GLASSHOUSE STUDIES ON THE RESISTANCE OF SOME ANCIENT WHEAT VARIETIES TO CEREAL APHIDS

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A Dissertation Submitted for the Degree of
DOCTOR OF PHILOSOPHY
at the University of Reading

Department of Zoology
University of Reading

1984

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ABSTRACT

Studies on the resistance of wheat to two cereal aphids (Sitobion avenae and Metopolophium dirhodum) were carried out in the glasshouse using some ancient wheats (Einkorn, Emmer and Spelt) as well as some modern wheat varieties (Bounty, Highbury, Mardler and Maris Kinsman).

The diploid ancient wheat Einkorn was the least preferred by both cereal aphids and both aphids were also least fecund on this wheat. Infestation by S. avenae led to least reduction in the growth of Einkorn of the wheat varieties studied while infestation by M. dirhodum led to a moderate reduction in the growth of this same wheat. S. avenae spent a short time on this wheat and a small proportion of the time was spent feeding; most of the time was spent wandering. In contrast with modern varieties, the mode of infestation of the ear of Einkorn by S. avenae did not follow any definite pattern. This ancient wheat was also the least affected by mildew. Einkorn has clearly shown a high level of resistance to both cereal aphids exhibiting two components of resistance (antibiosis and preference).

The ancient wheat Emmer (susceptible to M. dirhodum) and the hexaploid modern wheats Highbury and Mardler seem to show partial resistance to both cereal aphids but the primitive hexaploid wheat Spelt was very susceptible to both S. avenae and M. dirhodum.

This study has shown that some ancient wheats are potential genetic sources for the control of cereal aphids but that others may be as susceptible as modern varieties. In this study, at least one of the ancient wheats (Spelt) was as susceptible as the modern Maris Kinsman.

ACKNOWLEDGEMENTS

The author wishes to express his deep appreciation and sincere gratitude to Prof. H.F. van Emden for suggesting the problem, guiding the research with keen and continuing interest, helping in statistical analysis and correcting the manuscript.

Special acknowledgement is due to Prof. K. Simkiss and the late Prof. G. Williams in whose department this work was carried out. I am also very grateful for their encouragement.

In this project, I have benefitted greatly from the encouragement of Dr. N. G. M. Hague, Dr. R. H. Smith and Dr. S. Wallis.

I am very grateful to Mrs. T. Wise and Miss Elizabeth A. Wild for their encouragement and supply of research equipment and materials. I am also very grateful to Mrs. Denise Phillips for her careful and excellent typing.

I thank Dr. R. Stern of the Department of Applied Statistics for his help in the design of the experiments and Mr. Ben. Agbo. Oyejola for his help in statistical analysis.

I am greatly indebted to the Federal Government of Nigeria, Ahmadu Bello University Zaria and the Institute for Agricultural Research Samaru for their financial support. I am particularly grateful to the Institute for Agricultural Research Samaru, Nigeria for reinstating my scholarship after the expiration of my Federal Government scholarship.

1. INTRODUCTION

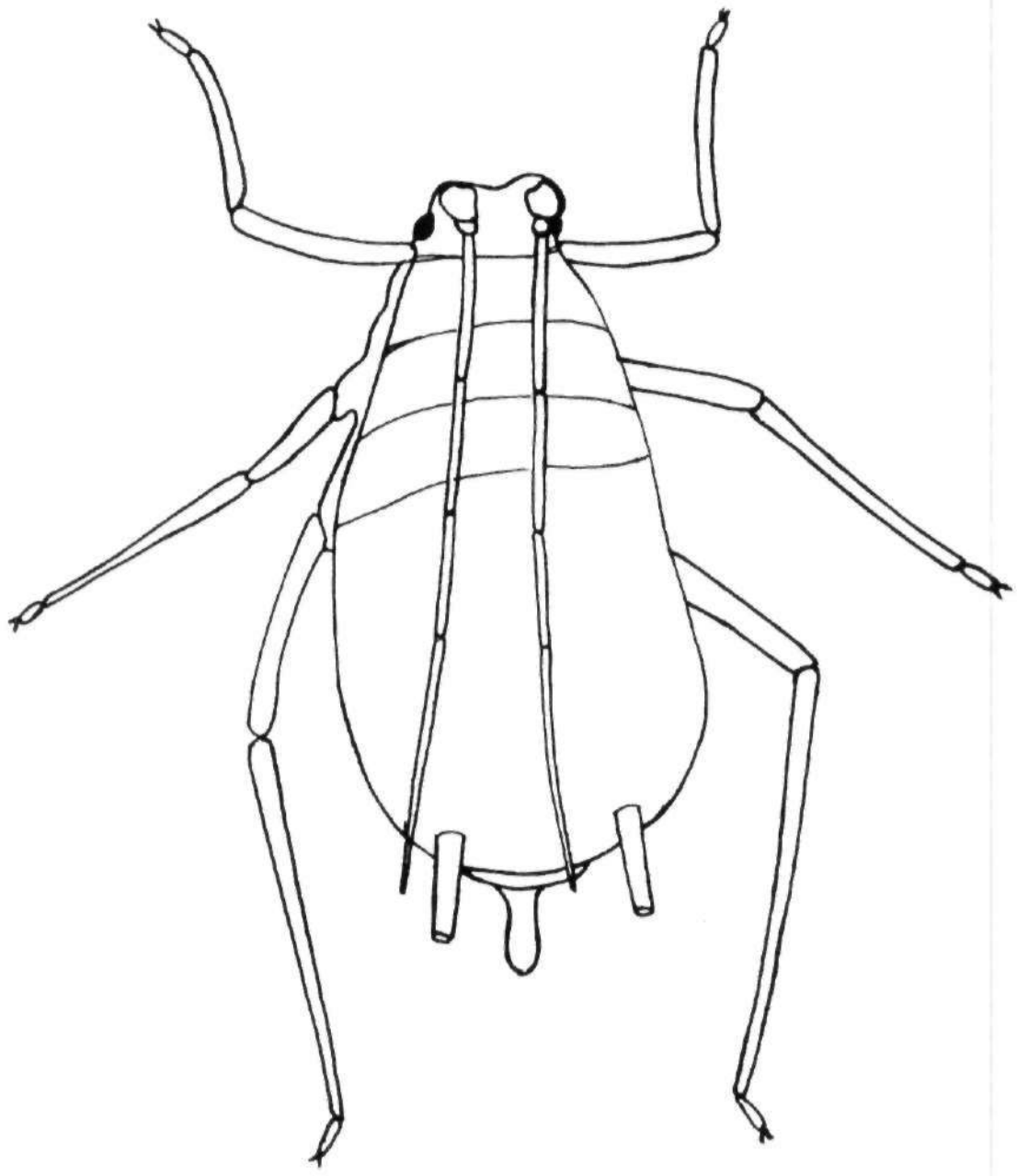
Great Britain is ranked fifth among the world's seven countries with the highest wheat yield per hectare. The annual average yielding capacity is 4573 kilograms per hectare (Fiddian 1977), well above Europe's average yielding capacity of 3027 kilograms per hectare (Spiertz 1978) and even almost triple the global average yielding capacity of 1557 kilograms per hectare (Spiertz 1978). About 1.4 million hectares are sown to wheat annually in the United Kingdom (Fertiliser Statistics 1976).

A wide variety of insects attack this crop amongst which the grain aphid Sitobion avenae (Fabricius) (Fig. 1) and the rose aphid Metopolophium dirhodum (Walker) (Fig. 2) are the most important.

A survey of the literature showed that there is a recent greater awareness of the benefits of using resistant varieties for the control of these aphids in Great Britain and other parts of the world (Rautapaa 1966 and 1968, Dean 1974c, Kolbe and Linke 1974, Wratten 1978, Lowe 1980 and Sotherton and van Emden 1982). The sudden shift to the search for resistant varieties to augment or replace chemical control is probably due to the global concern about the hazardous effects of chemicals on non-target organisms, high prices of the chemicals and the residues in the environment (Painter 1960 and 1968, Browning 1972, Dahms 1972, Harlan 1972, Baranyovits 1973, Green 1976, Newman 1976, van Emden 1977, Haskell 1977, Jenkins 1977, Robinson 1977, Way 1977, Brown 1978, van den Bosch 1980, Mackarness 1980 and Barrons 1981).

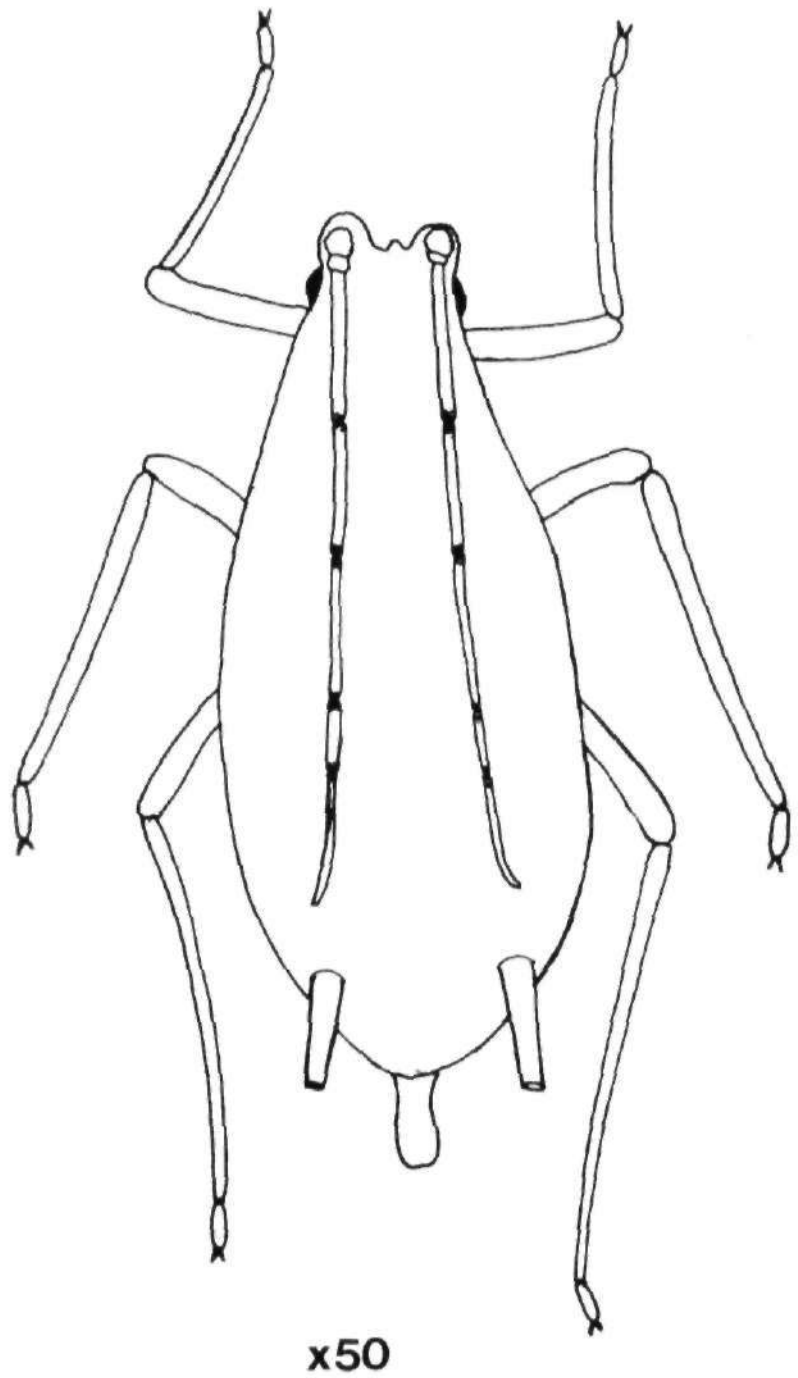
Except the recent publication of Sotherton and van Emden (1982), all the wheats and other cereal varieties used for investigations on plant resistance have been modern wheats. But Painter (1951), Harlan (1972) and Harris (1975) have emphasized the importance of ancient plants as possible

Fig. 1: Adult **Sitobion avenae**



x50

Fig. 2: Adult **Metopolophium dirhodum**



x50

sources of polygenic resistance which is what is needed nowadays to broaden the genetic basis of our crops. This polygenic type of resistance is what is needed to prevent existing resistant crop plants from being rendered susceptible by new strains of pathogens. Unfortunately, these ancient plants are being neglected in breeding programmes and some of them have become extinct (Harlan 1972). This present study attempts to find out whether three ancient wheats are resistant to cereal aphids and to make preliminary observations in relation to whether any mechanisms of resistance detected are chemical or physical in nature. The resistance or susceptibility of the ancient wheats were compared with that of modern counterparts.

Apart from a publication by Starks and Burton (1977) showing that nymphs of Schizaphis graminum (Rondani) moved more on the seedlings of resistant cereals than on susceptible seedlings, there seems to be no other information on the effect of resistance on the movement of cereal aphids. Particularly S. avenae is known to be a restless aphid (Otake 1966 and Dean 1973b).

Also there seems to be no information about the effect of resistance on the pattern of colonisation of the various plant parts by these cereal aphids, which in modern varieties show a predictable pattern from leaves to ear. This present study attempts to fill the gap in our knowledge on the effect of resistance on the movement of the cereal aphids and their pattern of colonisation on a limited number of wheat varieties.

2. LITERATURE SURVEY

2.1 Introduction

The cereals of which wheat is a member are indispensable daily components of every household dietary requirement. They are grown on about four million hectares in Great Britain and about 40 per cent of this hectarage is sown with wheat alone (Fertiliser statistics 1976 and Jenkins 1977). Pests (in particular insects) are major limiting factors to the production of wheat universally and in Great Britain the grain aphid Sitobion avenae (Fabricius) and the rose aphid Metopolophium dirhodum (Walker) are of paramount importance (Dean 1974 c and d, George 1974 and 1975, Plumb 1977, Lowe 1978, 1980 and 1981, Wratten 1978 and Sotherton and van Emden 1982). Apart from the sap sucked and the fouling of leaves and floral parts by the honeydew secreted by these aphids, both of them have been heavily implicated as vectors of barley yellow dwarf virus especially in spring sown cereals (Orlob 1961, Markkula and Myllymaki 1963 and Plumb 1977). Farmers seem to be more worried by the virus disease transmitted by these aphids than by the feeding and honeydew problems.

Apart from Africa, the Far East and Australia where these aphids have not been reported as pests, they have been rated as very important pests of wheat and other cereals in nearly all other countries of the World (Orlob 1961, Markkula and Myllymaki 1963, Kolbe 1969, 1970 and 1973, Dean and Luuring 1970, Rautapaa 1970 and 1976, Wratten 1978 and Vereijken 1979).

2.2 Origin of the ancient wheats used in the study

The diploid Einkorn wheat evolved as a cultivated plant in the early neolithic period about 4300 BC between Spain and Scandinavia (Kuckuck 1970).

Emmer is the oldest cultivated wheat and its domestication dates back to between 3000 BC and 4000 BC in the Nile Delta in Egypt and Mesopotamia while Transcaucasia is the centre of origin of the hexaploid wheat Spelt (Kuckuck 1970).

2.3 Biology of the cereal aphids used in the study

The biology of S. avenae and M. dirhodum has been given a lot of attention. Markkula and Myllymaki (1963) demonstrated that the development of alatae of S. avenae and M. dirhodum on Sisu oats at temperature regimes of 10.2°C and 14.4°C took on the average one day longer than development of apterae. The number of cereal aphids found infesting each tiller of five wheat, twenty barley and fifteen oat varieties ranged between 36 and 211 (Rautapaa 1976). On Proctor barley, Wratten (1977) showed that apterous forms of S. avenae and M. dirhodum produced an average of three nymphs more than alates, and apterae lived longer than alatae. On the ear, young leaves, mature leaves and senescent leaves of Aster oats, S. avenae reproduced on the average 5.95, 3.78, 2.17 and 2.08 nymphs respectively (Watt 1979). Markkula and Pulliainen (1965) working on Sisu oats and Dean (1974a) working on barley showed that the fecundity of S. avenae and M. dirhodum was largest at 20°C while Markkula and Rautapaa (1967) working on Sisu oats proved that exposure of reddish-brown virginoparous females of S. avenae for long periods in light encouraged the production of more reddish-brown forms.

2.4 Ecology of the cereal aphids

S. avenae is autoecious attacking only cultivated and wild grasses while M. dirhodum is heteroecious between Rosaceae and Graminae (ADAS 1978, Wratten 1978 and Vickerman and Wratten 1979). Aphids are found infesting the crop between one and four weeks after the first alate is caught in the

suction trap (Dean and Lurring 1970 and ADAS 1978). The main source of inoculum of the crop is the migrant alate (Orlob 1961 and ADAS 1978) with more alates being present in years with more days of frost (Dean 1974d and Vickerman and Wratten 1979). The optimum light requirements for take-off of alates are between 110 and 200 foot candles (Dry and Taylor 1970). Another possible source of inoculum is the resident population that survives the winter on the summer host (Orlob 1961). The subsequent spread of infestation within tillers is done by older nymphs and adult apterous aphids (Dean 1974d and Vickerman and Wratten 1979). The distribution of S. avenae in the field is peripheral while M. dirhodum is found further into the field (Dean and Luuring 1970 and Dean 1973b). S. avenae is mostly found on the ears while M. dirhodum is found on lower leaves (Orlob 1961, Dean and Luuring 1970, Dean 1973b, Rautapaa 1976, ADAS 1978, Wratten 1978 and Vickerman and Wratten 1979). One of the factors regulating the population buildup of these aphids is natural enemies such as coccinellids, syrphid larvae, hymenopterous parasites, dermapterous predators, carabid predators, linyphiid spiders and pathogens (Otake 1966, Dean 1974b and 1975, Wratten 1977, Vickerman and Wratten 1979, Sunderland and Vickerman 1980, Carter, Gardner, Fraser and Adams 1982 and Chambers, Sunderland, Stacey and Wyatt 1982). The ratio of natural enemies increases as the density of aphids increases but the effectiveness of the natural enemies really depends on their early appearance in the crop (Sunderland and Vickerman 1980 and Carter, Gardner, Fraser and Adams 1982). Other factors which regulate the buildup of the cereal aphids include weather conditions, changes in nutritional quality of the crop and emigration (Dean 1974d and Chambers, Sunderland, Stacey and Wyatt 1982).

2.5 Economic importance of the cereal aphids

The loss in yield caused by cereal aphids arises from three main sources.

These sources are the sucking of the sap, the spread of virus diseases and the secretion of the honeydew (Markkula and Myllymaki 1963 and Vereijken 1979). Rautapaa (1966 and 1968) showed that an aphid index of 1000 reduced the yield of wheat and barley by between 10 and 27 per cent. The aphid index is the sum of aphids on 100 main shoots. Apablaza and Robinson (1967) indicated that S. avenae drastically reduced the weight of grains while Kolbe (1969) and Kolbe and Linke (1974) showed that 20 to 50 aphids per ear reduced grain yield by between 10 and 25 per cent. In his study, George (1974) showed that infestation of the ear with 100 to 200 S. avenae reduced yield by between 12 to 17 per cent while Wratten (1975 and 1978) and Wratten and Redhead (1976) demonstrated that S. avenae and M. dirhodum reduced grain weight by 14 and 7 per cent respectively and each of the aphids equally reduced grain protein by 0.38 per cent. Wratten (1978) further established the damage threshold of S. avenae and M. dirhodum as being 21 to 25 peak units per ear; one aphid unit being either one adult or three aphids from the first to the third instar. Vereijken (1979) however suggested a different form of threshold for the control of S. avenae, the threshold being when 95 per cent of the ears were infested. Vereijken (1979) further showed that 30, 35, 20 and 10 per cent of the honeydew secreted by S. avenae was found on the ear, flagleaf, second leaf and third leaf respectively and 44 to 59 per cent of loss in yield was due to the fungi growing on this honeydew.

2.6 Work on the relative resistance of modern wheat varieties to cereal aphids

Wratten (1975) and Wratten and Redhead (1976) working with the winter wheat Capelle Desprez showed that S. avenae and M. dirhodum reduced grain yield

by 14 and 7 per cent respectively. In his study, Lowe (1978 and 1980) indicated that the wheat varieties Kador, Anna Miglori and EB921 and barley variety C116145 exhibited antibiotic resistance to the cereal aphids while Maris Huntsman wheat and Tyra barley were found to be especially susceptible. Sotherton and van Emden (1982) demonstrated that the cereal aphids only moderately preferred Sicco wheat and produced moderately few nymphs on this wheat while Timo wheat was very much preferred and many nymphs were produced on this wheat.

2.7 Control of the cereal aphids

Many control methods have been used against cereal aphids and some of them are enumerated below.

2.7.1 Cultural control

This is usually practised incidentally by farmers whenever they destroy cereal stubbles and various wild grasses where the resident population of these aphids normally survive the winter.

2.7.2 Forecasting

This is an important indirect aspect of control. Cereal aphids appear in suction traps between one and four weeks before aphids are spotted in cereal crops (Dean and Luuring 1970 and ADAS 1978), and work is progressing at Rothamsted Research Station to make such trap catches a basis for the timing of control measures, particularly in relation to the virus problem.

2.7.3 Biological control

This has been dealt with in section 2.4. The effectiveness of the natural enemies in the agroecosystem depends on their early appearance in the crop and the use of selective aphicides such as pirimicarb which kills the aphids and which is found to be ineffective against the natural enemies.

2.7.4 Chemical control

A narrow spectrum insecticide that is less toxic to bees commonly used in Great Britain against the cereal aphids is pirimicarb (Stone 1977 and van Emden personal Communication). Other insecticides occasionally used against the cereal aphids are Chlorpyrifos, demeton-S-methyl, dimethoate, formothion, oxydemetonmethyl, phosalone, thiometon and triazophos (ADAS 1978). Whatever the merits of insecticides, they are expensive, leave residues in food, kill beneficial insects and their constant use leads to the development of insect biotypes resistant to insecticides (Painter 1960 and 1968, Browning 1972, Dahms 1972, Harlan 1972, Baranyovits 1973, Green 1976, Newman 1976, van Emden 1977, Haskell 1977, Jenkins 1977, Robinson 1977, Way 1977, Brown 1978, van den Bosch 1980, Mackarness 1980 and Barrons 1981), although this has not yet happened with cereal aphids in the United Kingdom.

2.7.5 Integrated Control

One of the leading advocates of this method of insect control is Prof. Way of Silwood Park. Except the use of insecticides, nothing else seems to have been done on this method of insect control with respect to cereal aphids.

2.7.6 Resistant varieties

Because of the high prices of insecticides and their adverse effects on non-target organisms, the inefficiency of various biological and cultural control methods and because of the migrant power of the cereal aphids which cannot be controlled at various international borders, the search for resistant varieties has recently accelerated. This method of insect control is one of the safest and it leads to reduction in environmental pollution, use of less insecticides, less hazards to non-target organisms, reduction of insect population and compatibility with other control methods (Painter 1968, Dahms 1972 and Maxwell 1972). The main disadvantage of the use of resistant varieties is that it may encourage the development of insect biotypes to which the resistant crops become vulnerable (Snelling 1941, Dahms 1960, Gerhold 1966, Browning 1972, Gallun 1972, Harlan 1972, Maxwell 1972 and Fletcher 1974). At times, a crop resistant to one biological organism may become susceptible to another biological organism (Maxwell 1972 and Panda 1979).

Resistance to plants has been divided into three major components by Painter (1951). These sub-divisions are antibiosis, preference and tolerance.

Antibiosis:-

This mechanism reduces the population buildup of insects (Painter 1951 and Russell 1978) but it has the disadvantage that it selects biotypes through selection pressure (Gallun 1972).

Preference:-

In this case, the crop plants are unattractive to the insects (Painter 1951 and Russell 1978). This type of resistance mechanism does not so

strongly encourage the development of biotypes as does antibiosis, but the population buildup after the limited invasion may increase in the absence of any antibiosis to such an extent that neighbouring farms may be plagued by insects dispersing from the overcrowded plants (Gallun 1972).

Tolerance:-

Significant reduction in yield does not occur despite the buildup of insects on the plant (Painter 1951 and Russell 1978). This again has the disadvantage that the high population of insects on the crop may become a problem for an adjacent farm (Gallun 1972). The approach of the British entomologists to the work on resistance to S. avenae and M. dirhodum is dichotomous in outlook with Dean (1974d), George (1974 and 1975), Wratten (1978) and George and Gair (1979) gearing their research towards yield loss assessment (tolerance) while Lowe (1980 and 1981) (antibiosis) and Sotherton and van Emden (1982) work mainly on antibiosis and preference.

An important lesson for entomologists searching for sources of resistance is the potato famine of the 1840s (Hills 1964, Harlan 1972, Russell 1978 and Barrons 1981) and the panic which struck the whole of the United States of America because of the development of a new strain of corn blight fungus about twenty years ago (Tatum 1971, Browning 1972 and Harlan 1972). Though this is a disease problem, it is relevant to pests also since farmers all over the world now practise monocropping with crops of very narrow genetic bases. Hence any resistant varieties derived from narrow genetic bases are greatly at risk to different strains of the pest organisms.

The genetic bases of the world's crops are often narrow because plant breeders tend to rely solely on modern varieties and neglect the other genetic sources where they can obtain potent polygenic genes for resistance to biological organisms. The reason mainly given is that it is difficult to breed for high yield and resistance simultaneously (Robinson 1977). As a result of this type of reasoning, many of the ancient varieties of crops have been neglected and many of them have even become extinct (Harlan 1972). But Painter (1951) and Harris (1975) have both stressed the importance of ancient plants as being possible sources of polygenic resistance which is what is needed to improve the genetic bases of world crops from the point of view of pest control. The neglect and even extinction of ancient crops is a serious loss of genetic resources. These plants ought to have been kept in gene banks where they could be available for use when needed.

This present work touches on the genetic advantages that can be derived from the much neglected ancient wheats with respect to resistance to S. avenae and M. dirhodum and to determine the type of resistance exhibited if any.

Virtually all commercial wheats are vernalised but recently vernalisation has been shown to reduce the number of embryos in cereal aphids and change resistant rankings of cereal varieties (Kay, Wratten and Stokes 1981). This seems a significant finding in the sense that virtually all the observations already taken with vernalised wheats would need to be re-examined because the data did not show the maximum reproductive potential of the cereal aphids. Moreover, the resistant rankings made with vernalised wheats clearly do not necessarily apply in the absence of vernalisation.

3. GENERAL MATERIALS AND METHODS

3.1 Sources of wheat varieties

Einkorn, Emmer and Spelt varieties were obtained from Buster Ancient Farm Project Trust, Petersfield while Highbury spring wheat, Mardler winter wheat, Bounty winter wheat and Maris Kinsman wheats were obtained from NIAB in Cambridge. Lofa barley was obtained from the University of Reading farms.

3.2 Source of aphids

S. avenae was the green type while M. dirhodum was the yellowish green type, both from Rothamsted Research Station.

3.3 Soil

Fresh John Innes No. 2 compost was used for sowing the seeds.

3.4 Culturing of apterous aphids

At weekly intervals healthy grains of un-vernalised Lofa barley were selected. Vernalisation is an important commercial treatment for some of the varieties but it was omitted in this study. Either total vernalisation of all varieties or non-vernalisation creates problems of interpretation. It was decided to use un-vernalised plants throughout as most likely to show the maximum aphid performance; the implications of this are further considered in the general discussion. The plants were grown in a heated glasshouse (12 - 24°C) with supplementary lighting by high pressure sodium lamps (16 h photophase). The potted plants were infested with a few S. avenae and the plants were caged with muslin in order to exclude extraneous insects. The culture plants were maintained for two weeks

before the aphids were transferred to fresh plants to continue the culture. Twice every week, the infested plants were carefully examined for parasitised and mummified aphids. Any parasitised or mummified aphids found were removed and crushed. This same procedure was used for M. dirhodum. Aphids were cultured continuously on Lofa barley for about three months before commencement of an experiment.

