya Fahari	4.0±0.4a	46.9±4.6ab
Kenya Nyati	4.2±0.4a	44.8±4.0ab
Kenya Tembo	4.2±0.4a	42.7±3.4ab
Bounty	4.2±0.5a	47.9±3.7b
Leopard	5.4±0.5a	53.0±4.5b

Means followed by the same letter in each column are not significantly different at P = 0.05 (Tukey's multiple comparison test).

Correlation between means of alatae and apterae + nymphs (r = 0.74, 4 df P>0.05).

Table VII. Mean (± standard error) number of greenbugs per five plant sample taken randomly each week from 36 field plots of six wheat entries in 1985 antixenosis studies

Week	Alatae	Apterae
July 16	2.6±0.3b	18.5±2.6a
July 23	13.2±1.0d	99.2±9.3b
July 30	5.1±0.5c	196.8±13.5c
August 6	0.9±0.2a	233.5±15.0c

Means followed by the same letter in each column are not significantly different at P = 0.05 (Tukey's multiple comparison test).

Table VIII. Mean number of greenbugs at peak density of alatae (second week of sampling) in field plots in 1985 studies on antixenosis

Entry	Alatae week 2	Progeny week 2	Progeny week 4
Kenya Nyati	11.2	79.5	265.3
Bounty	11.6	80.7	221.3
Kenya Kuro	12.6	88.0	298.5
Kenya Fahari	12.8	106.0	152.2
Kenya Tembo	13.5	128.0	249.0
Leopard	14.0	109.2	207.5

Correlation coefficient between alatae and their progeny at peak density of alatae (second week) ($r = 0.92$, 4 df ($P<0.05$).

Correlation coefficient between alatae at peak density (week 2) and progeny in the fourth week ($r = -0.17$, 4 df $P>0.05$).

Partial correlation coefficient between alatae at peak density and progeny in the fourth week with e^{rc} (from antibiosis experiment) held constant ($r = 0.14$, 3 df $P>0.05$).

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Appendix 1. Mean net reproductive rate (R_o), cohort generation time (T_c) and capacity for increase (r_c) for three greenbug clones originating from Eldoret (ELD), Mau Narok (M/N) and Njoro (NJO) used in 1982 greenhouse experiment

	R_o			T_c (Days)			r_c (Per day)		
Entry	ELD	M/N	NJO	ELD	M/N	NJO	ELD	M/N	NJO
Kenya Kima	28.3	20.7	26.5	16.8	22.8	16.8	0.200	0.134	0.195
Kenya Kiboko	36.3	14.0	32.5	17.7	16.8	20.2	0.203	0.157	0.172
Leopard	7.3	34.0	37.0	18.9	15.5	18.0	0.105	0.228	0.201
Kenya Kulungu	38.8	4.3	46.8	19.3	8.9	19.1	0.189	0.162	0.201
K7155-36	17.3	20.0	29.5	15.6	17.1	16.8	0.183	0.175	0.202
R351	51.0	20.8	43.8	21.1	18.2	17.8	0.185	0.167	0.212
Kenya Fahari	25.0	36.0	41.8	17.9	20.1	17.8	0.180	0.178	0.210
Kenya Popo	14.8	23.3	29.0	16.7	15.1	16.6	0.161	0.209	0.202
R301	32.0	33.8	26.8	19.1	16.3	18.9	0.181	0.217	0.174
Kenya Mamba	11.3	42.0	70.8	18.4	18.3	18.1	0.132	0.204	0.236
Kenya Kongoni	18.5	20.8	23.8	15.0	15.5	16.9	0.194	0.195	0.187
Kenya Nyumbu	36.3	25.8	16.5	18.7	16.3	14.1	0.192	0.200	0.199
K6940-1	42.5	33.3	34.0	22.1	15.3	18.3	0.169	0.229	0.193
Kenya Ngiri	38.8	30.5	48.8	18.8	17.5	19.2	0.195	0.195	0.203
K7207-1	80.7	20.0	19.8	20.0	14.5	16.8	0.219	0.200	0.179
Kenya Nyangumi	29.8	48.8	46.5	18.1	18.0	19.5	0.188	0.216	0.197

Continued .....

Appendix 1 continued

	R_o			T_c (Days)			r_c (Per day)		
Entry	ELD	M/N	NJO	ELD	M/N	NJO	ELD	M/N	NJO
Kenya Nungu	27.8	31.0	45.3	16.1	18.9	17.7	0.206	0.182	0.215
Hunter	7.0	29.8	58.0	9.6	16.8	20.0	0.204	0.202	0.203
Kenya Nyati	51.0	39.3	34.5	18.8	16.7	19.4	0.209	0.220	0.183
K7002-13	55.5	27.8	43.0	18.6	16.9	19.0	0.216	0.197	0.198
R306	45.3	59.8	34.0	17.7	21.2	17.4	0.216	0.193	0.203
Africa Mayo	37.5	21.3	35.0	17.3	15.2	17.4	0.210	0.202	0.205
GB5764	28.3	30.3	43.8	17.1	15.2	19.3	0.195	0.224	0.198
K7000-1	39.8	59.0	49.0	19.1	20.2	17.0	0.193	0.202	0.229
Bounty	26.0	8.5	39.3	12.7	13.7	16.6	0.256	0.157	0.221
Kenya Swara	47.5	24.8	42.0	17.7	14.9	18.8	0.218	0.216	0.199
Kenya Bongo	56.5	79.5	27.5	19.7	17.3	18.9	0.205	0.253	0.175
K7207-19	26.5	33.3	35.3	16.4	17.9	14.7	0.200	0.194	0.241
Trophy	33.3	45.8	19.5	17.7	17.9	12.8	0.198	0.213	0.230
Kenya Kuro	58.0	21.8	42.8	16.5	17.1	17.0	0.245	0.181	0.220
Kenya Tembo	28.3	62.5	41.8	15.8	18.0	18.2	0.211	0.230	0.205
R325	39.3	42.0	37.8	17.8	17.5	16.1	0.206	0.214	0.226
Largo	19.3	28.5	37.3	16.1	14.4	16.6	0.183	0.233	0.219

Continued .....

Appendix 1 continued

	R_o			T_c (Days)			r_c (Per day)		
Entry	ELD	M/N	NJO	ELD	M/N	NJO	ELD	M/N	NJO
Kenya Kanga	33.0	33.5	58.7	16.0	16.8	18.3	0.219	0.209	0.223
Kenya Zabadi	20.0	18.3	43.3	12.2	15.2	17.3	0.246	0.191	0.218
K7186-1	53.0	33.3	45.3	16.9	15.8	19.5	0.235	0.222	0.196
Fanfare	25.0	52.0	49.3	14.3	17.3	19.2	0.225	0.229	0.203
R235	41.0	39.8	49.0	17.9	15.4	18.6	0.208	0.239	0.210
K7208-1	42.3	43.8	40.0	18.9	16.6	15.8	0.198	0.228	0.234
K7000-6	32.3	32.0	23.0	15.4	14.5	15.9	0.226	0.239	0.197
K6952-1	32.5	37.5	45.3	14.2	17.7	18.0	0.246	0.205	0.212
GB5766	48.3	51.0	46.3	17.6	16.4	18.9	0.220	0.240	0.202
Kenya Nyoka	71.5	58.0	21.8	19.6	17.2	14.8	0.218	0.237	0.208
Page	52.5	32.8	32.8	17.6	14.6	17.5	0.226	0.241	0.199
K7207-21	51.5	35.0	34.5	15.7	15.8	17.1	0.252	0.225	0.207
R253	47.3	26.3	64.8	16.7	13.5	19.8	0.231	0.242	0.211
Kenya Paa	34.3	72.5	32.0	14.9	20.3	14.5	0.238	0.211	0.239
Kenya Kudu	35.8	31.0	15.3	14.1	14.8	13.4	0.254	0.232	0.203
Kenya Paka	73.3	65.8	57.3	18.9	18.0	17.7	0.229	0.233	0.229
Kenya Kifaru	67.8	54.5	59.0	19.9	16.3	17.2	0.212	0.245	0.238

There were no significant differences between the entries, greenbug clones or interactions between entries and clones for each of the three variables (R_o, T_c or r_c) at P = 0.05.

Appendix 2. Effects of the feeding of greenbug on plant height at the end of feeding period, number of tillers and grain yield at harvest, of wheat entries in tolerance studies in 1982. Means are adjusted for population of greenbug 10 days after infestation

	Height[1] (cm)		Tillers[2]		Yield (g)	
Entry	Infested	Control	Infested	Control	Infested	Control
R306	38.3	39.2	5.7	5.8	3.08	2.25
Kenya Fahari	36.7	43.8	5.3	7.0	3.18	2.51
K7002-13	36.4	38.9	5.3	4.8	4.02	3.49
Kenya Nyumbu	43.3	50.1	6.1	5.3	2.80	2.47
K7155-36	40.1	46.0	6.3	6.5	2.65	2.54
Kenya Paa	37.5	43.6	3.4	5.3	3.36	3.51
K6952-1	42.3	46.0	6.7	7.0	3.08	3.14
Africa Mayo	46.4	50.9	6.4	7.2	4.62	4.99
Kenya Paka	28.4	36.7	4.8	5.8	4.05	4.19
GB5764	44.1	51.2	14.2*	17.3	1.15	1.26
Kenya Kima	46.4	49.8	5.6	6.0	4.01	4.44
R351	35.9	39.1	3.2	4.8	3.09	3.63
K7186-1	43.7	51.6	5.4	6.3	3.90	4.15
Kenya Kulungu	37.7	38.4	7.5	7.3	2.17	2.58
Kenya Nungu	38.5	38.8	4.3	5.0	4.72	5.43
Kenya Nyati	34.8	40.9	7.1	7.0	4.04	4.24
Kenya Mamba	39.5	46.4	7.6	5.8	4.51	5.02
Fanfare	37.8	46.1	6.6	6.3	4.32	4.99
K7000-1	36.9	47.8	5.6	5.8	4.76	5.84
Kenya Swara	35.7	36.5	7.2	7.5	3.49	3.75
K7207-19	41.6	50.1	6.2	6.8	4.17	4.72
Kenya Ngiri	33.2	38.1	8.3	7.5	5.07	6.01
Kenya Kongoni	34.5	35.1	5.7	6.3	3.48	4.20
Kenya Zabadi	39.2	42.3	5.9	6.0	3.14	3.85
Kenya Kanga	35.8	42.9	6.2	7.0	3.95	4.96

Continued .....

