

STUDIES ON ECOLOGY OF CEREAL
APHIDS AND PROSPECTS FOR INTEGRATED CONTROL

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by

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ABSTRACT

The increasing world-wide importance of cereal aphids has stimulated widespread research, yet many 'key' aspects of their ecology remain poorly understood. This thesis is concerned with some of these, namely overwintering, natural enemy impact and the effects of crop growth stage.

Different techniques were used at Silwood to study overwintering of virginoparous aphids (*Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi*) on wheat. These comprised:- observation of marked colonies naturally infesting crops in the autumn; monitoring artificial populations established in the field inside or outside shelters designed to reduce mortality from wind, rain or natural enemies; and testing effects of artificial wind on artificial populations. Between October - March, rainfall, predation and parasitism were negligible causes of mortality. Isolated nights of frost did not kill many aphids except when there was also heavy dew. Low temperature, however, contributed to the steady decline in numbers of *S. avenae* during winter. This long term effect resulted from prevention of much decreased reproduction; damage to the host plants; and possibly from metabolic imbalance and reduced nutrition at prolonged low temperatures. More striking losses due to wind were positively related both to wind velocity and gustiness. Gusty wind increased the 'shearing action' between leaves resulting in heavier losses of *S. avenae* than *M. dirhodum* and *R. padi* which feed lower down the plants.

To study natural enemy impact and the effect of crop growth stage on aphid populations (June - July) a large scale replicated experiment was set up. Physical and chemical methods were used to exclude predators from plots containing wheat of distinct growth stages. Whereas ground beetles had no effect, predation by Syrphidae substantially reduced *S. avenae* and *M. dirhodum* populations.

Similar patterns of population development and decline were observed on all three sowings but the timing of aphid attack coincided more closely to crop growth stage than to calendar time. These, together with supplementary studies with sequentially sown rows of wheat indicated a clear difference in growth stage preference between *S. avenae* and *M. dirhodum*. Plants first became attractive to larvipositing *S. avenae* alates after 'heading' but attractiveness steadily declined as the ear matured. In contrast *M. dirhodum* alates deposited most larvae on 'pre-heading' plants. Once plants reached the late milky ripe stage they became unattractive, even to established populations.

The results of this research indicate ways in which improved control of cereal aphids might be obtained. Progress towards this end will hopefully depend on the development of an integrated control programme that is nevertheless compatible with high yielding cereal production systems.

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CHAPTER 1

GENERAL INTRODUCTION

CHAPTER 1

GENERAL INTRODUCTION1.1 INTRODUCTION

Cereal aphids are currently one of Britain's more serious agricultural pests, both in terms of the potential damage they cause and difficulties in effectively controlling them. Despite extensive recent research, considerable ignorance still exists in relation to critical aspects of cereal aphid biology, and the biological reasons for their increased abundance and importance remain speculative.

The main purpose of this chapter is to provide a brief introduction to the biology and pest status of cereal aphids with special emphasis on the more controversial aspects. In addition, a survey is made of cereal aphid research in the U.K., and the objectives and approach of the present study defined. It is not intended to give exhaustive coverage of the literature on cereal aphids as this need has recently been fulfilled by the reviews of Vickerman and Wratten (1979) and Carter *et al* (1980).

1.2 APHID AND NATURAL ENEMY SPECIES

6 species of aphid commonly occur on the aerial parts of cereals in Europe; *Sitobion avenae*, *S. fragariae* (Walker), *Metopolophium dirhodum* (Walker), *M. festucae* (Theobald), *Rhopalosiphum padi* (L.) and *R. maidis* (Fitch). In addition, *R. insertum* is found on the roots. *S. avenae*, *M. dirhodum* and *R. padi* are generally considered to be the most important species in the U.K.

Potts (1977) has recently summarised records of predatory insects

in cereals. Considering 'aphid specific' predators, *Coccinella septempunctata* (L.) appears to be the most important coccinellid, and *Episyrphus balteatus* (Deg.), the main syrphid. Chrysodipae (*Chrysopa carnea* (Steph)), Anthocoridae (*Anthocoris*. spp.) also occur in small numbers.

There is commonly a wide variety of polyphagous or 'general' predators associated with cereals, many of which have been shown to climb plants and feed on cereal aphids (Vickerman and Sunderland, 1975; Sunderland and Vickerman, 1980). *Agonum dorsale* (Pont.), *Nebria brevicollis* (Fab.), *Pterontichus melanarius* (Illiger), *Harpalus rufipes* (Degeer) and *Demetrias* spp. all Carabidae and *Tachyporus* spp. (Staphylinidae) are some of the ground beetle species most likely to be important cereal aphid predators (Sunderland 1978, Edwards and George, 1977; Sunderland and Vickerman, 1980; Jones, 1979a). According to Vickerman and Wratten (1979), the main species of primary parasites are *Aphidius picipes* (Nees), *A. uzbekistanicus* (Luzhetskii), *A. ervi* (Haliday), *A. urticae* (Haliday), *A. equiseticola* (Stary), *Praon volucre* (Haliday), *P. gallicum* (Stary), *Lysiphletus fabarum* (Marshall), *Ephedrus plagiator* (Nees), *Trioscys auctus* (Haliday), *Monoctonus cerasi*, *Diaeretiella rapae* (M'Intosh) and *Aphelissus varipes* (Forster). These parasites are in turn parasitised by the following hyperparasites; *Asaphes vulgaris* (Walker), *A. suspensus* (Nees) and *Coruna clavata* (Walker) (Pteromalidae), *Lygocerus aphidivorus* (Kieffer) (Ceraphronidae), *Conostigmus* sp. (Ceraphronidae), *Dendrocerus* spp. (Ceraphronidae), *Phaenoglyphis* spp. and *Alloxysta* spp. (Cynipidae). (Also see Jones, 1972, 1976 and 1979b).

As well as occurring on commercially grown cereals, cereal aphids and many of their natural enemies are commonly found in wild and cultivated grassland (Dransfield, 1975).

1.3 FEEDING HABITS AND DAMAGE

The three major aphid species differ with respect to 'preferred feeding sites' on cereals and in the nature of the damage inflicted. *R. padi* feeds low down the plant on the stem and leaves and in the U.K. is primarily important as a vector of the 'severe' strain of barley yellow dwarf virus (B.Y.D.V.) (Plumb, 1974). Its relatively small importance in causing direct feeding losses in the U.K. remains one of the most puzzling questions in cereal aphid ecology. Thriving cultures develop on a range of cultivated cereals in the laboratory, large numbers are caught in Rothamsted suction traps (Dean 1974c) and they are serious primary pests in Finland. (Vickerman and Wratten, 1979). *S. avenae* and *M. dirhodum* both cause direct feeding losses but because *S. avenae* feeds on the ears of cereals, this species has usually caused most alarm to advisors and farmers. *M. dirhodum* is confined to the leaves and as such often passes unnoticed yet its feeding can reduce yield both in terms of 1000 grain weight (George, 1974; Wratten, 1975; Lowe, 1974) and 'grain nitrogen content'. (Wratten and Redhead, 1976; Wratten, 1978). Only damage inflicted prior to flowering (mainly *M. dirhodum*) appears to reduce spikelet number or grain number (Wratten, 1975). Infestations by these species during the seedling stages can disseminate the 'mild' strain of B.Y.D.V. and in this respect *M. dirhodum* appears to be increasing in importance especially in France.

It is not yet possible either to predict satisfactorily, the occurrence of aphids in a given year or to define the relationship between their numbers and losses due to virus (Plumb, 1977), but simulation models are being devised that should enable potential losses to be predicted from a knowledge of aphid and natural enemy abundance within a season (McLean *et al*, 1977; Rabbinge *et al*, 1979).

Yields from sprayed and unsprayed plots have been compared indicating up to 42% loss due to heavy infestations (species unspecified) (Kolbe 1969). Damage is critically dependent on timing as well as the intensity (aphid abundance) and duration of attack (Wratten *et al*, 1979) with heaviest losses likely to occur after flowering and during grain filling (George, 1978). The official A.D.A.S. recommendation to farmers reflects these dual considerations of intensity and timing and incorporates an element of prediction. Thus George (1975) recommends that if there is a mean of 5 or more aphids per ear at flowering and the population has increased a day or two later, one spraying is likely to be economically worthwhile. Elsewhere in Europe, (e.g. Belgium and Holland) higher thresholds have been adopted following the studies of Latteur (1976) but, according to Verijken (1979) these have been set too high for crops at the flowering - watery ripe growth stages although a high threshold remains appropriate for 'milky ripe' stage infestation.

1.4 OVERWINTERING

The question of overwintering by cereal aphids is characterized by its complexity resulting from the existence of both holocyclic and anholocyclic life cycles, the wide diversity of potentially important overwintering habitats and the need to consider at least the 3 major aphid species. These difficulties inevitably hamper any attempts to find correlations between winter conditions and subsequent aphid attack.

Holocyclic life cycles are considered to represent the primitive condition in aphids (Eastop, 1972) involving the production of sexual morphs which lay eggs on primary host plants during autumn. Eggs are well adapted to withstand adverse winter weather and, after hatching in the spring, aphids may ultimately migrate to crop habitats. Here

the aphids undergo pathenogenetic reproduction involving the telescoping of generations and consequent potential pest status. The primary hosts of *S. avenae*, *M. dirhodum* and *R. padi* are grasses, *Rosa* spp and the bird cherry tree *Prunus padus* (L.) respectively. The occurrence of anholocycly has been noted in all 3 major species (Hille Ris Lambers, 1939, 1947; Gair, 1953; Dean, 1974a; George 1974) but their relative importance compared to holocyclic clones is unknown. Their significance lies in their potential for rapid build up during the spring and summer, given short periods of favourable weather, possibly on the secondary hosts including cereals. Many authors, however have assumed that their survival as active stages is limited to mild winters. (Plumb, 1977,) but the mortality of exposed aphids in Dean's (1974a) experiments on potted seedlings showed no clear correlation with prevailing temperatures and rainfall. On the other hand, a similar group of aphids protected from wind, rain and snow survived substantially better. Dean concluded that 'all three species can survive pathenogenetically in grass tussocks and hedgerows where they are sheltered from wind, rain and snow,' and that the greater importance of anholocycly (and virus problems) in the west of England might be explained partly by the shelter conferred by improved plant growth due to milder weather. This hypothesis, however is difficult to assess objectively on the basis of Dean's (1974a) data, mainly because no descriptions are given of the methods used to protect his plants from wind, rain and snow. Unless considerable care was used, shelters would have substantially altered temperatures and the pattern of host plant growth to the benefit of aphids.

The potential overwintering sites of anholocyclic clones are enormously varied including wild grassland, meadows, cultivated grassland and cultivated cereals - indeed these habitats make up a substantial

part of the earth's surface. It is easy to envisage that changes in the management of these habitats (e.g. changes in varietal mixtures, increased pesticide and fertilizer applications, earlier sowing) might alter the pest status of cereal aphids and these possibilities have been considered (Potts, 1977; Potts and Vickerman, 1974; Baranyovits, 1973; Zuniga and Suzuki, 1970). At present, the relative importance of these habitats as sources of aphids and virus (see Plumb, 1978) is unknown.

1.5 POPULATION DYNAMICS ON THE CROP

The pattern of changing aphid abundance on cereal crops during summer has been the main subject of cereal aphid field studies. (Jones, 1979b; Dean 1974c; Wyatt, 1977; Dransfield 1975; Dedryver, 1980; Latteur, 1976). These studies have been mostly geared to the description of these patterns rather than their explanation. Thus many questions remain unanswered. Perhaps the most important of these relates to the relative importance of autumn, early spring, late spring and summer immigrants to the overall pest problem. It appears, however, that *S. avenae* infestations during 'outbreak' years are mainly attributable to massive 'inputs' of alates to the crop shortly after 'heading'. (George - pers. comm).

1.5.1 Colonization

Alate cereal aphids are usually first found on cereals during late May - early June, (Jones, 1979b), although their precise timing and abundance are poorly correlated with suction trap catches (Dean, 1973b). Aerial abundance is governed by weather factors (as with aphids in general: Jones and Jones 1974), the numbers leaving overwintering sites and possibly the numbers carried to the U.K. by air currents from the Continental mainland (N. Carter - pers. comm). (Carter *et al.* 1980). Settling on the crop probably involves additional factors (e.g. crop growth stage) but these have not been considered in detail in the literature.

1.5.2 Population development

McLean *et al.*, (1977) considered that 'the rate of build up of

the aphid population is predominantly governed by the weather conditions'. Supporting this conclusion, Jones (1979b) suggested that high temperatures and low rainfall accounted for the large populations found in 1975 and 1976 at Harpenden, U.K. McLean *et al* (1977) also stressed the importance of close synchrony between invasion and optimum crop growth stage for maximum growth rates to be achieved. The question of natural enemy impact is a controversial part of cereal aphid ecology but most workers would agree that at least during the build up phase, impact is limited, especially when weather (c.f. Dunn, 1952) and crop suitability 'favour' the aphid. I conclude that the main reasons for this are (a) the large and often sudden nature of aphid immigration, (b) the possibility that aphid populations need to exceed a certain threshold for 'specific predators' to remain in the field and oviposit, (c) the high reproductive rate of aphids relative to the rates of predation and parasitism and (d) the asynchrony between aphid attack and natural enemy impact.

Dean (1974c, 1974d) drew attention to the poor synchrony shown by syrphid predators but Jones (1979b) considered that parasites were 'more likely than predators to synchronize with and control cereal aphids.' Contrary to this suggestion, most studies indicate that parasites and disease only become effective towards the end of population build up (Jones, 1979b; Dean 1974d) with the result that they simply accelerate a population crash. Hence although large numbers of aphids may be killed by natural enemies, this may be of negligible benefit to the crop.

The most controversial question concerning predation has been the possible role of polyphagous predators, mainly ground beetles and spiders. Their importance as suggested by Potts and Vickerman (1974),

Potts, (1977) and Vickerman and Sunderland (1975) has challenged the assumptions of earlier field workers as well as the general premise that specific predators are best in biological control (Huffaker *et al*, 1971). The evidence in favour of polyphagous predator effectiveness has been (a) observed correlations between their diversity and abundance and the size of aphid populations (Potts and Vickerman, 1974, 1975), (b) the fact that large numbers of individuals and species have been found to climb plants and feed on aphids (Sunderland, 1975; Vickerman and Sunderland, 1975; Vickerman and Wratten, 1979), (c) the theoretical consideration that their acceptance of alternative prey can keep them in cereal-cropped land in the absence of aphids so that upon their arrival feeding preference might 'switch', leading to suppression without the delays associated with 'specific' predator impact (Southwood and Comins, 1976; Potts, 1977; Huffaker *et al*, 1976).

Very recently, experimental studies have shown that insecticidal exclusion of ground beetles from plots in March and April can increase aphid populations in the summer (Edwards and Steed, 1979; Edwards *et al*, 1979) but exclusion from May onwards had no effect.

Existing cereal varieties have been screened for aphid resistance at the seedling stage and seemingly large differences observed. For example, Elamin's (1975) experiments with *S. avenae* on spring barley showed that almost twice as many nymphs were deposited by female aphids on c.v. Zephyr than on Berac. Similar results were also obtained with *M. dirhodum* and *R. padi*. Although these, and other results (Adams and Drew, 1964b; Dean, 1973c and Wratten, 1977) of seedling stage screens for resistance are relevant to autumn and spring infestation and hence to the problem of virus transmission, they do not necessarily give an accurate indication of the likely level of resistance

to *S. avenae* attack after heading because at this time, these aphids move onto the ear where performance is dramatically improved (Watt, 1979). Some workers have ranked field attack of different cultivars (e.g. Kolbe 1969; Latteur 1971) but plots were normally unreplicated and even if differences were to occur in a particular year, those effects might be due to plant age effects rather than inherent resistance. Lowe (1977, 1978) for example, found major discrepancies between different field experiments. The critical importance of plant age has also hampered attempts to compare cultivar susceptibility using mature plants in the laboratory (Lowe, 1978).

1.5.3 Population Crash

Following the often rapid build up in aphid populations, the suddenness and speed with which they collapse can be even more spectacular (Carter *et al*, 1978a; McLean *et al*, 1977; Schaefer *et al*, 1979; Jones, 1979b; Dransfield, 1975; Adams and Drew, 1964a; Dean 1973b, Dean and Luuring, 1970; Forbes, 1962; Green, 1966; Latteur, 1970, 1976; Malyk and Robinson, 1971; Rautapaa, 1976; Watt, 1979). Field counts show an increasing predominance of alatiform 4th instar nymphs in the population prior to the crash (Dransfield, 1975; Carter *et al*, 1978; Dean, 1973b), possibly produced as a response to declining plant quality (Dean 1974c), and McLean *et al*, (1977) emphasise alate departure as a cause of the crash. Others have implicated predation as the predominant cause. Field exclusion experiments reported by Wyatt (1977) indicated a major role for natural enemies (braconid parasites and coccinellids), - a conclusion supported by subsequent experiments (Sunderland and Vickerman, in press; Vickerman and Wratten, 1979). Similarly Singer *et al*, (1977) claimed that on one occasion 'ladybirds killed all exposed cereal aphids observed on crops, grassland and woodland grasses during the first two weeks of July'. It

is possible that these contrasting interpretations of the crash simply reflect a multiplicity of causes operating in the field at different times and in different places. However, there is little doubt that more widespread use of experimental methods would enable the causes to be elucidated with greater certainty.

1.6 CAUSES OF PEST STATUS

Numerous possible reasons have been advanced to account for the recent upsurge of cereal aphid problems. Most fundamental have been the claims of Potts and Vickerman (1974) and Potts (1977) that pest problems may have been exacerbated by simplification of the cereal ecosystem. These workers based their suggestions on their experience monitoring the cereal ecosystem in Sussex, coupled with considerations of the simple relationship between diversity and ecosystem stability outlined by Elton (1966). Thus they 'felt that there is considerable virtue of complex trophic connections' despite the consensus of opinion today that there is not necessarily a causal relationship between stability and diversity (Van Emden and Williams 1974, Way, 1977a; Murdock 1975; May, 1971; May, 1973). The most useful conclusion that has been reached by critical analysis of the diversity - stability concept, is that stability is predominantly governed by the nature of ecosystem components and the form of their interrelations. In the context of pest control, therefore it is absurd to strive to preserve any form of diversity without consideration being given to possible 'key' species such as highly effective natural enemies. Collyer (1953), for example found that approximately 45 arthropod species feeding on orchard spider mites were often irrelevant to their overall suppression compared to a very few 'effective' species.

The fears expressed by Potts and Vickerman (1974) were fuelled by the accelerating rate of technological change taking place in

cereal growing in recent years (Way, 1978; Way and Cammell, 1979). In particular, they felt that the trend away from undersowing barley (associated with mixed farming) might have undesirable repercussions and that 'a decline in polyphagous predators (presumably due to pesticide usage and weed removal) could trigger pest outbreaks' (Potts, 1977). Other authors have implicated changes in agricultural practice as a likely cause of increased cereal aphid problems, many emphasising the possible contribution of agrochemical inputs (Baranyovits, 1973; Kolbe, 1973; Kolbe and Linke 1974; Way and Cammell, 1979).

The increased use of herbicides may have far reaching consequences for the regulation of pest populations (Perrin, 1978; Demster and Coaker, 1974). By removing weeds, ground beetle effectiveness is diminished (Vickerman, 1974; Speight and Lawton, 1976) and some herbicides may 'stimulate' (Coaker, 1977) pest reproduction directly. Adams and Drew (1965) found more aphids on oats treated with the selective herbicide, 2, 4-D than on untreated controls and the same result was obtained by Oka and Pimentel (1974) on maize. Fungicides have also had potentially undesirable side effects through stimulation of aphid reproduction (Sagenmuller, 1977), inhibition of germination in aphid pathogens (*Entomophthora* spp) (Zimmerman, 1976) and the deprivation of fungal food to polyphagous predators.

Despite the growing body of evidence on the relationship between plant nitrogen levels and insect attack (Dixon, 1970; 1973; Southwood 1973; Kennedy 1953; McNeill and Southwood, 1978; Lawton and McNeill 1979) not enough is known on the effects of fertilizer dressings on cereal aphids. This would seem to be a 'key' research area as Baranyovits (1973) considered that their increased use might explain not only the world-wide upsurge of cereal aphids, but aphids in general. Henderson and Parry (1978) found more aphids on crops having low nitrate concentrations

in plant sap in the early stages of growth, while Plumb (1977) has reported more B.Y.D.V. damage on barley treated with high levels of nitrogen compared to controls. (This could reflect increased disease expression rather than increased transmission by aphids.) Verijken (1975) found positive correlations between levels on nitrogen fertilizer and *S. avenae* performance in the laboratory although in the field, dressings 'hardly affected' aphid numbers.

Changes in cereal varieties (Way, 1978; Way and Cammell, 1979) and the composition of forage grass mixtures may be cited as further possible causes of aphid upsurge. Little data exists and study is beset by technical problems (see above) but it is noteworthy that in recent years radical shifts have occurred in the predominance of cereal cultivars (Potts and Vickerman 1974; Way 1978) without consideration to their aphid resistance status. The low genetic diversity of crop monocultures is generally believed to contribute to pest problems (Southwood and Way, 1970) and this might easily apply to cereals in the U.K. where much of the acreage is sown to a small number of cultivars (Way, 1978) - a possibility already being seriously considered by plant pathologists (Priestley, 1979; Priestley and Wolf, 1977; Burdon, 1978).

Finally, any discussion of changing pest status that considered technical matters alone would be incomplete. Farmers' decisions to spray insect infestations result from their knowledge of the pest, the availability of suitable pesticides and spray machinery, their perception of the risk to the crop and conflicting work commitments, elsewhere on the farm. Thus cereal aphids are more likely to be sprayed today than 10 years ago because of increased awareness of their presence and potential damage. In addition, farmers are now frequently on the land applying other pesticides and fertilisers, (Whittles, 1977; 1978). It is a simple matter, therefore to apply

an aphicide on one or more of these occasions. Economic factors have also had an important role. The spiralling price of wheat has tended to overshadow the cost of pest control inputs encouraging their almost indiscriminate use as part of a policy of yield maximisation that according to Way and Cammell (1979) is counterproductive to the farmer and to any long term pest control strategy.

1.7 CONTROL

It has been in recent years that farmers have considered control measures against aphids in cereals. Spraying has increased since the 1968 outbreaks (Fletcher and Bardner, 1969) until in 1975 over half the cereal acreage in the U.K. was treated (Stone, 1977). Very recently attention has been paid to the feasibility of autumn and early spring applications to reduce damage due to virus (B.Y.D.V.). In the U.K. farmers are encouraged to spray only in relation to the economic threshold defined by George (1975) although some have recommended spraying on the basis of mere presence of aphids in the crop (Whittles 1977), a suggestion challenged by Way (1978).

Although aerial application is effective, demand for aircraft during outbreaks often outstrips supply and so many fields have been sprayed too late to be worthwhile. Still more alarming is the possibility that farmers might overcome this problem by booking aircraft in advance regardless of attack. Tractor mounted equipment is also very widely used and although 'wheeling losses' are compensated for during heavy attacks (George, 1978), farmers are adopting the use of 'tramlines' to gain easy access to the crop. Although this might be seen as another step towards routine spraying, there is no doubt that it also facilitates timely applications and attention to economic thresholds. In the future controlled droplet application

methods are likely to be increasingly used in cereals (Pickin, 1978) offering further benefits of good timeliness. Many entomologists have strongly recommended the use of specific rather than 'broad spectrum' pesticides, not only to maximise the effectiveness of natural enemies within cereal fields but also to maintain high regional populations to check pest populations in other crops (Vickerman and Sunderland, 1977). Pirimicarb fulfills this need for cereal aphid control but broad spectrum materials such as 'demeton - S - methyl' and 'dimethoate' are also used, often unavoidably due to shortages of 'pirimicarb' supplies following exceptional demand.

Non-chemical methods of control have been considered, and ultimately much of the research conducted in universities and research establishments is directed towards this end. The prospects for varietal resistance is being investigated (Lowe, 1978) but McLean *et al*, (1977) considered that 'the artificial release of natural enemies is unlikely to be successful'. In Brazil, however, parasite release is currently being attempted (Salles and Gutierrez, pers. comm.) but in this case, the large early season populations of *M. dirhodum* and *Schizaphis graminum* (Rond) (Zuniga and Suzuki, 1970) may serve as a major parasite 'reservoir' for the control of aphids later in the season when crops are more prone to damage.

1.8 CEREAL APHID RESEARCH IN THE U.K.

The severe outbreaks of cereal aphids in 1968 (Fletcher and Bardner, 1969) highlighted a serious lack of knowledge on cereal aphid biology and control strategies. Since then, research has become more widespread. In 1978, a meeting of a 'cereal aphid group' at the University of East Anglia, Norwich, U.K. intended exclusively for active workers in the field, attracted more than 40 participants. At that meeting Dr. G.J. Dean agreed to circulate details of all projects

in progress in the U.K. to promote good communications and to avoid undesirable overlap between studies. The resulting document listed 38 workers in 5 university departments and 6 research institutes. In Rothamsted Experimental Station alone, a coordinator has been appointed to integrate their research. There is a similar high level of activity in the rest of Europe which is coordinated under the auspices of a subgroup of the International Organisation for Biological Control - Western Palaearctic Regional Section (I.O.B.C./W.P.R.S.). Dr. K.S. George (Plant Pathology Laboratory, Harpenden) is the U.K. representative at this group.

In the U.K. funding is channelled through a wide variety of bodies (Research Councils, Ministry of Agriculture, Fisheries and Food, Industry and Trusts etc)., and coordination between projects relies on the initiative of interested parties. There is no central direction of research goals and strategies; as a result some overlap between work has occurred. In itself, this is not necessarily undesirable but 'overlap by design' would be preferable to 'overlap in ignorance'. A more fundamental weakness of the fragmented nature of U.K. research is that despite an impressive pool of expertise, this is not readily tapped for large scale, intensive projects on any one site in any one season.

1.9 OBJECTIVES AND APPROACH OF THE PRESENT RESEARCH

A preliminary survey of the literature revealed a number of 'areas of ignorance' in cereal aphid ecology. Their resolution seemed to have been hindered by the bias of previous studies towards descriptive surveys of the cereal system, as distinct from experimentation (see above). It is a remarkable paradox that the early development of statistically based agricultural experimentation should have contributed so much to the development of new varieties, agricultural chemicals, and hence yield, without materially influencing the approach used to

study pest biology or evaluate biologically based control methods.

In the present work, predominantly experimental methods were used to study the following topics.

- (a) Survival and causes of mortality during winter.
- (b) Impact of natural enemies on summer populations, studied by quantitative methods.
- (c) Bearing of crop growth stage on aphid attack - especially the colonization by alates.

Over a year later, following their attempts to model cereal aphid populations, Carter *et al.*, (1978a) confirmed the significance of these topics.

'certainly more work still remains to be done on the biology of *S. avenae*, in particular on overwintering, migration and quantitative effects of natural enemies.'

More recently, Vickerman and Wratten (1979), concluding a major review on cereal aphids emphasised a number of fundamental biological features that are unknown.

'.....little is known about overwintering biology.....There is also little information on the factors that determine the distribution of alatae between fields.

Data have been collected by a number of workers on the prevalence of predators and parasites, in the course of studies on cereal aphids but there have been few attempts to quantify the effects of natural enemies on cereal aphid populations in the field.'

CHAPTER 2

SURVIVAL AND CAUSES OF MORTALITY ON A WHEAT

CROP, OCTOBER - APRIL

CHAPTER 2

SURVIVAL AND CAUSES OF MORTALITY ON A WHEAT
CROP, OCTOBER - APRIL

2.1 INTRODUCTION

As indicated in Chapter 1, the overwintering biology of cereal aphids is complex. Populations infesting cereals in the U.K. in the early summer for example, may be derived from four main sources.

- (a) aphids that have overwintered on the crop as virginoparae
- (b) aphids that have overwintered on non crop hosts (e.g. wild grass-land) as virginoparae,
- (c) aphids that have overwintered locally on primary hosts as eggs,
- (d) aphids that have left maturing crops on the continental mainland and migrated into the U.K.

A clear understanding of overwintering biology is valuable as a means of predicting the effect of winter weather or cultural practices on the size of pest populations in the summer. This, in turn could enable adequate preparation to be made to control heavy attacks, and permit deleterious changes in agricultural practice to be identified and avoided.

Two main approaches can be adopted to determine the importance of different mortality factors. First, the size of populations over successive years can be compared and an attempt made to relate summer abundance to weather conditions during the preceding winter and spring. Computers can be used for rapid regression analysis on a large number of experimental variables; e.g. number of frost days, rainfall, wind, predator abundance etc. Once correlated factors are identified, they can be monitored in future years to provide an early warning of pest

numbers. The advantage of such a scheme over crop monitoring is that all involved in pest control have time to react. Thus, farmers can perhaps know whether to apply systemic insecticides at the time of sowing and manufacturers are forewarned of the need for their insecticides. (Way and Cammell, 1977; Dunning 1977). Moreover, 'early warning' forecasts would be useful in situations where economic damage threshold are exceedingly low (e.g. with virus vectors). Regression analysis can sometimes reveal a good fit between certain environmental factors and pest numbers, even when the nature of the relationship is poorly understood. This need not reduce its value in predictive modelling but knowledge of its biological basis would certainly increase its value. Plant pathologists have implemented forecasts based on simple environmental parameters, but for arthropod pests, the need for more detailed ecological information on the organisms has hitherto limited the successful application of these models. Indeed the ecology of some pests may be so complex that long range forecasting may be practically impossible.

Being a relatively long range forecast, a scheme based on the relationship between winter weather and summer pest abundance is likely to be more prone to error than crop monitoring simply because the correlated variables are widely separated in time. Additional sources of error are likely to be fluctuations in the success of local migrations and shifts in the relative importance of local versus distant migrants. Watson *et al* (1975) showed a close correlation between weather factors and the incidence of virus yellows in sugar beet crops in the subsequent autumn during 1951 - 1971 but the prediction for 1974, based on these correlations seriously underestimated disease incidence (Heathcote, 1977). Similarly Sparrow (1974) reported a close correlation between March temperatures and the timing of crop colonisation by cereal aphids

but the relationship broke down after publication. (Turl 1978).

An alternative approach to understanding overwintering mortality, adopted in the present study is experimental. By manipulating the pest's environment during the winter, changes in abundance can be attributed to specific causes. The practical value of this knowledge is twofold. Firstly, it may be an important input to a predictive model for use in forecasting. Secondly it may reveal how overwintering survival might be influenced by changes in agricultural practice. For example, increased pesticide usage may pose a threat to regulation of pest numbers by natural enemies, the trend towards earlier sowing of cereals may increase the abundance of aphid colonists in the autumn (see Plumb, 1977); sparse sowings may alter the extent to which aphids are exposed to adverse weather.

Ideally the causes of overwintering mortality should be studied for all aphid species in both biological forms and in all potentially important habitats but this would require enormous resources. The studies reported here were confined to virginoparous aphids infesting wheat seedlings, but these were considered to be of special practical importance because;

- (1) Earlier sowing practices are increasing the numbers of aphids colonizing cereals in the autumn (Plumb, 1977),
- (11) These colonists can bring about rapid spread of BYDV that becomes manifest in the spring,
- (111) Aphids that have overwintered on the crop may be a major source of the summer population. Warm weather in the spring may enable reproduction to take place before conditions are right for alate migration into the crop. In the U.K, George (pers. comm.) has reported more serious aphid problems on the early autumn sown crops than on later ones.

Two major field experiments are reported using virginoparous aphids, artificially introduced to the field on potted wheat seedlings. The causes of overwintering mortality were separated experimentally by differentially protecting colonies from predation, wind and rain. In addition the development of *R. padi* colonies, naturally infesting field wheat were monitored. A range of simple experiments was also done to investigate the effects of wind on aphid populations, and the survival capacity of individuals dislodged by wind.

2.2 FIELD INVESTIGATION ON THE CAUSES OF MORTALITY, 1977 - 1978

2.2.1. MATERIALS AND METHODS

2.2.1.1. Conditioning of aphids and plants.*

For this experiment, standard laboratory cultures of parthenogenetic aphids were used to establish 'cold conditioned' cultures for subsequent introduction to the field on 'cold conditioned' seedlings.

Each aphid 'stock' culture was maintained on 4 - 10 12cm pots of wheat seedlings (approximately 25 per pot) (c.v. Maris Kinsman) growing in compost. Pots were watered and renewed as necessary. Each culture was enclosed by a wooden framed insect cage (0.5 x 0.5 x 0.5m) with a solid base, fine cotton mesh walls and a clear glass roof. Cages were kept in a 20° constant environment room under fluorescent strip light illumination.

3 cereal aphid species were cultured during the period of research; *S. avenae*, *M. dirhodum* and *R. padi* but only the first 2 were used in the present experiment.

In October 1977, several hundred aphids from each stock culture were transferred to new pots of seedlings placed in an unheated, open ended glasshouse. Early in the autumn, some reproduction occurred but later there was no obvious change in aphid numbers. Thermograph records showed that temperatures in the glasshouse frequently fell below 0°C so the aphids were considered to be 'cold conditioned'.

The experimental wheat seedlings (c.v. Maris kinsman) were sown during October 1977 in 12cm plastic pots and placed outside the glasshouse to germinate and grow at natural temperatures. Plant density was standardized to 5 per pot. At the beginning of November, batches of approximately 50 of the 'cold conditioned' aphids were put on each pot of 3 - 5 leaf stage seedlings (different pots for the 2 aphid species - 24 pots in total) and retained in the unheated, open glasshouse until

*According to recent laboratory studies (Griffiths & Wratten, 1979) acclimatisation has 'little effect' on cold tolerance.

the start of the experiment. A period of approximately 3 weeks was considered adequate for the aphids to adjust the experimental plants.

2.2.1.2. Transfer of infested plants to the field.

After 'marking out' the experiment and shelter construction, holes were dug in the soil for the infested plants. An empty plant pot, placed previously in each hole enabled the experimental pots to be sunk into the holes with minimum disturbance. A calm day (16/11/77) was chosen to start the experiment. After counting the aphids on each labelled pot of seedlings, the pots were carried to the experimental site and placed inside the empty pots already prepared.

2.2.1.3. Shelter Design

The aim of the experiment was to compare population development of aphids in 3 situations.

- | | |
|---|--|
| 1. exposed to wind, rain and predation. | |
| 2. protected from wind and rain | } referred to collectively
as 'protected' plants. |
| 3. protected from wind, rain and ground
based predators. | |

Plants in 'treatments' 2 and 3 were placed under shelters designed to eliminate rain and considerably reduce wind. Shelter roofs consisted of glazed metal window frames (1m^2) supported on bricks. The sides were made from plastic mesh with a material : airspace ratio of 32% (available commercially as 'Netlon' 'Greenhouse Shading Material'). For treatment 3, physical and chemical methods were used to exclude ground predators. Aluminium sheeting, pressed into the soil formed an oval barrier (height, 10cm) around the plants (material available commercially as 'lawn edging'). Methiocarb bait scattered inside the barriers was used to kill predators such as Carabidae and Staphylinidae that might cross the physical barrier (Figure 1) or occur in the cage.

FIGURE 1 : 'Exploded' diagram illustrating shelter design used for overwintering experiments 1977 - 1978.

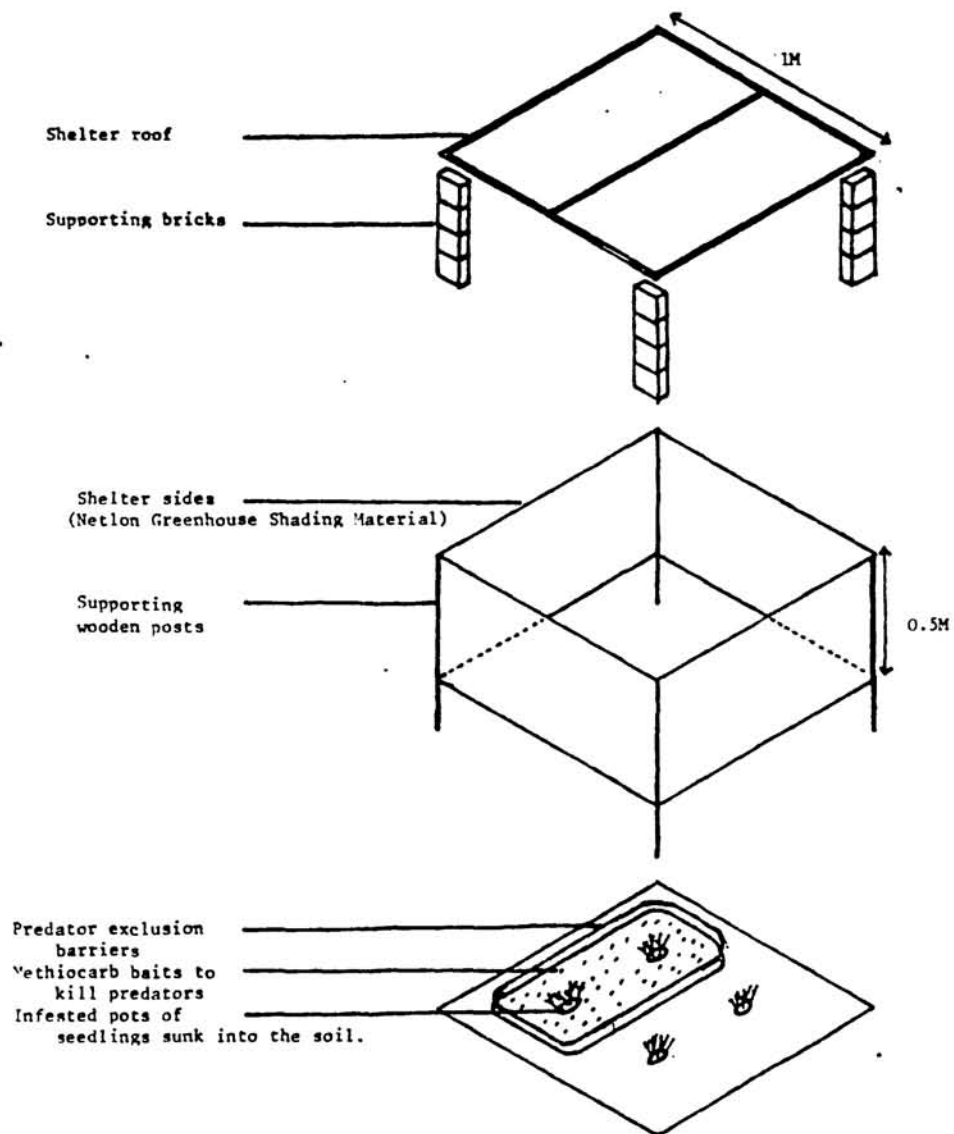
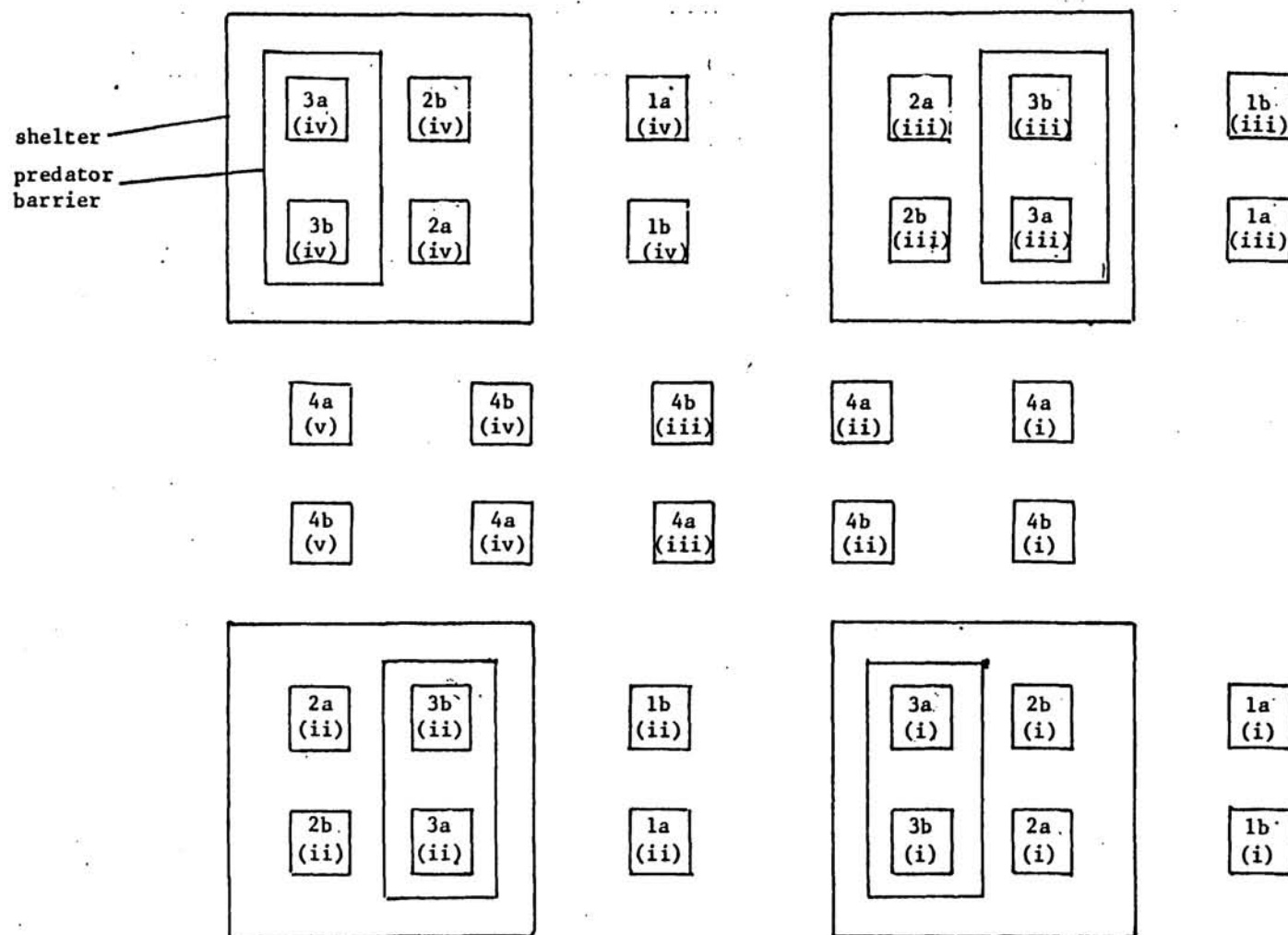


FIGURE 2 : Experiment Layout: Field investigation on the causes of mortality 1977-1978.

(1 = exposed, 2 = wind & rain protected, 3 = wind, rain and ground predator protected, 4 = supplementary batch of exposed plants; a = *S. avenae*, b = *M. dirhodum* ; (i), (ii), (iii), (iv) = replicate numbers.



2.2.1.4. Experimental Layout.

The treatments were replicated 4 times according to the layout in Figure 2 on an area of fallow land (approximately 20 x 20M) on the western edge of Silwood Bottom. When populations on exposed plants had diminished considerably by early February, a supplementary set of infested plants (5 pots for each species) was set up in the field. Approximately 10g of nitrogen fertilizer granules were applied to each pot on 2 occasions (December and February) and the sheltered plants were watered when necessary..

2.2.1.5. Environmental Monitoring.

General meteorological data were obtained from 2 sources; temperatures and rainfall from the Silwood House Meteorological Station, 300M away, and windspeeds from the Meteorological Office weather station at Heathrow. These data were presented graphically for each comparison with aphid population data (Figure 3). Windspeed and temperature were also measured inside and outside shelters so that their possible effects on microclimate could be assessed. Temperature was recorded using thermistor probes linked to a 'Grant' 9 channel recorder (Lewis and Siddorn, 1973). These probes were shielded from the direct effects of radiation by foil covered, cellulose acetate cylinders (3 x 5cm). A 'Porton' cup anemometer was used to measure windspeed (model AW1600, Vector instruments) (Painter, 1976).

2.2.1.6. Monitoring Colonies and interpretation of results.

Following introduction to the field on 16/11/77, aphids were counted at intervals of approximately 14 days. Separate counts were made of small (instars 1 and 2), large (instars 3, 4 and adult apterae) and alate aphids. Numbers of mummies and diseased aphids were also noted although host species was not distinguished.

Unfortunately, the need to accommodate 2 treatments under single shelters for economy of space and materials meant that the experimental design was non-random. Nevertheless analysis of variance (ANOVA) was considered worthwhile, especially to separate out error due to block effects, although results would need to be interpreted with caution. Separate ANOVAs were performed on the abundance of aphids (all stages) for the 2 species and for 8 census occasions. To normalize the data's distribution, the log transformation ($y = \log(x + 1)$) was applied and before analysis, counts were adjusted for covariance with respect to initial numbers which varied between plots. The difference between these logarithmic values on consecutive counts was used as an index of the rate of change in abundance and these data, in turn subjected to ANOVA (Appendices 1 and 2). Computer analysis made use of the ANOVA programme developed for 'Genstat,' - (Rothamsted Experimental Station, 1977). From the printed output, the 'F ratio' for treatment effects was tested using standard statistical tables and, if significant at the 5% level, particular comparisons were made between treatments. To simplify this process, 'least significant differences' (L.S.D's) were calculated from the 'standard errors of differences between means' (S.E.D's) included in the printed output (see Parker, 1973).

In addition to formal data analysis, aphid abundance and meteorological data were plotted graphically using a common time scale to facilitate comparison between observed population changes and weather (Figures 3 and 4). Through these complementary approaches, it was possible to identify the kinds of extreme weather that seemingly failed to influence aphid abundance as well as those having positive effects. Furthermore, effects that were too weak to attain statistical significance for any single occasion might be consistent enough in time to be acceptable as real effects.

2.2.2 RESULTS AND DISCUSSION

2.2.2.1. Effect of shelter on microclimate

Continuous temperature recordings showed that temperatures inside the shelters were slightly higher than outside. For example, during a period of relatively warm, sunny days and cold nights, this difference often exceeded 1°C (Table 1). Simple comparisons of windspeed showed that 10 M/S winds were reduced by about 20% by the shelters.

2.2.2.2. Survival and Mortality of *S. avenae*

(a) Treatment comparisons (Table 2)

5 days after transfer to the field on 15/11/77, aphid populations had declined similarly on all treatments (Figure 3). Exposed aphids had declined most at this time but the difference was not significant at the 5% level. (Table 2). Subsequently their rate of decline exceeded those of the two sheltered treatments, the difference being statistically significant ($P = 0.05$) on 17/1/80 and 28/2/80 (Table 2). Such differences never occurred however between the 2 sheltered treatments - 'predator exposed' and 'predator protected' (Table 2).

Accordingly the ANOVAs performed on the rates of change in aphid numbers between consecutive counts, no significant differences occurred between treatments (Table 2). Since the size of the exposed populations were significantly smaller on 17/1 and 28/2, compared to sheltered populations (Table 2), this difference must have developed gradually over several intervals between counts.

(b) Population change in relation to weather

16-25/11

As already mentioned, *S. avenae* populations declined similarly on all treatments over this period (Figure 3). Since the causal factor affected both sheltered and protected aphids alike, low temperature might

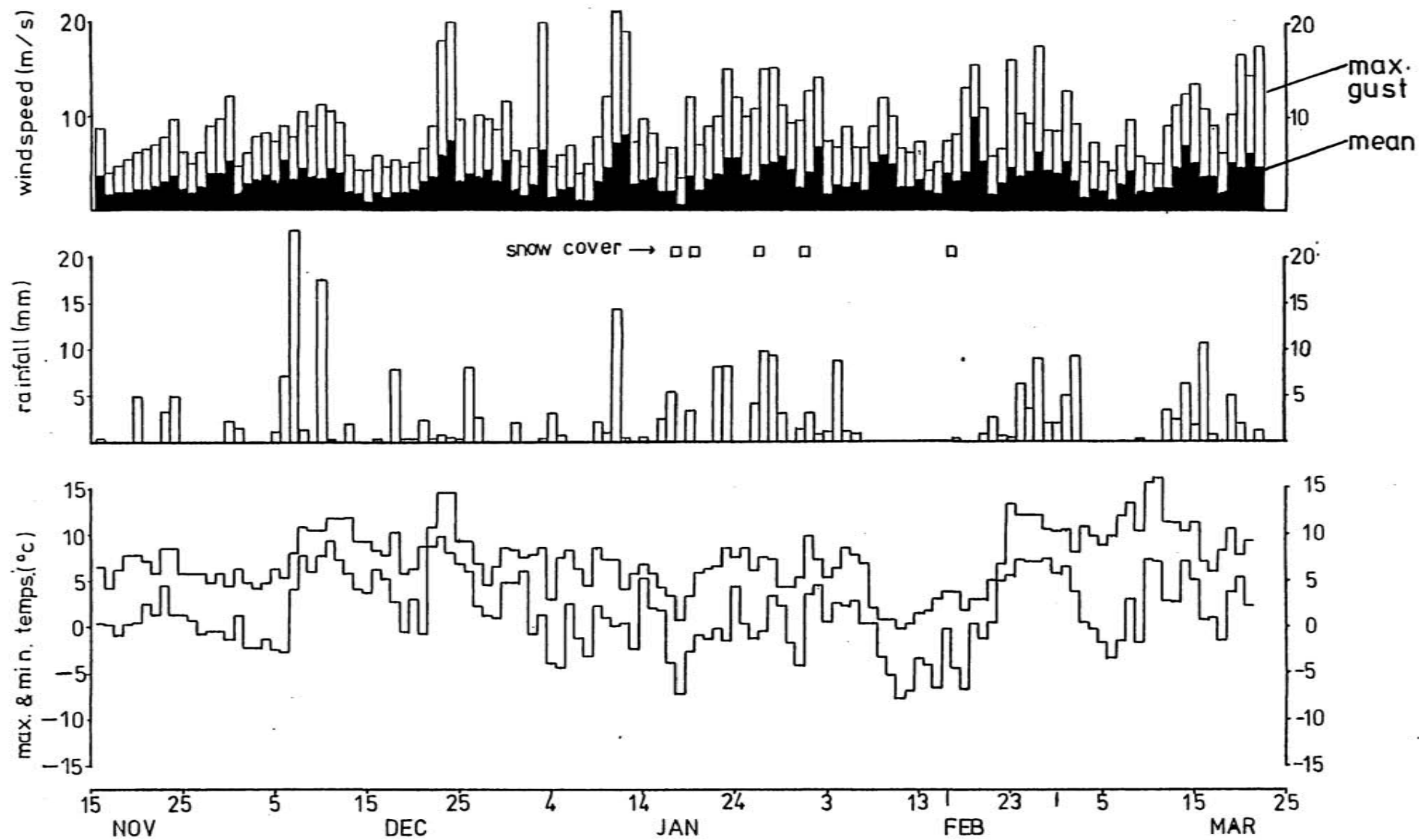


FIGURE 3 :

FIGURE 3 : Abundance of *S. avenae* during winter 1977 - 1978 in relation to shelter and weather (total aphids on 4 plots).

(x - x, exposed; 0 - - 0, protected from wind and rain; ● - . - . ●, protected from wind, rain and ground based predators).

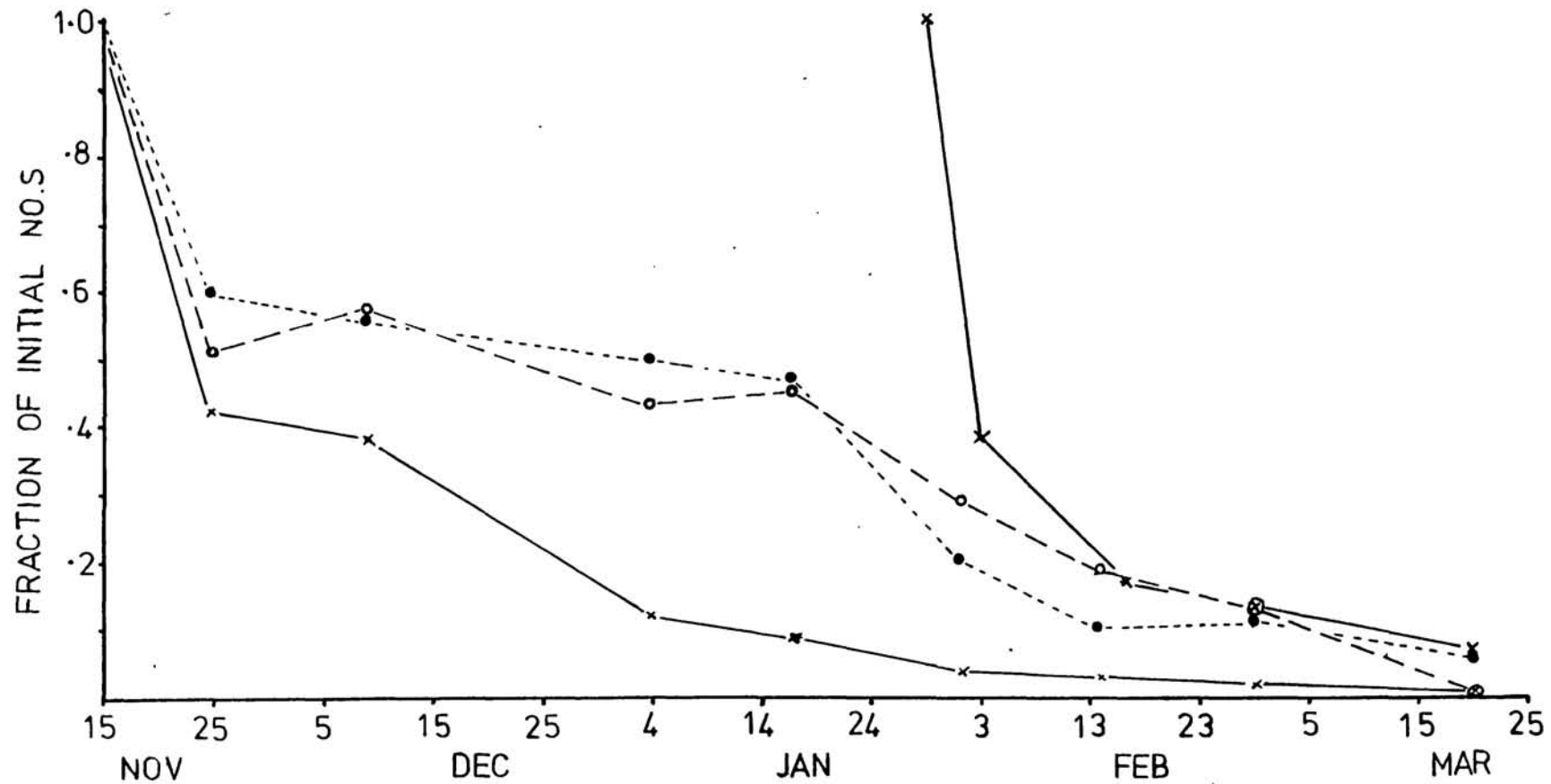


TABLE 1 : Temperature recordings inside and outside shelters: Sample data set for the period 3/3/78 - 5/3/78 ($^{\circ}\text{C}$).

TIME	LOCATION	
	Exposed	Shelter
3/3 15.00	13.00	12.81
17.00	10.00	10.25
19.00	2.75	3.69
21.00	- 0.25	1.13
23.00	- 0.70	0.45
4/3 01.00	- 1.75	- 0.69
03.00	- 2.00	- 0.90
05.00	- 1.75	- 1.13
07.00	1.00	1.00
09.00	3.50	3.56
11.00	5.05	5.19
13.00	11.00	10.94

TIME	LOCATION	
	Exposed	Shelter
4/3 15.00	10.95	10.50
17.00	6.75	6.81
19.00	3.00	2.81
21.00	0.75	1.38
23.00	0.50	1.00
5/3 01.00	- 2.00	- 1.25
03.00	- 2.85	- 2.19
05.00	- 4.00	- 2.88
07.00	- 3.95	- 2.94
09.00	5.75	3.88
11.00	10.30	8.56
13.00	11.80	10.81

TABLE 2 : Summary of Analysis of Variance - Winter 1977-1978

(** = significant at 1% level, * = significant at 5% level,

N.S. = not significant; treatment 1 = exposed, 2 = rain

protected, 3 = wind and rain protected).

Sitobion avenae

a) Total Aphids

		25/11	9/12	4/1	17/1	1/2	14/2	28/2	20/3
'F test'		N.S.	N.S.	N.S.	**	N.S.	N.S.	*	N.S.
Treatment comparisons	1, 3				**			*	
	1, 2				*			**	
	2, 3				N.S.			N.S.	

b) Rates of Change in Abundance Between Counts

		25/11	9/12	4/1	17/1	1/2	14/2	28/2	20/3
'F test'		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Treatment comparisons	1, 3								
	1, 2								
	2, 3								

TABLE 2 : Continued

Metopolophium dirhodum

a) Total Aphids

		25/11	9/12	4/1	17/1	1/2	14/2	28/2	20/3
'F test'		N.S.	N.S.	N.S.	**	**	**	**	**
Treatment comparisons	1, 3				**	**	**	**	**
	1, 2				**	**	**	**	**
	2, 3				*	N.S.	N.S.	N.S.	N.S.

b) Rates of Change in Abundance Between Counts

		25/11	9/12	4/1	17/1	1/2	14/2	28/2	20/3
'F test'		N.S.	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Treatment comparisons	1, 3		**						
	1, 2		N.S.						
	2, 3		**						

TABLE 3 : Causes of overwintering mortality 1977-1978 : (a) - raw data showing numbers of aphids on individual plots.

(Treatment 1 = exposed; 2 = wind and rain protected; 3 = wind, rain and predator protected)

<i>S. avenae</i>											<i>M. dirhodum</i>										
TREATMENT	REP.	16/11	25/11	9/12	4/1	17/1	1/2	14/2	28/2	20/3	TREATMENT	REP.	16/11	25/11	9/12	4/1	17/1	1/2	14/2	28/2	20/3
1	1	31	18	8	5	3	2	1	0	0	1	1	13	8	8	17	6	0	0	2	6
	2	25	12	14	2	2	1	0	1	0		2	35	20	11	31	15	8	7	1	6
	3	45	17	22	8	3	2	2	1	0		3	33	18	12	12	2	4	1	0	0
	4	41	13	22	2	4	0	1	0	1		4	32	27	18	6	10	3	1	1	0
2	1	24	11	7	19	8	4	2	2	0	2	1	58	78	76	135	95	167	118	127	347
	2	42	13	28	23	18	16	12	6	0		2	33	14	8	43	42	48	50	28	49
	3	36	16	15	2	5	4	1	2	0		3	45	16	14	35	17	28	16	10	7
	4	37	31	30	16	32	16	11	8	1		4	51	29	25	108	63	101	63	79	45
3	1	31	10	11	14	19	3	0	2	0	3	1	54	34	41	297	135	129	220	93	137
	2	38	17	15	20	33	4	4	6	2		2	33	25	20	114	72	82	48	77	87
	3	16	19	20	13	8	5	3	0	0		3	43	17	20	117	55	54	51	42	52
	4	102	65	58	46	29	25	11	12	8		4	126	60	66	47	178	185	110	67	98

Table 3 (cont) (b) - Numbers of mummies in relation to numbers of aphid hosts (both species).

(A = aphids; M = mummies)

TREATMENT	REP.	16/11 A M	25/11 A M	9/12 A M	4/1 A M*	17/1 A M*	1/2 A M	14/2 A M	28/2 A M	20/3 A M
1	1	44 0	26 0	16 0	22 0	9 0	2 0	1 0	2 1	6 0
	2	60 0	32 0	25 0	33 0	17 0	9 0	7 0	2 1	6 0
	3	78 0	35 0	24 0	20 0	5 0	6 0	3 0	1 0	0 0
	4	73 0	40 0	40 0	8 1	14 0	3 0	3 0	1 0	1 0
2	1	82 0	89 0	83 0	154 8	103 1	171 3	120 0	129 4	347 1
	2	75 0	27 0	36 0	66 3	60 1	64 0	62 0	34 0	49 0
	3	81 0	32 0	29 0	37 0	22 1	32 0	17 1	12 0	7 0
	4	88 0	60 0	55 0	134 0	95 2	117 2	74 7	87 4	46 3
3	1	85 0	44 0	52 0	311 0	154 3	132 0	220 0	95 2	137 1
	2	71 0	42 0	35 0	134 4	105 1	86 0	52 0	83 0	89 7
	3	59 0	36 0	40 0	130 6	63 1	59 1	54 2	42 4	52 0
	4	228 0	125 0	124 0	93 3	207 1	210 1	121 5	79 1	100 1

* Mummies removed for identification.

be the first potential cause to consider. Frosts did occur over this period (Figure 3) but later frosts failed to change aphid numbers. A more likely explanation is that wind was the cause. Although shelters were designed to reduce wind, they were not intended to eliminate it altogether (actual reduction in windspeed was approximately 20%). During their period of cold conditioning in the glasshouse, aphids would have selected feeding sites, virtually unconstrained by wind action. Those located on leaf extremities would be predisposed to wind action, so some losses were inevitable. Additional losses may have resulted from the departure of alates but alate adults and alatform 4th instars were not common enough on 16/11 to fully account for the substantial reduction in numbers by 25/1.