3.4.1 Culturing of alates

Alates were produced by allowing large numbers of aphids to build up on the culture plants. Alates used were those found walking on the muslin cages as these were believed to have performed the first test flight. The alates were collected as required into test tubes with an aspirator.

3.5 Basic preference technique for apterous aphids

Healthy grains of un-vernalised Bounty, Highbury, Mardler, Emmer, Einkorn, Spelt and Maris Kinsman wheats were selected.

Fourteen 12.5cm diameter pots were filled with compost and the soil in each pot carefully watered. The spot where the grains of each of the seven varieties of wheat would be sown in each pot was marked using a circular 11cm diameter cardboard template divided equally into seven sectors in such a way that each variety of wheat would be sown equally spaced around the circumference and equidistant from the centre of the pot. The plastic labels for each pot were randomised and sunk into their appropriate marked positions. Three grains of each variety other than Einkorn were sown at each appropriate location per pot. For Einkorn, six grains were sown at each position because of the poor rate of germination of this wheat. The pots were placed in the glasshouse according to a 7 x 7 Latin square design with 2 replicates.

At emergence, the seedlings were thinned to one seedling per position in each pot. Soon after emergence each potted plant was carefully examined daily for natural infestation by aphids and any aphid found was removed from the plant and crushed. The seedlings in these pots were used to test the aphids in the second and third weeks after sowing.

For subsequent weekly preference tests from the fourth week after sowing through to plant maturity, segments of leaves, stems and excised ears instead of seeds were positioned in the pots. The plant materials were obtained from over 40 pots of each wheat variety sown at the same time as the seeds for the initial preference trials and also thinned to one plant per pot.

Commencing from the fourth week after sowing, healthy potted plants were selected from each of the seven varieties of wheat and their middle leaves or stems were cut into about 9cm segments. A piece of white absorbent cotton wool was soaked in distilled water and wrapped round the basal 1cm of each leaf or stem segment to prevent dehydration. With excised ears, the absorbent cotton wool was wrapped round the culm of each ear.

Segments of leaves, stems and excised ears were used from the fourth week after sowing through to maturity since the size of the sown plants by then would have allowed aphids to hide in whorls and under leaf sheaths where the counting of aphids would have been practically impossible. Moreover, if segments of plant materials had not been used, all seven varieties of wheat would have grown together in a single pot from seedling to maturity. Under such conditions, competition would have occurred among the varieties resulting in vigorous growing varieties overshadowing their frail growing counterparts.

To perform a preference test, 50 apterous adult *S. avenae* cultured on Lofa

barley were carefully placed in the centre of each pot after which the pot was caged with muslin.

After 24 hours, the cage on each pot was carefully removed and the number of aphids on each piece of wheat variety counted and recorded.

3.5.1 Basic preference technique for alates

For experiments on the preference of alate aphids, 5cm diameter pots were filled with compost and labelled. Three grains of each variety of wheat were sown per pot and watered. The pots were arranged in the glasshouse according to a randomised block design with 3 replicates. At emergence, the seedlings were thinned to one per pot.

At the two leaf growth stage (Zadoks' growth stage 12 or Feekes' growth stage 1), a batch of four potted plants were arranged in each 20cm diameter plastic cage after which 50 alates aspirated into a test tube were carefully introduced into the cage from the top. The plastic cages were carefully arranged in a flight chamber, the circumference of which rotated at about 10 km per hour for 24 hours to eliminate positional effects. After 24 hours, the cages were removed and the number of alates selecting each variety of wheat counted and recorded.

4. PREFERENCE

4.1 Introduction

Some plant species offer better food sources to phytophagous insects than others (Gernert 1917, Kennedy and Booth 1951, Dethier 1954, Lipke and Fraenkel 1956, van der Poel and van Lenteren 1978 and Hodkinson and Hughes 1982). Even within a plant, an organ may offer a better source of food to an insect than another (Kennedy and Booth 1951, Cartier and Painter 1956, Wyatt 1970, van Emden 1972 and 1973, Maxwell 1972, Schoonhoven 1972 and Hodkinson and Hughes 1982). These differences occur because of various chemical and physical barriers which exist between insects and their host plants (Hsiao 1969, van Emden 1972, 1973 and 1978, Bernays, Chapman, Horsey and Leather 1974, Chapman 1977, Chapman and Bernays 1977, Panda 1979, Norris and Kogan 1980 and Hodkinson and Hughes 1982). The fundamental sensory cues which phytophagous insects use to locate host plants of their choice are colour, odour, taste and form (Painter 1951, Dethier 1954, Thorsteinson 1960, van Emden 1972 and 1973, Panda 1979 and Hodkinson and Hughes 1982) but the subsequent selection of the host plant involves a chain of processes (Painter 1951, Thorsteinson 1960, Dethier 1966, Hsiao 1972, Maxwell 1972, Schoonhoven 1972 and Hodkinson and Hughes 1982). Each step towards selection of the food involves a behavioural response. Hence if the insect perceives a stimulus to be correct it moves to the next, but if the stimulus is wrong the chain is broken and the insect rejects the host plant (Hodkinson and Hughes 1982). Thus 'preference' appears to be the most important component of host plant resistance because the best tactic a plant can deploy against an insect is to be inedible. If an insect cannot feed on a plant such an insect will not normally oviposit on such a plant. In fact, 'preference' is regarded as 'the very heart of agricultural Entomology' (Lipke and Fraenkel 1956 and Kennedy 1965).

There is still a great dearth of basic data on preference of cereal aphids for various cereal varieties commonly grown in Great Britain. Most of the research on cereal aphid/plant relationships in this country has been geared towards yield loss assessment (e.g. Dean 1973a and 1974d; George 1974; Wratten 1978; George and Gair 1979 and Wratten, Lee and Stevens 1979). Plumb (1977) stressed the importance of cereal aphids with regard to the transmission of virus diseases, where preference phenomena could be vital in the spread of diseases. Walters and Dixon (1982) recently reported that the take-off rate of alate S. avenae was influenced by the growth stage of wheat and the degree of overcrowding. Bardner and Fletcher (1974), Vickerman and Wratten (1979), and Carter, McLean, Watt and Dixon (1980) have extensively reviewed the literature on nearly all aspects of cereal aphid entomology. The only published work on the preference of cereal aphids among cereal varieties seems to be that of Sotherton and van Emden (1982) who reported that fewest alates in the field were found on an ancient wheat variety among five wheat varieties. Dean (1973a) had earlier shown that cereal aphids preferred cereal varieties to wild grasses.

As preference tests the degree of suitability of a host plant as food to an insect, this study reports some preference responses of S. avenae and M. dirhodum to some number of cereal varieties.

4.2 Preference of apterous S. avenae at weekly intervals for the leaves, stems and ears of seven varieties of wheat

4.2.1 Introduction

Aphids were usually found on certain plant organs while they were rarely found on others. This study was set up to find out which variety of wheat the aphids preferred most and which were least preferred, and whether these preferences changed with growth stage.

4.2.2 Methods

The experiment used the technique described earlier in section 3.5 with whole seedlings used up to the second week and plant segments thereafter. Soil used for the plant segments was prepared by sun-drying the compost, which was then sieved through a fine-meshed metal sieve. The fine loamy soil obtained was found to retain more water. After each weekly observation, the experiment was discarded, and soil collected, pulverised, sun-dried and re-used.

4.2.3 Results (Tables 1 and 2)

The results were subjected to analysis of variance and the means compared by Duncan's Multiple Range Test.

4.2.3.1 Seedlings (Zadoks' growth stages 12 and 13 or Feekes' growth stage 1) (Table 1)

Einkorn

The mean number of aphids selecting the seedlings of Einkorn during the 1st and 2nd weeks was consistently low (7th out of 7 varieties) and this mean was found to be significantly lower than the mean number of aphids selecting the seedlings of each of the other six varieties of wheat.

Bounty

The mean number of aphids selecting the seedlings of this wheat variety ranked 6th and 5th out of 7 varieties during the 1st and 2nd weeks respectively. This mean was found to be statistically inseparable from the mean number of aphids selecting the

Table 1: Mean number of apterous S. avenae selecting the seedlings, leaf segments and excised ears of seven wheat varieties at weekly intervals (out of 50 aphids per pot).

Wheat Material	Wheat varieties						
1st Wk Seedling	Highbury 9.07	Mardler 8.0	Spelt 7.0	Emmer 6.21	Kinsman 6.14	Bounty 4.57	Einkorn 1.78
2nd Wk Seedling	Mardler 10.85	Highbury 8.21	Spelt 7.14	Kinsman 6.64	Bounty 5.85	Emmer 5.42	Einkorn 1.42
3rd Wk Leaf Segment	Spelt 9.92	Kinsman 7.21	Mardler 6.42	Emmer 6.35	Highbury 6.28	Bounty 4.71	Einkorn 2.0
4th Wk Leaf Segment	Spelt 11.28	Kinsman 6.85	Emmer 6.42	Mardler 5.5	Highbury 4.14	Bounty 3.14	Einkorn 0.5

(Continued)

Table 1: (Continued)

Wheat Material	Wheat varieties						
5th Wk Leaf Segment	Spelt 9.0	Kinsman 7.28	Emmer 6.85	Mardler 5.21	Bounty 3.21	Highbury 2.92	Einkorn 1.5
6th Wk Leaf Segment	Highbury 9.85	Spelt 7.0	Mardler 6.85	Kinsman 5.92	Bounty 5.57	Emmer 5.42	Einkorn 1.35
7th Wk Leaf Segment	Emmer 11.07	Kinsman 8.71	Mardler 6.42	Spelt 5.35	Highbury 5.28	Bounty 3.14	Einkorn 1.0
8th Wk Leaf Segment	Kinsman 8.07	Spelt 7.21	Emmer 7.21	Highbury 6.14	Mardler 5.21	Bounty 4.71	Einkorn 1.42

(Continued)

Table 1: (Continued)

Wheat Material	Wheat varieties						
9th Wk Leaf Segment	Spelt 8.92	Emmer 8.14	Highbury 7.57	Kinsman 7.5	Mardler 6.28	Bounty 4.57	Einkorn 1.28
10th Wk Leaf Segment	Kinsman 9.64	Spelt 8.64	Emmer 7.0	Mardler 6.92	Bounty 5.92	Highbury 4.28	Einkorn 2.0
Flagleaf Segment	Mardler 11.21	Spelt 9.64	Kinsman 9.14	Highbury 7.85	Emmer 4.35	Bounty 2.92	Einkorn 1.78
Excised Ear	Kinsman 10.56	Mardler 8.42	Spelt 7.14	Emmer 6.64	Bounty 6.42	Highbury 4.42	Einkorn 1.42

Means of varieties connected by lines are not significantly different from each other (at P-O.05) as analysed by Duncan's Multiple Range Test.

seedlings of Emmer, Maris Kinsman and Spelt during the 1st week and that of all the remaining varieties other than Mardler (high preference) and Einkorn (low preference) during the 2nd week.

Emmer, Spelt and Maris Kinsman

The mean number of aphids selecting the seedlings of these varieties of wheat was moderately high in both weekly observations. There was always an overlap between the mean number of aphids selecting the seedlings of these wheat varieties and the mean number of aphids selecting the seedlings of the other varieties of wheat apart from Mardler (high preference) in the second week and Einkorn (low preference) in both weeks.

Highbury and Mardler

During the first and second weeks, the mean number of aphids selecting these two varieties was high. They were 1st or 2nd in order of preference. The means of aphids selecting these varieties of wheat were however statistically inseparable from the means of the intermediate varieties of wheat in the first week, though Mardler was statistically more preferred than all other varieties except Highbury in the second week.

4.2.3.2 Leaf (Table 1)

Einkorn

From the 3rd through to 10th week the mean number of aphids selecting the leaf of Einkorn was consistently low (7th out of

7 varieties) and this mean was found always to be significantly lower than the mean number of aphids selecting each of the other six varieties of wheat except for overlap into Highbury and Bounty on occasions. The mean number of aphids selecting the flagleaf of Einkorn was also found to be low (7th out of 7 varieties), though statistically inseparable from the mean number of aphids selecting the flagleaves of Bounty and Emmer.

Bounty

The mean number of aphids selecting this wheat was consistently fairly low (5th or 6th out of 7 varieties) from the 3rd through to the 10th week though statistically the mean overlapped with the mean number of aphids of several other varieties of wheat. A similar result was obtained for the selection of the flagleaf (6th out of 7 varieties) of this wheat variety.

Highbury, Emmer and Mardler

The mean number of aphids selecting these varieties of wheat tended to be moderately high. There was an overlap between the means of aphids selecting these wheats at four of the eight weekly observations. On the other three occasions, results were fluctuating and inconsistent with Highbury low twice and the most preferred variety once (6th week) and Emmer the most preferred once (7th week). Apart from Mardler, where the mean number of aphids selecting the flagleaf was high (1st out of 7 varieties), Highbury and Emmer again occupied a statistically inseparable and intermediate position.

Maris Kinsman and Spelt

The mean number of S. avenae selecting these two varieties was found to be high in about three quarters of the weekly observations. Apart from two occasions they were 1st or 2nd in order of preference. The mean number of aphids selecting Maris Kinsman was, however, always statistically inseparable from the means of aphids selecting varieties in the intermediate group, but Spelt was significantly most preferred in the 3rd and 4th weeks. Spelt and Maris Kinsman were 2nd and 3rd preferred in the flagleaf test, though there was overlap with other varieties.

4.2.3.3 Stem (Table 2)

Einkorn

Similar to what was observed in the case of the leaf segments, the mean number of aphids selecting the stem of Einkorn from the third through to the tenth week was the lowest of all the varieties though there was overlap with other varieties except for weeks 4 and 5.

Bounty, Highbury and Mardler

The mean numbers of aphids selecting the stem segments of these varieties were fairly low (3rd to 6th position out of 7 varieties). These means overlapped in most cases with the means of the other four varieties of wheat.

Table 2: Mean number of apterous S. avenae selecting the stem segments of seven wheat varieties at weekly intervals (out of 50 aphids per pot).

Wheat Material	Wheat varieties						
3rd Wk	Spelt	Kinsman	Highbury	Emmer	Bounty	Mardler	Einkorn
Stem segment	6.57	4.92	4.50	3.50	2.92	2.64	1.50
4th Wk	Kinsman	Emmer	Spelt	Highbury	Mardler	Bounty	Einkorn
Stem segment	10.71	7.14	5.57	4.07	3.71	2.92	0.42
5th Wk	Emmer	Kinsman	Spelt	Highbury	Mardler	Bounty	Einkorn
Stem segment	8.71	7.78	6.21	3.85	3.42	3.14	0.78
6th Wk	Emmer	Spelt	Kinsman	Highbury	Mardler	Bounty	Einkorn
Stem segment	7.64	7.57	5.64	4.57	3.14	2.42	1.57

(Continued)

Table 2: (Continued)

Wheat Material	Wheat varieties						
7th Wk	Emmer	Spelt	Mardler	Kinsman	Bounty	Highbury	Einkorn
Stem segment	6.64	5.64	5.0	3.78	3.64	2.42	0.85
8th Wk	Emmer	Kinsman	Mardler	Spelt	Bounty	Highbury	Einkorn
Stem segment	13.57	6.21	5.07	4.71	3.85	3.50	0.57
9th Wk	Mardler	Spelt	Kinsman	Bounty	Emmer	Highbury	Einkorn
Stem segment	7.71	6.50	6.42	4.78	4.42	3.07	1.0
10th Wk	Spelt	Kinsman	Bounty	Emmer	Mardler	Highbury	Einkorn
Stem segment	5.71	5.35	4.92	4.85	3.35	2.21	0.42

Means of varieties connected by lines are not significantly different from each other (at P=0.05) as analysed by Duncan's Multiple Range Test.

Emmer, Spelt and Maris Kinsman

The mean number of S. avenae selecting the stem segments of these wheat varieties ranked between 1st and 3rd position in order of preference out of seven varieties in most of the weekly observations and the most preferred variety each week was usually statistically separable from at least one of the means of the varieties in the intermediate group.

4.2.3.4 Ears (Table 1)

Einkorn

Similar to the results obtained with the seedlings, leaf and stem segments, the mean number of aphids selecting the ears of this wheat was the lowest of all the varieties and this mean was found to be significantly lower than that from the ears of the other six varieties of wheat.

Bounty, Highbury and Emmer

The ears of Emmer, Bounty and Highbury wheats were 4th, 5th and 6th respectively in order of preference by this aphid. This was again very similar to the preference shown by the aphid for these varieties on leaves and stems. The mean number of aphids selecting the ears of these wheats were statistically inseparable from the mean number of aphids selecting the ears of the other varieties apart from Einkorn (low) and Maris Kinsman and Mardler (high).

Spelt, Mardler and Maris Kinsman

The mean number of aphids selecting the ears of Maris Kinsman, Mardler and Spelt ranked 1st, 2nd and 3rd positions respectively in order of preference by S. avenae. Maris Kinsman was significantly more preferred than any other variety except Mardler.

4.3 Preference of apterous S. avenae for four varieties of wheat at different growth stages

4.3.1 Introduction

This study was set up as a partial repeat of the previous experiment to investigate the response of apterous S. avenae to just four of the varieties of wheat which had shown some degree of non-preference in the previous experiments. In this experiment the varieties were tested at five defined growth stages since the varieties grew differently and growth stages were not synchronised in the previous experiments. The four varieties selected were Highbury and Mardler which are modern varieties and have been widely grown by farmers and Emmer and Einkorn which are ancient varieties.

4.3.2 Methods

5cm diameter pots were used in these experiments to enable the aphids to make frequent contacts with the wheat varieties. The number of aphids placed in each pot was reduced to 20 because of the reduction in the number of wheat varieties. A Latin square design was used for all the experiments. For two, three, tillering, flagleaf and ear growth stages, 15, 3, 2, 2, and 3 replicates were used respectively.

4.3.3 Results (Table 3)

The results were subjected to analysis of variance and the means compared by Duncan's Multiple Range Test.

4.3.3.1 Two leaf growth stage (Zadoks' growth stage 12 or Feekes' growth stage 1)

The mean number of aphids selecting Einkorn was the lowest of all the varieties and this mean was significantly lower than the mean number of aphids selecting each of the other three varieties of wheat. The mean number of aphids selecting Emmer was the highest of all the varieties and this mean was also found to be significantly higher than the means of the other three varieties. Highbury and Mardler were 2nd and 3rd respectively in order of preference by this aphid.

4.3.3.2 Three leaf growth stage (Zadoks' growth stage 13 or Feekes' growth stage 1)

The mean number of aphids selecting Einkorn was the lowest of all the varieties and this mean was significantly lower than the mean number of aphids selecting each of the other three varieties of wheat. The mean number of aphids selecting Mardler was high (1st out of 4 varieties) and this mean was found to overlap with the mean of Emmer. Emmer and Highbury were 2nd and 3rd respectively in order of preference by this aphid, though not statistically separable.

Table 3: Mean number of apterous S. avenae selecting the seedlings, leaf segments and excised ears of four wheat varieties at different growth stages (out of 20 aphids per pot).

Wheat growth stage	Wheat varieties			
Two leaf growth stage	Emmer 6.18	Highbury 5.1	Mardler 4.16	Einkorn 2.25
Three leaf growth stage	Mardler 6.83	Emmer 5.67	Highbury 4.33	Einkorn 2.08
Tillering growth stage	Emmer 6.38	Mardler 5.25	Highbury 4.63	Einkorn 3.13
Flagleaf growth stage	Mardler 7.25	Highbury 6.0	Emmer 4.5	Einkorn 2.13
Ear growth stage	Emmer 7.33	Highbury 4.83	Mardler 4.33	Einkorn 1.41

Means of varieties connected by lines are not significantly different from each other (at P=0.05) as analysed by Duncan's Multiple Range Test.

4.3.3.3 Tillering growth stage (Zadoks' growth stage 24 or Feekes' growth stage 2)

No significant 'F' value at P=0.05 was obtained when the data on this section of the study were analysed. However, the mean number of aphids selecting Einkorn was still the lowest while the mean number of aphids selecting Emmer was the highest of all the varieties. Highbury and Mardler were 2nd and 3rd respectively in order of preference by this aphid.

4.3.3.4 Flagleaf growth stage (Zadoks' growth stage 39 or Feekes' growth stage 9)

The mean number of aphids selecting Einkorn was the lowest of all the varieties, but this mean was statistically inseparable from the mean number of aphids selecting Emmer. The mean number of aphids selecting Mardler was the highest and this mean overlapped with the means of Highbury and Emmer. Highbury and Emmer were 2nd and 3rd respectively in order of preference by this aphid.

4.3.3.5 Ear growth stage (Zadoks' growth stage 60 or Feekes' growth stage 10.51)

The mean number of aphids selecting Einkorn was the lowest of all the varieties and this mean was significantly lower than the mean number of aphids selecting each of the other three varieties of wheat. The mean number of aphids selecting Emmer was the highest and this mean was significantly higher than the other means. Highbury and Mardler were 2nd and 3rd respectively in order of preference by this aphid.

4.4 Preference of alate S. avenae for four varieties of wheat at different growth stages

4.4.1 Introduction

The preference response of apterous and alate morphs among cereal varieties have been reported to be similar (Sotherton and van Emden 1982). However, Cartier and Painter (1956) reported differences in the preferences of apterous and alate morphs of cereal aphids among cereal varieties.

This investigation was designed to verify the preference response of alate S. avenae among the same four wheat varieties tested with apterae in the previous experiment.

4.4.2 Methods

All experimental procedures were the same as for the apterous aphids. A randomised block design was used for the experiments. For two and three leaf growth stages, 3 and 15 replicates were used respectively.

4.4.3 Results (Table 4)

4.4.3.1 Two leaf growth stage (Zadoks' growth stage 12 or Feekes' growth stage 1)

The mean number of alates selecting Einkorn was the lowest of all the varieties and this mean overlapped with the means of the other varieties of wheat apart from Emmer. The mean number of alates selecting Emmer was high (1st out of 4 varieties) and this mean was found to overlap with the means of Mardler and

Table 4: Mean number of alate S. avenae selecting the seedlings of four wheat varieties at two growth stages (out of 50 aphids per cage).

Wheat Growth Stage	Wheat varieties			
Two leaf growth stage	Emmer	Mardler	Highbury	Einkorn
	14.67	9.67	9.0	3.67
Three leaf growth stage	Emmer	Highbury	Mardler	Einkorn
	12.13	8.53	6.07	2.0

Means of varieties connected by lines are not significantly different from each other (at P=0.05) as analysed by Duncan's Multiple Range Test.

Highbury. Mardler and Highbury were 2nd and 3rd respectively in order of preference by the alates.

4.4.3.2 Three leaf growth stage (Zadoks' growth stage 13 or Feekes' growth stage 1)

The mean number of alates selecting Einkorn was again the lowest of all the varieties and this mean was significantly lower than the mean number of alates selecting each of the other three varieties of wheat. The mean number of alates selecting Emmer was (as at the two leaf growth stage) the highest of all the varieties of wheat and at this growth stage this mean was significantly higher than the mean number of aphids selecting each of the other three varieties of wheat. Highbury and Mardler were 2nd and 3rd respectively in order of preference by the alates.

4.5 Preference of apterous M. dirhodum for four varieties of wheat at different growth stages

4.5.1 Introduction

The preference response of S. avenae and M. dirhodum among cereal varieties have been reported to be similar (Sotherton and van Emden 1982).

This experiment was designed to compare the preference response of apterous M. dirhodum with that of apterous S. avenae.

4.5.2 Methods

All experimental procedures were the same as for the apterous S. avenae.

As a result of excessive heat in the glasshouse which led to loss of part of the aphid culture and as a result of damage to experimental plants by birds and rodents, the number of varieties involved in this experiment from the tillering growth stage onwards was reduced from seven to four and the number of aphids placed at the centre of each pot was simultaneously reduced to 20. A Latin square design was used for all the experiments. For two, three, tillering, flagleaf and ear growth stages, 3, 2, 2, 2 and 3 replicates were used respectively.

4.5.3 Results (Table 5)

4.5.3.1 Two leaf growth stage (Zadoks' growth stage 12 or Feekes' growth stage 1)

The means of aphids selecting Einkorn and Maris Kinsman were the lowest of all the varieties and these means were statistically inseparable from the means of all other varieties except Emmer. The mean number of aphids selecting Emmer was the highest and this mean was significantly higher than the mean number of aphids selecting any of the other six varieties of wheat. Spelt, Highbury, Mardler and Bounty were 2nd, 3rd, 4th and 5th respectively in order of preference by this aphid.

4.5.3.2 Three leaf growth stage (Zadoks' growth stage 13 or Feekes' growth stage 1)

The mean number of aphids selecting Einkorn was significantly the lowest of all the varieties. Otherwise the remaining varieties could not be separated statistically though Spelt and Emmer were again the two most preferred varieties.

Table 5: Mean number of apterous M. dirhodum selecting the seedlings, leaf segments and excised ears of each wheat variety at different growth stages (out of 50 aphids per pot).

Wheat Growth Stage	Wheat varieties						
Two leaf growth stage	Emmer 8.67	Spelt 6.43	Highbury 5.90	Mardler 5.57	Bounty 4.1	Kinsman 3.86	Einkorn 3.86
Three leaf growth stage	Spelt 7.79	Emmer 7.29	Mardler 7.29	Kinsman 6.93	Bounty 6.79	Highbury 6.43	Einkorn 1.21
Tillering growth stage	Mardler 8.88	Emmer 5.25	Highbury 4.25	Einkorn 1.38			
Flagleaf growth stage	Emmer 6.5	Highbury 5.0	Mardler 3.75	Einkorn 2.38			
Ear growth stage	Emmer 6.42	Highbury 4.67	Mardler 3.75	Einkorn 0.75			

Means of varieties connected by lines are not significantly different from each other (at P=0.05) as analysed by Duncan's Multiple Range Test.

4.5.3.3 Tillering growth stage (Zadoks' growth stage 24 or Feekes' growth stage 2)

The mean number of aphids selecting Einkorn wheat was low (4th out of 4 varieties), but this mean was statistically inseparable from the mean number of aphids selecting Highbury. The mean number of aphids selecting Mardler was the highest of all the varieties and this mean was significantly higher than the mean number of aphids selecting each of the other three varieties of wheat. Emmer and Highbury were 2nd and 3rd respectively in order of preference.

4.5.3.4 Flagleaf growth stage (Zadoks' growth stage 39 or Feekes' growth stage 9)

No significant 'F' value at P=0.05 was obtained when the data on this section of the study were analysed. However, the mean number of aphids selecting Einkorn was again the lowest while the mean number of aphids selecting Emmer was the highest of all the varieties. Highbury and Mardler were 2nd and 3rd in order of preference.

4.5.3.5 Ear growth stage (Zadoks' growth stage 60 or Feekes' growth stage 10.51)

The mean number of aphids selecting Einkorn wheat was again the lowest of all the varieties and this mean was significantly lower than the mean number of aphids selecting each of the other three varieties of wheat. The mean number of aphids selecting Emmer was again the highest of all the varieties, but this mean was statistically inseparable from the mean number of aphids

selecting Highbury. Highbury and Mardler were 2nd and 3rd respectively in order of preference by this aphid.

4.6 Discussion

Einkorn wheat was least preferred among all varieties of wheat and during all growth stages by the apterous and alate morphs of S. avenae while Spelt and Maris Kinsman wheats were the most preferred. Bounty, Highbury, Emmer and Mardler wheats occupied an overlapping intermediate position.