Appendix 2 continued

	Height[1] (cm)		Tillers[2]		Yield (g)	
Entry	Infested	Control	Infested	Control	Infested	Control
K7000-6	35.2	40.8	4.5	4.8	3.20	4.16
R253	30.9	33.9	5.7	5.5	3.18	3.99
Kenya Popo	38.5	38.8	4.4	4.0	3.15	4.06
R325	38.6	38.7	5.1	5.3	4.39	5.58
R235	32.0	40.3	5.7	5.5	3.56	4.32
Leopard	38.9	40.3	8.6	8.5	3.43	4.33
Kenya Kudu	47.5	50.0	6.4	5.8	2.21	2.75
Kenya Kuro	37.4	38.3	6.9	5.0	3.16	4.03
K6940-1	38.3	46.6	5.5	5.0	4.85*	6.41
K7207-21	39.0	48.4	5.4*	7.8	3.25	4.34
Bounty	43.5	47.2	5.8	5.8	3.73*	5.14
K7208-1	32.6	38.1	7.2	7.5	3.67*	4.95
Kenya Kifaru	33.0	38.1	7.0	7.8	4.02*	5.51
Page	36.9	47.8	9.9	10.0	2.92	3.93
Trophy	35.7*	46.9	5.3	5.0	3.00	4.10
Kenya Nyoka	35.7	43.9	6.9	7.5	3.27	4.50
Kenya Kiboko	39.3	50.0	6.7	7.3	2.75	3.55
R301	36.9	42.5	4.6	4.3	3.95*	5.76
Kenya Tembo	37.5	39.5	4.1	4.8	2.87*	4.31
Hunter	39.8	46.5	9.3	7.8	1.47	2.27
Kenya Bongo	32.4	39.6	13.3*	11.3	1.26*	2.54

[1]Seedling height measured to the tip of longest leaf after 14 days of greenbug feeding.

[2]Means based on total number of tillers including those that did not yield grain.

*Mean for infested plant significantly different from that of respective control plant at P = 0.05 (one tailed t-test of contrast).

Appendix 3. Effects of three greenbug clones from Eldoret, Mau Narok and Njoro on seedling height, measured in cm to the tip of longest leaf, at the end of 14 days feeding period in 1982 studies on tolerance. Means (± standard error) not adjusted for greenbug numbers

	Greenbug clone			
Entry	Eldoret	Mau Narok	Njoro	Control
R306	38.4±1.34	36.2±2.49	34.9±1.39	39.2±1.55
Kenya Fahari	41.5±2.98	36.7±8.42	28.1±4.85	43.8±0.94
K7002-13	37.9±0.53	39.8±1.10	28.1±4.59	38.9±1.46
Kenya Nyumbu	49.1±0.39	45.9±2.10	34.2±5.64	50.1±0.92
K7155-36	44.9±3.00	46.7±1.13	28.3±4.23	46.0±3.58
Kenya Paa	41.0±1.43	34.0±5.33	34.6±4.96	43.6±0.83
K6952-1	48.0±0.71	48.6±1.18	29.8±1.81	46.0±1.34
Africa Mayo	46.4±4.19	46.3±2.80	42.5±3.50	50.1±2.24
Kenya Paka	31.7±2.68	34.1±0.55	23.3±0.97	36.7±1.44
GB5764	51.8±0.23	45.0±3.50	35.1±5.84	51.2±1.20
Kenya Kima	49.3±0.18	40.8±4.75	47.6±2.64	49.8±1.03
R351	37.8±1.11	34.8±2.62	29.5±4.64	39.1±3.03
K7186-1	48.3±6.35	52.9±0.50	33.5±4.47	51.6±2.46
Kenya Kulungu	36.5±4.20	38.6±1.64	34.3±6.20	38.4±1.60
Kenya Nungu	37.4±2.31	37.7±2.04	37.5±0.97	38.5±2.46
Kenya Nyati	40.1±5.89	36.7±7.18	34.9±0.36	40.9±3.92
Kenya Mamba	45.1±1.70	43.7±0.80	31.6±6.34	46.4±0.83
Fanfare	40.5±2.87	43.6±0.92	28.6±2.88	46.1±1.52
K7000-1	39.0±1.10	38.1±1.01	24.6±3.14	36.1±1.48
Kenya Swara	45.9±0.87	46.8±1.62	30.0±6.27	44.9±1.65
K7207-19	51.0±3.67	37.0±10.67	44.0±2.64	50.1±1.93
Kenya Ngiri	36.4±1.38	35.5±1.25	26.0±5.47	38.1±0.84
Kenya Kongoni	35.3±4.70	35.5±1.94	34.2±6.24	35.1±5.73
Kenya Zabadi	36.5±6.40	43.1±2.74	38.6±5.16	42.3±5.20
Kenya Kanga	39.9±4.18	38.3±1.42	28.7±3.75	42.9±4.57
K7000-6	39.9±1.42	35.2±6.48	27.3±5.83	40.8±1.84

Continued .....

Appendix 3 continued

Entry	Greenbug clone			
	Eldoret	Mau Narok	Njoro	Control
R253	33.0±3.76	30.2±5.12	29.3±2.60	33.9±3.04
Kenya Popo	38.2±4.30	38.5±4.38	37.9±4.17	38.5±2.59
R325	39.5±0.96	39.6±1.00	33.5±1.37	38.6±0.88
R235	36.2±2.62	36.4±4.83	28.1±0.83	40.3±0.97
Leopard	40.1±2.22	41.0±1.83	36.5±3.03	40.3±1.66
Kenya Kudu	50.5±2.73	48.5±1.16	45.4±4.30	51.0±1.50
Kenya Kuro	40.7±4.87	34.4±10.23	42.0±5.42	37.4±4.62
K6940-1	43.1±3.82	43.0±3.34	28.6±2.80	46.6±3.12
K7207-21	45.4±5.23	36.1±7.45	35.4±8.26	48.4±1.18
Bounty	44.6±2.03	45.4±1.88	37.3±2.31	47.3±2.92
K7208-1	36.0±2.26	40.1±1.63	21.2±1.64	38.1±2.57
Kenya Kifaru	34.1±1.12	36.5±1.76	26.9±1.45	38.2±0.44
Page	42.5±1.47	41.2±1.94	27.7±2.60	47.8±3.41
Trophy	41.6±2.01	40.9±4.92	24.8±7.80	46.9±1.03
Kenya Nyoka	41.5±3.08	40.9±1.13	25.1±1.81	43.9±0.87
Kenya Kiboko	46.1±1.66	47.0±1.78	29.6±4.08	50.0±1.17
R301	39.8±1.40	42.0±1.31	25.5±2.98	42.5±1.53
Kenya Tembo	39.1±1.85	37.8±1.36	33.8±2.73	39.5±0.61
Hunter	44.4±1.11	45.8±2.04	35.6±3.16	46.5±1.50
Kenya Bongo	29.5±8.74	38.1±1.30	26.9±2.54	39.6±0.83

Appendix 4. Effects of three greenbug clones from Eldoret, Mau Narok and Njoro on production of tillers by wheat entries in 1982 tolerance studies. Mean ± standard error, of four plants not adjusted for greenbug numbers

	Greenbug clone			
Entry	Eldoret	Mau Narok	Njoro	Control
R306	5.5±0.65	5.5±1.04	6.8±0.48	5.8±1.25
Kenya Fahari	4.0±1.29	5.5±1.26	6.8±1.18	7.0±0.71
K7002-13	5.8±0.48	5.0±0.41	5.5±0.50	4.8±0.63
Kenya Nyumbu	6.3±0.63	6.5±0.29	5.8±0.25	5.3±0.25
K7155-36	8.0±0.91	6.0±0.71	5.0±0.41	6.5±0.87
Kenya Paa	3.5±0.50	3.3±0.25	4.0±0.00	5.3±0.48
K6952±-1	6.3±0.63	7.5±0.65	6.3±0.25	7.0±0.41
Africa Mayo	8.0±0.41	6.5±0.50	5.0±0.58	7.3±0.48
Kenya Paka	4.8±0.75	5.0±0.41	4.3±0.48	5.8±0.48
GB57464	12.8±2.87	15.0±1.00	15.0±0.178	17.3±2.39
Kenya Kima	5.5±0.65	5.0±0.65	6.0±0.41	6.0±0.71
R351	3.8±0.48	3.8±0.48	2.8±0.25	4.8±0.75
K7186-1	5.0±0.41	5.0±0.41	5.8±0.63	6.3±0.48
Kenya Kulungu	7.3±0.48	7.3±0.63	8.3±0.85	7.3±0.48
Kenya Nungu	4.3±0.25	4.8±0.48	4.3±0.25	5.0±0.00
Kenya Nyati	8.8±0.25	6.0±1.87	5.8±0.48	7.0±0.58
Kenya Mamba	8.3±0.25	7.5±0.50	7.0±0.82	5.8±0.48
Fanfare	7.3±0.85	6.8±0.48	7.3±0.48	6.3±0.48
K7000-1	6.3±0.71	5.5±0.29	5.8±0.63	5.8±0.48
Kenya Swara	7.8±1.11	6.5±0.29	6.5±0.96	7.5±0.96
K7207-19	5.3±0.25	6.3±1.44	6.5±0.65	6.8±1.75
Kenya Ngiri	8.5±0.96	8.3±1.44	8.3±0.75	7.5±0.65
Kenya Kongoni	5.8±0.85	6.3±0.85	5.0±0.00	6.3±0.25
Kenya Zabadi	6.3±0.48	6.3±0.63	5.3±0.48	6.0±0.41
Kenya Kanga	6.0±0.91	6.3±0.75	6.5±0.29	7.0±1.94

Continued .....