25/11 - 9/12

On treatment 2, an unexpected increase in aphid numbers from 64 - 80 occurred (Figure 3). The observation of newly deposited nymphs behind adults on all treatments confirmed that reproduction had occurred although only in treatment 2 did this result in a net population increase. It is noteworthy that daily mean temperatures over this period were usually well below the commonly accepted 5°C threshold for physiological activity in aphids (Mean air temperatures at Silwood House : 3.3, 2.6, 2.0, 1.3, 2.6, 2.9, 4.0, 2.3, 1.4, 1.8, 3.0, 3.6, 5.8, 9.6, 8.4) and certainly, weekly mean temperature values would have not indicated the possibility for reproduction. Daily maximum temperatures, however, often exceeded 5°C and on the 7th, 8th and 9th December they reached 8, 11 and 10.5°C respectively. Hence, it appears that relatively short periods of warm weather are sufficient to allow reproduction in *S. avenae*. Frosts occurred on 9 nights over this period but from the data it is not possible to say whether resulting losses might have been offset by reproduction. What is clear however, is that frost did not have a 'catastrophic' effect on the populations.

Exposed populations experienced heavy rain (23mm) on 7/12 but over the period numbers declined only slightly; from 60 - 54. Winds were not strong, maximum gusts slightly exceeding 10m/s on just 2 occasions (30/11 and 8/12, Figure 3).

14/12 - 4/1

Modest losses of less than 25% on protected treatments contrasted sharply with approximately 67% losses on the exposed treatment (Figure 3). Rainfall was not exceptionally heavy (Figure 3) but winds were probably strong enough on 3/1 to have caused the fall in numbers (mean, 6.5; max. gust 20.2 : Figure 3) especially in view of the possibility that warm weather around 24/12 promoted movement of some aphids to more exposed feeding sites on the plants.

4/1 - 17/1

Frosts occurred on 6 nights, temperatures reaching -7°C on 18/1 yet numbers fell remarkably little (less than 10% on the protected treatments, about 30% on the exposed treatment). High winds on 11/1 and 12/1 seemingly had little effect - even on the exposed treatment. Perhaps aphids that survived the previous winds on 3/1 (see above) remained in relatively sheltered niches rendering them protected from subsequent winds. Indeed, aphids on these plants were often found to be located in new leaf 'funnels', at leaf bases low down the plants or under folds in large wind damaged leaves.

17/1 - 1/2

Although Figure 3 shows a marked decline in aphid numbers on the treatment protected from wind, rain and ground predators, this was not consistent between replicates (88% on replicate 2; 14% on replicate 4; Table 3a). Remarkably 5 individuals were still alive on the exposed plants on 1/2 despite more frosts and light snow (Figure 3).

1/2 - 16/2

A new batch of exposed aphids, set up in the field on 1/2 (see Figure 2) declined from 531 to 200 between 1/2 and 3/2. During this period there were no frosts and little rain but winds were moderately strong (mean = 6.8; maximum gust = 14.4 on 2/2; Figure 3). Numbers continued to fall reaching 90 by 16/2. Rainfall was moderate on 4/2 and there were frosts after 9/2 but moderate winds (Figure 3) were a more likely cause of mortality.

Over the period 1/2 - 14/2, aphids on the main treatments declined slightly, partly due to parasitism by *Aphidius uzbekistanicus*. Aphid mummies were first found on 4/1 when 25 were collected from the plants for identification. A further 10 were removed on 16/1. At that time, mummies comprised a very small proportion of the total population of both species (about 2%) but now that populations had declined, death due to parasitism became as important mortality factor (Table 3b).

14/2 - 20/3

The continuing decline on the 3 original treatments was associated with the occurrence of mummies on the plants (Table 3b). Although these were a small proportion of the combined *S. avenae* and *M. dirhodum* populations (Table 3b), a few deaths due to parasitism in *S. avenae* would represent a high percentage mortality now that their populations were low (Table 3a). Unfortunately host species were not differentiated during counts so this potential impact is not quantified.

The fall in numbers on the supplementary batch of exposed plants (Figure 3) was probably due to high winds, especially on 16/2 when mean speeds reached 6.4m/s and maximum gusts reached 17.5m/s (Figure 3).

Although temperatures during and after this period would have been suitable for reproduction (Figure 3), populations did not build up during April. This was probably due to parasitism (Table 3) and competition

from *M. dirhodum* that by now had built up large populations (see below) which were overwhelming plants originally infested with *S. avenae*.

2.2.2.3. Survival and Mortality of *M. dirhodum*

(a) Treatment Comparisons (Table 2)

Survival of *M. dirhodum* was considerably better than *S. avenae* (Figures 3 and 4). Fewer were lost between introduction (16/11) and first count (25/11) (Figure 4) and reproduction through the winter resulted in substantial population increase. During December, aphids on protected plants increased more rapidly than ones exposed to wind and rain (Figure 4). Large variations between the replicates made comparisons difficult but by 17/1, an 'F test' for treatment effects was significant ($p < .01$). 'T tests', used to compare mean numbers on protected treatments with those on the exposed treatment also proved to be significant ($p < .01$) and these differences were maintained for the duration of the experiment (Table 2).

There were significantly more ($p < .05$) aphids on 'predator protected' plants than on 'predator exposed' on a single occasion (17/1) (Table 2) and rates of change in abundance between 25/11 and 9/12 were also significantly higher on these plants.

In view of the 'short lived' nature of these differences and the limitations of experimental design (Section 2.2.1), it would be unreasonable to accept these results as conclusive evidence of predator effectiveness.

(b) Population change in relation to weather

16/11 - 25/11

Aphid populations on all treatments declined between introduction to the field and first count (35% on exposed plants, Figure 4). Aphids

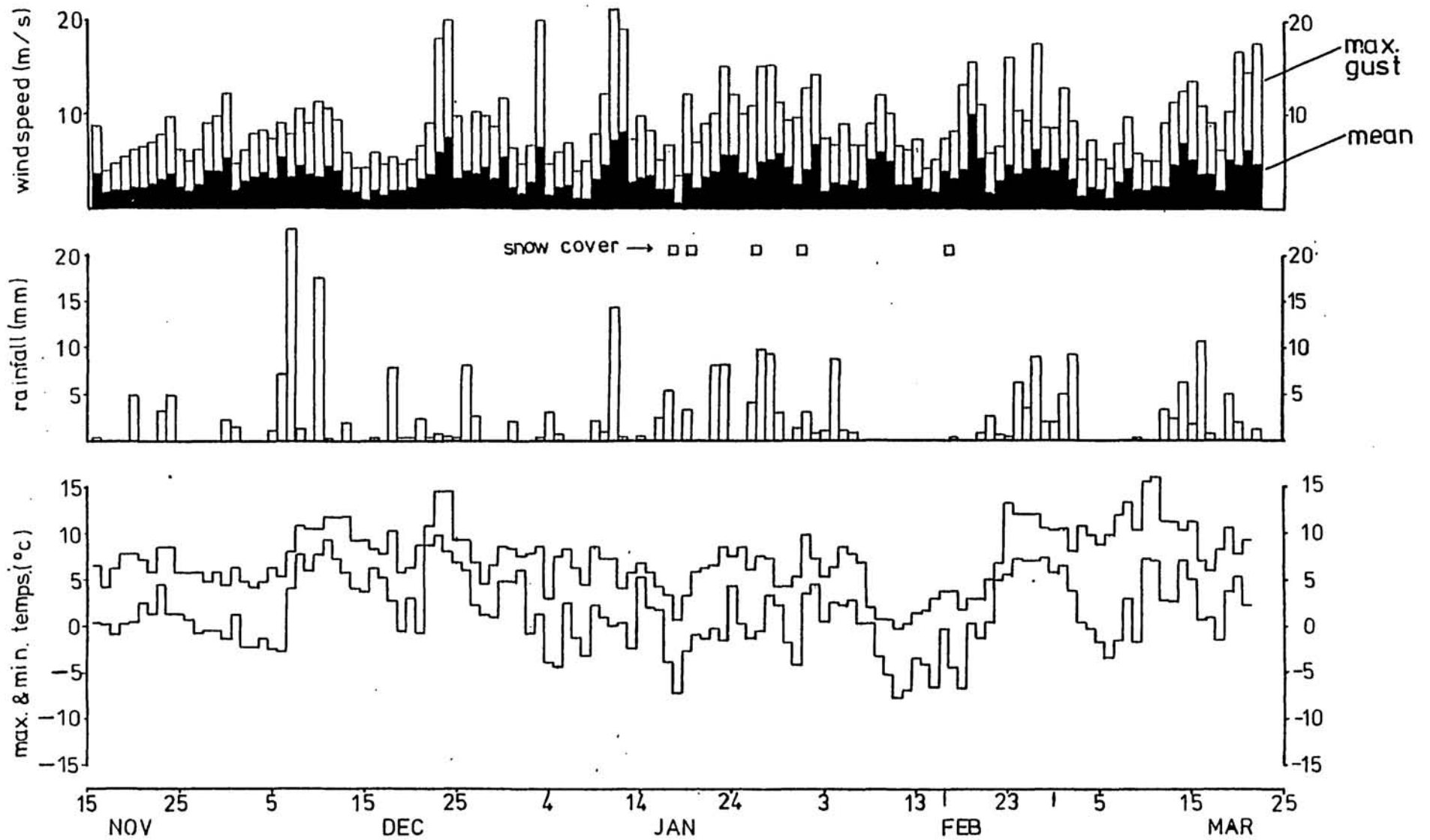
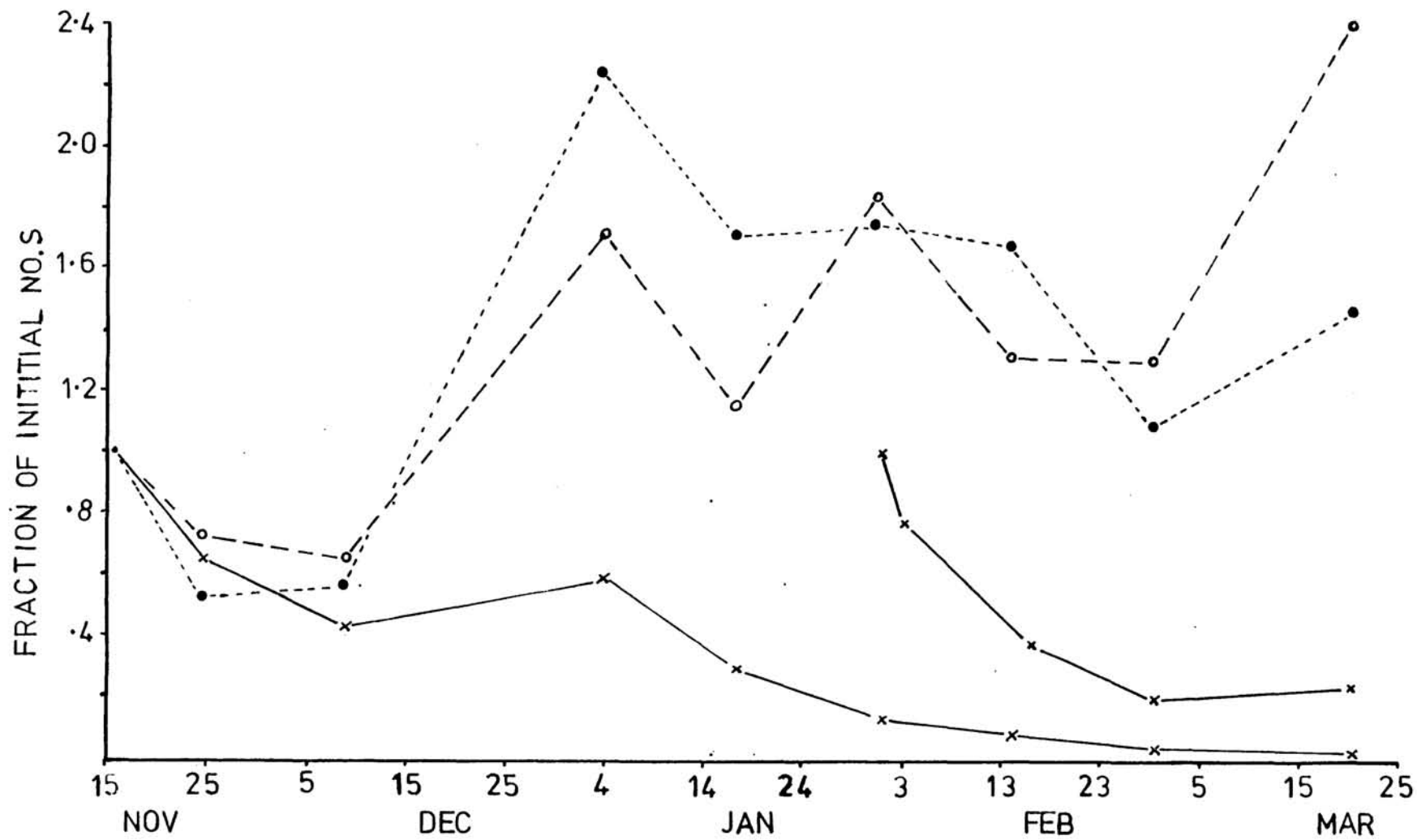


FIGURE 4 : (See adjacent page)

FIGURE 4 : Abundance of *M. dirhodum* during winter 1977 - 1978 in relation to shelter and weather (total aphids on 4 plots).

(x - x, exposed; 0 - - 0, protected from wind and rain; ● - · - · ●, protected from wind, rain and ground based predators).



kept in the glasshouse had probably occupied relatively exposed feeding sites rendering them especially susceptible to wind action (c.f. *S. avenae* already discussed).

25/11 - 9/12.

Adverse weather over this period included moderate winds, low temperatures with frosts on 9 nights and heavy rain on 7/12 (Figure 4). Despite this, none of the populations declined markedly. Perhaps reproduction helped to offset mortality (newly deposited nymphs were found on all treatments on 9/12) and in the case of treatment 3 (wind, rain and ground predator protected), this resulted in a net increase in aphid numbers (Figure 4).

9/12 - 4/1

Reproduction during this period occurred at an even faster rate during this period than in the previous one (Figure 4). Numbers rose from 123 to 321 on treatment 2 (wind and rain protected) and from 147 to 575 on treatment 3 (wind, rain and ground predator protected). Even on the exposed plants, a slight increase occurred from 49 to 66. Relatively short spells of warm weather had resulted in this reproduction although this could only have been predicted by close examination of daily mean and maximum temperature records (see Section on *S. avenae* (2.2.2.2.) for further details). Numerous night frosts (Figure 4) clearly had little or no deleterious effect on the population at this time. Lower rates of increase observed on the exposed plants must be explicable in terms of high rainfall (23mm) on 7/12 or moderate winds, exceeding 10m/s on 30/11 and 8/12 (Figure 4).

4/1 - 17/1

Very strong winds on 11/1 (mean, 7.3m/s; maximum gust, 21m/s) and 10/1 probably account for the observed losses on all treatments (Figure 4) since shelter walls only reduced wind by about 20%. Lower temperatures

after 12/1 (Figure 4) probably prevented reproduction from offsetting these losses.

17/1 - 1/2

Higher temperatures were no doubt responsible for increases in aphid numbers on protected plants (Figure 4), while on exposed plants they declined from 33 to 15, probably due to moderately strong (gusts over 10m/s) winds. Moderate rainfall during this period may also have accounted for aphid losses (Figure 4).

1/2 - 20/3

Between 1/2 and 28/2, numbers fell by 29% to 244 on treatment 2 and by 38% to 279 on treatment 3. Exposed populations also declined from 15 to 4 (Figure 4). These observations are not readily attributable to adverse weather conditions. Perhaps moderately strong (maximum gusts over 7m/s) winds on 22/2, 23/2 and 24/2 caused some losses, even from sheltered plants but high temperatures (Figure 4) might have been expected to have offset this through increased reproduction. Alternatively the losses could have resulted from increased dispersal stimulated by overcrowding, plant damage due to feeding, leaf senescence and higher temperatures. Between 28/2 and 20/3 all 3 populations increased, temperatures being relatively high, especially on 10/3 and 11/3 when maxima of 15.5 and 16.0 respectively were recorded (Figure 4). Winds, however were moderately strong between 12/3 and 17/3 reaching a peak on 15/11 when the mean windspeed was 5.1m/s and the maximum gust, 13.6m/s.

After 20/3, all populations declined, probably due to declining suitability of the plants, excessive temperatures inside the shelters and an increase in parasitism by (*Aphidius uzbekistanicus*). By early May, mummies had out-numbered non mummified aphids.

A new batch of exposed aphids (see Figure 2) declined sharply between introduction to the field on 1/2 and subsequent counts on 3/2, 16/2 and 28/2 (Figure 4). Little rain fell during this period but the moderately strong winds between 12/3 and 17/3 mentioned above probably caused some losses. In addition, dew combined with frosts may have been lethal to aphids conditioned to low temperature in a dry glasshouse (See results of 1978 - 1979 field experiment: 2.3). Silwood Park House meteorological data indicate that ground frosts occurred on every night between 1/2 and 21/2 except for 2/2. A slight increase in numbers between 28/2 and 20/3 occurred despite continuing frosts but by now, only fully 'conditioned' survivors remained.

2.3 FIELD INVESTIGATION ON THE CAUSES OF MORTALITY IN WINTER AND SPRING 1978 - 1979.

2.3.1. INTRODUCTION

Although essentially similar to the previous year's studies, except that only *S. avenae* was used, the present experiment incorporated changes in methods and approach. Better shelters were designed that provided maximum illumination and ventilation, while reducing wind more than in 1977-1978. Each 'treatment' was replicated 5 times and the spacing between shelters was increased to reduce the risk of interaction between plots (i.e. the creation of 'wind shadows' affecting neighbouring plots). The separate effects of wind and rain were assessed but the possible impact of ground predators was not tested. Numbers were counted more frequently, that is at approximately 7 day intervals.

2.3.2. MATERIALS AND METHODS

2.3.2.1. Conditioning of Aphids and Plants.

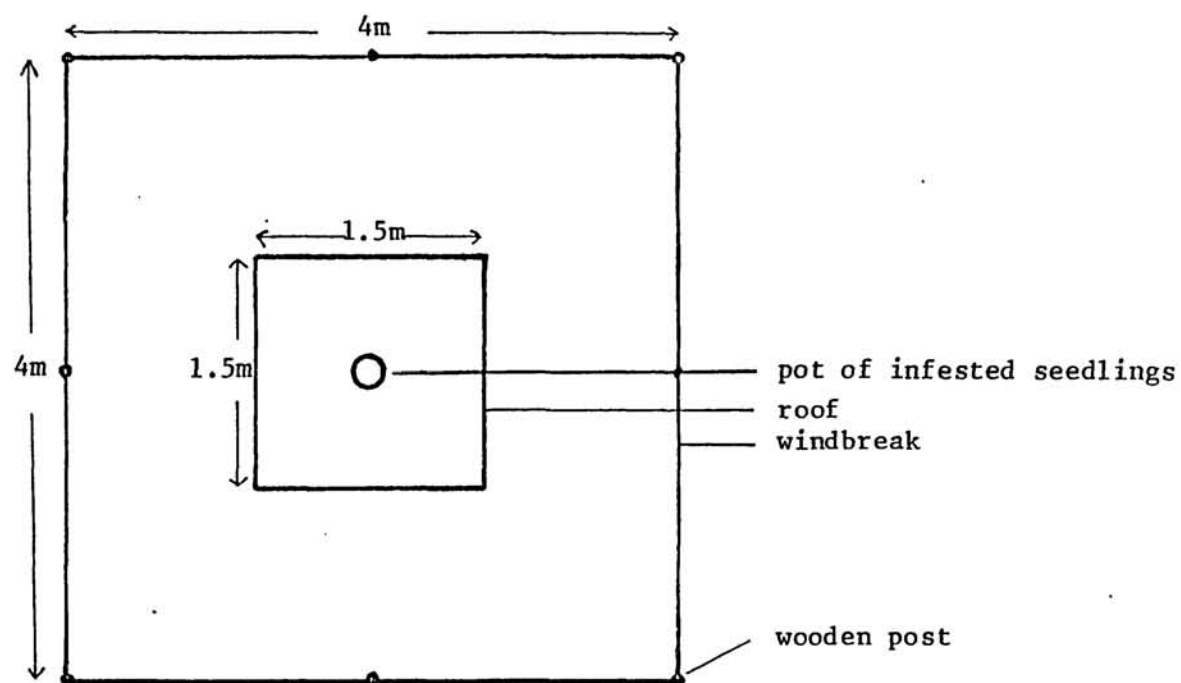
A 'cold conditioned' culture of *S. avenae* was established in mid September. The method was similar to the one described for the 1977-1978 experiment, except that each day the culture plants were inspected and newly deposited nymphs transferred to new culture plants. It was hoped that this would minimise crowding and so reduce alate production. The aphids used for the experiment came from the 4th or 5th generations produced in this way.

2.3.2.2. Shelter Design

To separate the effects of wind and rain, shelters were employed:-

(1) roof alone protecting aphids from rain (11) roof plus windbreak to protect from wind and rain. The first protected plants from rain by means of a roof consisting of corrugated clear plastic (available from 'Transatlantic Plastics Limited') built into a sturdy wooden frame. The legs of this

FIGURE 5 : Shelter Design: field investigation on the causes of mortality 1977-1978.



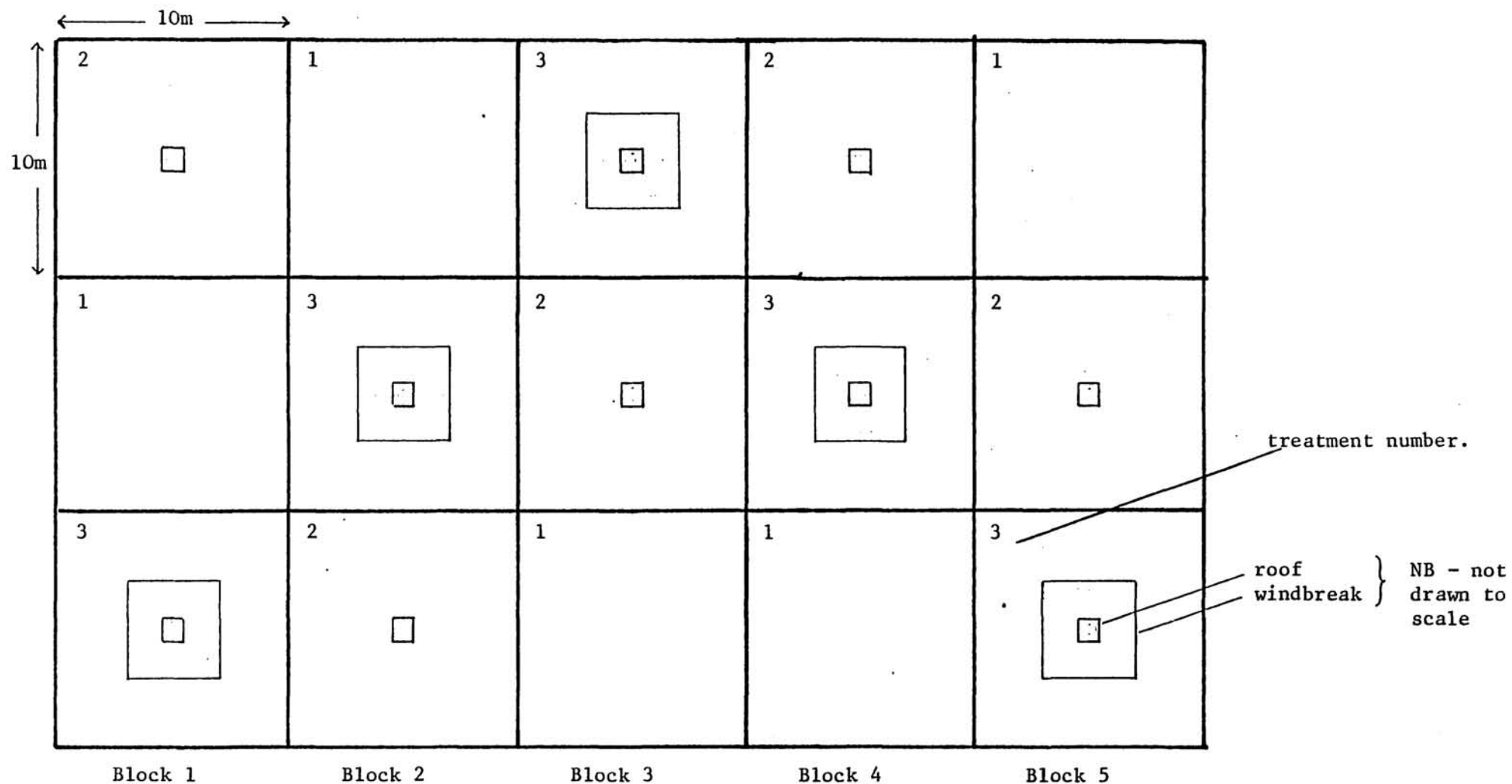
structure were sunk into the ground to a depth of approximately 0.3 M to provide anchorage against the action of strong wind. The second type of shelter consisted of a windbreak in addition to the roof already described. The windbreak material used was strong permiable plastic mesh capable of withstanding very high winds (known as Rokolene 60% shade quality netting manufactured by 'Roko containers' available through J. Bentley Limited). The material was supported on sturdy wooden posts firmly set in the ground to a depth of at least 0.5 M. 8 posts were used for each windbreak which surrounded a single roof (Plate 1 , Figure 5). The large gap between windbreak and roof provided good air circulation so that microclimate was reasonably realistic. A small space (approximately 3cm) between soil surface and windbreak allowed free access to ground predators. Indeed the shelters were unlikely to present a barrier to any group of aphid natural enemies.

2.3.2.3. Experimental Layout

The experimental site consisted of an area 30 x 50m on the western edge of Silwood bottom sown in winter wheat (c.v. Maris Huntsman). The treatments were replicated 5 times and arranged according to a randomised block design (Figure 6; Plate 2). In March a second batch of plants infested with aphids from standard cultures were set up in Block 1 where the overwintered aphids had all died. Experimental methods were the same in the main experiment except that in addition to re-establishing treatments 1, 2 and 3, one pot of infested seedlings was placed inside an insect cage (as used for standard aphid cultures: Section 2.2.1.1) and placed inside the windbreaks used for treatment 3. These aphids could be assumed to be completely protected from wind. Although unreplicated, this supplementary experiment was set up at a time when temperatures were high enough (Figure 8) for reproduction to occur, possibly enabling aphids to offset losses due to mortality.

FIGURE 6 : Experimental Layout: Field investigation on the causes of mortality 1978-1979

(1 = exposed, 2 = rain protected, 3 = wind and rain protected)



2.3.2.4. Environmental Monitoring

Rainfall data was collected at the Silwood House meteorological Station but all other important weather data were recorded within the experimental site. A 'Porton' cup anemometer (Model AW1600, Vector Instruments) (Painter 1976) linked to a chart recorder driven by mains electricity provided continuous wind recording. Maximum/minimum mercury and glass thermometers were used to record the range of temperatures experienced in the different 'treatments'. A pair of thermometers were fixed 5cm above ground level to posts placed either side of each pot of infested plants in block III of the experiment (Figure 6). The data collected in the exposed plot were plotted graphically using the same time scale as aphid data to facilitate interpretation of the results. The data collected from the other 2 'treatments' enabled the effect of shelter on temperature to be assessed. In combination with comparisons of windspeed, an overall picture of shelter effect was obtained. A thermograph provided continuous recordings of temperature from which daily mean temperatures were calculated.

2.3.2.5. Monitoring Colonies

Following their introduction to the field, aphids were counted after 24 hours and then at intervals of approximately 7 days except when snow covered the plants. In addition to recording the numbers of aphids, the occurrence of alateform aphids and newly deposited nymphs was noted.

As the experiment progressed some aphids were found to have moved to the newly emerging wheat seedlings adjacent to the experimental plants. Their numbers were recorded separately but later combined for purposes of analysis. From January onwards numbers of mummified aphids were noted and throughout the experiment miscellaneous additional notes were made (e.g. 'parasite searching plant', 'plants damaged by frost' etc).

2.3.2.6. Analysis of Results.

As in the previous season, an attempt was made to relate change in aphid numbers to prevailing weather conditions. Analysis of variance was performed on the data for each set of counts as well as the rate of change between observations (Appendix 3). The data were not adjusted to allow for covariance with initial numbers since these were similar on all plots.

2.3.3. RESULTS AND DISCUSSION

2.3.3.1. Effect of shelter on microclimate.

(a) Temperature

Table 4 shows temperature maxima and minima recorded within shelters and in the exposed plot. During December, January and February, the highest maxima were recorded in the two sheltered treatments but these temperatures usually exceeded those on the exposed plot by less than 1°C (Table 4).

During March and April the wind and rain protected treatment was consistently the warmest. The extent of this difference was highly variable - on some days as little as 0.5°C, on others greater than 4°C (e.g. 18/4 - Table 4). Strong sunshine combined with cold winds caused the largest discrepancies.

Although minimum temperatures were higher in the shelters, this difference was small. For example, on 20/12, 3/1 and 8/1, the following pairs of temperature minima were recorded in 'exposed' and 'wind and rain protected' treatments respectively : -7.25, -8.50; -11.50, -11.00; -10.50, -11.50.

Daily mean temperatures (Table 5) calculated from continuous thermograph recordings were compared with the data obtained outside Silwood Park House, in order to assess the value of 'on site' temperature

TABLE 4 : Records of temperature maxima and minima for winter 1978-1979
in relation to shelter ($^{\circ}\text{C}$).

TREATMENT DATE	EXPOSED		RAIN PROTECTED		WIND & RAIN PROTECTED		WARMEST TREATMENT	COLDEST TREATMENT
	Max	Min	Max	Min	Max	Min		
28/11	2.50	- 8.00	-	-	-	-	-	-
1/12	4.00	- 9.00	-	-	-	-	-	-
4/12	10.25	1.25	10.00	1.25	12.50	1.00	3	3
6/12	7.25	2.75	9.50	2.25	8.50	2.00	2	3
8/12	9.00	2.00	10.25	1.25	8.75	1.50	2	2
11/12	12.25	6.50	11.75	6.75	14.00	6.25	3	3
13/12	12.00	5.50	14.25	5.50	13.25	5.00	2	2
15/12	10.50	0.50	11.50	1.00	10.75	1.25	2	1
18/12	9.00	- 5.25	9.50	- 5.50	10.00	- 5.00	3	3
20/12	4.00	- 8.50	7.75	- 8.00	5.50	- 7.25	2	3
22/12	2.00	- 2.00	2.00	- 1.50	2.00	- 2.25	-	2
25/12	8.75	- 1.35	9.75	- 1.60	9.50	- 1.25	2	3
27/12	11.00	1.65	12.35	2.50	12.00	2.00	2	1
29/12	11.25	5.75	11.25	5.50	12.00	4.00	3	3
1/ 1	10.25	- 9.50	10.00	- 8.00	11.00	- 8.75	3	2
3/ 1	4.00	- 11.00	2.50	- 11.00	5.00	- 11.50	3	1 + 2
5/ 1	0.50	- 3.75	1.75	- 3.75	1.25	3.75	2	-
8/ 1	8.00	- 11.50	8.50	- 11.00	8.50	- 10.50	2 + 3	1
10/ 1	8.00	- 2.00	8.25	- 1.50	8.00	- 2.50	2	3
12/ 1	4.00	- 3.25	4.00	- 3.25	4.25	- 4.00	3	1 + 2
15/ 1	5.00	- 11.00	6.00	- 8.50	5.25	- 8.25	2	1
17/ 1	4.75	0.00	5.50	0.75	5.00	0.00	2	1 + 3
19/ 1	1.00	- 2.00	1.50	- 1.50	1.00	- 2.00	2	1 + 3
22/ 1	5.50	- 3.50	6.25	- 3.50	6.00	- 3.50	2	-
24/ 1	2.25	- 9.75	3.75	- 8.75	2.00	- 7.50	2	1
26/ 1	5.00	- 4.25	5.50	- 3.50	5.00	- 3.50	2	1
29/ 1	4.50	- 10.50	5.25	- 8.75	5.50	- 8.00	3	1
31/ 1	7.25	- 4.75	7.25	- 3.50	8.75	- 5.00	3	3
2/ 2	8.00	- 0.25	8.50	0.00	8.00	- 0.50	2	3

TABLE 4 : Continued

TREATMENT	EXPOSED		RAIN PROTECTED		WIND & RAIN PROTECTED		WARMEST TREATMENT	COLDEST TREATMENT
DATE	Max	Min	Max	Min	Max	Min		
5/ 2	6.00	- 5.75	7.50	- 5.50	7.75	- 5.75	3	1 + 3
7/ 2	7.00	- 6.25	7.00	- 5.75	7.75	- 5.75	3	1
9/ 2	6.25	- 2.00	6.25	- 1.25	7.00	- 2.25	3	3
12/ 2	3.00	- 0.75	3.00	0.50	3.25	0.00	3	1
14/ 2	7.00	- 1.00	7.00	- 1.00	7.25	- 1.00	3	-
17/ 2	0.25	- 4.00	0.50	- 4.50	2.00	- 3.75	3	2
19/ 2	1.00	- 2.00	1.50	- 2.50	2.00	- 2.00	3	2
21/ 2	2.00	- 0.75	2.50	- 0.50	3.00	- 0.75	3	1 + 3
23/ 2	9.75	- 2.50	10.50	- 2.25	3.25	- 2.75	2	3
26/ 2	7.50	- 7.25	10.00	- 7.50	11.00	- 6.50	3	2
28/ 2	9.00	- 2.75	10.50	- 2.50	11.75	- 3.00	3	3
3/ 3	12.00	- 4.00	12.00	- 5.00	13.00	- 4.75	3	2
5/ 3	11.00	- 3.50	12.00	- 3.25	15.25	- 3.50	3	1 + 3
7/ 3	12.00	- 1.00	13.50	0.50	12.50	- 0.75	2	1
8/ 3	11.50	- 2.00	12.50	- 2.25	14.00	- 2.50	3	3
10/ 3	15.50	- 2.50	15.50	- 2.25	13.50	- 2.75	1 + 2	3
13/ 3	12.00	0.25	12.50	0.00	14.00	1.00	3	2
19/ 3	10.50	- 3.00	11.50	- 3.00	13.50	- 2.50	3	1 + 2
21/ 3	11.75	1.75	12.00	1.75	14.50	2.00	3	1 + 2
23/ 3	11.00	- 5.00	11.75	- 5.00	12.50	- 5.25	3	3
26/ 3	14.00	- 6.00	14.25	- 6.25	14.50	- 6.25	3	2 + 3
30/ 3	12.00	0.00	12.25	0.50	12.50	1.25	3	0
2/ 4	13.00	- 2.25	13.50	- 1.75	14.50	- 1.75	3	1
6/ 4	10.50	- 4.00	10.25	- 3.75	12.00	- 3.25	3	1
9/ 4	15.75	- 1.50	15.50	- 1.00	17.50	- 1.00	3	1
11/ 4	16.00	6.75	16.50	7.25	18.50	7.00	3	1
13/ 4	16.75	5.00	17.00	5.50	19.25	5.00	3	1 + 3
17/ 4	25.50	2.00	25.50	3.25	27.25	3.00	3	1
18/ 4	11.00	- 3.00	10.75	- 3.00	15.50	- 2.25	3	3
20/ 4	17.00	3.50	16.50	4.00	19.75	4.00	3	1
24/ 4	16.25	0.00	15.75	0.75	18.75	0.75	3	1
25/ 4	15.00	0.00	15.25	1.25	19.00	2.00	3	1
27/ 4	14.00	3.50	14.00	4.25	15.50	4.50	3	1
30/ 4	17.00	- 1.50	16.50	0.00	17.75	0.50	3	1

TABLE 5 : Daily mean temperatures*, winter 1978-1979 derived from
continuous thermograph recordings in Silwood Bottom ($^{\circ}\text{C}$).

DATE	MEAN TEMP
Nov. 29	- 1.9
30	- 2.8
Dec. 1	- 4.0
2	- 0.1
3	2.0
4	3.2
5	1.0
6	2.6
7	0.2
8	9.0
9	10.5
10	11.5
11	10.9
12	10.6
13	7.0
14	5.0
15	5.0
16	5.15
17	2.6
18	- 1.8
19	- 2.2
20	- 0.6

DATE	MEAN TEMP
Dec. 21	- 1.8
22	0.2
23	0.5
24	1.6
25	5.0
26	3.8
27	7.3
28	6.5
29	7.3
30	4.3
31	- 1
Jan. 1	- 4
2	- 6.9
3	- 4
4	- 3.3
5	- 5.8
6	- 5.5
7	- 0.4
8	3.1
9	- 5.5
10	1.7
11	2.0

DATE	MEAN TEMP
Jan. 12	- 1.7
13	- 2.5
14	- 6.7
15	- 5.7
16	2.3
17	2.0
18	1.7
19	- 0.1
20	0.1
21	- 0.3
22	- 0.4
23	0.3
24	- 1.8
25	- 1.5
26	2.4
27	0.3
28	- 3.8
29	- 0.1
30	- 0.4
31	- 0.9
Feb. 1	3.1
2	3.1

DATE	MEAN TEMP
Feb. 3	- 0.9
4	- 0.4
5	0.2
6	- 0.3
7	- 0.3
8	1.7
9	0.8
10	1.3
11	0.8
12	1.3
13	2.0
14	3.2
15	- 1.0
16	- 1.0
17	- 1.8
18	- 1.1
19	- 1.1
20	- 0.7
21	0.1
22	- 0.3
23	1.1
24	1.4
25	- 1.0
26	- 3.3
27	0.8

DATE	MEAN TEMP
Feb. 28	3.5
Mar. 1	3.7
2	4.7
3	7.3
4	7.3
5	3.1
6	6.5
7	3.5
8	3.5
9	6.5
10	2.6
11	3.2
12	7.3
13	8.0
14	2.8
15	1.7
16	10.0
17	1.6
18	1.9
19	3.5
20	3.7
21	5.0
22	2.5
23	2.9
24	2.2

DATE	MEAN TEMP
Mar. 25	6.5
26	7.1
27	5.6
28	3.7
29	3.8
30	3.8
Apr. 1	3.7
2	5.2
3	5.0
4	3.4
5	3.5
6	6.6
7	5.0
8	5.3
9	5.9
10	10.3
11	9.8
12	9.1
13	8.5
14	9.2
15	11.3
16	13.0
17	10.3
18	4.7
19	8.3

DATE	MEAN TEMP
Apr. 20	9.8
21	2.9
22	7.0
23	9.2
24	13.6
25	5.0
26	7.1
27	8.0
28	7.7
29	5.8
30	10.4

* for 24 hour until 09.00 hours on the stated date.

TABLE 6 : Comparison of mean temperatures ($^{\circ}\text{C}$) recorded in Silwood Bottom and outside Silwood House in a Stevenson's Screen.

Date (April 1979)	Temperature $^{\circ}\text{C}$		
	Screen	Field	Difference
10	11.20	10.30	- 0.90
11	11.30	9.80	- 1.50
12	8.60	9.10	+ 0.50
13	11.60	8.50	- 3.10
14	14.20	9.20	- 5.00
15	13.60	11.30	- 2.30
16	8.90	13.00	+ 4.10
17	6.40	10.30	+ 3.90
18	6.60	4.70	- 1.90
19	7.60	8.30	+ 0.90
20	9.10	9.80	+ 0.70
21	8.70	7.90	- 0.80
22	8.80	7.00	- 1.80
23	8.50	9.20	+ 0.70
24	7.20	13.60	+ 6.40
25	6.40	5.00	- 1.40
26	7.70	7.10	- 0.60
$\bar{x}$	9.19	9.63	+ 0.44

TABLE 7 : Measurements of wind speed (m/s) in relation to shelter.

Experimental NotesWind Direction - N.E.Temperature - -1°C Time - 10.00-11.30Equipment - 'Wallac' hot wire thermo-anemometer

Method - Sensor held 10 cm above soil level adjacent to experimental plants in Block III. Wind speed measured for 1 minute and speed of maximum gust noted. Procedure repeated for each treatment in turn until 10 separate measurements had been obtained.

Results

TREATMENT REPLICATE	EXPOSED	RAIN PROTECTED	WIND AND RAIN PROTECTED
1	11.0	5.0	1.2
2	8.0	7.0	0.6
3	7.0	11.0	0.9
4	10.0	5.0	0.5
5	11.0	5.0	0.5
6	7.0	7.0	0.7
7	5.0	4.0	0.8
8	9.0	8.0	0.6
9	9.0	7.0	1.1
10	8.0	7.0	0.8
$\bar{x}$	8.5	6.6	0.8
Percent Reduction in Wind Speed Compared to Exposed	0	22	91

recording. During a period of wide daily variations in temperature in April, substantial differences were found between daily means (Table 6) although neither site was consistently warmer than the other. Over the 16 day 'sample' period in Table 6 the field temperature was, on average 0.44°C higher than outside Silwood House but in view of the large variation between days, this result is probably insignificant.

(b) Wind

Table 7 shows the results of windspeed comparisons in the three treatments during strong winds in February. In the exposed plots, maximum gusts of 5 - 11m/s were recorded whereas in the wind and rain protected plots maximum gusts ranged between 0.5 - 1.2m/s (Table 7). The range in gust strengths on the rain protected plots was the same as on wind and rain protected ones (5 - 11m/s; Table 7).

(c) Snow

Although shelter roofs mostly prevented snow from falling directly onto protected plants, wind frequently drifted snow to these plants (Plate 3). Between 20/12 and 5/1, this produced similar such deposits in all treatments but later snow falls drifted less onto plants in treatment 3 than in treatment 2.

2.3.3.2. Treatment Comparisons

The main purpose of this section is to present the results of statistical analysis (Table 8). The magnitude of treatment differences and their possible causes are discussed in the following section.

An 'F test' for treatment effects proved to be significant for every census occasion ($p < .01$ except on 13/12 and 1/2 where $p < .05$: Table 8). T tests, used to compare treatment means, in every case indicated a significant difference between one treatment and the other two. The results of these tests will therefore be described in terms

TABLE 8 : Summary of Analysis of Variance - Winter 1978-1979

(** = significant at 1% level, * = significant at 5% level,

N.S. = not significant; treatment 1 = exposed, 2 = rain

protected, 3 = wind and rain protected).

a) Total Aphids

		28/11	6/12	13/12	21/12	8/1	16/1	1/2	8/2	22/2
'F test'		**	**	*	**	**	**	*	**	**
Treatment comparisons	1, 3	**	**	*	*	*	**	N.S.	*	**
	1, 2	**	**	N.S.	*	N.S.	N.S.	N.S.	N.S.	N.S.
	2, 3	N.S.	N.S.	*	N.S.	*	**	N.S.	*	**

b) Rates of Change in Abundance Between Counts

		28/11	6/12	13/12	21/12	8/1	16/1	1/2	8/2	22/2
'F test'		**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Treatment comparisons	1, 3	**								
	1, 2	**								
	2, 3	N.S.								

TABLE 9 : Causes of overwintering mortality 1978-1979 - proportion of *S. aeneas* surviving between counts.

TREATMENT	REP.	27/11 28/11	28/11 6/12	6/12 13/12	13/12 21/12	21/12 8/1	8/1 16/1	16/1 1/2	1/2 8/2	8/2 22/2	22/2 7/3	7/3 21/3
1. Exposed Plants	1	.29	1.15	-	-	-						
	2	.47	.68	1.00	.58	.73						
	3	.32	1.00	.61	.36	1.50						
	4	.46	.71	.80	.33	1.75						
	5	.42	.96	.14	1.67	2.00						
$\bar{x}$		.39	.74	.68	.74							
Overall Survivorship on all Plots		.39	.86	.63	.53							

2. Plants Protected from Rain	1	.73	.63	.40	.88	.00	-					
	2	.63	.97	.47	.82	.29	.25					
	3	.82	1.14	.49	1.00	.75	.20					
	4	.78	.94	.21	1.14	.50	1.00					
	5	.76	.86	.54	.69	.22	1.00					
$\bar{x}$		.74	.91	.42	.91	.35	.61					
Overall Survivorship on all Plots		.73	.92	.42	.89	.43	.40					

TREATMENT	REP.	27/11 28/11	28/11 6/12	6/12 13/12	13/12 21/12	21/12 8/1	8/1 16/1	16/1 1/2	1/2 8/2	8/2 22/2	22/2 7/3	7/3 21/3
3. Plants Protected from Wind and Rain	1	.94	.93	.24	.30	1.33	.75	.00	-	-	1.00	1.00
	2	.98	1.08	.85	.76	.65	.55	1.00	.58	.14	4.00	.00
	3	.81	1.06	.92	.79	.65	.53	.56	1.80	.78	.00	-
	4	.57	1.36	.50	1.21	.78	1.33	.58	.57	.25	1.00	.00
	5	.79	1.10	.76	.68	.47	.88	.00	"	1.00	.33	.00
$\bar{x}$		.82	1.11	.63	.75	.85	.81	.43	.98	.54	1.27	.25
Overall Survivorship on all Plots		.82	1.09	.65	.78	.67	.80	.56	.87	.52	.57	.13

of 'the exceptional treatment'.

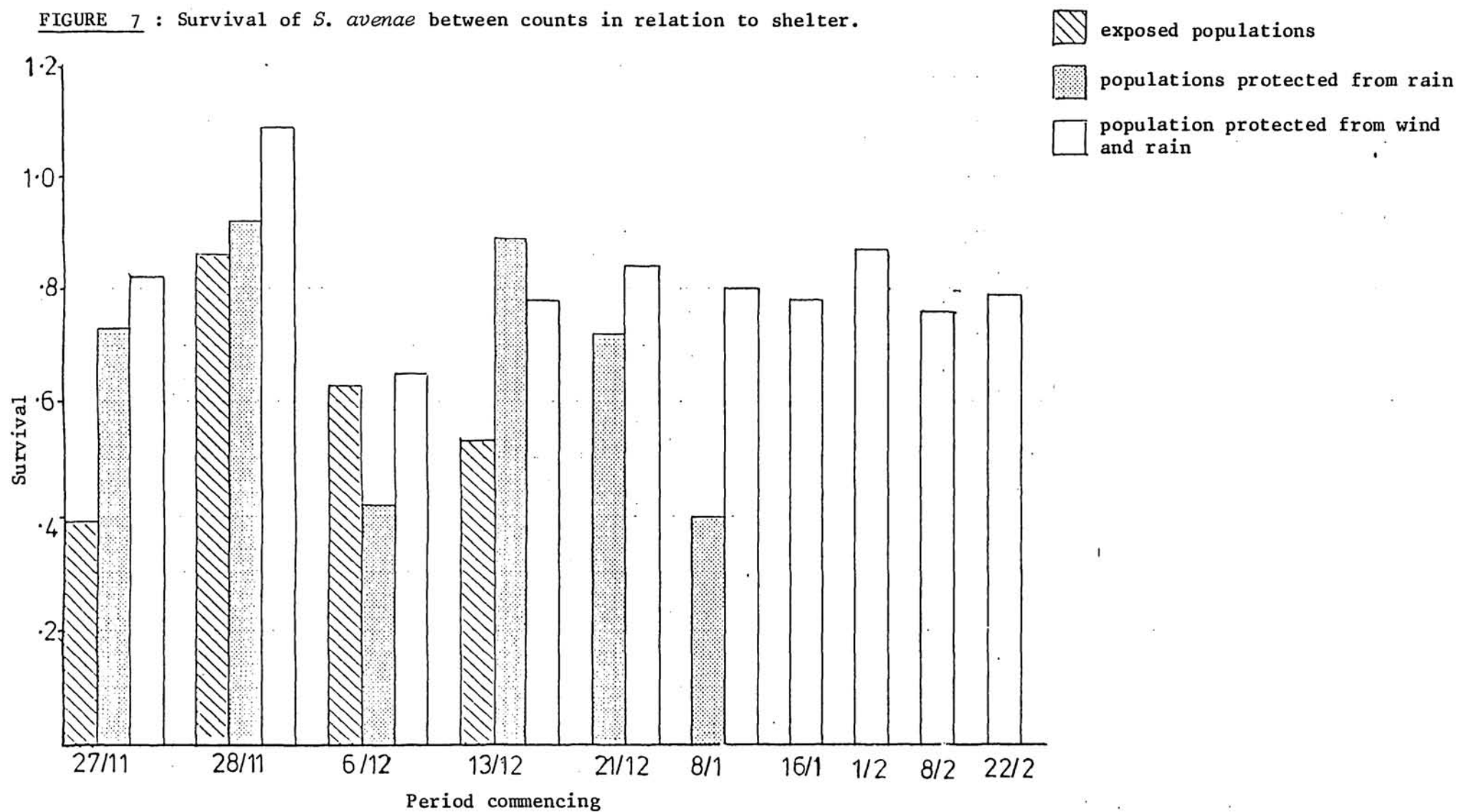
On 28/11 and 6/12 exposed populations were smaller than those on the sheltered treatments. ($p < .01$). By 13/12, treatment 3 (wind and rain protected) had become the exceptional treatment retaining more aphids than treatments 1 and 2 ($p < .05$) - a difference that persisted for the rest of the experiment although not statistically significant ($p = .05$) on 21/12. Differences between treatments 1 (exposed) and 2 (rain protected) became very small and statistically insignificant ($p = .05$) after 8/1.

Analysis of variance on the rates of change in numbers between counts was significant for one interval only, 27/11 - 28/11 ($p < .01$) when there were heavier losses on exposed plants than on sheltered treatments. Survival between counts was tabulated (Table 9) and plotted graphically (Figure 7) to supplement formal analysis of variance. This facilitated comparisons between survival rates at different times of the year. When numbers fell below 2 individuals on 2 or more replicate, the data were omitted so that spurious changes (e.g. due to counting error) would not lead to misleading interpretations. The most conspicuous feature of Figure 6 is the remarkable consistency in mean weekly survival on treatment 3. Apart from 28/11 - 6/12 when temperatures were high enough for reproduction to occur, fluctuations were confined to the range 0.65 - 0.87 despite widely differing weather conditions. Other noteworthy features include the consistently greater survival of colonies on treatment 3 compared to other treatments and the lack of consistent differences between treatments 1 and 2. This is discussed in detail in the following section.

2.3.3.3. Population change in relation to weather.

(a) Main experiment (Table 10, Figures 8 and 9)

FIGURE 7 : Survival of *S. avenae* between counts in relation to shelter.



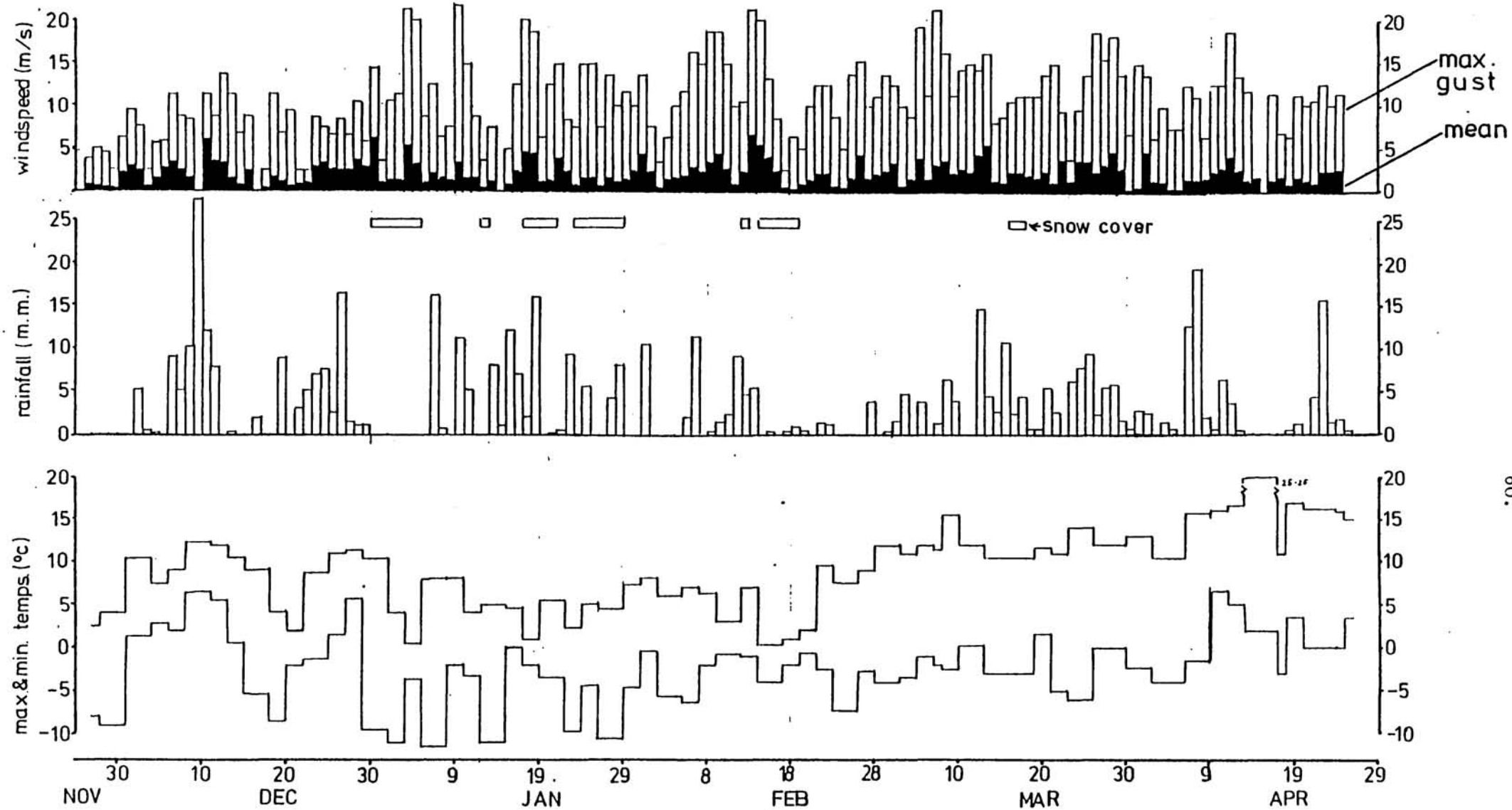
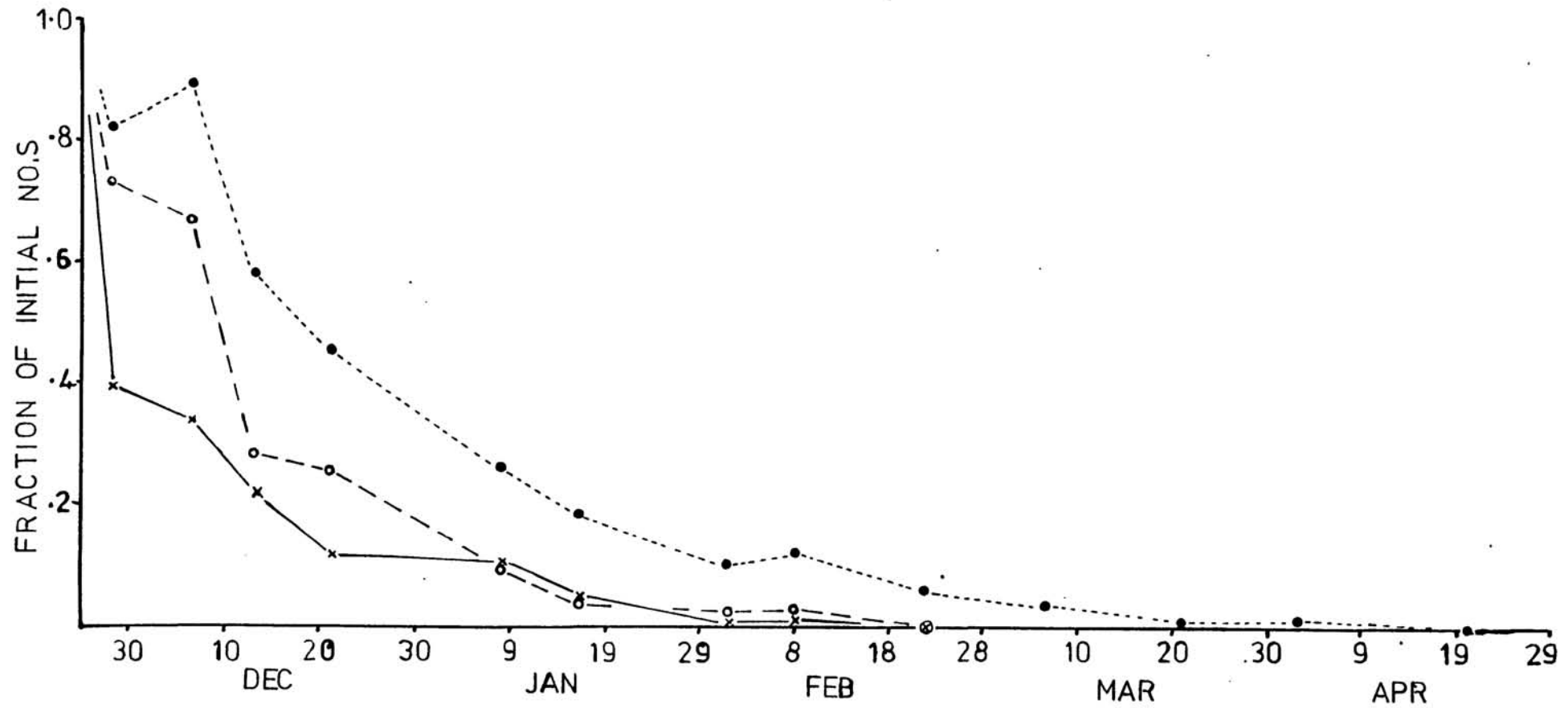


FIGURE 8 : (See adjacent page)

FIGURE 8 : Abundance of *S. avenae* in relation to shelter and weather - total aphids on 5 replicates plotted on an arithmetic scale. (x - x, exposed; 0 - - 0, protected from rain; ● --- ●, protected from wind and rain).



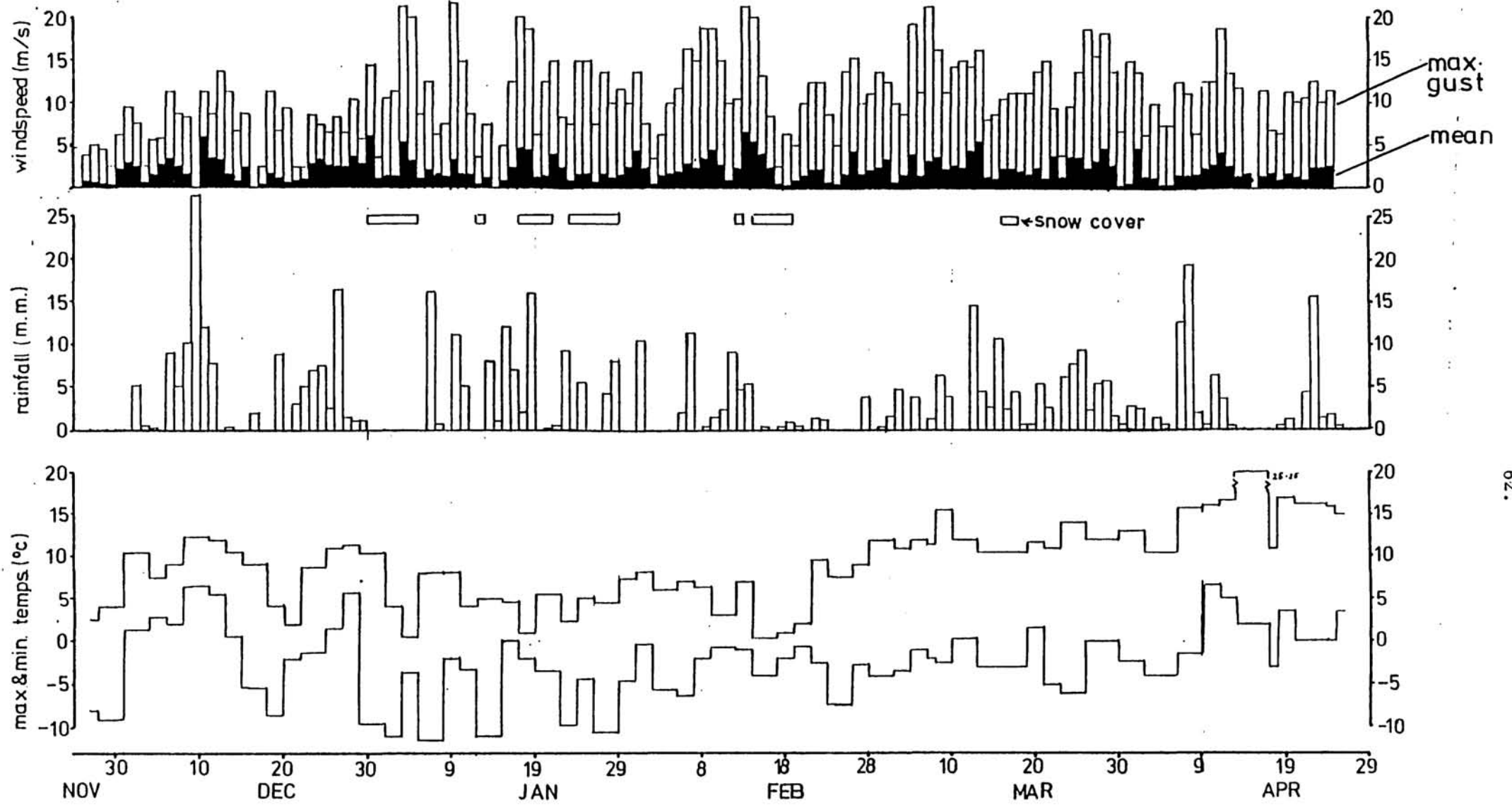


FIGURE 9 : (See adjacent page)

FIGURE 9 : Abundance of *S. avenae* in relation to shelter and weather - total aphids plotted on a logarithmic scale.