In the case of M. dirhodum, Einkorn wheat was again least preferred during all the growth stages while Spelt and Emmer contrary to the result obtained with S. avenae were most preferred. Bounty, Maris Kinsman, Highbury and Mardler wheats occupied an overlapping intermediate position.

The pattern of preference of apterous and alate morphs of S. avenae was found to be similar (Tables 3 and 4). Schuster and Starks (1973) and Sotherton and van Emden (1982) obtained similar results with apterous and alate morphs of aphids.

In the tests involving S. avenae the ancient wheat Spelt was as susceptible as the modern Maris Kinsman variety which was regarded as a standard susceptible check. In the case of M. dirhodum, Emmer, another ancient wheat, was as susceptible as Mardler and Highbury which are modern varieties. It appears that the inherent ability of some of the ancient wheats to be preferred by the cereal aphids could be as high as those of their modern counterparts.

Vernalisation of cereal varieties has been shown to change the ranking of resistant varieties (Kay, Wratten and Stokes 1981). However, in this study, none of the wheats used was vernalised but Bounty and Mardler normally need

vernalisation. It is strongly felt that the resistance ranking of these two wheats would be lowered if these wheats had been vernalised.

In some cases a small fraction of the aphids did not select any of the plant materials provided. This was probably due to the restlessness of S. avenae as well as the changes in the temperature regimes in the glass-house. Schuster and Starks (1973) in a preference experiment with S. graminum reported that only 74% of all the adult aphids selected plants.

5. ANTIBIOSIS

5.1 Introduction

For the past two decades that entomologists from both the eastern and western hemispheres of the World have been searching for sources of resistance among cereal varieties to the cereal aphids, modern cereal varieties have mostly been used for their investigations (Rautapaa 1966 and 1968; Apablaza and Robinson 1967; Kolbe 1969 and 1970; Dean and Luuring 1970; Malyk and Robinson 1971; Dean 1973a and 1974d; George 1974; Kolbe and Linke 1974; Bakker and Robinson 1975; Wratten 1975, 1977 and 1978; A'Brook and Dewar 1977; Dewar 1977; Starks and Burton 1977; Vereijken 1979; Wratten, Lee and Stevens 1979; Lowe 1980 and 1981; Kay, Wratten and Stokes 1981 and Walters and Dixon 1982). Though ancient in origin, the neglected primitive cereals may well possess potent heritable resistant genes against the cereal aphids which can be combined with commercially acceptable cereal varieties in breeding programmes. An example of the possibilities of primitive cereal varieties serving as sources of resistance to the cereal aphids was recently shown by the study of Sotherton and van Emden (1982) where they demonstrated that an ancient wheat was non-preferred and antibiotic to both S. avenae and M. dirhodum. The chemical or morphological sources of resistance in this ancient wheat have not been reported by these two authors. However, this seems a positive step towards the exploration of a probable wealth of genetic resources embalmed in these ancient cereal varieties.

As antibiosis is a resistant component which adversely affects the reproductive potential of insects, this study was designed to compare the rate of reproduction of S. avenae and M. dirhodum on two ancient and two modern wheats. The two primitive varieties of wheat were Einkorn and Emmer while their modern counterparts were Highbury and Mardler. In a previous study

(Chapter 4) Einkorn was shown to be non-preferred by these aphids while Emmer, Highbury and Mardler were shown to be moderately preferred.

5.2 Experimental techniques

Unvernalised grains of Highbury, Mardler, Emmer and Einkorn wheats were placed between separate moistened Bowater tissue papers and the grains incubated in a warm glasshouse. This technique was used to facilitate rapid germination of the grains of Einkorn. Moreover, choice of seedlings of the same size was found to be possible with this method.

On the fourth day, sixteen 12.5cm diameter pots were filled with compost and labelled. Four germinating grains whose plumules were of equal length were selected from each variety. Each of these seedlings was transplanted singly into a separate pot and watered and the pots placed in the glass-house as a randomised block design with 4 replicates.

Fifty tight 1.5cm diameter leaf clip-cages were selected, soaked in distilled water for 24 hours, washed, rinsed and dried. This was a precautionary measure against accidental contamination of used cages with insecticides. At the two leaf growth stage (Zadoks' growth stage 12 or Feekes' growth stage 1), three 4th instar nymphs of the aphid, cultured on the same wheat variety as that to which they were transferred, were caged on the older of the two leaves of each seedling for five days. On the fifth day, each cage was removed and the number of nymphs reproduced counted. For subsequent weeks fresh aphids were caged on the middle leaf of each plant and finally on the flagleaf at the flagleaf growth stage (Zadoks' growth stage 39 or Feekes' growth stage 9). The study was conducted only on the leaves because cages that would in no way interfere with the morphological activities of the ear could not be obtained.

5.3 Results

The results at each plant age and each aphid species were separately subjected to analysis of variance and the means compared by Duncan's Multiple Range Test. Regression analysis was carried out for the number of nymphs produced by the two aphids on each wheat variety at weekly intervals.

5.3.1 S. avenae (Table 6)

Einkorn

From the 1st week through to the flagleaf growth stage, the lowest number of nymphs was produced on the leaves of Einkorn. However, a significant 'F' value at P = 0.05 was obtained only during the 5th and 6th weeks and on the flagleaf. During the 5th week, the number of nymphs produced on Einkorn was statistically separable from those of all other varieties except Highbury while during the 6th week, the number of offspring produced on Einkorn overlapped with those of all other varieties except Emmer. On the flagleaf, the number of young born on this ancient wheat overlapped with those of all other varieties except Mardler.

Highbury

Except on the 8th week when the greatest number of nymphs were produced on the leaf of Highbury, this modern wheat occupied an intermediate position. On the 5th week, the number of nymphs produced on this wheat variety overlapped with that of all other varieties except Einkorn but during the 6th week, the number of young produced on this wheat was statistically inseparable from those of all other varieties except Emmer. On the flagleaf, the number of young born on this wheat overlapped with

TABLE 6: Mean number of nymphs produced by a single S. avenae in 5 days on four wheat varieties at weekly intervals (means of 4 replicates).

Time of incubating with aphids	Wheat varieties			
First Week	Emmer	Highbury	Mardler	Einkorn
	15.0	14.5	13.75	9.8
Second Week	Mardler	Highbury	Emmer	Einkorn
	6.0	5.5	4.75	3.75
Third Week	Emmer	Highbury	Mardler	Einkorn
	11.5	10.75	7.25	5.5
Fourth Week	Emmer	Highbury	Mardler	Einkorn
	12.0	10.75	7.25	6.25
Fifth Week	Mardler	Emmer	Highbury	Einkorn
	18.25	14.5	11.0	5.25
Sixth Week	Emmer	Mardler	Highbury	Einkorn
	24.25	15.0	14.25	11.0

(Continued)

TABLE 6: (Continued)

Time of incubating with aphids	Wheat varieties			
Seventh Week	Emmer	Mardler	Highbury	Einkorn
	23.25	20.0	17.0	11.0
Eighth Week	Highbury	Emmer	Mardler	Einkorn
	13.75	13.5	11.0	4.75
Ninth Week	Mardler	Emmer	Highbury	Einkorn
	14.5	10.0	9.75	4.75
Flagleaf	Mardler	Highbury	Emmer	Einkorn
	15.25	8.25	8.0	4.75

Means of varieties connected by lines are not significantly different from each other (at $P = 0.05$) as analysed by Duncan's Multiple Range Test.

those of all other wheats except Mardler.

Emmer and Mardler

From the 1st through to the 9th week, the number of nymphs produced on Emmer and Mardler was usually fairly high. More nymphs seemed to be produced on the leaves of Emmer than on the leaves of Mardler. During the 5th week, the number of nymphs produced on these two wheats was statistically inseparable but this number was statistically separable from those of all other varieties except Highbury while during the 6th week, the number of young born on Emmer was both significantly greater than the number of nymphs born on Mardler and those of all other wheats. On the flagleaf, the number of nymphs produced on Mardler was also both significantly greater than the number of offspring produced on Emmer and those of all other wheat varieties. However, the number of nymphs produced on the flagleaf of Emmer overlapped with those of all other wheats except Mardler.

5.3.2 M. dirhodum (Table 7)

Einkorn

Except during the 4th week and on the flagleaf, fewest nymphs were again produced on the leaves of Einkorn. A significant F value at $P = 0.05$ was obtained only during the 2nd and 3rd weeks. During the 2nd week, the number of young produced on Einkorn was significantly less than the number of young produced on all other varieties while during the 3rd week, the number of offspring produced on Einkorn was statistically lower than the number produced on all other varieties except Highbury. In contrast to the result obtained on the flagleaf of Einkorn with S. avenae, the greatest number of M. dirhodum nymphs

TABLE 7: Mean number of nymphs produced by a single M. dirhodum in 5 days on four wheat varieties at weekly intervals (means of 4 replicates).

Time of incubating with aphids	Wheat varieties			
First Week	Emmer	Mardler	Highbury	Einkorn
	13.25	13.25	12.5	9.75
Second Week	Highbury	Mardler	Emmer	Einkorn
	19.75	18.0	17.75	11.75
Third Week	Emmer	Mardler	Highbury	Einkorn
	22.25	17.75	14.25	9.5
Fourth Week	Highbury	Einkorn	Emmer	Mardler
	20.25	15.75	14.25	11.75
Fifth Week	Emmer	Highbury	Mardler	Einkorn
	22.0	21.5	16.5	14.25
Sixth Week	Emmer	Mardler	Highbury	Einkorn
	25.0	25.0	23.75	16.5

(Continued)

TABLE 7: (Continued)

Time of incubating with aphids	Wheat varieties			
Seventh Week	Mardler	Highbury	Emmer	Einkorn
	24.0	18.5	16.75	14.0
Eighth Week	Emmer	Highbury	Mardler	Einkorn
	18.25	17.75	15.75	6.75
Ninth Week	Emmer	Mardler	Highbury	Einkorn
	18.75	16.75	15.5	13.25
Flagleaf	Einkorn	Mardler	Highbury	Emmer
	19.75	14.25	13.0	12.0

Means of varieties connected by lines are not significantly different from each other (at P = 0.05) as analysed by Duncan's Multiple Range Test.

was produced on the flagleaf of Einkorn.

Highbury

With the exception of the 2nd and 4th weeks when the greatest number of nymphs were produced on Highbury, this wheat again occupied an intermediate position. During the 2nd and 3rd weeks, the number of young produced on this wheat was statistically inseparable from those of all other varieties except Einkorn. On the flagleaf, the number of nymphs produced on this modern wheat was moderately low.

Emmer and Mardler

Similar to the result obtained with S. avenae the number of nymphs produced on Emmer and Mardler was high in most cases. Again more young seemed to be produced on the leaves of Emmer than on the leaves of Mardler. In both the 2nd and 3rd weeks, the number of nymphs born on these two wheats was statistically inseparable from each other and this number was also statistically inseparable from those of all other varieties except Einkorn. The number of nymphs born on the flagleaf of Emmer was the lowest of all the varieties while the number of young born on the flagleaf of Mardler was moderately high.

5.4 Discussion

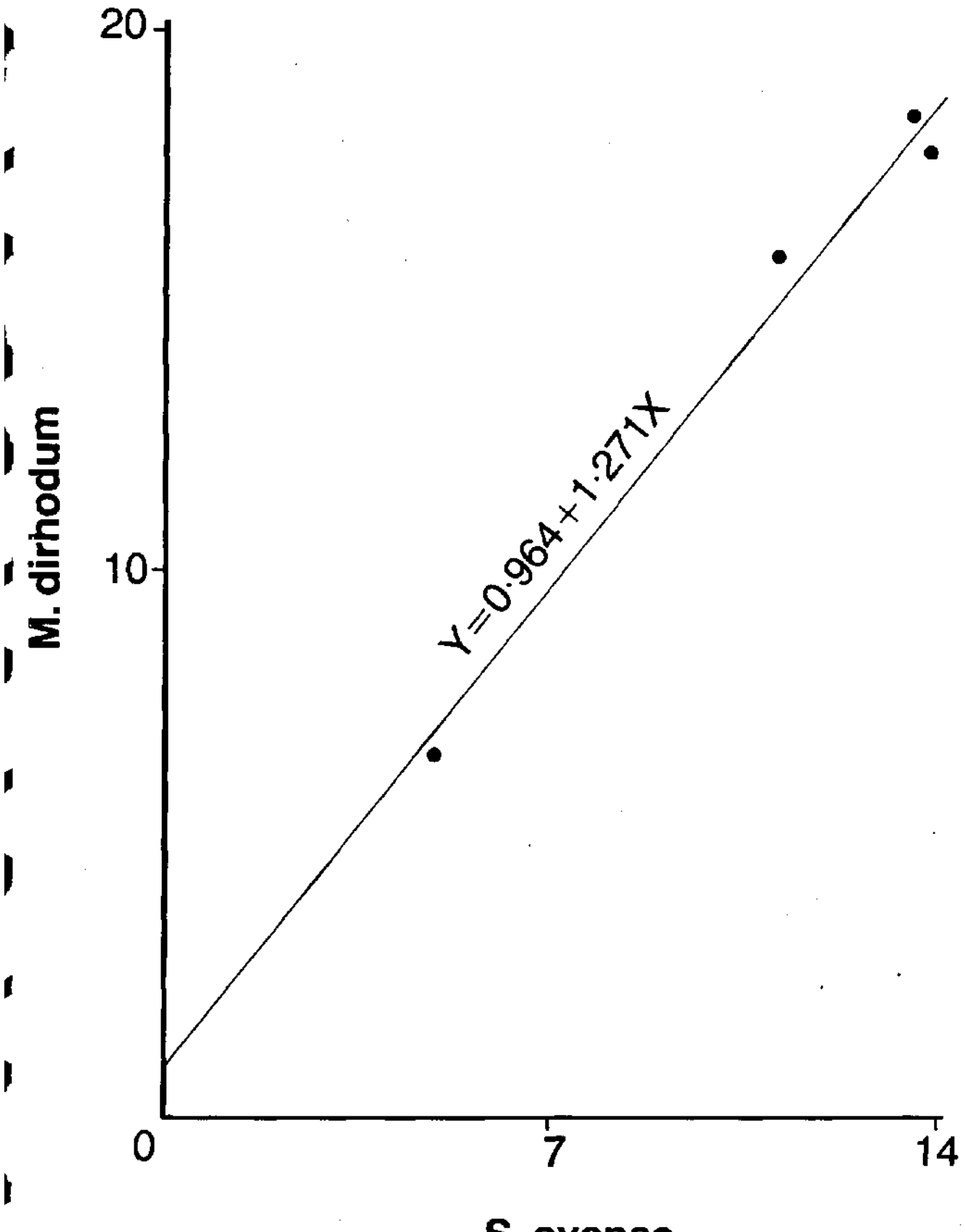
Fewest nymphs were produced on the leaves of Einkorn by both S. avenae and M. dirhodum. On the flagleaf of this wheat, a sharp contrast occurred between the two aphids. While fewest nymphs were produced on the flagleaf of Einkorn by S. avenae, the greatest number was produced by M. dirhodum. This probably suggests differences in the suitability of various plant organs as sources of food to these two aphids.

The number of nymphs produced on Highbury by these two aphids occupied an intermediate position while many nymphs were produced on both Emmer and Mardler by both aphids. The ancient wheat Einkorn seems to be the only cereal variety on whose leaves these two aphids consistently produced remarkably few nymphs, but Einkorn seems to be more susceptible to M. dirhodum than S. avenae. The total number of nymphs that M. dirhodum produced on Einkorn was on average nearly twice the total number of nymphs that S. avenae produced on this ancient wheat, a higher factor than that on the other varieties (Table 8). Regression analysis for the total number of nymphs produced by the two aphids on each wheat variety showed that there was no correlation between the aphids on any wheat. However, the regression analysis for the number of nymphs produced on the four wheat varieties at weekly intervals showed that there was correlation between the aphids only during the 8th week ($F = 141.18$, $R = 0.99$) (Fig. 3).

TABLE 8: Comparison of the total number of nymphs produced by S. avenae and M. dirhodum on four different wheats.

Wheat varieties	Aphids		Ratio of total nymphs produced by S. avenae to that of M. dirhodum
	S. avenae	M. dirhodum	
Emmer	136.75	180.25	1 : 1.32
Mardler	128.25	173.0	1 : 1.35
Highbury	115.5	176.75	1 : 1.53
Einkorn	66.8	131.25	1 : 1.96

Fig. 3: Number of nymphs produced by **S. avenae** and **M. dirhodum** on the leaves of four wheats during the 8th week



6. EFFECT OF INFESTATION BY S. AVENAE AND M. DIRHODUM ON CEREAL GROWTH

6.1 Introduction

The subsequent adverse effects on the quantity and quality of cereal grains due to the infestation of cereal varieties by cereal aphids is perhaps one of the aspects of cereal entomology that most European entomologists have geared their research efforts towards.

The objective of this investigation was to test how far the type of infestation of the cereal aphids (S. avenae and M. dirhodum) which would develop on two ancient and two modern wheat varieties would be reflected in the reduction of the growth of these four wheat varieties. The selected wheat varieties were the ancient wheats Einkorn and Emmer which have been shown to be non-preferred and moderately preferred respectively while the modern varieties were Highbury and Mardler which were both moderately preferred by these aphids.

Damage to the vegetative parts of the plants was studied because severe infestation of the vegetative parts would reduce the vigour of the plant, hence causing a reduction in the yield; and much less is known about damage at this stage than about damage from feeding on the ear.

6.2 Experimental technique

Two hundred and twenty four 12.5cm diameter pots were filled with compost and labelled. Three unvernalised grains of each of Highbury, Mardler and Emmer and six grains of Einkorn were sown in 32 separate pots (24 pots for M. dirhodum). The pots were placed in the glasshouse as a split plot design with 16 replicates for S. avenae and 12 replicates for M. dirhodum. The main plots were infested versus noninfested while the sub-plots were

the varieties. At emergence, the seedlings were thinned to one per pot. At the two leaf growth stage (Zadoks' growth stage 12 or Feekes' growth stage 1), the number of leaves were counted. The length of leaf, length of stem (distance between soil level and base of the youngest leaf) and the height of each plant (distance between soil level and tallest leaf) were measured.

16 potted seedlings of each wheat variety were separately infested with ten 4th instar S. avenae which had been cultured on the same wheat variety as the seedling to which they were transferred. The plants were caged with muslin. 12 potted seedlings of each wheat variety were given similar treatments using M. dirhodum. For every infested plant, there was a corresponding uninfested caged plant. 24 and 48 hours later, each infested plant was carefully checked to ensure that the correct number of aphids were on each plant and that there were no natural enemies accidentally caged with the aphids. Similarly, each uninfested plant was checked to make sure that no uninfested plant had become infested in error.

Though the number of aphids infesting each plant was not counted yet it was strongly felt that the number of aphids infesting each of the four wheat varieties would differ. This was clear from the results obtained for the 'antibiosis' experiment.

Two weeks later the aphids were carefully brushed off each plant and the aphids were crushed. The plant organs were counted and all measurements were repeated. Each plant was cut at ground level, divided into leaf and stem components and each plant component enclosed in a labelled polythene bag and immediately put in a deep freezer. The roots and soil were removed from the pot, placed in a fine metal sieve into which a piece of muslin cloth was placed, bathed carefully in a bucket of water, carefully washed in three separate plastic containers filled with distilled water and rinsed

in the fourth plastic container. The roots were then stored in the same way as the other plant parts. All the plant components were freeze-dried and weighed.

6.3 Results

The percent difference between the final and initial plant organ count and measurements and the percent difference between noninfested and infested plant organ dry weights were calculated using the following formulae:

(1) Plant organ count and measurement

$$\frac{\text{((Final-Initial) Uninfested)-((Final-Initial) Infested)}}{\text{((Final-Initial) Uninfested)}} \times 100$$

(2) Plant organ dry weight

$$\frac{\text{Dry weight uninfested-Dry weight infested}}{\text{Dry weight uninfested}} \times 100$$

These percentages were subjected to analysis of variance and the means compared by Duncan's Multiple Range Test.

6.3.1 S. avenae (Table 9)

Leaf

The percent decrease in the length of the leaf of Einkorn due to the infestation of this aphid was the highest and this decrease overlapped

TABLE 9: Percent reduction in plant growth caused by free infestation of *S. avenae*.

Plant Measurement	Wheat varieties			
Increment in number of leaves	Einkorn 33.5	Highbury 29.0	Emmer 25.5	Mardler 17.6
Increment in length of leaf cm	Einkorn 68.0	Highbury 38.3	Mardler 26.3	Emmer 19.9
Dry weight of leaf gm	Highbury 48.9	Emmer 46.4	Mardler 41.1	Einkorn 27.3
Increment in length of stem cm	Highbury 42.4	Emmer 27.2	Mardler 22.5	Einkorn 21.4
Dry weight of stem gm	Highbury 68.1	Emmer 67.8	Einkorn 63.9	Mardler 57.4
Dry weight of root gm	Highbury 70.4	Emmer 65.7	Mardler 59.0	Einkorn 58.2
Increment in height of plant cm	Einkorn 29.9	Highbury 25.4	Emmer 24.0	Mardler 12.3

Means of varieties connected by lines are not significantly different from each other (at P = 0.05) as analysed by Duncan's Multiple Range Test.

with that of Highbury but statistically separable from those of Mardler and Emmer while the percent decrease in the length of the leaf of Emmer was the smallest and this decrease overlapped with those of all other wheats except Einkorn. The two modern wheats (Highbury and Mardler) occupied an intermediate and statistically inseparable position.

Stem

The percent reduction in the length of the stem of Highbury was the highest and this reduction was significantly higher than those of all other varieties while the percent decrease in the length of the stem of Einkorn was the smallest and this decrease overlapped with those of all other varieties except Highbury. Emmer and Mardler occupied an intermediate and statistically inseparable position.

Root

The percent decrease in the dry weight of the root of Highbury was again the highest while that of Einkorn was again the smallest. Emmer and Mardler again occupied an intermediate position.

Generally, the percent reduction of the plant organs of Highbury due to the infestation of S. avenae tended to be high while that of Einkorn tended to be small but Emmer and Mardler occupied an intermediate position.

6.3.2 M. dirhodum (Table 10)

Leaf

Percent decrease of the dry weight of the leaf due to the infestation of M. dirhodum was highest on Emmer and this decrease was statistically

TABLE 10: Percent reduction in plant growth caused by free infestation of M. dirhodum.

Plant Measurement	Wheat varieties			
Increment in number of leaves	Einkorn	Emmer	Mardler	Highbury
	38.3	36.1	34.7	23.6
Increment in length of leaf cm	Einkorn	Emmer	Highbury	Mardler
	40.0	34.6	13.1	9.2
Dry weight of leaf gm	Emmer	Mardler	Einkorn	Highbury
	59.8	52.3	46.2	45.6
Increment in length of stem cm	Einkorn	Mardler	Highbury	Emmer
	90.9	86.2	65.1	29.7
Dry weight of stem gm	Emmer	Mardler	Einkorn	Highbury
	74.5	72.7	66.3	57.8
Dry weight of root gm	Highbury	Emmer	Einkorn	Mardler
	46.3	44.8	40.1	34.0
Increment in height of plant cm	Mardler	Einkorn	Highbury	Emmer
	62.2	53.9	51.4	31.0

Means of varieties connected by lines are not significantly different from each other (at P = 0.05) as analysed by Duncan's Multiple Range Test.

separable from those of all other varieties except Mardler while the decrease in the weight of the leaf of Highbury was the smallest and this decrease overlapped with those of all other varieties except Emmer. Einkorn and Mardler occupied an intermediate and statistically inseparable position.

Stem

The percent reduction in the length of the stem of Einkorn was the highest and this reduction was statistically inseparable from those of all other varieties except Emmer, where the percent decrease was significantly smaller than those of all other varieties. The percent decrease in the dry weight of the stem of Emmer was the highest and this decrease was statistically inseparable from those of all other wheats except Highbury while the decrease in the dry weight of the stem of Highbury was the smallest and this dry weight was statistically separable from those of all other varieties except Einkorn. Mardler and Einkorn occupied an intermediate and overlapping position.

Root

Due to the infestation of M. dirhodum, the percent decrease in the dry weight of the root of Highbury was the highest while that of Mardler was the smallest. The decrease in the dry weight of the root of the two ancient wheats (Einkorn and Emmer) occupied an intermediate position.

Generally, the percent reduction of the plant organs of Emmer tended to be high while that of Highbury tended to be small. Einkorn and Mardler occupied an intermediate position.

6.4 Discussion

The percent decrease of the leaf, stem and root due to the infestation of S. avenae was high for Highbury while this percentage decrease was small for Einkorn but Emmer and Mardler occupied an intermediate position. Contrasted to the result obtained for S. avenae, percent decrease due to the infestation of M. dirhodum tended to be high on Emmer while it was small on Highbury. Einkorn and Mardler occupied an intermediate position.

The result obtained for Einkorn with M. dirhodum should be interpreted with caution because the percent decrease in the dry weights of the leaf, stem and root difference of Einkorn (moderately affected) and Highbury (least affected) was small. Hence there seems to be a very little difference between the reaction of Einkorn and Highbury to the infestation of M. dirhodum.

The result obtained for 'antibiosis' indicated that the number of aphids infesting each wheat variety differed hence Einkorn wheat would be infested with the fewest aphids if the aphid-plant burden had been counted. But for certain parameters tested (e.g. number of leaves and length of leaf) in this experiment, percent decrease due to the infestation of both S. avenae and M. dirhodum was found to be the highest for Einkorn wheat. If these few aphids which infested this ancient wheat could cause such remarkable percent decrease in plant organs, it would appear that Einkorn has not got the inherent ability to tolerate the infestation of these aphids if they are forced to feed on it.

7. RESTLESSNESS

7.1 Introduction

In recent years resistant cereal varieties have been developed as a part of a package for the control of cereal aphids but the mechanisms involved in resistance are still only partially known. Among the mechanisms of resistance to cereal aphids studied in this country were those described by Lowe (1980 and 1981) who reported that Kador and Amigo wheats were antibiotic to S. avenae while Sotherton and van Emden (1982) showed that an ancient wheat exhibited both non-preference and antibiosis to S. avenae. There has not been any published work on the effect of resistance on the settling behaviour of cereal aphids on various aerial organs of cereal varieties in Great Britain. Similarly, in other parts of the world very little attention has been paid to this aspect of cereal entomology. The only published work seems to be that of Starks and Burton (1977) in the United States of America who demonstrated that apterous nymphs of S. graminum were more restless on seedlings of resistant barley, wheat, oat and rye than on their susceptible counterparts. In their study, the nymphs were placed on the cereal plants and the distance walked calculated every 24 hours. These American entomologists did not, however, watch the activities of the aphid between observations.

The present study was designed to investigate the effect of any plant resistance on the movement of adult apterous S. avenae on the surfaces of three plant organs at three different growth stages using four varieties of wheat. The four varieties of wheat selected were the ancient wheat Einkorn which in the previous experiments had been least (7th out of 7 varieties) preferred by S. avenae and Spelt which was most preferred. Emmer and Mardler wheats were intermediate in their degree of preference

by this aphid. Thus the experiment involved one modern and three ancient wheats.

7.2 Experimental technique

At weekly intervals, sixteen 12.5cm diameter pots were filled with compost and each pot was labelled. Unvernalised seeds of each of the four varieties of wheat were sown in four of the pots. The pots were placed in the glass-house as a completely randomised design with 31 replicates. At emergence, the seedlings were thinned to one per pot.

At each defined growth stage, the length of the plant organ to be tested was measured. A rectangular strip measuring about 60cm in length and 20cm in breadth was cut from 0.1mm squared graph paper. The strip was pinned on a piece of bamboo stick and this was carefully staked adjacent to the whole length of the plant organ. With dangling leaves, the tip of the leaf was carefully clamped with a 1.5cm diameter insect cage attached with string to an improvised support. This enabled all the activities of the aphid to be seen clearly.