Appendix 4 continued

	Greenbug clone			
Entry	Eldoret	Mau Narok	Njoro	Control
K7000-6	5.0±0.41	4.0±1.00	4.8±0.25	4.8±0.48
R353	5.5±0.29	5.3±0.48	6.3±0.25	5.5±0.65
Kenya Popo	4.5±0.29	4.5±0.50	4.3±0.25	4.0±1.08
R325	4.8±0.48	5.5±0.50	5.0±1.00	5.3±0.48
R235	5.5±0.65	6.3±0.85	4.8±1.03	5.5±0.65
Leopard	8.8±0.95	8.3±0.25	8.5±0.50	8.5±0.87
Kenya Kudu	6.5±0.87	5.8±1.11	6.8±0.95	5.8±0.95
Kenya Kuro	7.8±0.48	5.3±0.48	7.5±0.50	5.0±0.71
K6940-1	6.0±0.91	6.0±0.91	4.5±0.29	5.0±0.41
K7207-21	5.5±1.55	3.5±1.44	7.3±0.48	7.8±1.03
Bounty	6.5±0.87	5.3±0.48	6.3±0.71	5.8±0.25
K7208-1	7.5±0.87	6.5±0.95	7.8±1.44	7.5±0.87
Kenya Kifaru	6.8±0.85	7.8±0.25	6.8±0.48	7.8±0.63
Page	11.3±1.80	10.0±0.58	8.5±0.50	10.0±0.41
Trophy	6.5±1.19	5.3±1.03	4.3±1.18	5.0±0.41
Kenya Nyoka	8.0±1.00	6.8±0.75	6.0±0.41	7.5±1.50
Kenya Kiboko	5.8±1.11	6.3±1.32	8.5±0.29	7.3±0.48
R301	5.3±0.63	4.5±0.65	4.3±0.25	4.3±0.48
Kenya Tembo	4.5±0.29	3.8±0.48	4.5±0.65	4.8±0.25
Hunter	9.8±1.44	8.8±1.93	9.0±1.53	7.8±1.03
Kenya Bongo	13.0±1.08	13.0±0.82	13.3±1.32	11.3±0.63

Appendix 5. Effects of three greenbug clones from Eldoret, Mau Narok and Njoro on grain yield (g) of wheat entries tested for tolerance in 1982. Mean ± standard error, of four plants, not adjusted for greenbug numbers

	Greenbug clone			
Entry	Eldoret	Mau Narok	Njoro	Control
R306	3.8±1.12	2.9±0.32	3.8±1.26	2.3±0.66
Kenya Fahari	3.0±0.52	3.5±0.32	3.6±0.32	2.5±0.28
K7002-13	4.5±0.42	4.3±0.26	3.7±0.64	3.5±0.48
Kenya Nyumbu	3.4±0.42	2.6±0.24	2.5±0.40	2.5±0.62
K7155-36	3.3±1.02	2.4±0.50	2.3±0.58	2.5±0.16
Kenya Paa	3.7±0.44	2.3±0.38	4.5±1.22	3.5±0.20
K6952-1	3.3±0.26	3.1±0.28	2.9±0.30	3.1±0.44
Africa Mayo	4.8±0.30	4.8±0.50	4.7±0.82	5.0±0.68
Kenya Paka	3.3±1.02	3.6±0.66	4.5±0.50	4.2±0.14
GB5764	1.9±0.72	1.1±0.54	0.57±0.36	1.3±0.30
Kenya Kima	4.3±0.22	3.4±0.24	4.5±0.28	4.4±0.50
R351	4.0±0.20	3.2±1.00	2.8±0.80	3.6±0.26
K7186-1	4.3±0.42	4.1±0.96	2.9±1.22	4.2±0.82
Kenya Kulungu	2.1±0.48	3.0±0.60	1.9±0.40	2.6±0.58
Kenya Nungu	5.5±0.22	5.0±0.20	4.2±0.16	5.4±0.42
Kenya Nyati	3.9±0.52	3.0±0.46	4.4±0.58	4.2±0.44
Kenya Mamba	4.9±0.28	3.8±0.54	4.6±0.42	5.0±0.12
Fanfare	3.6±0.68	4.7±1.00	4.7±1.00	5.0±0.54
K7000-1	5.4±0.48	5.8±0.24	3.8±0.96	5.8±0.70
Kenya Swara	4.2±0.58	3.2±1.32	3.1±0.68	3.8±0.32
K7207-19	3.8±0.62	2.8±0.70	5.2±1.42	4.7±0.34
Kenya Ngiri	5.0±0.40	5.2±0.20	4.6±0.56	6.0±0.44
Kenya Kongoni	4.4±0.48	3.2±0.44	2.7±0.56	4.2±0.70
Kenya Zabadi	3.7±0.54	3.3±0.44	2.4±0.78	3.9±0.44
Kenya Kanga	3.4±0.30	3.7±0.56	4.9±0.82	5.0±0.36

Continued .....

Appendix 5 continued

Entry	Greenbug clone			
	Eldoret	Mau Narok	Njoro	Control
K7000-6	3.4±0.46	3.4±0.50	3.3±0.90	4.2±0.26
R253	3.8±0.58	1.9±0.90	3.9±0.36	4.0±0.54
Kenya Popo	4.0±0.58	1.9±0.78	3.8±1.22	4.1±0.54
R325	5.6±0.24	4.3±0.56	4.4±0.78	4.6±0.48
R235	3.1±0.78	3.8±0.50	3.2±0.20	4.3±0.90
Leopard	4.1±0.18	2.7±0.78	3.3±0.60	4.3±0.28
Kenya Kudu	2.6±0.34	1.6±0.58	2.3±0.56	2.8±0.52
Kenya Kuro	3.4±0.30	2.3±0.30	3.5±0.40	4.0±0.36
K6940-1	5.1±0.30	4.9±0.96	4.7±1.26	6.4±0.82
K7207-21	4.9±0.52	1.6±1.18	3.4±0.90	4.3±0.28
Bounty	3.5±0.72	4.3±0.26	3.8±0.82	5.1±0.52
K7208-1	4.3±0.98	4.5±0.40	2.2±0.82	5.0±0.32
Kenya Kifaru	4.1±0.66	3.5±0.74	4.6±0.12	5.5±0.10
Page	2.6±0.66	4.2±0.62	2.9±0.96	3.9±0.42
Trophy	4.3±0.74	2.6±0.82	2.1±0.80	4.1±0.86
Kenya Nyoka	3.3±0.60	3.6±0.44	2.9±0.14	4.5±0.20
Kenya Kiboko	2.6±0.12	2.9±0.52	1.3±0.22	3.6±0.54
R301	4.1±0.52	4.8±0.18	3.4±0.90	5.8±0.18
Kenya Tembo	2.3±0.62	3.5±0.24	3.1±0.70	4.3±0.20
Hunter	1.1±0.90	1.4±0.38	1.5±0.80	2.3±0.74
Kenya Bongo	1.6±0.66	0.8±0.72	1.4±0.74	2.5±0.74

CHAPTER III

Part II

Flight periods of greenbug, *Schizaphis graminum* (Rondani) (Homoptera:Aphididae), and development of infestations on wheat crops in Kenya

by

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Flight periods of greenbug, *Schizaphis graminum* (Rondani) (Homoptera:Aphididae), and development of infestations on wheat crops in Kenya

ABSTRACT

Greenbugs, *Schizaphis graminum* (Rondani), were not captured in yellow water traps placed in a field of wheat that they invaded in 1982 at Njoro in Kenya. Clear sticky traps, used from August 1983 to July 1985, were effective in catching airborne greenbugs. The annual pattern of greenbug flight activity was classified into two periods associated with rainy seasons. 1. June-September when catches were numerous and peaked in July or August, 2. October-February or March, when catches were low. No greenbugs were caught between March and May. The numbers caught at 1.5, 3.0, 4.5 and 6 m diminished with height during August-September 1983, and during the October 1983-March 1984 flight periods but not at other times. More greenbugs were caught in wet years (1983 and 1985) than in the dry year (1984).

Arrival of greenbugs on a crop was not always followed by a rapid population increase, and in one field greenbug population became locally extinct. Precipitation seemed to influence the rate of population increase of greenbugs on wheat. It is recommended that late planting of wheat (late May-June) be avoided so that the vulnerable seedling stage is passed before greenbugs appear in June or July.

Les périodes de vols du puceron vert des graminées Schizaphis graminum Rondani (Homoptera:Aphididae) et le développement des infestations des récoltes de blé au Kenya.

RÉSUMÉ

Les pucerons verts des graminées, Schizaphis graminum (Rondani), qui envahirent un champ de blé à Njoro au Kenya en 1982, ne furent pas capturés dans des trappes d'eau jaunes qui étaient placées dans le champ. Des trappes claires et collantes, utilisées depuis août 1983 à juillet 1985 furent efficaces pour attraper les pucerons verts des graminées qui sont aéroportés. Le patron de vol annuel du puceron vert des graminées fut classifié en deux périodes associées avec les saisons pluvieuses: 1. Juin à septembre, lorsque les prises étaient nombreuses et la période de pointe était en juillet ou août, 2. Octobre à février ou mars, lorsque les prises étaient peu nombreuses. Aucun puceron vert des graminées ne fut attrapé entre la période de mars à mai. La quantité attrapée à 1.5, 3.0, 4.5 et 6 mètres diminua avec l'élévation pendant août à septembre 1983, et pendant la période de vol d'octobre 1983 à mars 1984, mais ne diminua pas pendant les autres périodes. Plus de pucerons verts des graminées furent attrapés pendant les années pluvieuses (1983 et 1985) que pendant l'année sèche (1984).

L'arrivée des pucerons verts des graminées sur la récolte n'était pas toujours suivie par une augmentation rapide de la population et dans un champ la population des pucerons fut détruite dans la localité. La précipitation semblait influencer le taux d'augmentation de la population des pucerons verts des graminés sur le blé. Il est recommandé d'éviter la plantation tardive de blé (fin mai-juin) afin que la phase du vulnérable semis soit passée avant que les pucerons verts des graminées apparaissent en juin ou juillet.

INTRODUCTION

Greenbugs, *Schizaphis graminum* (Rondani), can fly long distances before invading crops (Kieckhefer et al., 1974). For example, mass movement of greenbugs from the southern United States, considered to be migration (Johnson, 1969) is the probable cause of outbreaks of greenbug in the northern United States and Canada (Robinson and Hsu, 1963; Berry and Taylor, 1968; Taylor and Palmer, 1972). The distance over which greenbugs fly ranges from a few metres to several hundred kilometres (Taylor and Palmer, 1972). Migrating greenbugs have been sampled in low-level jet streams blowing at heights between 500-1000 m (Berry and Taylor, 1968). It is suggested that aphids may fly for up to 36h (Taylor and Palmer, 1972).

Various traps have been used for monitoring aphids, e.g. yellow water traps (Moerike traps) for catching landing aphids (Eastop, 1957), suction traps such as the Rothamsted insect survey trap sampling airborne aphids (Taylor, 1977), and sticky traps catching both landing and migrating aphids (Broadbent, 1948; Heathcote, 1966). There are conflicting reports regarding the response of greenbugs to yellow traps. Taylor and Palmer (1972) suggested that greenbugs are not attracted to yellow while other authors report that they are attracted to yellow (Roach and Agee, 1972; Harvey et al., 1982).

Information on greenbug movements has been used to predict infestations and to provide recommendations on planting dates for wheat and sorghum (Kieckhefer et al., 1974; Harvey et al., 1982). Despite frequent outbreaks of greenbug on wheat in Kenya (Wanjama, 1979), the flight periods of this aphid are not known. Such information would be

useful for predicting periods of possible high infestation, and establishing planting dates to avoid extensive damage to seedling wheat. The objectives of this study were to find a convenient method for monitoring greenbug, to determine greenbug flight periods, and to investigate the pattern of development of infestations on young wheat crops.