(x - x, exposed; 0 - - 0, protected from rain; ● --- ●, protected from wind and rain)

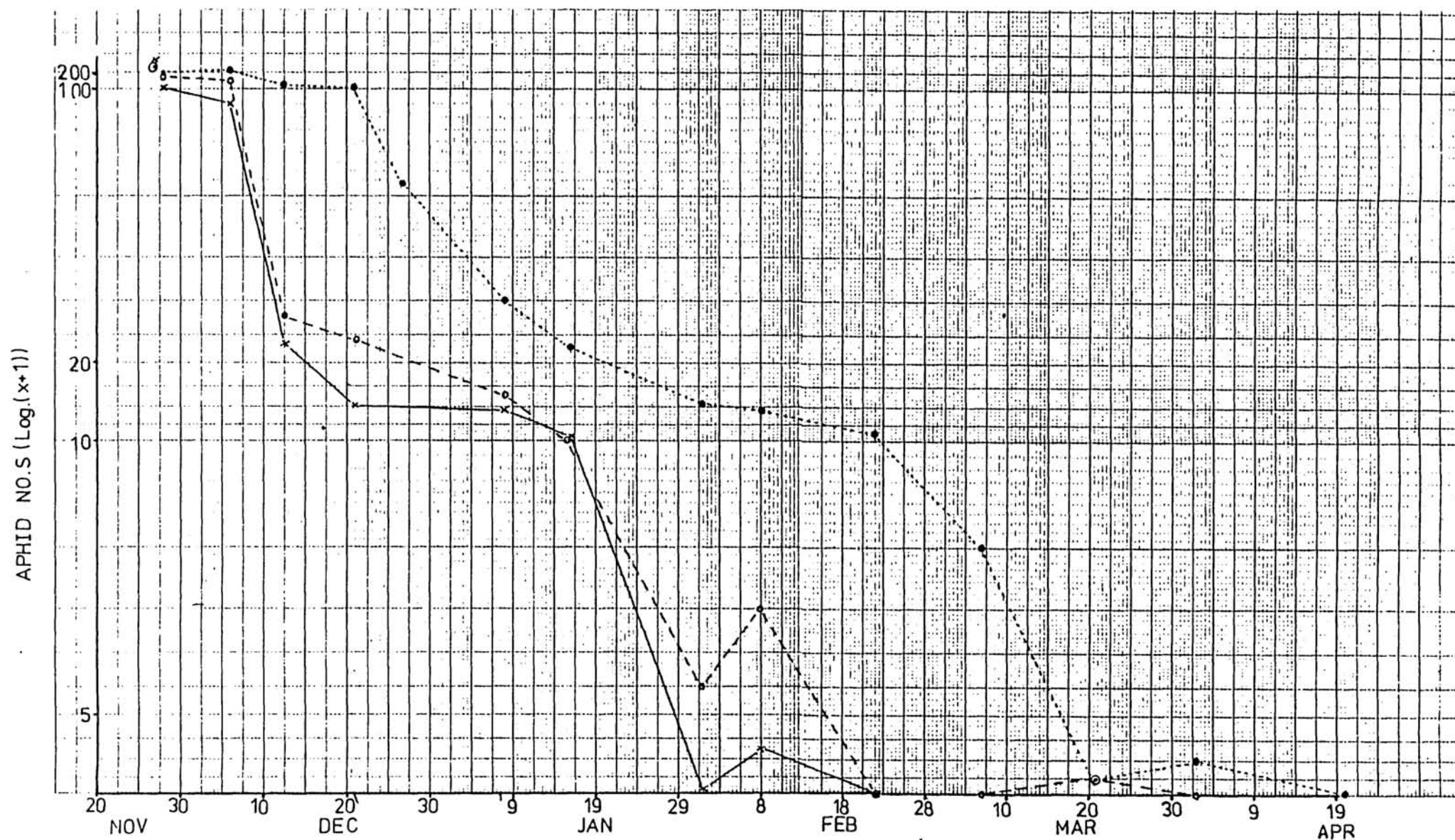


TABLE 10 : Causes of overwintering mortality 1978-1979 - raw data showing numbers of *S. avenae* (and 'mummies') on individual plots.

TREATMENT	REP.	27/11	8/11	6/12	13/12	21/12	8/1	16/1	1/2	8/2	22/2	7/3	21/3	2/4	20/4
1. Exposed	1	45	13	15	*	-	-	-	-	-	-	-	-	-	-
	2	59	28	19	19	11	8	2	1	1	0	0	0	0	0
	3	56	18	18	11	4	6	1	0	1	0	0	0	0	0
	4	46	21	15	12	4	7	5 (1)	0	0 (1)	0	0	0	0	0
	5	55	23	22	3	5	1	2	0	0	0	0	0	0	0
2. Protected from Rain	1	44	32	20	8	7	0	0	0	0	0	0	0	0	0
	2	59	37	36	17	14	4	1	2	2	0	0	0	0	0
	3	44	36	41	20	20	15	3	2	4	0	0	0	0	0
	4	45	35	33	7	8	4	4	0	0	0	0	0	0	0
	5	37	28	24	13	9	2	2	1	1	0	0	0	0	0
3. Protected from Wind and Rain	1	48	45	42	10	3	4	3	0	0	1	1	1	0 (1)	0
	2	50	49	53	45	34	22	12 (3)	12	7	1	4	0	0	0
	3	42	34	36	33	26	17	9	5	9	7	0	0 (2)	0 (1)	0
	4	49	28	38	19	23	18	24	14	8	2	2	0 (2)	2 (1)	1
	5	38	30	33	25	17	8	7	0	3	3	1	0	0	1

* Plant grazed by rabbits, inspections terminated and totals adjusted.

27/11 - 28/11

The most striking differences between treatments occurred 24 hours after transfer of aphids to the field. The 60% decrease in numbers of 'exposed' aphids significantly ($p < .01$) exceeded losses suffered on other treatments (see above). The absence of rain (Figures 8 and 9) rules out a simple explanation of this result. Dew may possibly have caused the difference. It occurred in combination with frost on exposed plants while on the other treatments it settled out on shelter roofs leaving plants relatively dry. Aphids survived slightly better on wind and rain protected plants than on plants protected from rain alone but this difference was statistically insignificant ($p = .05$; Table 8) and small in magnitude (survival = .82 compared with .73; Table 9). This was not surprising in view of the low windspeeds recorded for this period (maximum gusts = $<5\text{m/s}$; Figure 8).

28/11 - 6/12

During this period of light winds and little rain (Figure 8), reproduction occurred on all plots. 'On site' measurements of temperature maxima exceeded 10°C between 1 - 4 December although mean daily temperatures never exceeded 5°C (a commonly used 'developmental threshold' for growth and reproduction in aphids). Clearly, short periods of favourable weather were sufficient for reproduction by *S. avenae*.

6/12 - 13/12

During this period of relatively high temperatures and light/moderate winds, rain fell almost every day. On 9/12 exceptionally heavy rainfall was recorded (over 27mm; Figure 8). Despite this, survival on exposed plants (Treatment 1) were slightly better than on plants protected from rain (Treatment 2) (survival = .63 compared to .42; Table 9).

13/12 - 21/12

Widely varying temperatures were recorded during this period, minima

reaching -8.5°C (Figure 8). Despite this, populations declined at a much slower rate than during the previous 7 days. This is shown clearly by comparing slopes of population curves plotted on a log. scale (Figure 9) for the 2 periods. Perhaps the key difference between this and the previous period was relatively light winds (mean $< 3\text{m/s}$, maximum gust $< 12\text{m/s}$ compared with mean $< 6\text{m/s}$, maximum gust $< 15\text{m/s}$; Figure 8).

21/12 - 8/1

Exceptionally severe weather conditions were recorded during this period. Rainfall was moderate but on 2 days heavy (over 16mm on 27/12 and 7/1; Figure 9), winds were strong (maximum gusts in excess of 20m/s), frosts were severe (below -10°C ; Figure 9) and frequent (only 4 days in 12 without frost; Figure 9) and drifting snow covered all infested plants. Surprisingly, the fall in aphid numbers was not exceptional compared to other periods. Total numbers on treatments 1, 2 and 3, before and after were 24, 22; 58, 25; 105, 69 respectively (Table 10). Indeed, the fact that any aphids survived these conditions is noteworthy.

8/1 - 16/1

Although rainfall was moderate (not exceeding 12mm in a single day; Figure 8) and temperatures continued to fall below -10°C (Figure 8), snow was only present for 1 day. Aphids on treatments 1 and 2 declined faster than in the previous period, perhaps because snow had previously protected aphids from adverse weather. Alternatively, plant damage caused by cold in the previous period may have become manifest after 8/1, so depriving aphids of shelter and food and forcing them to move away and be killed by exposure or food shortage. At this time field grown winter wheat had also been damaged by frost.

16/1 - 1/2

This period was characterised by high winds, (maximum gusts of over 10m/s

on 10 days, over 18m/s on 2 days in the 16 day period; Figure 8); moderate rain and daily frosts - below -9°C on 5 days; Figure 8). By 1/2, numbers had fallen from 10 to 1 on the exposed plants, 10 to 5 on rain protected plants and 55 to 31 on wind and rain protected plants (Table 10, Figure 8). On 7 plots, aphids could no longer be found (Table 10) so quantitative comparisons between treatments became unreliable. On the wind and rain protected plants, 14 dead aphids were found compared with 31 that were still alive. These may have been killed directly by prolonged low temperature or else by starvation resulting from plant damage caused by frost.

1/2 - 20/4

By 22/2 there were no aphids on Treatments 1 and 2. Populations protected from wind and rain (treatment 3) continued to decline despite warmer weather. (Maxima usually exceeding 9°C after 21/2; Figure 8). Reproduction was observed on 8/2 but this was offset by mortality. More dead aphids were found on the plants on 8/2 and 22/2 (1 and 7 dead compared with 27 and 14 still alive respectively) and later most were killed by aphid parasites - *Aphidius uzbekistanicus*. On 7/3 there were 8 individuals still alive but on 21/3 and 2/4 5 had mummified (Table 10). Searching adult parasites were found on experimental plants much earlier in the winter - first on 13/12 and then on 8/1 and 16/1 during sunny weather.

(b) Supplementary experiment during March - April.

The results of this experiment (Figure 10), described above (Section 2.3.2.3) need to be interpreted with caution as treatments were unreplicated.

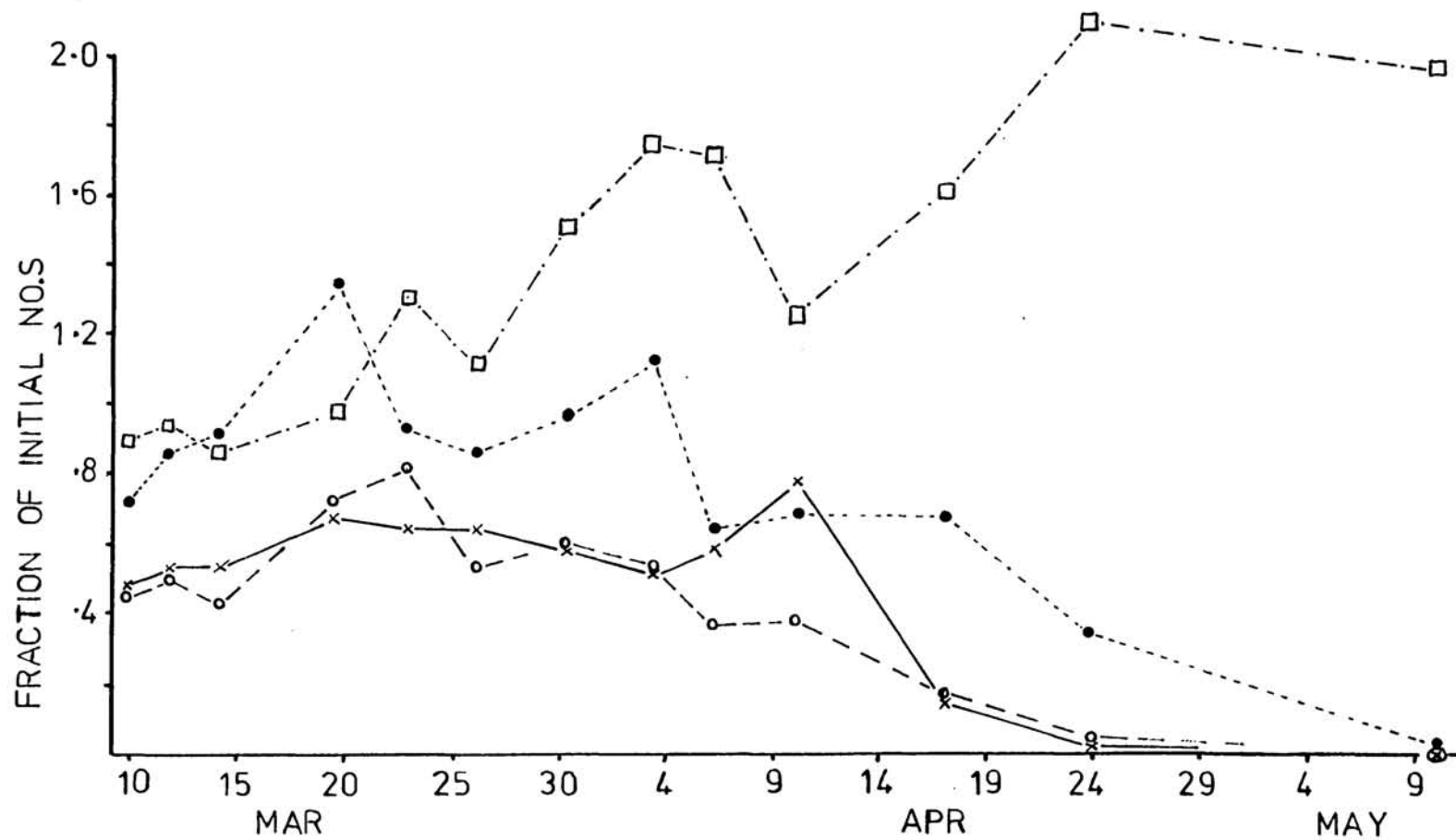
As in the main experiment, notable losses occurred 24 hours after the introduction of plants to the field on 8/3 on treatments 1 (51%) and 2 (45%), and to a lesser extent, 3 (28%) (Figure 10). In contrast, few were lost from the caged plants (12%) (Figure 10) supporting the hypothesis that in the glasshouse, many aphids occupy feeding sites from which they can be readily dislodged even by light wind (see above). Although strong winds were recorded on 8/3 and 9/3, (maximum gusts = 16 and 11m/s respectively), the losses in treatment 3 were associated with substantially reduced (approximately 90% (Section 2.3.3.1) winds due to the effect of windbreaks.

Subsequent aphid counts showed that reproduction was taking place on all plants no doubt due to relatively high temperatures (mean temperatures over 5°C on 11 days in March, 25 days in April; maxima exceeding 15°C on 2 days in March, 18 days in April). Differences in the size of aphid populations were potentially the result of differential rates of mortality and/or reproduction but these were not separable in this experiment. (In the main experiment, differences were mainly attributable to mortality).

As in the main experiment, populations on treatments 1 and 2 differed little, indicating that rain was not an important mortality factor. Wind and rain protected populations built up considerably from 137 on 10/3 to 258 on 19/3 when seedlings clearly became overcrowded. Subsequently numbers fell to 166 on 26/3 (perhaps due to overcrowding and departure

FIGURE 10 : Abundance of *S. avenae* in relation to shelter - results of an unreplicated experiment during spring.

(x - x, exposed; 0 - - 0, protected from rain; ● --- ●, protected from wind and rain;
 □ - - - □ , fully caged)



of alates) but built up again to 215 on 3/4. Numbers fell to 124 on 6/4 and remained similar on 10/4 and 17/4 but subsequently declined (Figure 10) due to parasitism (there were 2 mummies on 24/4, 15 on 10/5) and possibly predation by ground beetles. (*Notiophilus biguttatus* was a particularly conspicuous diurnal carabid during March and April).

Aphid survival and build up was substantially higher on the fully caged plants (Figure 10). Although the virtual elimination of wind by the cage was a prime cause of this difference, other factors may also have been important; for example:-

- (1) The maximum temperature in the fully caged system over the period 27/4 - 30/4 was 20°C compared with 18.5°C in treatment 3 and 17°C outside. Differences of this magnitude could significantly increase rates of growth and reproduction.
- (11) The cage may have prevented alate aphids from leaving the experimental plants.
- (111) The cage excluded ground predators which were abundant and active during March and April.

2.4 FIELD OBSERVATIONS ON THE DEVELOPMENT OF NATURAL APHID POPULATIONS ON DIFFERENT AGED WHEAT PLANTS DURING WINTER.

2.4.1 INTRODUCTION

During Autumn 1977, winter wheat plots in Silwood Bottom were inspected for the occurrence of cereal aphids. On one area, winter wheat was sown in 3m rows at intervals of approximately 3 weeks, starting 14/9. This provided the opportunity to study the development of natural populations in relation to different plant growth stages. The plants first became infested at the end of October 1977, by which time 3 sowings had been made. The present study was concerned with aphid population development on these plants through the winter. Additional rows were sown throughout the winter and spring in order to study the relationship between wheat growth stage and aphid attack during summer (Section 4.3.1.2).

2.4.2 MATERIALS AND METHODS

Each experimental block comprised an area 3 x 6m (Figure 11) divided into 20 plots which consisted of 3 rows of winter wheat (c.v. Maris Kinsman) sown with a manually operated 'Stanhay' seed drill. Instead of sowing plots at regular time intervals, the period between sowings was modified to maximise the range of growth stages that were likely to be present in the spring. (See Chapter 4). Instead of randomising the position of plots, sowings were made sequentially across the blocks (Figure 11) because in the spring, close proximity of short and tall tillers could bias plant selection by colonising alates. The system of sequential sowing would present alates with a 'wedge' of increasingly mature wheat plants. There were 4 experimental blocks, each facing a different direction so that directional effects during colonisation could be separated from 'growth stage selection'.

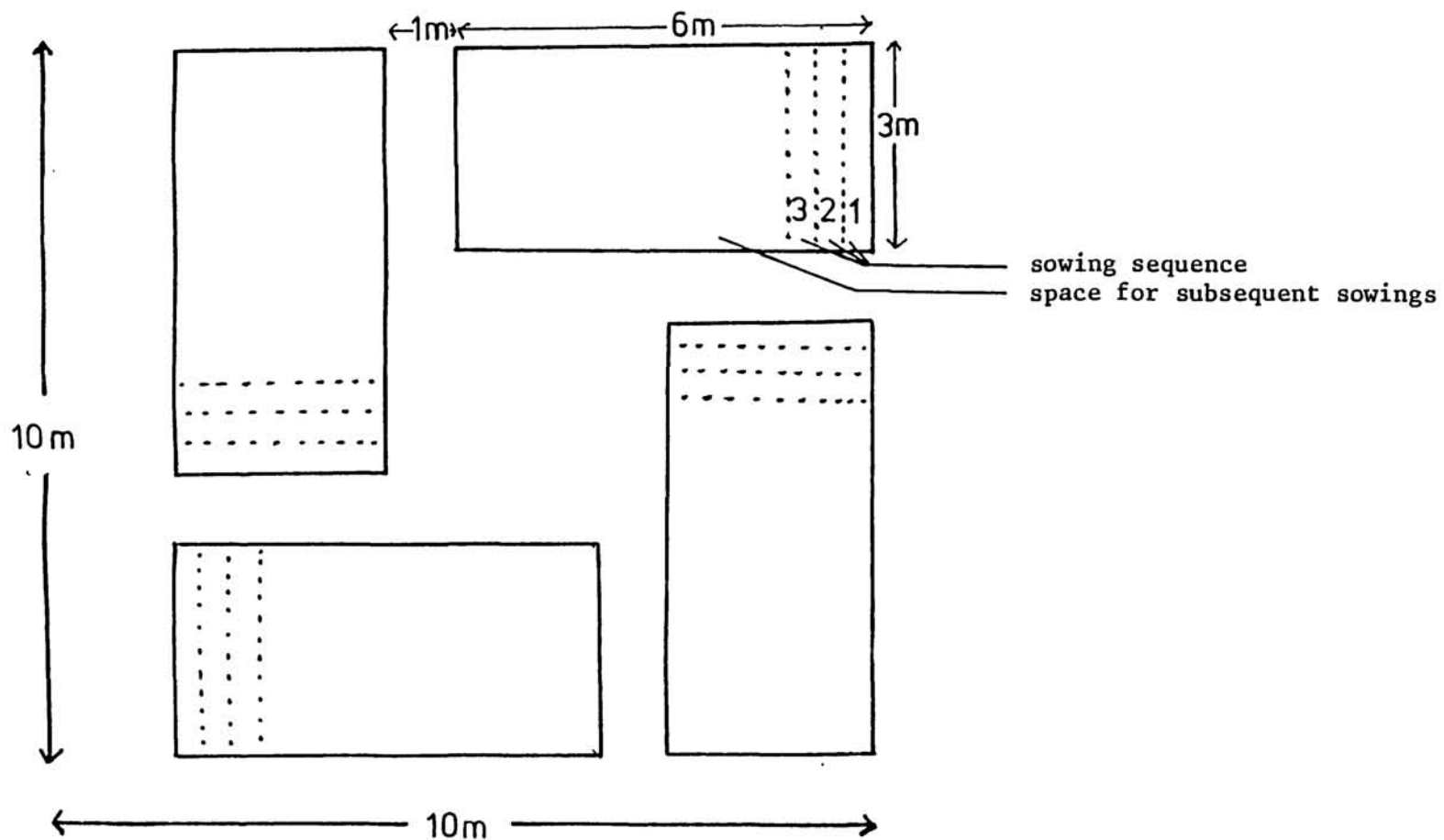


FIGURE 11: Development of natural colonists on winter wheat-plot plan - experimental layout.

Aphids were counted on all seedlings at intervals of 1 - 4 days during November and 1 - 10 days in December and January until all aphids had died. White plastic plant labels were pressed into the soil beside infested plants to aid relocation on later counts. These methods were considered preferable to random sampling on large plots which would suffer unacceptable sampling errors once overwintering populations had declined to low levels. A similar approach has been used by Joyce (1938) and Davies (1932) to study movement of aphids between potato plants.

In addition to providing population estimates (Table 11), the 'search and mark' method enabled the progress and performance of individual colonies to be recorded. *R. padi* were sufficiently numerous for these records to be 'pooled' and mean estimates derived (Table 12). These values should be regarded as rough estimates rather than precise measures because they incorporate a number of errors. For example, the parameter '% larviposition' ignores reproduction by alates that alighted and departed between counts; 'number of progeny' ignores new individuals disappearing between counts; 'alate duration' is taken as the period between its first and last 'sighting'*

In the case of *S. avenae*, numbers of colonists were so low that these measures of performance were unlikely to be very accurate. Nevertheless, the estimates obtained have been included in the results section for comparison with *R. padi*. The performance of one *S. avenae* colony was so good that full details of its development are tabulated. (Table 13).

* If an alate, first recorded on day x, had disappeared on the next count (day y); alate duration = $\frac{y - x}{2}$. This assumes that aphids disappear on average half way through the period between counts.

2.4.3 RESULTS AND DISCUSSION

2.4.3.1. Population change in relation to weather (Table 11 Figure 12).

High maximum temperatures during the first half of November resulted in crop colonisation by alates, larviposition and the subsequent growth of progeny.

A fall in aphid numbers of both species (approximately 30%, Table 11, Figure 12) 4/11 - 8/11 coincided with heavy rain on 5/11 but a more substantial decline in *R. padi* (53% on the youngest plants; Table 11, Figure 12) 8/11 - 10/11 occurred in the absence of 'adverse' weather (Figure 12). A further reduction by 11/11 coincided with high winds on 11/11 (maximum gusts over 20m/s; Figure 12). Continuing strong winds until 15/11 were associated with further losses (from 24 to 17 *R. padi* on the youngest plants; Figure 12). On 18/11 the first frost of the winter was recorded without obvious effect on aphid numbers (Table 11, Figure 12). More frosts 27/11 - 6/12 were associated with a decline in the *R. padi* population but the steady nature of this change precludes a simple explanation of its lethal effect. Furthermore, *S. avenae* numbers remained stable over this period complementing observations made on artificial populations (Section 2.2.2.2b). Heavy rain (over 20mm; Figure 12) on 7/12 did not noticeably effect *S. avenae* and although *R. padi* declined from 9 to 5 individuals on the youngest plants (Table 11, Figure 12) between 29/11 - 9/12, numbers were too small to attach significance to the change. A sharp fall in *S. avenae* numbers (from 20 to 10 individuals on the youngest plants; Table 11, Figure 12) 13/12 - 16/12 surprisingly coincided with favourable weather; perhaps high temperatures (maxima over 5°C on 5 days; Figure 12) promoted dispersal. Their subsequent build up 16/12 - 20/12 (from 10 to 28 on the youngest plants) occurred when temperature maxima ranged between 5 and 10°C (Figure 12) and winds were very light (maximum gusts approximately 5 m/s; Figure 12).

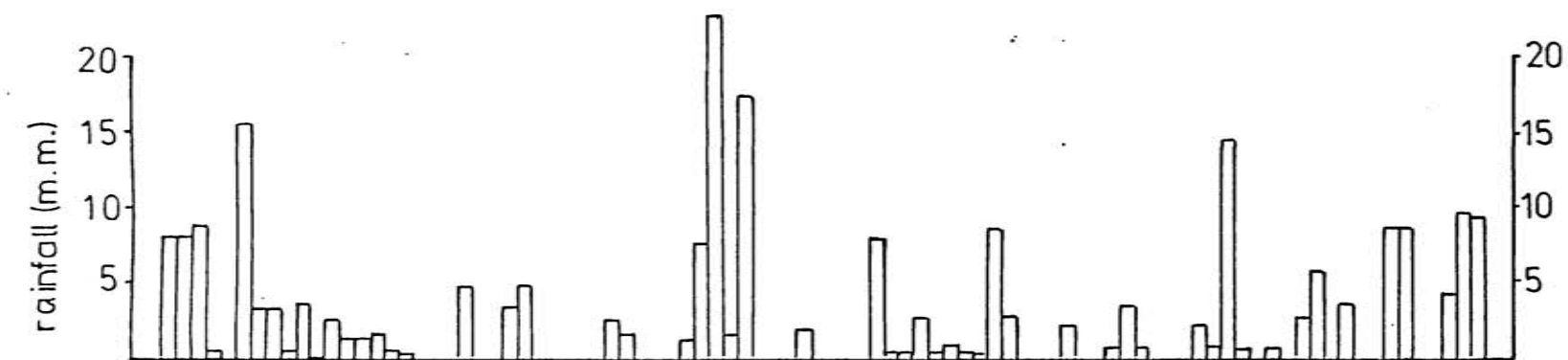
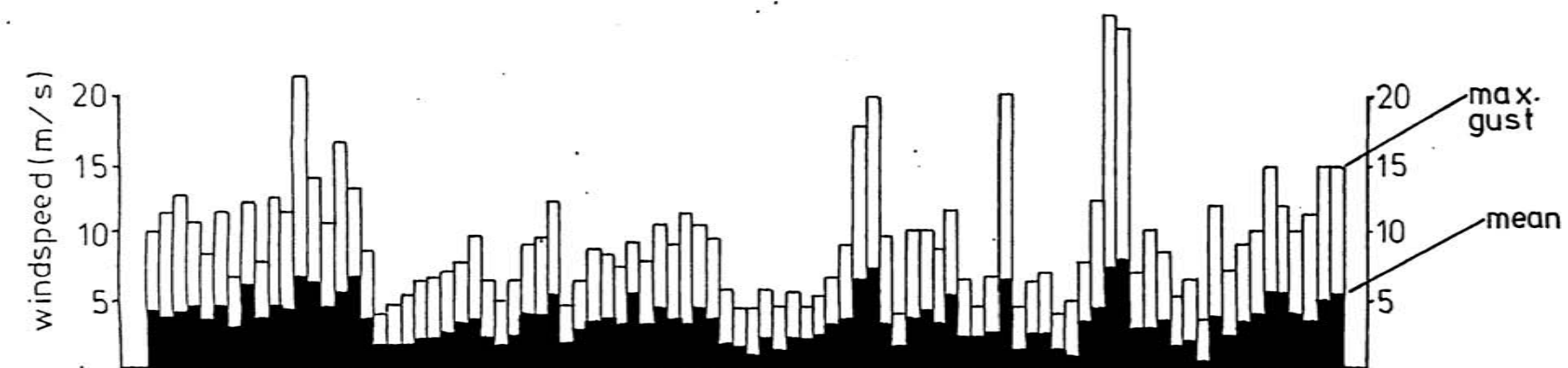


FIGURE 12 :

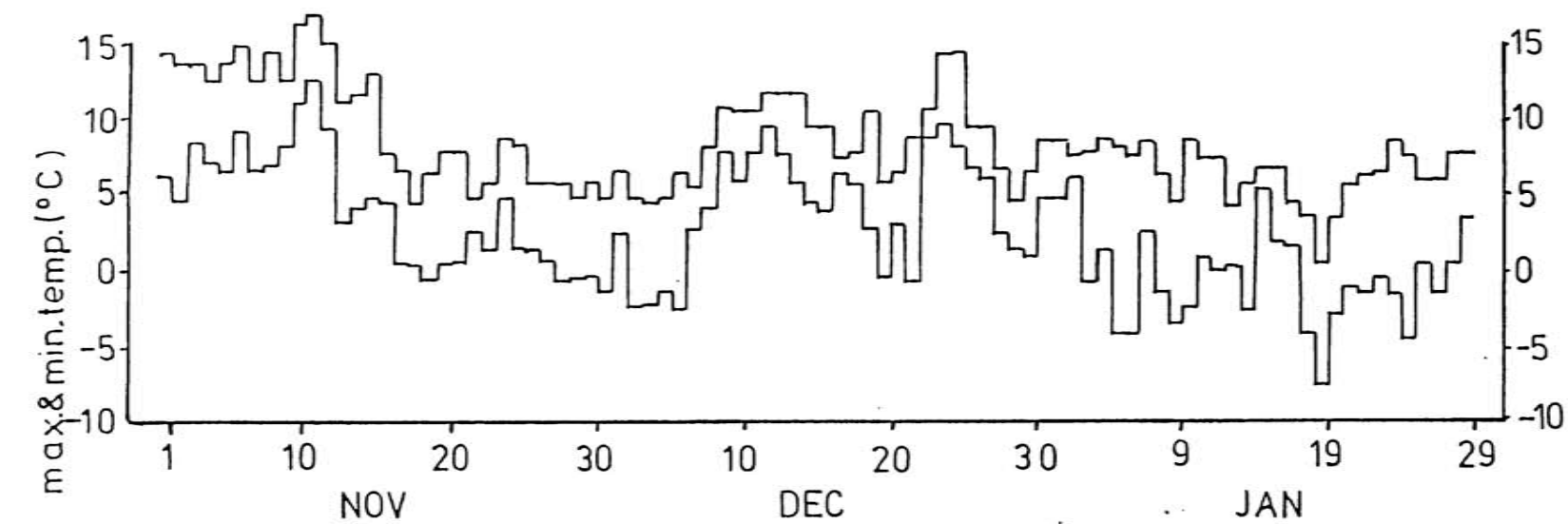


FIGURE 12: Abundance of aphids naturally infesting winter wheat in relation to weather - number of aphids in marked colonies on 4 plots.

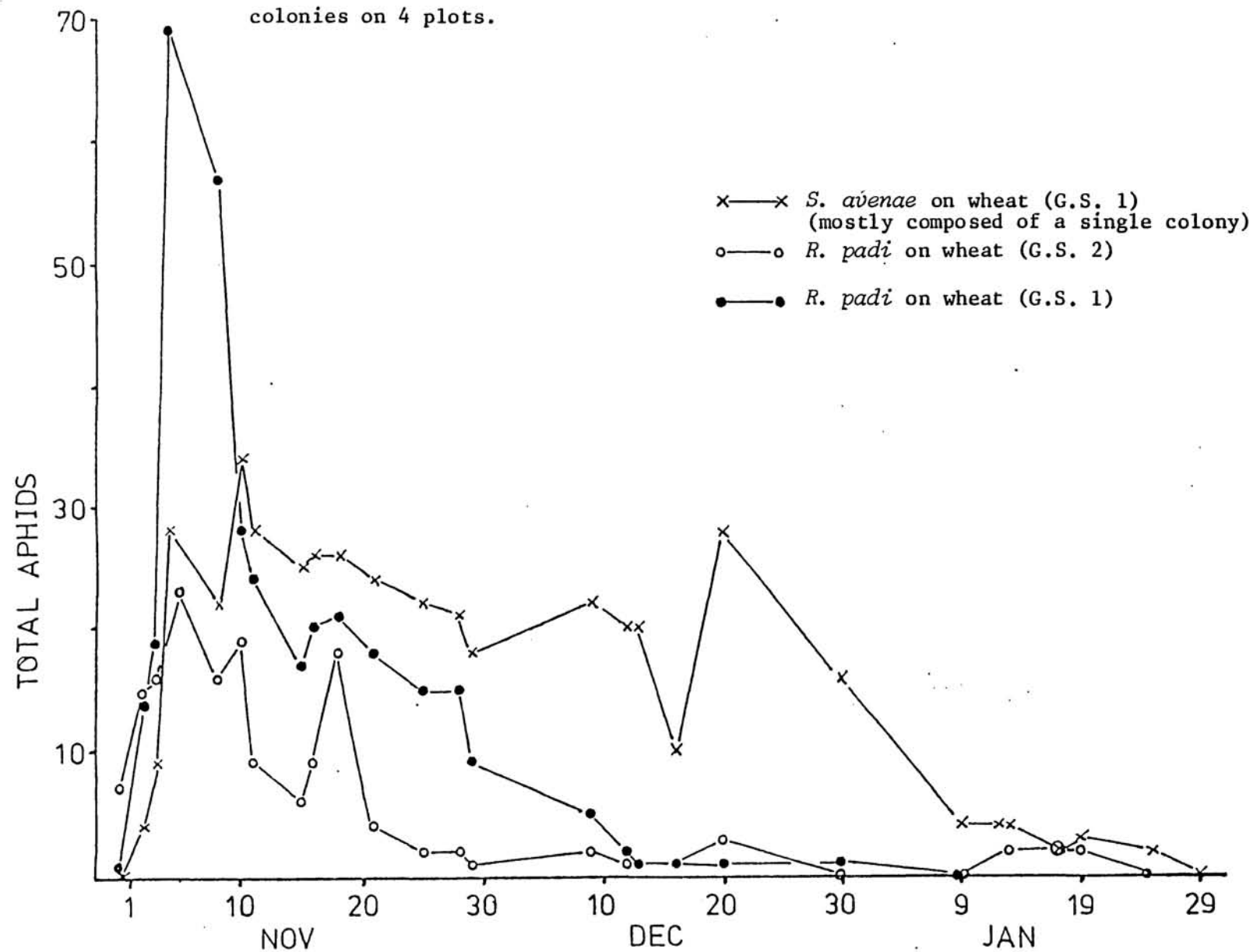


TABLE 11 : Abundance of naturally occurring cereal aphids (all stages) on winter wheat seedlings at 3 growth stages.

APHID SPECIES	<i>S. avenae</i>			<i>R. padi</i>		
SOW DATE	14/9	30/9	14/10	14/9	30/9	14/10
GROWTH STAGE*	3	2	1	3	2	1
CENSUS DATE						
31/10	0	1	0	0	7	1
2/11	1	1	4	5	15	14
3/11	1	4	9	1	16	19
4/11	1	9	28	2	23	69
8/11	0	5	22	0	16	57
10/11	0	5	34	0	19	27
11/11	0	3	28	0	9	24
15/11	0	2	25	0	6	17
16/11	0	2	26	0	9	20
18/11	0	2	26	0	7	21
21/11	0	2	24	0	4	18
25/11	0	2	22	0	2	15
28/11	0	2	21	0	2	15
29/11	0	2	18	0	1	9
9/12	0	1	22	0	2	5
12/12	0	0	20	0	1	2
13/12	0	0	20	0	1	1
16/12	0	0	10	0	1	1
20/12	0	0	28	0	3	1
30/12	0	0	16	0	0	1
9/ 1	0	0	4	0	0	0
12/ 1	0	3	4	0	0	0
13/ 1	0	4	4	0	2	0
17/ 1	0	3	2	0	2	0
19/ 1	0	3	3	0	2	0
25/ 1	0	1	2	0	0	0
27/ 1	0	0	0	0	0	0

* 'Feekes' Growth Stage (Large (1954)).

The return of high winds 23/12 - 24/12 (maximum gusts over 18 m/s; Figure 12) probably caused the losses recorded on 30/12 and 9/1 respectively (Table 11, Figure 12). By this time, there were just 4 *S. avenae* surviving and *R. padi* had all died.

2.4.3.2. *R. padi* colony development - overall estimates of performance

All the parameters used to estimate colony performance show a relationship with plant age. On the younger plants, alates settled in larger numbers and remained for a longer period of time (Table 12, Figures 13 and 14). More of them reproduced and the number of nymphs deposited was higher (Table 12, Figures 13 and 14). As a result aphid colonies were substantially more abundant on the younger plants (peak numbers on plants at growth stages 1, 2 and 3 were 69, 23 and 2 for *R. padi* and 34, 5 and 0 for *S. avenae* respectively; Table 11) and survival was better than on older sowings (i.e. on average, the longest surviving colony member passed through more moults; Figure 14).

Only a few individuals reached maturity and reproduced.

2.4.3.3. *S. avenae* colony development - detailed observations of a single colony

On average, *S. avenae* colonies were few in number, small in size and short lived compared to *R. padi* (Table 12). One colony, however was an outstanding exception to this general rule. (Table 13). When first recorded, the colony consisted of a single alate and 9 second instar progeny. By 8/11, 6 of these had become third instars and on 15/11, fourth instar were recorded. 6 individuals had become apterous adults by 21/11 but only 2 remained long enough to start reproduction on 20/12. 19 first instar progeny, recorded on 20/12 gave rise to 13 third instars on 30/12 but only 2 remained on 9/1. 16 days later these aphids had moulted to third instars but 2 days later these were missing.

FIGURE 13: Performance of *R. padi* on winter wheat at 3 growth stages (see text for details).

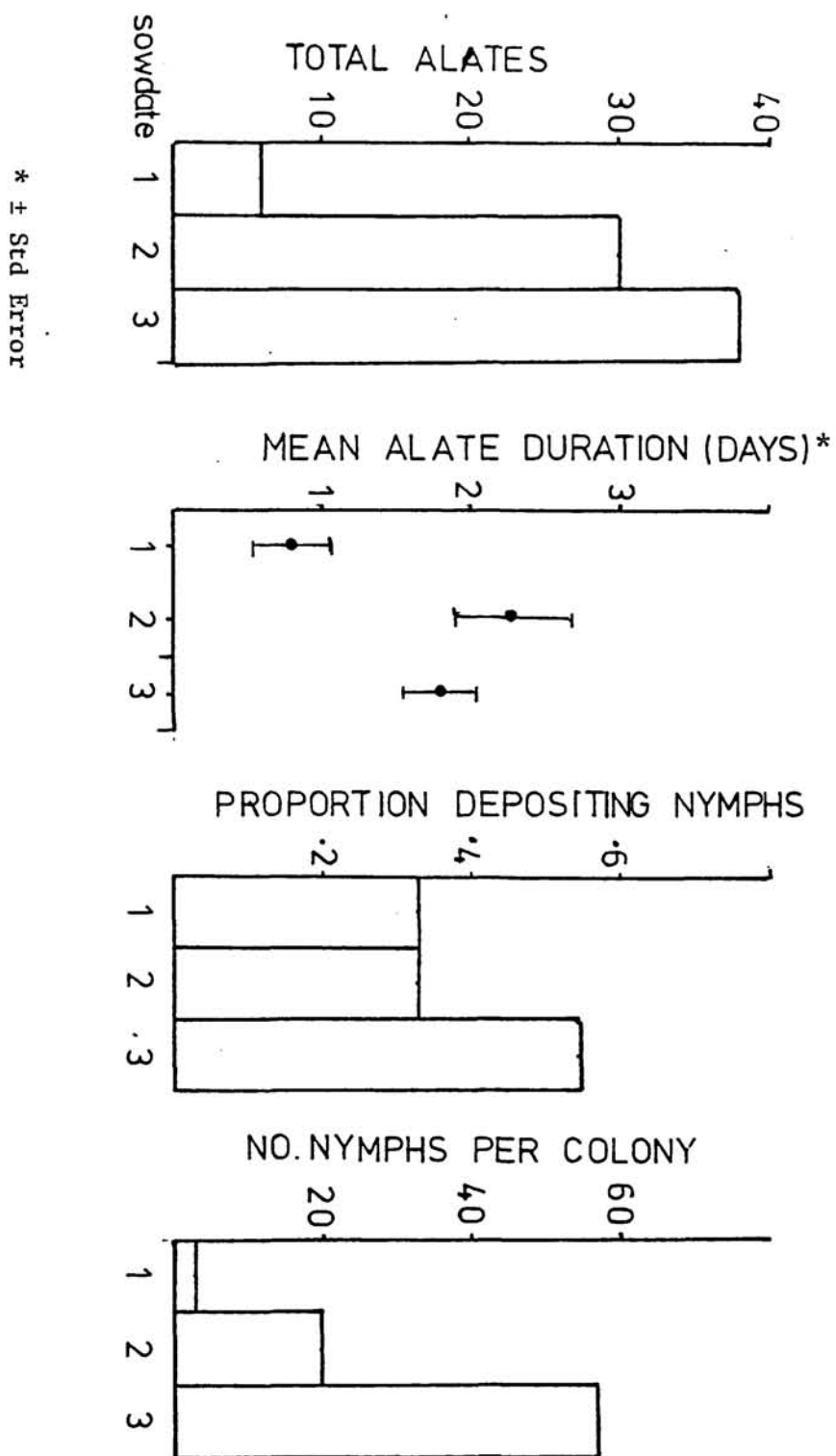


FIGURE 14: Performance of *R. padi* on winter wheat at 3 growth stages
(continued). Colony duration (see text and Table 12 for details).

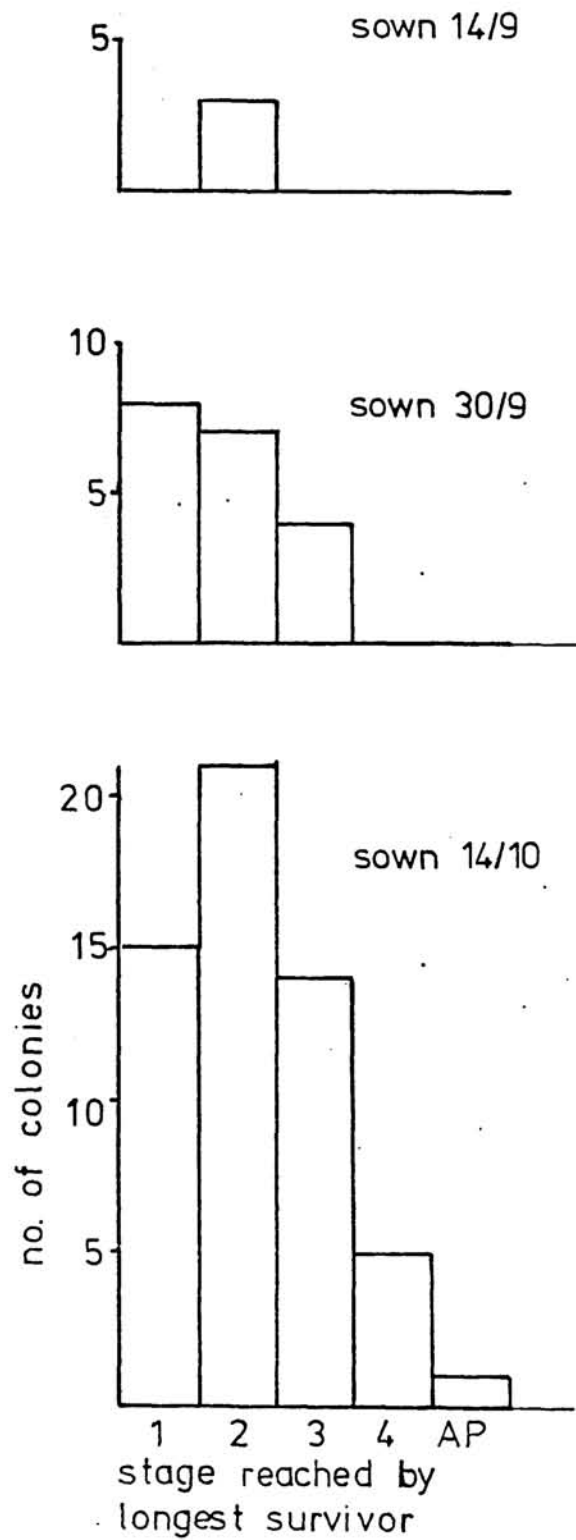


TABLE 12 : Performance of cereal aphids on winter wheat seedlings at 3 growth stages. - Autumn 1977 (a) *R. padi*

SOW DATE	REPLICATE	NO. ALATES	MEAN ALATE DURATION (DAYS $\pm$ STD. ERROR)	PROPORTION OF TAGGED ALATES DEPOSITING NYPHS	NO. NYMPHAL COLONIES [†]	MEAN NO. PROGENY PER COLONY ($\pm$ STD. ERROR)	COLONY DURATION*				
							I	II	III	IV	AP
<i>R. padi</i>	1 (14/9)	2	2.0	0.50	1	1.00	0	1	0	0	0
		2	0.5	0.33	2	1.00	0	2	0	0	0
		3	0.5	0.00	0	0.00	0	0	0	0	0
		4	0.0	0.00	0	0.00	0	0	0	0	0
		Total	6	0.80 $\pm$ 0.27	3	0.50	0	3	0	0	0
	2 (30/9)	1	1.75	0.50	2	1.00	0	2	0	0	0
		2	2.79	0.36	8	2.38	4	1	3	0	0
		3	1.06	0.22	8	1.13	3	4	1	0	0
		4	3.00	0.33	1	1.00	1	0	0	0	0
		Total	30	2.30 $\pm$ 0.40	19	1.60 $\pm$ 0.32	8	7	4	0	0
	3 (14/10)	1	2.10	0.33	4	2.00	1	2	1	0	0
		2	2.25	0.60	18	1.94	7	6	4	0	0
		3	1.63	0.50	21	1.48	2	7	7	4	1
		4	1.50	0.64	14	2.43	5	6	2	1	0
		Total	38	1.82 $\pm$ 0.24	57	2.00 $\pm$ 0.20	15	21	14	5	1

[†] Not necessarily derived from tagged alates.

* Derived from records of individual colony development; each colony catagorized according to the stage attained by its longest lived member, then number of colonies in each catagory tabulated.

TABLE 12 : Continued (b) - *S. avenae*

	SOW DATE	REPLICATE	NO. ALATES	MEAN ALATE DURATION (DAYS $\pm$ STD. ERROR)	PROPORTION OF TAGGED ALATES DEPOSITING NYMPHS	NO. NYMPHAL COLONIES [†]	MEAN NO. PROGENY PER COLONY ($\pm$ STD. ERROR)	COONY DURATION*				
								I	II	III	IV	AP
<i>S. avenae</i>	1 (14/9)	1	0	-	-	0	-	-	-	-	-	-
		2	0	-	-	0	-	-	-	-	-	-
		3	0	-	-	0	-	-	-	-	-	-
		4	0	-	-	0	-	-	-	-	-	-
		Total	0	-	-	0	-	-	-	-	-	-
	2 (30/9)	1	0	-	-	0	-	-	-	-	-	-
		2	1	1.00	0.00	1	1.00	0	0	0	0	1
		3	2	3.25	0.00	1	1.00	1	0	0	0	0
		4	2	4.00	0.50	3	1.31	0	2	1	0	0
		Total	5	3.00 $\pm$ 1.44	0.20	5	1.20 $\pm$ 0.20	1	2	1	0	1
	3 (14/10)	1	2	1.57	1.00	4	2.50	0	2	2	0	0
		2	1	2.00	1.00	6	1.00	0	3	3	0	0
		3	2	8.00	1.00	7	3.14	0	3	1	1	2
		4	2	4.00	1.00	5	1.80	3	1	1	0	0
		Total	7	3.64 $\pm$ 1.78	1.00	22	1.91 $\pm$ 0.70	3	9	7	1	2

[†] Not necessarily derived from tagged alates.

* Derived from records of individual colony development; each colony categorized according to the stage attained by its longest lived member, then number of colonies in each category tabulated.

TABLE 13 : Development of a single *S. avenae* colony during winter 1977-1978.

DATE	NO.S OF EACH INSTAR						TOTAL
	I	II	III	IV	AP	AL	
4/11		9				1	10
8/11		3	6			2	11
10/11	2	7	7			1	17
11/11	2	7	7			1	17
15/11	1		8	6		1	16
16/11	1		8	6		1	16
18/11	1		8	6		1	16
21/11		3	7		6		16
25/11		4	5		5		14
28/11		4	5		5		14
29/11		4	6		6		16
2/12		4	6		6		16
9/12		4	3	1	5		13
12/12		4	2	2	5		13
13/12		4	2	2	5		13
16/12				2	4		6
20/12	19			2	2*		23
30/12			13	1			14
9/ 1			2				2
12/ 1			2				2
13/ 1			2				2
16/ 1			2				2
17/ 1			2				2
19/ 1			2				2
24/ 1			2				2
25/ 1				2			2
27/ 1							0

* The disappearance of these aphids from the tagged plant is thought to be due to dispersal. One individual was found on an adjacent seedling 6 cm away on 30/12 but was missing on 9/1.

Although this probably marked the colony's extinction, some individuals may have dispersed from the tagged seedling and colonised new plants without being noticed. Factors that might have promoted dispersal include lower leaf senescence and the spattering of sandy soil onto foliage following soil erosion caused by rain.

2.5 INVESTIGATIONS ON THE EFFECT OF WIND ON APHIDS ON POTTED SEEDLINGS.

2.5.1 INTRODUCTION.

Field studies reported above (2.2 and 2.3) demonstrate the considerable importance of wind in reducing aphid populations during winter. To obtain a more thorough understanding of the causes of the losses incurred by *S. avenae*, experiments were carried out under controlled conditions, mostly using artificial wind sources.

In addition to considering key properties of wind (velocity and gustiness) and their interaction with other weather factors (low temperature), this work was concerned with the relative susceptibility of different aphid species, the possible long term adverse effects of wind and the influence of plant canopy structure on survival.

The general methods described below are supplemented by experimental notes accompanying the results of specific experiments.

2.5.2 GENERAL METHODS

In October 1978 winter wheat (c.v. Maris Kinsman) was sown in single rows in 5" plant pots, and left to germinate outside the glasshouse at natural temperatures. The growth form of the resulting seedlings closely resembled their counterparts sown in the field at Silwood Park. After thinning, each pot contained 5 young seedlings, 10 - 15 cm in height ('Feekes' growth stage 2 (Large 1954)).

The aphids used in the experiments were cultured at 20°C. A replicated experiment conducted at sub-zero temperatures (-1°C) showed no difference in the susceptibility of these insects compared to the cold cultured aphids used in field experiments. (Past treatment % survival on 4 replicates was as follows:- laboratory culture; 6.6, 6.0, 5.3, 8.0: cold conditioned culture; 12.2, 4.4, 9.2, 6.2).

Prior to each experiment, plants were brought into the laboratory

to be infested with 50-200 aphids per pot. After 24 hours they were transferred to an unheated glasshouse where they remained for at least 3 days to adjust to the experimental plants and new environmental conditions.

For most experiments, wind was provided by a motorised airblast sprayer (commonly known as a mist blower) (designed for crop spraying). Later this was substituted by an electrically driven fan which drove air into an unheated glasshouse through a 7cm diameter hose. Wind velocity was then controlled by placement of pots at measured distances from the wind source. In all experiments wind was directed at right angles to the rows of seedlings.

Aphid populations were counted before and after treatment and the proportion remaining calculated. The normality of these data was compared (c.f. Ryan and Joiner 1978) with arc sine transformed data and the data set most closely approaching normality was subjected to analysis of variance.

2.5.3 DESCRIPTION OF INDIVIDUAL EXPERIMENTS.

Experimental details including meteorological recordings are shown in note form with the relevant tables of results.

2.5.3.1 Effect of Wind Speed.

(a) Results and Discussion

Analysis of variance showed a highly significant effect of wind-speed on survival ($p > .01$). Losses at the lowest windspeed (3 m/s) were negligible, but winds of 8, 10 and 20 m/s caused increasingly heavy losses (Figure 15). However, survival levelled off at about 0.2 (Figure 15). Observations made during the experiment indicated that these survivors occupied basal feeding sites on the plants. In these positions aphids were probably protected from being dislodged directly by wind as well as from the shearing action between leaves also caused

FIGURE 15: Effect of wind speed on *S. avenae* (survival $\pm$ 95% confidence limits).

Experimental Details

Weather - Light rain, 5.5°C, calm

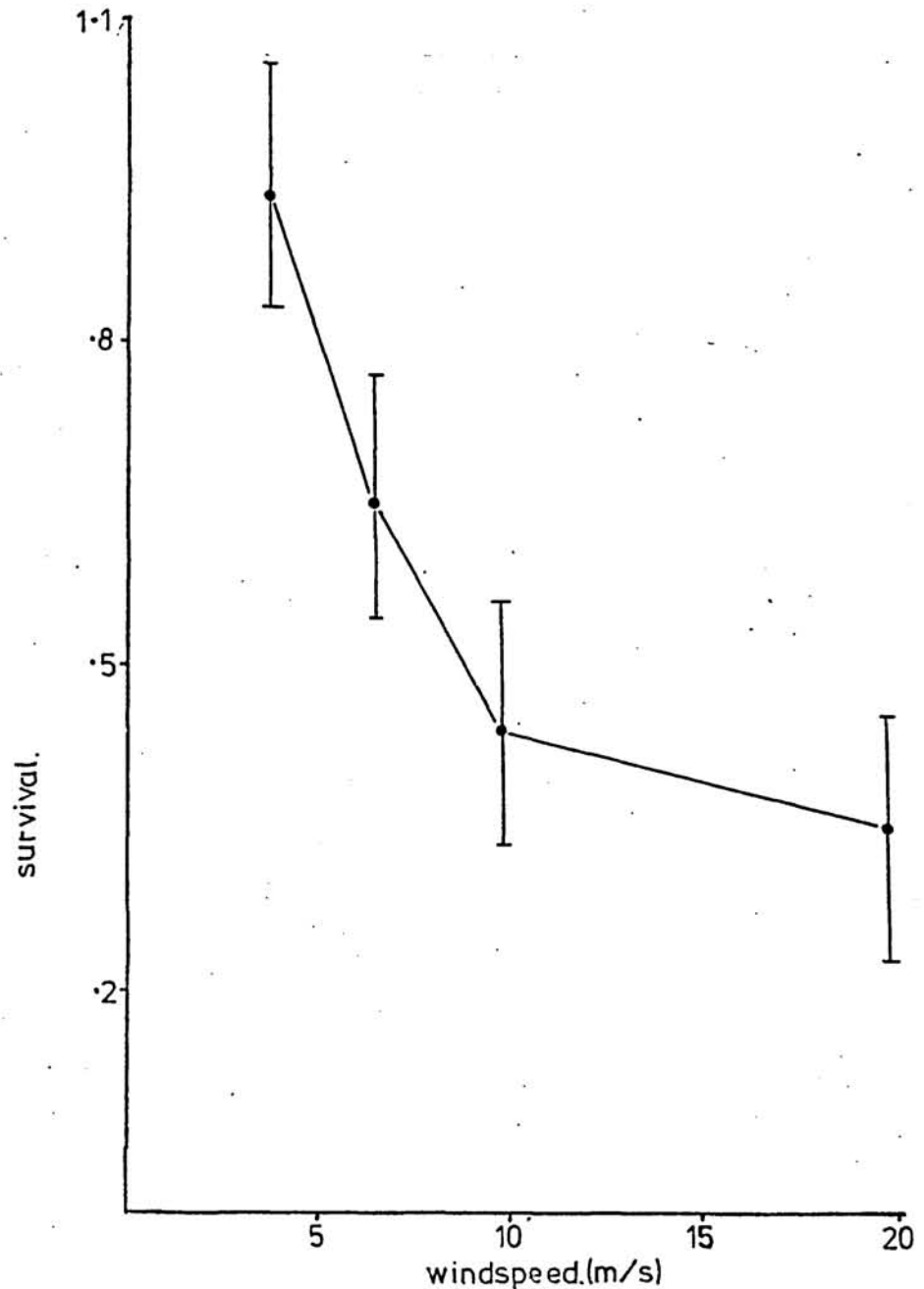
Layout - plants randomly arranged on a 4 x 4 grid

Duration of artificial wind - 5 minutes shared equally between 4 rows of pots.

Statistical Analysis

Data transformation - none

Analysis of variance - F test for treatment effects highly significant ($p < .01$). No significant effect of aphid size (large or small).



by wind. Small aphids survived better than large, but the difference was not statistically significant.

2.5.3.2 Continuous versus gusty wind.

(a) Introduction

This experiment aimed to test the hypothesis that interrupted wind might dislodge more aphids than continuous wind due to increased shearing action between leaves.

(b) Results and Discussion.

According to analysis of variance, wind gustiness and aphid size significantly influenced survival ($p < .01$). There was no significant interaction between these factors (Table 14).

The higher survival shown by small aphids is consistent with results obtained in the previous experiment (Section 2.5.3.1) where the effect was too weak to attain statistical significance. Perhaps small aphids rest sufficiently close to leaf surfaces to partially evade the shearing effect of moving leaves. T. tests based on pooled standard deviation show a significant difference between continuous wind and the two 'gusty' treatments ($p < .05$) but no difference between levels of gustiness (Table 14).

The experiment demonstrates clearly the importance of gusty wind but possibly underestimates the magnitude of its effect in the field because the 'continuous' windstream produced experimentally was not entirely free of turbulence. First, air leaving the mist blower fluctuated in velocity and secondly intermittent natural wind may have disturbed the velocity of artificial wind.

2.5.3.3. Comparative susceptibility of 3 aphid species.

(a) Introduction

To compare the susceptibility of *S. avenae*, *M. dirhodum* and *R. padi*

TABLE 14 : Effect of continuous versus gusty wind on *S. avenae*. - proportion surviving.

Experimental Details

Weather - Dry, 5°C, moderate wind.

Layout - Each pot of plants individually subjected to wind blast in random order.

Wind speed 8 m/s

Duration of artificial wind - 2 minutes

Statistical Analysis

Data transformation - none

Analysis of variance F test significant for treatment effects and for the differing response of the 2 aphid size classes ($p < .01$). No significant interaction.

APHID SIZE	WIND GUSTINESS			ROW MEANS
	Continuous	10 Interuptions/minute	50 Interuptions/minute	
Large	.1467	.0614	.0394	.0825
Small	.2732	.1336	.2107	.2058
Column Means	.2100	.0975	.1250	.1442

FIGURE 16 : Effect of wind in relation to aphid size and species (mean survival $\pm$ 95% confidence limits). (A) following first windblast (5 m/s); (B) following second windblast (8 m/s).