An adult *S. avenae* cultured on Maris Kinsman wheat was carefully placed with a camel hair brush at one end of the plant organ to be tested and the stop watch was simultaneously started. The activities of the aphid such as the number of stops made and the time spent at each stop, the number of times honeydew was produced, the number of times nymphs were produced and the total time spent in walking were recorded on the adjacent graph paper without disturbing the aphid. The stop watch was switched off immediately the aphid reached the other end of the plant organ. Each plant organ was used only once. Any aphid which accidentally fell off the surface of the plant organ during the course of an observation was killed and the results discounted. Similarly, aphids which successfully walked through the whole

length of the plant organ were killed after the observation. This was a precautionary measure against the repetitive use of an aphid as this could influence the duration of feeding of the aphid.

7.3 The movement of adult apterous S. avenae on the surfaces of the leaf of seedlings, flagleaves and ears of four varieties of wheat

7.3.1 Introduction

Wherever they are present, hairs are major physical features of leaf surfaces. Hairs have been shown to influence the movement of phytophagous insects (Johnson 1953 and 1956; Thurston, Smith and Cooper 1966; Gibson 1971; Smith, Wilson and Wilson 1975 and Chapman 1977). These outgrowths entangle the insects (Johnson 1953 and Smith, Wilson and Wilson 1975).

Among the four varieties of wheat selected, the leaves of Spelt were hairy while the leaves of Emmer and Mardler were rather smooth. The leaves of Einkorn were intermediate between these two types but coarse and very much reduced in size particularly in width.

7.3.2 Results

Except 'feeding time' on the seedling, flagleaf and ear, all the data required normalisation by transformation to natural logarithms. The data were subjected to analysis of variance and the means compared by Duncan's Multiple Range Test.

Very few nymphs and drops of honeydew were produced during the experiment; the erratic results could not be used.

7.3.2.1 Two leaf growth stage (Zadoks' growth stage 12 or Feekes' growth stage 1) (Table 11).

Total time spent on the leaf per centimetre

The results were expressed in this way to take account of differences between the varieties in the length of the plant organs. This was considered important as the variety on which the aphid was most restless (Einkorn) also had the shortest leaves (Fig. 4).

No significant 'F' value at P = 0.05 was obtained when the data were analysed. However, time/cm on the seedling of Einkorn was the shortest of all the varieties and this time was shorter than those on Emmer, Spelt and Mardler by factors of 1.7, 2.2 and 3.5 respectively. Emmer and Spelt occupied an intermediate position. The longest time/cm was spent on the seedling of Mardler and this time was longer than the times spent on the seedlings of Spelt, Emmer and Einkorn by factors of 1.6, 2 and 3.5 respectively.

Feeding time

Though again no significant 'F' value at P = 0.05 was obtained when the data on this aspect of the study were analysed yet again the shortest time was spent feeding on the seedling of Einkorn of all the varieties and this time was 2.7, 3.2 and 6 times shorter than the time spent feeding on the seedlings of Emmer, Spelt and Mardler respectively. Emmer and Spelt again occupied an intermediate position. Longest time was spent feeding on the seedlings of Mardler and this time was 1.8, 2.2 and 6 times as long as those on Spelt, Emmer and Einkorn

TABLE 11: Activity of adult apterous S. avenae on the leaves of seedlings of four wheat varieties at two leaf growth stage

Activity	Wheat varieties			
Log total time in seconds per centimetre (Actual time in brackets)	Mardler 2.61 (37.9)	Spelt 2.21 (23.6)	Emmer 2.18 (19.1)	Einkorn 1.82 (10.8)
Feeding time in seconds	Mardler 372	Spelt 197	Emmer 167	Einkorn 61
Wandering time as per cent of total time (Logarithm transformation. Actual percentage in brackets)	Einkorn 4.49 (93.4%)	Spelt 4.30 (83.3%)	Emmer 4.29 (83.5%)	Mardler 3.95 (72.0%)

Means of varieties connected by lines are not significantly different from each other (at P = 0.05) as analysed by Duncan's Multiple Range Test.

respectively.

Wandering time as per cent of total time

Few significant differences were recorded, which is related to the lack of significant differences in feeding time. On the seedling of Einkorn, the longest proportion of the time was spent wandering out of all the varieties and this time was 1.1, 1.1 and 1.3 times longer than the time spent wandering on the seedlings of Spelt, Emmer and Mardler. Again Emmer and Spelt occupied an intermediate position, with a very similar proportion of the time spent wandering on the seedlings of these two wheats. The shortest proportion of the time was spent wandering on Mardler and this time was significantly shorter than those on Emmer, Spelt and Einkorn by factors of 1.2, 1.2 and 1.3 respectively. It seems that this aphid spent a fairly high proportion of the time wandering on the seedlings of each of the four wheat varieties hence there was little difference between varieties.

7.3.2.2 Flagleaf growth stage (Zadoks' growth stage 39 or Feekes' growth stage 9) (Table 12).

Total time spent on the flagleaf per centimetre

Similar to the results obtained during the seedling growth stage, the time/cm on the flagleaf of Einkorn wheat was again the shortest of all the varieties and this time was significantly shorter than the time spent on Mardler, Emmer and Spelt by factors of 9, 14 and 23 respectively. The times/cm spent on the flagleaves of Mardler and Emmer occupied an intermediate

TABLE 12: Activity of adult apterous S. avenae on the flagleaves of four wheat varieties at flagleaf growth stage

Activity	Wheat varieties			
Log total time in seconds per centimetre (Actual time in brackets)	Spelt 3.07 (165)	Emmer 2.96 (100)	Mardler 2.90 (62)	Einkorn 1.73 (7)
Feeding time in seconds	Spelt 3246	Emmer 1640	Mardler 1079	Einkorn 34
Wandering time as per cent of total time (Logarithm transformation. Actual percentage in brackets)	Einkorn 4.42 (86.0%)	Mardler 3.78 (61.8%)	Emmer 3.52 (53.6%)	Spelt 3.45 (56.4%)

Means of varieties connected by lines are not significantly different from each other (at P = 0.05) as analysed by Duncan's Multiple Range Test.

position. The longest time/cm was spent on the flagleaf of Spelt and this time was 1.6, 2.6 and 23 times as long as the time spent on the flagleaves of Emmer, Mardler and Einkorn respectively. However, statistically only Einkorn was separable from the other varieties.

Feeding time

Consistent with the trend obtained at the two leaf growth stage, a short time was spent feeding on the flagleaf of Einkorn and this time was significantly shorter than the times spent on the flagleaves of Mardler, Emmer and Spelt by factors of 32, 48 and 95 respectively. As with total time/cm, Emmer and Mardler occupied an intermediate position. A significantly long time was spent feeding on the flagleaf of Spelt and this time was longer than the times on Emmer, Mardler and Einkorn by factors of 2, 3 and 95 respectively.

Wandering time as per cent of total time

Also similar to the results obtained during the seedling growth stage, the greatest proportion of the time was spent wandering on the flagleaf of Einkorn and this time was 1.4, 1.5 and 1.6 times as great as and significantly distinguishable from the times on Mardler, Spelt and Emmer respectively. Mardler occupied an intermediate position. The proportion of time spent wandering on the flagleaves of both Spelt and Emmer wheats was almost equal and this time was about 1.1 and 1.6 times as long as the times spent on Mardler and Einkorn respectively.

7.3.2.3 Ear growth stage (Zadoks' growth stage 60 or Feekes' growth stage 10.51) (Table 13)

Total time spent on the ear per centimetre

Consistent with the results obtained during both the seedling and flagleaf growth stages, the least time/cm was again spent by this aphid on the ear of Einkorn wheat out of all the varieties and this time was significantly shorter than the times on Emmer, Spelt and Mardler by factors of 15, 27 and 71 respectively. Emmer and Spelt occupied an intermediate position. The longest time/cm was spent on the ear of Mardler and this time was longer than the times spent on the ears of Spelt, Emmer and Einkorn by factors of 2.5, 4.6 and 71 respectively, and statistically distinguishable from Emmer and Einkorn.

Feeding time

In agreement with the results obtained during the two previous growth stages, the shortest time was spent feeding on the ear of Einkorn and this time was shorter than the time spent on the ears of Emmer, Spelt and Mardler by factors of 163, 362 and 739 respectively. The difference with Mardler was statistically significant. Similar to the result obtained during the seedling growth stage, Emmer and Spelt occupied an intermediate position. The longest time was spent feeding on the ear of Mardler of all the varieties and this time was significantly longer than the time spent feeding on the ears of Spelt, Emmer and Einkorn by factors of 2, 4.5 and 739 respectively.

TABLE 13: Activity of adult apterous S. avenae on the ears of four wheat varieties at ear growth stage

Activity	Wheat varieties			
Log total time in seconds per centimetre (Actual time in brackets)	Mardler 5.49 (1133)	Spelt 4.76 (440)	Emmer 3.99 (244)	Einkorn 2.53 (16)
Feeding time in seconds	Mardler 7392	Spelt 3616	Emmer 1634	Einkorn 10
Wandering time as per cent of total time (Logarithm transformation. Actual percentage in brackets)	Einkorn 4.53 (93.7%)	Emmer 3.69 (63.5%)	Spelt 3.36 (48.6%)	Mardler 2.61 (38.9%)

Means of varieties connected by lines are not significantly different from each other (at P = 0.05) as analysed by Duncan's Multiple Range Test.

Wandering time as per cent of total time

Also similar to the results obtained during the two previous growth stages (seedling and flagleaf) a long proportion of time was spent wandering on the ear of Einkorn and this time was 1.4, 2 and 2.4 times as long as and significantly distinguishable from the times on Emmer, Spelt and Mardler respectively. Emmer and Spelt again occupied an intermediate position. The shortest proportion of the time was spent wandering on the ear of Mardler and this time was significantly shorter than those on Spelt, Emmer and Einkorn by factors of 1.2, 1.6 and 2.4 respectively.

7.4 Discussion

S. avenae spent a short total time (as time/cm) on Einkorn at all three growth stages; this was significantly shorter than on the other varieties on the flagleaf and ear of this ancient wheat. A small proportion of this time was devoted to feeding while the rest of the time was spent wandering. On the leaves, this aphid was observed making repetitive attempts to feed, but the efforts were abortive with the attempts ending in short jabs while on the ear the aphid found it almost impossible to feed at the base of the spikelet. It seems that this aphid not only would not feed on this variety but tried to leave its surface as quickly as possible. This would seem a valuable resistance phenomenon if it could be combined into a commercially acceptable variety.

Except on the flagleaf, a fairly long time was spent feeding by S. avenae on the three plant organs of Emmer and therefore a fairly short time was devoted to wandering. Observations showed that aphids find it moderately difficult to feed at the base of the spikelet.

With the exception of the flagleaf of Mardler where the time spent feeding was 3rd out of 4 varieties, the times spent feeding on the plant organs of Mardler and Spelt wheats were either 1st or 2nd out of 4 varieties. Aphids were observed moving and feeding very easily at the bases of the spikelets of Spelt but very much less so at the bases of the spikelets of Mardler. Hairs were not observed acting as deterrents to the movement of this aphid on the leaf of Spelt. The fact that this aphid spent a relatively short time on the three plant organs of Einkorn was not because the average length of the plant organs of Einkorn was always the shortest (Figs. 4, 5 and 6). Firstly, the time was corrected for length of plant organ for the analysis. Secondly, the average length of the ear of Einkorn was the same as that of Mardler (6.5cm, Fig. 6) but the mean time spent feeding on the ear of Mardler was longer than the mean time spent feeding on the ear of Einkorn by a factor of over 700. This shows that Einkorn has some special anatomical or chemical characteristics quite separate from general size and appearance which made this ancient wheat to be non-preferred by S. avenae.

Fig. 4: Relationship of the length of plant organ to the time spent by adult apterous **S. avenae** at two leaf growth stage

Ei = Einkorn
Em = Emmer
M = Mardler
Sp = Spelt

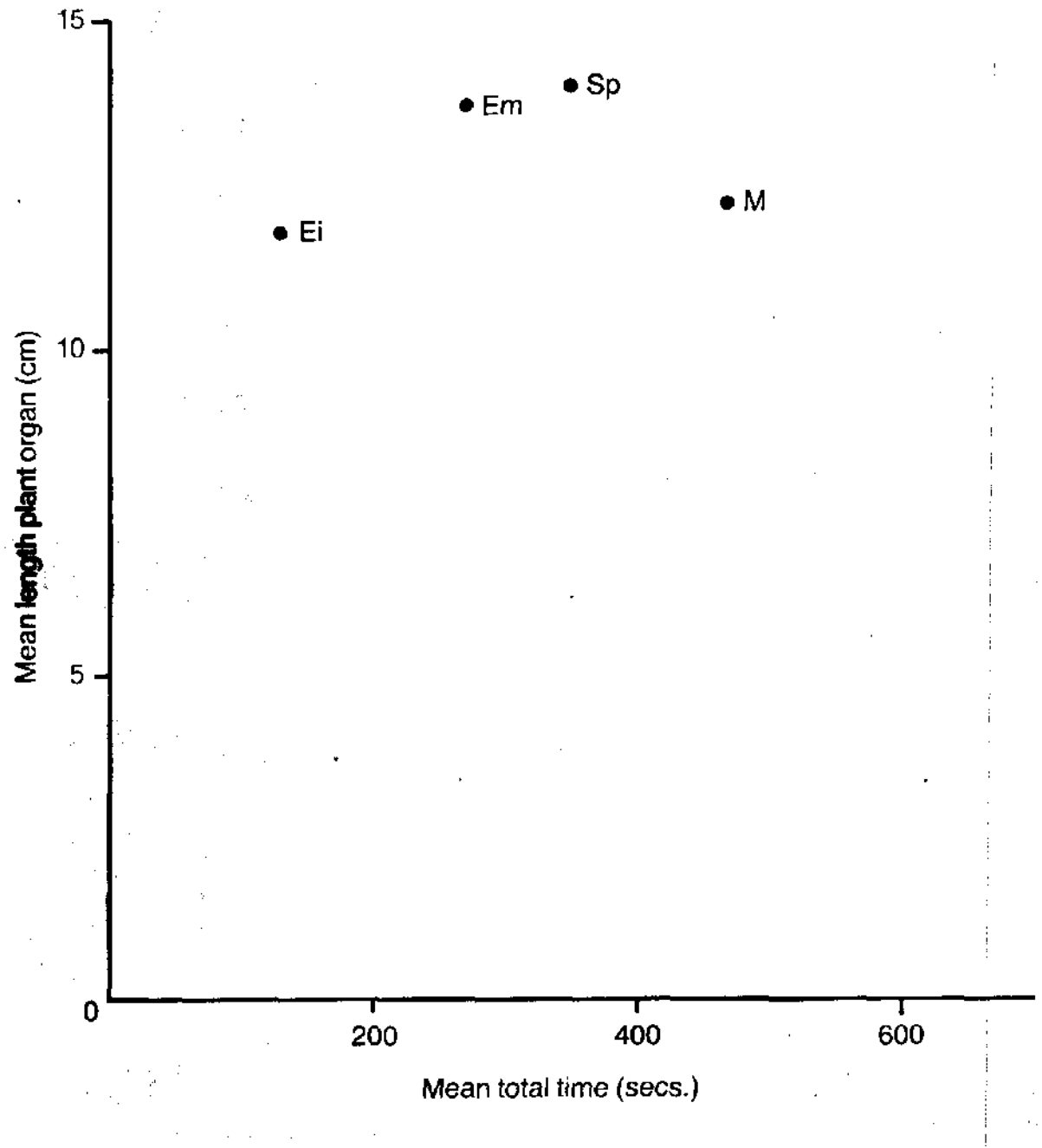


Fig. 5: Relationship of the length of plant organ to the time spent by adult apterous **S. avenae** at flagleaf growth stage

Ei = Einkorn
Em = Emmer
M = Mardler
Sp = Spelt

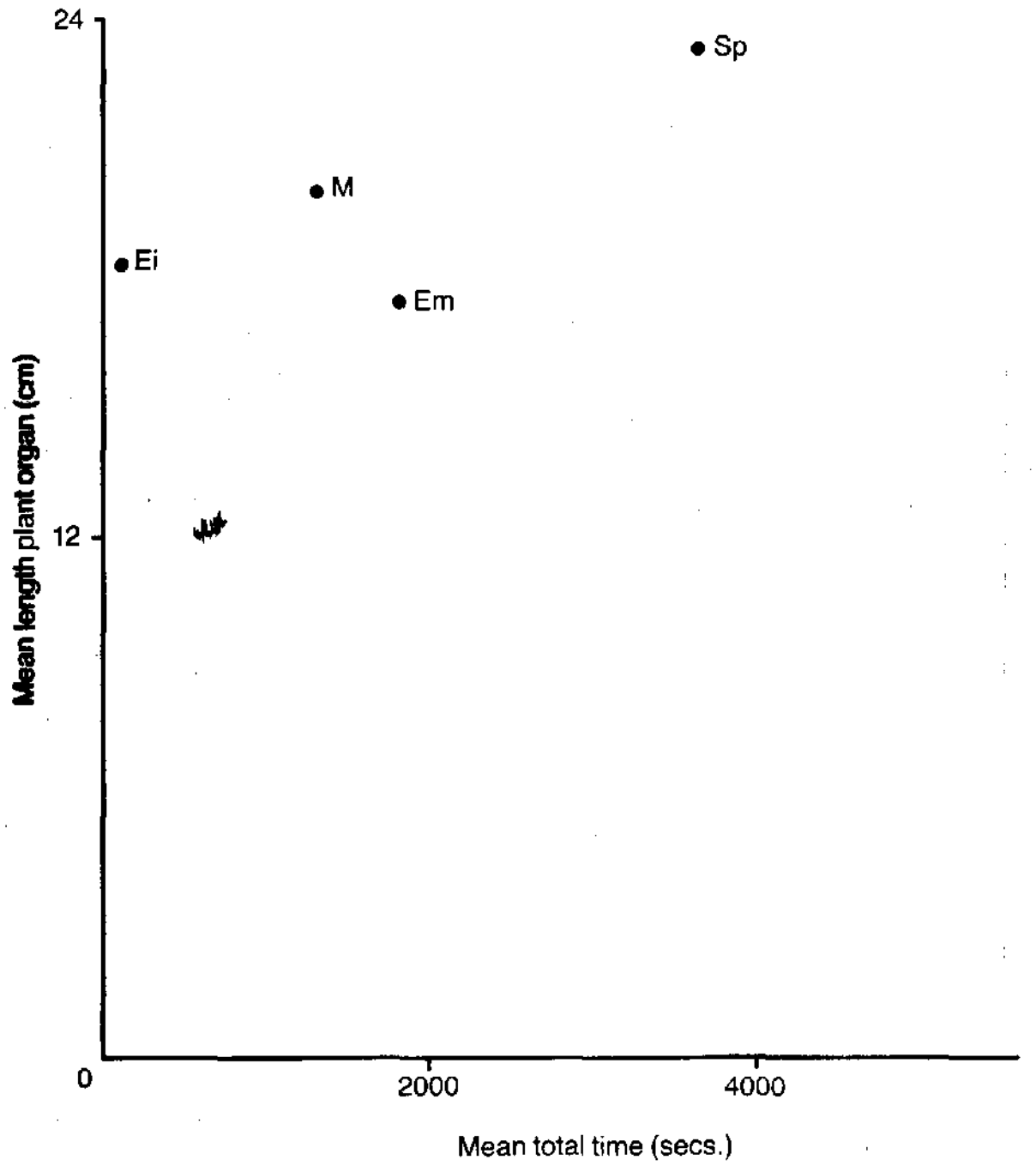
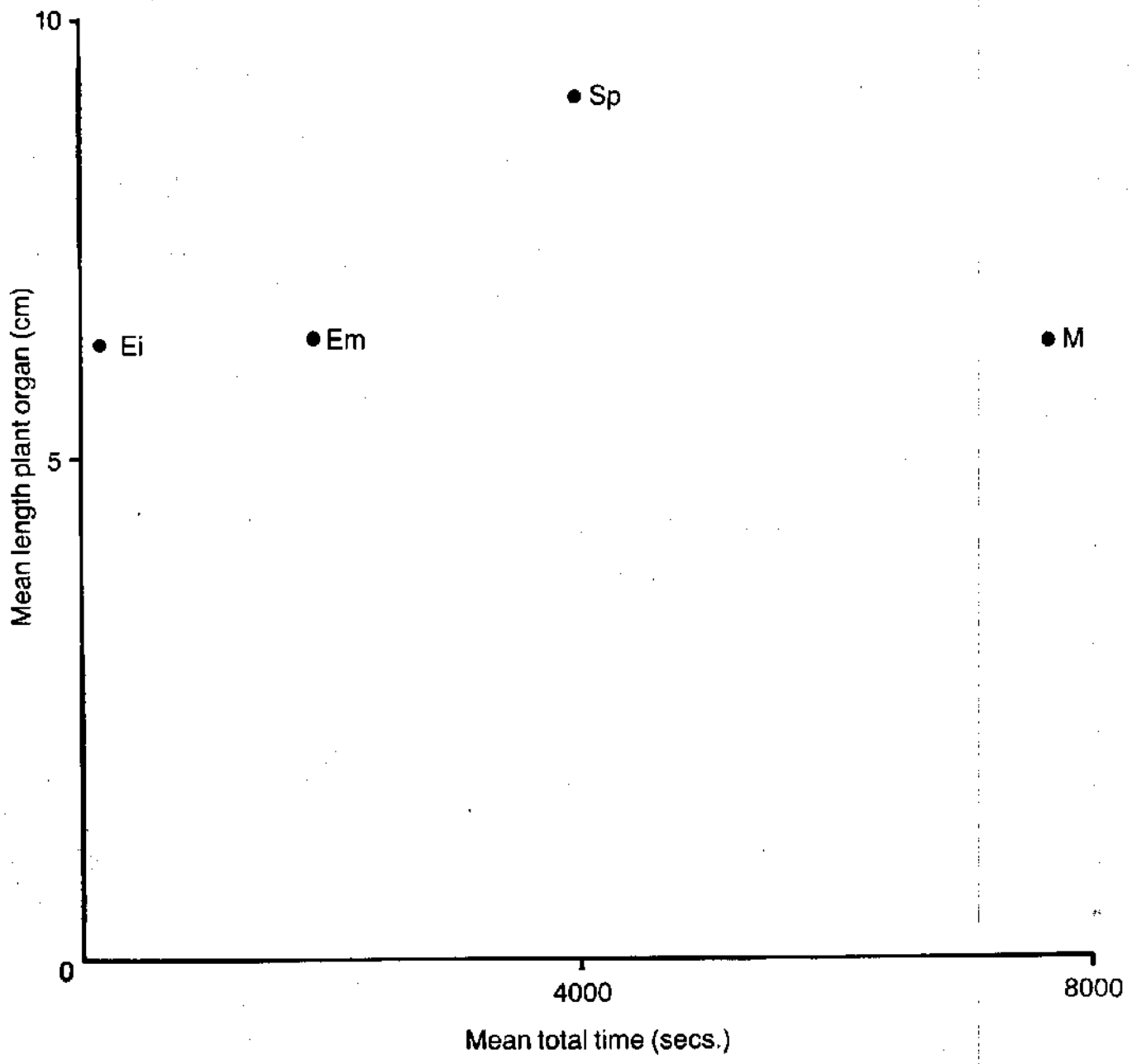


Fig. 6: Relationship of the length of plant organ to the time spent by adult apterous **S. avenae** at ear growth stage

Ei = Einkorn
Em = Emmer
M = Mardler
Sp = Spelt



8. PATTERN OF COLONISATION OF S. AVENAE ON EINKORN, EMMER AND SPELT WHEATS FROM FLAGLEAF TO SENESCENCE GROWTH STAGE

8.1 Introduction

Since the beginning of this study, I had the impression that the pattern of colonisation of S. avenae on various wheat varieties under investigation appeared to differ when aphids were cultured on these wheats from seedling to senescence (Zadoks' growth stage 12 to 92). Moreover, Wratten (1978) established that at the peak of infestation of cereals the percentage distribution of S. avenae on the ear, flagleaf, leaf two and leaf three was 89, 5, 4 and 2 respectively. The flagleaf was reported as a plant organ which contributed most of assimilates used for the production of the ear (Spiertz 1978). Hence it appears that infestation of the plant including the flagleaf and ear by S. avenae can be very damaging to the plant. A study was therefore set up to verify how this aphid colonised the part of the plant including the flagleaf and ear from flagleaf growth stage to senescence growth stage. Particular attention was paid to the movement of the aphid from one newly formed plant organ to another. The order in which the plant organs are formed is as follows: flagleaf - awn - spikelet - ear. The wheat varieties selected for the study were Einkorn, Emmer and Spelt which were least, moderately and most preferred respectively in previous experiments.

8.2 Experimental technique

At weekly intervals, nine pots were filled with compost and labelled. Three unvernalised seeds of Emmer and Spelt and six of Einkorn were sown separately with three pots per variety. The pots were randomised and placed in the glasshouse. At emergence the seedlings were thinned to one plant per pot.

At the stem extension growth stage (Zadoks' growth stage 31 or Feekes' growth stage 6) the plants were placed among infested Bounty, Highbury, Mardler, Emmer, Einkorn, Spelt and Maris Kinsman wheats. At Zadoks' growth stage 39, tillers of Einkorn, Emmer and Spelt whose flagleaves had been infested by a single aphid were selected and the population allowed to develop from this one aphid. These tillers were subsequently examined daily and the number of times aphids were found on various plant organs in only the area between the flagleaf and the ear were noted. Also the number of aphids selecting the awn, base of the spikelet, culm, stem, dorsal part of the spikelet, lateral part of the spikelet, rachis, ventral part of the spikelet and flagleaf as feeding sites were noted. The pattern of movement of the aphids from one newly formed plant organ to another was recorded in only the area between the flagleaf and the ear.

8.3 Results

Selection of feeding sites

The mean number of aphids selecting each feeding site was converted to percentages using the formula below:

$$\frac{\text{Mean number of aphids selecting a feeding site e.g. awn throughout the duration of the experiment}}{\text{Mean number of aphids selecting all the nine feeding sites throughout the duration of the experiment}} \times 100$$

The percentage number of times aphids were found infesting any location e.g. 'point of ear emergence' at any growth stage was computed using the formula below:

$$\frac{\text{Number of times aphids were found on a location e.g. 'point of ear emergence' throughout the duration of each growth stage}}{\text{Total number of times the location e.g. 'point of ear emergence' was checked throughout the duration of each growth stage}} \times 100$$

The percentage number of times that S. avenae was present on different plant organs at each growth stage was computed using the formula below:

$$\frac{\text{Number of times aphids were present on a plant organ e.g. 'spikelet' throughout the duration of each growth stage}}{\text{Total number of times aphids were present on all the plant organs (e.g. awn, spikelet, rachis and flag-leaf) throughout the duration of each growth stage}} \times 100$$

8.3.1 Pattern of infestation of the wheat varieties (Figs. 7 and 8)

The pattern of colonisation of Emmer and Spelt was similar but that of Einkorn differed in certain respects and these are pointed out at relevant places below.