MATERIALS AND METHODS

A 12 ha field at the National Plant Breeding Station, Njoro, Kenya was seeded with the wheat variety Kenya Ngiri, on June 8, 1982. About one week later, 18 yellow water traps (cans 15 cm diameter and 5 cm deep) were placed 30 m apart in three rows 30 m apart. Each trap was placed on a stage 1 m above the ground and partly filled with soap solution (Teepol$^{(R)}$) (Broadbent, 1948; Evans and Medler, 1966). Traps were examined every 2-3 days, and captured aphids taken to the laboratory for identification. Plants in the same field were searched, and sweep net samples taken, to determine whether greenbugs were present in the field.

Between August 1983 and July 1985 sticky traps were used to catch flying greenbugs. Wire-supported polyethylene rectangles 10 x 15 cm were covered on both sides with Tanglefoot$^{(R)}$. At each trapping height four rectangles were held vertically radiating at 90^{o} intervals from a central pole. Trapping heights were 1.5, 3.0, 4.5 and 6 m above the ground. The sticky surfaces could be raised and lowered on the pole by a rope and pulley so that aphids could be removed. Four such trap assemblies were erected in the field, forming a square 200 x 200 m. Aphids were removed from the traps three times a week. Weekly total catches for each flight period were subjected to analysis of variance to determine whether catch was dependent on height.

In 1983, observations on the build up of greenbug populations were made in two fields. A 30 x 200 m strip of wheat, variety Leopard, was planted on June 27th. Five transects each across 100 rows were marked so that transects were 30 m apart. On each sampling date, 10 plants

from each transect were selected randomly and searched in situ for greenbugs.

The second field was planted on October 28th with six wheat entries including local varieties (Kenya Fahari, Kenya Kiboko, Kenya Kifaru and Africa Mayo), one plant introduction (R306) and one local breeder's line (K7002-13). These were planted in a randomized complete block design with four blocks each containing six plots 1.5 x 6 m. There was no adequate rain at the time of planting and overhead irrigation was applied on 29th October, one day after seeding, then on 4th, 11th and 19th November. Five plants taken randomly in each plot were searched in situ for greenbugs each week.

Rainfall records were obtained from the weather station at the National Plant Breeding Station, Njoro.

RESULTS

Yellow water traps attracted other aphid species but not *S. graminum* (Table 1). Direct observations of the crop, and sweep net sampling indicated that a large number of greenbugs had colonised the young plants in the field.

The catches of greenbugs on sticky traps between August 1983 and July 1985 are shown in Figure 1. There are two rainfall seasons in Kenya; the "long rains" season (March to May) and "short rains" season (October to December (Morris and Freeman, 1965). Three flight patterns were found to be influenced by the rainy seasons. Two flight periods may be distinguished: 1. June-September, with a peak in July/August, and 2. October-February/March. There are no greenbugs flying between March and May. A linear relationship of catch with trapping heights was significant for two periods, August-September 1983 and October 1983-March 1984, when catches decreased with increasing trapping height (Table 2). A field adjacent to the trapping field was under an irrigated wheat crop during the latter period and supported an infestation of greenbugs. This may have influenced the trap catches and contributed to the prolonged flight activity (up to mid March 1984) as compared to the same period in 1984-85 when no greenbugs were caught after mid February (Figure 1).

In the first field crop (Figure 2), the greenbug population increased from July 12-28 and then declined to extinction by August 13. There were heavy rains during the period of sampling and this may account for the slow population growth and subsequent decline.

In the second field crop (Figure 3), planted with six wheat entries, the population ofthe greenbugs increased gradually from the third week of November to the first week of December. The number of greenbugs dropped in mid-December and again in the first week of January.

DISCUSSION

Yellow water traps undoubtedly catch a wide range of aphid species (Eastop, 1957; Gonzalez and Rawlins, 1968), but there is no evidence that *S. graminum* is caught in such traps. Yellow water traps did not attract any greenbugs in this study even when immigrants of this species had landed on young wheat in the same field. Where greenbugs have been reported to be attracted by yellow in the field, sticky traps have been used (Roach and Agee, 1972; Harvey et al., 1982). The effects of attraction to colour and of impaction of flying greenbugs on the traps may not be easily differentiated in such cases. Even where different colours are provided for the sticky traps (Roach and Agee, 1972), indifference to some colours and avoidance of others can easily be misinterpreted as attraction and lack of attraction respectively. The sticky traps used in this study were effective in catching flying greenbugs. Because traps were almost transparent, it is probable that greenbugs were intercepted by, rather than attracted to them.

Aerial densities of insects are known to decrease with increasing height (Johnson, 1969), but during the periods of greenbug flight, a decrease in catch with increasing trapping height was significant only for two flight periods, August-September 1983 and October 1983-March 1984 (Table 2). This may indicate that for most of the times the greenbugs caught on these traps are flying above the boundary layer. Aphids are capable of flights below boundary layer only in calm conditions (Taylor and Palmer, 1972).

January to March is the dry season with sparse vegetation, and no greenbugs were caught in the following two months (April and May). In years of abundant rainfall (1983 and 1985) 55 greenbugs or more were caught weekly in July or August, but in the dry year (1984) weekly catches were lower than five (Figure 1). This probably means that the density of migrants in the June-September period is dependent upon populations building up to densities at which alatae are produced on the available vegetation. In dry years there is little vegetation, and perhaps rates of increase are reduced by poor host quality (Eastop, 1983).

Wheat crops planted from late May-June are likely to be at the vulnerable seedling stage should the greenbugs appear in June or July. Harvey et al. (1982) recommended that early planting in spring be avoided in Kansas in order to avoid having wheat or sorghum at the vulnerable seedling stage when the early spring greenbug migrants reach Kansas. In Kenya, as a result of this study, we recommend that late planting of wheat around Njoro be avoided so that the crop can escape heavy greenbug infestation at the seedling stage. The "long rains" season starts at the end of March or beginning of April and most of the planting is done in April although planting may continue up to June. The time lag from onset of rains to the first appearance of greenbugs is long enough for an early planted crop (planted in April) to escape infestation in the vulnerable seedling stage.

The greenbug of the first flight period infested Leopard wheat in July 1983. Although the infestation was low its timing shows that short term prediction may be possible from the flight pattern. In one field study of antixenosis of wheat to greenbug in 1985 (Wanjama and Holliday,

1986a) infestation was first noticed during the third week of July; the third week after the first greenbug catch on the sticky traps. The infestation in November/December 1983 could also have been predicted from the trap catches. Greenbugs were caught, though in low numbers, at the time of planting (third week of October). The build up of infestation was slow at first probably for the same reason that the immigrants landing on the crop were few. Therefore, although the trapping period was short, there is evidence that trap data on greenbug catches can be used to predict infestations.

Table 1. Mean (± standard error) number of aphids per trap caught in yellow water traps weekly in 1982

Aphids	June 10-17	June 17-24	June 24 -July 1	July 1-8
Total	4.8±0.66	3.8±0.57	1.5±0.34	2.0±0.36
S. graminum	0	0	0	0

Table 2. Mean greenbug catches per four rectangles during each flight season

Period	Height (m)				Significance of regression
	1.5	3.0	4.5	6.0	
August-September 1983	110	115	77	56	$P<0.05$
October 1983-March 1984	20	18	15	11	$P<0.05$
July-September 1984	2	3	1	2	NS
October 1984-February 1985	11	11	12	11	NS
June-July 1985	14	16	13	15	NS

Figure 1. Total number of greenbug caught each week on sticky trap (o---o) and monthly rainfall (histogram bars) at the National Plant Breeding Station, Njoro, Kenya. Trapping took place from August 1983 - July 1985.

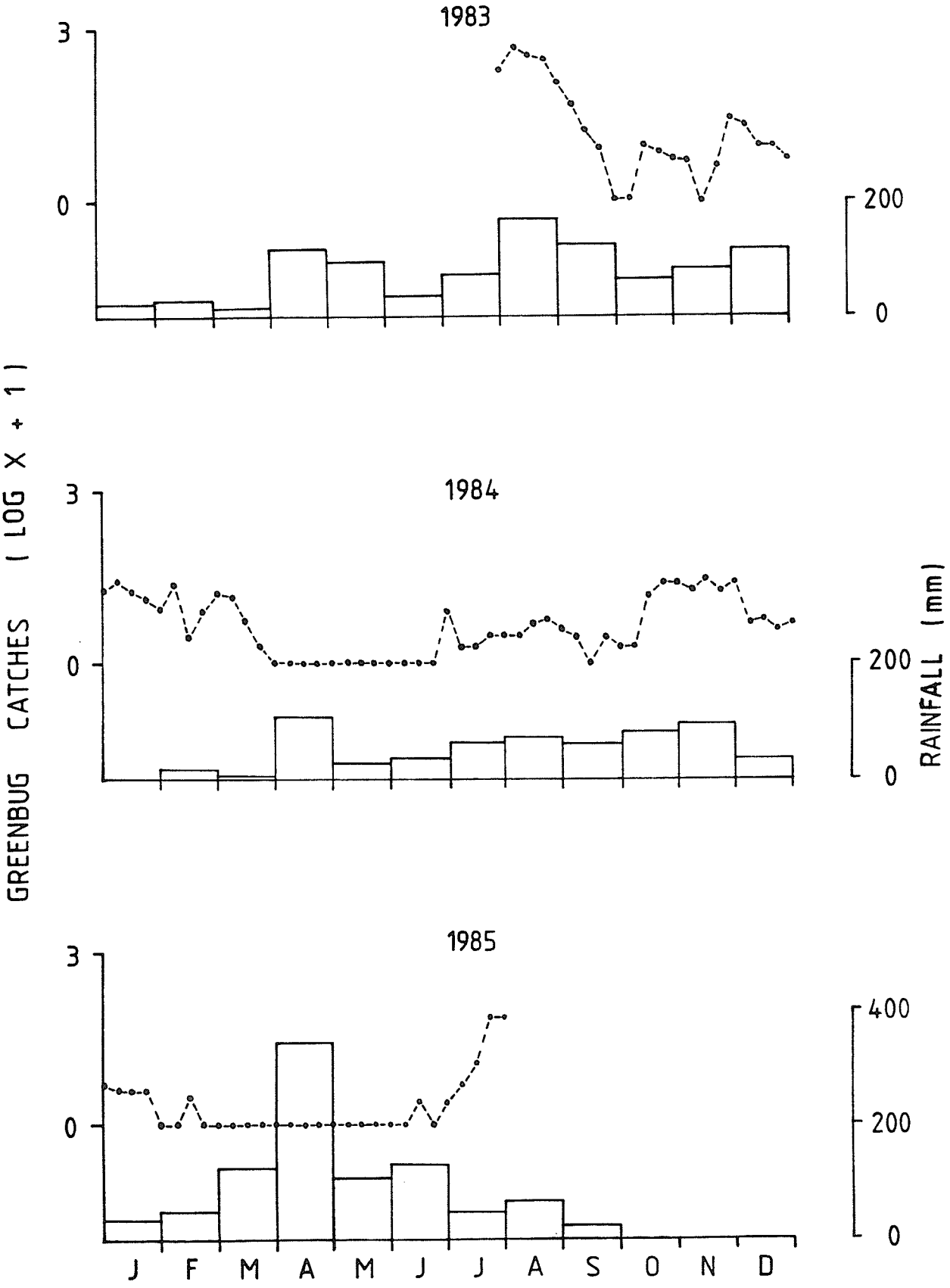

1983
1984
1985
3
0
200
0
400
GREENBUG CATCHES (LOG X + 1)
RAINFALL (mm)
J F M A M J J A S O N D

Figure 2. Mean (± standard error) of greenbugs/plant (o---o) recorded on wheat variety Leopard in the field in 1983, and the rainfall (histogram bars) for the week preceding each sampling, recorded at the National Plant Breeding Station, Njoro, Kenya.