Experimental Details

Weather records - Dry, -1.5°C , moderate wind (< 6 m/s)

Layout - pots arranged in a line at random

Artificial wind speed - 5 m/s (windblast 1.), 8 m/s (windblast 2)

Duration - 5 minutes (all pots)

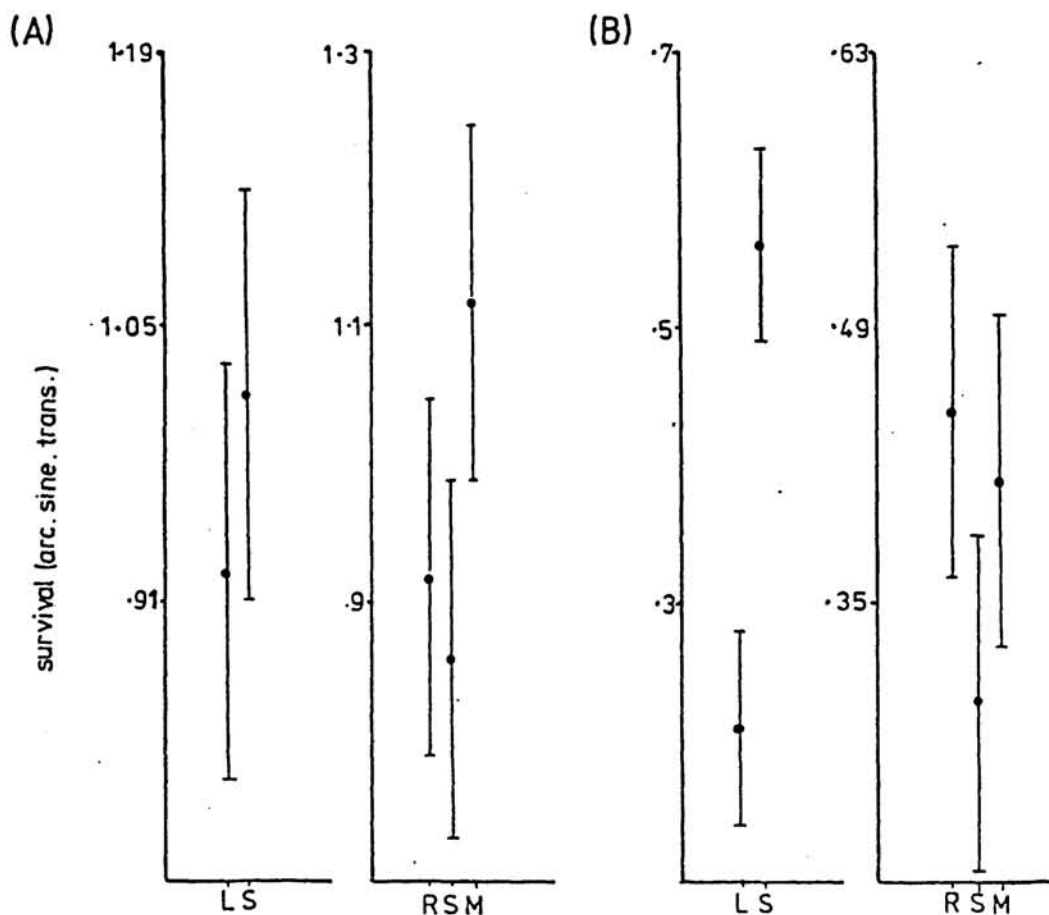
Statistical Analysis

Transformation - arcsine $\sqrt{x}$

Analysis of variance - F test for treatment effects significant for windblast 1; F test for aphid size significant for windblast 2; other F tests not significant.

L = large } Aphid size
S = small }

R = *R. padi* } Aphid species
S = *S. avenae* }
M = *M. dirhodum* }



separate colonies were subjected to 2 consecutive 5 minute periods of wind. During the first period a windspeed of 5 m/s was used and this was increased to 8 m/s for the second period.

(b) Results and Discussion

Following the first windblast more large aphids were dislodged than small (Figure 16) but this difference was not statistically significant. After the second windblast, the difference was highly significant ($p < .01$).

The first period of wind reduced *S. avenae* significantly more than the 2 other aphid species (Figure 16). Its losses were also greatest following the second period of wind but the difference was no longer statistically significant. *M. dirhodum* responded very differently to the 2 windblasts, only the second, stronger winds causing appreciable loss. *R. padi* responded similarly to *M. dirhodum* but its losses were more evenly spread between the 2 periods (Figure 16).

S. avenae more commonly infest the terminal parts of wheat seedlings than the other 2 species. These are probably the most exposed parts of wheat seedlings so these individuals are, perhaps easily dislodged by wind.

2.5.3.4. Influence of Aphid feeding site on susceptibility.

(a) Introduction

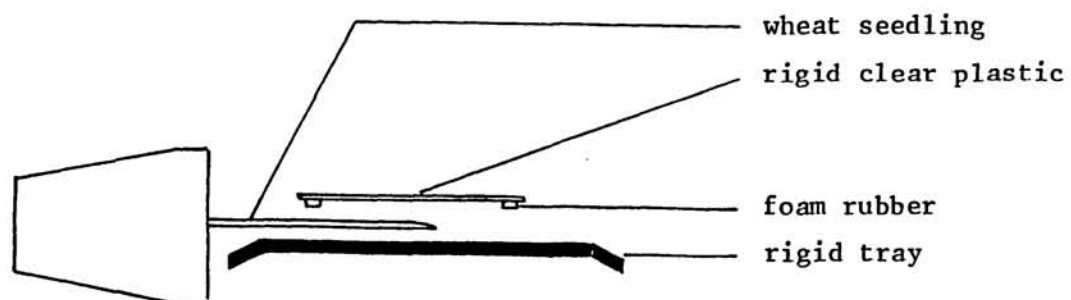
The previous experiment (Section 2.5.3.3) showed that *S. avenae* was more readily dislodged from plants than *M. dirhodum* or *R. padi*. There are 2 main possible explanations of this difference.

a) greater tenacity of *M. dirhodum* and *R. padi*.

b) lower feeding sites of *M. dirhodum* and *R. padi* reducing their losses due to less shearing action of moving leaves.

The present experiment aimed to test the importance of feeding site

FIGURE 17 : Method used to restrict *S. avenae* to basal or terminal feeding sites on wheat seedlings.



NB. After local infestation, separation was maintained by pushing the rigid clear plastic against the tray using rubber bands.

by comparing the losses of *S. avenae* from basal and terminal parts of plants. Aphids were confined to these feeding sites using the method illustrated in Figure 17.

(b) Results and Discussion

Aphids infesting terminal parts of wheat seedlings suffered losses, almost 4 times as heavy as their counterparts lower down the plant ($p < .01$) (Table 15). The 2 aphid size classes responded similarly to treatment.

2.5.3.5 Effect of prolonged exposure to freezing natural winds.

(a) Introduction

The experiments described so far have been concerned with the straightforward 'acute' effect of wind, dislodging aphids from plants. Although this probably accounts for substantial mortality during winter, additional losses possibly occur through wind acting in more subtle ways.

- e.g. a) by damaging the host plants forcing aphids to move to new feeding sites.
- b) by restricting aphids to sheltered niches that are nutritionally inadequate.
- c) by enhancing the chilling effect of low temperature.
- d) by increasing dessication when temperatures are too low for aphids to feed.

A period of strong freezing winds in February provided the opportunity to test the possible importance of enhanced chilling as a cause of aphid death. 18 infested pots of seedlings were placed in an exposed location and batches of 3 pots returned to the unheated glasshouse at intervals over a 4 hour period.

(b) Results and Discussion

The reduction in aphid numbers occurring over a 4 hour period can be

TABLE 15 : Influence of feeding site on susceptibility - proportion surviving.Experimental DetailsWeather - Dry, 7°C, light wind (max. gust = 4 m/s)Layout - pots arranged in a line at random.Wind speed 8 m/sDuration of artificial wind - 5 minStatistical AnalysisData transformation - none

Analysis of variance 'F test' showed highly significant effect of treatment ($p < .01$), no effect of aphid size and no interaction.

FEEDING SITE	LARGE	SMALL	ROW MEANS
Terminal	.184	.293	.239
Basal	.933	.883	.908
Column Means	.559	.588	.594

accounted for mainly by those dislodged within the first 5 minutes. (Table 16). According to analysis of variance, the additional losses incurred after 1 hour (approximately 8%) cannot be considered significant ($p = .05$) but the observation of dead aphids on the '2 hour' and '4 hour' treatments suggest that additional mortality did occur over this period.

Although the dead aphids observed were few in number and their contribution to overall losses insignificant, the possible importance of enhanced chilling in the field needs to be emphasised. In nature, aphids are exposed to winds that are stronger, colder and longer in duration than those used in the present experiment and this form of mortality may be important to survival of aphids located in niches that protect them from being dislodged by wind.

2.5.3.6. Further experiment on the effect of prolonged wind.

(a) Introduction

Following the previous experiment (Section 2.5.3.5), the present work aimed to study the consequences of wind lasting for more than 4 hours. A continuous airstream was directed into an unheated glasshouse by an electrically driven fan that could be conveniently left running for several weeks. Unreplicated pots of plants, infested with *S. avenae* were placed at intervals from the wind source to obtain a gradation of windspeeds. At 0.5m strong winds (18 m/s) were recorded but these decayed rapidly with distance such that 'acute' losses were likely to be negligible at 2.5m (3.5 m/s)(c.f. previous experiments). A 'control' pot of plants was placed in the same glasshouse adjacent to the airstream. Aphid losses after 3 minutes corresponded to the 'acute' effect of wind investigated in previous experiments. Any subsequent mortality over the next 4 weeks would represent the 'chronic' effect of wind. Wind temperature was monitored by a maximum - minimum thermometer placed close to the fan inlet, outside the glasshouse (Table 17).

TABLE 16 : Effects of prolonged exposure to freezing natural winds.Experimental DetailsWeather Records (using 'Wallac' thermo-anemometer)

a) Wind speed (max. gust for 8 consecutive minutes (m/s)

11.30 hours 6, 4, 6, 3, 3, 2, 4, 3 ($\bar{x}$ = 3.9)14.15 hours 3, 3, 5, 4, 7, 5, 4, 5 ($\bar{x}$ = 4.5)b) Temp ($^{\circ}$ C) 11.30 hours - 1.5, 14.15 hours - 1.0Layout - pots placed at random in an east-west line at right angles to northerly wind.Statistical AnalysisTransformation - arc sine $\sqrt{x}$ Analysis of variance F test not significant

EXPOSURE DURATION	% SURVIVAL		
	LARGE APHIDS	SMALL APHIDS	ROW MEANS
5 min	10.67	24.43	17.55
15 min	17.00	24.70	20.85
30 min	10.30	23.43	16.87
1 hour	13.10	21.80	17.45
2 hour*	5.20	12.47	8.84
4 hour†	7.02	17.43	12.21
Column Means	10.55	20.71	15.63

* 4 dead aphids (21 live)

† 3 dead aphids (17 live)

(b) Results and Discussion

After 3 minutes, aphid populations were reduced in proportion to windspeed (Figure 18). Little additional loss was recorded after 30 minutes, probably because insects surviving the initial blast of wind occupied protected niches on the plant. During the next 11 days, the 2 highest windspeeds resulted in total loss of aphids, due partly to the damage inflicted by wind on the host plants. Leaves appeared to lose the waxy surface layers leading to wilting and necrosis. Aphids exposed to 6 m/s winds also declined over this period but appeared to reach equilibrium at 9 surviving individuals. In contrast, aphids exposed to slower winds increased in numbers. The population exposed to 3.5 m/s winds fully recovered from its 'acute' losses at the start of the experiment (Figure 18). This evidence of reproduction, supplemented by observations of nymph deposition after day 4 is not surprising in view of the high temperature maxima recorded over the period (e.g. 10°C on day 5; Table 17). It is noteworthy, however, that low minimum temperatures were recorded over the same period illustrating the ability of aphids to reproduce during short periods of warm weather. Furthermore, it is significant that no appreciable losses (Figure 18) were recorded following nights of frost (e.g. days 5, 11, 20 and 29; Table 17).

Reproduction on 'control' plants caused rapid growth in aphid numbers but this was partly offset by departure of alates. The rate of increase shown by this population is not strictly comparable with aphids placed in the airstream due to the build up of temperatures in the wind-free parts of the glasshouse.

The experiment failed to confirm the suggestion that aphids might be killed directly by the combination of frost and wind but this cannot be ruled out at this stage. During the experiment, frosts were neither severe nor prolonged and the passage of air through a hose from the fan must have raised temperatures slightly.

FIGURE 18: Effect of prolonged wind in relation to windspeed on *S. avenae*.

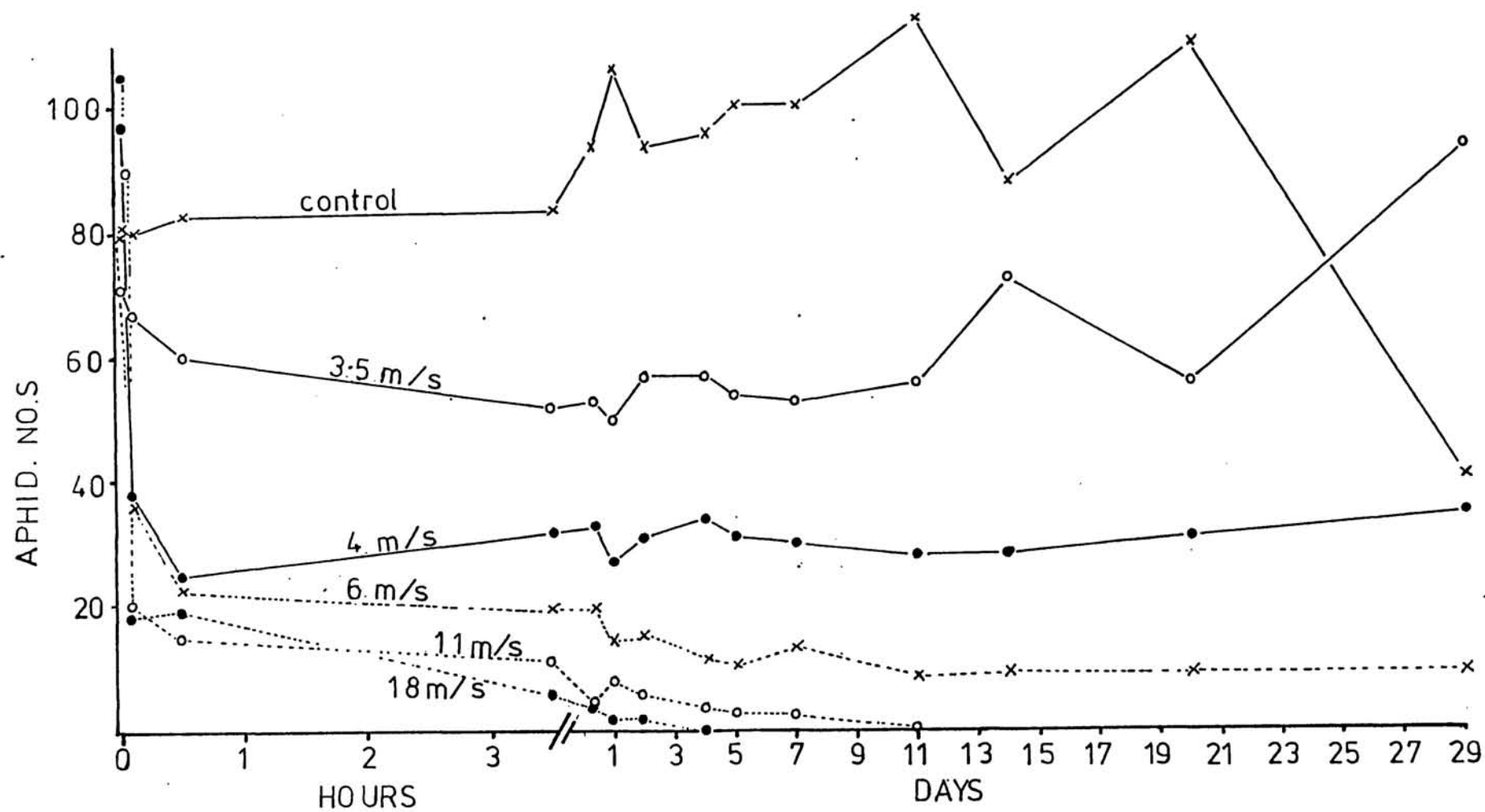


TABLE 17 : Effects of prolonged wind in relation to wind speed - temperature maxima and minima ($^{\circ}\text{C}$).

	DAY NO.									
	8 HR	1	2	4	5	7	11	14	20	29
MAX	1.5	1.0	1.0	4.8	10.0	9.0	13.0	11.0	12.0	15.0
MIN	1.0	0.0	0.0	0.0	- 1.5	3.0	- 0.5	1.0	- 1.5	- 1.0

Mortality following wind induced plant damage (destruction of the wax layer leading to wilting and necrosis) was another chronic effect of wind that was clearly highlighted by the experiment. The availability of niches on the plant protected from the direct effects of wind are limited: plant damage due to wind limits these still further.

2.5.3.7. Effect of prefreezing on susceptibility

(a) Introduction

In the course of field counts (Section 2.3.2.5) aphids were sometimes found hanging by their stylets from plants during freezing weather. This raised the possibility that these aphids might differ in their susceptibility to the acute effects of wind, compared with unfrozen insects. A simple experiment aimed to test this hypothesis. Preliminary studies showed that an infested pot of seedlings could be placed in a 'deep freeze' for 5 or 10 minutes in order to freeze aphids on the plants without causing aphid mortality or plant damage. Experimental pots of infested plants were frozen in this way for 7 minutes and immediately subjected to wind at 0.5°C for 2 minutes. Frozen aphids remained in the immobilised state throughout the test period.

(b) Results and Discussion

Losses of frozen aphids did not differ from unfrozen 'controls' and there was no difference in the susceptibility of large and small aphids (Table 18)

2.5.3.8 Effect of plant density on susceptibility

(a) Introduction

An earlier comparison between the effects of continuous and gusty wind (Section 2.5.3.2) raised the possibility that the shearing action between moving leaves was a prime cause of 'acute' aphid losses. The present experiment tested this hypothesis by comparing losses at 3 plant densities. Plants sown at the lowest density were too widely spaced

TABLE 18 : Effect of prefreezing on susceptibility of *S. avenae* to wind action.Experimental DetailsAir temperature - 0.5°CWind source electric fan directed into glasshouse.Wind speed 6 m/sWind duration 2 minutes.Layout pots placed in airstream sequentially at random.Statistical AnalysisTransformation - noneAnalysis of variance - no significant F tests.

	PROPORTION SURVIVING		
	Large Aphids	Small Aphids	Row Means
20°C Aphids	.64	.71	.675
Frozen Aphids	.66	.67	.665
Column Means	.650	.690	.670

for contact to occur, so aphids infesting these plants could not be dislodged by mutual contact between leaves. The densities chosen corresponded approximately to the recommended seedling densities associated with three distinct cereal growing systems (Whittles 1975): conventional, 'Schleswig - Holstein' and 'Laloux'. Because wheat seedlings give rise to approximately two established tillers (MAFF, 1977), seedling densities used experimentally (Table 19) were roughly half the 'recommended tiller densities' quoted by Whittles (1977).

The single stem seedlings were arranged in 2 rows in 30 x 20cm seed trays and the experiment was unreplicated. Each infested tray of plants was subjected to 2 five minute periods of wind (4 m/s followed by 11 m/s) produced by electric fan (as in previous 2 experiments).

(b) Results and Discussion

Aphids on the sparse sowing survived more than 10% better than insects on densely sown plants (Table 19) and although firm conclusions cannot be drawn from this unreplicated experiment, differences may be attributable to the lack of mutual contact between plants.

The intermediate losses observed on the densest sowing can perhaps be explained on the grounds that very dense seedlings benefit from considerable mutual support that increases stability and reduces wind speed and shearing action between leaves.

TABLE 19 : Effect of plant density on susceptibility

Experimental Details

Air temperature - 12°C

Wind source - electric fan directed into glasshouse

Wind speed - 4 m/s (windblast 1), 11 m/s (windblast 2)

Wind duration - 5 minutes

SYSTEM OF CULTIVATION SIMULATED IN EXPERIMENT	RECOMMENDED* TILLER DENSITY/m ²	DERIVED [⊕] PRE-TILLERING SEEDLING DENSITY/m ²	NO. SEEDLINGS PER 20 cm ROW	PRE-TREATMENT APHID NOS. PER SEEDLING	% SURVIVAL	
					Following First Windblast	Following Second Windblast
'Laloux'	190-220	103	2	8.5	97.06	64.71
'Schleswig-Holstein'	400-480	220	4	9.9	79.75	40.51
Conventional	880	440	16	7.8	82.80	51.12

* Whittles 1977

⊕ MAFF 1977

2.6 SURVIVAL OF DISLODGED APHIDS.

2.6.1 INTRODUCTION

Most of the experiments reported in the previous section relate to the ability of wind to dislodge aphids from their host plants. Although dislodgement does not constitute mortality, field observations suggested that dislodged *S. avenae* usually failed to colonise new plants (very few individuals were found on field wheat seedlings adjacent to exposed experimental plants). Low winter temperatures, limiting aphid movement possibly account for this.

Once isolated from their host plants, aphids build up a water and nutrient deficit which may ultimately cause death. At ground level in winter, they run the risk of being consumed by a wider spectrum of predators such as ground beetles and spiders than on the foliage and rain combined with soil erosion may cause injury and burial.

The following experiments investigated first, the capacity of aphids to move at low temperatures and second, the influence of temperature and humidity on survival.

2.6.2 MATERIALS AND METHODS

2.6.2.1 Mobility in relation to temperature.

Groups of 10 *S. avenae*, freshly removed from wheat seedlings were placed in a small glass beaker (diameter - 5cm, height 4 cm) floating inside an insulated flask (Figure 19). The flask was almost filled with an ethanol/water/ice mixture previously prepared to a required temperature. After a 15 minute equilibration period each aphid was probed with a fine paintbrush and the number capable of sustained movement recorded.

2.6.2.2 Mortality in relation to temperature and humidity.

Aphids confined in 1" plastic specimen tube caps were placed inside airtight plastic containers (Figure 20) to control humidity. The inclusion

FIGURE 19 : Method used to study aphid movement at low temperature.

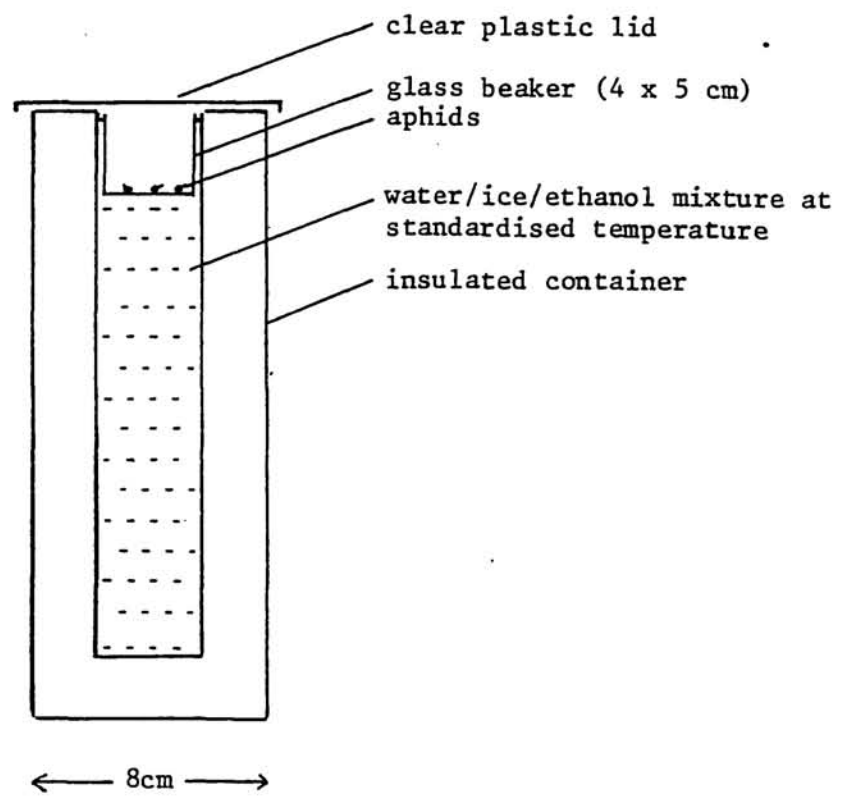
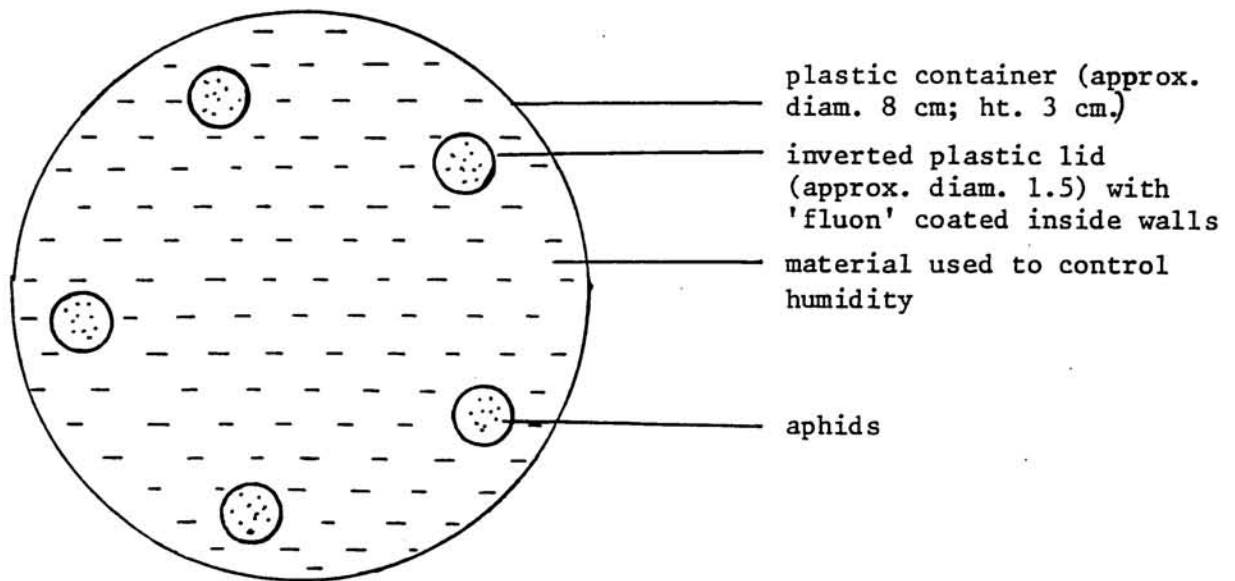


FIGURE 20 : Method used to study aphid survival in relation to temperature and humidity.



of phosphorus pentoxide, saturated sodium chloride solution or distilled water controlled humidity at 0%, 70% and 100% respectively, independent of temperature (Spencer, 1926). Containers were maintained at one of 4 temperatures in constant environment rooms and survival monitored until all aphids had died.

2.6.3 RESULTS AND DISCUSSION

2.6.3.1 Mobility in relation to temperature.

At 3°C, all aphids were capable of movement (Figure 21). As the temperature was lowered an increasing proportion of first instars became immobilised until at -1°C none were capable of walking. Much lower temperatures were required to prevent movement of fourth instars, presumably due to their relatively low surface area: volume ratio conferring partial independence from ambient temperatures through better conservation of metabolic heat. Only temperatures of -4°C or below resulted in their complete immobilisation.

Seemingly aphids in the field would not normally be prevented from recolonising plants by quite low temperatures. During periods of exceptionally prolonged frost, delay in recolonisation would not necessarily result in mortality, due to the reduced metabolic demand of frozen insects.

2.6.3.2 Mortality in relation to temperature and humidity.

The longevity of isolated aphids was negatively correlated with temperature, insects kept at 5°C living approximately 4 times as long as at 20°C (Figures 22 and 23; Tables 20 and 21). Humidity was relatively unimportant except in the case of aphids kept at 5°C where survival of fourth instars was considerably prolonged at 100% R.H.

The effects of temperature and aphid size can be explained on the basis of the more rapid depletion of energy reserves at higher temperatures and the possession of relatively large quantities of reserves by fourth instar aphids compared with the firsts.

FIGURE 21 : Proportion of aphids capable of movement in relation to temperature.

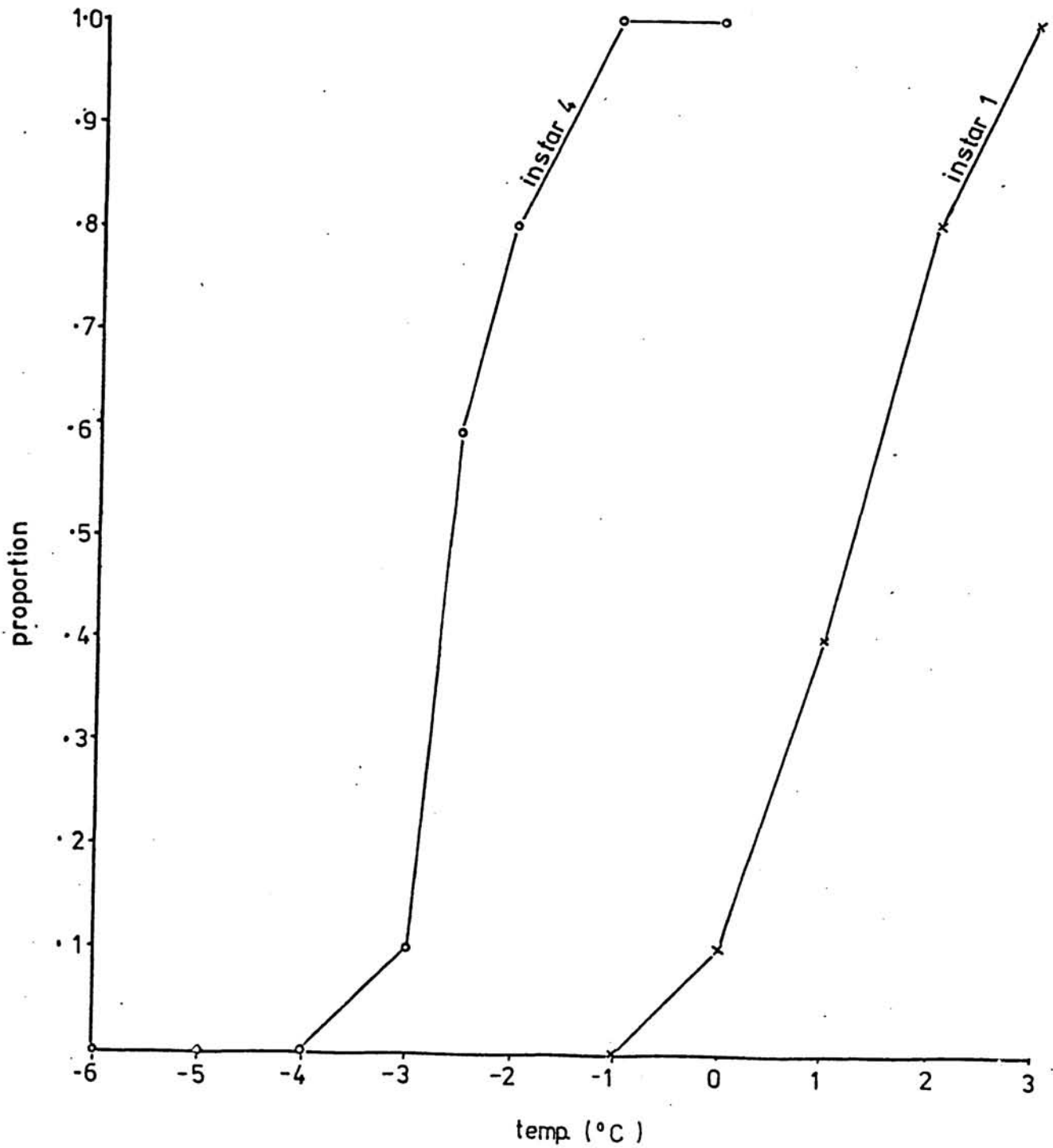


FIGURE 22: Survival of starved 4th instar *S. avenae* in relation to temperature and humidity (expressed as mean survival period in hours).

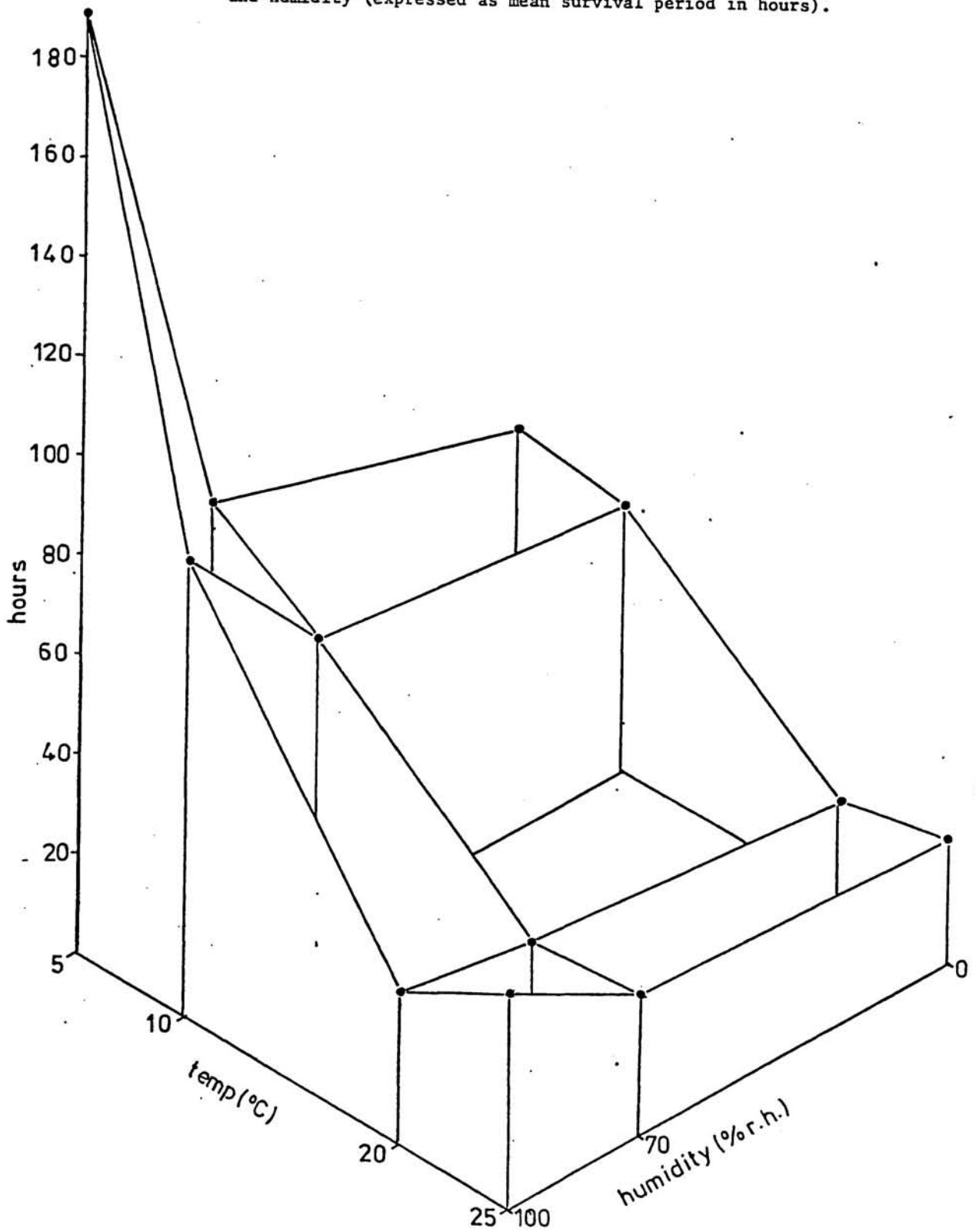


FIGURE 23: Survival of starved 1st instar *S. avenae* in relation to temperature and humidity (expressed as mean survival period in hours).

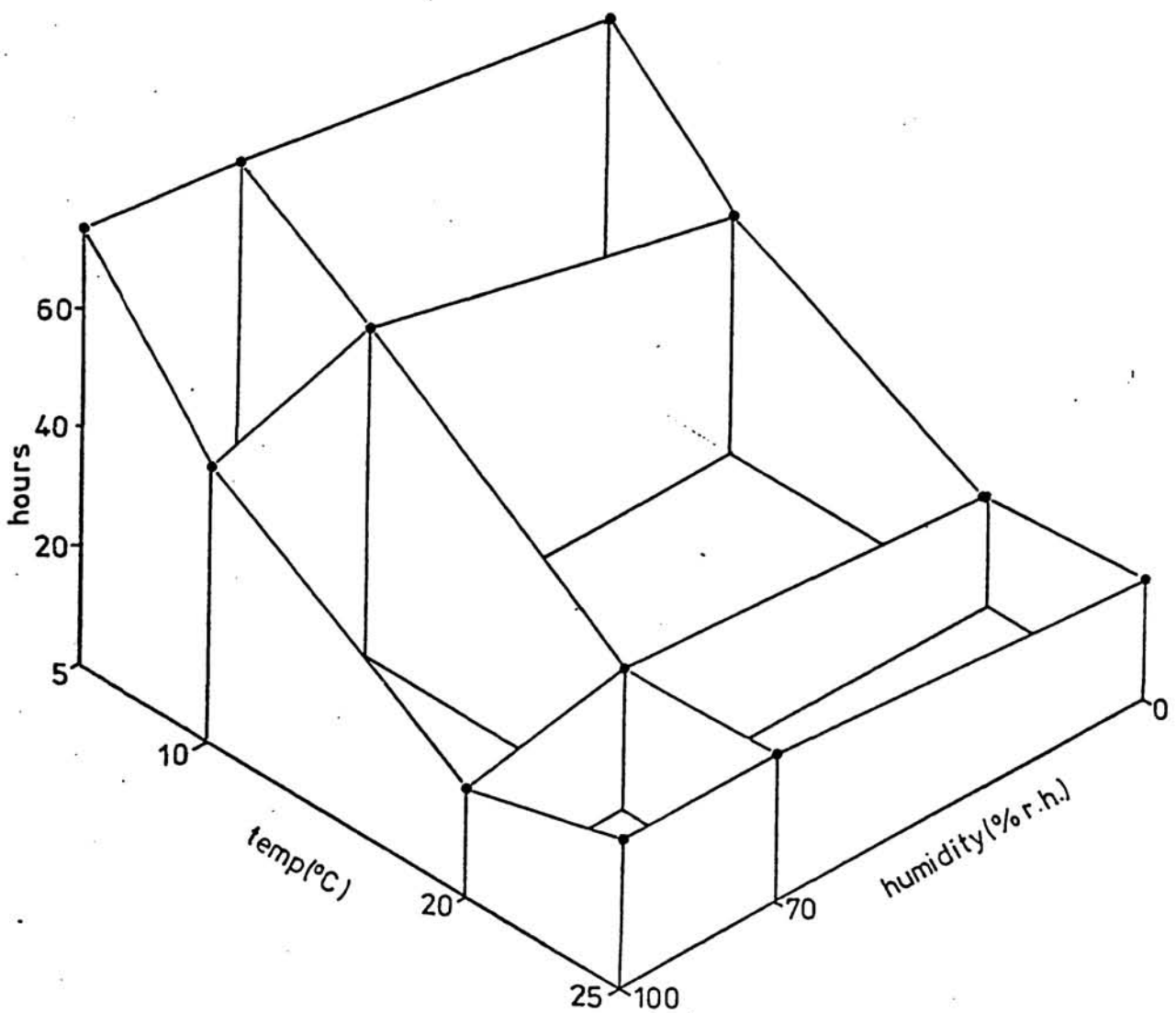


TABLE 20 : Mortality of 1st instar *S. avenae* in relation to temperature and humidity. (proportion dead)

TEMP.	5°			10°			20°			25°		
% R.H.	0	70	100	0	70	100	0	70	100	0	70	100
NO. APHIDS*	45	19	16	38	34	4	50	41	9	38	40	7
TIME (HOURS)												
14	.14	.04	.03	.26	.14	.00	.96	.48	.50	.47	.43	.25
24	.29	.17	.34	.31	.23	.00	1.00	.76	1.00	.92	.73	.67
40	.44	.30	.62	.60	.42	.60		.95		1.00	.95	.75
66	.71	.76	.68	.74	.77	.80		1.00			1.00	1.00
88	.88	.78	.68	1.00	.86	.80						
96	.93	.79	.68		.97	.80						
120	1.00	.79	.68		.97	1.00						
144		.95	.68		1.00							
168		1.00	.72									
192			.82									
216			.88									
240			.88									
288			.94									
312			.94									
336			.94									
360			1.00									
384												

* Fluon failed to prevent aphid escape in the 100% R.H. treatments.

TABLE 21 : Mortality of 4th instar *S. avenae* in relation to temperature and humidity. (proportion dead)

TEMP.	5°			10°			20°			25°		
% R.H.	0	70	100	0	70	100	0	70	100	0	70	100
NO. APHIDS*	42	45	23	31	25	11	41	35	6	45	25	8
TIME (HOURS)												
14	.04	.04	.03	.05	.04	.06	.63	.41	.25	.28	.32	.14
24	.28	.09	.03	.09	.18	.13	.90	.67	.27	.76	.64	.19
40	.37	.40	.04	.52	.50	.19	1.00	.91	.83	1.00	.92	.36
66	.63	.57	.14	.78	.59	.45		1.00	1.00		1.00	1.00
88	.77	.73	.23	.91	.78	.53						
96	.93	.87	.20	1.00	.88	.64						
120	.98	.87	.38		.92	.64						
144	1.00	.89	.41		.96	.69						
168		.96	.41		1.00	.77						
192		.98	.55			.77						
216		1.00	.73			.83						
240			.77			.83						
288			.91			.91						
312			.91			1.00						
336			.91									
360			.96									
384			1.00									

* Fluon failed to prevent aphid escape in the 100% R.H. treatments.

The potential importance of humidity was only manifest at 5°C where perhaps low metabolic demand removed starvation as the limiting factor to survival. In other words, aphids were killed by dessication before food reserves were depleted.

2.7 GENERAL DISCUSSION

2.7.1 CAUSES OF POPULATION CHANGE ON WINTER WHEAT, OCTOBER - APRIL

2.7.1.1 Predation

The long term winter experiments (Section 2.2 and 2.3) made use of infested pots of seedlings placed in the field where natural cereal aphids were absent. Predation on these colonies might be expected to be unrealistically high yet the results show no consistent effect of predation on colony size. *M. dirhodum*, protected from weather, actually increased in numbers during 1977-1978 (Section 2.2) despite exposure to ground based predators. There are several reasons however why the possible importance of winter predation cannot be ruled out.

- a) It is likely that epigeal predators differ in their impact in different locations. This may arise from differences in composition of the predator community, because of differences in the abundance of alternative prey (e.g. Collembola) or simply due to different levels of abundance. Carter *et al* (1978a) for example, found that ground beetles important as cereal aphid predators in Sussex were low in abundance in East Anglia. Vickerman and Sunderland (1975) working in Sussex have demonstrated that a large number of epigeal species climb plants and feed on cereal aphids. Some of these, such as *Agonum dorsale* appear to be extremely efficient at searching for prey, sometimes finding aphids in the field when they are too scarce to be found in field samples (also see Sunderland and Vickerman, 1980).
- b) The possible impact of predation during March and April was not fully tested by 'shelter' experiments. In the first season (Section 2.2) populations were reduced considerably by parasitism obscuring the possible role of predation. In the second, differences were observed between 'fully caged' and 'weather protected' populations but serious limitations of the caging technique as a means of assessing predator

exclusion (eliminating wind, elevating temperatures and preventing aphid dispersal) and the lack of replication preclude confident conclusions.

Experiments on predator impact during summer (Chapter 3) were concerned with the period late May - early August and these indicated no significant effect of ground based predators on aphid populations. Hence from the present research, no conclusions can be drawn on the possible importance of predation during late March, April and May. Recently published experiments carried out at Rothamsted Experimental Station and at North Farm, West Sussex (Edwards and George, 1977; Edwards and Steed., 1979; Edwards *et al*, 1979) have shown that predation by polyphagous predators over this period was effective in reducing the size of summer populations. It is noteworthy however that predator effectiveness declined steadily until they had no effect on the populations during June (Edwards *et al*, 1979). Hence, polyphagous predators appear to be important in reducing populations that have overwintered in cereal crops but they are unlikely to have an effect on populations of summer immigrants arriving when the crop reaches the heading stage. Hence the overall value of these predators to the farmer depends heavily on the relative importance of overwintered and summer immigrant aphids to the size of summer populations. Summer immigrants are thought to be primarily responsible for damage in 'outbreak years' (George, pers. comm) but the value of polyphagous, predators could lie in preventing overwintered aphids from building up into 'outbreak populations'.

2.7.1.2 Parasitism

Populations sheltered from wind and rain suffered heavy losses due to parasitism during 1977-1978 (*Aphidius* spp)(Section 2.2.2).

The extent to which this simulates natural parasite impact is difficult to assess because host densities were unnaturally high and the parasites could have been introduced into the populations while in the glasshouse during autumn. Further evidence of the natural impact of parasites came in March, 1979 when most of the sparse winter survivors became parasitized following the appearance of the first mummy in mid January (Section 2.3.3.3). Adult *Aphidius* spp were sometimes observed searching plants during warm weather in winter (13/12/78, 8/1/79, 16/1/79) and on 25 October 1978 parasites belonging to 3 species were reared through from 50 *S. avenae* placed in the field for just 3 hours (*Aphidius ervi*, Nees; *A. picipes* Haliday;) *A. uzbeckistanicus* (Luzhetzlei)).

2.7.1.3 Adverse effect of low temperature

Observations on natural (Section 2.4) and artificially established cereal aphid colonies (Section 2.2 and 2.3) showed that periods of severe frost were not associated with exceptionally heavy aphid mortality. Nevertheless, populations did decline during the winter, even on plots protected from wind and rain so low temperatures must have played some part.

First, low temperatures are important from the viewpoint of population dynamics as they prevent reproduction that would otherwise offset the effects of mortality (see below: Section 2.7.1.4). Secondly, low temperatures can cause mortality at a steady rate during prolonged cold, and this is likely to be enhanced by wind (Section 2.7.1.5). Thirdly, frost can damage host plants (cell rupture leading to wilting and death) thereby depriving aphids of food so forcing them to move to new feeding sites. Fourthly, low temperature may prevent feeding.

Many workers have assumed that low winter temperatures reduce

aphid populations, especially those of anholocyclic clones (Vickerman and Wratten, 1979; Dixon, 1973) but there has been little direct evidence for this in the case of cereal aphids. Frosts provided a useful indicator of *M. persicae* abundance on sugar beet (Watson *et al*, 1975) and Short (1978) used a similar approach with respect to the aerial abundance of cereal aphids. Vickerman (1977a) however found a negative relationship between summer abundance and spring temperatures. His hypothesis for this surprising result was that in cold springs, natural enemy build up is reduced and the migration of aphids to cereal fields delayed. As a result, the eventual arrival of aphids coincides with the crop growth stage most suitable for aphid build-up (flowering - watery ripe) so resulting in a population 'explosion' before natural enemy action can check the increase.

From the physiological viewpoint, the ability of cereal aphids to withstand frost is not surprising. The literature contains numerous remarkable examples of extreme cold tolerance in insects (see reviews of Salt (1961) and Asahina (1969)). Some Lepidoptera larvae, for example can survive temperatures below -30°C although development to the adult stage may be impaired. There are fewer published accounts of cold tolerance in aphids but Carter (1972) showed that the Green Spruce aphid *Elatobium abietinum* could survive at -8°C . Parry (1978) demonstrated supercooling points of below -20°C for unfed first instar *M. persicae*.

Cold hardiness in insects is achieved in 2 ways : avoidance of freezing and frost resistance. To avoid freezing, body fluids may be concentrated (by water excretion or solute production) so lowering the freezing point, or by supercooling.

A liquid can potentially freeze once its temperature falls to freezing point but ice formation normally depends on inoculation by external ice crystals on the body surface or in the gut. A much lower temperature is required to induce spontaneous freezing without inoculation

and this is referred to as the supercooling point (less than -20°C for many insects (Asahina 1969)).

Many cold hardy insects produce 'protective substances' which (a) concentrate the blood (so reducing its freezing point), (b) protect the cells from the damaging effects of ice formation and (c) lower the supercooling point (Asahina, 1969). The most important of these protective substances is probably glycerol, occurring in some insects at very high concentrations (e.g. 25% of body fresh weight in the parasitic wasp *Bracon cephi*) but in the green spruce aphid, mannitol is probably more important (Parry 1979). These are supplemented by a number of low molecular weight sugars (e.g. trehalose). Some insects have been found to produce these substances according to need (Morrissey and Baust, 1976; Mansingh and Smallman, 1972) accounting for the phenomenon of acclimatisation, but their possible significance in cereal aphids is not known.

The ability of an insect to survive freezing depends not only on the concentrations of these substances in the blood but on body size, severity of frost and duration of frost (Salt 1966). Indeed, mortality depends on the duration of cold whether body contents are frozen or supercooled (Asahina, 1969). For example, Adams (1962) found that mortality of *Mysus persicae* (Sulz) kept at -2°C increased steadily with time. Perhaps this helps explain the gradual nature of population decline during winter in *S. avenae* observed in the present experiments (Section 2.3).

The formation of ice in the insect body normally originates in the blood, and subsequently spreads through the tissues. Free water on the insects' body surface can be an important cause of nucleation inside the haemocoel but this is unimportant to insects protected by over-wintering cases (eggs, puparia etc). In anholocyclic aphids, however, contact with moisture is potentially a common occurrence, although prevented by wax particles on the cuticle in *Elatobium abietinum* (Bevan and Carter, 1980). In the 1978-1979 experiment (Section 2.3.3.3), the combination of dew and low temperature accounted for significantly heavier mortality than low temperature alone

suggesting that, in *S. avenae*, protective wax is either absent or less than completely effective. Griffiths and Wratten (1979) found no such effect in laboratory experiments.

2.7.1.4 Winter temperatures and aphid reproduction

Frequent observations on aphid colonies (Section 2.2 and 2.3) indicated the remarkable ability of aphids to continue reproducing during winter. In many cases this followed very short periods of warm weather (several hours) underlining the inadequacy of daily mean temperature data as a predictor of aphid population growth.

During 1977 - 1978 (Section 2.2) *M. dirhodum* reproduced substantially more than *S. avenae* resulting in considerable population increase in December and March of sheltered colonies. Separate observations on natural colonies (Section 2.6) indicated growth and reproduction in both *R. padi* and *S. avenae* during October, November and December. Reproduction on the crop between October and April contributes to eventual yield reduction in 3 ways.

- (1) Nymph deposition by colonizing alates in autumn establishes winter populations that (a) form a source of damaging summer populations (b) transmit barley yellows dwarf virus to wheat plants at the sensitive seedling stage. (Plumb, 1977).
- (11) Winter reproduction in the crop offsets losses due to mortality that might otherwise result in colony extinction.
- (111) Reproduction during Spring increases the size of populations in the summer. (N.B. often considerably supplemented by immigration).

George (1974, pers. comm) reports more serious aphid problems on winter sown cereals, possibly indicating the importance of aphids over-wintering on the crop. Furthermore, aerial photography has shown a relationship between aphid damage and crop sowing date in the autumn. (George, pers. comm).

The observations of colonization and reproduction by *R. padi* at

Silwood Park (Section 2.4) refutes the recent suggestion (George, per. comm), that alates of this species flying in autumn are only capable of reproduction on their primary host, *Prunus padus*.

2.7.1.5 Wind and Rain

Field experiments during the winter 1977 - 1978 (Section 2.2) showed that wind and rain was the main factor reducing numbers of *S. avenae* and *M. dirhodum*. A similar experiment the following year (Section 2.3) separated the effects of wind and rain and found that wind alone could account for losses incurred by *S. avenae*.

The importance of wind and rain as a mortality factor in natural insect populations has been stressed by a number of authors (Richards, 1961; Andrewartha and Birch, 1954) and Jones 1979b has correlated the decline in summer populations of cereal aphids with periods of high wind. Few workers, however have investigated its effects by experiment. In the present studies, a range of simple experiments investigated the nature of wind's effect on *S. avenae* infesting wheat seedlings (Section 2.5). From the outset, a distinction was made between the straightforward, acute effect of wind dislodging aphids from plants and the potentially important chronic effects that might occur such as

- (1) Damaging host plants,
- (11) enhancing the chilling effect of low temperature.
- (111) increasing dessication when temperatures are too low for aphids to feed.
- (1V) restricting aphids to sheltered niches that are nutritionally inadequate.

The proportion dislodged by wind increased as expected with wind velocity (Section 2.5.3.1) but also with gustiness (Section 2.5.3.2) and with aphid size. A few aphids survived even the strongest winds tested.

These survivors were normally found on the lower parts of the wheat seedlings. *R. padi* and *M. dirhodum* were less easily dislodged than *S. avenae* because they feed lower down the plants (Section 2.5.3.3 and Section 2.5.3.4). This partly explained the improved survival of *M. dirhodum* over *S. avenae* during winter 1977 - 1978 (Section 2.2). Although some aphids are blown directly from their feeding sites by wind, the majority are probably dislodged by the shearing action between moving leaves. The shearing effect is likely to be considerably influenced by seedling density. Widely spaced plants do not come into contact, densely planted seedlings are likely to stabilize by mutual support and also cut down local wind speed. At intermediate densities, shearing action is likely to be of considerable importance and although a preliminary experiment (Section 2.5.3.8) supported this conclusion, no general statement on the effect of plant density on wind mortality can be made at this stage. Laboratory experiments indicated that dislodged large aphids might reinfest plants at sub zero temperatures (Section 2.6.3.1) and they are potentially able to survive for at least 4 days below 5°C (Section 2.6.3.2). Nevertheless, seedlings growing beside infested test plants in the field rarely became infested with aphids, suggesting that other mortality factors operating at soil level accounted for the loss of dislodged aphids. These probably include predation, and injury caused by attrition through the combination of rain and soil erosion.

Two examples of 'chronic' loss due to wind were highlighted. First, wind resulted in leaf damage followed by wilting and necrosis that forced aphids to leave plants. Secondly, dead aphids were found on plants exposed to freezing winds for more than 1 hour (Section 2.5.3.5) probably because wind enhanced the chilling effect of low temperature. It is also possible that temperatures were too low for the aphids to

feed meaning that they were unable to recover from dessication which is enhanced by wind.

2.7.2 SCOPE FOR FURTHER RESEARCH

Studies on the survival and causes of winter mortality in cereal aphids have indicated important gaps in knowledge and prospects for improved control. A number of possibly fruitful topics for research are therefore listed briefly below.

Source of Spring immigrants

- Sample potential 'source' habitats during Autumn and spring use radiotracers to 'label' a potential source population, sample aphids on the crop in Spring.

Relative importance of overwintered versus immigrant aphids.

- Spray large field plots with a short persistence aphicide (e.g. pirimicarb) in February, March, April and May and compare peak aphid numbers in summer to assess the contribution of overwintered aphids to summer populations.

Predator and parasite impact

- Place infested plants inside shelters for periods of 1 week throughout the winter and spring. Assess losses due to predators and rear through parasites. Relate natural enemy activity to weather.

Forecasting

- Test the possible value 'winter wind velocity' as a predictor of cereal aphid abundance.

Impact of changes in agricultural practice

- Examine effects of minimal tillage and reduced plant densities on overwintering survival.

Biological Control

- Evaluate the value of parasite release in the spring (potentially

capable of inflicting heavy losses on aphid populations already low following winter).

Varietal control

- Screen cereal cultivars for resistance in the seedling stage to attack during autumn.

Chemical control

- Devise optimal useage of selective materials for virus control (i.e. timings, rates, application methods).

CHAPTER 3

FIELD STUDIES ON THE CAUSES OF POPULATION CHANGE

DURING SUMMER

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FIELD STUDIES ON THE CAUSES OF POPULATION CHANGE
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3.1 INTRODUCTION

In all branches of science, progress has been accelerated by the adoption of experimental study methods. This holds well for the field of insect ecology where our knowledge has progressed from the 'insights' of natural historians to a relatively thorough understanding, tested through the application of simulation models. Not surprisingly, the greatest progress in population ecology has been made in laboratory systems, where conditions are readily controlled to test the effects of experimental variables. Although laboratory systems are usually very artificial, and results can usually only be applied to the field with great caution, these studies are justified on the grounds that they promise to further general theories of population ecology (Southwood, 1977a)

There is little doubt that field studies have benefited from the growth of an analytical approach to population ecology. Many field ecologists today extend their field observations by analysis, through life table analysis (Varley *et al* 1973; Hughes, 1972) or model construction (Crawley, 1973; Norton and Holling 1976) - techniques that potentially provide an understanding of practically important processes such as pest mortality due to natural enemies. But these techniques suffer from important drawbacks that limit their widespread application. For example, the life table analysis of Varley and Gradwell (Varley *et al*, 1973) is best suited to populations with discrete generations, ideally just one per year (Southwood, 1975). The Hughes method (Hughes, 1972), although suitable for insects with overlapping generations such as aphids, assumes stable instar distribution which, according to Carter *et al* (1978b) 'is rarely achieved' in the field. Furthermore, the technique makes no distinction

between losses due to predation and dispersal and utilises unreliable estimates of reproductive rate (Carter *et al* 1978 and Dixon, 1977).

Paradoxically it is the relative instability of many pest populations (Conway, 1976, Southwood 1977b) that (a) confers pest status and (b) limits their suitability for life table analysis. Nevertheless, these insects have demanded study due to their economic importance. The quantitative assessment of natural enemy impact has been recognised as a 'key' research area providing a basis for biological or integrated control (Debach *et al* (1976), Kiritani and Dempster (1973), Hodek *et al* (1972)), and in this field important experimental methods have emerged. These approaches involve the manipulation of pest and natural enemy populations in the field, and it is this important respect that they differ from the life table approach. In principle there is no reason why similar experimental methods could not be extended to the study of all population processes in the field to obtain a 'total view' of insect populations as sought through life table construction. The experimental techniques used to quantify natural enemy effectiveness all suffer from significant drawbacks but 'the insecticidal check method', 'hand removal of predators', 'mechanical exclusion of predators' etc., have produced convincing proof that natural enemies can effectively limit the size of many insect populations (Debach *et al*, 1976). It is surprising, therefore that these methods should not have become more widespread. Thus, Hodek *et al*, (1972) concluded:

'what is important is that workers should abandon sole reliance on the data resulting from field samples and make more extensive use of the more effective experimental methods which have as yet been little used.'

Later, Debach *et al*, (1976) reaffirmed these views:

'we reiterate that the best, the clearest, and the only reliable means of evaluation is through the use of experimental or comparison methods. We are convinced that they warrant far greater use....'

A survey of the methods used to assess natural enemy impact on cereal aphid populations indicates that these recommendations have gone largely unnoticed. Until very recently (c.f. Edwards *et al.*, 1979) few studies have involved experimentation (see Vickerman and Wratten, 1979) contrasting sharply with the numerous 'descriptive' surveys of aphid and natural enemy abundance in cereal fields. This seems remarkable in view of the controversy that centres over cereal aphid predation and the possible adverse effects, on natural enemies, of pesticides that are being increasingly used on farmland (Vickerman and Wratten, 1979).

In the present study, considerable emphasis was placed on the use of quantitative, experimental methods. Although the evaluation of natural enemy impact was the prime objective, it seemed highly probable that a similar approach could be used to measure other population processes such as natality, dispersal of apterae, immigration and emigration of alatae.

In 1977 an experiment was set up at Silwood Park to measure a number of factors, potentially important in determining aphid abundance (Section 3.2). These included mortality due to ground based predators, aerial predators and parasitism as well as crop suitability. The objective was to obtain these measurements on a continuous basis through the summer so that the results could be related to the natural abundance of aphids and prevailing environmental conditions. The 'key' features of the approach were the use of:

- (a) exclusion methods to assess the separate roles of 'ground based' and 'aerial' predators.
- (b) artificially infested test plants, to enable potential natural enemy impact to be assessed even when there were no naturally occurring aphids in the field.
- (c) immature aphids, left in the field for short periods to remove

reproduction as a possible cause of population change.

The ambitious goals of this experiment were not satisfactorily realised in 1977, but it is described in this thesis on its merits of approach and methodology. The discussion section ascribes failure to the low level of natural attack, dispersal of artificially infested aphids and the invalid assumption that test plants, placed in the field were 'at risk' to predation to the same extent as field plants. Possible refinements are recommended but these would have involved too much work to have been attempted in the subsequent summer. Instead, research in the following season set more limited objectives but met these with a large scale replicated experiment (Section 3.3). Large plots of winter wheat were manipulated with respect to levels of predation and sowing date and the associated aphid populations monitored. The experimental design enabled the results to be analysed statistically and the effects of sow date, predation and their interactions to be tested.

3.2 1977 FIELD EXPERIMENT

3.2.1 MATERIALS AND METHODS

3.2.1.1 Layout

The experimental site consisted of an area (36 x 24m) of winter wheat (c.v. Maris huntsman) in Silwood Bottom.. This was divided into 36 square plots (4 x 4m) arranged as 6 experimental 'blocks'. The 9 plots comprising each block were assigned plot numbers at random which corresponded to their subsequent purpose. Some were used to study components of population change. Others, to monitor natural populations of aphids and predators.

<u>PLOT NO.</u>	<u>'TREATMENT' APPLIED</u>	<u>PURPOSE</u>
1	plants removed and transferred to laboratory	assessment of suitability for aphid growth.
2	test plant placed in cage	measurement of losses in the absence of predation, wind and rain.
3	test plant protected from ground predators (by barriers and 'methiocarb' baits) and aerial predators (by treatment of surrounding plants with 'azinphos methyl')	measurement of losses in the absence of predation.
4	test plant protected from ground predators only	measurement of losses in the absence of ground based predators.
5	test plants unprotected	measurement of total losses and percentage parasitism.
6	test plants cleared of aphids	to distinguish subsequent alate colonists from alates produced on the crop.
7	none	census of aphid populations on the crop.
8	none	census of conspicuous predator populations.
9	none	census of alate aphids (using water traps) and ground predators (using pitfall crops).

3.2.1.2 Experimental Procedure.

Plot 1 (Crop suitability)

Wheat plants, dug up from the field were placed in pots, cleared of

aphids and kept in a 20°C constant temperature room. A batch of 25 first instar *S. avenae*, taken from standard cultures, were weighed using a 'Cahn' microbalance (Adams and Van Emden, 1972) and introduced to the terminal parts of the plants. The aphids were reweighed after 3 days and their collective 'relative growth rate' (Van Emden, 1969) calculated. The experiment was replicated 6 times.