On all varieties, S. avenae was found in close proximity to the point of ear emergence on the flagleaf at Zadoks' growth stage 39. This location was selected as the starting point because observations showed that apart from this stage of plant growth, aphids are rarely found at this location. I had the impression that the aphids maintained this position until they received a particular stimulus probably coincident with the protrusion of the first strand of the awn. On Einkorn, the flagleaf adjacent to the point of ear emergence was checked 28 times and out of these 28 times aphids were found on the flagleaf adjacent to the point of ear emergence 8 times (28.6 per cent) and during this time also the aphids were found on the leaf blade of the flagleaf 2 times (7.1 per cent). The aphids were neither found on the flagleaf adjacent to the point of ear emergence nor on the leaf blade of the flagleaf 18 times (64.3 per cent). Out of the 10 times that this aphid was present on both the flagleaf adjacent to the point of ear emergence and the leaf blade of the flagleaf, S. avenae was found on the flagleaf adjacent to the point of ear emergence 80 per cent of the time while at the remaining 20 per cent of the time this aphid was found on the leaf blade of the flagleaf. On Emmer, the flagleaf adjacent to the point of ear emergence was checked 16 times and out of these 16 times, aphids were found on the flagleaf adjacent to the point of ear emergence 13 times (81.2 per cent) while in the remaining 3 times (18.8 per cent) the aphids were found on the leaf blade of the flagleaf. The flagleaf adjacent to the point of ear emergence was

Fig. 7: Pattern of colonisation of Emmer by **S. avenae** between the flagleaf and the ear

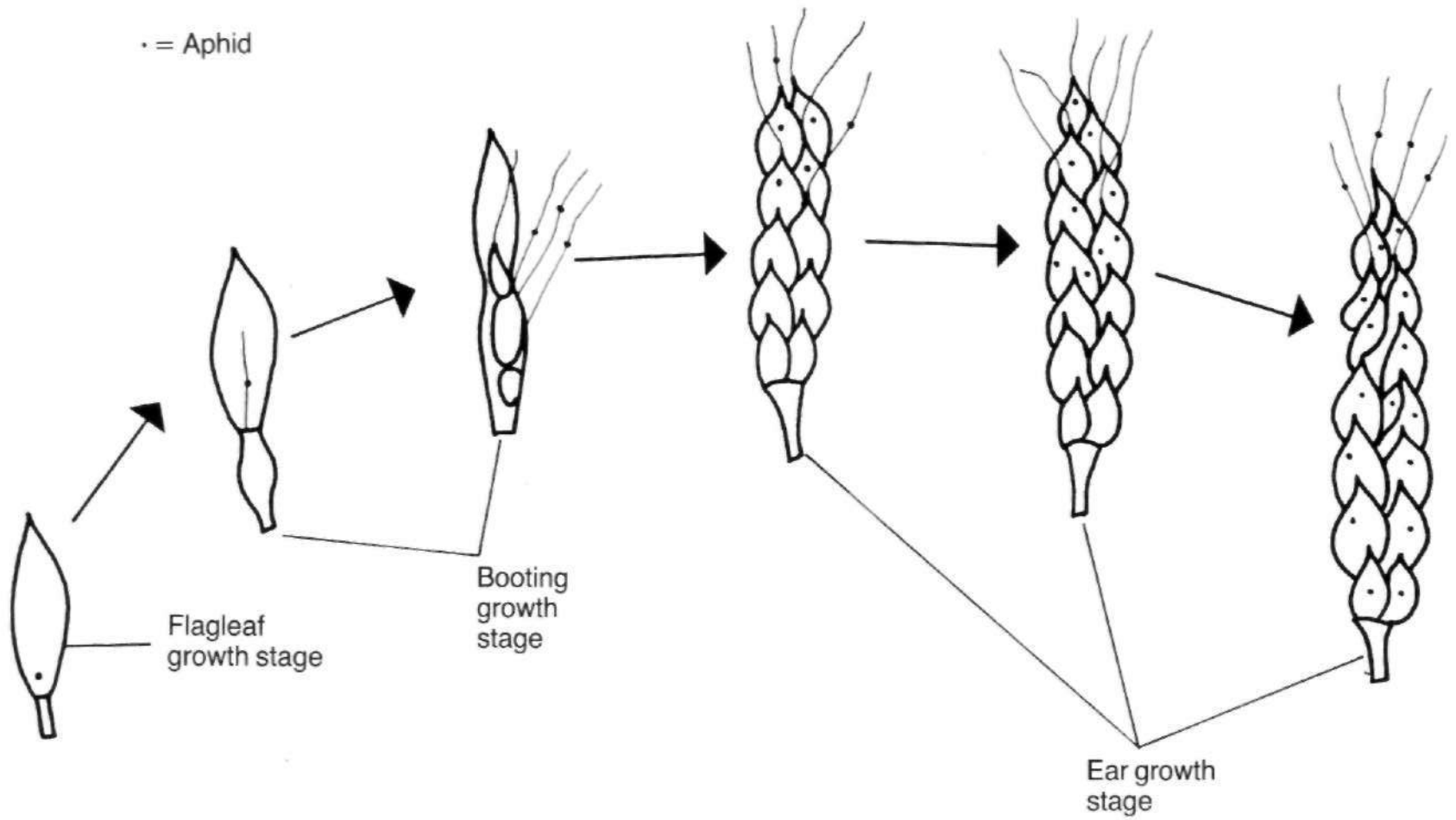
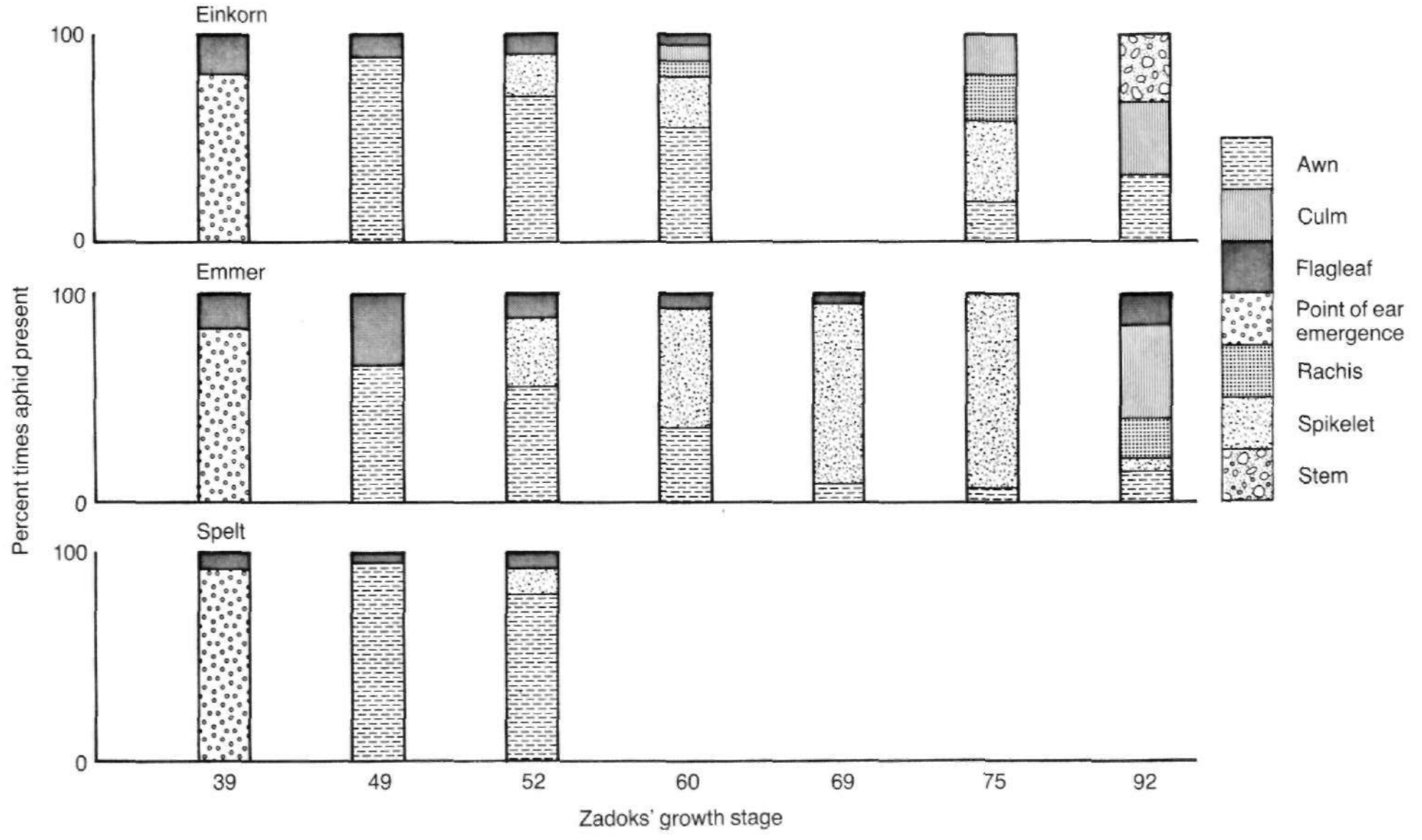


Fig. 8: Percentage number of times that **S. avenae** was present on different plant organs, at each growth stage on three wheat varieties



checked on Spelt 44 times and of these 44 times, aphids were found on the flagleaf adjacent to the point of ear emergence 41 times (93.2 per cent) while at the other 3 times (6.8 per cent) these aphids were found on the leaf blade of the flagleaf.

One possible explanation for the reason why this aphid was neither found on the flagleaf adjacent to the point of ear emergence nor on the leaf blade of the flagleaf of Einkorn a high percentage (64.3 per cent) of the times was that the preference tests suggested that the non-preference of S. avenae for Einkorn could be classified at least as a high level of resistance and sometimes immunity. Apart from the preference experiments, the inability of S. avenae to stay and feed on Einkorn was also shown during the 'restlessness' tests where this aphid spent a very short time on this diploid ancient wheat and also spent a very short time feeding on the seedling, flagleaf and ear.

↓

After the protrusion of the first awn at the booting growth stage (Zadoks' growth stage 49), this first awn became infested. This first awn was checked on Einkorn 37 times and aphids were found on the awn 8 times (21.6 per cent) while the aphids were found infesting the leaf blade of the flagleaf only once (2.7 per cent). Neither the awn nor the leaf blade of the flagleaf was infested 28 times (75.7 per cent). Out of the 9 times that this aphid was found on both awn and the leaf blade of the flagleaf, S. avenae was present on the awn and the leaf blade of the flagleaf in 88.9 and 11.1 per cent of the time respectively. On Emmer, the awn was checked 17 times and in 11 times (64.7 per cent) aphids were found infesting the awn while at the remaining 6 times (35.3 per cent) the aphids were found infesting the leaf blade of the flagleaf. Also on Spelt the awn was checked 31 times

and in 30 times (96.8 per cent) the aphids were found on the awn while the aphids were found on the leaf blade of the flagleaf only once (3.2 per cent).

At the advanced booting growth stage (Zadoks' growth stage 52) which was usually accompanied by the exposure of the spikelets, the flagleaf and awns were both usually infested but occasionally the developing spikelets became infested also. These organs were checked on Einkorn 36 times and the aphids were found on the organs 10 times (27.8 per cent). Out of the ten times that this aphid was found on the awn, flagleaf and spikelet, the percentage number of times that this aphid was found on the awn, flagleaf and spikelet was 70, 10 and 20 respectively. On Emmer, these plant organs were checked 17 times and in 16 times (94.1 per cent) the aphids were found on the plant organs. Out of the 16 times that this aphid was found on the awn, flagleaf and spikelet, the percentage number of times that this aphid was found on the awn, flagleaf and spikelet was 56.3, 12.5 and 31.2 respectively. In 109 times these organs were checked on Spelt and the aphids were found on the plant organs in all the 109 times. Out of the 109 times that this aphid was found on the awn, flagleaf and spikelet the percentage number of times that S. avenae was found on the awn, flagleaf and spikelet was 80.7, 7.3 and 12 respectively.

At complete ear emergence (Zadoks' growth stage 60), the upper one-third of the ear from above was included among the areas infested on Emmer but on Einkorn any part of the ear, culm and flagleaf could be infested. All the tillers of Spelt had been killed by the aphids

before complete ear emergence. On Emmer the upper one-third of the ear was examined 14 times and the aphids were found infesting this location (upper one-third of the ear) in all the 14 times (100 per cent). Out of the 14 times that S. avenae was found on the awn, flagleaf and spikelet, the percentage number of times that this aphid was found on the awn, flagleaf and spikelet was 35.7, 7.2 and 57.1 respectively. The ear of Einkorn was checked for the erratic mode of infestation 170 times and the aphids were found infesting the ear in 135 times (79.4 per cent). Out of the 135 times that S. avenae was found on the awn, flagleaf, spikelet, rachis and culm, the percentage number of times that this aphid was found on the awn, flagleaf, spikelet, rachis and culm was 56.3, 4.4, 26, 8.1 and 5.2 respectively.

↓

Infestation on the ear of Emmer then spread to the central and basal parts (Zadoks' growth stage 69). The central and basal parts of the ears of Emmer were checked 22 times and aphids were found infesting these locations (central and basal parts of the ears) in all the 22 times (100 per cent). Out of the 22 times that S. avenae was found on the awn, flagleaf and spikelet, the percentage number of times that this aphid was found on the awn, flagleaf and spikelet was 9, 4.7 and 86.3 respectively.

↓

Soon the aphid population was beyond the carrying capacity of the ear (Zadoks' growth stage 75) and overcrowding (fifty aphids or more per ear) ensued on the ear of Emmer. The ears of Emmer were examined for overcrowding 16 times and the ears were found overcrowded in all the 16 times (100 per cent). Out of the 16 times that S. avenae was found

on the awn and spikelet during overcrowding, the percentage number of times that this aphid was found on the awn and spikelet was 6.2 and 93.8 respectively. At this time, the ears of Einkorn were checked 28 times for the erratic mode of infestation and the aphids were found infesting the ear of Einkorn 5 times (17.9 per cent). Out of the 5 times that S. avenae was found on the awn, spikelet, rachis and culm, the percentage number of times that aphids were found on the awn, spikelet, rachis and culm was 20, 40, 20 and 20 respectively.

When the spikelets began to dry up (Zadoks' growth stage 92) on the ear of Emmer, the aphids infested any fresh organ of the plant including the culm and rachis. On the ears of Emmer these locations were checked 19 times and aphids were found infesting these fresh organs in all the 19 times (100 per cent). Out of the 19 times that S. avenae was found on the awn, flagleaf, spikelet, rachis and culm, the percentage number of times that this aphid was found on the awn, flagleaf, spikelet, rachis and culm was 15.8, 15.8, 5.3, 21, and 42.1 respectively. On the ears of Einkorn these fresh organs were checked 34 times and aphids were found infesting these fresh organs 3 times (8.8 per cent). Out of the 3 times that the aphids were found on the awn, culm and stem, the percentage number of times that this aphid was found on the awn, culm and stem was 33.4, 33.3 and 33.3 respectively.

8.3.2 Observations on the ear of Einkorn

The arrangements of the spikelets of the ear of Einkorn could appear in any of six forms:

The commonest type of ears were ones in which all the spikelets were closely arranged in such a way that a very small gap occurred between one spikelet and another from ear emergence through to maturity. This type of ear formed over 99 per cent of the whole population.

Other categories of ears were those in which the arrangement of the spikelets widened from grain ripening onwards at any of the following locations - apex, middle, basal and lateral parts. Moreover, biological organisms such as mice, birds, squirrels and even man at times tampered with the ears in such a way as to simulate the types of ears described above. The high percentage (over 99 per cent) of ears of Einkorn with the close arrangement of the spikelets might well be a factor in the resistance of this ancient wheat in that the aphid would find it very difficult to gain access to the base of the spikelet which is the most preferred feeding site (Chapter 10).

8.3.3 Population development (Fig. 9)

On the three wheats the population development began slowly, increased sharply to a peak and then declined. The population remained lowest on Einkorn of all the varieties. The only moderately high peak population of Spelt was achieved early because Spelt was the most preferred wheat in this study, but the aphids did not reach higher population levels and declined early because the tillers of this wheat were killed by the aphids before the ear growth stage (Zadoks' growth stage 60) was reached.

8.3.4 Feeding sites (Table 14)

The most preferred feeding site on the ears of Emmer and Einkorn was 'Base of the spikelet' while the awn was the most preferred feeding

Fig. 9: Development of **S. avenae** Populations on Emmer, Einkorn and Spelt

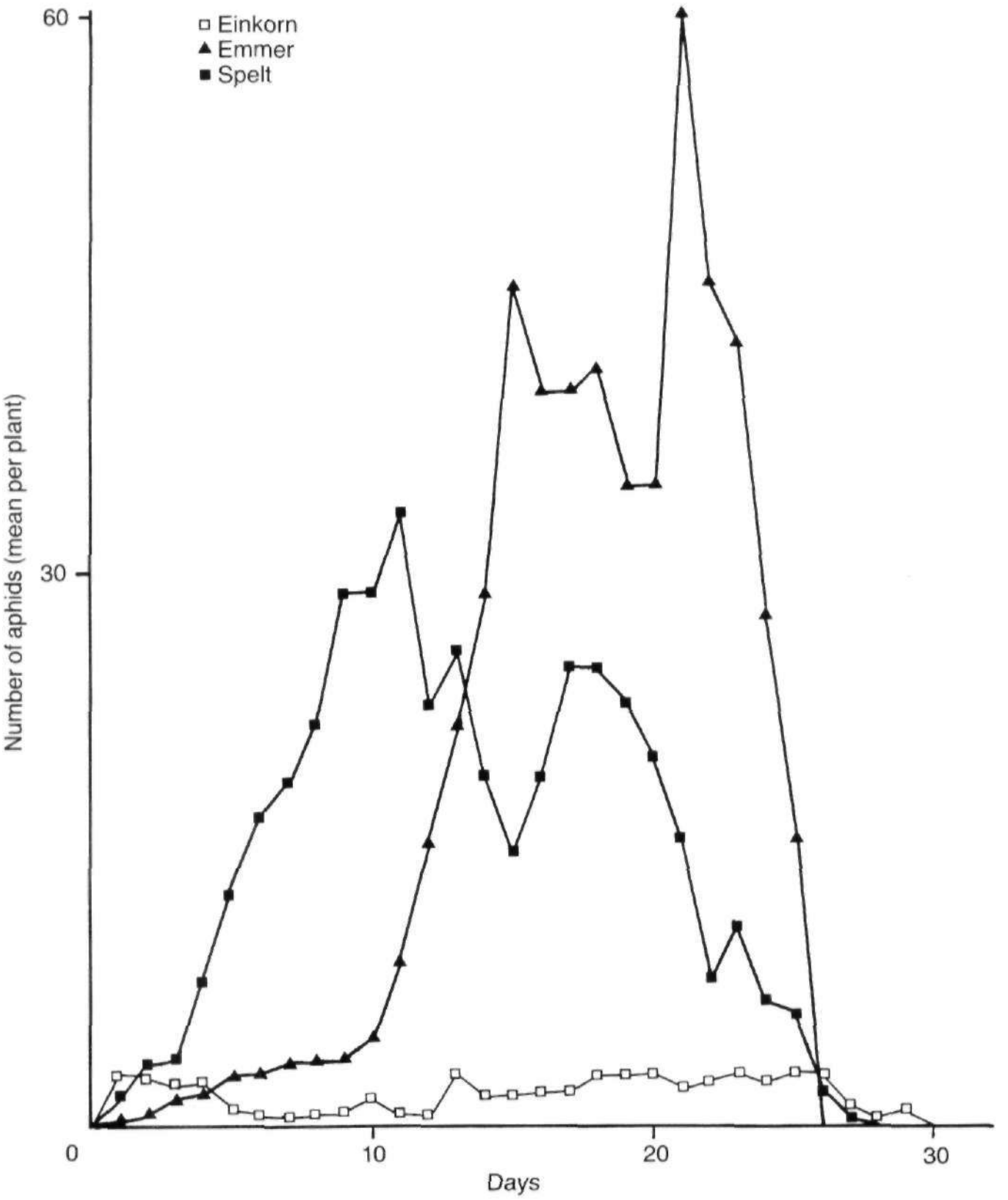


TABLE 14: Percentage of aphids selecting each of the nine feeding sites on three wheat varieties

Wheat varieties	Total aphids	Feeding Sites								
	All aphid morphs	Awn	Base of the spikelet	Culm	Stem	Dorsal part of the spikelet	Lateral part of the spikelet	Rachis	Ventral part of the spikelet	Flagleaf
Emmer										
Total	2157	486	1497	8	0	71	0	3	57	35
Mean per tiller	539.25	121.5	374.25	2	0	17.75	0	0.75	14.25	8.75
Mean per tiller as per cent of total aphid population		22.53	69.40	0.37	0	3.29	0	0.15	2.64	1.62
Einkorn										
Total	532	40	357	42	1	66	0	12	1	13
Mean per tiller	76	5.71	51	6	0.14	9.42	0	1.71	0.14	1.85
Mean per tiller as per cent of total aphid population		7.52	67.11	7.89	0.19	12.41	0	2.25	0.19	2.44

(Continued)

TABLE 14: (Continued)

Wheat varieties	Total aphids	Feeding Sites								
	All aphid morphs	Awn	Base of the spikelet	Culm	Stem	Dorsal part of the spikelet	Lateral part of the spikelet	Rachis	Ventral part of the spikelet	Flagleaf
Spelt										
Total	3464	1833	218	0	0	179	10	0	16	1208
Mean per tiller	433	229.12	27.25	0	0	22.37	1.25	0	2	151
Mean per tiller as per cent of total aphid population		52.92	6.29	0	0	5.17	0.29	0	0.46	34.87

site on Spelt. The likely explanation for a high proportion (52.92 per cent) of the aphids selecting the awn on the developing ear of Spelt was that all the tillers were killed by this aphid at the booting growth stage; hence most of the aphids did not come in contact with the spikelets. For a similar reason the rachis, which was not completely exposed to this aphid, had no aphids recorded selecting this location on Spelt.

8.4 Discussion

The pattern of colonisation of Einkorn from complete ear emergence to senescence was quite different from that of Emmer. While this aphid would infest the ear of Emmer systematically from the apex to base, the pattern of infestation of the ear of Einkorn was erratic and did not follow any pattern. There were no visible morphological barriers on the ear of Einkorn acting as impediments to the movements of the aphid apart from the close arrangement of the spikelets.

The base of the spikelet was the most preferred feeding site on both Einkorn and Emmer but not on Spelt. The possible explanation for the choice of the awn as the preferred feeding site on Spelt was that awns are normally produced from the booting growth stage and as soon as the first piece of awn protruded from a small orifice at the base of the flagleaf, it became infested by this aphid. Subsequent awns produced were infested in the same way with the result that before the ear emerged completely, most of the awns would have been infested. In fact, aphids normally moved from the awns to the spikelets. But during this observation, all the tillers of Spelt were killed at the advanced booting growth stage by the aphids when most of the awns had protruded but before complete emergence of the ear on which the spikelets were borne. Hence most of the aphids did not come in contact with the spikelets.

9. ACCESSIBILITY OF THE BASES OF THE SPIKELETS OF THE EARS OF FOUR WHEAT VARIETIES TO S. AVENAE

9.1 Introduction

In the preceding experiments, the base of the spikelet proved the most preferred feeding site by S. avenae (see also Rautapaa 1966; Kolbe 1969, 1970 and 1973; Dean and Luuring 1970; George 1974; Kolbe and Linke 1974; Wratten 1978 and Vereijken 1979) but observations during the culturing of S. avenae on different wheat varieties at the ear growth stage and when conducting the experiment on 'restlessness' suggested that whereas aphids moved easily into the bases of the spikelets of certain wheat varieties, the aphids found it much more difficult to gain access to the bases of the spikelets of other wheats. To quantify these observations, a study was set up to verify whether there was a morphological barrier to the movement of S. avenae at the bases of the spikelets on some varieties.

The four wheat varieties selected were Einkorn and Emmer whose spikelets were closely arranged and Spelt whose spikelets were widely arranged. The arrangement of the spikelets of Mardler was intermediate between the two. The distance between pairs of spikelets was the datum measured, since aphids gained access to the bases of spikelets through the small gaps between spikelets.

9.2 Experimental technique

At weekly intervals, twelve 12.5cm diameter pots were filled with compost and labelled. Unvernalised seeds of each of Einkorn, Emmer, Mardler and Spelt wheat varieties were sown in three of the pots and placed in the glasshouse as a completely randomised design with 150 replicates.

At the ear growth stage (Zadoks' growth stage 60 or Feekes' growth stage 10.51), the distance between one spikelet and another was measured at random at the top, middle and basal parts of the ears by inserting feeler guages of various thicknesses (0.05mm to 1.5mm) into gaps between pairs of spikelets starting with the thinnest guage. One gap was measured per ear. The thickness of the guage which fitted accurately into the gap between any pair of spikelets was taken as the width of the gap.

9.3 Results (Fig. 10)

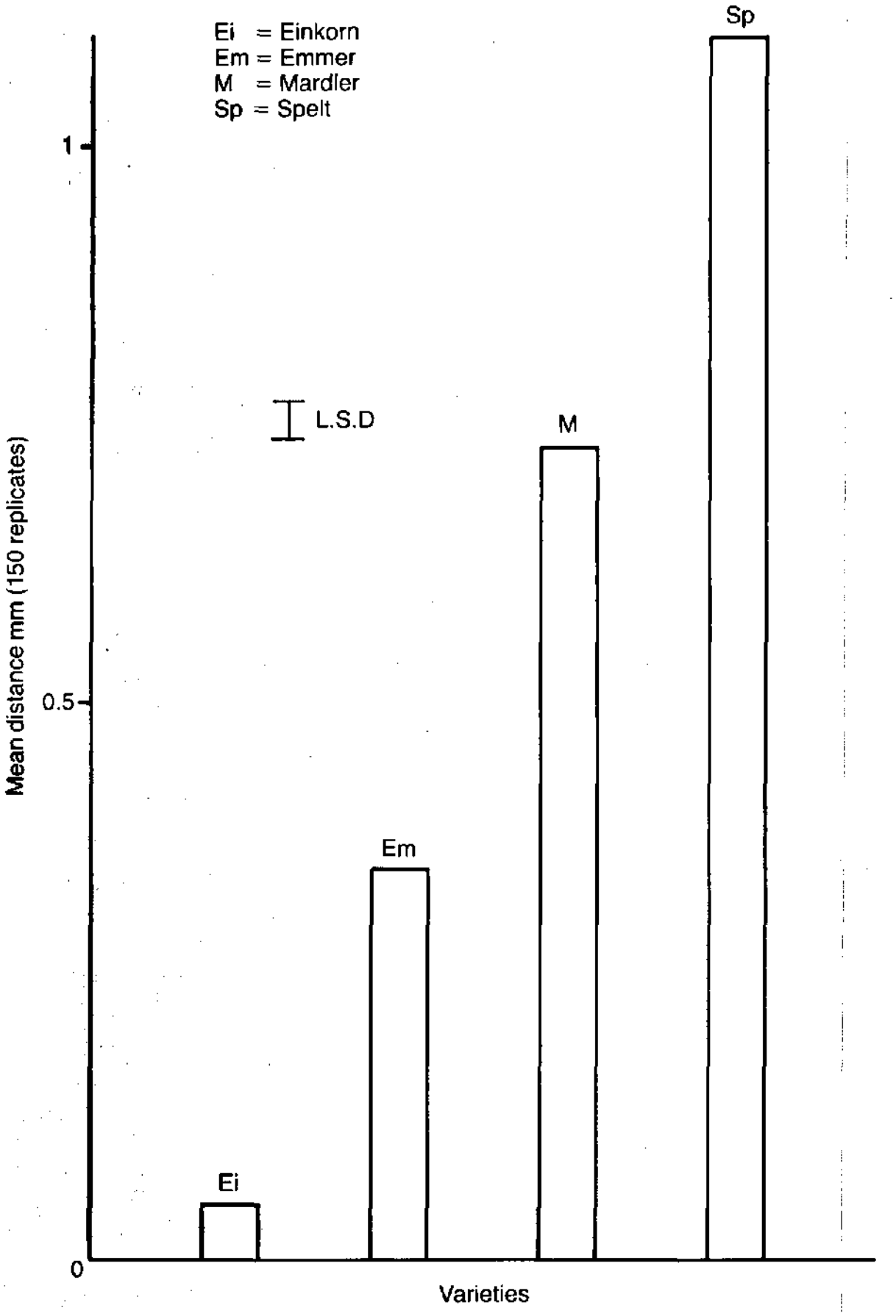
The results were subjected to analysis of variance, and the means compared by Duncan's Multiple Range Test. All varieties differed significantly from each other.