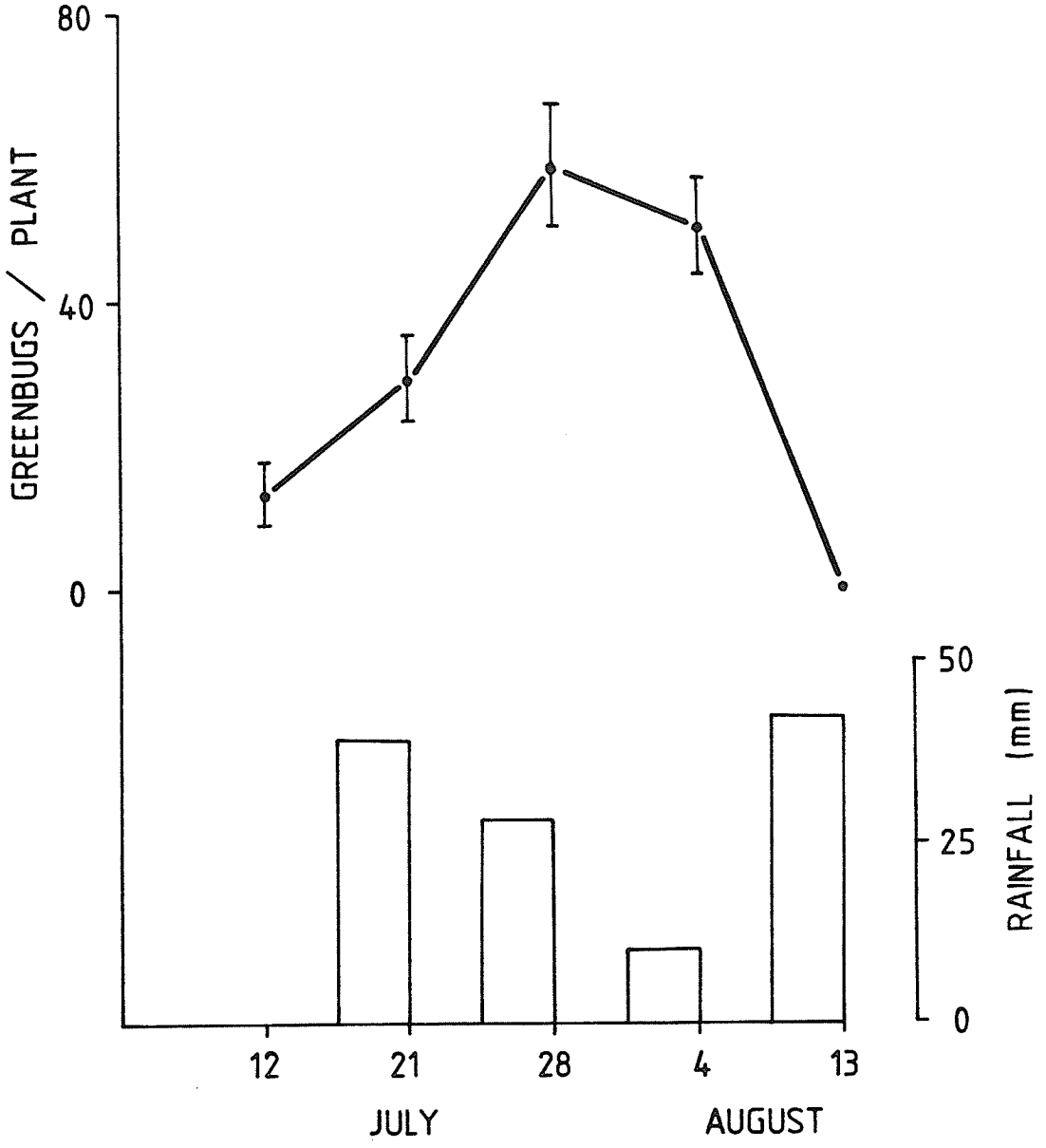
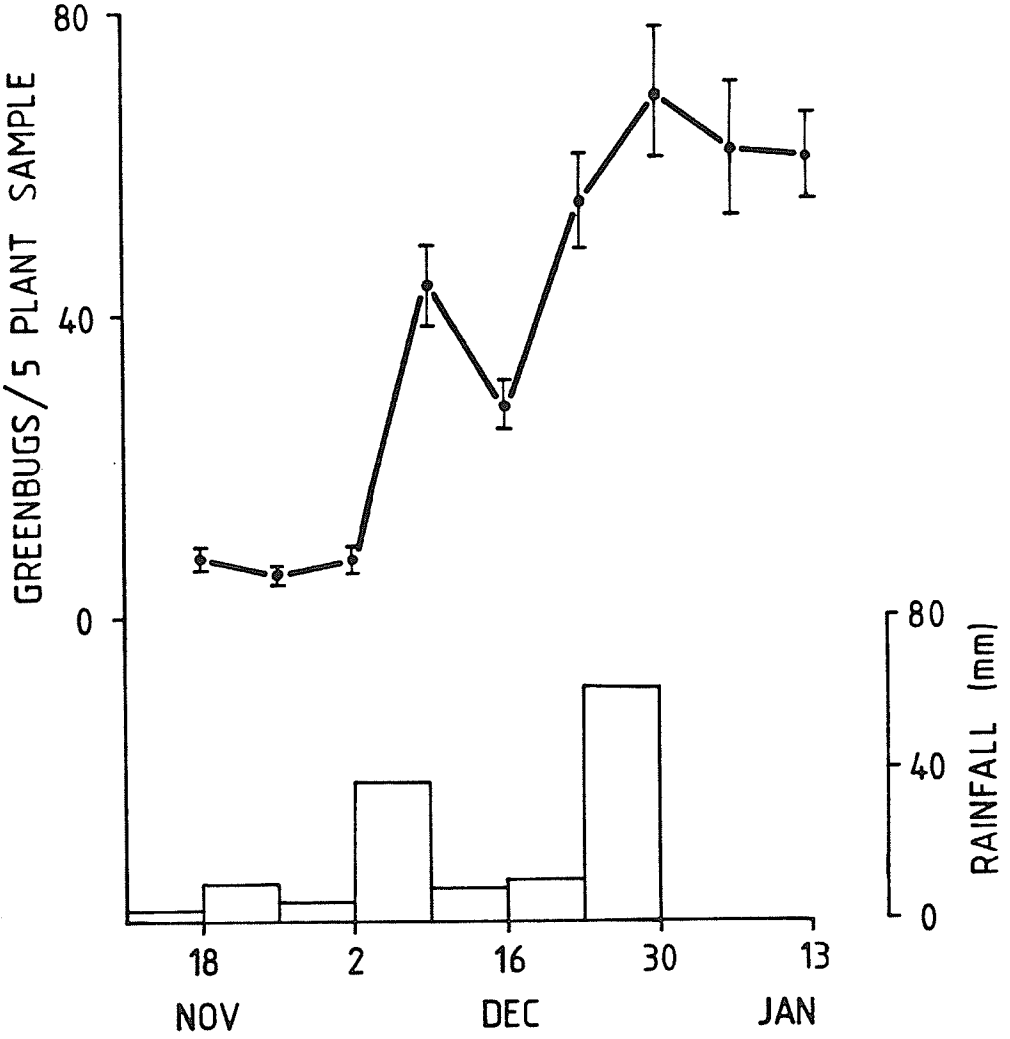

80
40
0
GREENBUGS / PLANT
50
25
0
RAINFALL (mm)
12
21
28
4
13
JULY
AUGUST

Figure 3. Mean (± standard error) number of greenbugs counted on six wheat entries each week in the field in 1983 (o---o) and rainfall (histogram bars) for the week preceding each sampling.


80
40
0
GREENBUGS/5 PLANT SAMPLE
80
40
0
RAINFALL (mm)
18
2
16
30
13
NOV
DEC
JAN

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CHAPTER III

Part III

Variation among greenbugs from different localities in Kenya

by

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Variation Among Greenbugs From Different Localities in Kenya

ABSTRACT

Wheat fields infested with greenbugs, *Schizaphis graminum* Rondani were sampled in 1983 and 1985; from each field a single parthenogenetic female was used to start a separate clone in a greenhouse culture. Using seedlings of wheat, variety Kenya Kifaru, reproductive performance and longevity of each clone were determined. Significant differences in the capacity for increase (r_c) were found among greenbug clones that were tested in 1983 ($P<0.001$); the intraclass correlation in 1983 (the proportion of variance which was genetically determined) was $r_I = 0.59$; with 90% confidence limits of 0.297 to 0.810. In 1985, there were no significant differences among clones in r_c ($P>0.10$) and intraclass correlation was, $r_I = 0.065$ with 90% confidence limits of 0 to 0.228. It is suggested that selection occurred during the drought year of 1984 and that this reduced heterogeneity within the greenbug population. Heterogeneity of clones might be increased by mutation or by the influence of migrants.

La variation parmi les pucerons verts des graminées venant de différentes localités du Kenya

Resumé

Des échantillons furent pris de champs de blé infestés de pucerons verts des graminées, Schizaphis graminum (Rondani) en 1983 et en 1985; une seule femelle parthénogénétique fut utilisée pour commencer un total de 16 clones de serres séparés. En utilisant des semis de blé de la variété Kenya Kifaru, la performance reproductive et la longévité de chaque clone ont pu être déterminées. Des différences significatives dans la possibilité d'augmentation (r_c) furent trouvées parmi les clones des pucerons verts des graminées qui furent mis à l'épreuve en 1983 ($P<0.001$); la corrélation interne en 1983 (la proportion de contradiction qui fut déterminée génétiquement) était $r_I=0.59$; avec des limites de confiance de 90%, de 0.297 à 0.810. En 1985, il n'y avait aucune différence significative parmi les clones en r_c ($P>0.10$) et la corrélation interne était $r_I=0.065$ avec des limites de confiance de 90% de 0 à 0.228. Il y a raison de croire que la sélection a eu lieu pendant l'année sèche de 1984 et que cela a réduit l'hétérogénéité parmi la population des pucerons verts des graminées. L'hétérogénéité des clones peut être augmentée par la mutation ou par l'influence des migrateurs.