Plots 2, 3, 4 and 5 (Impact of predators and parasites)

Wheat plants, newly dug up from the field were infested with 30 second or third instar nymphs in the laboratory. Aphids at this developmental stage were considered to be sufficiently large to be accepted as hosts for aphid parasites but young enough to be incapable of reproduction during the experiment. The plants were carefully replaced in the field on the same day in their prescribed locations on the experimental site. The cages used in plot 2 were cylindrical in shape (approximately 20cm diameter, 100cm height) consisting of cotton mesh (parasite proof) supported on a steel framework. The roofs were made from clear cellulose acetate to maximise the illumination received by the plants.

After 2 days the plants were taken from the field to the laboratory. Remaining aphids were counted immediately and the number of mummies scored after 15 days.

Plot 6 (Crop colonization by alates)

Frequent applications of 'pirimicarb' on this plot were planned as a means of clearing plants of aphids in order to monitor the arrival of new alates. The eventual scarcity of cereal aphids at Silwood Park in 1977 prevented this experiment from being carried out.

Plot 7 (aphid census)

15 tillers were selected at random in each plot (making 90 tillers

per sampling occasion) and the numbers of aphids recorded.

Plot 8 (predator census)

The scarcity of predators during 1977 made absolute estimates of population density impossible. Instead a visual search for predators (2 minutes/plot) was used as a relative method that could be used to compare predator abundance through the season.

Plot 9 (aerial aphid populations, epigeal predators)

Each plot contained 1 standard yellow water trap (Taylor and Palmer, 1972) to sample aerial aphid populations and 2 pitfall traps (Southwood, 1979; Greenslade, 1964) to sample epigeal predator populations.

3.2.2 RESULTS AND DISCUSSION

3.2.2.1 Crop suitability

Aphid growth rates during the summer (Figure 24) were exceptionally high when plants became 'watery ripe' (Feekes growth stage 10.5.4 (Large 1954)) but these were not sustained through the 'milky ripe' stage (Feekes growth stage 11.1), and declined substantially when the ears became 'mealy ripe' (Feekes growth stage 11.2). These findings correspond closely to those of Watt (1979) working with *S. avenae* on oats, as well as to the rates of change observed in the field population (Section 3.2.2.3).

3.2.2.2 Impact of Predators and Parasites

The experiment failed to show differences between treatments during the summer (Table 22), but in view of serious shortcomings of the experimental technique, the possible importance of natural enemies cannot be refuted. First, a substantial proportion of aphids disappeared from plants even in the absence of mortality factors. This was mainly due to natural dispersal and experimental disturbance but on several occasions coccinellids were found inside the cages. Second, the 'azinphos methyl' treatment used in Plot 3 clearly failed to exclude natural enemies. In fact Table 22b shows that the highest levels of parasitism occurred on these plots. Finally, it is questionable whether introduced aphids on Plot 5 were 'at risk' to the same extent as aphids in the natural population. The test plants were planted into disturbed soil and they remained in the field for just 2 days so less mobile predators (e.g. spiders, syrphid larvae) may not have encountered the test aphids.

3.2.2.3 Abundance of aphids and predators

S. avenae was the only abundant aphid species present during 1977, and coccinellids were the main 'aphid specific' predators. Their changes in abundance through the summer are shown in Figure 25. Alates reached their maximum numbers on 24/6 (growth state 11.1 - milky ripe) and

FIGURE 24 : Relative growth rates (R.G.R.) of *S. avenae* on winter wheat (means of 6 replicates $\pm$ std errors).

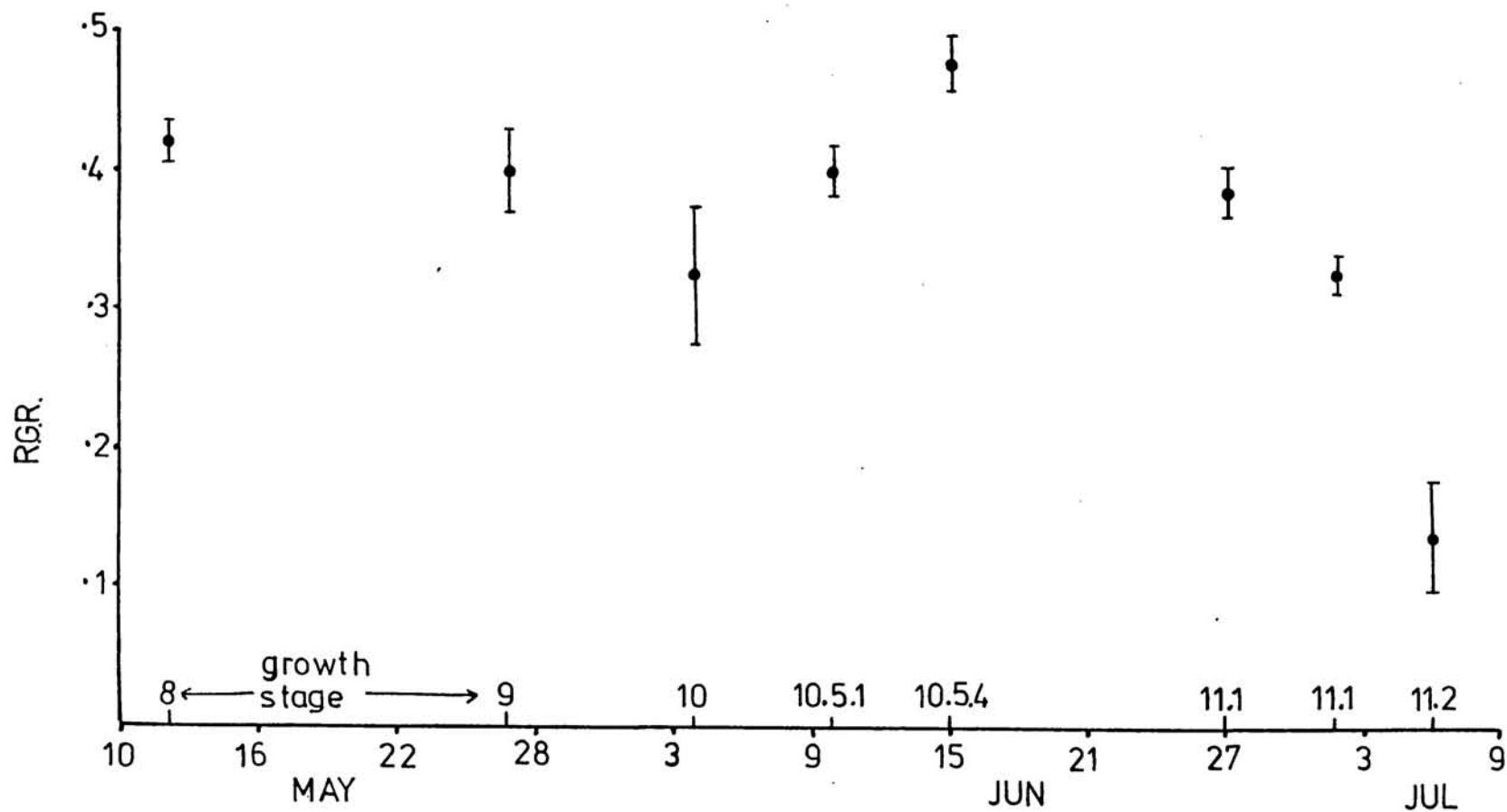


TABLE 22 : Results of experiments designed to assess the impact of predation and parasitism on *S. avenae* populations.

(A) Mean % Loss

<u>Treatment</u>	<u>11/5</u>	<u>18/5</u>	<u>27/5</u>	<u>1/6</u>	<u>10/6</u>	<u>16/6</u>	<u>24/6</u>	<u>29/6</u>	<u>6/7*</u>
2	48	47	40	49	28	36	24	59	100
3	-	-	-	55	46	41	25	37	33
4	50	47	42	46	39	48	17	28	73
5	54	55	48	55	34	39	27	24	93

(B) Mean % Parasitism

2	0	0	0	0	0	0	1	2	0
3	0	0	0	0	0	0	14	3	0
4	0	0	0	0	0	0	5	3	0
5	0	0	0	0	0	0	9	1	0

* unreplicated

KEY TO TREATMENTS

2 - caged.

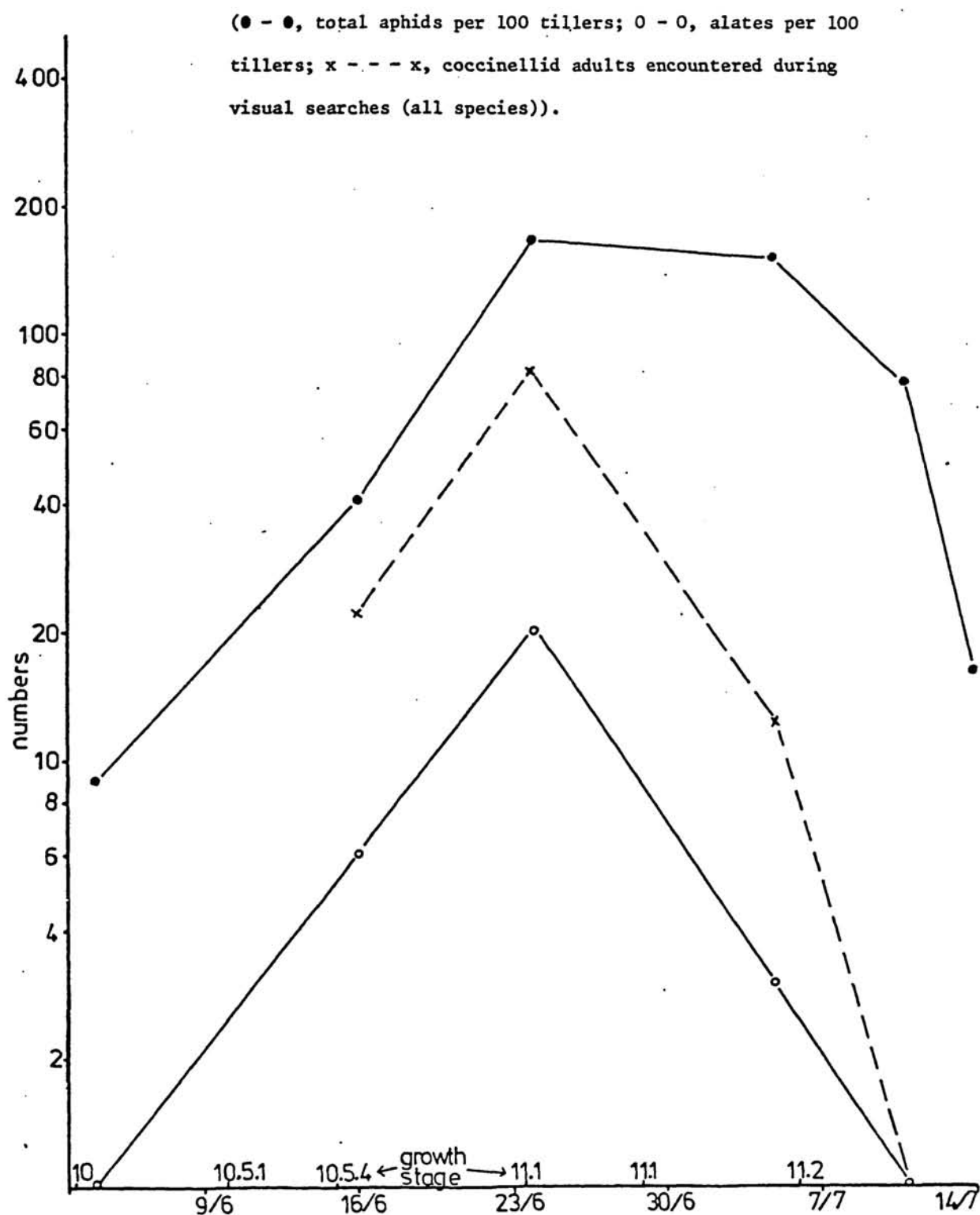
3 - protected from ground predators by barriers and 'methiocarb' baits.

Protected from aerial predators by 'azinphos-methyl' sprayed onto surrounding plants.

4 - protected from ground predators by barriers and methiocarb baits.

5 - exposed plants.

FIGURE 25: Numbers of *S. avenae* and coccinellids on winter wheat, 1977.



subsequently declined substantially. Total aphids remained at similar levels of abundance between 24/6 and 5/7 (growth stage 11.2 - mealy ripe) and then declined. Coccinellid adults, mainly *Coccinella septempunctata* (L.) were relatively scarce and left the field in large numbers between 24/6 and 5/7 despite little change in the abundance of prey (Figure 25). No immature stages were found during sampling. Some syrphid larvae were seen feeding on aphids at night around 25/6 but their abundance was not measured.

3.2.2.4 Aerial aphid populations

The small numbers of aphids caught in 6 water traps are shown in the following table:

	13/5	27/5	4/6	16/6	27/6	5/7	10/7	18/7	1/8
<i>S. avenae</i>	0	4	0	0	2	2	1	2	3
<i>M. dirhodum</i>	0	1	1	0	0	0	0	0	3

3.2.3 GENERAL DISCUSSION AND RECOMMENDATIONS

Field studies during summer 1977 produced useful 'descriptive' data on the population changes of cereal aphids and predators. In addition, measurements of crop suitability through the summer helped explain the rapid rates of population build up observed in the third week of June. Nevertheless the main goal of the studies, namely to obtain accurate field measurements of predation and other population processes, was not achieved. The reasons for this have already been described but, essentially the problems encountered in 1977 originated from:-

(a) the use of introduced plants. (b) the disturbance of artificially infested aphids during transfer to the field. (c) the small size of plots used for insecticidal exclusion of predators. (d) the low density of aphids and predators occurring in 1977.

The first 3 of these problems could easily be overcome by the use of larger plots and the establishment of aphid colonies in the field. Single leaf or ear cages could be used to confine first instar aphids on tagged plants and these could be removed once aphids reached third instars. Aphid density and distribution could be easily manipulated and the response of predators and parasites monitored. These studies, providing data on the independent effects of aphid mortality components could be supplemented by similar investigations on the other pathways of population change (natality, immigration and emigration). Tagged colonies could be used to study alate production and the rates of alate take off in relation to aphid density; uninfested plants could enable monitoring of crop colonization by alates (see above); caged adults could provide data on fecundity on the crop at field temperatures.

Obviously, some of these measurements can most conveniently be made by sequential observations on caged aphids. However, the considerable effects of caging on microclimate inevitably limit their accuracy. It follows

that improved methods of field caging would radically improve the prospects of field experimentation. Surprisingly, there have been no attempts to mechanically ventilate field cages despite their frequent use in predator exclusion experiments (Debach *et al*, 1976; Hodek *et al*, 1972). It would be a relatively simple matter to operate an electric fan in the field which drew air through bifurcating tubes from a large number of field cages.

3.3 1978 FIELD EXPERIMENT

3.3.1 MATERIALS AND METHODS

3.3.1.1 Layout and treatments

The study site consisted of an area (50 x 50m) of winter wheat (c.v. Maris Kinsman) on the western edge of Silwood Bottom. The area was divided into plots according to a split plot latin square design (Cochran and Cox, 1957) (see Figure 26). Main plots were subjected to 1 of 3 'treatments'.

<u>TREATMENT NO.</u>	<u>TREATMENT DESCRIPTION</u>	<u>PURPOSE</u>
1	untreated	- experimental 'control' with natural levels of predators and parasites
2	'methiocarb' baits and 'fonofos' granules applied broadcast to the soil	- to kill ground based predators (c.f. Edwards and Steed, 1979)
3	as treatment 2, plus carbaryl applied to the foliage as a spray	- to kill ground based and aerial natural enemies (c.f. Meier, 1966).

For convenience these treatments are referred to by number or by the names adopted for computer data tabulation : 'CONTROL', 'NOGRPRED' and 'NOPRED' respectively. Table 23 gives application details for the insecticides used to exclude natural enemies from plots. It also contains details of other pesticide applications used to control weeds and disease. Although intrinsically aphicidal, carbaryl was applied by methods designed to maximise its kill of natural enemies while minimising its effect on aphids. The first application was made prior to the immigration of aphids and the second directed to the lower half of plants thereby avoiding *S. avenae* feeding on the ears and flag leaves. Because there was uncertainty over the likely success of these attempts to obtain

TABLE 23 : Details of pesticide applications.

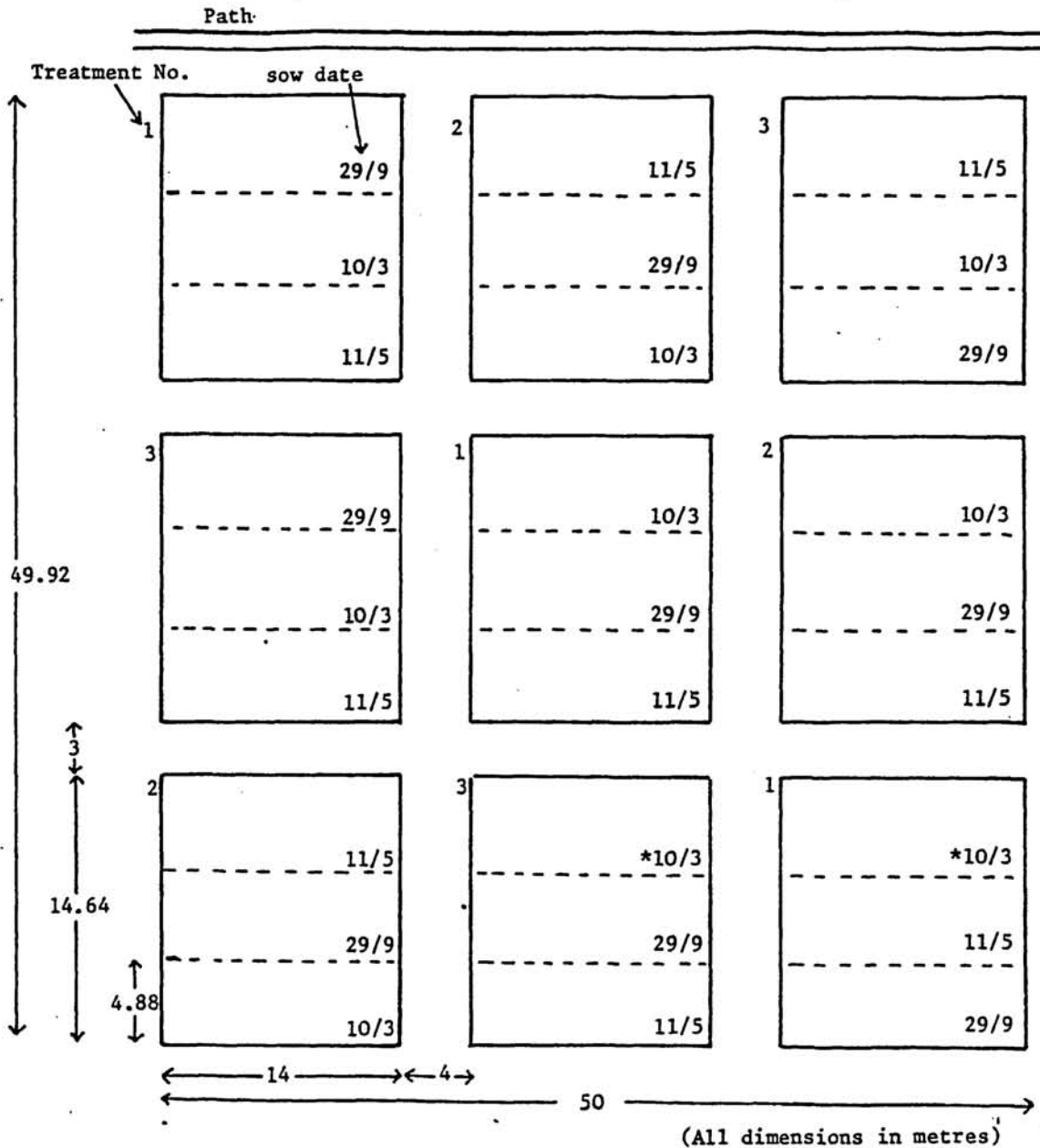
CHEMICAL COMMON NAME	FORMULATION	APPLICATION DETAILS			PURPOSE
		Rate (kg/ha)	Dates	Method	
'fonofos'	granules	20.4	19/5, 20/6, 27/7, 11/8	broadcast by hand	} to kill ground based predators
'methiocarb'	baits	11.0	19/5, 20/6, 27/7, 11/8	broadcast by hand	
'carbaryl'	wettable powder	3.3	26/5, 20/6, 27/7, 11/8	manually operated hydraulic knapsack sprayer	} to kill 'aerial' predators
'mecoprop' (herbicide)	emulsifiable concentrate	2.0	10/7	"	broad leaf weed control
'triadimefon' (fungicide)	wettable powder	0.25	7/7	C.D.A. stacked - disc sprayer (diluent = 8 L water, 2 L Ulvapon)	mildew and rust control

selectivity, a 2M zone across the subplots (Figure 26) was left unsprayed. Hopefully, this zone would be significantly predator depleted due to mortality occurring during movement through the remainder of the plot while the aphids would be unaffected directly by the insecticide.

At the end of May, each treated plot was surrounded by a barrier consisting of 45cm wide flattened polythene tubing, partially buried below soil level (approximate depth, 10cm) to prevent the ingress of ground beetles. (c.f. Edwards and Steed, 1979; Shires 1980). Steel wire running through the tubing facilitated the vertical support of the polythene by wooden stakes (Plate 4), and bridging of the barriers by weeds, was prevented by local applications of 'paraquat' herbicide. Wide 'corridors' between main plots ensured that all 'CONTROL' plots were accessible to ground beetles that might disperse from hedgerow overwintering sites adjacent to the path (Figure 26). The effectiveness of exclusion was monitored by 2 methods. 5 pitfall traps (Southwood, 1978) placed in each plot belonging to treatments 1 and 2 were used to compare numbers of Carabidae and Staphylinidae. Numbers of 'aerial' predators were recorded at the times of each aphid census. (See section 3.3.1.2 below).

Each main plot was divided into 3 subplots (Figure 26, Plate 5) differing with respect to sowing date. The first sowing was made on 29/9/77 to correspond to typical agricultural practice for winter wheat. The second on 10/3/78 corresponded to a spring sowing. The timing of the third (11/5/78) sowing was not agriculturally realistic but provided the opportunity to study the potential for population increase after mid July when conventionally sown crops become unsuitable for aphids. The commonly observed coincidence between deteriorating plant condition and increased natural enemy abundance normally hinders the evaluation of natural enemy impact.

FIGURE 26: Plot plan - 1978 field experiment.



* omitted in error during drilling.

EXPERIMENTAL DESIGN - split plot latin square

<u>KEY TO TREATMENTS</u>	<u>No.</u>	<u>Description</u>	<u>Reference</u>
	1	Untreated control	'CONTROL'
	2	'Fonofos' and 'methiocarb' applied to kill ground based predators	'NOGRPRED'
	3	'Fonofos', 'methiocarb' and 'carbaryl' applied to kill all predators	'NOPRED'

3.3.1.2 Monitoring cereal aphids and predators

The first population census was on 7/6 when 'countable' numbers first appeared in the field. In each sub plot 100 tillers were selected at random and the numbers of *S. avenae* and *M. dirhodum* recorded. Separate counts were made for each instar and the records for each tiller were kept separate so that the percentage of tillers infested could be calculated.

The aerial abundance of aphids was monitored by 2 methods (see Taylor and Palmer, 1972); the Rothamsted 12.2M suction trap at Silwood Park and 6 yellow water traps (diameter 15cm) within the experimental site.

Ground beetle populations were monitored by pitfall trapping (see above) and conspicuous predators counted during timed searches in each plot. These searches were abandoned when numbers failed to build up during June. Counts of mummified and diseased aphids and immature syrphids were made during each of aphid census.

3.3.1.3 Monitoring cereal growth stage and nutrient status.

Crop growth stages of all 3 sowings were recorded using the Zadoks decimal code (Zadoks *et al*, 1974, Appendix 7). The main advantage of this, over the Feekes scale (Large 1954) was its discrimination between different stages of 'milky ripe'. Cereal aphid populations usually collapse during this stage and the Zadoks code offered the prospect of identifying this with precision.

The main purpose of plant nutrient analysis was to supplement records of crop growth stage and to contribute to an understanding of the causes of population collapse in *S. avenae*. Thus, samples were confined to ears and flag leaves and these were only collected after heading. Later in the summer it became clear that a more comprehensive sampling programme

would have been required to fully explain the observed pattern of aphid attack, especially crop colonisation.

Plant samples consisted of 50 ears and flag leaves collected from the central main plot in the experiment (Figure 26). After cutting the material into small pieces, half the sample was used to measure 'percent dry weight' (see Bannister 1976) and the remainder freeze dried and set aside for later analysis of soluble nitrogen and soluble carbohydrate using the methods of Hill (1976) (modified from Broadstreet (1965)) and Golterman (1969) respectively.

3.3.1.4 Analysis of Results

The use of a computer for analysis was virtually essential due to complexity of the data and the experimental design, plus the problems of 2 missing plots (omitted in error during sowing 2; see Figure 26). 'Genstat' (Rothamsted Experimental Station 1977) was used to perform analysis of variance (ANOVA), to tabulate data and to extract key values for graphical presentation. All ANOVA's were performed in 2 stages; first using counts obtained in the sprayed area of treatment 3; second using counts from the unsprayed zone. Aphid counts were read into the computer as raw data and the following parameters calculated within the programme (see Appendix 4).

<u>Parameter</u>	<u>Parameter description.</u>	<u>Relevance to treatment comparison</u>
C20	Total aphids per 100 tillers (Log (x + 1))	} aphid abundance is partly a function of predation pressure and plant suitability
C32	Total aphids per M ² (Log (x + 1))	
C21	Alates per 100 tillers (Log (x + 1))	} alate settling is partly a function of plant suitability
C33	Alates per M ² (Log (x + 1))	
C40	First instars per 100 tillers (Log (x + 1))	} nymph deposition is partly a function of plant suitability
C42	First instars per M ² (Log (x + 1))	
C9	Ratio of first instars : total aphids	
C10	Ratio of alatiform forth instars - alate production is partly a function of plant suitability.	

These parameters are of 2 kinds; numbers and proportions. All the numbers were analysed on the basis of 'numbers per M^2 ' as well as 'numbers per 100 tillers' to allow for the difference between tiller densities on the 3 sow dates. Log ($x + 1$) transformations were applied to these numbers to normalise their distributions. Modified programmes were used to analyse records of 'percent infested tillers' (Appendix 5) and counts of natural enemies (Appendix 6) (disease, parasites and syrphid eggs).

3.3.1.5 Problems of interpretation.

For each of the 9 sampling occasions there were 9 treatment means for every parameter analysed. Significant interactions between sow dates and main treatments justified comparisons between these means but potentially, 36 such comparisons could be made in each case. Unfortunately, as the number of comparisons increase, the risk of accepting a chance difference as real, also increases. When using the 95% confidence level, one in twenty comparisons should appear significant simply due to chance (Murdie, 1972).

Duncan (1955) has attempted to overcome this problem by making acceptance of individual comparisons more rigorous as the total number of comparisons increases. The penalty for this refinement however is an increased risk of making type 2 errors (accepting a null hypothesis that no difference exists when, in reality it does). There is no simple solution to this dilemma other than to exercise great caution and common sense in interpreting the results of ANOVA. In the present work, particular comparisons were only made when the appropriate F tests were significant; only pre planned comparisons were made (between levels of factor x within a single level of factor y); and firm conclusions were generally based on differences achieving high levels of statistical significance ($p < .01$) or persisting over several sampling occasions.

3.3.2 RESULTS AND DISCUSSION

3.3.2.1 Aerial abundance of aphids.

Large catches of cereal aphids were only obtained around mid-July when populations were leaving crops (Tables 24 and 25). An earlier peak occurring around late May/early June (Table 24), just prior to the arrival of alates on the crop, may represent spring aphid migrations but numbers are too low to justify confident conclusions.

3.3.2.2 Efficiency of insecticide exclusion.

The use of 'fonofos' and 'methiocarb' proved to be a very efficient means of eliminating ground beetles from plots. Overall reduction of carabid populations approached 90% (Table 26) and no species appeared to escape substantial mortality. Staphylinids were not immediately reduced by treatment but by 28/6, they were reduced by over 80% compared to control plots (Table 27).

The 'carbaryl' treatment on 'NOPRED' did not notably reduce counts of mummies, diseased aphids or syrphid eggs (Tables 28 - 41). Nevertheless, results described below indicate that predator mortality was achieved and the most likely explanation is that syrphid larvae were killed after emergence from eggs by residual deposits of carbaryl. Unfortunately, this explanation remains speculative due to the difficulties of obtaining accurate population estimates for syrphid larvae (see Vickerman and Sunderland 1975) especially when at low levels of abundance. Dean (1974d) for example underestimated populations since he found higher numbers of pupae than larvae.

3.3.2.3 Aphid Abundance in Relation to Predation.

The 'raw data' derived on each aphid census are shown in Tables 42 - 50 (*S. avenae*) and 52 - 59 (*M. dirhodum*). Records of 'percent infested tillers' are given in Tables 51 (*S. avenae*) and 60 (*M. dirhodum*).

TABLE 24 : Numbers of *S. avenae* and *M. dirhodum* caught in the Rothamsted
12.2 M suction trap, summer 1978.

<u>Period</u>	<u><i>S. avenae</i></u>	<u><i>M. dirhodum</i></u>
1/5 - 7/5	0	0
8/5 - 14/5	0	3
15/5 - 21/5	0	0
22/5 - 28/5	7	7
29/5 - 4/6	7	6
5/6 - 11/6	1	2
12/6 - 18/6	2	2
19/6 - 25/6	2	6
26/6 - 2/7	1	1
3/7 - 9/7	10	13
10/7 - 16/7	56	84
17/7 - 23/7	88	39
24/7 - 30/7	240	16
31/7 - 6/8	111	1

NB. Data extracted with permission from Rothamsted Insect Survey
weekly bulletins.

TABLE 25 : Numbers of alate cereal aphids caught in 6 yellow water traps
1978.

APHID SPECIES	2/6	12/6	20/6	28/6	4/7	21/7	28/7	4/8	11/8
<i>S. avenae</i>	2	2	0	0	1	9	13	10	1
<i>M. dirhodum</i>	0	1	0	0	2	13	1	1	0
<i>S. fragariae</i>	0	0	0	0	0	0	0	2	0
<i>M. festucae</i>	0	0	0	2	0	0	0	0	0

TABLE 26 : Numbers of Carabidae caught in 15 pitfall traps.

SPECIES	PRE TREATMENT*						POST TREATMENT																								
	Untreated Plots			Treated Plots			Untreated Plots												Treated Plots												
	14/5	21/5	Tot	14/5	21/5	Tot	28/5	4/6	28/6	7/7	14/7	21/7	28/7	4/8	11/8	Tot	28/5	4/6	28/6	7/7	14/7	21/7	28/7	4/8	11/8	Tot					
<i>Carabus violaceus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	4	0	0	0	0	0	0	0	0	0	0	0				
<i>Carabus nemoralis</i>	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	1	0	0	1					
<i>Helorus brevicollis</i>	1	3	4	2	6	8	10	18	2	1	0	1	0	0	0	32	0	1	0	0	0	0	0	0	0	1					
<i>Notiophilus biguttatus</i>	1	2	3	4	1	5	7	6	0	0	0	0	1	0	0	14	0	0	0	0	0	0	0	0	0	0					
<i>Notiophilus palustris</i>	0	0	0	0	1	1	3	3	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0					
<i>Loricera pilicornis</i>	22	6	28	20	1	21	13	10	0	2	2	1	2	5	7	42	0	0	1	0	1	0	0	0	0	2					
<i>Clivina collaris</i>	20	0	20	0	0	0	0	1	0	0	2	0	0	0	0	3	1	0	0	0	0	0	0	0	0	1					
<i>Trochus quadristriatus</i>	2	1	3	2	0	2	0	0	0	2	3	4	6	3	5	23	5	0	0	0	0	0	0	0	0	5					
<i>Trochus obtusus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0					
<i>Acaphidion flavipes</i>	26	2	28	20	0	20	16	10	0	3	3	0	0	2	0	34	5	0	0	0	0	0	0	0	0	5					
<i>Bembidion lampros</i>	11	10	21	9	5	14	17	6	0	0	2	1	6	4	4	40	0	0	0	0	1	1	1	2	0	3					
<i>Bembidion tetracolum</i>	2	6	8	10	5	15	2	0	0	1	0	1	2	0	1	7	0	0	0	0	0	0	0	0	0	0					
<i>Bembidion guttula</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>Bembidion lunatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	3						
<i>Pterostichus versicolor</i>	6	8	14	5	1	6	6	34	6	2	0	0	0	0	0	48	0	0	0	0	0	0	0	0	0	0					
<i>Pterostichus malidus</i>	1	1	2	2	0	2	0	2	5	2	3	15	22	23	24	96	0	0	0	0	0	3	1	2	2	10					
<i>Pterostichus melanarius</i>	0	0	0	1	0	1	0	0	10	4	12	12	12	31	18	99	0	0	3	0	0	0	1	2	4	10					
<i>Pterostichus strenuus</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>Pterostichus niger</i>	0	0	0	0	0	0	0	0	0	0	0	0	2	1	3	6	0	0	0	0	0	0	0	0	0	0					
<i>Abax parallelepipedus</i>	0	0	0	0	0	0	1	1	2	0	0	0	1	0	2	7	0	0	0	0	0	0	0	0	0	0					
<i>Culathus fuscipes</i>	0	0	0	0	0	0	0	0	1	0	0	2	2	1	9	15	0	0	6	0	0	0	0	0	0	6					
<i>Culathus melanocephalus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0					
<i>Agonum dorsale</i>	8	6	14	4	8	12	15	12	3	0	0	0	0	0	0	30	1	1	0	3	0	0	0	0	0	5					
<i>Agonum muelleri</i>	5	5	10	6	2	8	3	1	0	0	0	0	0	0	1	0	5	0	0	0	0	0	0	0	0	0					
<i>Amara plabeja</i>	0	1	1	2	1	3	1	1	0	3	4	1	3	0	0	13	0	0	0	0	1	0	0	0	0	1					
<i>Amara similata</i>	2	4	6	0	5	5	6	10	2	2	1	1	1	1	2	26	2	0	1	0	1	0	0	0	0	4					
<i>Amara ovata</i>	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0					
<i>Amara anthobia</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0					
<i>Amara bifrons</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1					
<i>Amara calica</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0	0	0	1	1	1	0	0	3					
<i>Amara familiaris</i>	3	3	6	2	4	6	4	5	2	0	1	0	1	0	0	13	0	1	0	0	0	0	0	0	0	1					
<i>Amara aenea</i>	19	12	31	6	3	9	10	18	0	3	0	0	0	1	0	32	1	0	0	0	0	0	0	0	0	1					
<i>Amara laticollis</i>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>Harpalus rufipes</i>	0	0	0	0	1	1	0	4	0	12	9	6	23	15	13	82	0	0	0	0	0	0	1	2	1	4					
<i>Harpalus aeneus</i>	4	3	7	4	1	5	1	3	1	3	6	2	2	3	2	23	0	0	0	0	0	0	0	3	0	3					
<i>Harpalus tardus</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0					
<i>Anisodactylus binotatus</i>	6	8	14	5	2	7	4	7	1	1	0	0	1	0	0	14	2	0	0	0	0	0	0	0	0	2					
<i>Metalictus foveatus</i>	0	0	0	2	0	2	1	1	0	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0					
<i>Acupalpus meridionalis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	3	1	4					
	223			154															732												78

* methiocarb baits and 'fenofos' granules first applied 1915.

TABLE 27 : Numbers of Staphylinidae caught in 15 pitfall traps.

	PRE TREATMENT*						POST TREATMENT																					
	Untreated Plots			Treated Plots			Untreated Plots									Treated Plots												
	14/5	21/5	Tot	14/5	21/5	Tot	28/5	4/6	28/6	7/7	14/7	21/7	28/7	4/8	11/8	Tot	28/5	4/6	28/6	7/7	14/7	21/7	28/7	4/8	11/8	Tot		
<i>Tachyporus</i> spp.	10	6	16	9	14	23	6	7	0	9	18	9	12	4	3	68	8	7	4	1	3	0	0	1	0	24		
Others	21	10	31	16	14	32	8	10	1	4	18	3	16	5	2	67	9	9	5	0	3	2	1	0	2	31		
Total	31	16	47	25	28	1	14	17	1	13	36	12	28	9	5	135	17	16	9	1	6	2	1	1	2	55		

* methiocarb baits and 'fonofos' granules first applied 1915.

TABLES 28 - 35 ARE CONTAINED IN APPENDIX 8 p 374

TABLE 36 : Effect of 'exclusion' treatments on the numbers of mummies per 100 tillers - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		N.S.	N.S.	N.S. §	Δ	N.S.	N.S.	N.S.	N.S.	N.S.
Sow date	Main treatment comparisons									
1	1, 2			N.S.						
	2, 3			N.S.						
	1, 3			N.S.						
2	1, 2			N.S.						
	2, 3			N.S.						
	1, 3			N.S.						
3	1, 2			N.S.						
	2, 3			N.S.						
	1, 3			N.S.						

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons		N.S.	N.S.	N.S.	Δ	N.S. §	N.S.	N.S.	N.S.	N.S.
Sow date	Main treatment comparisons									
1	2, 3					N.S.				
	1, 3					N.S.				
2	2, 3					N.S.				
	1, 3					N.S.				
3	2, 3					N.S.				
	1, 3					N.S.				

KEY

N.S. - not significant

Δ - incomplete data.

§ - significant interaction between main treatments and sow date.

TABLE 37 : Effect of 'exclusion' treatments on the ratio of mummies: total aphids - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		N.S.	N.S.	N.S. [§]	Δ	N.S.	N.S.	N.S.	N.S.	N.S.
Sow date	Main treatment comparisons									
1	1, 2			N.S.						
	2, 3			N.S.						
	1, 3			N.S.						
2	1, 2			N.S.						
	2, 3			N.S.						
	1, 3			N.S.						
3	1, 2			N.S.						
	2, 3			N.S.						
	1, 3			N.S.						

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons		*	N.S.	N.S.	Δ	N.S.	N.S.	N.S.	N.S.	N.S.
Sow date	Main treatment comparisons									
1	2, 3	N.S.								
	1, 3	N.S.								
2	2, 3	*								
	1, 3	N.S.								
3	2, 3	N.S.								
	1, 3	N.S.								

KEY

N.S. - not significant

* - significant ($p < .05$)

§ - significant interaction between main treatments and sow date.

Δ - incomplete data.

TABLE 38 : Effect of 'exclusion' treatments on the numbers of syrphid eggs per 100 tillers - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		N.S.	N.S.	N.S.	Δ	N.S.	N.S.	N.S.	N.S.	N.S.
Sow date	Main treatment comparisons									
1	1, 2									
	2, 3									
	1, 3									
2	1, 2									
	2, 3									
	1, 3									
3	1, 2									
	2, 3									
	1, 3									

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons		N.S.	*	N.S.	Δ	N.S.	N.S.	N.S.	N.S.	N.S.
Sow date	Main treatment comparisons									
1	2, 3		N.S.							
	1, 3		*							
2	2, 3		N.S.							
	1, 3		*							
3	2, 3		N.S.							
	1, 3		N.S.							

KEY

N.S. - not significant

* - significant ($p < .05$)

Δ - incomplete data.

TABLE 39 : Effect of 'exclusion' treatments on the ratio of syrphid eggs:
total aphids - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		N.S.	N.S.	N.S.	Δ	N.S.	N.S.	N.S.	N.S.	N.S.
Sow date	Main treatment comparisons									
1	1, 2									
	2, 3									
	1, 3									
2	1, 2									
	2, 3									
	1, 3									
3	1, 2									
	2, 3									
	1, 3									

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	*	N.S.
Sow date	Main treatment comparisons									
1	2, 3								N.S.	
	1, 3								N.S.	
2	2, 3								N.S.	
	1, 3								N.S.	
3	2, 3								*	
	1, 3								*	

KEY

N.S. - not significant

* - significant ($p < .05$)

Δ - incomplete data.

TABLE 40 : Effect of 'exclusion' treatments on the numbers of aphids killed by disease (*Entomophthora* spp.) per 100 tillers - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects	N.S.	N.S.	N.S.	Δ	N.S.	N.S.	N.S.	N.S.	*
Sow date	Main treatment comparisons								
1	1, 2								N.S.
	2, 3								N.S.
	1, 3								N.S.
2	1, 2								N.S.
	2, 3								N.S.
	1, 3								N.S.
3	1, 2								**
	2, 3								N.S.
	1, 3								*

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons	N.S.	N.S.	N.S.	Δ	N.S.	N.S.	N.S.	N.S.	*
Sow date	Main treatment comparisons								
1	2, 3								
	1, 3								N.S.
2	2, 3								N.S.
	1, 3								N.S.
3	2, 3								N.S.
	1, 3								N.S.

KEY

N.S. - not significant

* - significant ($p < .05$)

** - highly significant ($p < .01$)

Δ - incomplete data.

TABLE 41 : Effect of 'exclusion' treatments on the proportion of aphids killed by disease (*Entomophthora* spp.) - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		N.S.	N.S.	N.S.	Δ	N.S. [§]	N.S.	N.S.	N.S.	N.S.
Sow date	Main treatment comparisons									
1	1, 2					N.S.				
	2, 3					N.S.				
	1, 3					N.S.				
2	1, 2					N.S.				
	2, 3					N.S.				
	1, 3					N.S.				
3	1, 2					N.S.				
	2, 3					N.S.				
	1, 3					N.S.				

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons		N.S.	N.S.	N.S.	Δ	N.S. [§]	N.S.	N.S.	N.S.	*
Sow date	Main treatment comparisons									
1	2, 3					N.S.				N.S.
	1, 3					N.S.				N.S.
2	2, 3					N.S.				*
	1, 3					N.S.				*
3	2, 3					N.S.				*
	1, 3					N.S.				N.S.

KEY

N.S. - not significant

* - significant ($p < .05$)

[§] - significant interaction between main treatments and sow date.

Δ - incomplete data.

3.3.2.3.1 Role of Ground based predators

Patterns of population development were similar on 'CONTROL' and 'NOGRPRED' treatments for all 3 sow dates and for both aphid species (Figures 27 - 32). Where differences between these treatments did exist, they were towards lower aphid populations on NOGRPRED compared to control. In some cases, these differences appeared to be significant according to ANOVA, but the level of significance never exceeded $p = .05$ and they did not persist between consecutive population counts (Tables 61 - 64). According to Figures 31 and 32, the application of insecticides on 20/6 was followed by a reduction in *M. dirhodum* populations on sow dates 2 and 3. Although this suggests a direct adverse effect of the insecticides on the aphids, the lack of an effect on the aphids on sow date 1 is difficult to explain. Perhaps they could have evaded contact with the chemicals if they moved across the soil surface between plants less often than aphids on younger plants. In the case of *S. avenae* there were no indications of direct insecticide effects on sow dates 1 and 2 although on sow date 3, rates of increase after insecticide application on 20/6 were higher on 'CONTROL' than all the treatments.

Although the possibility of a direct insecticidal effect on aphids demands the use of great caution in interpreting the data obtained on sow dates 2 and 3, the results from sow date 1 constitute good evidence that ground beetles predation was a negligible source of mortality in *S. avenae* and *M. dirhodum*.

3.3.2.3.2 Role of 'aerial' predators

Coccinellids were so scarce in 1978 that formal counts were abandoned soon after the beginning of the experiment. Syrphids (mainly *Erisyrphus balteatus* (Deg.)) were the only 'aerial' or 'aphid specific' predators occurring in significant numbers. Syrphid eggs were not evenly

TABLES 42 - 60 ARE CONTAINED IN APPENDIX 9 p 382

spread between sowings 1, 2 and 3. Instead, oviposition occurred after the arrival of aphids which sequentially colonised sowings 1, 2 then 3 (Section 3.3.2.4).

In interpreting the data, greatest weight is placed on comparisons between 'NOGRPRED' and 'NOPRED', both having been treated with 'fonofos' and 'methiocarb', only NOPRED having received carbaryl sprays to kill aerial predators.

The 'NOPRED' treatment resulted in considerably increased numbers of both *S. avenae* and *M. dirhodum* on sow date 1 (Figures 27 and 30). On 11/7 there were means of 80.7 *S. avenae*/100 tillers on NOPRED compared with 6.3 on NOGRPRED (Table 47). On 6/7 there were 62.3 *M. dirhodum* compared with 5.0 (Table 55). ANOVA for *S. avenae* showed that these differences were significant in terms of 'numbers per 100 tillers' ($p < .05$) (Table 61) and 'percent infested tillers' ($p < .01$) (Table 62) and the effect remained significant for 2 consecutive sampling dates (11/7 and 17/7). *M. dirhodum* populations reached their peak earlier, but again the difference persisted over 2 sampling occasions (6/7 and 11/7) in the case of 'numbers per 100 tillers' ($p < .05$), although in terms of percent infested tillers, differences were significant only on 6/7 ($p < .05$). On the later sown plots, much smaller differences were found between 'NOPRED' and 'NOGRPRED'. On sow date 2, *S. avenae* populations were highest on 'NOPRED' ($\bar{x} = 118$ compared with 86.3 on 'NOGRPRED' on 17/7 (Table 48) and their rate of decline was slower during the eventual 'crash' compared to other treatments (Figure 28) but their numbers did not differ significantly from NOGRPRED (Tables 61, 62). In the case of *M. dirhodum*, increases on NOPRED appeared more obvious (Figure 66) ($\bar{x} = 111.5$ compared to 25.0 on 'NOGRPRED' on 11/7 (Table 50); 163.5 compared to 81.0 on 17/7 (Table 57)) but this was not significant ($p = .05$) (Tables 63 and 64). On sow date 3, comparisons for *S. avenae* were similar

to those on sowdate 2; highest numbers on NOPRED on 3/8 (Figure 29) ($\bar{x}$ = 115.0 compared to 46.0 on 'NOGRPRED' (Table 50) but no significant differences (Tables 61 and 62).

M. dirhodum was more abundant and declined more slowly on NOPRED and this proved to be significant on 3/8 ($\bar{x}$ = 14.3 compared to 1.0 on 'NOGRPRED' (Table 59)) in terms of 'numbers per 100 tillers' ($p < .05$) (Table 63).

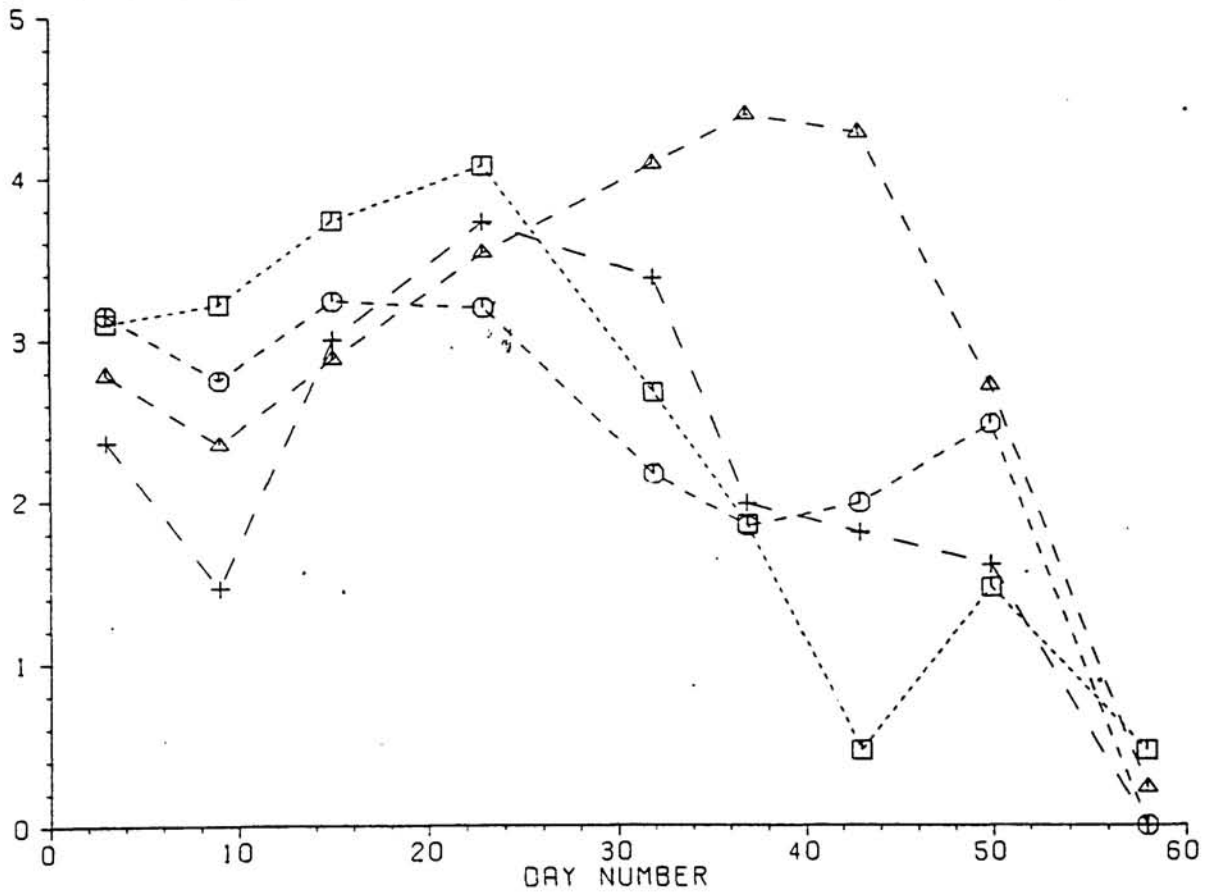
The results suggest that syrphids are capable of considerable impact on the abundance of cereal aphids. In addition to causing a 'premature' population crash in both species, they significantly reduced peak population levels of *M. dirhodum*. This finding is particularly remarkable in view of the seemingly low abundance of syrphids. The maximum number of eggs found during '100 tiller' searches was 34 (Tables 28 - 35) and very few larvae were found. The low resting sites used by syrphid larvae during daytime (Vickerman and Sunderland, 1975) explains how abundance can readily be underestimated during counts. Considerations of voracity in relation to syrphid development may explain the suddenness of effect on prey populations. Laboratory studies on syrphid voracity show remarkable increases in predation rates during larval development. Benestad (1970a, b) demonstrated that *Syrphus corollae* (Fabr) obtained 90% of their entire aphid intake during the third instar. O'Donnell (1972), working with *E. balteatus* obtained similar results and found that each individual consumed more than 1000 aphids.

In a synchronous field syrphid population, moulting to the final larval instar could suddenly result in substantially increased predation rates, sufficient to induce an aphid population crash. In this context it is significant that close inspection of Dean's data (Dean, 1974d - Figures 3 and 4) supports this hypothesis, population collapse following rapidly after the final larval moult.

There are 3 possible explanations for the reduced impact of syrphids .

FIGURE 27 :

S.AVENAE-TOTAL APHIDS PER 100 TILLERS (LOG(X+1))-SOWDATE 1

KEYAssessment
dateDay
No.

7/6

3

13/6

9

19/6

15

27/6

23

6/7

32

11/7

37

17/7

43

24/7

50

3/8

58

□ - CONTROL

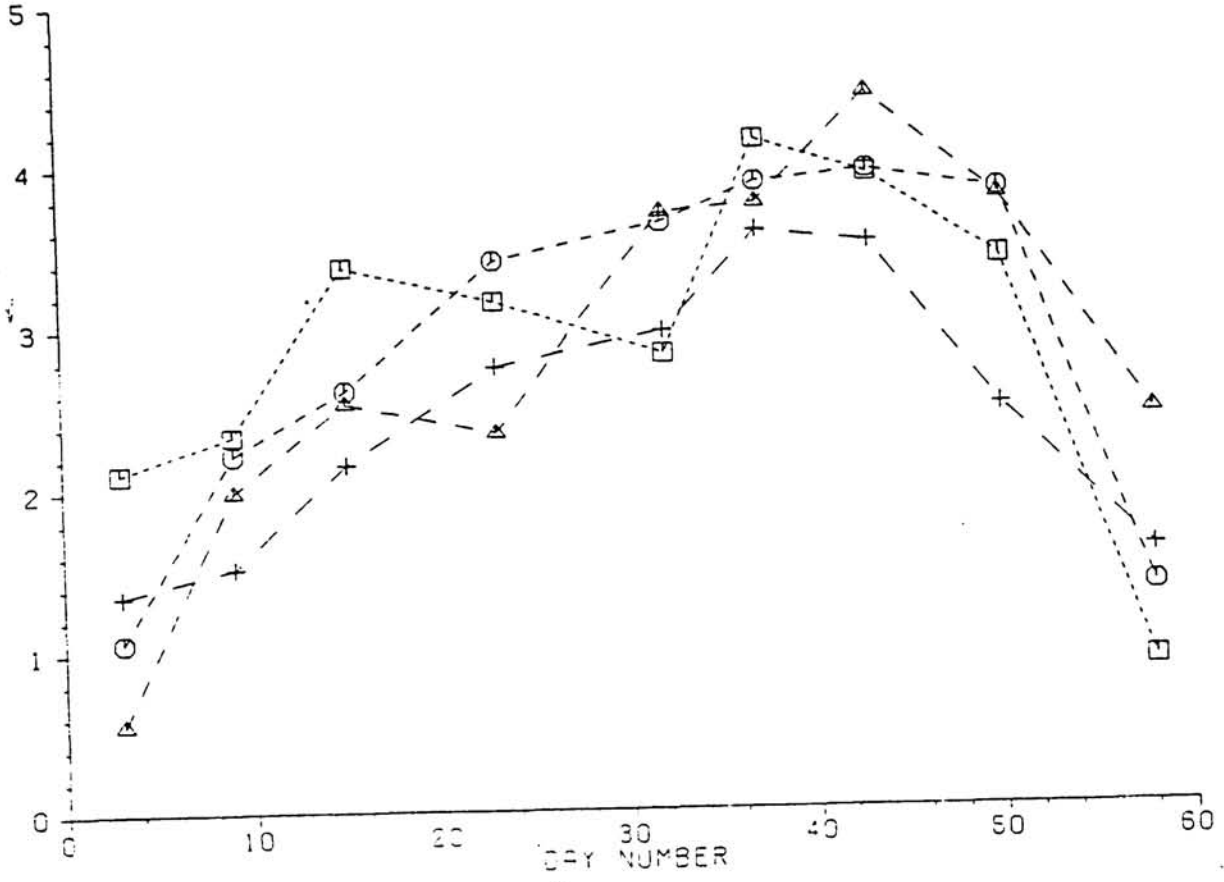
○ - NOGRPRED

△ - NOPRED

+ - NOPRED (UNSPRAYED)

FIGURE 28 :

S.AVENAE-TOTAL APHIDS PER 100 TILLERS (LOG(X+1))-SOWDATE 2

KEYAssessment
dateDay
No.

7/6

3

13/6

9

19/6

15

27/6

23

6/7

32

11/7

37

17/7

43

24/7

50

3/8

58

□ - CONTROL

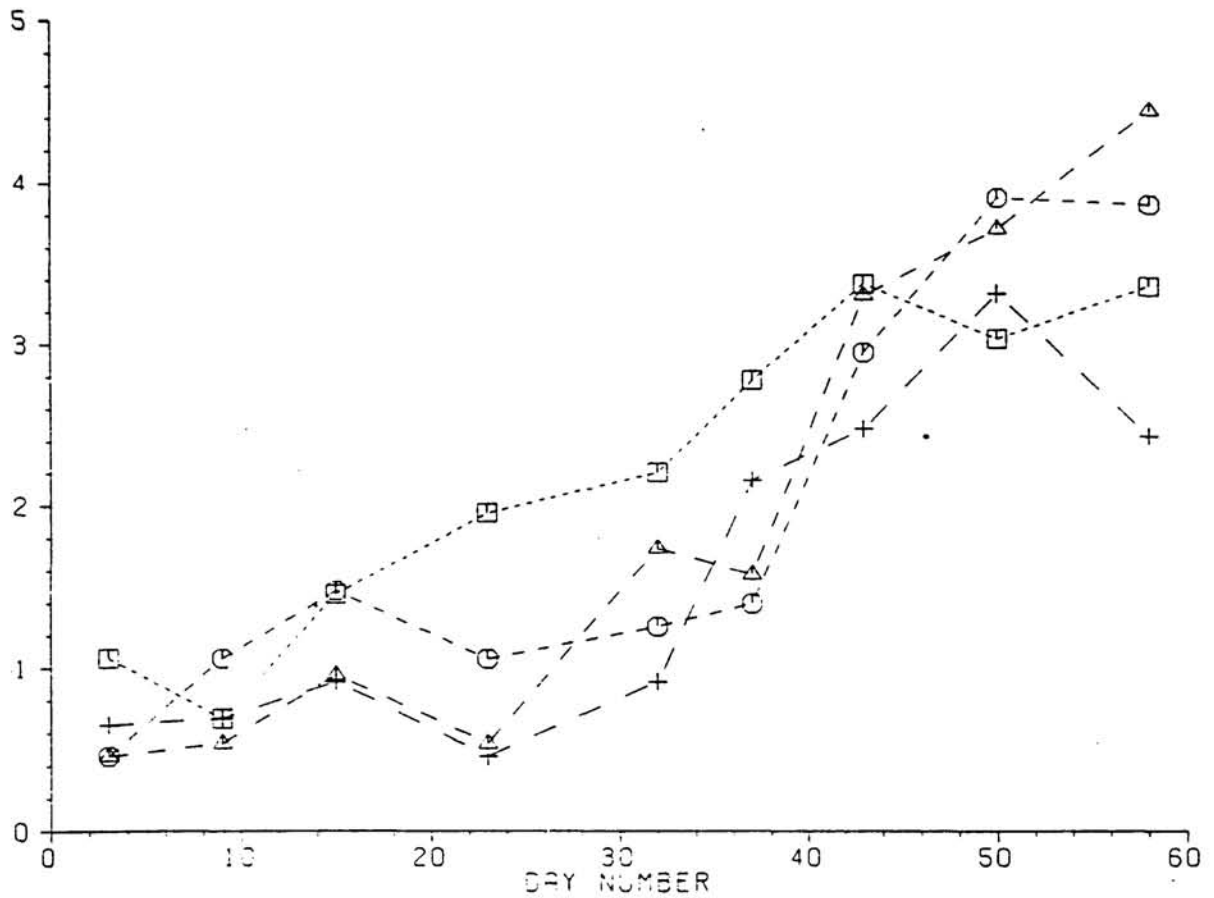
○ - NOGRPRED

△ - NOPRED

+ - NOPRED (UNSPRAYED)

FIGURE 29 :

S. AVENAE-TOTAL APHIDS PER 100 TILLERS (LOG(X+1))-SOWDATE 3

KEY

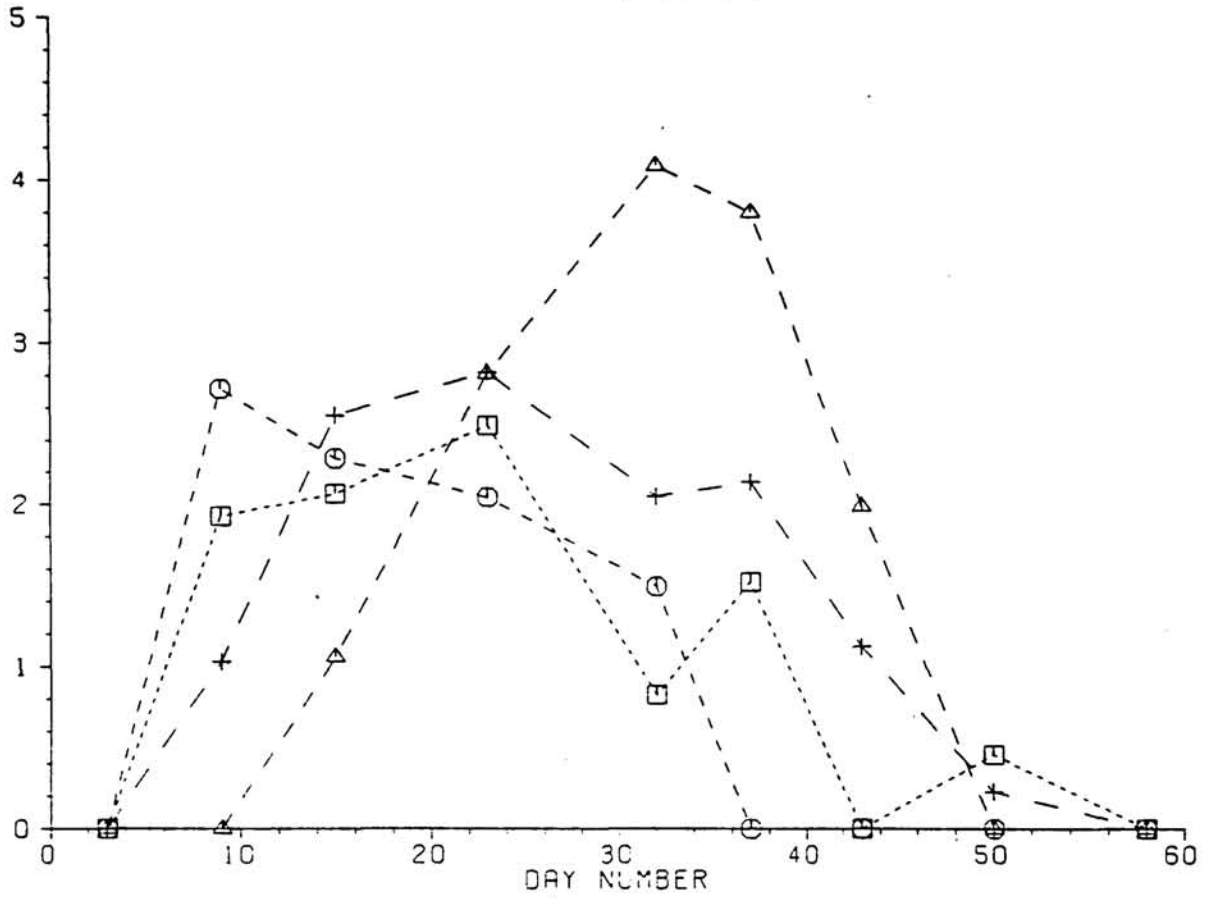
Assessment date	Day No.
-----------------	---------

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- CONTROL
○	- NOGRPRED
△	- NOPRED
+	- NOPRED (UNSPRAYED)

FIGURE 30 :

M.DIRRHODUM-TOTAL APHIDS PER 100 TILLERS (LOG(X+1))-SOWDATE 1

KEYAssessment
dateDay
No.