The distance between one spikelet and another was smallest on the ear of Einkorn. This gap was 7, 15 and 22 times smaller than the gaps between the spikelets of Emmer, Mardler and Spelt respectively. The distance between the spikelets of Emmer and Mardler occupied an intermediate position. The gaps between the spikelets of Emmer were half the size of those of Mardler. Gaps between the spikelets of Spelt were the widest of all the varieties and these gaps were 1.5, 3 and 22 times wider than the gaps between the spikelets of Mardler, Emmer and Einkorn respectively.

9.4 Discussion

The gap between adjacent spikelets on the ear of Einkorn was clearly the smallest of all the varieties and this could be the mechanism depriving S. avenae of the opportunity of feeding at the base of the spikelet. Moreover, the small gap also protects the rachis from being attacked by this aphid. This type of morphological feature, if responsible for the resistance, would seem a valuable resistance phenomenon. Emmer and Mardler

Fig. 10: Mean distance between adjacent spikelets on the ears of four wheat varieties



occupied an intermediate position while the bases of the spikelets and the rachis of Spelt were the most exposed to the infestation of this aphid.

10. SELECTION OF FEEDING SITES BY S. AVENAE

10.1 Introduction

It has been pointed out (Chapter 8) that the most preferred feeding site of the grain aphid (S. avenae) on the ear is the 'Base of the spikelet'. 'Base of the spikelet' is however an inadequately defined term because it embraces the area from a few millimetres above the junction of the sessile spikelet with the rachis to the rachis itself.

This experiment was conducted to ascertain more exactly the spot where S. avenae most frequently fed on the spikelets of Einkorn and Emmer wheats, and whether the preferred location differed between the varieties. These two wheats were selected because their spikelets were closely arranged (Chapter 9) hence aphids normally find it difficult to feed at the bases of the spikelets. The sites tested were 'Base of the spikelet but dorsal below' (B S D B), 'Base of the spikelet but junction with the rachis' (B S J R), 'Base of the spikelet but ventral below' (B S V B), 'Dorsal part of the spikelet' (D P S P), 'Lateral part of the spikelet' (L P S P), 'Ventral part of the spikelet' (V P S P) and the 'Rachis' (R A C H) (Fig. 11).

10.2 Experimental technique

At weekly intervals, six pots were filled with compost and labelled. Three unvernalised seeds of Emmer and six of Einkorn were sown separately with each variety in three of the pots. The pots were placed in the glasshouse as a randomised block design with 6 replicates. At emergence the seedlings were thinned to one plant per pot.

At the ear growth stage (Zadoks' growth stage 60) all spikelets were removed from the ears of three tillers of each wheat variety thus leaving the aphid

with a choice of four feeding sites (B S J R, R A C H, B S D B and B S V B). B S D B was included because it was practically impossible to remove the spikelet without leaving a fragment of this portion of the spikelet. From yet another six tillers of wheat (three tillers from each variety), the spikelets were removed alternately thus making it easy for the aphid to reach all seven feeding sites. The spikelets were removed in order to expose hidden sites at the base and ventral parts of the spikelets which were normally difficult for the aphid to reach. The treated tillers were placed among infested Bounty, Highbury, Mardler, Emmer, Einkorn, Spelt and Maris Kinsman wheats in the glasshouse. Each treated ear was examined daily using a magnifying glass and the number of aphids selecting each site counted and accumulated over the daily observations.

10.3 Results (Fig. 11 and Table 15)

The number of aphids selecting various sites were converted to percentages of the total number of aphids, transformed to degrees using angular transformation, subjected to analysis of variance and the means compared by Duncan's Multiple Range Test.

10.3.1 Selection among four sites

The feeding site most frequently selected on both Einkorn and Emmer by S. avenae when the spikelets had been removed was B S J R and the proportion of aphids selecting this site was significantly greater than that selecting any other site. That this site was most preferred, yet presented the smallest feeding area shows that a clear preference must have been involved. The R A C H occupied an intermediate and statistically separable position from other sites. The proportions of aphids selecting B S D B and B S V B were statistically inseparable and very low.

TABLE 15: Per cent of S. avenae selecting each feeding site.

(Data are means of angular transformation of percentages)

Varieties		Sites			
		B S J R	R A C H	B S D B	B S V B
Selection among four sites	Emmer	74.326	14.908	2.491	0
	Einkorn	71.176	15.55	4.678	3.203
	Combined	72.75	15.22	3.58	1.60

(Continued)

TABLE 15: (Continued)

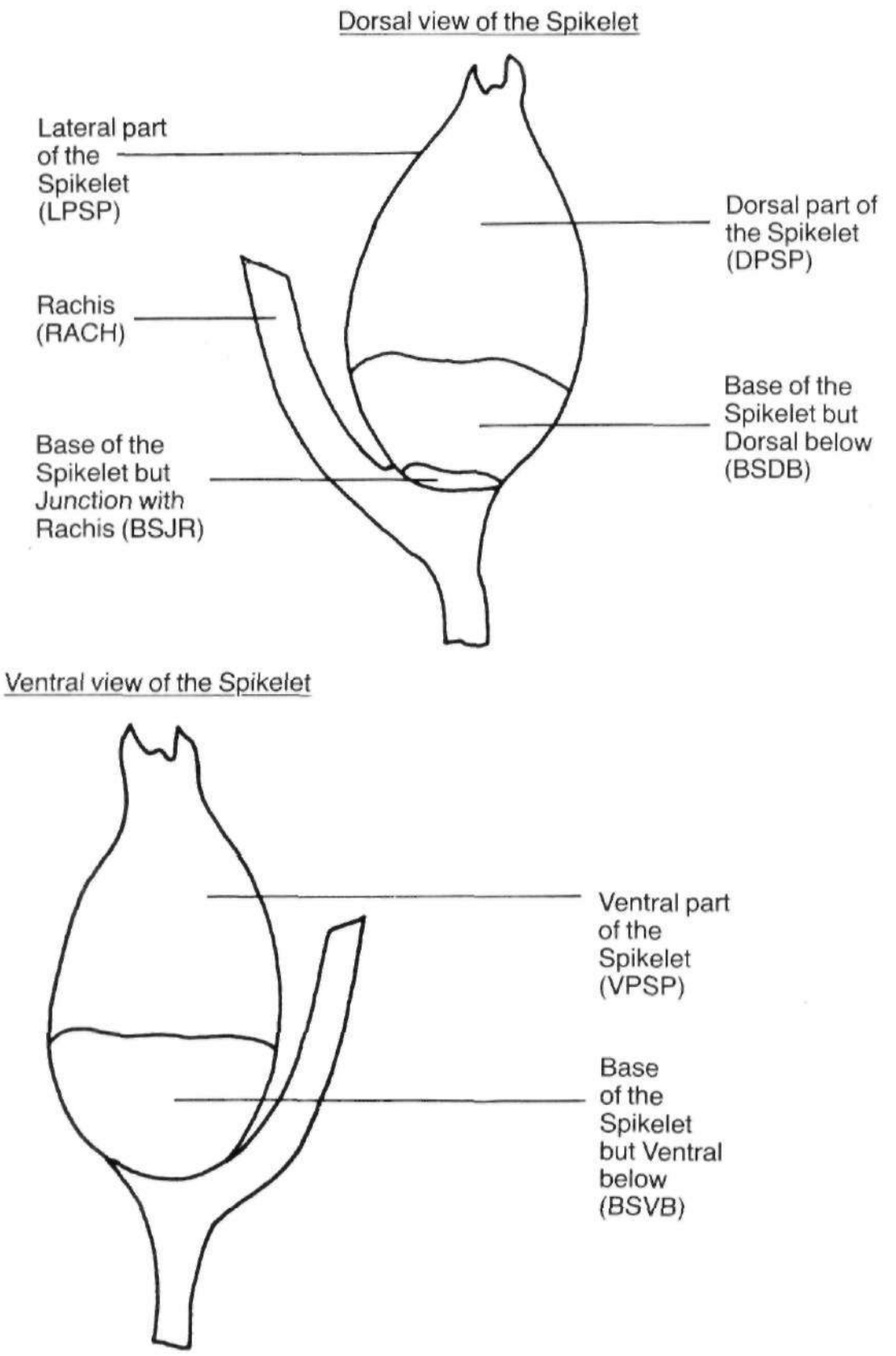
Varieties		Sites						
		B S J R	R A C H	B S D B	L P S P	V P S P	D P S P	B S V B
Selection among	Emmer	71.996	12.33	4.81	5.736	6.55	2.48	0
seven sites	Einkorn	67.693	9.746	8.96	7.836	5.806	5.43	6.166
	Combined	69.84	11.04	6.88	6.78	6.18	3.95	3.08

B S J R = BASE OF SPIKELET BUT JUNCTION WITH RACHIS
R A C H = RACHIS
B S D B = BASE OF SPIKELET BUT DORSAL BELOW
L P S P = LATERAL PART OF THE SPIKELET
V P S P = VENTRAL PART OF THE SPIKELET
D P S P = DORSAL PART OF THE SPIKELET
B S V B = BASE OF SPIKELET BUT VENTRAL BELOW

Means of varieties connected by lines are not significantly different from each other (at P = 0.05) as analysed by Duncan's Multiple Range Test.

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Fig. 11: A Spikelet showing locations of feeding sites



10.3.2 Selection among seven sites

Similar to the result obtained in the previous experiment, even when spikelets were present (with alternative spikelets removed) the proportion of aphids selecting B S J R was significantly higher than that of other sites on both varieties. The proportions of aphids choosing R A C H, B S D B, L P S P, V P S P, D P S P and B S V B were statistically inseparable.

10.4 Discussion

B S J R was clearly the most preferred feeding site on both Einkorn and Emmer. Observations showed that at a few occasions the rostrum was not directly in contact with the junction but slightly above it. This site must offer particular nutritional advantages to the aphid since it is rather inaccessible. One would expect a more conspicuous feeding site like D P S P to be more frequently selected by this aphid but the reverse was the case. It is possible that this aphid comes into contact with the phloem very easily at this location.

The moderate preference shown for the R A C H also seems surprising. One would expect this aphid to prefer any part of the spikelet to the R A C H which was rather woody in texture. More aphids were found selecting B S J R and R A C H on Emmer than on Einkorn in both tests.

In contrast to the result obtained above, the result obtained in a previous investigation (Chapter 8) where S. avenae selected for feeding sites on the ears of Einkorn and Emmer with all the spikelets on the ears intact, the 'Base of the spikelet' was the most preferred feeding site. In this same test, very few aphids were recorded selecting the rachis while no aphid was found selecting 'Lateral part of the spikelet'.

One possible explanation for the selection of the 'Base of the spikelet' as the most preferred feeding site, was the close arrangement of the spikelets on the ears of Einkorn and Emmer (Chapter 9). This type of spikelet arrangement prevented S. avenae from gaining access to the B S J R which was selected as the most preferred feeding site when the spikelets were removed. For the same reason, few aphids were recorded selecting the rachis and no aphid was even recorded selecting 'Lateral part of the spikelet'.

11. INCIDENCE OF MILDEW DISEASE (ERYSIPHE GRAMINUM) AMONG FOUR WHEAT VARIETIES AT THREE GROWTH STAGES

11.1 Introduction

Since the inception of this study, it was observed that whenever there was a sporadic outbreak of mildew disease in the glasshouse, the intensity of symptoms differed among the cereal varieties under study.

One of the problems of plant resistance in agricultural crops is that after a variety of crop is found resistant to a particular biological organism, the same crop plant may be very susceptible to another biological organism (Maxwell, Lafever and Jenkins 1965, van den Bosch and Messenger 1973, Panda 1979, Norris and Kogan 1980 and Phillips, Gutierrez and Adkisson 1980). Hence a study was set up to investigate whether wheat varieties resistant to the aphid would also be resistant to the mildew.

The cereal varieties selected were the ancient wheat Einkorn which was the least preferred by S. avenae and Spelt which was most preferred by this aphid. Both Emmer and Mardler were intermediate in their degree of preference by this aphid.

11.2 Experimental technique

All unvernalised seedlings of Einkorn, Emmer, Mardler and Spelt meant for experimental use at any occasion were carefully examined daily for the sporulated spots of the mildew disease using a magnifying glass and the seedlings scored for the incidence of this disease using the following criteria.

Clean plants: Plants with no visible sporulated spot

Slightly infected plants:

Plants with between one and three sporulated spots

Heavily infected plants:

Plants with between three and six sporulated spots

and

Very heavily infected plants:

Plants with over six sporulated spots.

11.3 Results

Histograms of the frequency of the categories of the incidence of the mildew disease on each wheat variety are shown in Figs. 12 - 15. The results were analysed separately for each growth stage using the chi-square test on the frequencies of each disease incidence category. At each occasion that the incidence of this disease gave a significant chi-square between the wheat varieties (i.e. there were differences in the frequencies between varieties) the variety making the highest contribution to the total chi-square was eliminated and the remaining varieties re-tested. This elimination process continued until no significant chi-square was obtained.

11.3.1 Two leaf growth stage (Zadoks' growth stage 12 or Feekes' growth stage 1) (Table 16)

No significant 'F' value at P = 0.05 was obtained when the data on this section of the study were analysed. There was no appreciable difference in the reactions of the four wheat varieties to the

Fig. 12: Incidence of mildew disease on Mardler at two, three and four leaf growth stages

A = Two leaf growth stage
B = Three leaf growth stage
C = Four leaf growth stage

Cl = clean
Sl = slight
He = heavy
Vh = very heavy

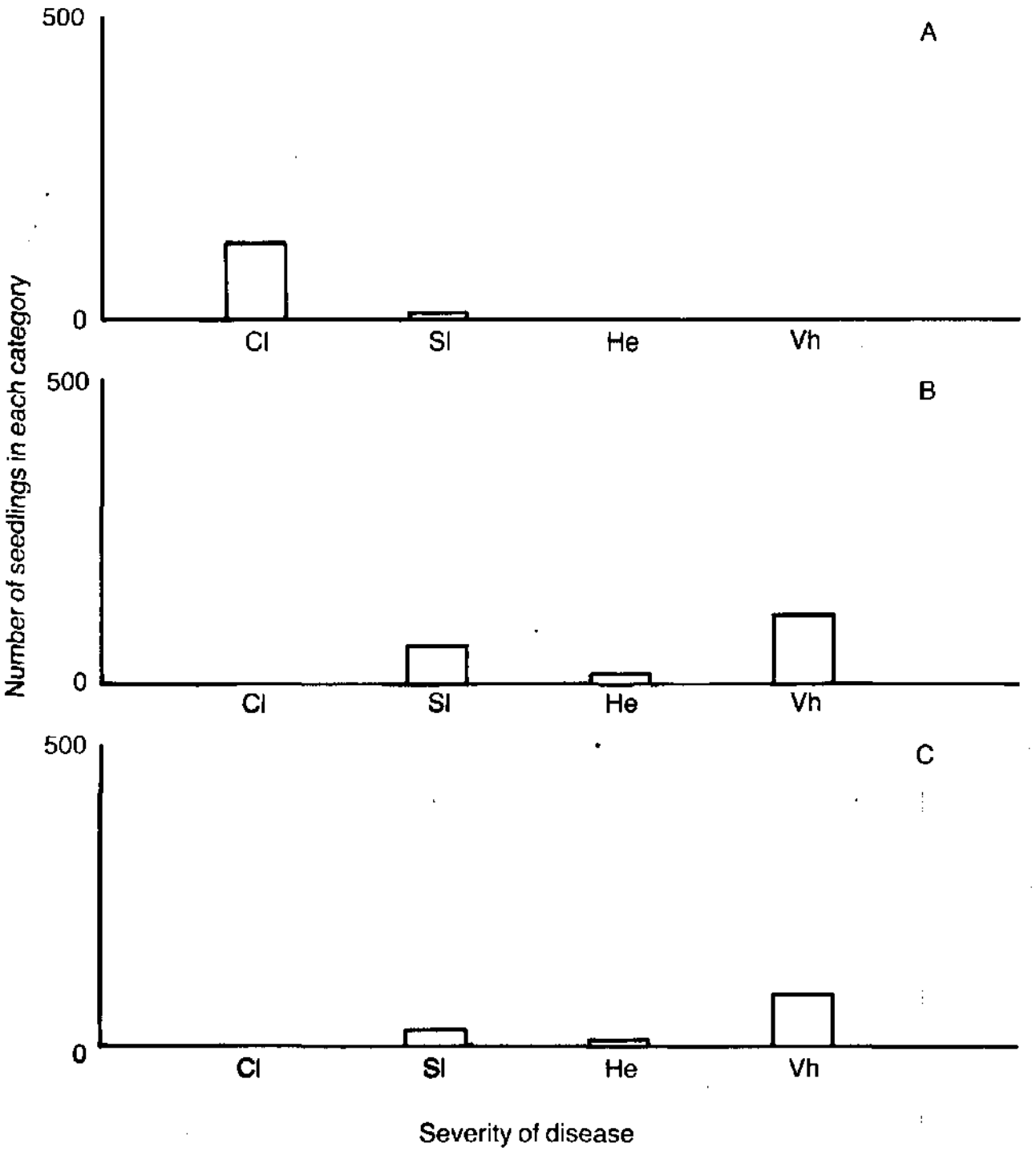


Fig. 13: Incidence of mildew disease on Emmer at two, three and four leaf growth stages

A = Two leaf growth stage
B = Three leaf growth stage
C = Four leaf growth stage

Cl = clean
Sl = slight
He = heavy
Vh = very heavy

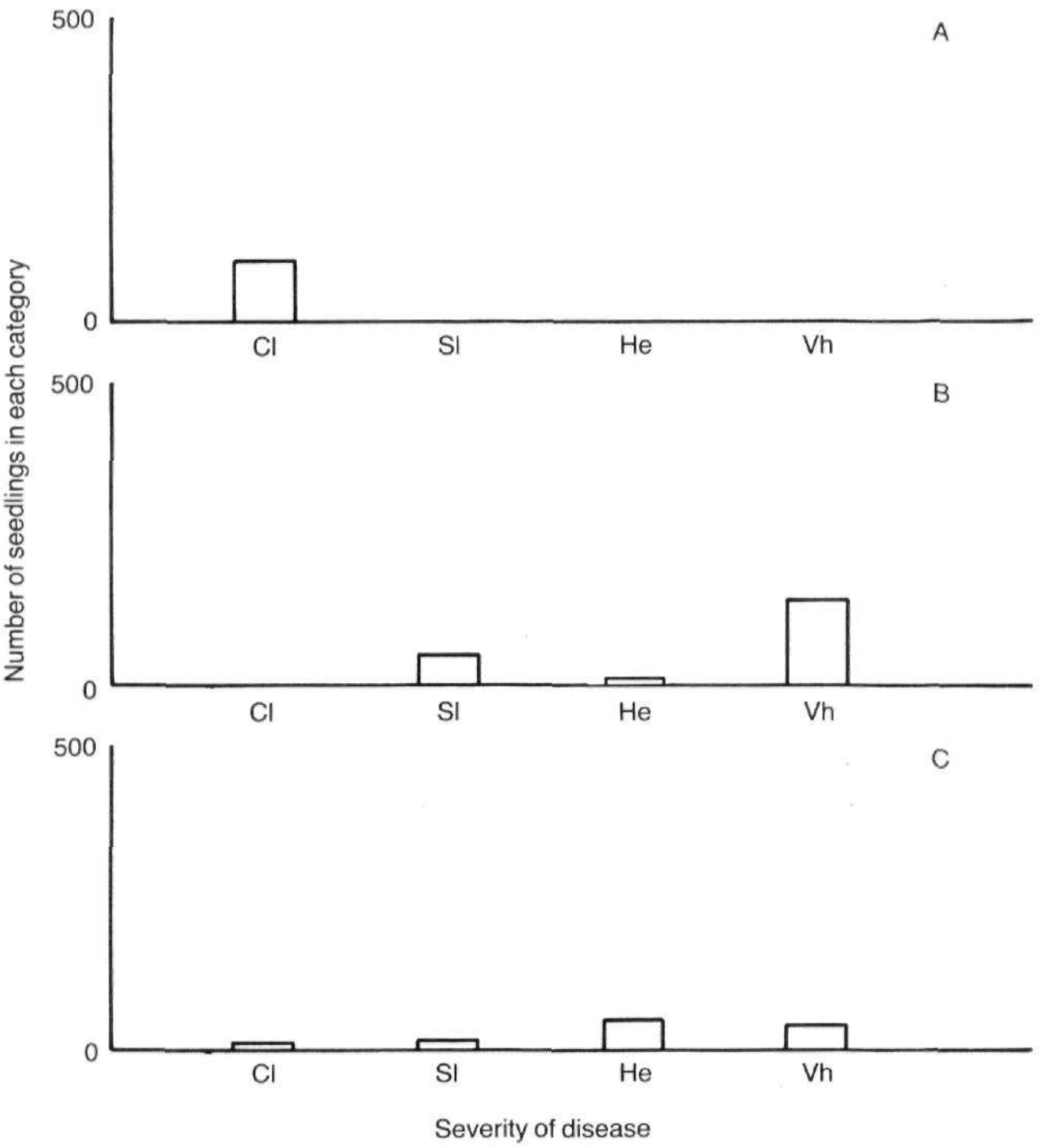


Fig. 14: Incidence of mildew disease on Einkorn at two, three and four leaf growth stages

A = Two leaf growth stage
B = Three leaf growth stage
C = Four leaf growth stage

Cl = clean
Sl = slight
He = heavy
Vh = very heavy

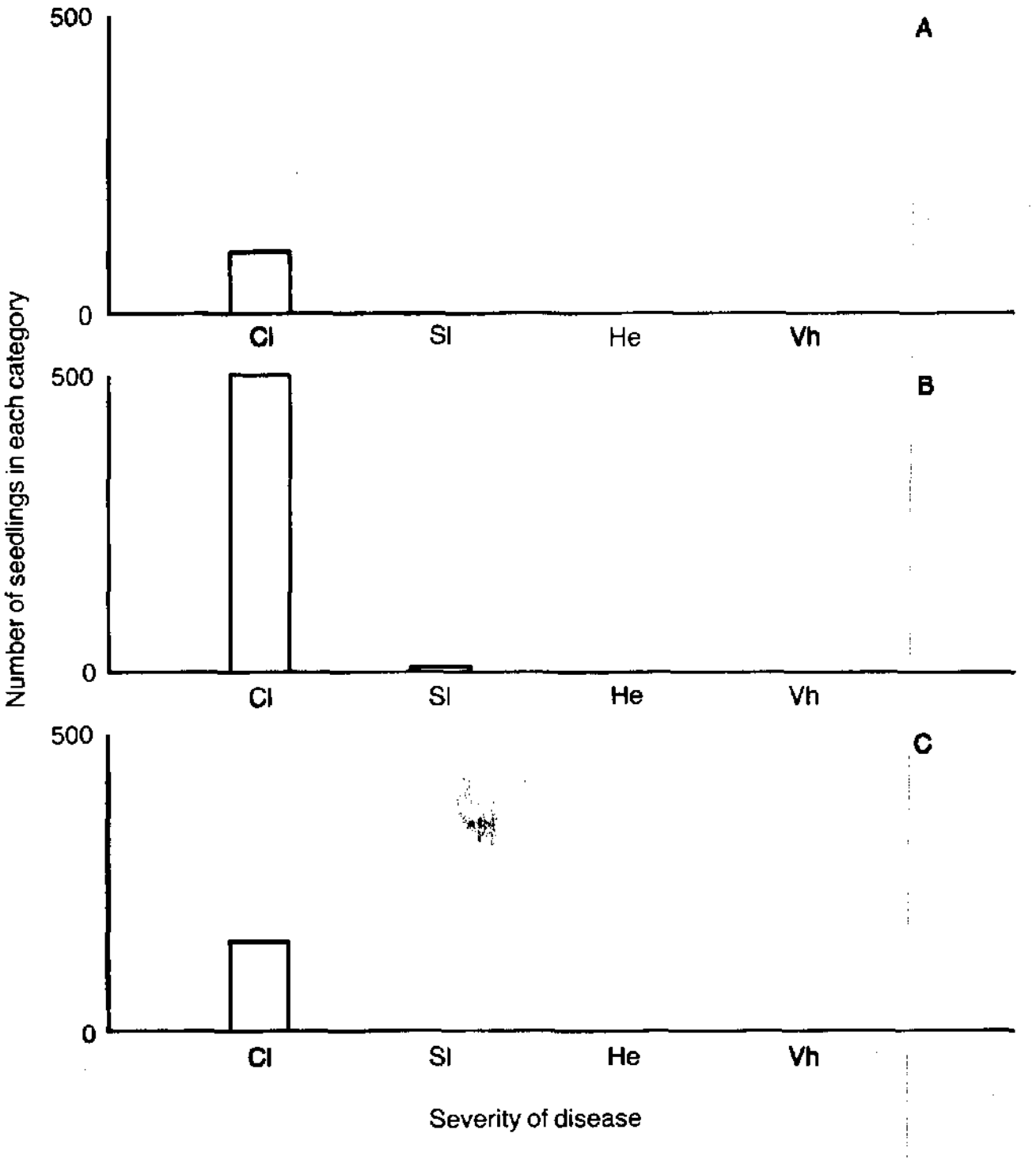


Fig. 15: Incidence of mildew disease on Spelt at two, three and four leaf growth stages

A = Two leaf growth stage
B = Three leaf growth stage
C = Four leaf growth stage

Cl = clean
Sl = slight
He = heavy
Vh = very heavy

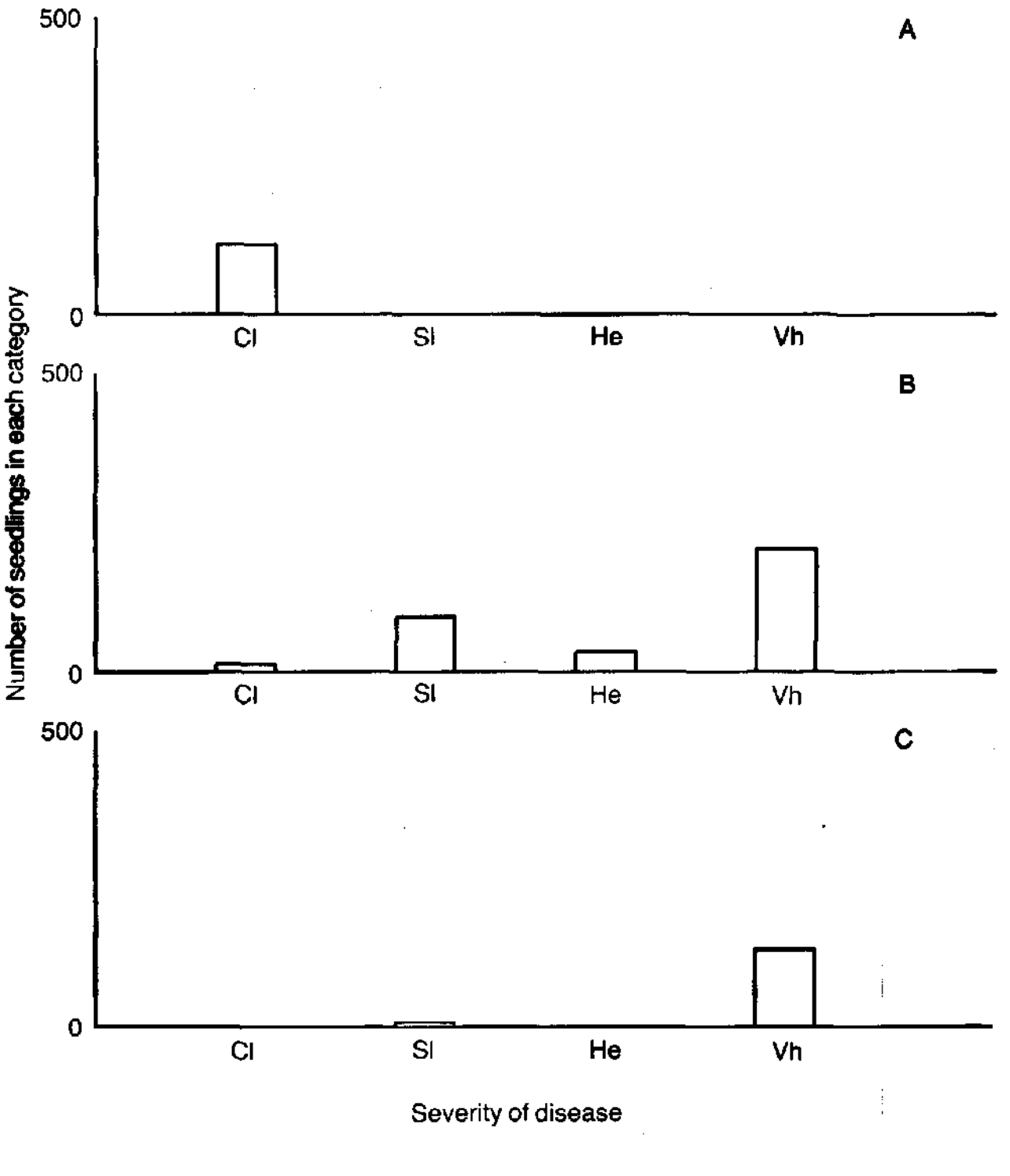


TABLE 16: Analysis of the incidence of mildew disease among four wheat varieties at two leaf growth stage

Analysis of the incidence of mildew disease among Mardler, Emmer, Einkorn and Spelt.