INTRODUCTION

The greenbug, *Schizaphis graminum* (Rondani), is believed to undergo continuous parthenogenesis in the tropics (Eastop, 1983). In the temperate regions, where sexuales are known to occur, it was for a long time thought that their eggs never hatch (Washburn, 1908; Mayo and Starks, 1972; Purteka and Slosser, 1983). But it has been reported that greenbug eggs can overwinter and hatch in spring (Niemczyk and Power, 1982). In aphid species where sporadic parthenogenesis occurs, new genotypes are produced each time sexual reproduction takes place (Dixon, 1985a, b). Subsequent aphid populations are therefore comprised of a number of genetically different clones. In areas where continuous parthenogenesis in aphids occurs, appearance of new clones in the population is through genetic mutation (Blackman, 1979).

An invasion of cereal crops by greenbugs sometimes results from long distance migration of windborne greenbugs (Kieckhefer et al., 1974). Therefore new genotypes may be introduced to a habitat from other areas where sexual reproduction may have taken place.

Variability in greenbug populations in Kenya has not been investigated. Studies were therefore undertaken to investigate whether clones with different characteristics are found within the greenbug population. The studies were conducted at the National Plant Breeding Station, Njoro, Kenya.

MATERIALS AND METHODS

Greenbugs were collected from wheat fields around Njoro, Kenya (0.15°S and 35.5°E, at 2,100 m a.s.l.) with a minimum distance of 5 km between any two fields. In the greenhouse, greenbugs from each field were separately placed on caged potted plants (caged prior to emergence to avoid contamination). One adult female was taken from each sample to start a clone which was maintained on caged potted wheat seedlings in a separate greenhouse.

Wheat seedlings were raised in plant pots and were thinned to one/pot at growth stage 12 (GS 12) (Zadoks et al., 1974; Tottman and Makepeace, 1979). Apterous adults were taken from each clone and placed singly on potted seedlings and left for 24 h to larviposit and then removed. All but one nymph were removed after 4 days, and the remaining nymph observed daily until it matured and started to reproduce. The offspring were counted and removed every two or three days until reproduction stopped or the reproducing female died.

In 1983, greenbugs were collected from 10 fields. One wheat variety, Kenya Kifaru, was used to test the 10 clones that were raised from the 10 field populations. At GS 12 each clone was introduced onto wheat seedlings in four replicates.

In 1985, six greenbug populations were tested using Kenya Kifaru; each clone was observed on nine seedlings. Tests with the six clones were also done using five other wheat varieties, Kenya Kiboko, Kenya Kima, Kenya Kulungu, Leopard and Kenya Paka.

The data for each year were used to construct life tables using

life schedules of individual greenbugs, in order to portion the genetic components of variation. Lenski and Service (1982) have shown that estimates of population growth rate based on few cohorts of many individuals may be more biased than those based on life schedules of individuals making the cohort. The net reproductive rate (R_o), mean generation time (T_c) and capacity for increase (r_c) were then computed.

$$R_o = \Sigma l_x m_x$$

where l_x is the proportion of live adults at each sampling and m_x is the age specific reproduction (Laughlin, 1965). The T_c is the age, in days, when 50% of the offspring are produced, and

$$r_c = \log_e R_o / T_c$$

The values for R_o, T_c and r_c were subjected to analysis of variance and the variation due to environmental and genetic components differentiated by using Model II analysis of variance (Wald, 1940; Snedecor and Cochran, 1980). The intraclass correlation coefficients (r_I) were computed for each parameter and 90% confidence limits determined.

RESULTS

The greenbug clones tested in 1983 showed significant differences in r_c but not in R_o, T_c or longevity (Table 1). The correlation was positive and significant between R_o and r_c ($r = 0.88$, 8 df $P<0.05$), negative and significant between T_c and r_c ($r = -0.69$, 8 df $P<0.05$) and negative and nonsignificant between R_o and T_c ($r = -0.39$, 8 df $P>0.05$). The nonsignificant negative relationship of R_o and T_c may explain why there are significant differences in r_c and not in R_o or T_c: reducing T_c and increasing R_o both increase r_c and vice versa. Longevity was not correlated with higher r_c ($r = -0.17$, 8 df $P>0.05$).

In 1985, there were no significant differences in any of the parameters, R_o, T_c, r_c or longevity, among the six greenbug clones that were tested on Kenya Kifaru, (Table 2), nor in the respective parameters for those greenbugs feeding on the other five varieties (Appendix 1). In all these cases genetic components of variance were not significantly greater than those due to environment (within clone) (Table 3). The 90% confidence limits for r_I for r_c for greenbugs feeding on Kenya Kifaru were 0.297 to 0.810 in 1983 and 0 to 0.228 in 1985.

DISCUSSION

The term clone, as used in aphid literature, refers to the progeny of a single parthenogenetic female (Eastop, 1973). The capacity for increase, r_c, varied significantly for greenbug clones tested in 1983 (Table 1). The importance of r_c in determining the rate of population growth of greenbugs feeding on different wheat varieties has been demonstrated by Wanjama and Holliday (1986a). The greenbugs tested in 1983 and 1985 originated from the same area and the lack of significant differences among clones in 1985 probably suggests that a homogeneous population inhabited the same area in the latter year. Results obtained with three greenbug clones in 1982 (from Wanjama and Holliday, 1986a) also showed no significant differences, although they were collected from the field in February (during the dry season) and tested in June and only one clone originated from Njoro. The 90% confidence limits for r_I based on r_c for the 1983 and 1985 do not overlap, indicating that the probability that the r_I of the populations in the two years is the same and is less than 0.10. It is therefore apparent that greenbug populations in Kenya may be homogeneous in some years and heterogeneous in other years.

A number of hypotheses could be advanced to explain the variation shown by these results. The first hypothesis is that differences were due to some statistical artifact that lead to the rejection or acceptance of the null hypothesis in the earlier or later years respectively. Even in a population that is expected to be homogeneous, there is a chance that some deviants will occur and the most deviant of these may mislead

one to believe that there is variation (Sokal and Rohlf, 1981). However the results for 1983 were significant at $P<0.001$ which indicates that the probability of a type I error is very small.

A second hypothesis is that the differences may be attributed to differences in experimental procedure followed in the two years. The greenbugs were obtained from the fields in June and experiments run in September/October during the two years. Observations were made separately for individual greenbugs except there were four individuals for each clone in 1983 and 10 in 1985. The environmental components of variance in 1983 and 1985 (0.00084 and 0.00077) were very similar (Table 3) which suggests that the differences in the results of the two years were due to genetic variation of the greenbugs.

The last hypothesis is that variation in the clones comprising greenbug populations does indeed occur from one year to another and that the results obtained represent a real situation in regard to field greenbug populations in Kenya and is more plausible. At the end of a growing season, aphid mortality is very high (Dixon, 1985b) and for greenbugs the dry season in the tropics (January to March in Kenya) is passed in available patches of green vegetation (Eastop, 1983) which may be assumed to diminish with increasing severity of drought. Therefore selection may be more intense in very dry years, for example 1984 (Wanjama and Holliday, 1986b), with a consequence that greenbug populations are more homogeneous in the following year (e.g. 1985, Table 2). There is no evidence that sexual reproduction in aphids occurs in the tropics (Eastop, 1983) and therefore reproduction is assumed to be through constant parthenogenesis.

Under such conditions a homogeneous population would be expected to result, and if not, then other forces must be operative to bring about heterogeneity. Blackman (1979) suggested that heterogeneity in aphid populations in the tropics could result from frequent genetic mutations. *S. graminum* is also known to migrate long distances borne by wind (Taylor and Palmer, 1972) and this species has been reported in southern Africa (Brown, 1972) and in the Mediterranean Region (Hill, 1975). Therefore wind-assisted migration from areas where sexual reproduction takes place cannot be ruled out. It is therefore suggested that genetic mutation and migration increase genetic heterogeneity of greenbugs in Kenya, while selection during the dry seasons results in populations that are more homogeneous.

Table 1. Variation of greenbug clones as shown by mean net reproductive rate (R_o), cohort generation time (T_c), capacity for increase (r_c) and longevity using Kenya Kifaru in 1983

Clone	R_o	T_c (days)	r_c/day	Longevity (days)
1	29.0	18.4	0.185	36.5
2	30.7	17.3	0.189	46.0
3	65.3	19.5	0.214	34.5
4	69.8	19.6	0.217	39.5
5	61.3	18.7	0.218	35.8
6	56.0	16.8	0.219	26.0
7	70.3	17.5	0.222	18.3
8	66.3	15.9	0.228	18.8
9	76.5	15.6	0.278	29.8
10	97.0	15.1	0.310	36.3
P	>0.05	>0.05	<0.05	>0.05
r_I	0.034	0	0.596	0.036
90% confidence limits for r_I	0 to 0.685	-	0.297 to 0.810	-

Table 2. Variation of greenbug clones as indicated by mean net reproductive rate (R_o), cohort generation time (T_c), r_c and longevity using Kenya Kifaru in 1985

Clone	R_o	T_c (days)	r_c/day	Longevity (days)
A	65.2	17.6	0.230	27.4
B	68.8	18.1	0.237	32.0
C	60.4	16.0	0.250	31.3
D	51.5	17.4	0.227	30.7
E	78.2	17.0	0.257	33.2
F	52.4	15.7	0.234	24.1
r_I	0.039	0	0.065	0
90% confidence limits for r_I	0 to 0.165	-	0 to 0.228	-

Means within each column are not significantly different ($P>0.05$).

Table 3. Analysis of variance table showing the environmental and genetic components of variance for the capacity for increase (r_c) for greenbug clones tested on Kenya Kifaru in 1983 and 1985

Source	df	SS	MS	F	P
Among clones 1983	9	0.0486	0.00540	4.29	<0.10
Among clones 1985	5	0.0063	0.00126		
Within (environment) 1983	27	0.0227	0.00084	1.09	>0.10
Within (environment) 1985	48	0.0371	0.00077		

Variance components:

Due to genetics 1983 (S_A^2) = 0.00124

Due to genetics 1985 (S_A^2) = 0.00005

Appendix 1. Variation of greenbug clones as shown by mean net reproductive rate (R_o), cohort generation time (T_c), and capacity for increase using five wheat varieties in 1985

Clone	R_o	T_c (days)	r_c/day	Longevity
A	58.7	16.3	.240	28.4
B	66.7	17.4	.238	31.3
C	73.3	17.5	.244	31.6
D	54.0	16.0	.237	29.3
E	72.5	17.2	.243	32.1
F	61.8	16.1	.247	27.7
r_I	0.054	0.001	0	0.003
90% confidence limits for r_I	0 to 0.393	0.069 to 0.491	-	0 to 0.907

Means within the same column are not significantly different.