7/6

3

13/6

9

19/6

15

27/6

23

6/7

32

11/7

37

17/7

43

24/7

50

3/8

58

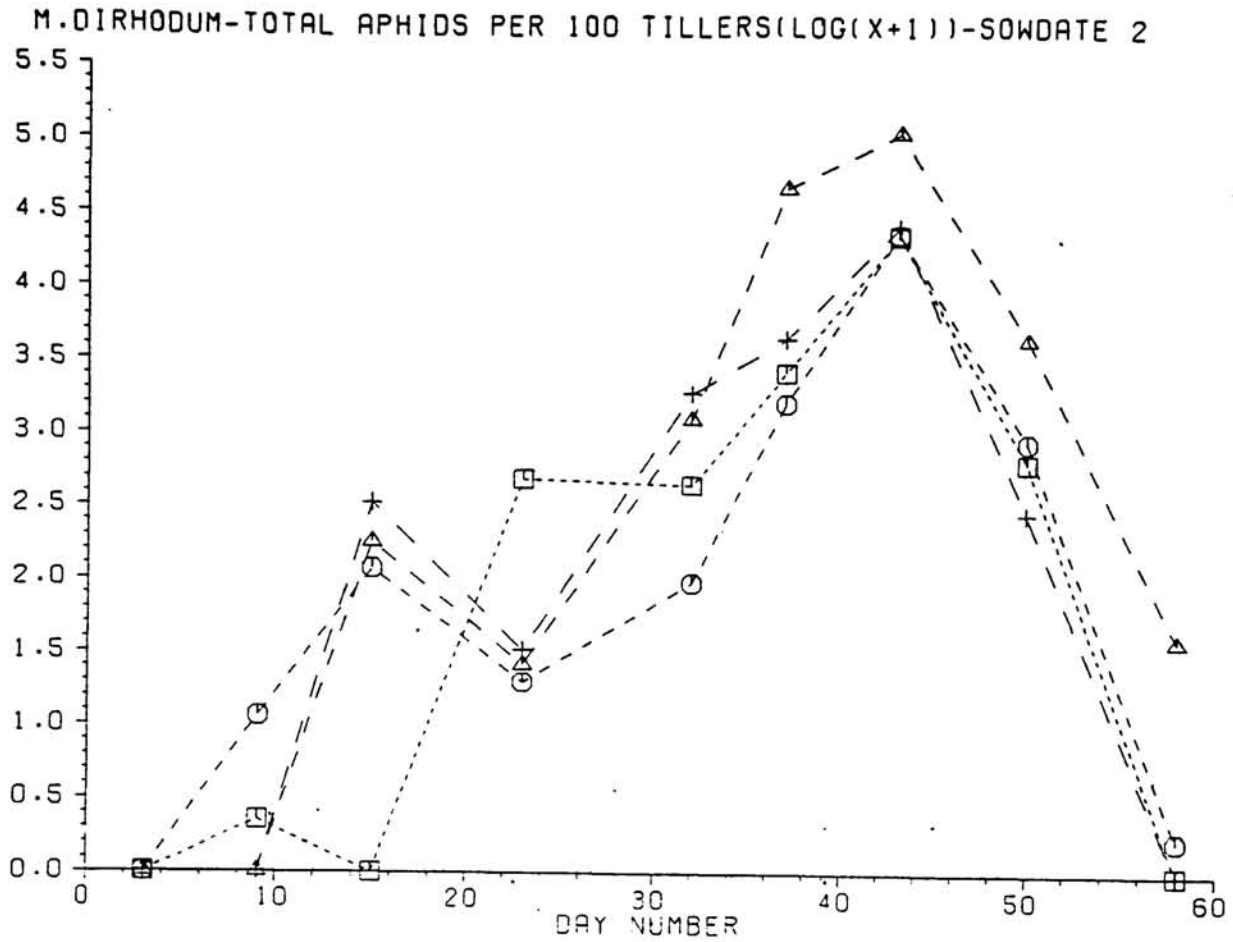
□ - CONTROL

○ - NOGRPRED

△ - NOPRED

+ - NOPRED (UNSPRAYED)

FIGURE 31 :

KEYAssessment
dateDay
No.

7/6

3

13/6

9

19/6

15

27/6

23

6/7

32

11/7

37

17/7

43

24/7

50

3/8

58

□ - CONTROL

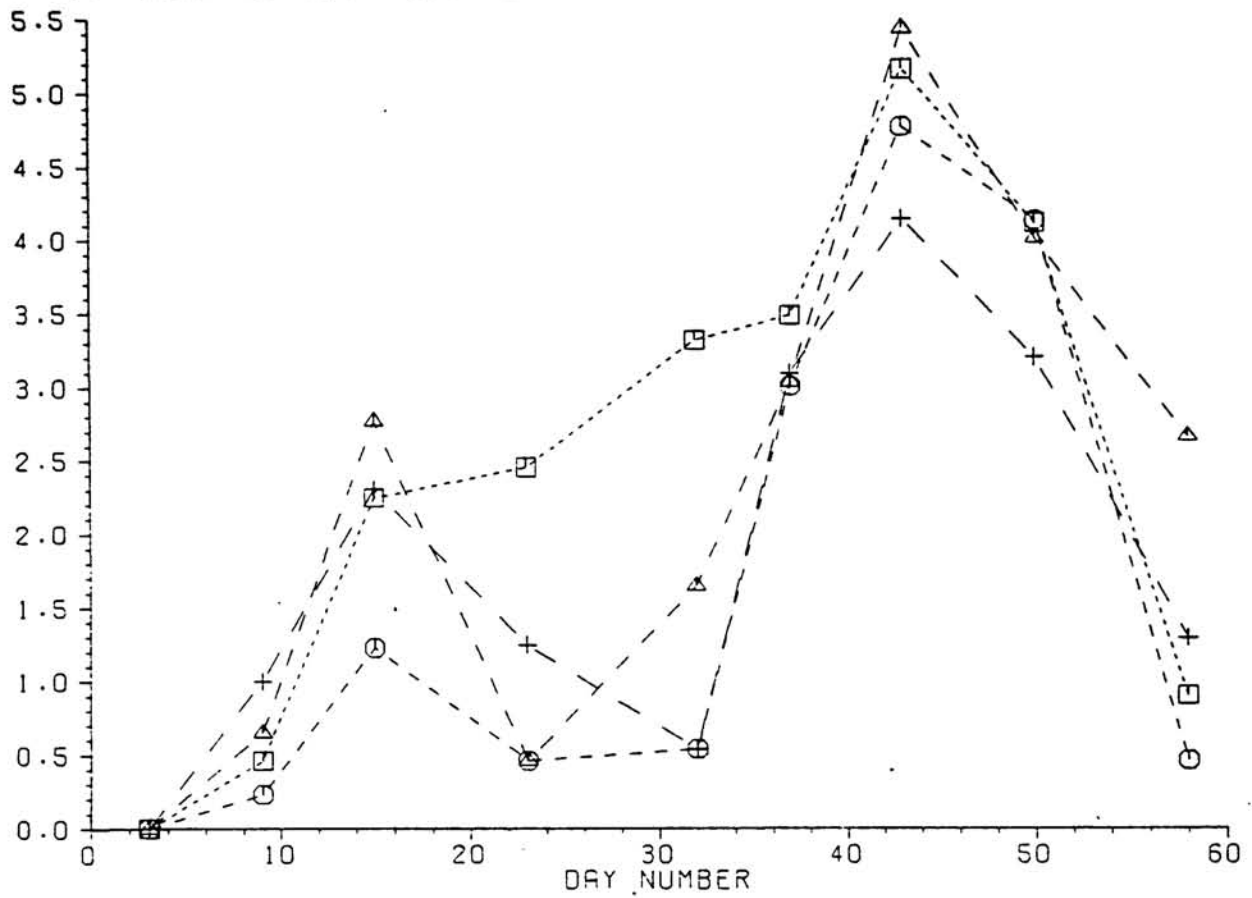
○ - NOGRPRED

△ - NOPRED

+ - NOPRED (UNSPRAYED)

FIGURE 32 :

M.DIRRHODUM-TOTAL APHIDS PER 100 TILLERS (LOG(X+1))-SOWDATE 3

KEYAssessment
dateDay
No.

7/6

3

13/6

9

19/6

15

27/6

23

6/7

32

11/7

37

17/7

43

24/7

50

3/8

58

□ - CONTROL

○ - NOGRPRED

△ - NOPRED

+ - NOPRED (UNSPRAYED)

TABLE 61 : Effect of predator exclusion on *S. avenae* populations (numbers per 100 tillers) - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects	N.S.	*	N.S.	N.S.	N.S.	N.S. [§]	N.S. [§]	N.S.	N.S. [§]
Sow date	Main treatment comparisons								
1	1, 2		N.S.			N.S.	N.S.		N.S.
	2, 3		N.S.			*	*		N.S.
	1, 3		N.S.			*	**		N.S.
2	1, 2		N.S.			N.S.	N.S.		N.S.
	2, 3		N.S.			N.S.	N.S.		N.S.
	1, 3		N.S.			N.S.	N.S.		*
3	1, 2		N.S.			N.S.	N.S.		N.S.
	2, 3		N.S.			N.S.	N.S.		N.S.
	1, 3		N.S.			N.S.	N.S.		N.S.

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S. [§]	N.S.	N.S.
Sow date	Main treatment comparisons								
1	2, 3						N.S.		
	1, 3						N.S.		
2	2, 3						N.S.		
	1, 3						N.S.		
3	2, 3						N.S.		
	1, 3						N.S.		

KEY

N.S. - not significant

* - significant ($p < .05$)

** - highly significant ($p < .01$)

[§] - significant interaction between main treatments and sow date.

TABLE 62 : Effect of predator exclusion on *S. avenae* populations (percentage of tillers infested) - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects	Δ	*	N.S.	Δ	N.S.	**	N.S. [§]	N.S.	Δ
Sow date	Main treatment comparisons								
1	1, 2		*			N.S.	N.S.		
	2, 3		N.S.			**	**		
	1, 3		N.S.			**	**		
2	1, 2		*			N.S.	N.S.		
	2, 3		N.S.			N.S.	N.S.		
	1, 3		**			N.S.	N.S.		
3	1, 2		N.S.			N.S.	N.S.		
	2, 3		*			N.S.	N.S.		
	1, 3		*			*	N.S.		

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons	Δ	N.S.	N.S.	Δ	N.S.	N.S.	N.S.	N.S.	Δ
Sow date	Main treatment comparisons								
1	2, 3								
	1, 3								
2	2, 3								
	1, 3								
3	2, 3								
	1, 3								

KEY

N.S. - not significant

* - significant ($p < .05$)

** - highly significant ($p < .01$)

[§] - significant interaction between main treatments and sow date.

Δ - incomplete data.

TABLE 63 : Effect of predator exclusion on *M. dirhodum* populations (numbers per 100 tillers) - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		Φ	N.S.	N.S.	*	N.S. [§]	*	*	N.S.	*
Sow date	Main treatment comparisons									
1	1, 2				N.S.	N.S.	N.S.			N.S.
	2, 3				N.S.	*	*			N.S.
	1, 3				N.S.	*	*			N.S.
2	1, 2				N.S.	N.S.	N.S.			N.S.
	2, 3				N.S.	N.S.	N.S.			N.S.
	1, 3				N.S.	N.S.	N.S.			N.S.
3	1, 2				N.S.	*	N.S.			N.S.
	2, 3				N.S.	N.S.	N.S.			*
	1, 3				N.S.	N.S.	N.S.			*

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons		Φ	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Sow date	Main treatment comparisons									
1	2, 3									
	1, 3									
2	2, 3									
	1, 3									
3	2, 3									
	1, 3									

KEY

N.S. - not significant

* - significant ($p < .05$)

[§] - significant interaction between main treatments and sow date.

Φ - too few aphids to analyse.

TABLE 64 : Effect of predator exclusion on *M. dirhodum* populations (percentage of tillers infested) - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Main set of analyses

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		♦	N.S.	N.S.	Δ	N.S. [§]	N.S.	N.S. [§]	N.S.	Δ
Sow date	Main treatment comparisons									
1	1, 2					N.S.		N.S.		
	2, 3					*		N.S.		
	1, 3					*		N.S.		
2	1, 2					N.S.		N.S.		
	2, 3					N.S.		N.S.		
	1, 3					N.S.		N.S.		
3	1, 2					*		N.S.		
	2, 3					N.S.		N.S.		
	1, 3					*		N.S.		

(B) Supplementary analyses using data from the unsprayed zone of treatment

3

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment comparisons		♦	N.S.	N.S.	Δ	N.S.	N.S. [§]	N.S. [§]	N.S.	Δ
Sow date	Main treatment comparisons									
1	2, 3						N.S.	N.S.		
	1, 3						N.S.	N.S.		
2	2, 3						N.S.	N.S.		
	1, 3						N.S.	N.S.		
3	2, 3						N.S.	N.S.		
	1, 3						N.S.	**		

KEY

N.S. - not significant

* - significant ($p < .05$)

** - highly significant ($p < .01$)

[§] - significant interaction between main treatments and sow date.

Δ - incomplete data.

♦ - too few aphids to analyse.

on sow dates 2 and 3 compared with sow date 1.

(1) syrphid eggs were more abundant and evenly distributed on the early sowing.

(11) since plants were taller on sow date 1, selective application of carbaryl was easier to achieve by directing the spray to the lower half of the wheat plants.

(111) since sow dates 2 and 3 remained attractive for larviposition longer than sow date 1, natality may have overwhelmed the effects of differential mortality on the different treatments. If aphid nymphs deposition is a density dependent process, natality could cancel out any differences that might be caused by mortality.

The use of insecticidal check methods always carries the risk that the insecticides might have direct effects (positive or negative) on prey (Hodek *et al*, 1972; De Bach *et al*, 1976). Even the evidence of a direct detrimental effect of carbaryl on aphids at the time of spraying is no guarantee that stimulation of fecundity (as is known to occur in mites (Coaker, 1977; Dittrich *et al*, 1974)) could not result in population increase later on. Although unlikely, this possibility does warrant further study. Perhaps, further light can be shed on this question by considering the timing of the population crashes attributed to predation. Figures 50 and 54 show that the decline in 'CONTROL' aphids on sow date 1 occurred at the same time for both *M. dirhodum* and *S. avenae*; a result entirely compatible with a hypothesis of non-discriminating Syrphid predation. Other causes of population crash (e.g. changing host plant nutrient status) would be less likely to reduce populations of both species simultaneously.

3.3.2.4. Aphid attack in relation to sow date.

The 'raw data' derived on each aphid census are shown in Tables

42 - 50 (*S. avenae*) and 52 - 59 (*M. dirhodum*). Records of 'percent infested tillers' are given in Tables 51 (*S. avenae*) and 60 (*M. dirhodum*).

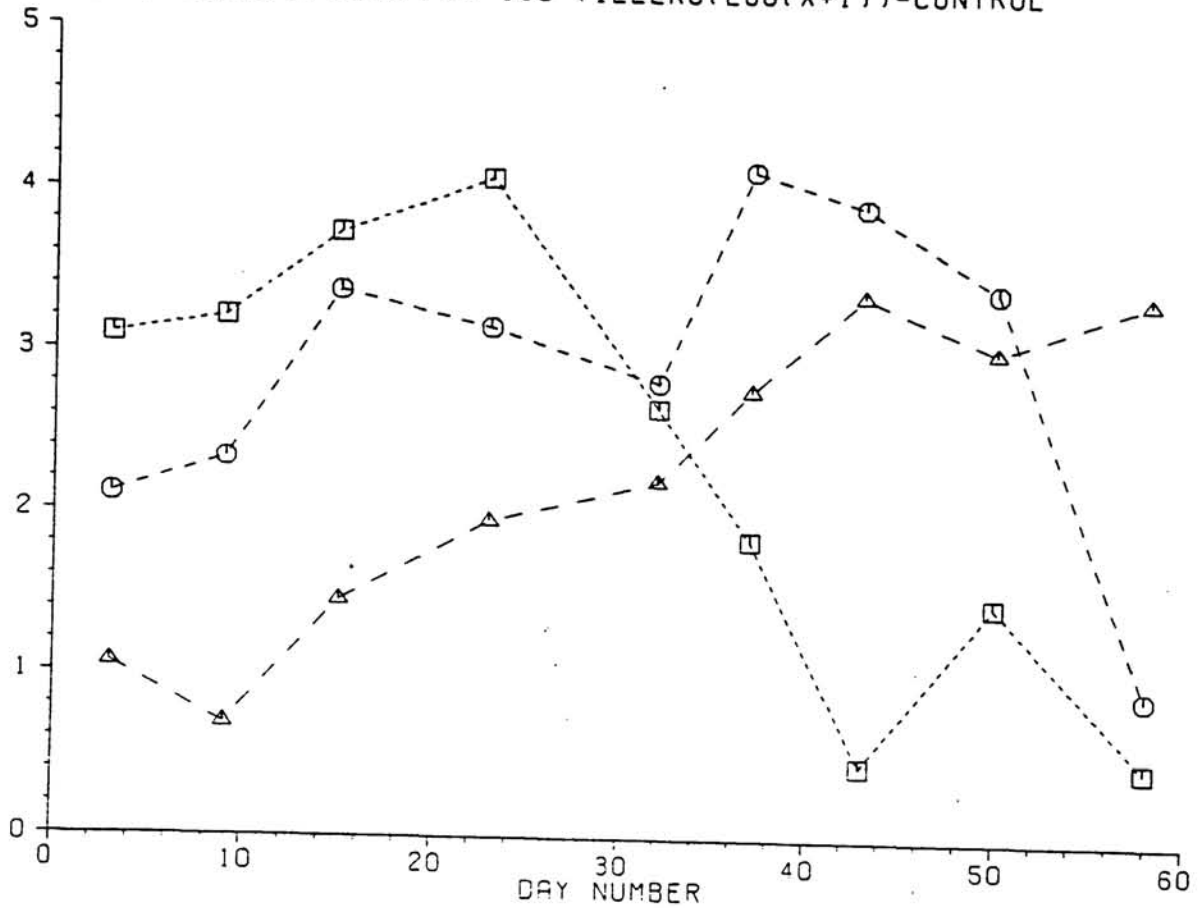
The most striking feature of the results was the successive exploitation, by aphids of winter, early spring and late spring sown crops. This pattern is discussed in detail in terms of the abundance of aphids, settling of alates and larviposition by alates for both aphid species.

3.3.2.4.1 Total aphids (all stages)

S. avenae (Figures 33, 34 and 35)

As the summer progressed, each sowing in turn became the preferred crop in terms of aphid abundance. Although the sequence of preference shift was consistent between main treatments, the timing of the sow date 1 population crash was brought forward on 'NOGRPRED' and 'CONTROL' due to the impact of syrphid predation (Figures 33 and 34). On the 'NOPRED' treatment, population levels were sustained until after 17/6 (Figure 35) when numbers 'collapsed', probably due to a change in host plant 'suitability'. Although populations on all sowings followed a similar cycle of population build up and decline, input of immigrants to the crop occurred over a much shorter period on sow date 1 compared to later crops which showed a prolonged attractiveness to aphid colonists (see below). On sow dates 1 and 2, population build up followed colonisation and nymph deposition during crop growth stages 50 - 59 (inflorescence emergence), corresponding closely to the findings on growth stage preference reported in Chapter 4. Colonisation of sow date 3 occurred prior to 'heading' but the non-availability of alternative crops late in the season may have resulted in the decay of any inherent behavioural preference. Thus, on 3/8, sow date 3 supported large populations of *S. avenae* after populations had declined on the earlier crops (Figures 33, 34 and 35) clearly indicating the importance of reduced plant suitability as a cause of aphid decline. On 10/8, virtually no aphids remained on the experimental plots and the causes of this population crash are unknown. Weather was not especially

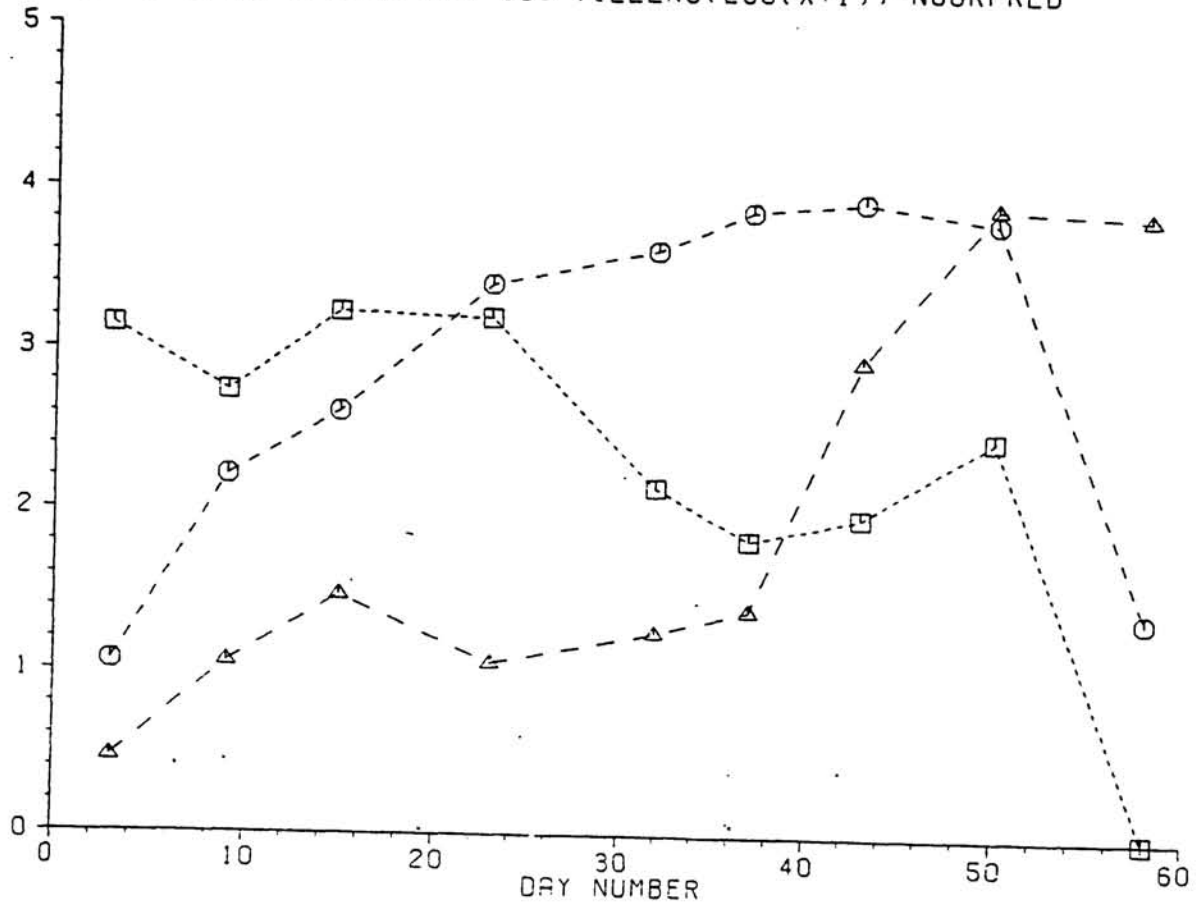
FIGURE 33 :

S.AVENAE-TOTAL APHIDS PER 100 TILLERS($\text{LOG}(X+1)$)-CONTROLKEY

Assessment date	Day No.	
7/6	3	□ - SOWDATE 1
13/6	9	○ - SOWDATE 2
19/6	15	△ - SOWDATE 3
27/6	23	
6/7	32	
11/7	37	
17/7	43	
24/7	50	
3/8	58	

FIGURE 34 :

S.AVENAE-TOTAL APHIDS PER 100 TILLERS (LOG(X+1))-NOGRPREO

KEYAssessment
dateDay
No.

7/6 3

13/6 9

19/6 15

27/6 23

6/7 32

11/7 37

17/7 43

24/7 50

3/8 58

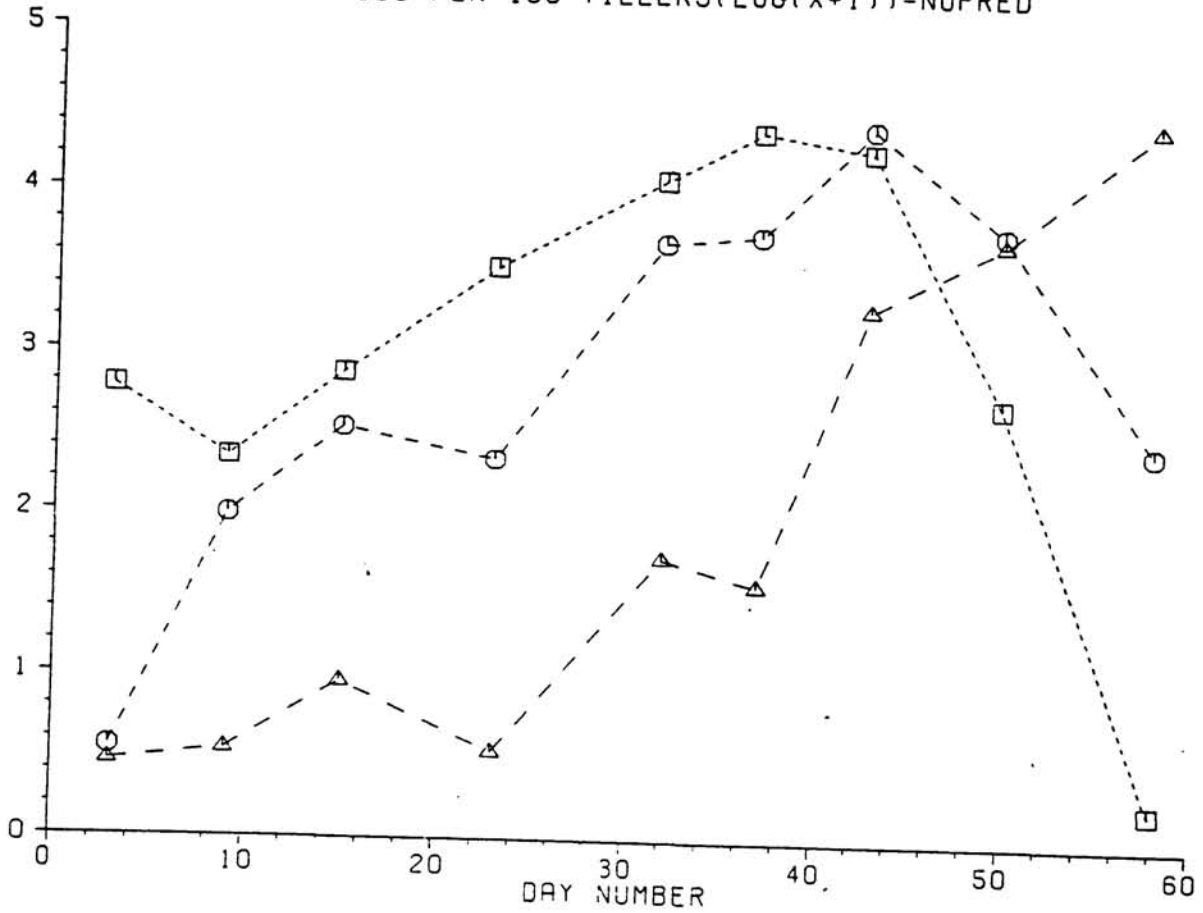
□ - SOWDATE 1

○ - SOWDATE 2

△ - SOWDATE 3

FIGURE 35 :

S.AVENAE-TOTAL APHIDS PER 100 TILLERS (LOG(X+1))-NOPRED

KEYAssessment
dateDay
No.

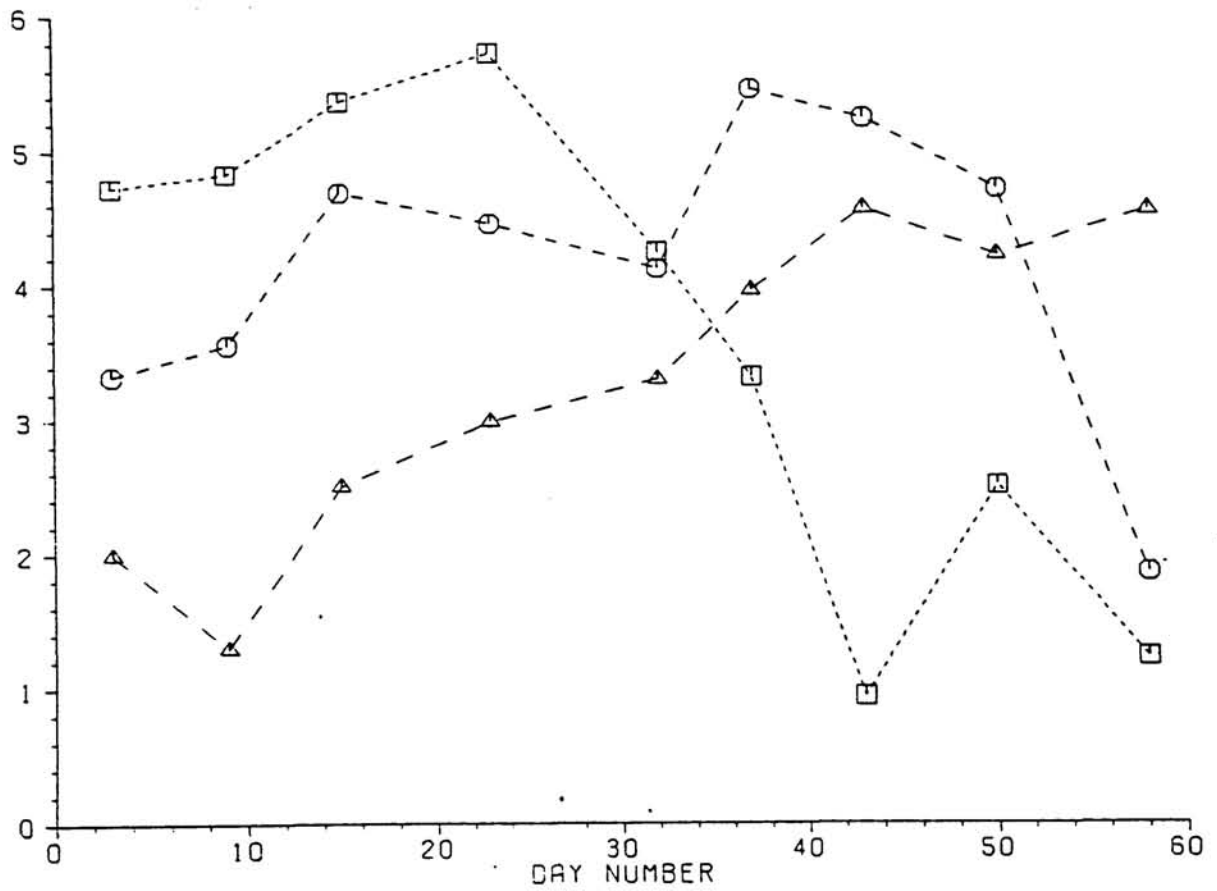
7/6
13/6
19/6
27/6
6/7
11/7
17/7
24/7
3/8

3
9
15
23
32
37
43
50
58

□ - SOWDATE 1
○ - SOWDATE 2
△ - SOWDATE 3

FIGURE 36 :

S.AVENAE-TOTAL APHIDS PER METRE SQUARED (LOG(X+1))-CONTROL

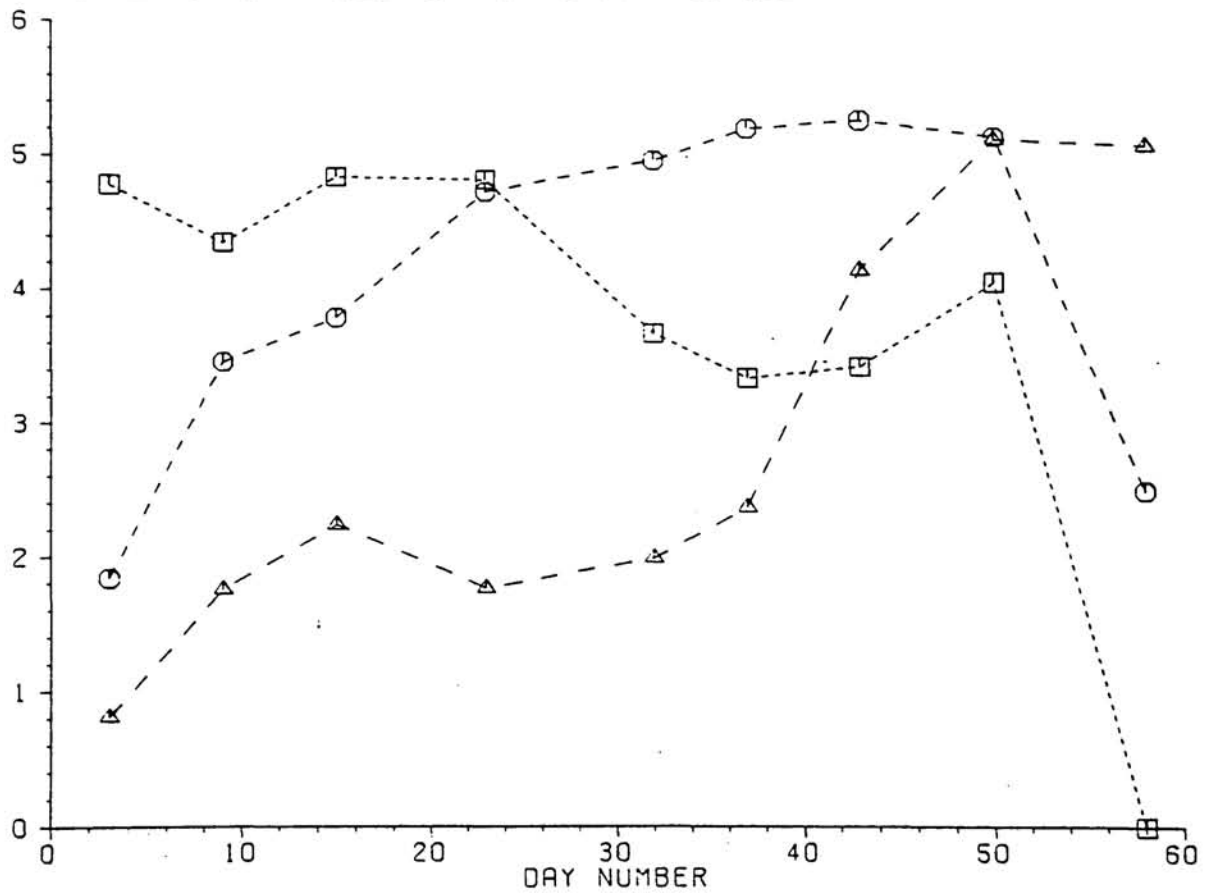
KEYAssessment
dateDay
No.

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

FIGURE 37 :

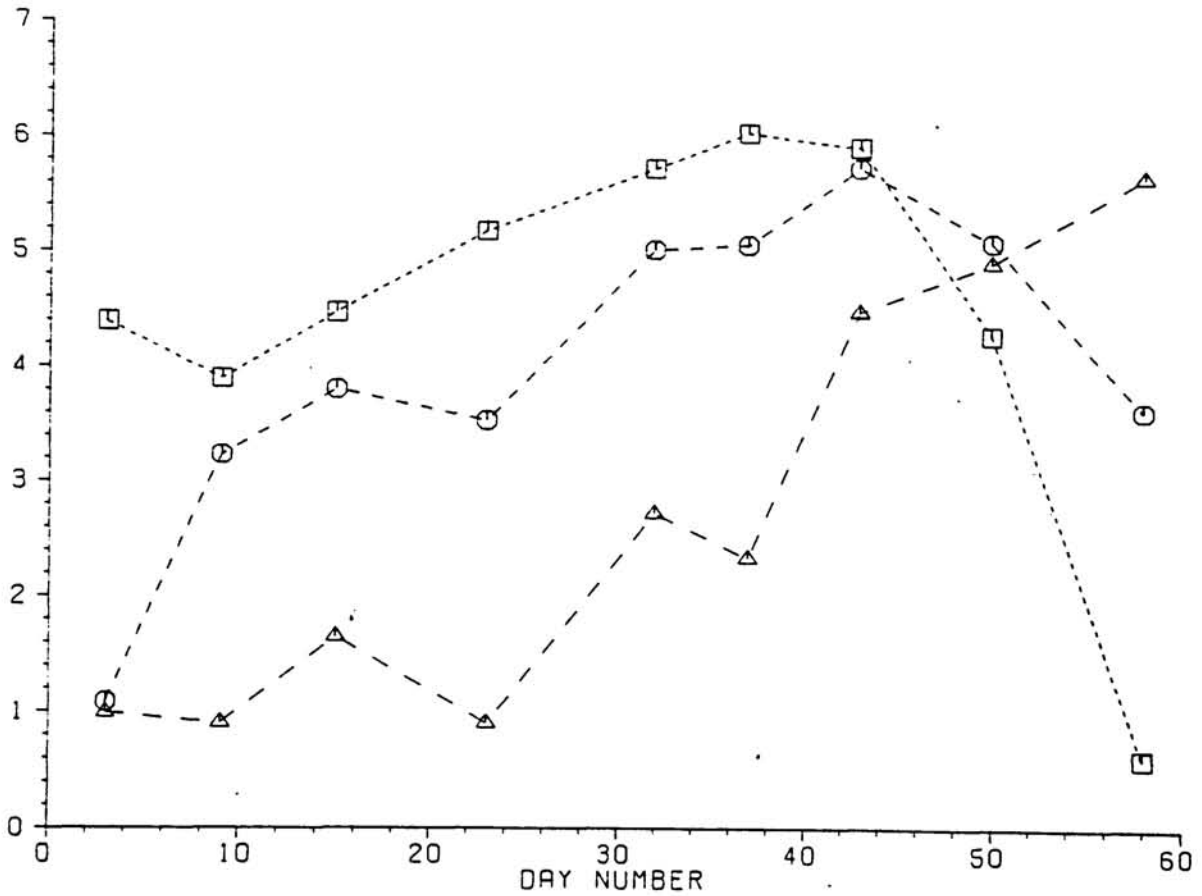
S. AVENAE-TOTAL APHIDS PER METRE SQUARED (LOG(X+1))-NOGRPRED

KEY

Assessment date	Day No.	
7/6	3	□ - SOWDATE 1
13/6	9	○ - SOWDATE 2
19/6	15	△ - SOWDATE 3
27/6	23	
6/7	32	
11/7	37	
17/7	43	
24/7	50	
3/8	58	

FIGURE 38 :

S.AVENAE-TOTAL APHIDS PER METRE SQUARED (LOG(X+1))-NOPRED

KEYAssessment
dateDay
No.

7/6
13/6
19/6
27/6
6/7
11/7
17/7
24/7
3/8

3
9
15
23
32
37
43
50
58

□ - SOWDATE 1
○ - SOWDATE 2
△ - SOWDATE 3

TABLE 65 : Effect of crop age on *S. avenae* populations (total aphids) - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Numbers per 100 tillers

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for sow date effects		**	**	**	**	*	** [§]	** [§]	**	** [§]
Treatment	Main sow date comparisons									
1	1, 2	*	N.S.	N.S.	N.S.	N.S.	**	**	**	N.S.
	2, 3	*	*	N.S.	N.S.	N.S.	*	N.S.	N.S.	**
	1, 3	**	**	*	**	N.S.	N.S.	**	**	**
2	1, 2	**	N.S.	N.S.	N.S.	N.S.	**	**	*	**
	2, 3	N.S.	N.S.	N.S.	**	*	**	N.S.	N.S.	**
	1, 3	**	*	N.S.	**	N.S.	N.S.	N.S.	*	**
3	1, 2	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	**
	2, 3	N.S.	N.S.	N.S.	N.S.	*	**	N.S.	N.S.	**
	1, 3	**	*	*	**	*	**	N.S.	N.S.	**

(B) Numbers per m²

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for sow date effects		**	**	**	**	**	** [§]	** [§]	**	** [§]
Treatment	Main sow date comparisons									
1	1, 2	N.S.	N.S.	N.S.	N.S.	N.S.	*	**	**	N.S.
	2, 3	N.S.	*	N.S.	N.S.	N.S.	*	N.S.	N.S.	**
	1, 3	**	**	*	**	N.S.	N.S.	**	**	**
2	1, 2	**	N.S.	N.S.	N.S.	N.S.	*	*	N.S.	**
	2, 3	N.S.	*	N.S.	**	*	**	N.S.	N.S.	**
	1, 3	**	*	*	**	N.S.	N.S.	N.S.	N.S.	**
3	1, 2	**	N.S.	N.S.	*	N.S.	N.S.	N.S.	N.S.	**
	2, 3	N.S.	*	N.S.	*	*	**	N.S.	N.S.	**
	1, 3	**	**	*	**	**	**	N.S.	N.S.	**

(C) Percentage of tillers infested

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		Δ	**	*	Δ	*	**	* [§]	**	Δ
Sow date	Main treatment comparisons									
1	1, 2		**	N.S.		N.S.	**	**	**	
	2, 3		**	N.S.		N.S.	*	N.S.	N.S.	
	1, 3		**	N.S.		N.S.	N.S.	*	N.S.	
2	1, 2		**	N.S.		N.S.	*	*	N.S.	
	2, 3		**	N.S.		N.S.	**	*	N.S.	
	1, 3		**	*		N.S.	N.S.	N.S.	**	
3	1, 2		*	N.S.		N.S.	N.S.	N.S.	N.S.	
	2, 3		*	N.S.		N.S.	**	*	N.S.	
	1, 3		*	N.S.		**	**	*	N.S.	

KEY

N.S. - not significant

* - significant ($p < .05$)

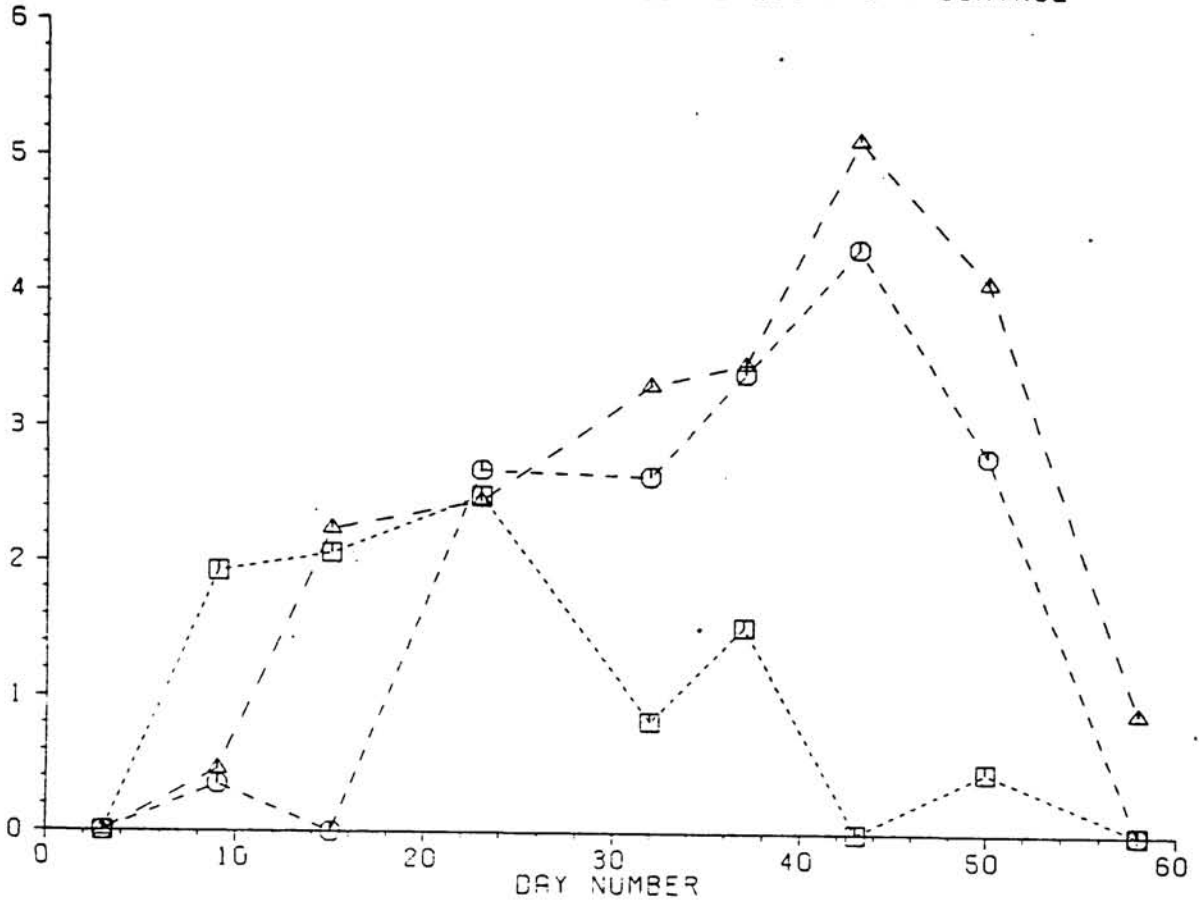
** - highly significant ($p < .01$)

[§] - significant interaction between main treatments and sow date.

Δ - incomplete data

FIGURE 39 :

M.DIRRHODUM-TOTAL APHIDS PER 100 TILLERS (LOG(X+1))-CONTROL

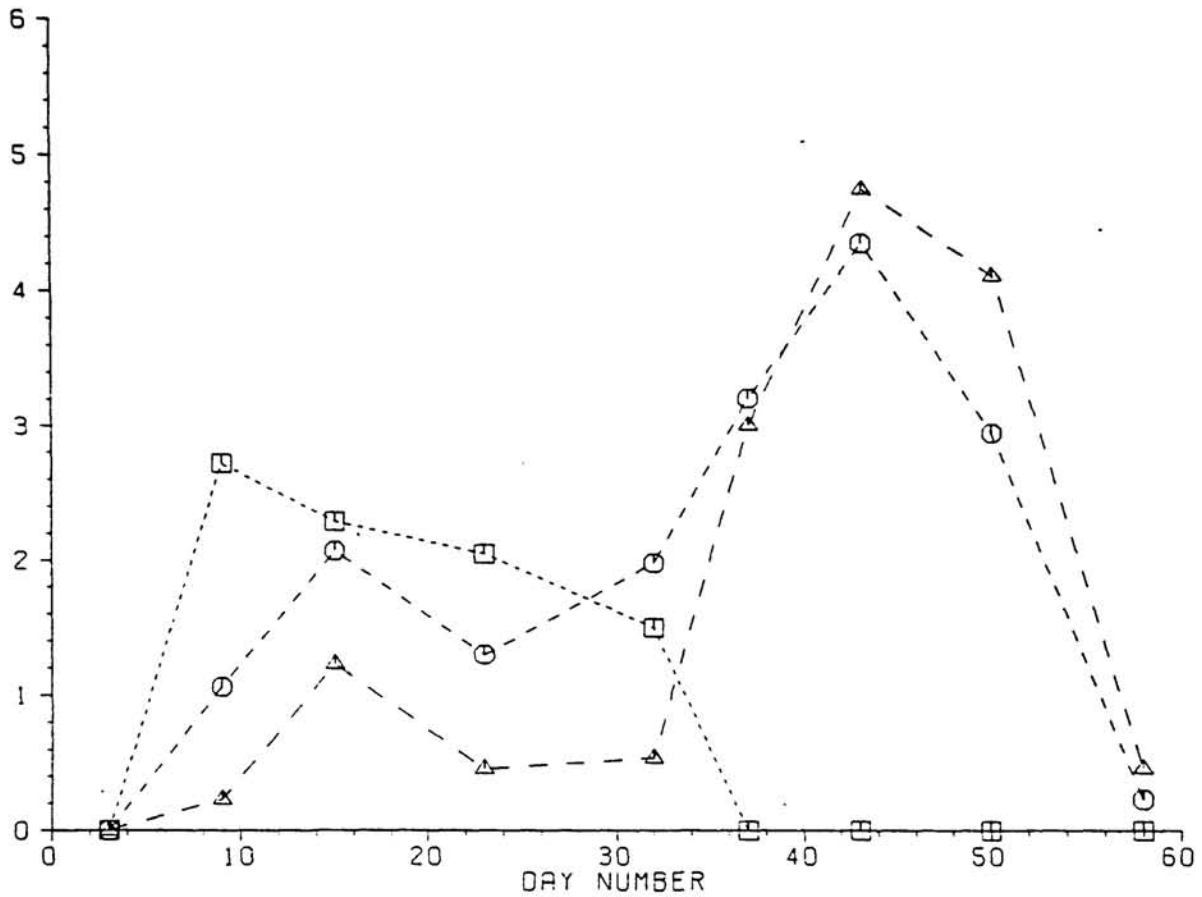
KEYAssessment
dateDay.
No.

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

FIGURE 40 :

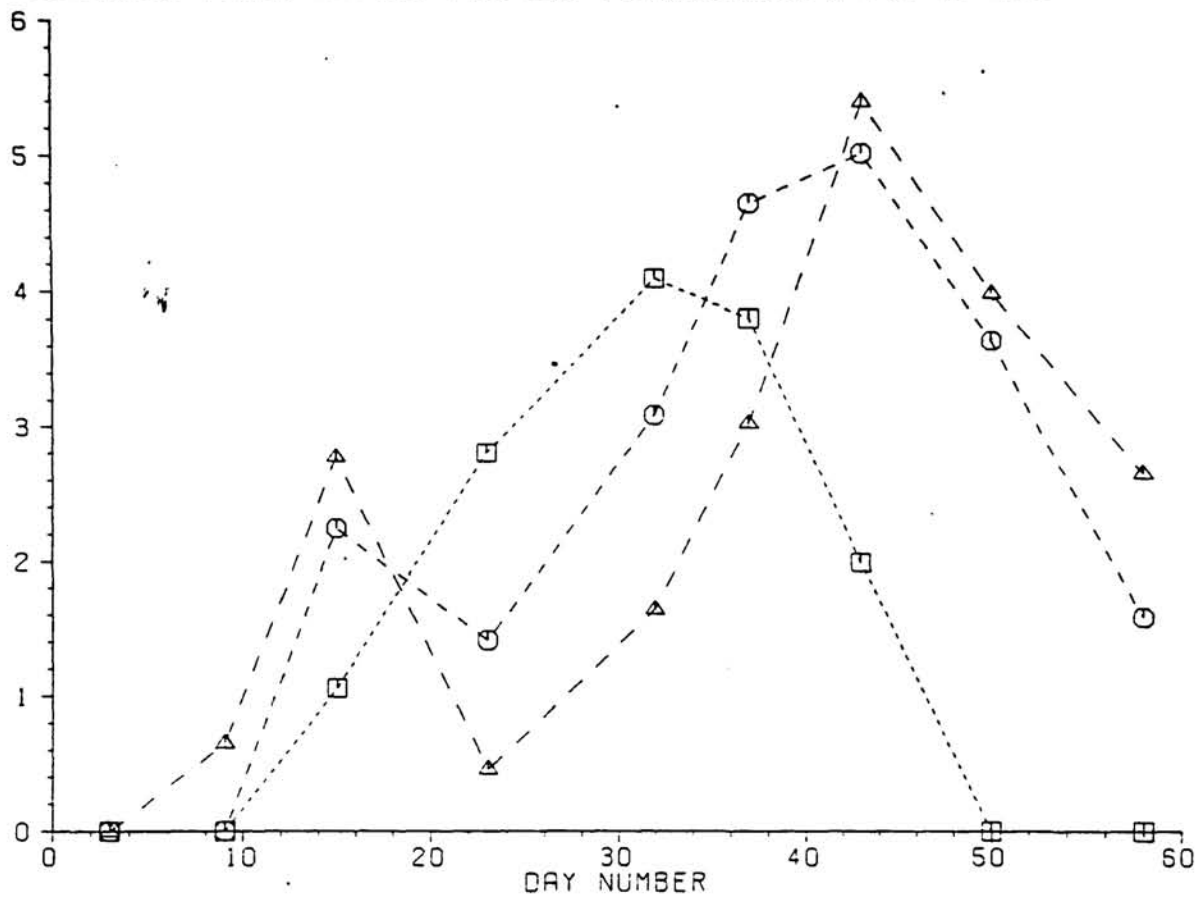
M.DIRHODUM-TOTAL APHIDS PER 100 TILLERS(LOG(X+1))-NOGRPREP

KEY

Assessment date	Day No.	
7/6	3	□ - SOWDATE 1
13/6	9	○ - SOWDATE 2
19/6	15	△ - SOWDATE 3
27/6	23	
6/7	32	
11/7	37	
17/7	43	
24/7	50	
3/8	58	

FIGURE 41 :

M.DIRRHODUM-TOTAL APHIDS PER 100 TILLERS (LOG(X+1))-NOPRED

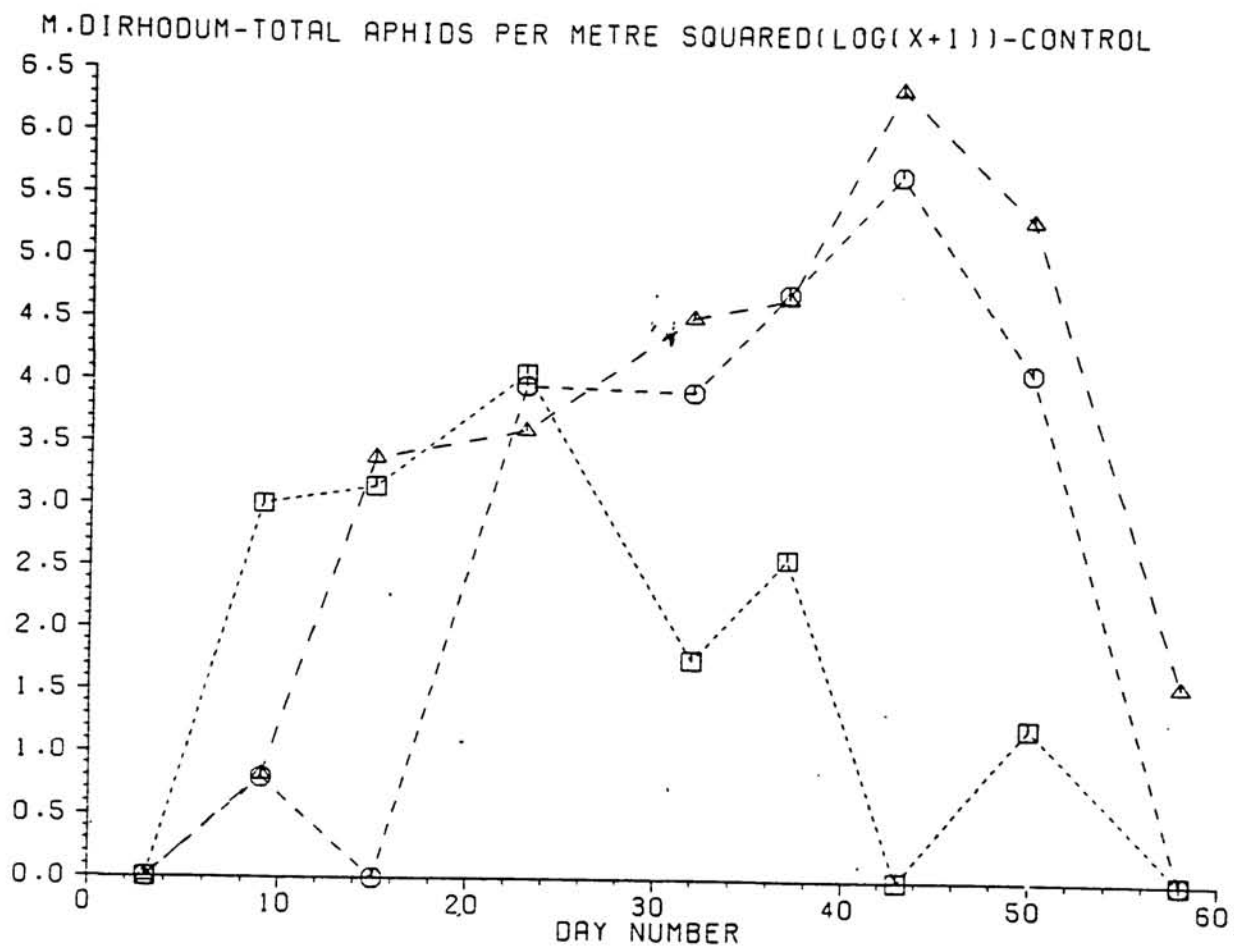
KEY

Assessment date	Day No.
-----------------	---------

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

FIGURE 42 :

KEYAssessment
dateDay
No.