χ^2 = 2.88

D F = 9

P = > 0.95 N.S.

. . No significant difference between varieties.

TABLE 17: Analysis of the incidence of mildew disease among four wheat varieties at three leaf growth stage.

Analysis of the incidence of mildew disease among Mardler, Emmer, Einkorn and Spelt.

$$\chi^2 = 1163.14$$
$$DF = 9$$
$$P = < 0.001$$

∴ There is a significant difference between varieties. Highest contribution was from Einkorn (Significantly less susceptible).

Analysis of the incidence of mildew disease among Mardler, Emmer and Spelt.

$$\chi^2 = 26.86$$
$$DF = 6$$
$$P = < 0.001$$

∴ Still there is a significant difference between varieties. Highest contribution to chi-square was from Mardler (Significantly less susceptible).

Analysis of the incidence of mildew disease between Emmer and Spelt.

$$\chi^2 = 5.74$$
$$DF = 3$$
$$P = < 0.10 \text{ n.s.}$$

∴ No significant difference between varieties.

∴ Order of mildew susceptibility was Spelt = Emmer > Mardler > Einkorn.

TABLE 18: Analysis of the incidence of mildew disease among four wheat varieties at four leaf growth stage.

Analysis of the incidence of mildew disease among Mardler, Emmer, Einkorn and Spelt.

$$\chi^2 = 635.33$$
$$DF = 9$$
$$P < 0.001$$

∴. There is a significant difference between varieties. Highest contribution to chi-square was from Einkorn (Significantly less susceptible).

Analysis of the incidence of mildew disease among Mardler, Emmer and Spelt.

$$\chi^2 = 154.1$$
$$DF = 6$$
$$P < 0.001$$

∴. Still there is a significant difference between varieties. Highest contribution to chi-square was from Emmer (Significantly less susceptible).

Analysis of the incidence of mildew disease between Mardler and Spelt.

$$\chi^2 = 29.34$$
$$DF = 3$$
$$P < 0.001$$

∴. Still there is a significant difference between varieties. Highest contribution to chi-square was from Mardler (Significantly less susceptible).

∴. Order of mildew susceptibility was Spelt > Mardler > Emmer > Einkorn.

infection of this disease at this growth stage.

11.3.2 Three leaf growth stage (Zadoks' growth stage 13 or Feekes' growth stage 1) (Table 17)

Fewest seedlings of Einkorn were infected by this disease ($P < 0.001$) while the greatest number of the seedlings of Emmer and Spelt were infected ($P > 0.10$ between Emmer and Spelt). The incidence of this disease on the seedlings of Mardleroccupied an intermediate position ($P < 0.001$ between Einkorn and Emmer/Spelt).

11.3.3 Four leaf growth stage (Zadoks' growth stage 14 or Feekes' growth stage 1) (Table 18)

At this growth stage disease development continued in the order of varieties already noted in the previous growth stage (Three leaf growth stage) with the seedlings of Einkorn again being the least affected by the disease ($P < 0.001$) while the seedlings of Spelt were again the most affected ($P < 0.001$). Emmer and Mardler occupied an intermediate position ($P < 0.001$) between the least and most affected wheats.

11.4 Discussion

At the two leaf growth stage the disease had not developed sufficiently to show differences between wheat varieties, with only very few leisons showing on just one variety, Mardler. However, at both the three and four leaf growth stages, Einkorn was the least affected by the disease while Spelt was the most affected. Emmer and Mardler occupied an intermediate position but Emmer was more vulnerable to the disease than Mardler during the three

leaf growth stage. It appears that the ancient wheat Einkorn exhibits 'multiple resistance' in the sense that apart from being resistant to the aphid, it also possesses some degree of resistance to the mildew disease, a very valuable property in cereal where aphids and mildew are two economically important problems.

12. DISCUSSION

12.1 Aim

The objective of the study was to contribute to non-chemical control of cereal aphids (S. avenae and M. dirhodum) which for nearly two decades have become a problem for farmers all over Europe and particularly in Great Britain. Apart from the yield losses due to removal of sap by these aphids, aphids have also been heavily implicated as agents transmitting virus diseases. In fact, farmers are mostly concerned with the transmission of virus diseases by these aphids as the virus problem is serious and there is no instant chemical treatment for the virus disease similar to that of the aphids. Moreover, the honeydew produced by the aphids fouls the leaves and floral parts and encourages the growth of moulds.

Broad spectrum and specific insecticides have been developed for the control of aphids and other insects but short and long term environmental hazards especially to non-target organisms have been a persistent problem to ecologists, agriculturists and environmentalists. As an extreme example (though not of an aphid) fumes of dioxin which escaped from a chemical factory in Seveso, Northern Italy on July 10, 1976 were reported to have caused environmental hazards to birds, livestock and man shortly after the incident. Even seven years after the incident, several hectares of the affected area were being excavated and re-buried because of the residual effect of this chemical (TV a.m. news of 17/4/83, BBC.1 9 o'clock p.m. news of 18/4/83, BBC.1 5 o'clock p.m. news round of 18/5/83, BBC.1 9 o'clock p.m. news of 19/5/83, ITV 1 o'clock p.m. news of 20/5/83, ITV 5.45 o'clock p.m. news of 20/5/83, BBC.1 9 o'clock p.m. news of 20/5/83, Daily Star of 21/5/83 page 6, ITV World in Action programme between 8.30 and 9 o'clock p.m. on 25/7/83 and TV a.m. news of 26/7/83. This case is presently being

heard in one of the highest Courts of Justice in Italy.

As 'plant resistance' is one of the safest methods of insect control, this study was aimed at comparing the relative susceptibility of a number of wheat varieties. The wheat varieties involved were Einkorn, Emmer and Spelt which were ancient varieties and Bounty, Highbury, Mardler and Maris Kinsman which were modern varieties.

12.2 Critique of material and method

12.2.1 General

Perhaps the two most important limiting factors during this study were lack of glasshouse space and lack of growth room facilities. The amount of space available determined the number of experiments that could be conducted simultaneously, the number of replicates involved in each experiment and the number of plants that could be grown for cases of emergency. Also, certain varieties had to be grown well beforehand in order to synchronise the heading dates with their more rapidly maturing counterparts. The number of such plants were seriously curtailed by the limited space available.

The temperature in the glasshouse was at times well above the ambient temperature resulting in aphid cultures being lost through excessive heat at critical phases of certain experiments. Hence aphid cultures and even experimental potted plants were at times arranged in a shed outside the glasshouse where the temperature was cooler.

All the wheat varieties used were not vernalised hence a few of the varieties flowered out of season. The wheats were not vernalised because vernalising cereals changes the resistance rankings of cereal varieties (Kay, Wratten and Stokes 1981). In order to overcome this problem, grains of such varieties were sown well ahead of time to

bring about synchrony in their heading dates with the wheats not requiring vernalisation.

Mildew, rodents, birds, squirrels, spider mites and extraneous insects (e.g. thrips) constituted significant threats to certain experiments. In fact, the infection of mildew and attack by birds and rodents led to the need to repeat the growing of plants for some experiments.

Working with several varieties seriously limited the number of experiments and the number of replicates per sowing involved in experiments.

Use of stakes and twist ties became a problem in experiments involving counts of S. avenae on various parts of the plant because this aphid was also found wandering on these materials.

Heat problems and parasites at times adversely affected aphid cultures. Hence in 'preference', 'antibiosis' and 'restlessness' experiments involving daily or weekly use of aphids, cultures were examined daily.

Had time and space permitted, separate tests should really have been conducted at two leaf, three leaf, four leaf, tillering, flagleaf, booting and ear growth stages in 'antibiosis', restlessness', 'effect of infestation on cereal growth' and 'pattern of wheat colonisation' experiments. This would have enabled each of these experiments to be better related to more growth stages which were not synchronous between the varieties.

In 'restlessness', 'pattern of wheat colonisation' and 'choice of feeding sites' tests, the rose aphid (M. dirhodum) should have been used in addition to the grain aphid (S. avenae) had space permitted.

This would have enabled the behaviour of these two aphids to be compared.

In addition to the tests in the glasshouse, 'restlessness', 'pattern of wheat colonisation' and 'choice of feeding sites' experiments should have been conducted in the field and the growth room. It would have been possible to test whether the behaviour of this aphid would change under different temperature regimes at each location.

But for the limitation of space and time, more wheats should have been involved in 'restlessness', 'pattern of wheat colonisation', 'choice of feeding sites', 'effect of infestation on cereal growth' and 'distance between adjacent spikelets' experiments. The behaviour of this aphid on more wheats and the relative susceptibility of such wheat varieties to this aphid would have been known.

12.2.2 Suggestions for future and additional work relating to specific experiments

Preference

Aphids of different instars should be used separately in this experiment. This would ascertain whether the behaviour of aphids of different stadia differs between growth stages.

The sections of various plant organs on which the aphids were tested should be taken to ascertain whether there are anatomical features adversely affecting the probing activities of the aphid.

Distance between adjacent spikelets

Thinner feeler guages of various thicknesses between 0.005mm and 0.05mm would be required for measuring the distance between adjacent spikelets

which are very closely arranged on the ear of Einkorn.

The thickness of the head of S. avenae at different instars should be measured. This would be necessary to determine the minimum thickness of the head at each instar that might easily penetrate the distance between adjacent spikelets on the ear of each wheat variety.

12.3 Conclusions on methodology

The importance of being able to keep clean cultures all the year round was found to be critical. It became vital to gain familiarity with problems of fluctuating temperature conditions and natural enemies, in spite of which clean aphid cultures had to be maintained and used for daily or weekly experiments.

'Preference', 'antibiosis', 'restlessness' and 'pattern of aphid colonisation' experiments are probably better carried out in a growth room.

Because of the shortage of space, it is strongly felt that only a few varieties could be compared. For the same reason, experimental design was kept as simple as possible.

12.4 Discussion of the results

Spelt

This ancient and hexaploid wheat was the most preferred by both S. avenae and M. dirhodum. S. avenae spent a fairly long time feeding on this wheat while a fairly short time was devoted to wandering. The pattern of infestation of this wheat (flagleaf - awn - spikelet) by S. avenae was similar to that of Emmer until advanced booting growth stage when all the tillers of Spelt were killed. The inability of the tillers of Spelt to tolerate the

infestation of S. avenae showed that this ancient wheat was very susceptible to this aphid, thus confirming the result obtained during the 'preference' test. Thus, in spite of the old origin of this wheat, it proved as or more susceptible to the two aphid species as modern varieties. The gaps between adjacent spikelets on the ears of Spelt were wide hence aphids could easily move into the bases of the spikelets. This primitive wheat developed the greatest incidence of mildew disease. In conclusion, this wheat seems to be very susceptible to both S. avenae and M. dirhodum and to the mildew disease at three and four leaf growth stages.

Maris Kinsman

The hexaploid modern Maris Kinsman wheat was preferred by S. avenae while it was moderately preferred by M. dirhodum. Few tests were done with this variety because of lack of glasshouse space.

Bounty

Both S. avenae and M. dirhodum moderately preferred this modern wheat. Limited experiments were conducted with this wheat because of lack of glasshouse space.

Highbury

The cereal aphids (S. avenae and M. dirhodum) moderately preferred this modern wheat and the number of nymphs produced on this wheat by these two aphids occupied an intermediate position between Einkorn and Emmer. Highbury wheat infested with S. avenae were severely affected but the infestation of M. dirhodum least reduced the growth of this wheat. From the overlapping intermediate position with Mardler and Bounty which this wheat held in preference tests with S. avenae and M. dirhodum, the moderately high

number of nymphs which both S. avenae and M. dirhodum produced on this wheat in 80 per cent of the times that observations were taken and the small reduction in growth which the feeding of M. dirhodum caused on Highbury, this modern wheat seems to be partially resistant to both cereal aphids.

Mardler

This modern wheat was moderately preferred by both S. avenae and M. dirhodum and this wheat was moderately affected by the feeding activities of these aphids. Both cereal aphids produced moderately high numbers of nymphs on this wheat and S. avenae spent a long time feeding on the seedling, flagleaf and ear of this modern wheat and a small proportion of the time was devoted to wandering. The gaps between adjacent spikelets on the ears of Mardler were moderately wide hence aphids find it relatively easy to gain access to the bases of spikelets. During the three and four leaf growth stages, this wheat was moderately susceptible to the infection of the mildew disease. This wheat seems to exhibit partial resistance to both grain (S. avenae) and rose (M. dirhodum) aphids.

Emmer

The primitive tetraploid Emmer wheat was moderately preferred by S. avenae but most preferred by M. dirhodum and many nymphs were produced on the leaf of this wheat by both aphids. Emmer was moderately affected when infested by S. avenae but the infestation of M. dirhodum severely affected this wheat. On the three plant organs (seedling, flagleaf and ear) tested, S. avenae spent a fairly long time feeding while a fairly short time was spent wandering. The grain aphid (S. avenae) infested Emmer in a definite pattern with the daily population development being high and reaching over-crowding

on the ear. The gaps between adjacent spikelets were moderately wide hence aphids find it moderately easy to gain access to the bases of spikelets. This ancient wheat was also moderately affected by the pathogenecity of the mildew disease. Generally, Emmer seems to be partially resistant to the grain aphid (S. avenae) and the mildew disease but susceptible to the rose aphid (M. dirhodum).

Einkorn

The seedling, leaf, stem, flagleaf and ear of this diploid ancient wheat were least preferred by apterous S. avenae. Also fewest alates (at two leaf and three leaf growth stages) and fewest apterous S. avenae selected this wheat during the two leaf, three leaf, tillering, flagleaf and ear growth stages. Moreover, this wheat was also least preferred by apterous M. dirhodum during the two leaf, three leaf, tillering, flagleaf and ear growth stages. Fewest nymphs were produced on the leaf of Einkorn by apterous S. avenae and M. dirhodum (except during the 4th week and on the flagleaf for M. dirhodum). The mean number of nymphs produced by M. dirhodum on the leaf of Einkorn was almost twice that produced by S. avenae. Einkorn wheat infested by S. avenae and M. dirhodum was slightly and moderately affected respectively. Though the aphid - plant burden of this wheat was not counted yet from the results obtained during the 'antibiosis' tests, few aphids would have been found infesting this wheat. Hence it was to be expected that few aphids would give small decreases in plant growth and dry weights. In certain cases, however, (Table 9) the effect on the plant of the small infestation was the highest of the four wheat varieties tested. If these few aphids were able to cause such remarkable decreases in the growth of plant organs, it would appear that Einkorn has not got the inherent ability to tolerate the infestation of the aphids if they are forced

to feed on it.

S. avenae spent a short total time on the seedling, flagleaf and ear of Einkorn. A small proportion of the total time was spent feeding on each of these three plant organs and therefore a greater proportion of the time was spent wandering. The pattern of colonisation on the ear of Einkorn was quite different from that on Emmer from complete ear emergence to senescence. As from complete ear emergence on Einkorn, the culm, stem and rachis were infested whereas on Emmer, these organs were normally infested only in overcrowded cultures and during senescence. The development of S. avenae population on this primitive wheat was the lowest of the three wheats studied and the population was not observed reaching overcrowding on the ear. The gaps between adjacent spikelets on the ears of Einkorn were found to be the narrowest out of four wheat varieties. This type of spikelet arrangement made the bases of the spikelets of this wheat almost inaccessible to the aphids. Apart from resistance to the cereal aphids, this ancient wheat exhibited a high level of resistance to the mildew disease at the three and four leaf growth stages. Out of the seven wheat varieties tested, the diploid ancient wheat Einkorn clearly showed a high level of resistance to both S. avenae and M. dirhodum in the glasshouse but confirmatory tests would be required to ascertain whether this high level of resistance would be maintained in the field.

12.5 Further work

All experiments conducted in the glasshouse should now be repeated in the field. This is necessary because results of experiments conducted in the glasshouse are known to be slightly different from the results obtained in the field (Done and Whittington 1978 and van Emden 1978).

All the wheats used were not vernalised but some of them require vernalisation. These experiments should now be repeated subjecting all the wheats to a vernalisation treatment. This is to test whether vernalisation would change the resistance rankings of the wheats.

Cross sections of all the organs of Einkorn should now be taken because this might reveal whether there is any evidence of an anatomical mode of resistance.

Chemical analysis of various organs of Einkorn should now be carried out at various growth stages to seek deterrent compounds or the absence or low level of certain essential amino acids.

Distillates of various organs of Einkorn should be made and used to treat the leaves of susceptible varieties. Aphids would be introduced to the treated leaves and their behaviour watched. This is necessary to test whether the painting of the distillates of Einkorn on the leaves of a susceptible variety would confer temporary resistance on such a susceptible wheat.

An experiment should be conducted with the most preferred feeding site (B S J R) made unavailable to the aphid by painting a non-toxic substance on its locations on the ear. The behaviour of the aphid should be watched as to the choice of the other feeding sites. It would be interesting to find out whether this aphid would still try to feed on the blocked feeding site.

More growth stages (e.g. seedling, tillering, flagleaf, booting and ear growth stages) should be included in 'antibiosis', 'effect of infestation on cereal growth', 'restlessness' and 'pattern of aphid colonisation' experiments. This would enable each of the experiments to be more related to the growth stages.

Einkorn has clearly shown a high level of resistance to the cereal aphids and this appears to be a breakthrough in the search for resistance to the cereal aphids in that no similar high level of resistance combining two major components of resistance (antibiosis and preference) has yet been detected in modern hexaploid wheats. Hence at present Einkorn seems to be the only genetic source of a high degree of resistance to the cereal aphids. However, this primitive wheat will not be acceptable to the farmers because of certain undesirable agronomic characters e.g. small grains. The only solution to this problem would be to transfer the desirable characters of this primitive wheat into a commercially acceptable wheat variety through breeding. This proposition will certainly give rise to another breeding problem because Einkorn is a diploid wheat while the modern wheats are hexaploid. Crosses between diploid and hexaploid plants give rise to sterile F1 hybrids (Niles 1980). One possible way of solving this problem would be to cross Einkorn with a tetraploid wheat (e.g. T. timopheevi) to produce an hexaploid wheat (T. zhukovskyi) (Kuckuck 1970). T. zhukovskyi could then be crossed with a modern hexaploid wheat.

Even after the desirable characters of Einkorn have been successfully transferred to a modern hexaploid wheat, the new plant should be exhaustively tested to ascertain that it does not become susceptible to other biological organisms. Cases have been reported where crop plants resistant to certain biological organisms have become susceptible to different biological organisms (Gerhold 1966, Hawkes 1970, Maxwell 1972, van den Bosch and Messenger 1973, Panda 1979, Norris and Kogan 1980 and Phillips, Gutierrez and Adkisson 1980). It is interesting to note that in this study, Einkorn has been shown to be resistant to the mildew disease which is an economically important problem in cereal production.

If the new plant resistant to the cereal aphids does not become susceptible to different pathogens, new biotypes of the cereal aphids may suddenly

develop to which the new wheat might become susceptible (Maxwell 1972, Russell 1978, Panda 1979 and Ortman and Peters 1980). A possible solution to this problem would be to make the genetic base of the new wheat very polygenic by incorporating more resistant genes into the new wheat variety from other wheats thus enabling the new wheat to tolerate the infestation of the new strains of aphids (Panda 1979).

SUMMARY

The literature on the importance of cereal aphids as one of the limiting factors to the production of wheat and other cereals and the various ways by which they can be controlled are discussed. The importance of the use of resistant varieties for the control of the cereal aphids is emphasized. Moreover, the importance of the ancient plants as potential sources of potent genes for the control of the cereal aphids is discussed.

Using seedlings, excised leaves, stems and ears, preference tests were conducted at weekly intervals and at various growth stages. The diploid ancient wheat Einkorn was the least preferred by both cereal aphids. In antibiosis tests, three fourth instar aphids were caged on leaves at weekly intervals and the number of nymphs produced counted after five days. Fewest number of nymphs were produced on Einkorn wheat by both cereal aphids. Ten fourth instar aphids were used to infest seedlings of four wheat varieties for two weeks. Infestation of S. avenae and M. dirhodum slightly and moderately stunted Einkorn wheat respectively.

In restlessness tests, adult S. avenae were placed on the leaves of seedlings, flagleaves and ears of four wheat varieties and allowed to walk through the whole length of the plant organ. The shortest time was spent on each of the plant organs of Einkorn. A very small proportion of this short time was spent feeding while a greater proportion of the time was spent wandering on each of the three plant organs of Einkorn.

The pattern of colonisation of three wheats by S. avenae was studied by watching the movement of this aphid daily from flagleaf growth stage to senescence growth stage. The movement of this aphid on Emmer and Spelt followed a definite pattern (flagleaf - awn - spikelet) while that of Einkorn differed from complete ear emergence in the sense that the ear was

not colonised systematically from apex to the base.

The distance between adjacent spikelets on the ears of four wheats was measured using feeler guages of different thicknesses. The distance between adjacent spikelets on the ear of Einkorn was found to be the narrowest. Spikelets were removed alternately on the ears of two wheats and the number of S. avenae found selecting each feeding site was recorded daily. 'Base of the spikelet but junction with the rachis' was the most preferred feeding site on all varieties. When this result was compared with that of the previous investigation (Chapter 8) when observations were taken with the spikelets intact on the ears of these same two wheats (Einkorn and Emmer), 'Base of the spikelet' was selected as the most preferred feeding site. This sharp contrast in the choice of the most preferred feeding site when all the spikelets were intact on the ears was due to the close arrangement of the spikelets on the ears of Einkorn and Emmer (Chapter 9) which prevented the aphids from gaining access to B S J R which was proved to be the most preferred feeding site.

Incidence of mildew disease was studied on four wheats at two, three and four leaf growth stages by scoring for the severity of this disease on these seedlings. The ancient Einkorn wheat showed the least development of the disease at three and four leaf growth stages.

Emmer (susceptible to M. dirhodum), Mardler and Highbury wheats were moderately resistant to the cereal aphids but the primitive Spelt wheat was found to be very susceptible to both the grain (S. avenae) and the rose (M. dirhodum) aphids.

In this study, not all the ancient wheats were found resistant to the cereal aphids. At least one of the ancient wheats (Spelt) was susceptible as the modern Maris Kinsman susceptible check.

REFERENCES

A'BROOK, J. and DEWAR, A.M. (1977).
Evaluation of different screening technique for testing resistance in barley to cereal aphids.
In: International organisation for biological control of noxious animals and plants - Breeding for resistance to insects and mites - Wageningen, The Netherlands, pp. 31-35.

ADAS, (1978).
Cereal aphids.
Ministry of Agriculture, Fisheries and Food advisory leaflet 586, (Revised edition) 7 pp.

APABLAZA, J.U. and ROBINSON, A.G. (1967).
Effects of three species of aphids on barley, wheat or oats at various stages of plant growth.
Can. J. Plant Sci. 47, 367-373.

BAKKER, T. and ROBINSON, A.G. (1975).
Population trends of the English grain aphid, Macrosiphum avenae (Homoptera : Aphididae), on cereal crops in Manitoba, 1971-72.
The Manitoba Entomologist 9, 17-22.

BARANYOVITS, F. (1973).
The increasing problem of aphids in agriculture and horticulture.
Outlook on Agriculture 7, 102-108.

BARDNER, R. and FLETCHER, K.E. (1974).
Insect infestations and their effects on the growth and yield of field crops: a review.
Bull. ent. Res. 64, 141-160.

BARRONS, K.C. (1981).
Are pesticides really necessary?
Regnery Gateway, Inc. Chicago, Illinois. 245 pp.

BBC.1 9 o'clock pm news of 18/4/83, 5 o'clock pm news round of 18/5/83, 9 o'clock pm news of 19/5/83 and 9 o'clock pm news of 20/5/83.

BERNAYS, E.A., CHAPMAN, R.F., HORSEY, J. and LEATHER, E.M. (1974).
Inhibitory effects of seedling grasses on feeding and survival of acridids.
Bull. ent. Res. 64, 413-420.

van den BOSCH, R. (1980).
The pesticide conspiracy.
Prism Press, Dorset. 226 pp.

van den BOSCH, R. and MESSENGER, P.A. (1973).
Biological control.
Intext Press, Inc. New York. 180 pp.

BROWN, L.R. (1978).
The twenty-ninth day - Accommodating human needs and numbers to the earth's resources.
Norton and Company Inc., New York. 363 pp.

BROWNING, J.A. (1972).
Corn, wheat, rice, man : Endangered species.
J. Environ. Quality 1, 209-211.

CARTER, N., GARDENER, S., FRASER, A.M. and ADAMS, T.H.L. (1982).
The role of natural enemies in cereal aphid population dynamics.
Ann. appl. Biol. 101, 190-195.

CARTER, N., McLEAN, I.F.G., WATT, A.D. and DIXON, A.F.G. (1980).
Cereal aphids : a case study and review.
Applied Biology 5, 271-348.

CARTIER, J.J. and PAINTER, R.H. (1956).
Differential reactions of two biotypes of the corn leaf aphid to resistant and susceptible varieties, hybrids and selections of sorghums.
J. econ. Entomol. 49, 498-508.

CHAMBERS, R.J., SUNDERLAND, K.D., STACEY, D.L. and WYATT, I.J. (1982).
A survey of cereal aphids and their natural enemies in winter wheat in 1980.
Ann. appl. Biol. 101, 175-178.

CHAPMAN, R.F. (1977).
The role of the leaf surface in food selection by acridids and other insects.
Colloq. Int. C.N.R.S. 265, 133-149.

CHAPMAN, R.F. and BERNAYS, E.A. (1977).
The chemical resistance of plants to insect attack.
Scr. varia pont. Acad. Sci. 41, 603-643.