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CHAPTER III

Part IV

Paedogenesis and alata production by alate greenbugs (Homoptera:Aphididae)

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Paedogenesis and Alata Production by Alate Greenbugs (Homoptera:Aphididae)

ABSTRACT

Tests on the occurrence of paedogenesis in greenbug, *Schizaphis graminum* (Rondani), were done at 15, 21 and 25°C with alate and apterous greenbugs. Reproduction in immature instars occurred only in the fourth instar and ranged from one to three nymphs/reproducing nymph; reproducing nymphs moulted to adults and continued to reproduce. Among the alatae the proportions of fourth instars that reproduced before the final moult were 0, 0.46 and 3.93% at 15, 21 and 25°C respectively, while among the apterae no fourth instars reproduced at 15 and 21°C and 0.93% did so at 25°C.

When apterae were crowded as fourth instars and as adults, between 80 and 100% produced alate offspring. When alate greenbugs were crowded as fourth instars and again soon after the last moult 12% produced alate offspring. Alate greenbugs did not produce alate offspring when crowded only as fourth instars or as adults. It is suggested that both paedogenesis and alate production by alatae may enhance the greenbugs ability to utilize ephemeral resources.

INTRODUCTION

Paedogenesis is precocious reproduction in the larval or pupal stages (Wyatt, 1961) and is associated with parthenogenesis (Dixon, 1985b). It occurs in the families Cecidomyiidae (Wyatt, 1961, 1963) and Chironomidae (Gillot, 1980) in Diptera, Micromalthidae (Crowson, 1981) in Coleoptera and Aphididae (Wood and Starks, 1975) in Homoptera. In Aphididae, ovulation in embryos and lack of a haploid phase in the development of the gonad products have been considered to fulfill conditions for paedogenesis (Uichanco, 1924; Bodenheimer and Swirski, 1957). However parturition in immature stages in aphids has only been reported among alate fourth instars of *S. graminum* (Wood and Starks, 1975). In the present studies the use of the term paedogenesis will be limited to parturition in immature stages.

The production of alate offspring by alate aphids is not common and has only been reported in *Aphis craccivora* Koch (Johnson and Birks, 1960). It was found not to occur in *Aphis fabae* Scopoli (Shaw, 1970), *Myzus persicae* (Sulzer) (Blackman, 1979) or *Acyrthosiphum pisum* (Harris) (MacKay, 1977). Conversely apterous aphids are easily stimulated to produce alate offspring when crowded (Lees, 1966) with the highest percentage of alatae being produced within the first 2 days after the crowding stimulus (MacKay, 1977).

Paedogenetic reproduction and production of alate offspring by alate adult greenbugs were observed in a greenhouse at Njoro, Kenya. This work was started to determine whether paedogenesis occurs in both alate and apterous greenbugs and whether it is influenced by temperature, and to investigate the effects of crowding alate adults on production of alate offspring.

MATERIALS AND METHODS

A greenbug clone originating from a wheat field near Njoro in 1982, and maintained on seedling wheat in a greenhouse culture thereafter, was used in all the tests, which were conducted in 1985. To prevent contamination of experimental greenbugs with stray ones, experiments were carried out on greenbugs confined to petri dishes in controlled environmental chambers. Each petri dish contained a 6 cm long portion of a wheat leaf; this leaf section was kept fresh by inserting its base into a heap of moist sand at the periphery of the dish. Apical portions of the leaves were not used because they deteriorated rapidly. Leaf sections were replaced every four days.

Experiments on paedogenesis were carried out in controlled environment chambers at 12:12 L:D and at temperatures of 15, 21 or 25°C. Adult greenbugs were placed individually in petri dishes, with leaf sections, to larviposit and then removed after 24 h. After 4 days one nymph from each dish was transferred to a fresh leaf section in a new petri dish; the remaining nymphs were discarded. Each nymph was observed daily until it started to reproduce. It was then examined to determine whether it had matured by observing the shape of the cauda (and size of wings in case of alatae). Occurrence of a fourth molt after reproduction further confirmed paedogenetic individuals.

To determine the effects of crowding on the reproduction of alate offspring by alate greenbugs, 25 individuals, of either fourth instar or adult greenbugs, were placed in a plastic vial (4x1 cm) for 8 h at 25°C and 12:12 L:D. The crowded greenbugs were then transferred singly to

leaf sections in petri dishes, and removed after 15 h and the nymphs they produced were reduced to one/dish as described for the paedogenesis experiment. When fourth instar nymphs were crowded, they were transferred and left to mature; the resulting adults were either allowed to remain on the leaf sections and reproduce or were subjected to crowding for a second time and transferred to fresh leaf sections for 15 h. Nymphs were reduced to one per dish as before. The remaining nymphs were observed for development of wings.

RESULTS

All greenbugs that reproduced while in the fourth instar continued development to become adults. The number of nymphs produced by fourth instar mothers varied from one to three. Incidence of paedogenesis was significantly different ($\chi^2 = 4.37$, df = 1, $P<0.05$) between alatae and apterae at 25°C but not at lower temperatures: at 25°C, a higher percentage of alatae than of apterae reproduced paedogenetically (Table 1). Among the alatae, there were significant temperature effects ($\chi^2 = 13.76$, df = 2, $P<0.05$) on the number of fourth instar greenbugs that produced nymphs, with more reproducing fourth instars being observed at 25°C than at lower temperatures. Paedogenesis among apterous greenbugs was only observed at 25°C.

Apterous greenbugs, when crowded for 8 h at 25°C, responded by producing alate offspring (Table 2). Twelve percent of alate greenbugs from crowded colonies in the greenhouse culture produced alate offspring without further crowding. Alatae produced alate offspring in response to crowding, but only when crowded as fourth instars and again soon after the final moult (Table 2). Intermediates (adults with very short wings) were observed among the offspring of the individuals that received the double crowding stimulus and apterae crowded as fourth instars (Table 2).

DISCUSSION

Paedogenesis in greenbugs occurs among the alatae and also, though to a lesser extent, among apterae (Table 1). Paedogenesis as used here refers to parturition in nymphal instars, as opposed to the definition of Uichanco (1924) and Bodenheimer and Swirski (1957). In a greenhouse, Wood and Starks (1975) found that 1.8% of alate greenbugs reproduced while in the fourth instar.

Temperature was found to influence the incidence of paedogenesis in alate fourth instars; the highest percentage, 3.93%, was obtained at 25°C (Table 1). The percentage of apterae that reproduced in the fourth instar was low, while no paedogenesis in apterous fourth instars was observed at 15 or 21°C. The lower incidence of paedogenesis in apterae may explain Wood and Starks' (1975) failure to observe its occurrence.

Small changes in time to first reproduction results in large changes in the intrinsic rate of increase of a population (Lewontin, 1970; Wyatt and White, 1977). The capacity to reproduce early in an aphid's life is enhanced by parthenogenesis (Clark, 1973). An adaptation by individuals reproducing by parthenogenesis to reproduce paedogenetically would permit them to reproduce even earlier. Although *S. graminum* has not widely adapted to paedogenetic reproduction, the history of this phenomenon is not understood and may well be a recent one. But, even now, the low percentage that reproduce paedogenetically may constitute an enormous number of greenbugs when the whole field population is considered (Wood and Starks, 1975) and may make a big difference to the rate at which that population grows. Greenbugs infest seedling wheat (Starks

et al., 1975) and in order to exploit such a transient crop stage, any adaptation for a rapid rate of population increase would be an added advantage.

The crowding period of 8 h (MacKay, 1977) at 25°C provides enough stimulus for greenbugs to produce alate offspring. The production of alate offspring by alate greenbugs and the high percentage of apterae that produce alate offspring after crowding is probably an indication of a high sensitivity of the species to a crowding stimulus. It is apparent from these results that for alate greenbugs to respond to crowding and produce alate offspring, they must be in crowded colonies in immature (fourth) instars and as teneral adults. The factors that resulted in the occurrence of intermediates were not understood.

A constant decline of alate greenbugs, in a field population may result from emigration (Summy and Gilstrap, 1983). The migratory tendencies of aphids (*A. pisum*) can be measured in terms of the proportion of a population that develops into alatae (Lamb and MacKay, 1979). The increased capacity to produce alate offspring by alate greenbugs may be viewed as an increase in migratory efficiency of the species that might allow it to escape from deteriorating habitats.

Table 1. Effects of temperature on reproduction by alate and apterous fourth instar greenbugs

	Temp.	Reproducing 4th instars	Mean number of young/ nymph	Non-reproducing 4th instars	% Paedogenesis
Alatae					
	25°C	13	2.1	318	3.93
	21°C	1	2.0	218	0.46
	15°C	0	-	195	0
Apterae					
	25°C	2	2.0	214	0.93
	21°C	0	-	31	0
	15°C	0	-	5	0

Table 2. Effects of crowding on the production of alate offspring

Morph	Crowded instar	Number of crowded individuals	Number producing alatae	% Producing alatae
Apterae				
	Adults	50	50	100
	4th instar	25	20(2)*	80
	4th instar + adults	25	24(1)*	96
Alatae				
	Adults	100	0	0
	4th instars	50	0	0
	4th instars + adults	50	6(2)*	12

*The number of individuals shown in brackets produced intermediates; not included in the number reproducing alatae (20, 24 and 6).

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CHAPTER III

Part V

Tolerance of six cereal crops to infestation of seedlings by *Schizaphis graminum* (Homoptera:Aphididae)

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Tolerance of six cereal crops to infestation of seedlings by *Schizaphis graminum* (Homoptera:Aphididae)

ABSTRACT

Six cereal crops, bread wheat, durum wheat, sorghum, barley, oats and triticale, were tested for resistance to greenbug, *Schizaphis graminum* (Rondani). The wheat and sorghum varieties, Kenya Kifaru and BJ28 respectively, were found to be more sensitive to greenbug attack while the other crop varieties were tolerant.

INTRODUCTION

There are cultivars of several crop species that are resistant to greenbug, *Schizaphis graminum* (Rondani), e.g. some wheat selections (Starks and Merkle, 1977), sorghum (Schuster and Starks, 1973), oats (Wilson et al., 1978) and triticale (Wood et al., 1974). In most of these examples all the three mechanisms of resistance (antibiosis, tolerance and antixenosis) have been found to operate in the same cultivar. However Gaucho triticale is not resistant by antixenosis but antibiosis and tolerance provide it with adequate resistance to greenbug (Wood et al., 1974).