7/6
13/6
19/6
27/6
6/7
11/7
17/7
24/7
3/8

3

9

15

23

32

37

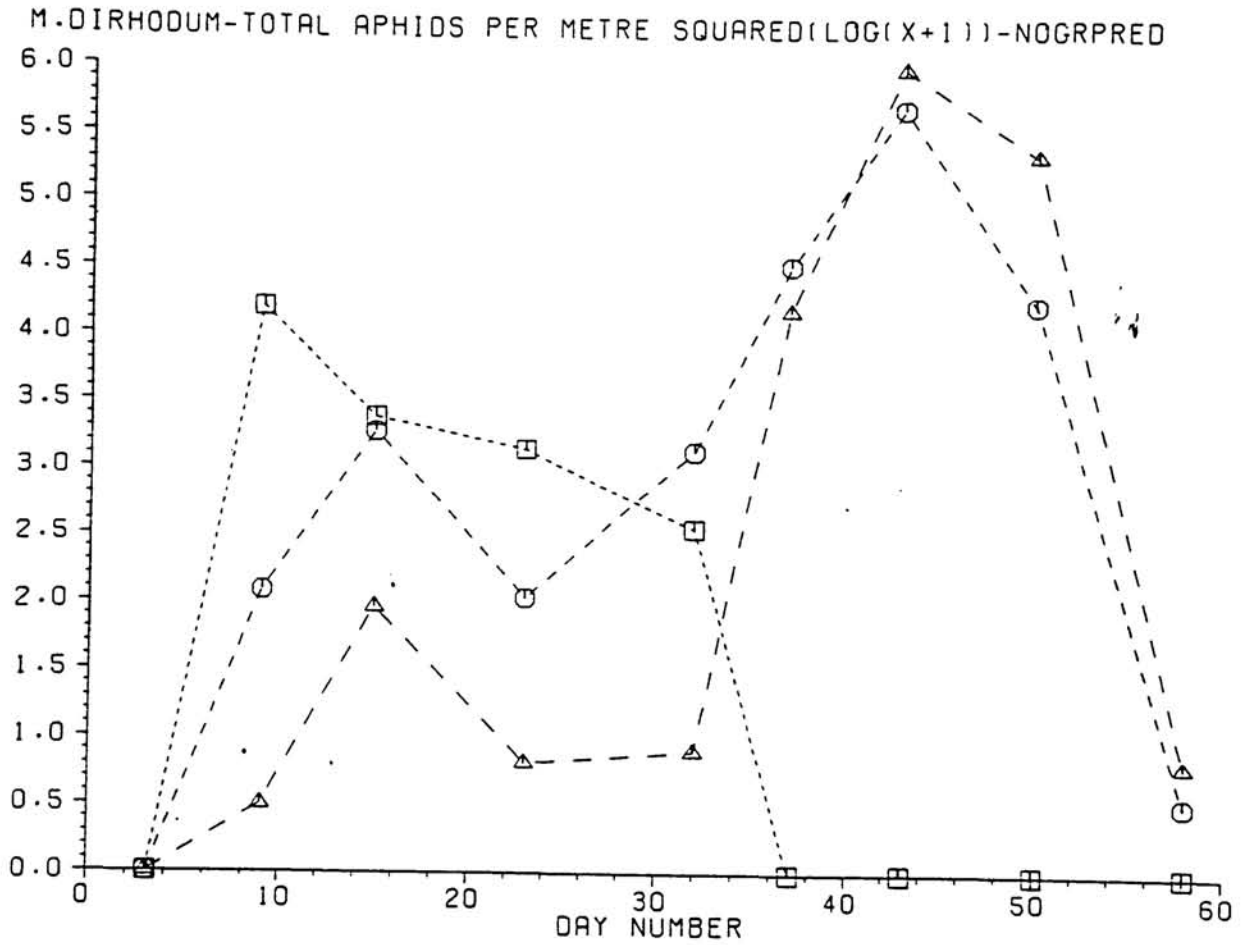
43

50

58

□ - SOWDATE 1
○ - SOWDATE 2
△ - SOWDATE 3

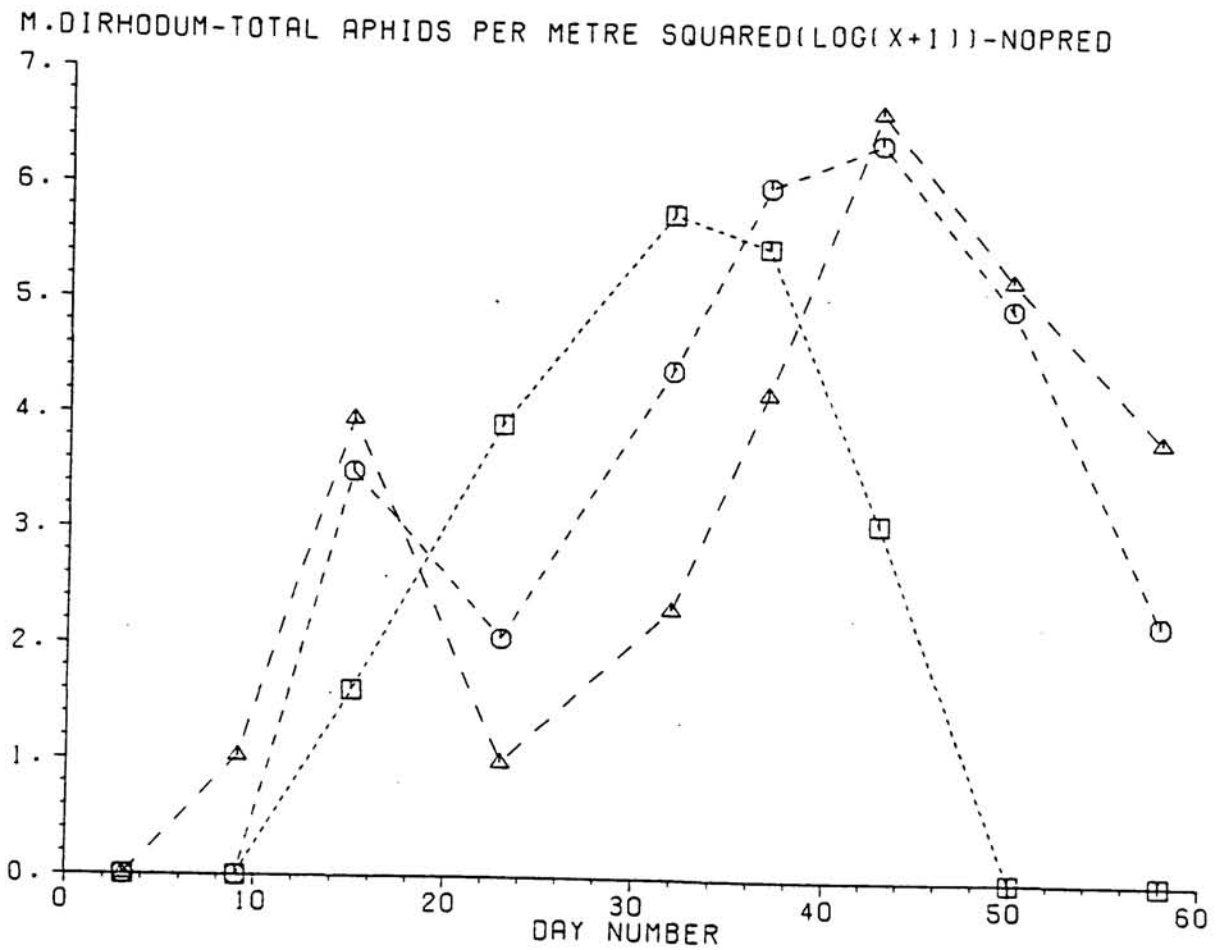
FIGURE 43 :

KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

FIGURE 44 :

KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

TABLE 66 : Effect of crop age on *M. dirhodum* populations (total aphids) - summary of ANOVA†.

† see text for guide to interpretation.

(A) Numbers per 100 tillers

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for sow date effects		φ	N.S.	N.S.	N.S.	N.S. §	**	**	**	*
Treatment	Main sow date comparisons									
1	1, 2					N.S.	*	**	**	N.S.
	2, 3					N.S.	N.S.	N.S.	*	N.S.
	1, 3					*	*	**	**	N.S.
2	1, 2					N.S.	**	**	**	N.S.
	2, 3					N.S.	**	N.S.	*	N.S.
	1, 3					N.S.	N.S.	**	**	N.S.
3	1, 2					N.S.	N.S.	**	**	*
	2, 3					*	*	N.S.	**	N.S.
	1, 3					*	N.S.	**	**	**

(B) Numbers per m²

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for sow date effects		φ	N.S.	N.S.	N.S.	N.S.	**	**	** §	*
Treatment	Main sow date comparisons									
1	1, 2						*	**	**	N.S.
	2, 3						N.S.	N.S.	**	N.S.
	1, 3						*	**	**	N.S.
2	1, 2						**	**	**	N.S.
	2, 3						N.S.	N.S.	N.S.	N.S.
	1, 3						**	**	**	N.S.
3	1, 2						N.S.	*	**	*
	2, 3						*	N.S.	N.S.	N.S.
	1, 3						N.S.	**	**	**

(C) Percentage of tillers infested

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		φ	*	N.S.	Δ	N.S. §	**	** §	**	Δ
Sow date	Main treatment comparisons									
1	1, 2		*			N.S.	**	**	N.S.	
	2, 3		*			N.S.	N.S.	**	**	
	1, 3		N.S.			N.S.	**	**	**	
2	1, 2		N.S.			N.S.	**	**	**	
	2, 3		N.S.			N.S.	N.S.	N.S.	**	
	1, 3		*			N.S.	**	**	**	
3	1, 2		N.S.			N.S.	*	**	**	
	2, 3		N.S.			N.S.	**	N.S.	N.S.	
	1, 3		N.S.			*	N.S.	**	**	

KEY

N.S. - not significant

* - significant ($p < .05$)** - highly significant ($p < .01$)

§ - significant interaction between main treatments and sow date.

Δ - incomplete data

φ - too few aphids to analyse

adverse after 3/8 and there was no ingress of predators into the crops. The differences between sow dates were endorsed by the results of ANOVA performed both on 'numbers per 100 tillers' and 'percent infested tillers' (Table 65), in which differences at the 99% significance level were often found. Furthermore, differences did not arise simply as a response to the variation in plant densities over the 3 sow dates; conversion of the data to numbers per M^2 made little difference to the comparison of population trends (Figures 36, 37 and 38) or to the outcome of statistical analysis (Table 65).

M. dirhodum (Figures 39, 40 and 41)

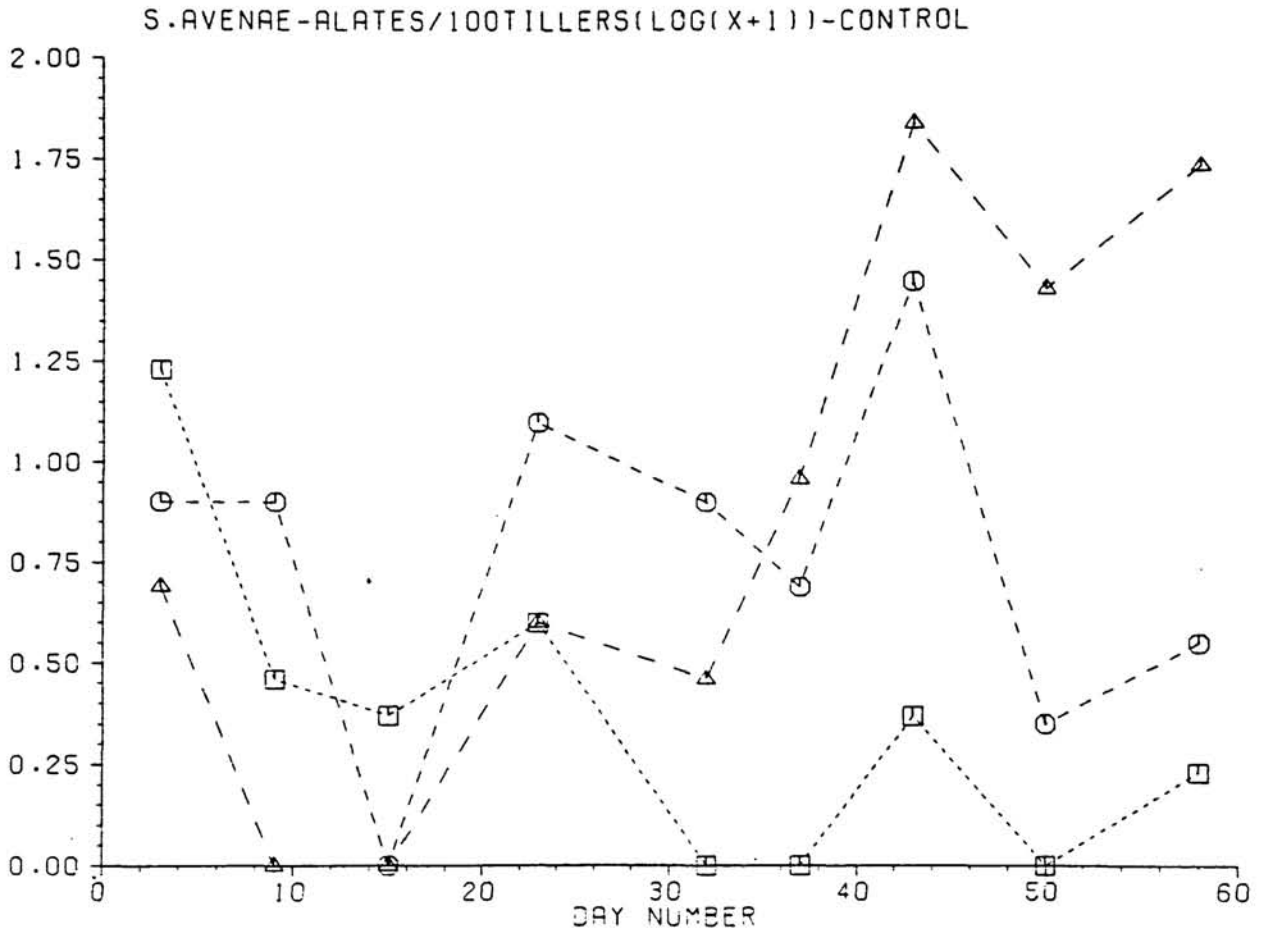
At the first aphid census on 7/6 there were very few *M. dirhodum* (less than 1 per 100 tillers) but rapid population build up followed on sow date 1 (Figure 41). Similar patterns of increase occurred subsequently on sow dates 2 and 3, but the onset of aphid attack was not clearly associated with crop growth stage (contrasting with *S. avenae* above). Population decline on sow dates 1 and 2 did however coincide with growth stage 77 (late milk) when extensive senescence of lower leaves occurred. An 'earlier' crash in the sow date 3 population after growth stage 50 (flowering) was contrary to pattern on the older sowings but the reasons for this are not understood. The effects of sow date on *M. dirhodum* numbers often attained high levels of statistical significance regardless of whether analysis was performed on 'numbers per 100 tillers' or 'numbers per M^2 .' (Table 66, also see Figures 42, 43 and 44). Separate analyses showed that significant differences existed between the proportions of tillers infested on the 3 sow dates (Table 66).

3.3.2.4.2 Alate aphids

S. avenae (Figures 45, 46 and 47)

Alate preference for different sow dates shifted through the summer

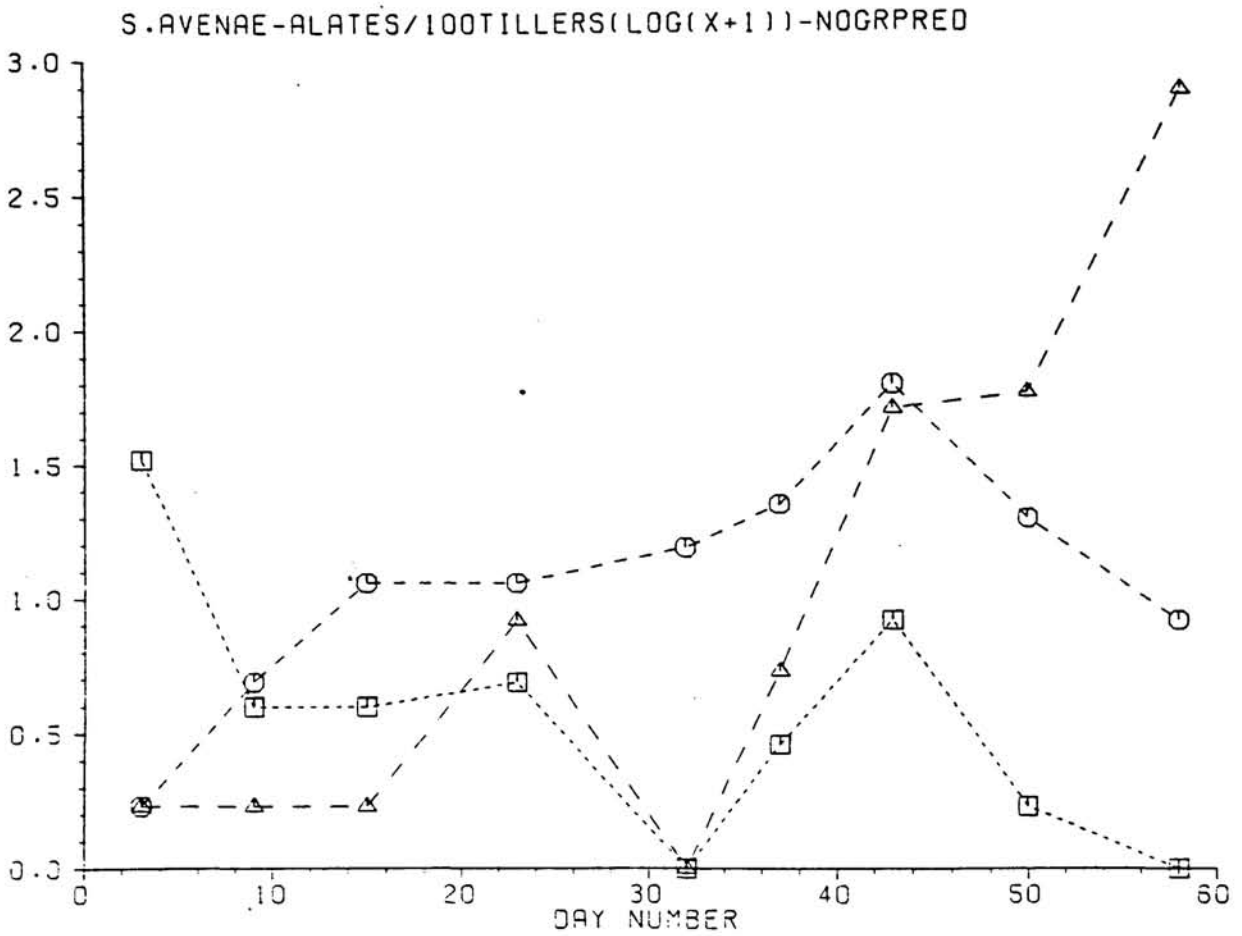
FIGURE 45 :

KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

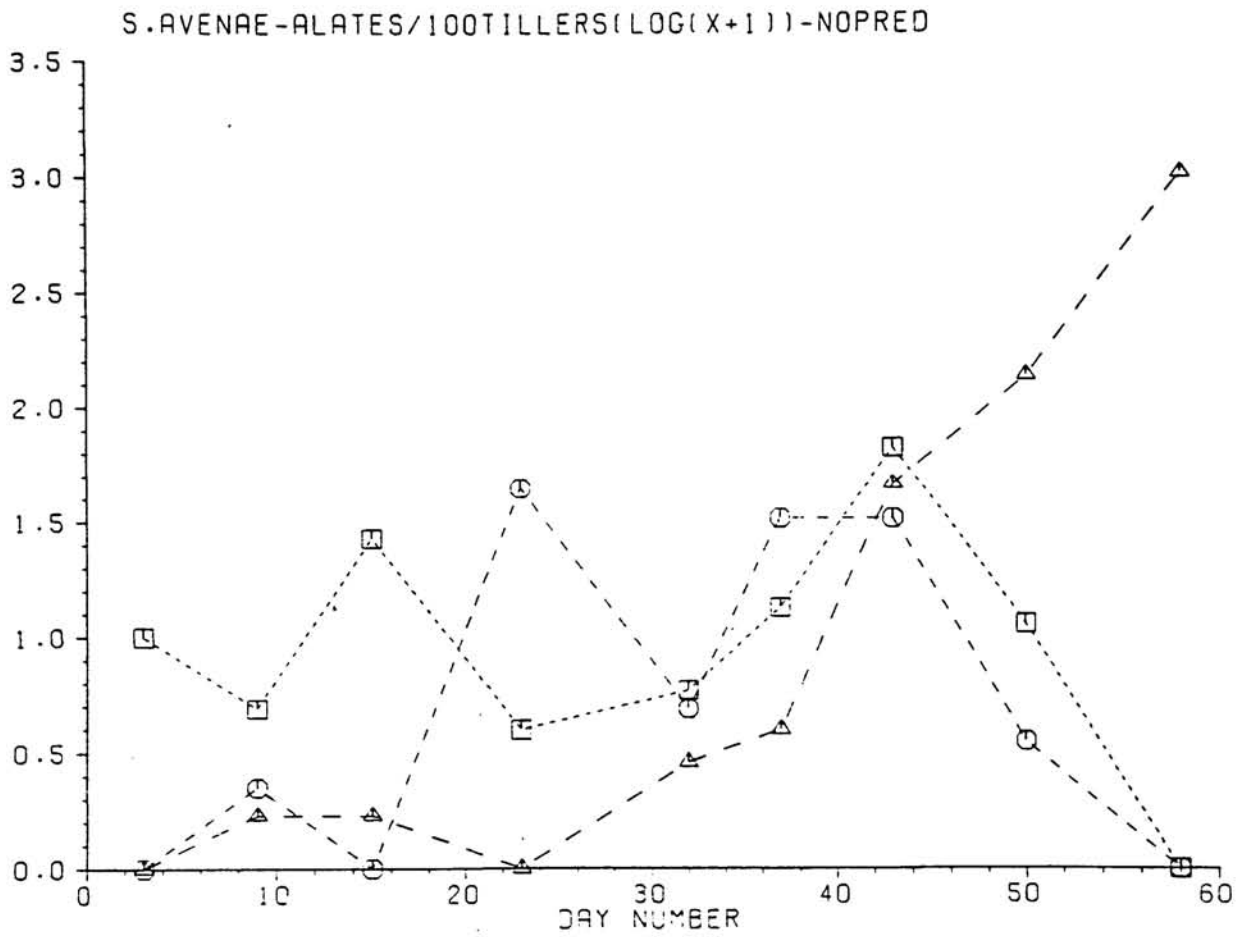
FIGURE 46 :

KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

FIGURE 47 :

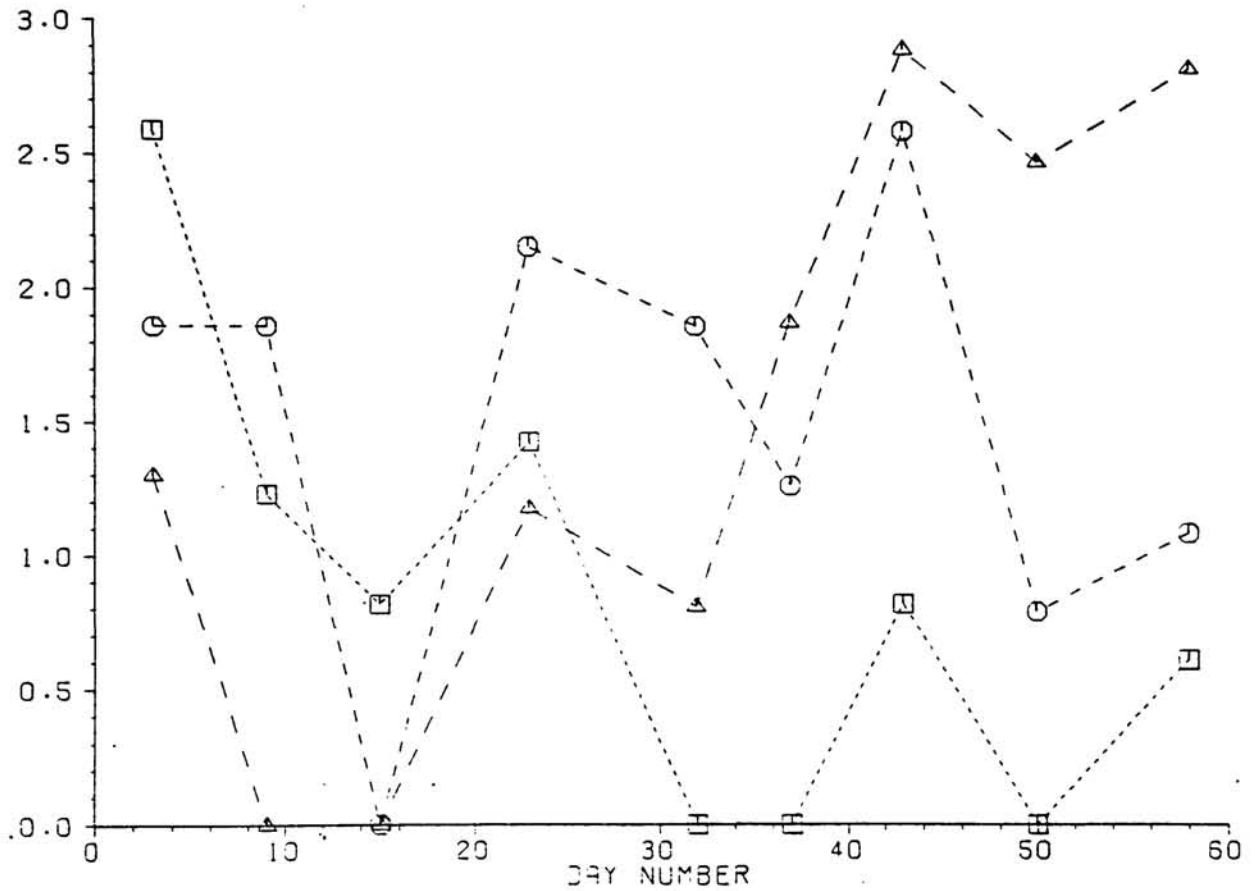
KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

FIGURE 48 :

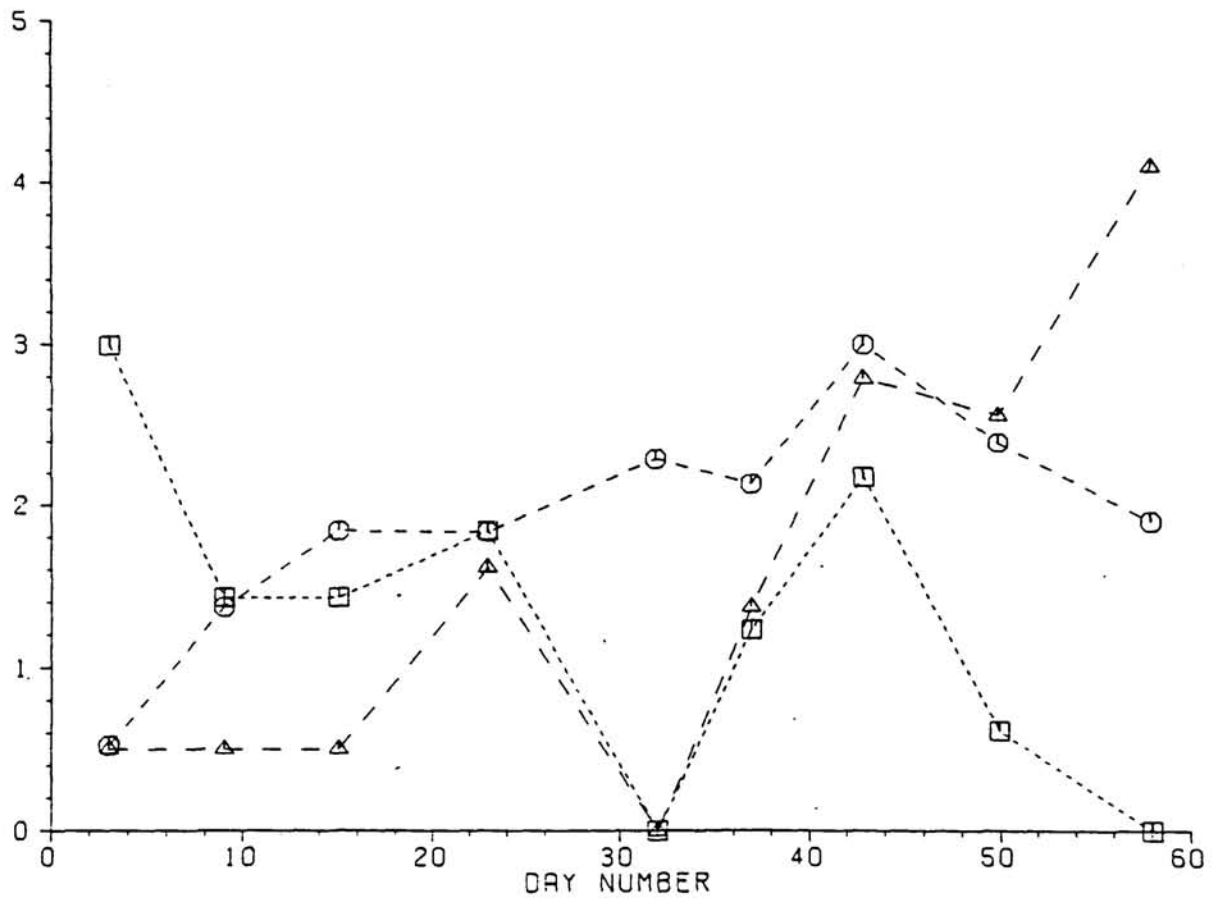
S. AVENAE-ALATES PER METRE SQUARED (LOG(X+1))-CONTROL

KEY

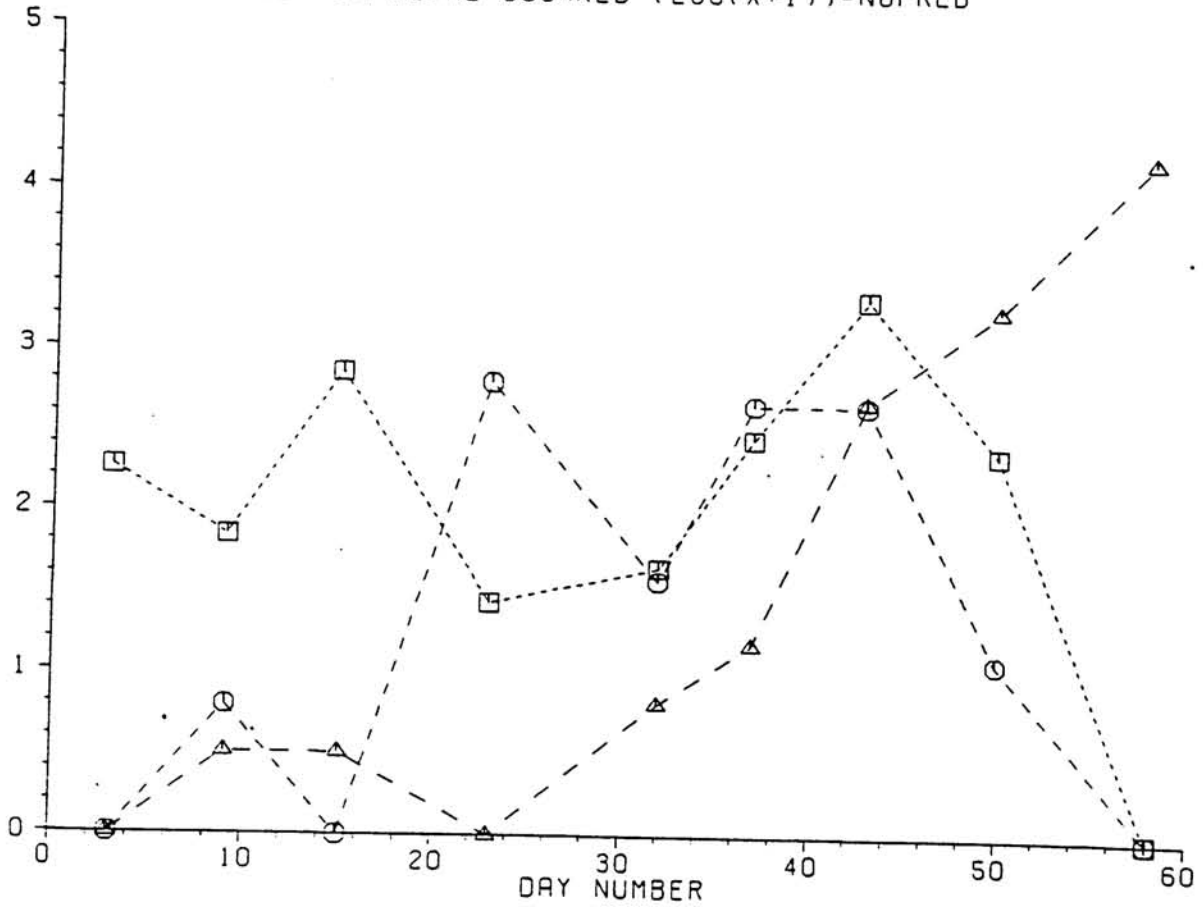
Assessment date	Day No.	
7/6	3	□ - SOWDATE 1
13/6	9	○ - SOWDATE 2
19/6	15	△ - SOWDATE 3
27/6	23	
6/7	32	
11/7	37	
17/7	43	
24/7	50	
3/8	58	

FIGURE 49 :

S.AVENAE-ALATES PER METRE SQUARED (LOG(X+1))-NOGRPRED

KEY

Assessment date	Day No.	
7/6	3	□ - SOWDATE 1
13/6	9	○ - SOWDATE 2
19/6	15	△ - SOWDATE 3
27/6	23	
6/7	32	
11/7	37	
17/7	43	
24/7	50	
3/8	58	

FIGURE 50 :S. AVENAE-ALATES PER METRE SQUARED ($\text{LOG}(X+1)$)-NOPRED**KEY**

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

TABLE 67 : Effect of crop age on *S. avenae* populations (alate aphids) -
summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Numbers per 100 tillers

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects	**	N.S.	**	*	**	N.S.	**	**	**
Sow date	Main treatment comparisons								
1	1, 2	N.S.		N.S.	N.S.	**		**	N.S.
	2, 3	N.S.		N.S.	N.S.	N.S.		N.S.	*
	1, 3	N.S.		N.S.	N.S.	N.S.		**	**
2	1, 2	**		N.S.	N.S.	**		*	*
	2, 3	N.S.		*	N.S.	**		N.S.	N.S.
	1, 3	**		N.S.	N.S.	N.S.		*	**
3	1, 2	*		**	*	N.S.		N.S.	N.S.
	2, 3	N.S.		N.S.	*	*		N.S.	**
	1, 3	*		**	N.S.	N.S.		N.S.	*

(B) Numbers per m²

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects	**	N.S.	**	N.S.	**	N.S.	*	**	**
Sow date	Main treatment comparisons								
1	1, 2	N.S.		N.S.		**		**	N.S.
	2, 3	N.S.		N.S.		N.S.		N.S.	*
	1, 3	*		N.S.		N.S.		**	**
2	1, 2	**		N.S.		**		N.S.	*
	2, 3	N.S.		*		**		N.S.	N.S.
	1, 3	**		N.S.		N.S.		N.S.	*
3	1, 2	**		**		N.S.		N.S.	N.S.
	2, 3	N.S.		N.S.		*		N.S.	*
	1, 3	**		**		N.S.		N.S.	N.S.

KEY

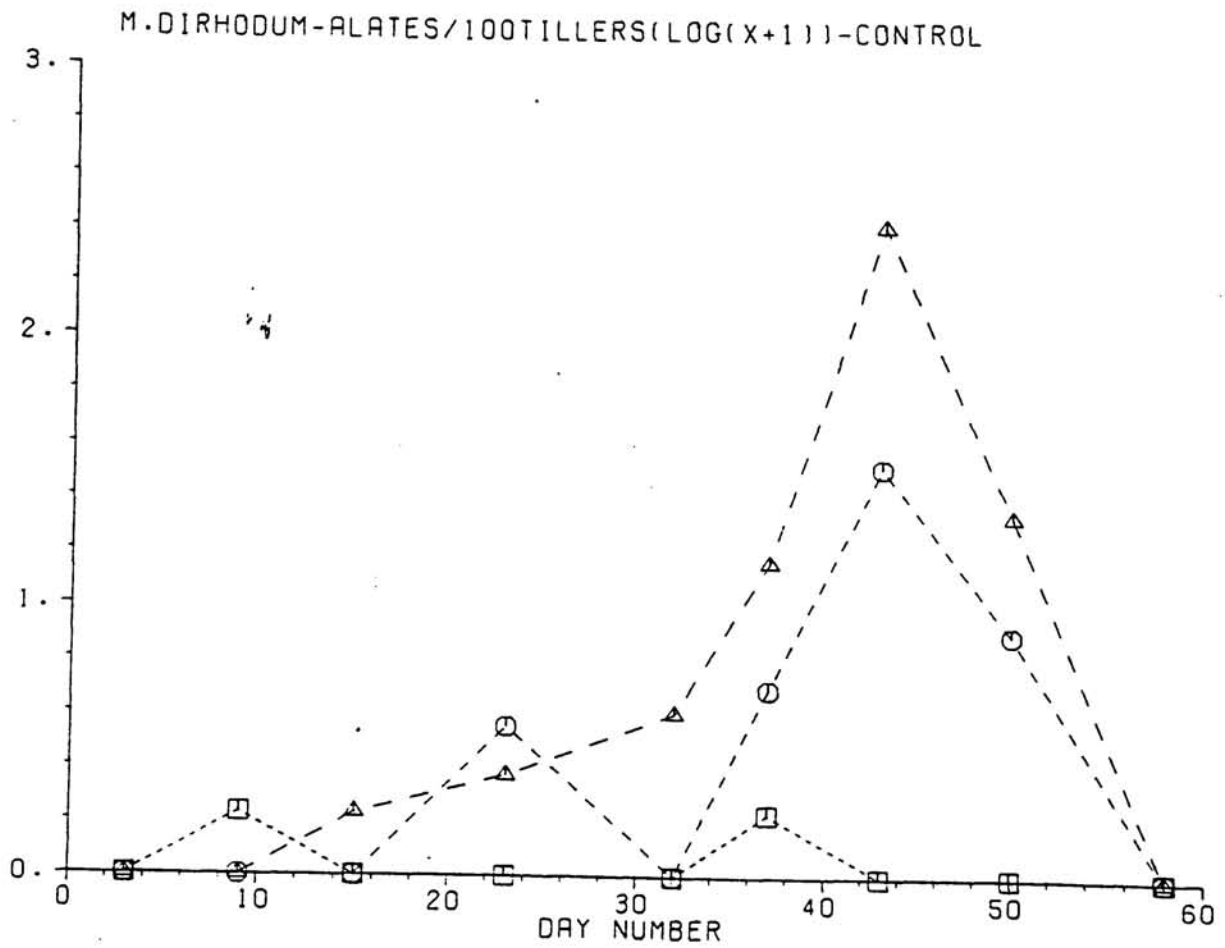
N.S. - not significant

* - significant ($p < .05$)

** - highly significant ($p < .01$)

§ - significant interaction between main treatments and sow date.

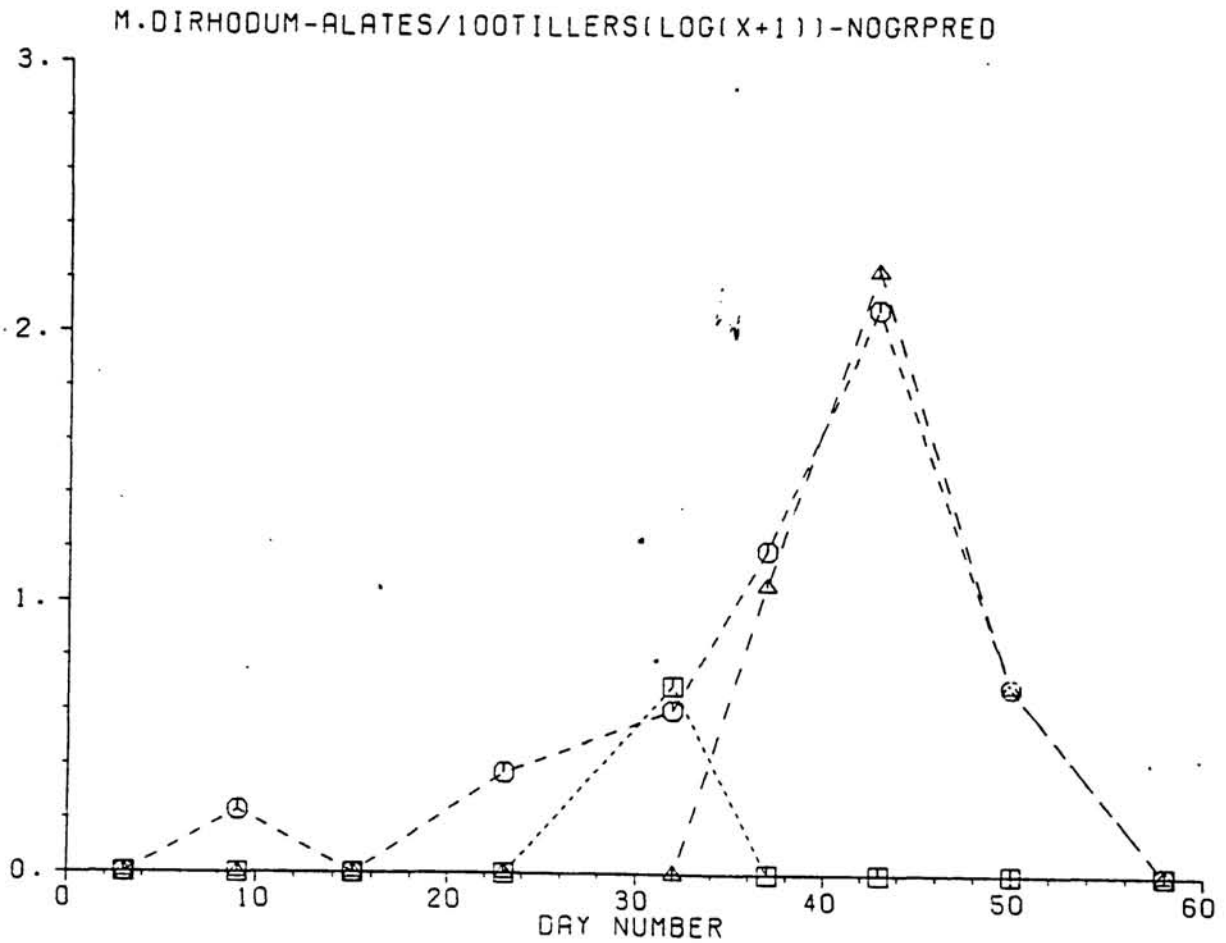
FIGURE 51 :

KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

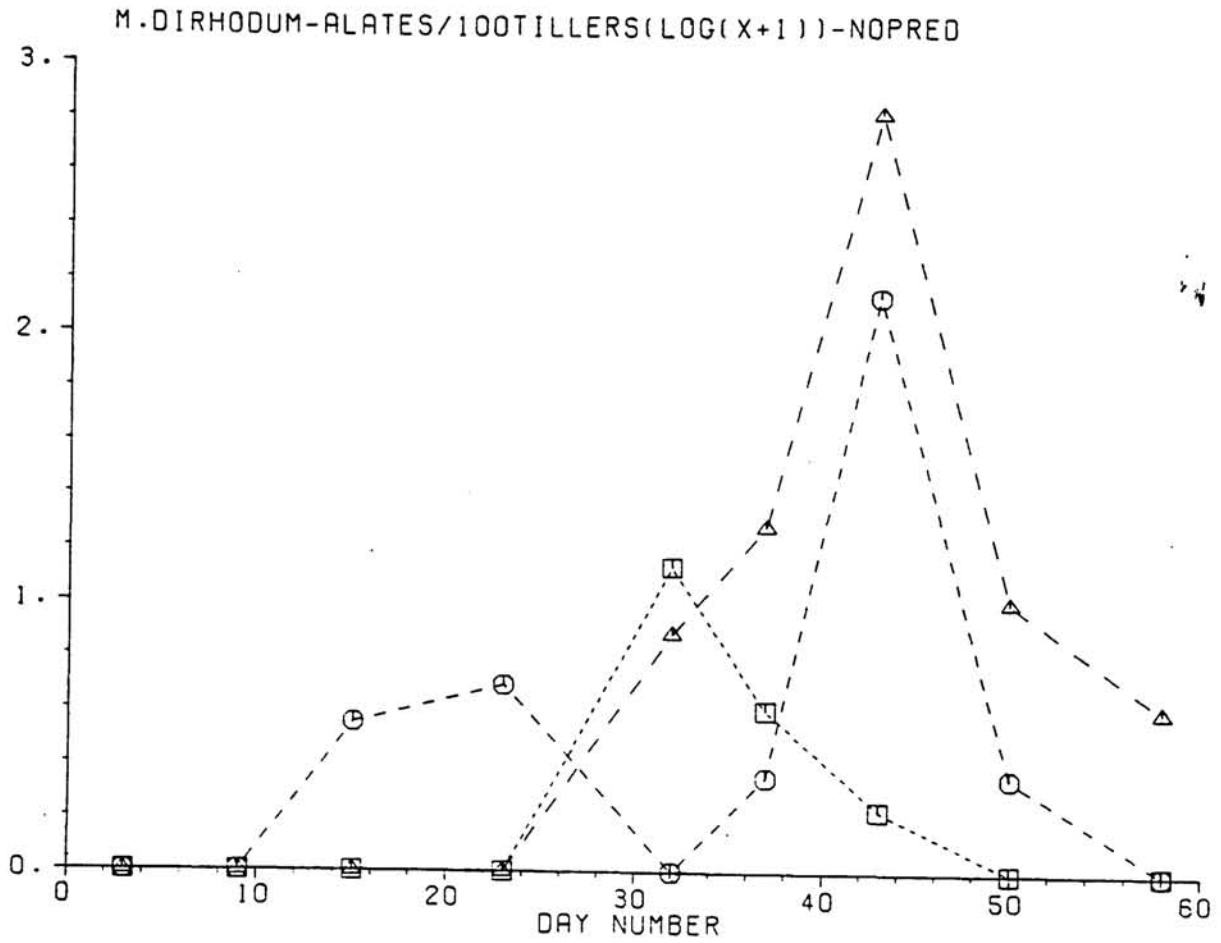
FIGURE 52 :

KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

FIGURE 53 :

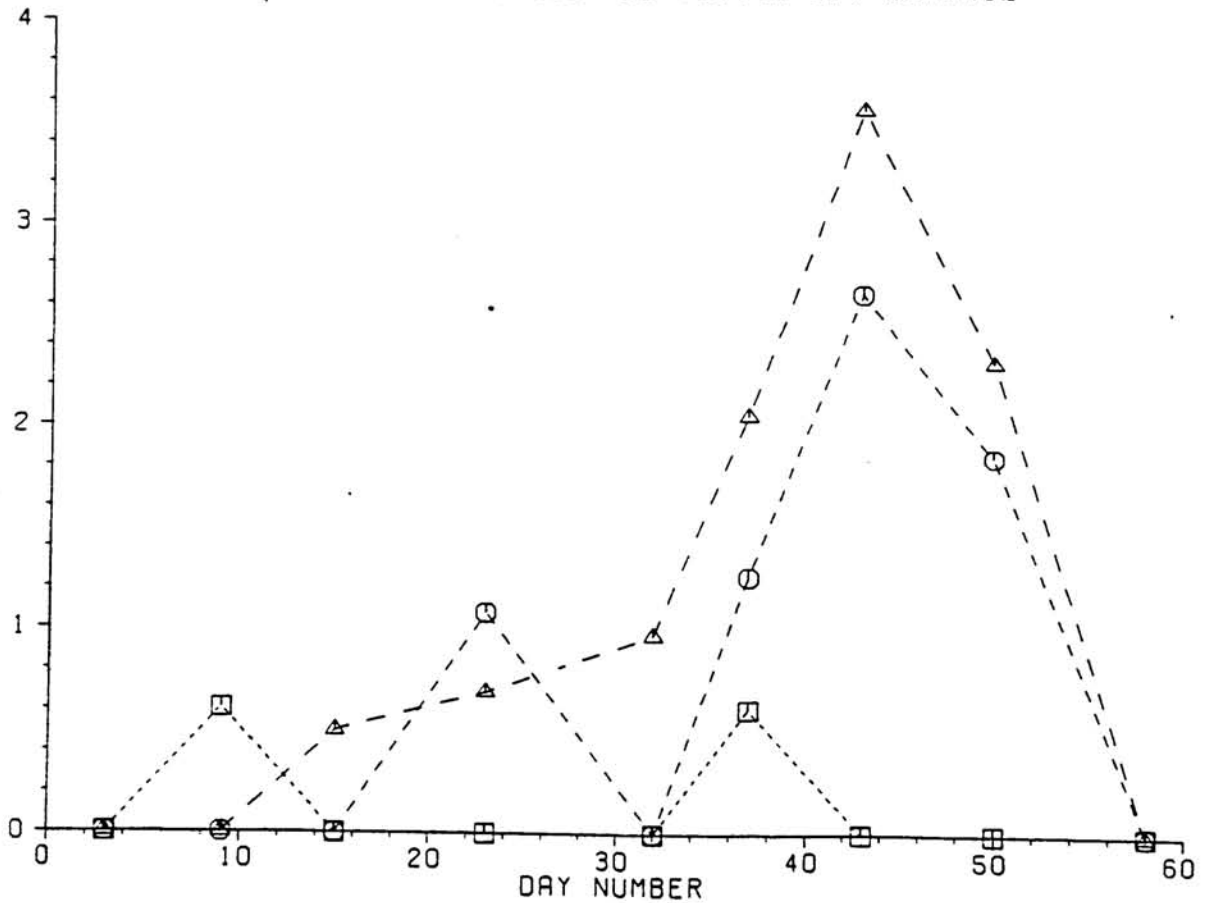
KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

FIGURE 54 :

M.DIRRHODUM-ALATES PER METRE SQUARED (LOG(X+1))-CONTROL

KEYAssessment
dateDay
No.

7/6

3

13/6

9

19/6

15

27/6

23

6/7

32

11/7

37

17/7

43

24/7

50

3/8

58

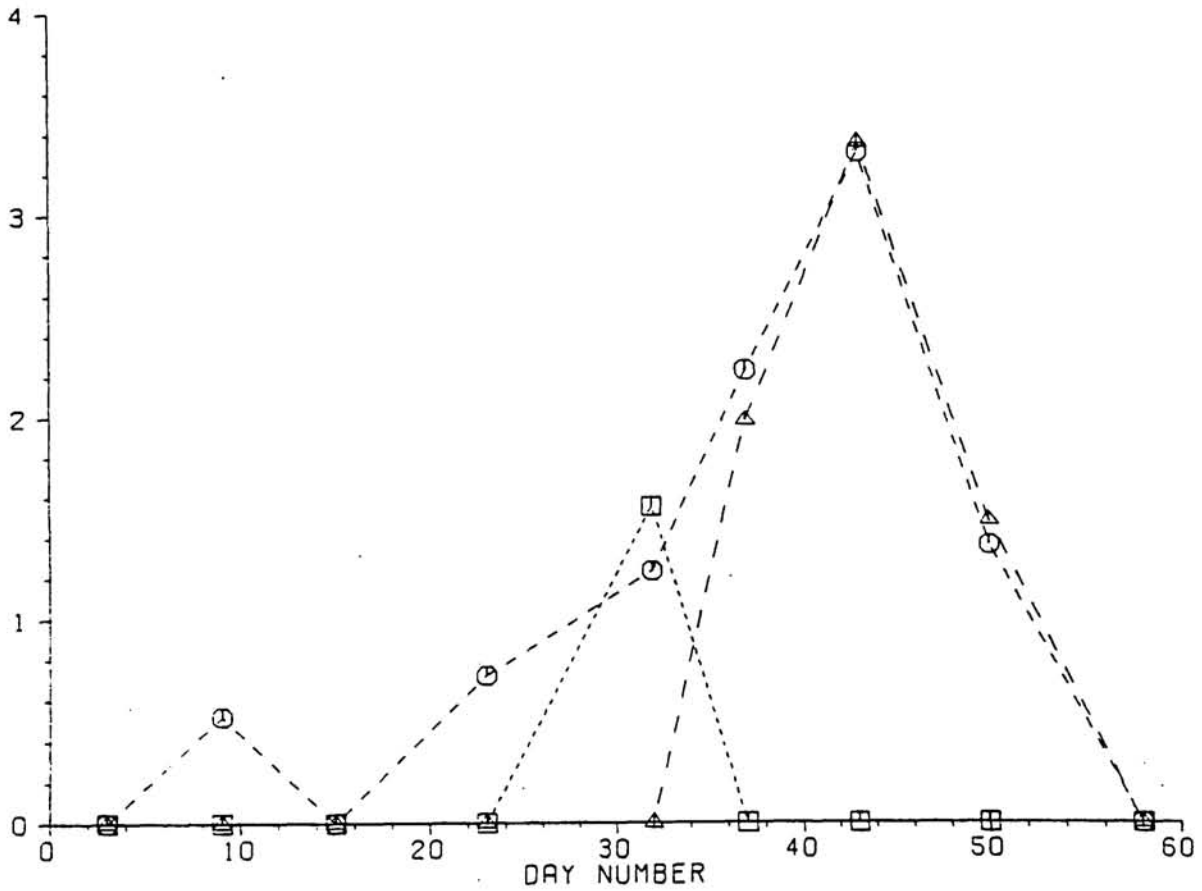
□ - SOWDATE 1

○ - SOWDATE 2

△ - SOWDATE 3

FIGURE 55 :

M.DIRRHODUM-ALATES PER METRE SQUARED (LOG(X+1))-NOGRPREO

**KEY**

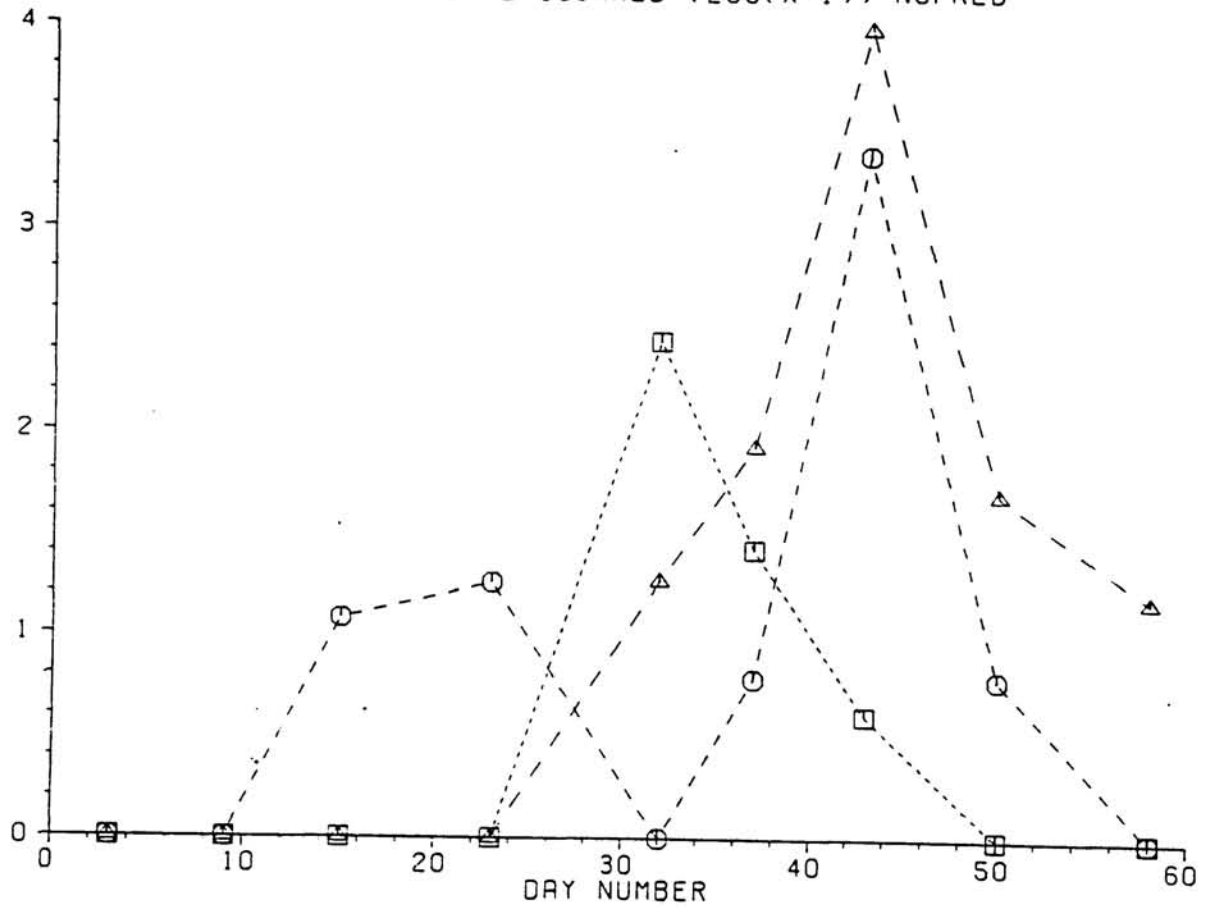
Assessment date	Day No.
-----------------	---------

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

FIGURE 56 :

M.DIRHODUM-ALATES PER METRE SQUARED (LOG(X+1))-NOPRED

KEY

Assessment date	Day No.
-----------------	---------

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

TABLE 68 : Effect of crop age on *M. dirhodum* populations (alate aphids) - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Numbers per 100 tillers

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects	φ	N.S.	N.S.	N.S.	N.S.	N.S.	**	**	N.S.
Sow date	Main treatment comparisons								
1	1, 2						**	N.S.	
	2, 3						**	N.S.	
	1, 3						**	**	
2	1, 2						**	N.S.	
	2, 3						N.S.	N.S.	
	1, 3						**	N.S.	
3	1, 2						**	N.S.	
	2, 3						N.S.	N.S.	
	1, 3						**	**	

(B) Numbers per m²

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects	φ	N.S.	N.S.	N.S.	N.S.	N.S.	**	**	N.S.
Sow date	Main treatment comparisons								
1	1, 2						**	*	
	2, 3						*	N.S.	
	1, 3						**	**	
2	1, 2						**	*	
	2, 3						N.S.	N.S.	
	1, 3						**	*	
3	1, 2						**	N.S.	
	2, 3						N.S.	N.S.	
	1, 3						**	**	

KEY

N.S. - not significant

* - significant ($p < .05$)

** - highly significant ($p < .01$)

§ - significant interaction between main treatments and sow date.

φ - too few aphids to analyse

as the crops aged. Each crop, in turn became the favoured sow date in terms of alate density and this partly explains the cycles in abundance of total aphids on the 3 sowings described above.

On 7/6, alates were most abundant on sow date 1 ($p < .01$ on 'NOGRPRED', $p < .05$ on 'NOPRED', NS on 'CONTROL' (Table 67)) but subsequently declined. A second peak in alates on 11/7 probably resulted from the production of alates on the crop; fourth instar alates had first been recorded on 6/7 (Table 46). On sow date 2, alates reached their maximum numbers around 27/6 - 6/7 differing significantly from those on other sow dates ($p < .01$ on 'CONTROL' and 'NOGRPRED' (Table 67)). After mid July most alates were found on sow date 3, the difference reaching high levels of statistical significance by 3/8 (Table 67). Analysis of the data in terms of numbers per M^2 made no material difference to the appearance of population trends (Figures 72, 73 and 74) or to the overall conclusions of statistical analysis (Table 67).

M. dirhodum (Figures 51, 52 and 53)

Despite the large size of *M. dirhodum* populations developing on sow date 1, aphid records do not indicate the initial appearance of large numbers of 'founder' alates. Perhaps the founders alighted, reproduced and departed within a short period of time between counts. Much larger numbers were found later in the season but these were probably produced on the crop. It is noteworthy that on 'NOPRED', where aphids reached their greatest abundance, the highest numbers of alates were also found (Figure 53).

The most spectacular difference between sow dates occurred on 17/7 (all treatments) when no alates remained on sow date 1 and sow dates 2 and 3 supported their highest numbers for the season, most occurring on sow date 3 ($p < .01$ on 'CONTROL' (Table 68)). The especially high levels of alate abundance on sow dates 2 and 3 probably resulted from the large

numbers leaving earlier maturing crops, both locally (i.e. from adjacent plots (see Figure 53)) and regionally.

Data expressed in terms of 'numbers per M^2 ' are shown in Figures 54, 55 and 56. The appearance of population trends and the conclusions of statistical analysis (Table 68) are similar to those described above for 'numbers per 100 tillers'.

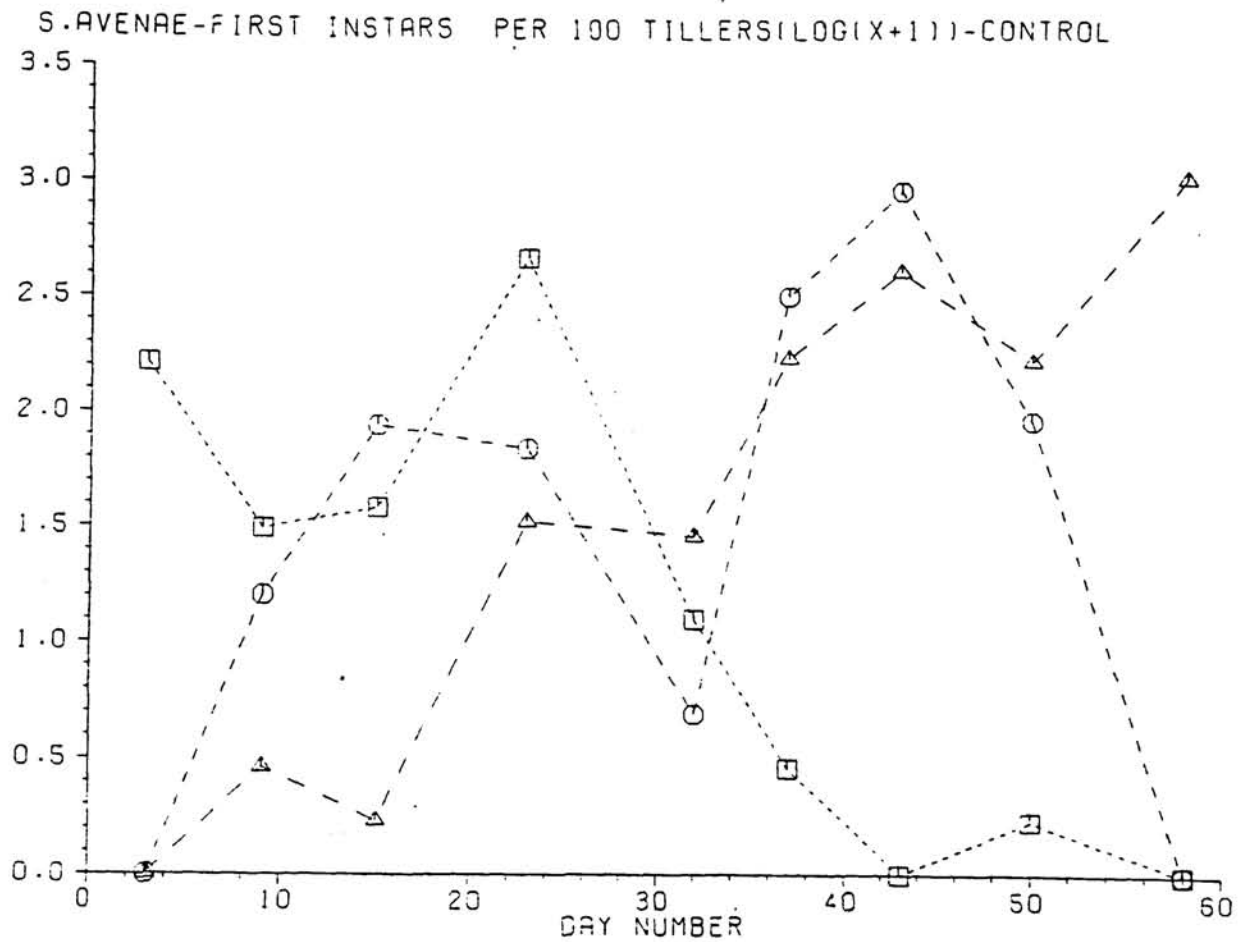
3.3.2.4.3. First instar aphids.