DAHMS, R.G. (1960).
Use of resistant varieties - the ideal way to control insects.
In: Handbook on biological control of plant pests (Westcott, C. and Nelson, P.K. eds.). Brooklyn Botanic Garden, New York. pp. 82-87.

DAHMS, R.G. (1972).
Managing insect pests to reduce environmental problems.
J. Environ. Quality 1, 211.

DAILY STAR of 21/5/83 p. 6.

DEAN, G.J. (1973a).
Bionomics of aphids reared on cereals and some Gramineae.
Ann. appl. Biol. 73, 127-135.

DEAN, G.J. (1973b).
Distribution of aphids in spring cereals.
J. appl. Ecol. 10, 447-462.

DEAN, G.J. (1974a).
Effect of temperature on the cereal aphids Metopolophium dirhodum (Wlk.), Rhopalosiphum padi (L.) and Macrosiphum avenae (F.) (Hem., Aphididae).
Bull. ent. Res. 63, 401-409.

DEAN, G.J. (1974b).
Effects of parasites and predators on the cereal aphids Metopolophium dirhodum (Wlk.) and Macrosiphum avenae (F.) (Hem., Aphididae).
Bull. ent. Res. 63, 411-422.

DEAN, G.J. (1974c).
The overwintering and abundance of cereal aphids.
Ann. appl. Biol. 76, 1-7.

DEAN, G.J. (1974d).
The four dimensions of cereal aphids.
Ann. appl. Biol. 77, 74-78.

DEAN, G.J. (1975).
The natural enemies of cereal aphids.
Ann. appl. Biol. 80, 130-132.

DEAN, G.J. and LUURING, B.B. (1970).
Distribution of aphids in cereal crops.
Ann. appl. Biol. 66, 485-496.

DETHIER, V.G. (1954).
Evolution of feeding preferences in phytophagous insects.
Evolution 8, 33-54.

DETHIER, V.G. (1966).
Feeding behaviour.
In: Symposia of the Royal Entomological Society of London (Haskell, P.T., ed.) 3, 46-58.

DEWAR, A.M. (1977).
Assessment of methods for testing varietal resistance to aphids in cereals.
Ann. appl. Biol. 87, 183-190.

DONE, A.A. and WHITTINGTON, W.J. (1978).
The restoration of male fertility f_1 hybrids.
Ann. appl. Biol. 89, 489-493.

DRY, W.W. and TAYLOR, L.R. (1970).
Light and temperature thresholds for take-off by aphids.
J. Anim. Ecol. 39, 493-504.

van EMDEN, H.F. (1972).
Aphids as phytochemists.
In: Phytochemical Ecology (Harborne, J.B., ed.).
Academic Press, London and New York pp. 25-43.

van EMDEN, H.F. (1973).
Aphid host plant relationships - some recent studies (Lowe, A.D., ed.).
N.Z. ent. Soc. Bull. No. 2, pp. 54-64.

van EMDEN, H.F. (1977).
Insect-pest management in multiple cropping systems - a strategy.
In: Symposium on cropping systems research and development for the Asia rice farmers.
IRRI, Manila pp. 325-343.

van EMDEN, H.F. (1978).
Insects and secondary plant substances - an alternative viewpoint with special reference to aphids.
In: Biochemical aspects of plant and animal coevolution (Harborne, J.B., ed.).
Academic Press, London and New York pp. 309-323.

van EMDEN, H.F. (personal communication).

FERTILISER STATISTICS (1976).
The fertiliser manufacturers association. Alembic House, London 8 pp.

FIDDIAN, W.E.H. (1977).
Factors affecting cereal yield.
Proceedings 1977 British Crop Protection Conference - Pests and Diseases. pp. 755-761.

FLETCHER, W.W. (1974).
The pest war.
Basil Blackwell, Oxford. 218 pp.

GALLUN, R.L. (1972).
Genetic interrelationships between host plants and insects.
J. Environ. Quality 1, 259-265.

GEORGE, K.S. (1974).
Damage assessment aspects of cereal aphid attack in autumn and spring-sown cereals.
Ann. appl. Biol. 77, 67-74.

GEORGE, K.S. (1975).
The establishment of economic damage thresholds with particular reference to cereal aphids.
Proceedings 8th British Insecticide and Fungicide Conference. pp. 79-85.

GEORGE, K.S. and GAIR, R. (1979).
Crop loss assessment on winter wheat attacked by the grain aphid, Sitobion avenae (F.), 1974-77.
Pl. Path. 28, 143-149.

GERHOLD, H.D. (1966).
In quest of insect-resistant forest trees.
In: Breeding pest-resistant trees (Gerhold, H.D., Schreiner, E.J., McDermott, R.E. and Winieski, J.A., eds.).
Pergamon Press Oxford, London and New York pp. 305-318.

GERNERT, W.B. (1917).
Aphis immunity of teosinte-corn hybrids.
Science 46, 390-392.

GIBSON, R.W. (1971).
Glandular hairs providing resistance to aphids in certain wild potato species.
Ann. appl. Biol. 68, 113-119.

GREEN, M.B. (1976).
Pesticides : Boon or Bane?
Elek Books Limited, London. 111 pp.

HARLAN, J.R. (1972).
Genetics of disaster.
J. Environ. Quality 1, 212-215.

HARRIS, M.K. (1975).
Allopatric Resistance : Searching for sources of insect resistance for use in agriculture.
Environ. Entomol. 4, 661-669.

HASKELL, P.T. (1977).
Integrated pest control and small farmer crop protection in developing countries.
Outlook on Agriculture 9, 121-126.

HAWKES, J.G. (1970).
Potatoes. In: Genetic resources in plants - their exploration and conservation (Frankel, O.H. and Bennett, E., eds.).
Blackwell Scientific Publication, Oxford and Edinburgh pp. 311-319.

HILLS, L.D. (1964).
Pest control without poisons.
The Henry Doubleday Research Association, Bocking, Braintree, Essex, England. 64 pp.

HODKINSON, I.D. and HUGHES, M.K. (1982).
Insect herbivory.
Chapman and Hall, London, New York. 77 pp.

HSIAO, T.H. (1969).
Chemical basis of host selection and plant resistance in oligophagous insects.
Ent. exp. et appl. 12, 777-788.

HSIAO, T.H. (1972).
Chemical feeding requirements of oligophagous insects. In: Insect and mite nutrition, significance and implications in ecology and pest management (Rodriguez, J.G. ed.).
North-Holland Publishing Company Amsterdam pp. 225-240.

ITV 1 o'clock pm news of 20/5/83, 5.45 o'clock pm news of 20/5/83 and World in Action programme between 8.30 and 9 o'clock pm on 25/7/83.

JENKINS, J.E.E. (1977).
Future strategy for pest and disease control in cereal production systems.
Proceedings 1977 British Crop Protection Conference - Pests and Diseases pp. 785-793.

JOHNSON, B. (1953).
The injurious effects of the hooked epidermal hairs of French beans (Phaseolus vulgaris L.) on Aphis craccivora Koch.
Bull. ent. Res. 44, 779-788.

JOHNSON, B. (1956).
The influence on aphids of the glandular hairs on tomato plants.
Pl. Path. 5, 131-132.

KAY, D.J., WRATTEN, S.D. and STOKES, S. (1981).
Effects of vernalisation and aphid culture history on the relative susceptibilities of wheat cultivars to aphids.
Ann. appl. Biol. 99, 71-75.

KENNEDY, J.S. (1965).
Mechanism of host plant selection.
Ann. appl. Biol. 56, 317-322.

KENNEDY, J.S. and BOOTH, C.O. (1951).
Host alternation in Aphis fabae Scop. 1. Feeding preferences and fecundity in relation to the age and kind of leaves.
Ann. appl. Biol. 38, 25-64.

KOLBE, W. (1969).
Studies on the occurrence of different aphid species as the cause of cereal yield and quality losses.
Pflanzenschutz-Nachrichten Bayer 22, 171-204 (English edition).

KOLBE, W. (1970).
Further studies on the reduction of cereal yields by aphid infestation.
Pflanzenschutz-Nachrichten Bayer 23, 144-162 (English edition).

KOLBE, W. (1973).
Studies on the occurrence of cereal aphids and the effect of feeding damage on yields in relation to infestation density levels and control.
Pflanzenschutz-Nachrichten Bayer 26, 396-410 (English edition).

KOLBE, W. and LINKE, W. (1974).
Studies of cereal aphids : their occurrence, effect on yield in relation to density levels and their control.
Ann. appl. Biol. 77, 85-87.

KUCKUCK, H. (1970).
Primitive wheats. In: Genetic resources in plants - their exploration and conservation (Frankel, O.H. and Bennett, E., eds.).
Blackwell Scientific Publications, Oxford and Edinburgh pp. 249-266.

LARGE, E.C. (1954).
Growth stages in cereals. Illustration of the Feekes scale.
Pl. Path. 3, 129-130.

LIPKE, H. and FRAENKEL, G. (1956).
Insect nutrition.
Ann. Rev. Entomol. 1, 17-44.

LOWE, H.J.B. (1978).
Detection of resistance in cereals.
Ann. appl. Biol. 88, 401-404.

LOWE, H.J.B. (1980).
Resistance to aphids in immature wheat and barley.
Ann. appl. Biol. 95, 129-135.

LOWE, H.J.B. (1981).
Resistance and susceptibility to colour forms of the aphid Sitobion avenae in spring and winter wheats (Triticum aestivum).
Ann. appl. Biol. 99, 87-98.

MACKARNESS, R. (1980).
Chemical victims.
Pan Books Limited, London and Sydney. 203 pp.

MALYK, M.R. and ROBINSON, A.G. (1971).
Population trends of aphids on cereal crops in Manitoba, 1968-1969.
The Manitoba Entomologist 5, 79-88.

MARKKULA, M. and MYLLYMAKI, S. (1963).
Biological studies on cereal aphids, Rhopalosiphum padi (L.), Macrosiphum avenae (F.), and Acyrthosiphum dirhodum (Wlk.) (Hom., Aphididae).
Ann. Agric. Fenn. 2, 33-43.

MARKKULA, M. and PULLIAINEN, E. (1965).
The effect of temperature on the lengths of the life periods of the English grain aphid Marcrosiphum avenae (F.) (Hom., Aphididae) and on the number and colour of its progeny.
Ann. Ent. Fenn. 31, 39-45.

MARKKULA, M. and RAUTAPAA, J. (1967).
The effect of light and temperature on the colour of the English grain aphid, Macrosiphum avenae (F.) (Hom., Aphididae).
Ann. Ent. Fenn. 33, 1-13.

MAXWELL, F.G. (1972).
Morphological and chemical changes that evolve in the development of host plant resistance to insects.
J. Environ. Quality 1, 265-270.

MAXWELL, F.G., LAFEVER, H.N. and JENKINS, J.N. (1965).
Blister beetles on glandless cotton.
J. econ. Entomol. 58, 792-793.

NEWMAN, J.F. (1976).
Assessment of the environmental impact of pesticides.
Outlook on Agriculture 9, 9-15.

NILES, G.A. (1980).
Breeding cotton for resistance to insect pests. In: Breeding plants resistant to insects (Maxwell, F.G. and Jennings, P.R. eds.). John Wiley and Sons, New York and Chichester pp. 337-369.

NORRIS, D.M. and KOGAN, M. (1980).
Biochemical and morphological bases of resistance. In: Breeding plants resistant to insects (Maxwell, F.G. and Jennings, P.R. eds.). John Wiley and Sons, New York and Chichester pp. 23-61.

ORLOB, G.B. (1961).
Biology and taxonomy of cereal and grass aphids in New Brunswick (Homoptera : Aphididae).
Can. J. Zool. 39, 495-503.

ORTMAN, E.E. and PETERS, D.C. (1980).
Introduction to 'Plant Resistance to Insect'. In: Breeding plants resistant to insect (Maxwell, F.G. and Jennings, P.R. eds.). John Wiley and Sons, New York and Chichester pp. 3-13.

OTAKE, A. (1966).
Studies on aphid populations.
Hokuriku Regional Agricultural Experimental Station, Tadada, Niigata Prefecture, Japan 108 pp.

PAINTER, R.H. (1951).
Insect resistance in crop plants.
The Macmillan Co., New York. 520 pp.

PAINTER, R.H. (1960).
Possibilities and methods of breeding for resistance to insects in forage crops.
Proceedings of the eighth International Grassland Congress held at the University of Reading, Berkshire, England from 11th to 21st July, 1960 pp. 81-83.

PAINTER, R.H. (1968).
Crops that resist insects provide a way to increase World food supply.
Kans. State Agric. Exp. Stn. Bull. No. 520 22 pp.

PANDA, N. (1979).
Principles of host-plant resistance to insect pests.
Hindustan Publishing Corporation, Delhi. 386 pp.

PHILLIPS, J.R., GUTIERREZ, A.P. and ADKISSON, P.L. (1980).
General accomplishments toward better insect control in cotton.
In: New technology of pest control (Huffaker, C.B., ed.).
John Wiley and Sons, New York and Chichester. pp. 123-153.

PLUMB, R.T. (1977).
Aphids and virus control on cereals.
Proceedings 1977 British Crop Protection Conference - Pests and Diseases pp. 903-913.

verschoor-van der POEL, P.J.G. and van LENTEREN, J.C. (1978).
Host-plant selection by the greenhouse whitefly Trialeurodes vaporariorum (Westwood) (Homoptera : Aleyrodidae).
Med. Fac. Landbouww. Rijksuniv. Gent 43, 387-396.

RAUTAPAA, J. (1966).
The effect of the English grain aphid Macrosiphum avenae (F.) (Hom., Aphididae) on the yield and quality of wheat.
Ann. Agric. Fenn. 5, 334-341.

RAUTAPAA, J. (1968).
Changes in the yield and protein quantity of oat caused by Rhopalosiphum padi (L.) (Hom., Aphididae).
Ann. Agric. Fenn. 7, 95-104.

RAUTAPAA, J. (1970).
Preference of cereal aphids for various cereal varieties and species of Gramineae, Juncaceae and Cyperaceae.
Ann. Agric. Fenn. 9, 267-277.

RAUTAPAA, J. (1976).
Population dynamics of cereal aphids and method of predicting population trends.
Ann. Agric. Fenn. 15, 272-293.

ROBINSON, R.A. (1977).
Crop resistance may be our best crop protection.
World crops 29, 104-106.

RUSSELL, G.E. (1978).
Plant breeding for pest and disease resistance.
Butterworths, London and Boston. 485 pp.

SCHOONHOVEN, L.M. (1972).
Some aspects of host selection and feeding in phytophagons insects.
In: Insect and mite nutrition, significance and implications in ecology and pest management (Rodriguez, J.G. ed.).
North-Holland Publishing Company Amsterdam pp. 557-566.

SCHUSTER, D.J. and STARKS, K.J. (1973).
Greenbugs: Components of host-plant resistance in Sorghum.
J. econ. Entomol. 66, 1131-1134.

SMITH, R.L., WILSON, R.L. and WILSON, F.D. (1975).
Resistance of cotton plant hairs to mobility of first-instars of the pink bollworm.
J. econ. Entomol. 68, 679-683.

SNELLING, R.O. (1941).
Resistance of plants to insect attack.
Botanical Review 7, 543-586.

SOTHERTON, N.W. and van EMDEN, H.F. (1982).
Laboratory assessments of resistance to the aphids Sitobion avenae and Metopolophium dirhodum in three Triticum species and two modern wheat cultivars.
Ann. appl. Biol. 101, 99-107.

SPIERTZ, J.H.J. (1978).
Grain production and assimilate utilization of wheat in relation to cultivar characteristics, climatic factors and nitrogen supply. Agricultural Research Report No. 881, Centre for Agricultural Publishing and Documentation Wageningen. 35 pp.

STARKS, K.J. and BURTON, R.L. (1977).
Greenbugs: A comparison of mobility on resistant and susceptible varieties of four small grains.
Environ. Entomol. 6, 331-332.

STONE, L.E.W. (1977).
The incidence and economic significance of pests in cereals in England and Wales.
Proceedings of the 1977 British Crop Protection Conference - Pests and Diseases pp. 713-720.

SUNDERLAND, K.D. and VICKERMAN, G.P. (1980).
Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields.
J. appl. Ecol. 17, 389-396.

TATUM, L.A. (1971).
The southern corn leaf blight epidemic.
Science 171, 1113-1116.

THORSTEINSON, A.J. (1960).
Host selection in phytophagous insects.
Ann. Rev. Entomol. 5, 193-218.

THURSTON, R., SMITH, W.T. and COOPER, B.P. (1966).
Alkaloid secretion by trichomes of Nicotiana species and resistance to aphids.
Entomologia exp. et appl. 9, 428-432.

TV am news of 17/4/83 and 26/7/83.

VEREIJKEN, P.H. (1979)
Feeding and multiplication of three cereal aphid species and their effect on yield of winter wheat.
Agricultural Research Report No. 888, Centre for Agricultural Publishing and Documentation Wageningen. 58 pp.

VICKERMAN, G.P. and WRATTEN, S.D. (1979).
The biology and pest status of cereal aphids (Hemiptera : Aphididae) in Europe : a review.
Bull. ent. Res. 69, 1-32.

WALTERS, K.F.A. and DIXON, A.F.G. (1982).
The effect of host quality and crowding on the settling and take-off of cereal aphids.
Ann. appl. Biol. 101, 211-218.

WATT, A.D. (1979).
The effect of cereal growth stages on the reproductive activity of Sitobion avenae and Metopolophium dirhodum.
Ann. appl. Biol. 91, 147-157.

WAY, M.J. (1977).
Integrated control - practical realities.
Outlook on Agriculture 9, 127-135.

WRATTEN, S.D. (1975).
The nature of the effects of the aphids Sitobion avenae and Metopolophium dirhodum on the growth of wheat.
Ann. appl. Biol. 79, 27-34.

WRATTEN, S.D. (1977).
Reproductive strategy of winged and wingless morphs of the aphids Sitobion avenae and Metopolophium dirhodum.
Ann. appl. Biol. 85, 319-331.

WRATTEN, S.D. (1978).
Effects of feeding position of the aphids Sitobion avenae and Metopolophium dirhodum on wheat yield and quality.
Ann. appl. Biol. 90, 11-20.

WRATTEN, S.D. and READHEAD, P.C. (1976).
Effects of cereal aphids on the growth of wheat.
Ann. appl. Biol. 84, 437-440.

WRATTEN, S.D., LEE, G. and STEVENS, D.J. (1979).
Duration of cereal aphid populations and the effects on wheat yield and quality.
Proceedings 1979 British Crop Protection Conference - Pests and Diseases pp. 1-8.

WYATT, I.J. (1970).
Susceptibility of year-round chrysanthemums to aphids.
Gardeners Chronicle 167, 10-12.

ZADOKS, J.C., CHANG, T.T. and KONZAK, C.F. (1974).
A decimal code for the growth stages of cereals.
Weed Research 14, 415-421.

A P P E N D I X

*	=	Significant at 5% level
* *	=	Significant at 1% level
* * *	=	Significant at 0.1% level
n.s.	=	Non significant

APPENDIX 1: Analysis of variance table for the number of apterous S. avenae selecting the seedlings, leaf segments and excised ears of seven wheat varieties at weekly intervals.

Source of variation	df	Mean Squares for each week											
		1	2	3	4	5	6	7	8	9	10	Flagleaf	Excised ear
Replicates	1	0.092	4.08	4.500	1.020	6.90	0.00	4.94	0.37	0.37	0.65	0.50	0.83
Rows	6	2.163	2.01	0.296	1.136	3.24	3.40	2.52	1.19	2.35	1.13	0.70	1.37
Columns	6	8.211	23.51	14.391	4.898	22.10	14.52	9.02	18.02	15.14	26.94	24.30	34.03
Varieties	6	79.830***	115.82***	81.272***	159.874***	103.38***	90.26***	156.83***	69.67***	96.81***	93.84***	187.15***	118.34***
Residual	78	8.852	13.36	7.859	8.451	13.83	11.99	11.01	14.90	19.56	16.10	31.73	12.93

APPENDIX 2: Analysis of variance table for the number of apterous S. avenae selecting the stem segments of seven wheat varieties at weekly intervals.

Source of variation	df	Mean Squares for each week							
		3	4	5	6	7	8	9	10
Replicates	1	1.020	0.163	0.826	6.915	6.897	2.295	2.295	0.653
Rows	6	0.914	1.248	2.843	2.653	15.571	7.285	1.295	2.897
Columns	6	7.795	2.153	10.938	17.224	8.928	37.047	29.367	9.302
Varieties	6	39.486**	152.248**	111.653**	82.057**	54.142**	227.047**	73.700**	52.61**
Residual	78	5.739	6.250	7.657	13.674	13.785	19.896	16.079	13.382

APPENDIX 3: Analysis of variance table for the number of apterous *S. avenae* selecting the seedlings, leaf segments and excised ears of four wheat varieties at different growth stages.

Two leaf growth stage

Source of variation	df	Mean Square
Replicates	14	2.903
Rows	3	0.161
Columns	3	2.694
Varieties	3	166.894 ***
Residual	216	5.716

Three leaf growth stage

Source of variation	df	Mean Square
Replicates	2	1.271
Rows	3	3.299
Columns	3	0.132
Varieties	3	49.854 ***
Residual	36	4.363

Tillering growth stage

Source of variation	df	Mean Square
Replicates	1	0.781
Rows	3	27.281
Columns	3	0.281
Varieties	3	14.698 n.s.
Residual	21	9.460

(Continued)

APPENDIX 3: (Continued)

Flagleaf growth stage

Source of variation	df	Mean Square
Replicates	1	0.031
Rows	3	1.865
Columns	3	0.115
Varieties	3	38.865*
Residual	21	7.924

Ear growth stage

Source of variation	df	Mean Square
Replicates	2	5.895
Rows	3	0.076
Columns	3	1.187
Varieties	3	70.687***
Residual	36	7.509

APPENDIX 4: Analysis of variance table for the number of alate *S. avenae* selecting the seedlings of four wheat varieties at two growth stages.

Two leaf growth stage

Source of variation	df	Mean Square
Replicates	2	1.750
Varieties	3	60.750.
Residual	6	9.083

Three leaf growth stage

Source of variation	df	Mean Square
Replicates	14	4.945
Varieties	3	272.194...
Residual	42	6.123

APPENDIX 5: Analysis of variance table for the number of apterous *M. dirhodum* selecting the seedling, leaf segments and excised ears of each wheat variety at different growth stages.

Two leaf growth stage

Source of variation	df	Mean Square
Replicates	2	65.76
Rows	6	4.48
Columns	6	4.82
Varieties	6	64.50***
Residual	126	12.03

Three leaf growth stage

Source of variation	df	Mean Square
Replicates	1	0.163
Rows	6	16.473
Columns	6	2.639
Varieties	6	71.497***
Residual	78	5.491

Tillering growth stage

Source of variation	df	Mean Square
Replicates	1	0.125
Rows	3	9.708
Columns	3	0.125
Varieties	3	76.708***
Residual	21	8.673

(Continued)

APPENDIX 5: (Continued)

Flagleaf growth stage

Source of variation	df	Mean Square
Replicates	1	0.78
Rows	3	7.61
Columns	3	1.28
Varieties	3	24.78 n.s.
Residual	21	15.52

Ear growth stage

Source of variation	df	Mean Square
Replicates	2	2.895
Rows	3	2.743
Columns	3	7.576
Varieties	3	67.465...
Residual	36	4.981

APPENDIX 6: Analysis of variance table for the number of nymphs produced by a single S. avenae in 5 days on four wheat varieties at weekly intervals.

Source of variation	df	Mean Squares for each week									
		1	2	3	4	5	6	7	8	9	Flagleaf
Replicates	3	33.00	34.167	4.17	30.73	12.17	114.75	103.23	8.33	20.17	8.56
Varieties	3	22.87 n.s.	3.833 n.s.	32.50 n.s.	30.23 n.s.	122.17 *	129.42 * *	108.56 n.s.	70.17 n.s.	63.50 n.s.	78.23 *
Residual	9	22.17	6.667	11.89	16.90	17.11	16.58	28.78	21.11	33.33	15.40

APPENDIX 7: Analysis of variance table for the number of nymphs produced by a single M. dirhodum in 5 days on four wheat varieties at weekly intervals.

Source of variation	df	Mean Squares for each week									
		1	2	3	4	5	6	7	8	9	Flagleaf
Replicates	3	11.06	36.396	43.40	32.17	90.73	145.23	34.23	22.92	176.06	67.50
Varieties	3	11.06 n.s.	48.729 *	116.56 *	51.00 n.s.	57.73 n.s.	66.73 n.s.	71.23 n.s.	114.92 n.s.	21.23 n.s.	47.83 n.s.
Residual	9	21.56	9.896	17.45	21.83	28.28	90.01	33.23	52.69	50.34	42.33

APPENDIX 8: Analysis of variance table for the percent reduction in plant growth caused by free infestation of S. avenae.

Source of variation	df	Mean Squares for each plant measurement						
		Increment in number of leaves	Increment in length of leaf	Dry weight of leaf	Increment in length of stem	Dry weight of stem	Dry weight of root	Increment in height of plant
Replicates	15	1949	4398	1719	726.5	266.3	745.8	945
Variety	3	722n.s.	7272*	1496n.s.	1498.3*	399.2n.s.	535.2n.s.	901n.s.
Residual	45	1003	1875	1984	361.5	319.0	886.2	1070

APPENDIX 9: Analysis of variance table for **the percent reduction in plant growth caused by free** infestation of M. dirhodum.

Source of variation	df	Mean Squares for each plant measurement						
		Increment in number of leaves	Increment in length of leaf	Dry weight of leaf	Increment in length of stem	Dry weight of stem	Dry weight of root	Increment in height of plant
Replicates	11	539.4	728.5	796.7	404.2	925.4	566.9	1399.6
Variety	3	516.4n.s.	2828.9*	525.6*	9333.3***	683.6*	366.6n.s.	2104.9n.s.
Residual	33	194.6	965.8	130.7	671.0	156.2	960.6	888.6

APPENDIX 10: Analysis of variance for the activity of adult apterous *S. avenae* on the leaves of seedlings of four wheat varieties at two leaf growth stage.

Source of variation	df	Mean Square for each activity		
		Log total time in seconds per centimetre	Feeding time in seconds	Log wandering time in seconds per cent.
Varieties	3	3.248n.s.	517769n.s.	1.5633.
Residual	120	1.225	334677	0.5110

APPENDIX 11: Analysis of variance for the activity of adult apterous *S. avenae* on the flagleaves of four wheat varieties at flagleaf growth stage.

Source of variation	df	Mean Square for each activity		
		Log total time in seconds per centimetre	Feeding time in seconds	Log wandering time in seconds per cent.
Varieties	3	12.228**	5576000*	6.068**
Residual	120	2.425	1949000	1.176

APPENDIX 12: Analysis of variance for the activity of adult apterous *S. avenae* on the ears of four wheat varieties at ear growth stage.

Source of variation	df	Mean Square for each activity		
		Log total time in seconds per centimetre	Feeding time in seconds	Log wandering time in seconds per cent.
Varieties	3	49.821***	31380000***	19.555***
Residual	120	2.734	3832000	1.567

APPENDIX 13: Analysis of variance for the accessibility of the bases of the spikelets of the ears of four wheat varieties to *S. avenae*.

Source of variation	df	Mean square
Variety	3	31.329733***
Residual	596	0.0251153

APPENDIX 14: Analysis of variance for the selection of feeding sites by S. avenae.

Selection among four feeding sites

Source of variation	df	Mean Square
Varieties	1	6.2280021n.s.
Sites	3	13480.417***
Residual	32	40.162183

Selection among seven feeding sites

Source of variation	df	Mean Square
Varieties	1	12.815238n.s.
Sites	6	3497.6759***
Residual	28	35.403433