Low level resistance may be sufficient to prevent losses (Starks and Merkle, 1977) but only cultivars with high resistance are useful in a breeding programme (Webster and Inayatullah, 1984). Such resistant crop cultivars may be useful as a source of resistance for developing new resistant varieties of the same crop or for interspecific crosses using appropriate technology. For example Sebesta and Wood (1978) transferred greenbug resistance from rye to wheat using X-rays. Occurrence of resistance of cereal crops grown in Kenya to greenbug is not understood and this paper is a report on preliminary studies on tolerance resistance to greenbug of six cereal crop varieties tested at the National Plant Breeding Station, Njoro, Kenya.

MATERIALS AND METHODS

The six cereal crop varieties tested were: Kenya Kifaru - bread wheat, *Triticum aestivum* L.; Kenya Njiwa - durum wheat, *Triticum turgidum* L. var *durum*; BJ28 - sorghum, *Sorghum bicolor* L.; Proctor - barley, *Hordeum vulgare* L.; Suregrain - oats, *Avena sativa* L. and T65 - triticale, Triticale. The experiment was conducted in a greenhouse using the three greenbug clones and the procedure described by Wanjama and Holliday (1986). Potted seedlings, one seedling/pot, were caged at emergence using nylon netting supported on a frame. Two apterous adult greenbugs of the same clone were introduced onto four seedlings of each crop species and the total number of aphids on each seedling counted after 10 days. The greenbugs were allowed a total feeding period of 14 days and then killed using malathion 6.25 g a.i./ℓ, and the seedling height to the tip of longest leaf was measured. The plants were allowed to mature and the grain yield determined. The grain was dried to constant weight.

The seedling height and yield of infested plants were adjusted for greenbug numbers by analysis of covariance and subjected to analysis of variance. There were no significant differences between the three clones and the data for the three clones were pooled for each crop variety and tested using one way analysis of variance. The means of infested plants and respective control plants were tested for significant differences by using one tailed t-tests of contrasts (Sokal and Rohlf, 1981).

RESULTS

Reduction in seedling height as a result of greenbug infestation was significant for oats (Table 1). Significant reductions in yield occurred only in the wheat variety Kenya Kifaru and sorghum variety BJ28. Oats which has shown significant reductions in seedling height yielded (non-significantly) more than did oats which had not been infested.

The number of greenbug on the different varieties after 10 days was highest on triticale followed by barley and lowest for sorghum and bread wheat but the differences were not significant.

DISCUSSION

Comparison of seedling height of infested and control plants was considered a good measure of tolerance to greenbug in sorghum (Schuster and Starks, 1973) but not in wheat (Wanjama and Holliday, 1986). It did not seem to be an appropriate measure of tolerance in oats in this test because the oats variety had significant height reduction, but the mean grain yield for the infested plants was greater than that of the control plants, probably due to recovery by attacked plants. Grain yield was therefore the criterion used in determining tolerance in this test. Greenbugs on bread wheat and sorghum had the lowest rate of population increase though not significantly different from the others, but these two crops suffered significant yield loss. Kenya Kifaru does not exhibit antibiosis (Wanjama and Holliday, 1986) and it is therefore apparent that all the six varieties do not possess resistance by antibiosis.

Wheat resistance to greenbug is not common (Harvey et al., 1980) and the wheat variety used in this test (Kenya Kifaru) has also been shown to be susceptible (Wanjama and Holliday, 1986). This test confirms the susceptibility of Kenya Kifaru to greenbug attack. The sorghum variety BJ28 is also susceptible while the other crop varieties are tolerant. Reports on resistance to greenbug seem to indicate that it is more frequent in other cereal crops, e.g. sorghum (Schuster and Starks, 1973), oats (Wilson et al., 1978), barley (Webster and Starks, 1984) and triticale (Wood et al., 1974) than in wheat (Harvey et al., 1980). Although the results of this test appear to be in agreement with previous reports, more varieties of each of these crops will need to be evaluated in future work to verify this resistance.

Table 1. Mean number of greenbugs per plant, seedling height and grain yield of plants of six crop varieties tested for greenbug tolerance in 1982

Crop	Variety	Greenbugs/ plant	Seedling height (cm)		Grain yield (g)	
			Infested	Control	Infested	Control
Oats	Suregrain	52.3	34.6*	49.8	5.96	4.88
Barley	Proctor	64.9	41.7	45.7	2.16	2.39
Triticale	T65	78.0	39.1	38.5	4.06	4.87
Durum	Kenya Njiwa	53.7	28.7	32.1	2.09	3.19
Wheat	Kenya Kifaru	41.1	45.8	49.8	2.02*	3.87
Sorghum	BJ28	40.5	39.0	43.1	4.87*	6.12

Means of infested plants are adjusted for number of greenbugs that were feeding on them by analysis of covariance.

*Mean of infested plants significantly lower than that of respective control plants at $P \leq 0.05$ (one tailed t-test of contrasts).

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CHAPTER IV

GENERAL DISCUSSION

Heretofore literature on various aspects of greenbug population in Kenya has been scanty despite the seriousness of this pest on cereal crops (Harder, 1974; Wanjama, 1979). The extent of the variation within the greenbug populations is not clear although it has been suggested that aphids in the tropics undergo constant parthenogenesis (Dixon, 1985b), with genetic mutation the only mechanism promoting heterogeneity (Blackman, 1979). From this work, the greenbug population occurring in Kenya may be homogeneous in some years and heterogeneous in others. There is no evidence that sexual reproduction takes place, but besides genetic mutation, it may be that migration from other areas where sexual reproduction takes place may also play a part in bringing about heterogeneity. Kenya lies on the equator and the trade winds blowing towards opposite hemispheres (Pedgley, 1982) could probably carry greenbugs from southern Africa where greenbug is known to occur (Brown, 1972). Possibly, migrants could also reach Kenya from the north where greenbug occurs in the Mediterranean region (Ilharco et al., 1982). Long distance migration of greenbug, over several thousand kilometers, has been reported (Taylor and Palmer, 1972) and it is therefore likely that greenbugs in Kenya are not entirely a resident population.

The movement of greenbug in Kenya starts with a flight period in June which occurs when some wheat crops are still in the early seedling stage which is the most susceptible stage (Starks et al., 1975). Because of the small size of greenbugs they are not easily seen as they fly

and land on the crop and almost invariably, the farmers detect greenbug invasion through visible damage, sometimes too late for economical control (Wanjama, 1979). The use of sticky traps provides an effective method of detecting the arrival of greenbugs, allowing adequate time for local monitoring of infestations. Two levels of monitoring are suggested; one at strategic places, for example research stations, and another at the farm level. At the former level, forecasts based on greenbug catches should be sent to local agricultural offices and farmers so that field monitoring at the latter level is itensified when an outbreak is imminent.

Although the results on flight periodicity of greenbug have shown that greenbug movements start when an early planted crop is likely to have passed the vulnerable stage, there are factors that favour rapid growth of their population. The occurrence of parthenogenesis minimizes the time lost, on landing on the crop, in search of a mate (Clark, 1973). The incidence of paedogenesis may allow a proportion of the population to reproduce early and influence the rate of population increase. Greenbugs feeding on susceptible cultivars also have a high rate of increase while the production of alate offspring by alate greenbugs may increase the dispersal ability of this species. Therefore a sudden population explosion is likely to occur and devastate available crop still in the seedling stage at the time of infestation. Besides enhancing the virulence on the crop, these adaptations may contribute to the success of the greenbug in escaping from a habitat that is rapidly deteriorating due to the feeding and toxic saliva ejected while feeding (Pfadt, 1978).

Development of wheat resistant to greenbug in Kenya could not have been possible in a situation so deficient of necessary information

regarding the target pest. Among the entries that were screened, some were found to rank high in resistance by one mechanism or another. This probably indicates that the different resistance mechanisms (antibiosis, tolerance and antixenosis) are controlled by different genes (Horber, 1980). The resistance found among the entries that were screened is not a result of deliberate breeding for resistance and it is, therefore, not known which of the parents used in the crosses carried the genes for greenbug resistance. Kenya Fahari ranked high in resistance by different mechanisms but the source of this resistance is still unknown. However this variety is now available for use in developing future greenbug-resistant varieties.

Although most of the screening work was carried out in the greenhouse, Starks and Burton (1977) reported that resistance to greenbug detected under greenhouse conditions also operates under field conditions.

FUTURE WORK

a) Integrated Pest Management

The long term goal for the greenbug studies in Kenya is to establish an integrated pest control programme.

These studies provide some basic information concerning the greenbug and together with other factors in the environment may be used as the first step towards an integrated pest management (IPM) programme. The programme will then be improved as more information becomes available from experimental work. For a start a simple stepwise programme may be adopted:

STEP I

Avoid planting that synchronizes the susceptible seedling stage with the expected time of greenbug invasion. Wheat planted in late May and in June would be at a vulnerable stage when the first flight period of greenbugs start in June or early July. Wheat planted in April will be less susceptible.

STEP II

Use resistant varieties. Kenya Fahari and Africa Mayo are the best but other varieties that show resistance by one of the mechanisms are preferred to the susceptible ones. Low level resistance is effective in an integrated programme (Adkisson and Dyck, 1980) in maintaining pest populations at low levels that may not require control with an insecticide.

STEP III

Establish a greenbug monitoring programme. Two levels have been suggested, one at strategic points, e.g. research stations, to facilitate greenbug forecasting and the other at farm level, for local field monitoring. This will require a well defined communication system so that information reaches local agricultural offices and farmers without much time wastage.

STEP IV

Use selective insecticides. Select insecticides that spare the natural enemies but are effective against greenbugs and other aphids. If Steps I-III are followed then insecticide use will be limited to incidences of high infestation only and unnecessary use of insecticides will therefore be avoided.

b) Experimental Work

1. Development of resistant varieties.

This will be the first effort to develop varieties that are resistant to greenbug in Kenya. It is desirable that this is done locally because selections that have been developed in the United States for greenbug resistance were not found to be superior to locally available lines which had not been selected on the basis of resistance to greenbug. Cooperative efforts between plant breeders and entomologists will be necessary.

2. Determination of natural enemies.

In order for an integrated pest management (IPM) programme to be effective a knowledge of the natural enemies that help to check the population growth of greenbug is needed. An understanding of the life cycle of the natural enemies will provide guidance in determining the right time to apply an insecticide to control greenbugs.

3. Establishment of economic injury levels.

In order to justify the use of insecticides in controlling greenbug infestations, it is desirable to establish the level of infestation that results in economic crop losses. This will assist in establishing the economic thresholds at which control measure should be applied and will therefore be a useful tool in the proposed IPM programme.

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