S. avenae (Figures 57, 58 and 59)

On 7/6, relatively large numbers of first instars had been deposited on sow date 1 (e.g. on 'NOPRED' : $\bar{x} = 7/100$ tillers) but fewer were found on the two subsequent counts (e.g. on 'NOPRED' $\bar{x} = 3$ and $1.3/100$ tillers respectively; Table 43 and 44). A second peak occurred on 27/6 (Figure 57), probably due to reproduction by apterae produced on the crop. It is noteworthy that on 'NOPRED' (Figure 59) this peak was greater in magnitude and duration than on 'CONTROL'; this difference ultimately accounting for the substantially increased total populations on 'NOPRED' (Figure 35). These differences between counts and between treatments were not simply a reflection of the differences in overall population levels. Analysis of the data in the form of 'first instar : total aphid ratios' showed that peaks in the absolute numbers of first instars were the result of higher rates of nymph deposition (Figures 63, 64 and 65).

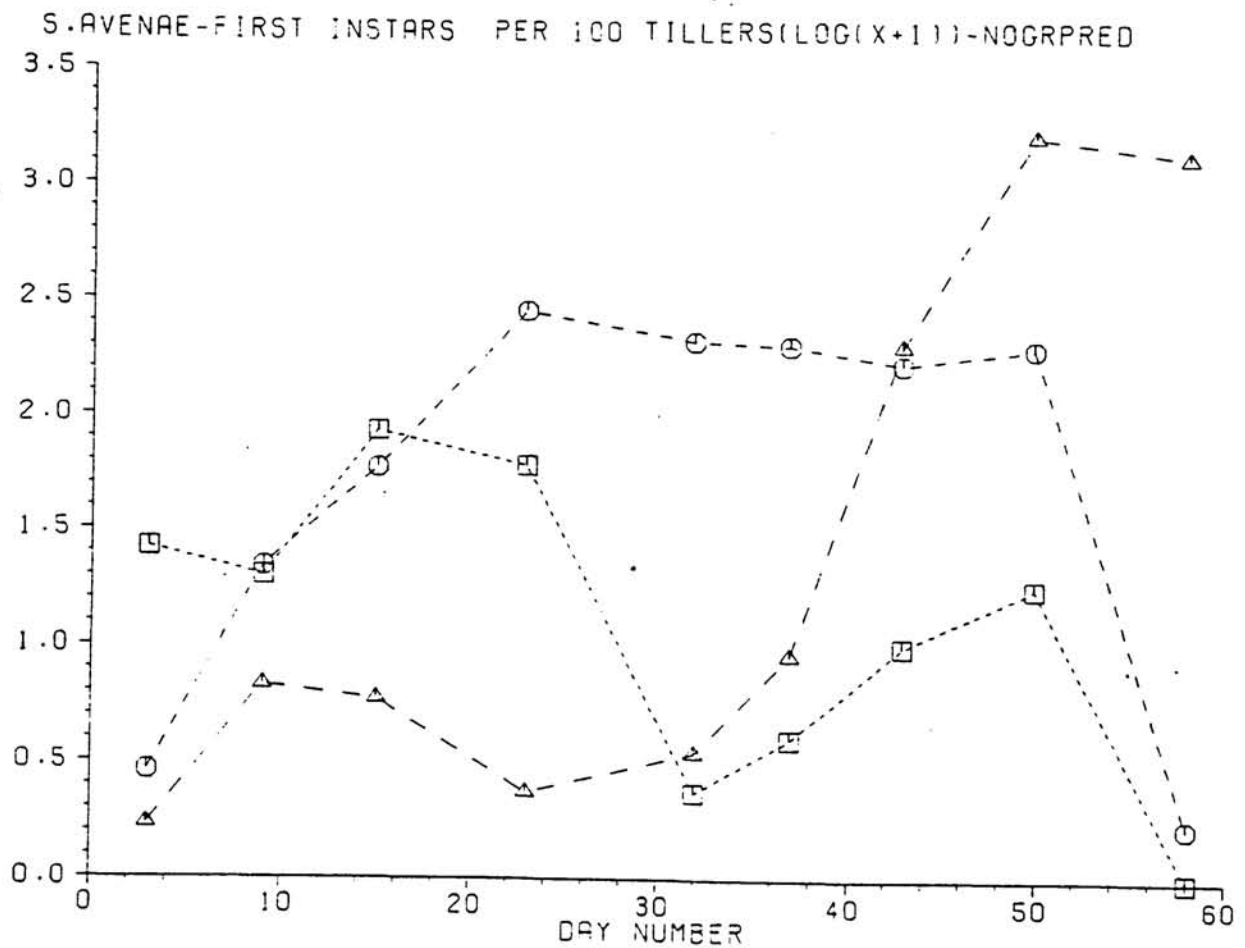
On the other sowings, separate peaks for apterous and alate reproduction were not easily recognised, probably due to the extended period of crop attractiveness to alates. Although initially alates discriminated against sow date 2 ($p < .01$; Table 69) this clear difference was no longer apparent by 13/6. Indeed, it is likely that on 27/6 the preference had reversed. On 'NOPRED' for example, there were similar numbers of first instars on sow dates 1 and 2 ($\bar{x} = 11.7$ and $9.5/100$ tillers respectively; Table 43) yet on the older crop, it is likely that a higher

FIGURE 57 :

KEY

Assessment date	Day No.	
7/6	3	□ - SOWDATE 1
13/6	9	○ - SOWDATE 2
19/6	15	△ - SOWDATE 3
27/6	23	
6/7	32	
11/7	37	
17/7	43	
24/7	50	
3/8	58	

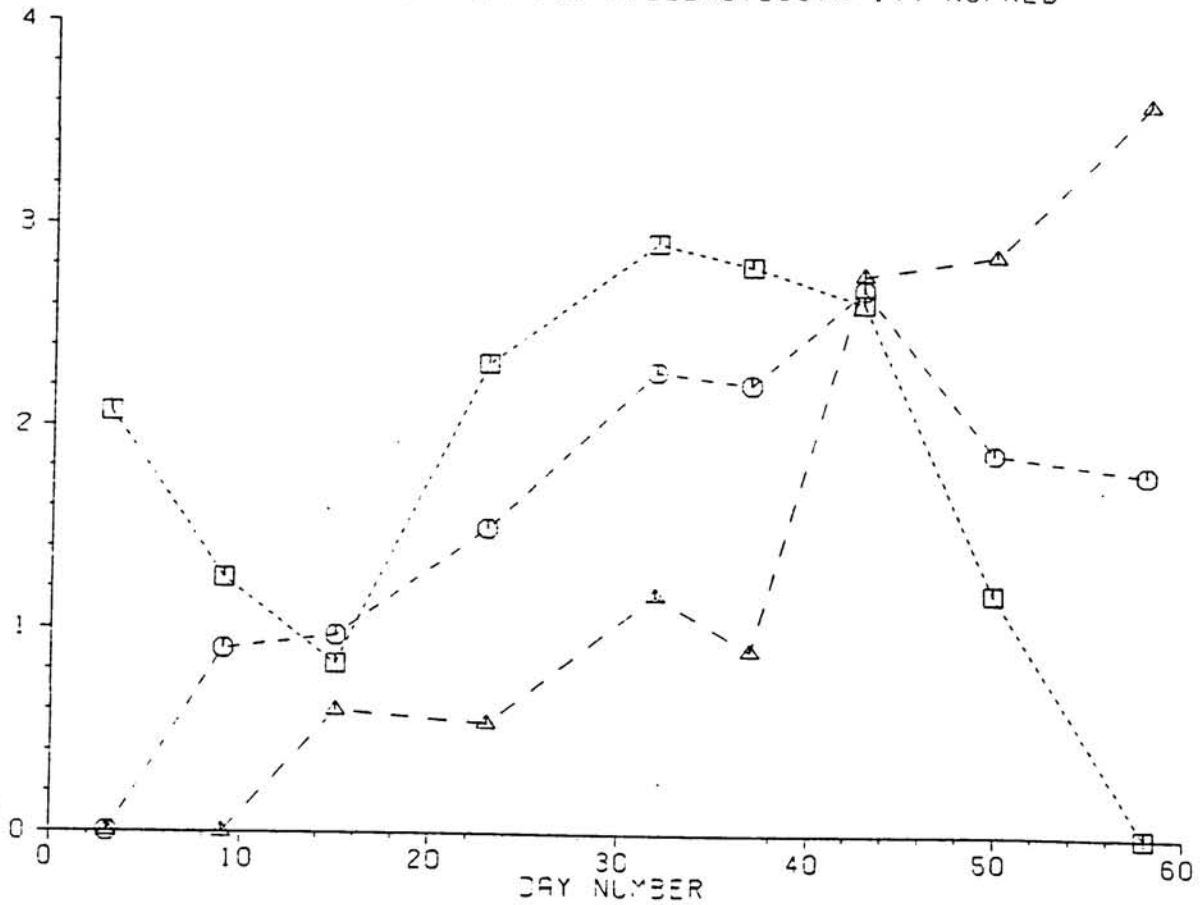
FIGURE 58 :

KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

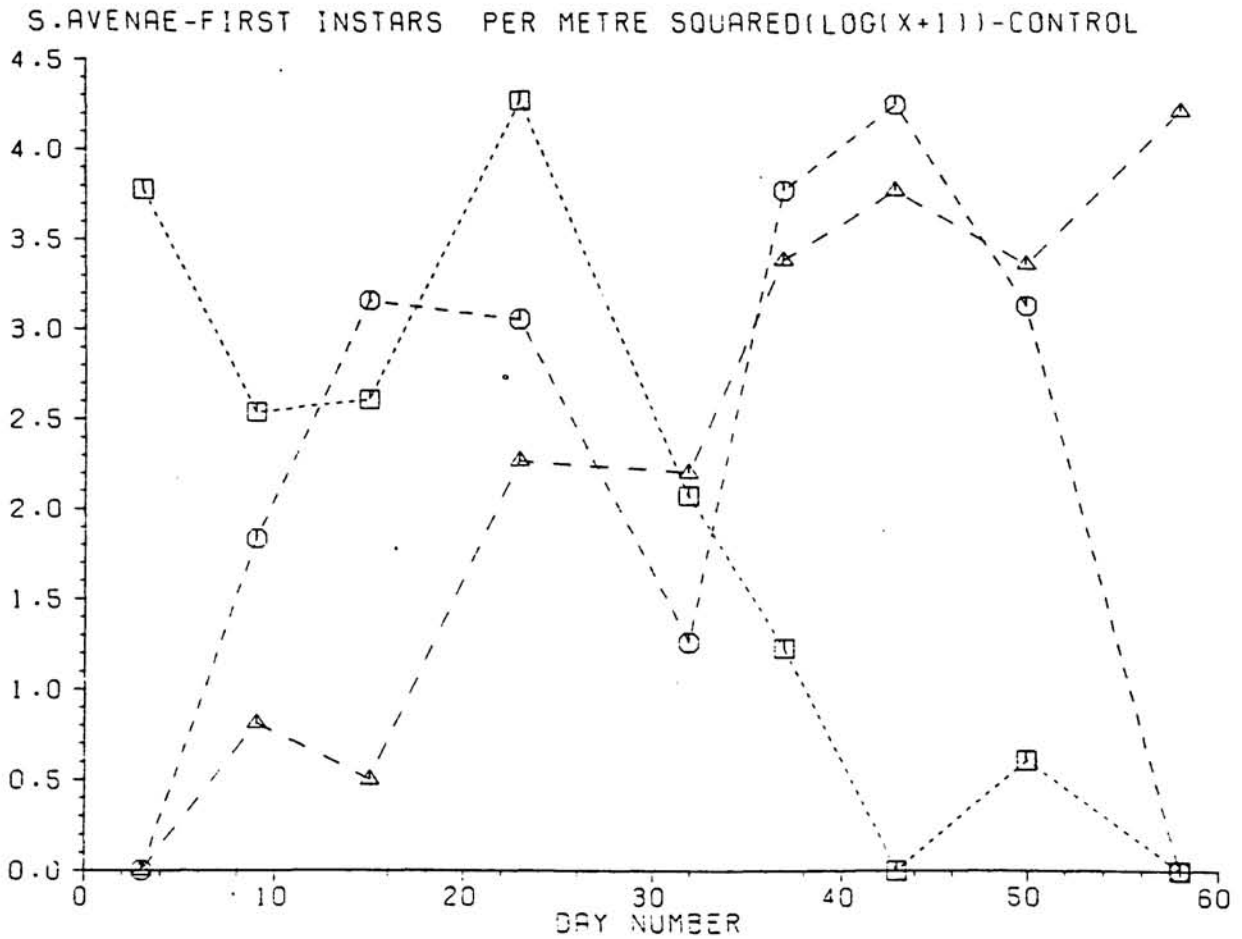
FIGURE 59 :

S.AVENAE-FIRST INSTARS PER 100 TILLERS($\text{LOG}(X+1)$)-NOPREDKEYAssessment
dateDay
No.

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

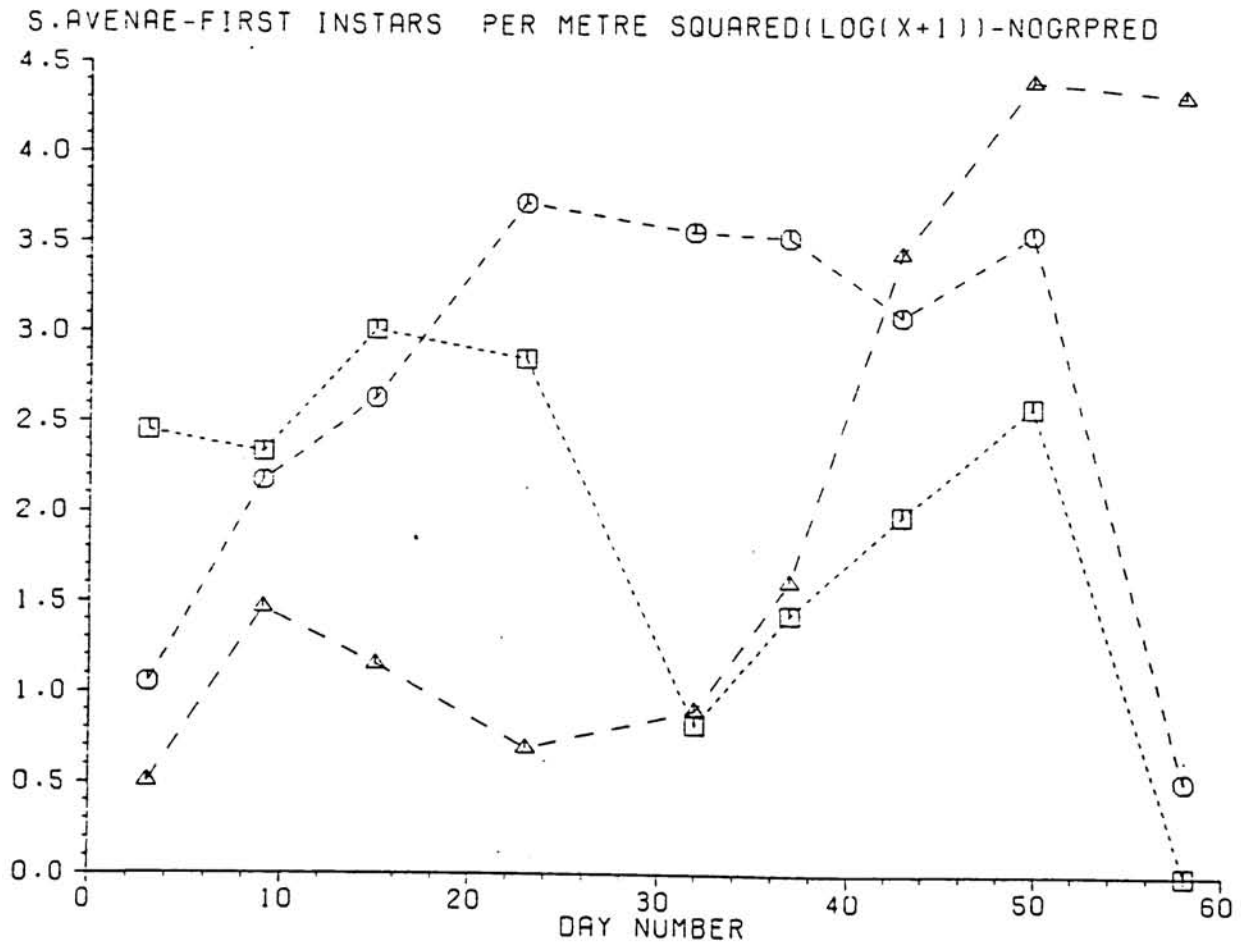
FIGURE 60 :

KEYAssessment
dateDay
No.

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

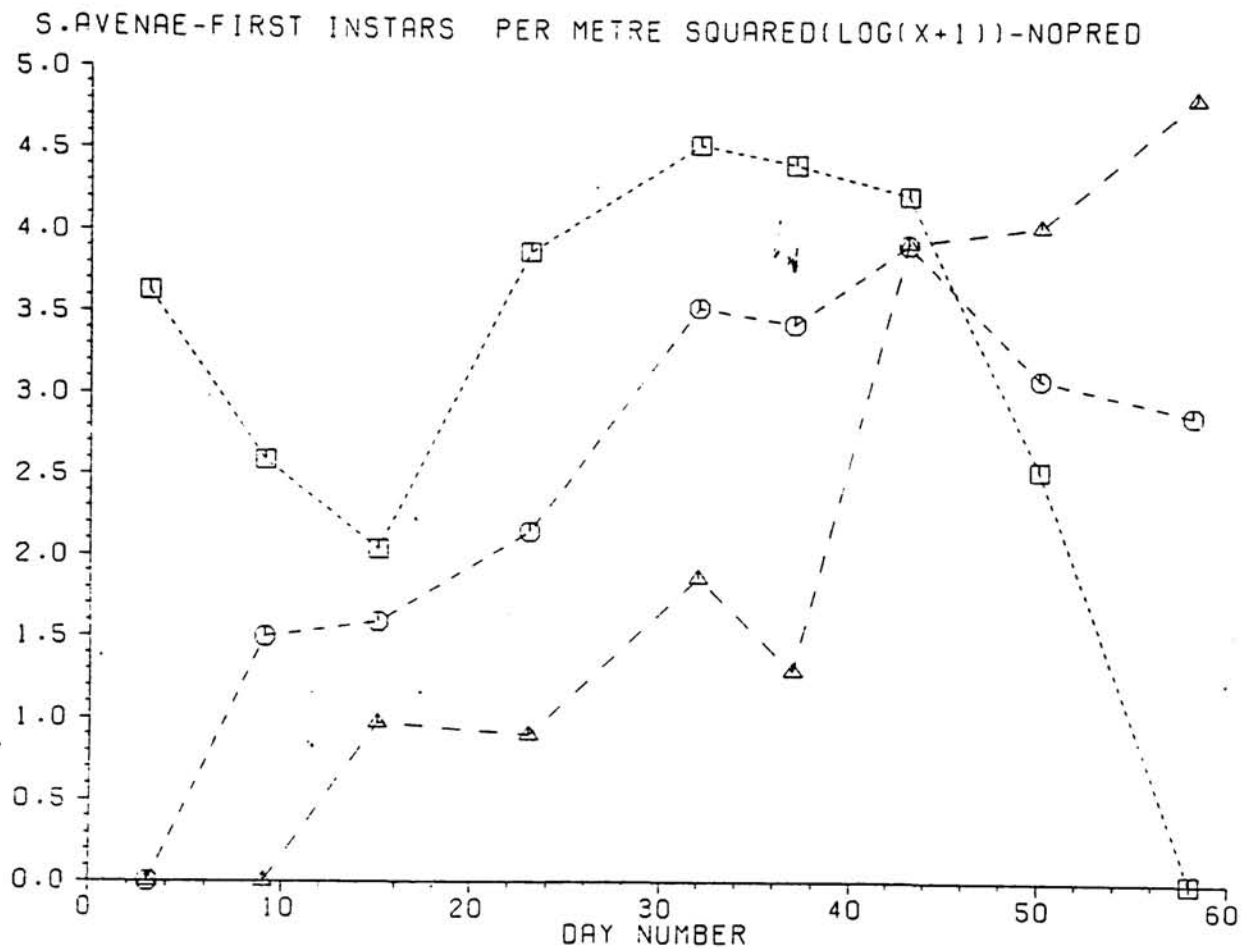
FIGURE 61 :

KEYAssessment
dateDay
No.

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

FIGURE 62 :

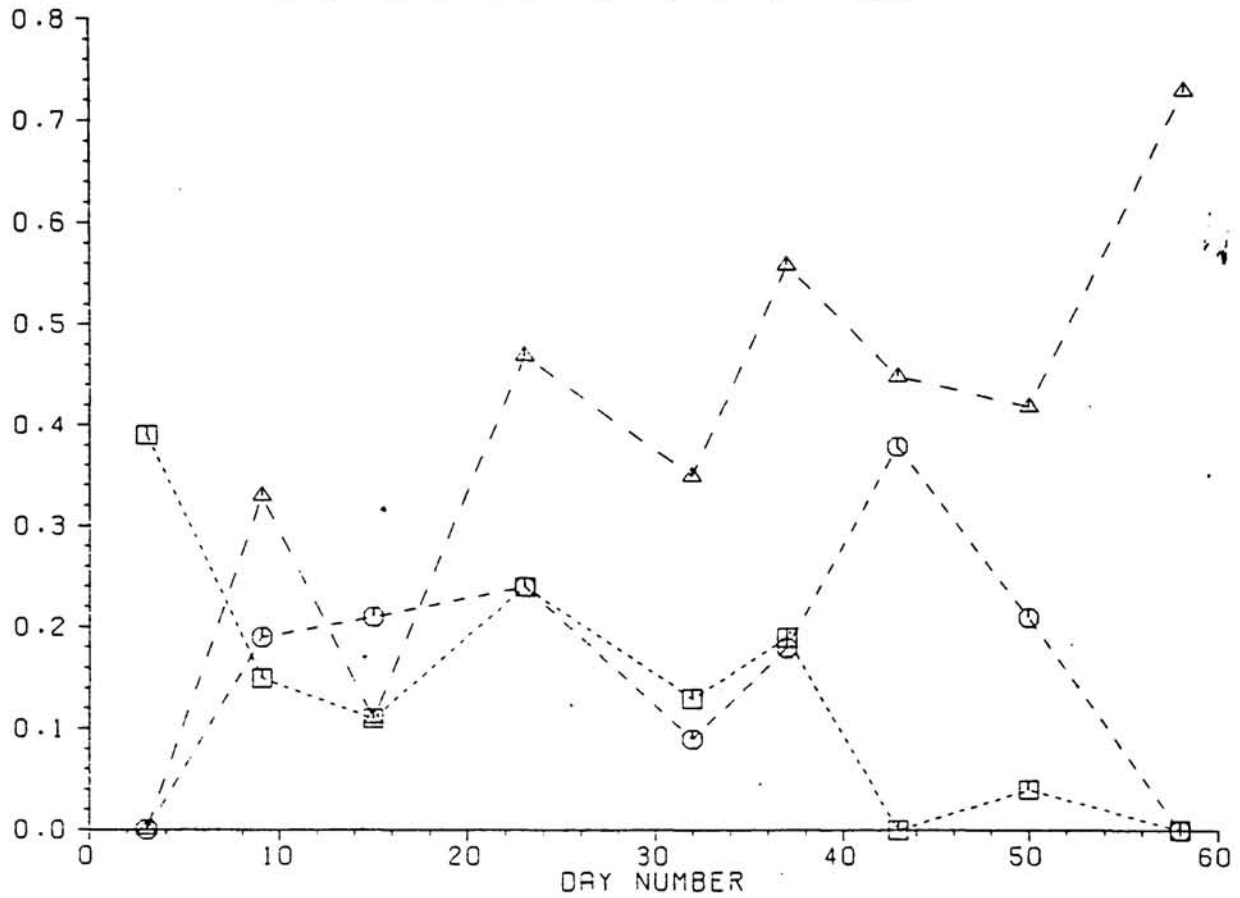
KEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

FIGURE 63 :

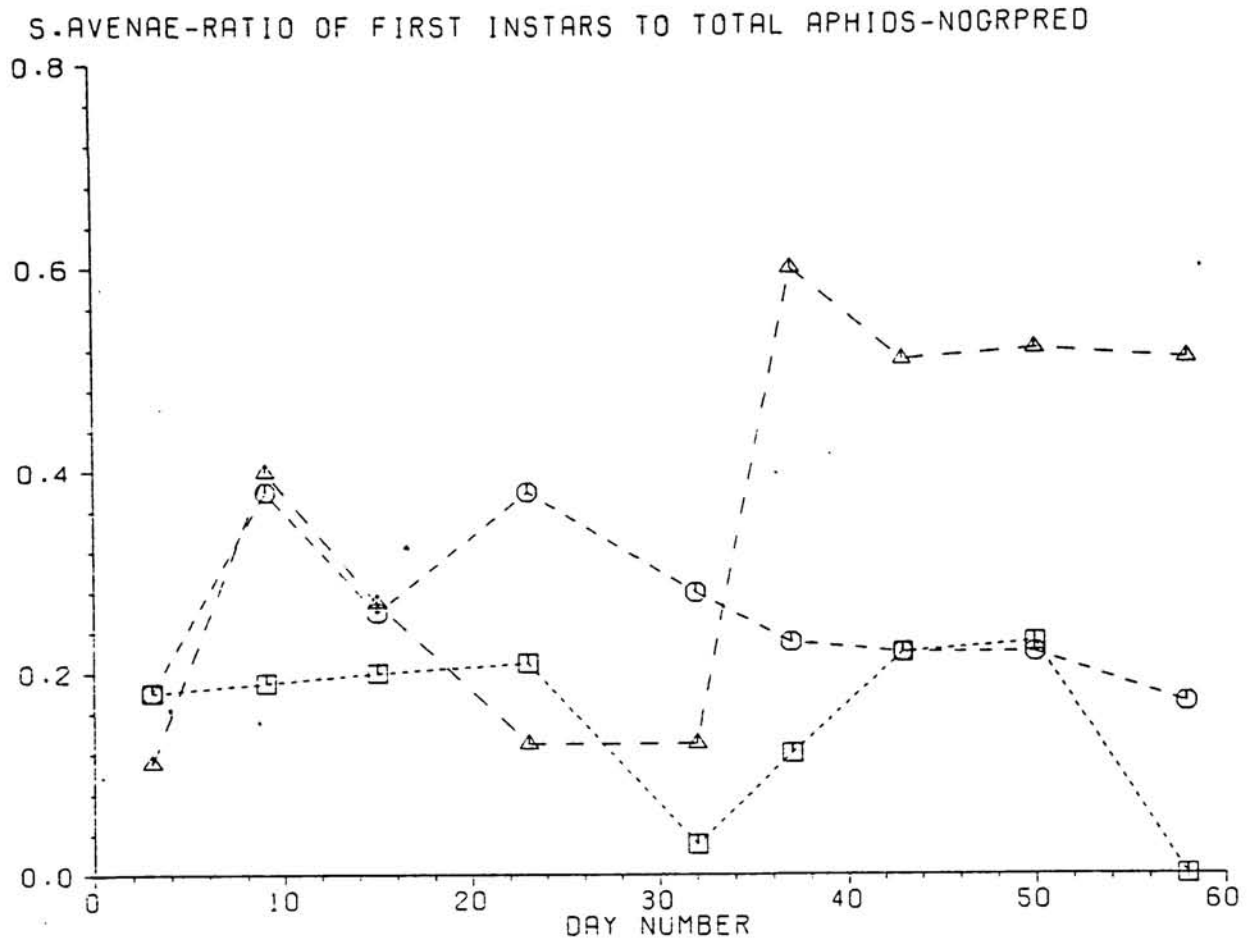
S.AVENAE-RATIO OF FIRST INSTARS TO TOTAL APHIDS-CONTROL

KEYAssessment
dateDay
No.

7/6 3
 13/6 9
 19/6 15
 27/6 23
 6/7 32
 11/7 37
 17/7 43
 24/7 50
 3/8 58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

FIGURE 64 :

KEYAssessment
dateDay
No.

7/6

3

13/6

9

19/6

15

27/6

23

6/7

32

11/7

37

17/7

43

24/7

50

3/8

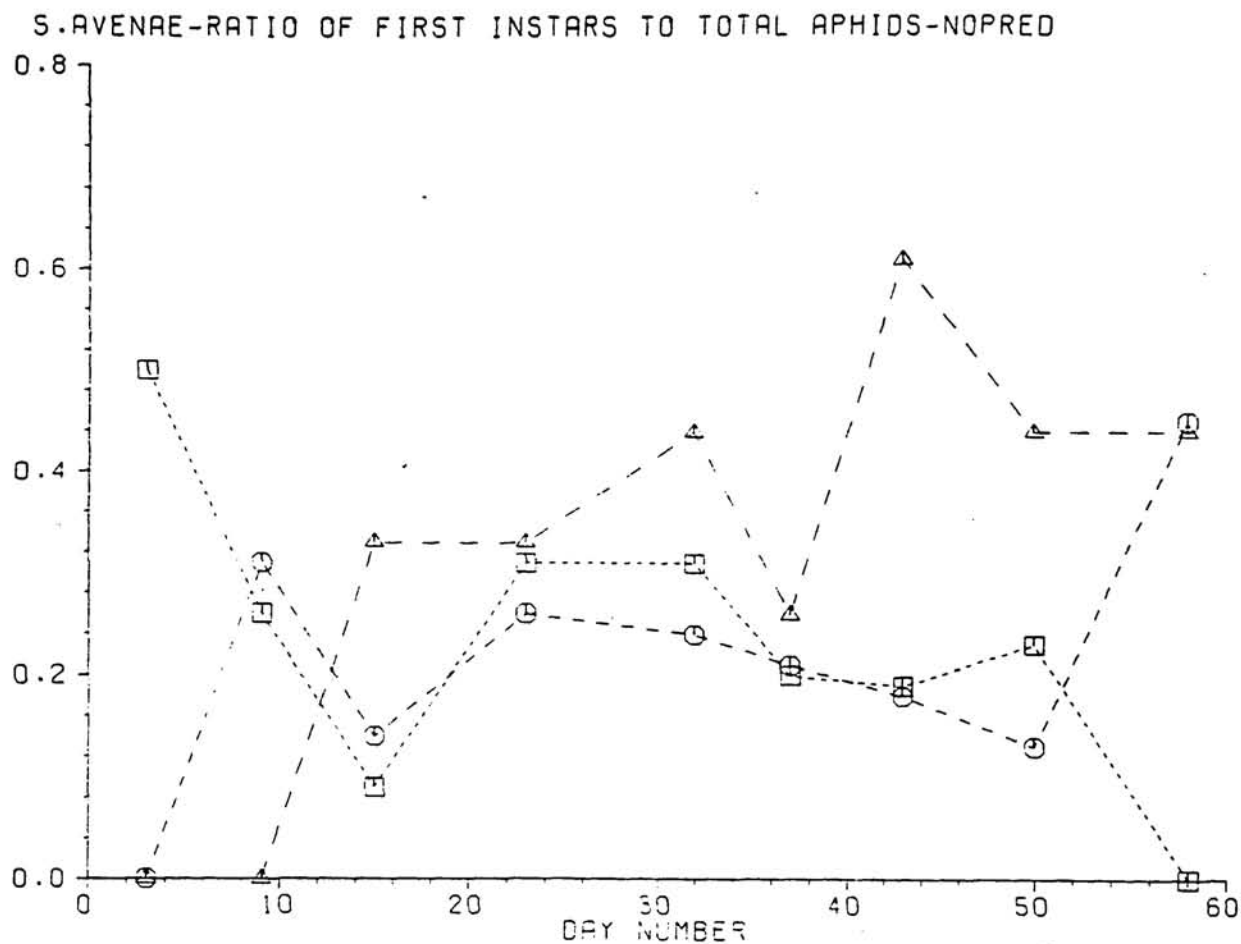
58

□ - SOWDATE 1

○ - SOWDATE 2

△ - SOWDATE 3

FIGURE 65 :

KEYAssessment
dateDay
No.

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

TABLE 69 : Effect of crop age on *S. avenae* populations (first instar aphids) - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Numbers per 100 tillers

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for sow date effects	**	N.S.	N.S.	*	N.S.	*	*	**	**
Treatment	Main sow date comparisons								
1	1, 2	**		N.S.		*	*	**	N.S.
	2, 3	N.S.		N.S.		N.S.	*	N.S.	**
	1, 3	**		N.S.		*	N.S.	**	**
2	1, 2	*		N.S.		N.S.	N.S.	*	N.S.
	2, 3	N.S.		*		N.S.	N.S.	**	**
	1, 3	**		N.S.		N.S.	N.S.	**	**
3	1, 2	**		N.S.		N.S.	N.S.	*	**
	2, 3	N.S.		N.S.		N.S.	N.S.	N.S.	**
	1, 3	**		N.S.		*	N.S.	**	**

(B) Numbers per m²

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for sow date effects	**	N.S.	*	*	N.S.	*	*	**	**
Treatment	Main sow date comparisons								
1	1, 2	**	N.S.	N.S.	-	*	*	**	N.S.
	2, 3	N.S.	**	N.S.		N.S.	N.S.	N.S.	**
	1, 3	**	N.S.	N.S.		*	*	**	**
2	1, 2	*	N.S.	N.S.		N.S.	N.S.	*	N.S.
	2, 3	N.S.	N.S.	*		N.S.	N.S.	*	**
	1, 3	**	N.S.	N.S.		N.S.	N.S.	**	**
3	1, 2	**	N.S.	N.S.		N.S.	N.S.	*	**
	2, 3	N.S.	N.S.	N.S.		*	N.S.	N.S.	**
	1, 3	**	N.S.	N.S.		*	N.S.	**	**

(C) Ratio of first instars: total aphids

Date	7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for sow date effects	**	N.S.	N.S.	N.S.	N.S.	N.S.	*	**	**
Treatment	Main sow date comparisons								
1	1, 2	**					N.S.	*	N.S.
	2, 3	N.S.					N.S.	*	**
	1, 3	**					*	**	**
2	1, 2	N.S.					N.S.	N.S.	N.S.
	2, 3	N.S.					N.S.	**	**
	1, 3	N.S.					N.S.	**	**
3	1, 2	**					N.S.	N.S.	**
	2, 3	N.S.					*	N.S.	N.S.
	1, 3	**					*	*	**

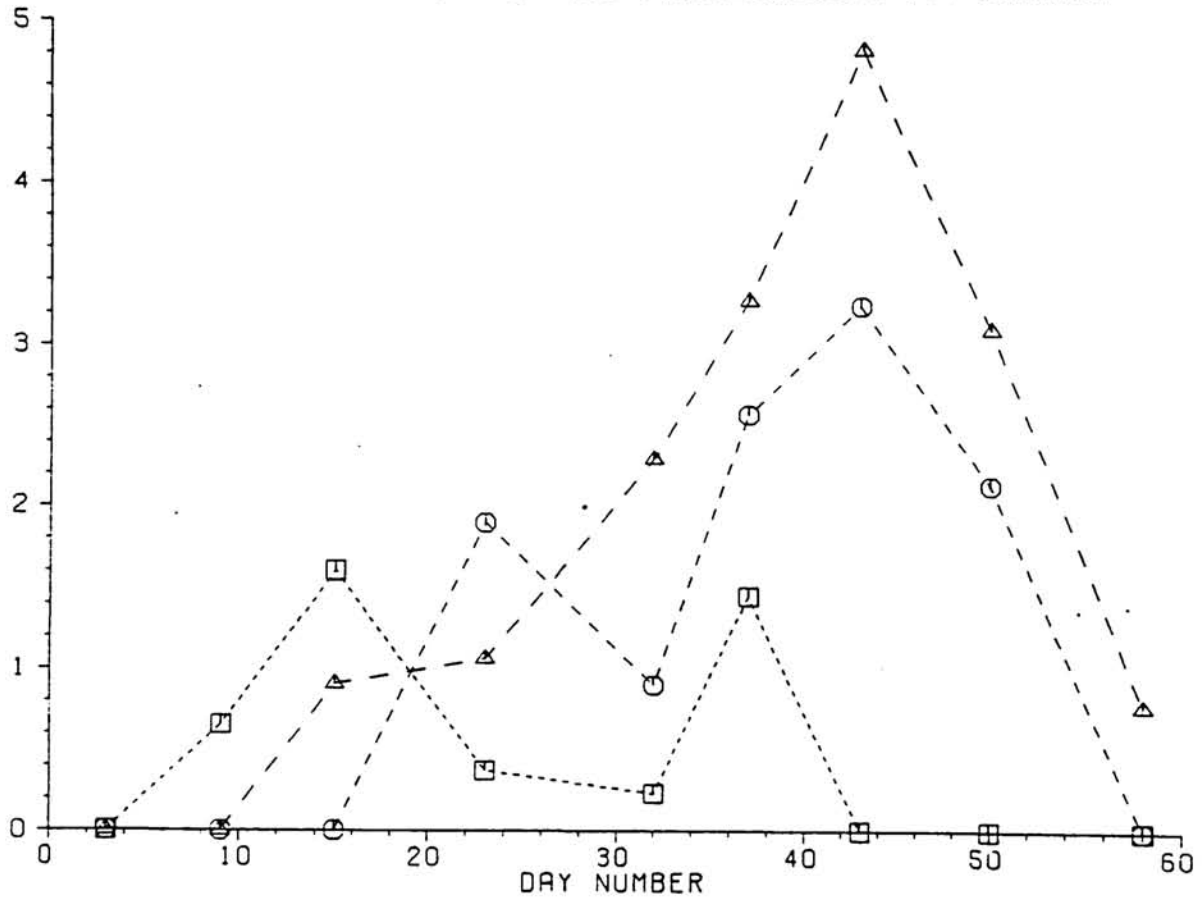
KEY

N.S. - not significant

* - significant ($p < .05$)

** - highly significant ($p < .01$)

FIGURE 66 :

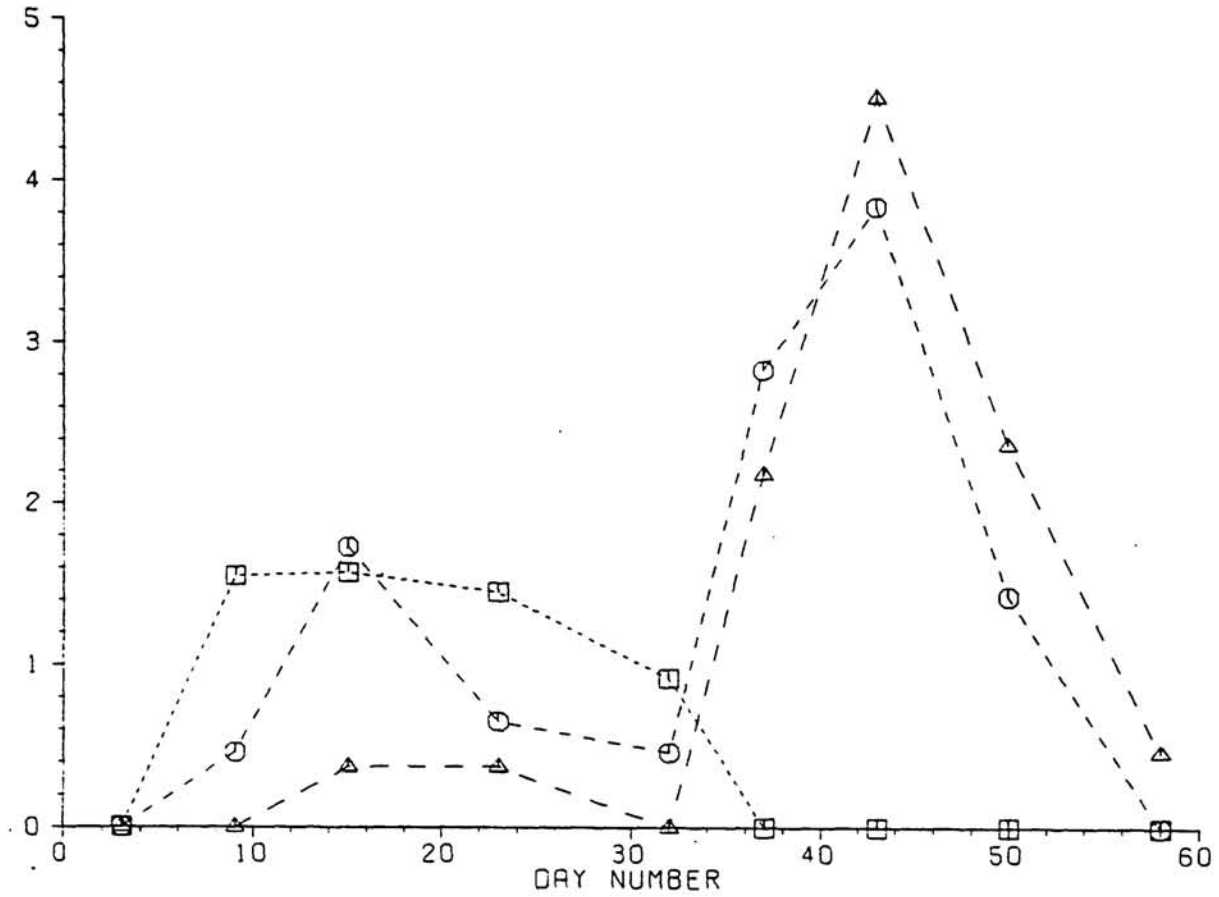
M.DIRRHODUM-FIRST INSTARS PER 100 TILLERS($\text{LOG}(X+1)$)-CONTROLKEY

Assessment date	Day No.
7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

FIGURE 67 :

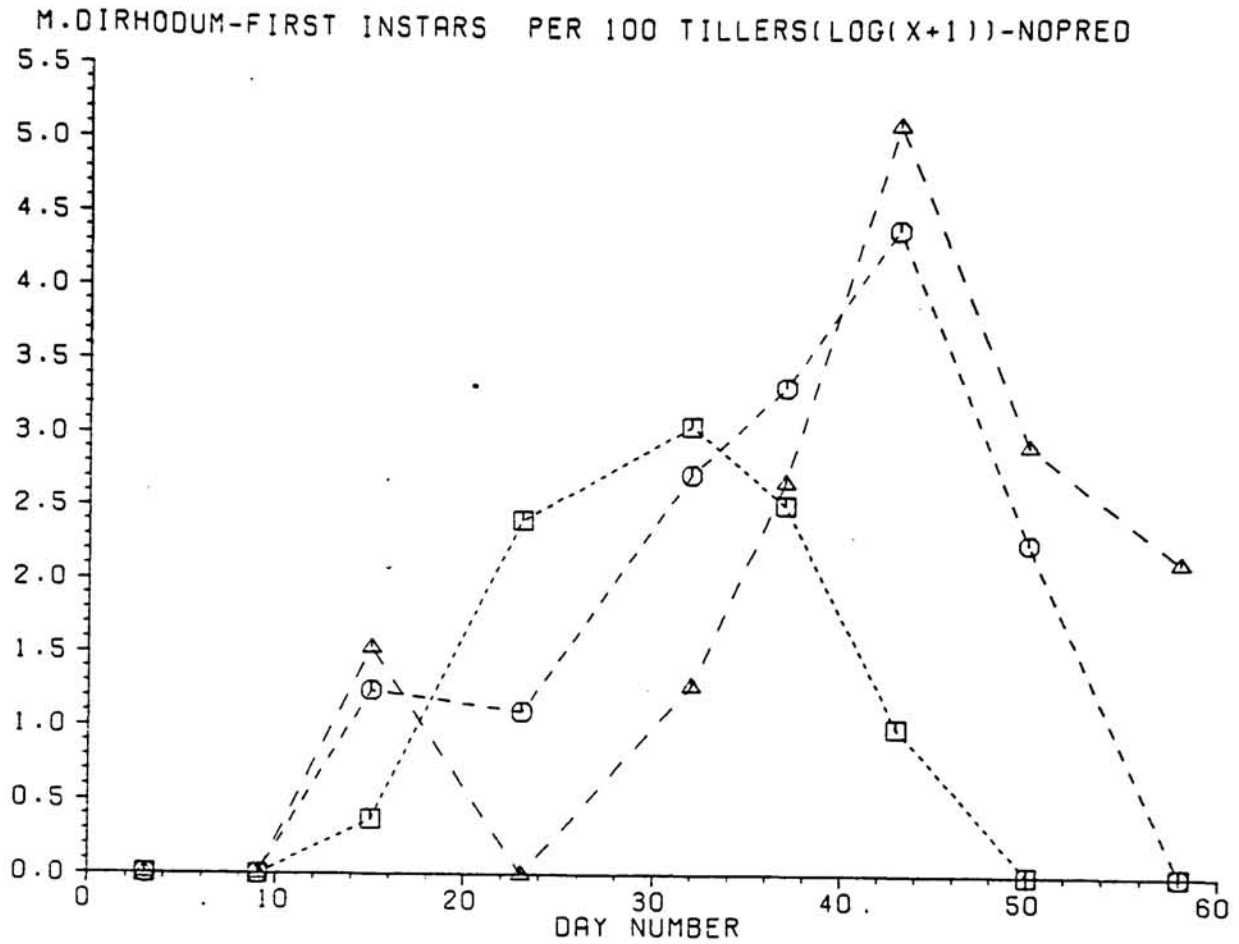
M.DIRRHODUM-FIRST INSTARS PER 100 TILLERS (LOG(X+1))-NOGRPREO

KEYAssessment
dateDay
No.

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

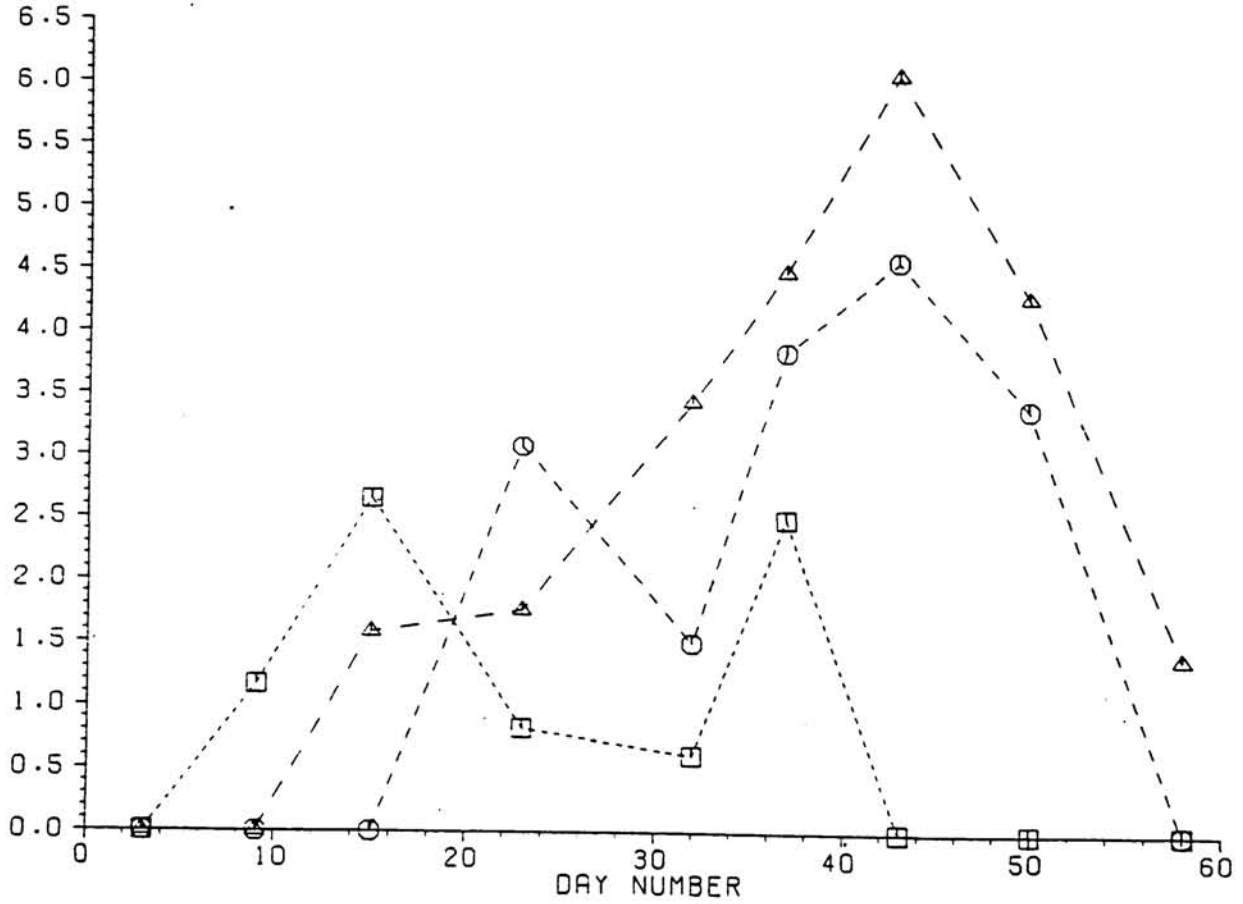
FIGURE 68 :

KEY

Assessment date	Day No.	
7/6	3	□ - SOWDATE 1
13/6	9	○ - SOWDATE 2
19/6	15	△ - SOWDATE 3
27/6	23	
6/7	32	
11/7	37	
17/7	43	
24/7	50	
3/8	58	

FIGURE 69 :

M.DIRRHODUM-FIRST INSTARS PER METRE SQUARED (LOG(X+1))-CONTROL

KEY

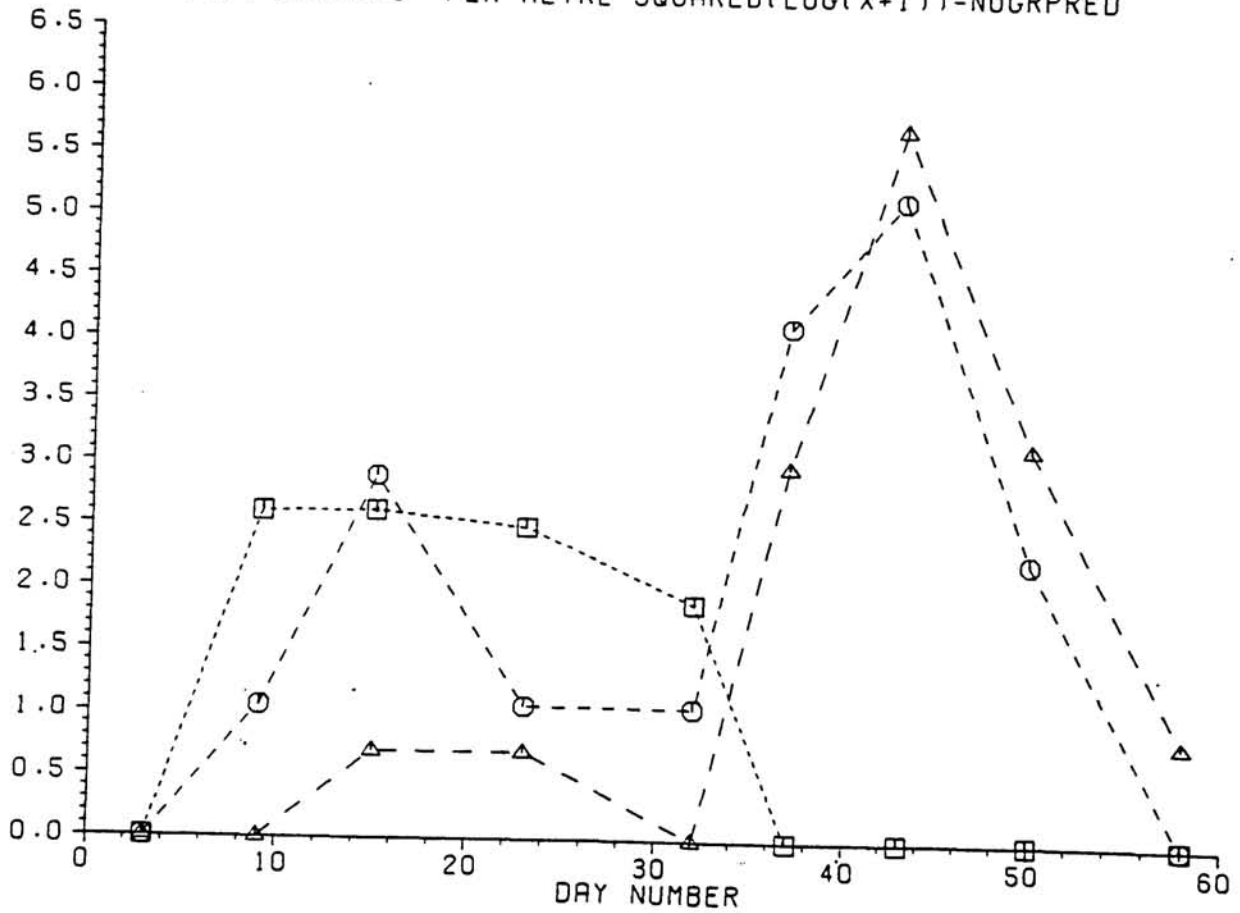
Assessment date	Day No.
-----------------	---------

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

FIGURE 70 :

M.DIRRHODUM-FIRST INSTARS PER METRE SQUARED (LOG(X+1))-NOGRPREP

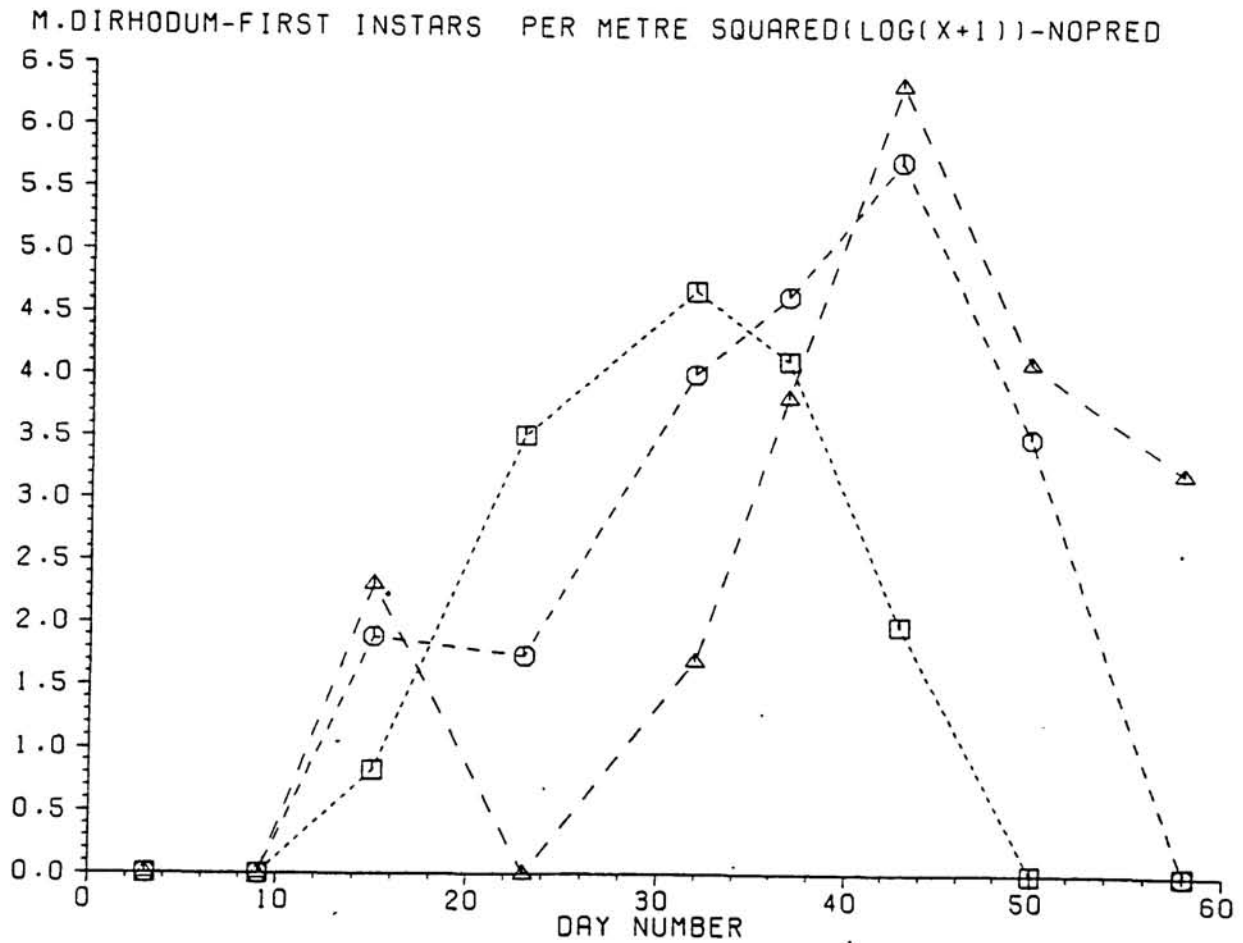
KEY

Assessment date	Day No.
-----------------	---------

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

FIGURE 71 :

KEY

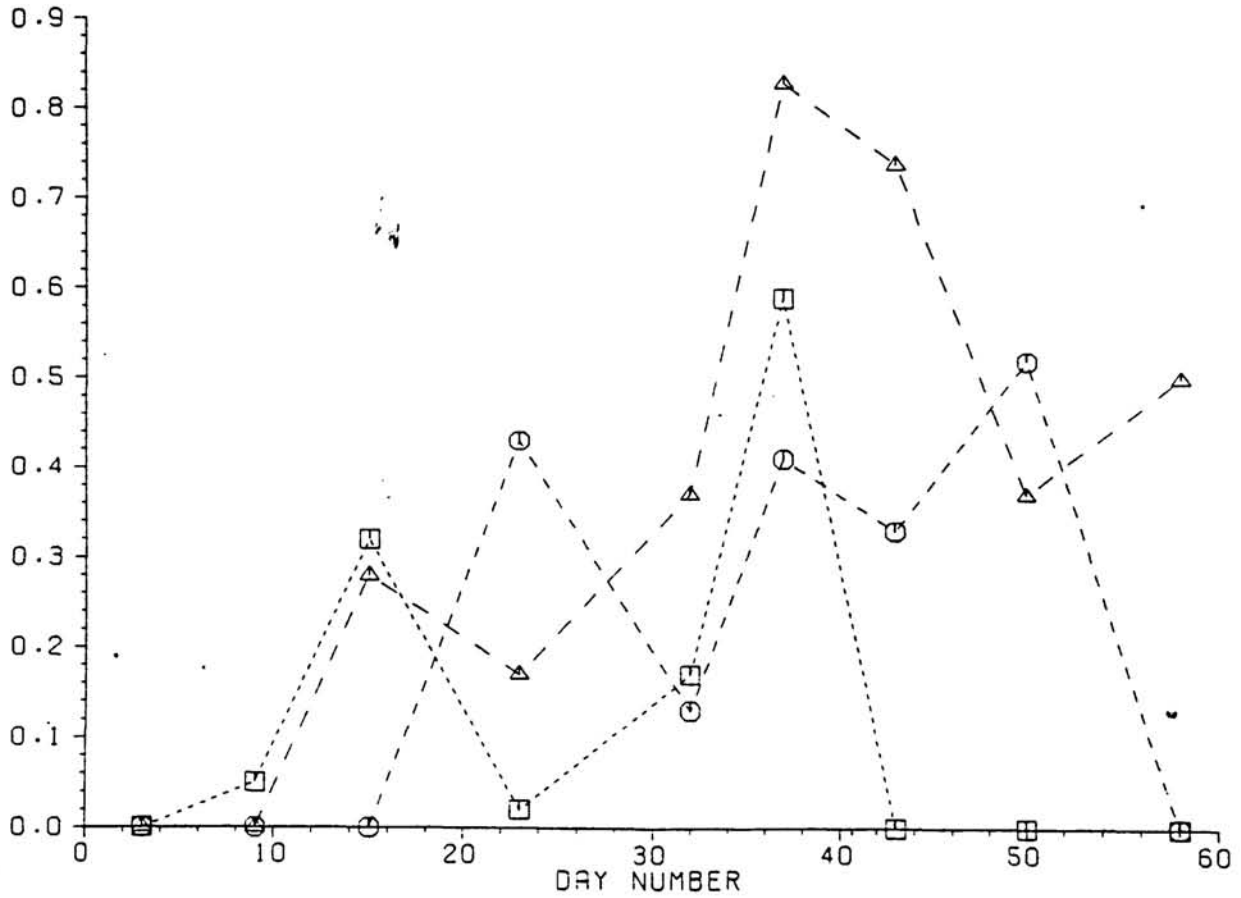
Assessment date	Day No.
-----------------	---------

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

FIGURE 72 :

M.DIRRHODUM-RATIO OF FIRST INSTARS TO TOTAL APHIDS-CONTROL

KEYAssessment
dateDay
No.

7/6

3

13/6

9

19/6

15

27/6

23

6/7

32

11/7

37

17/7

43

24/7

50

3/8

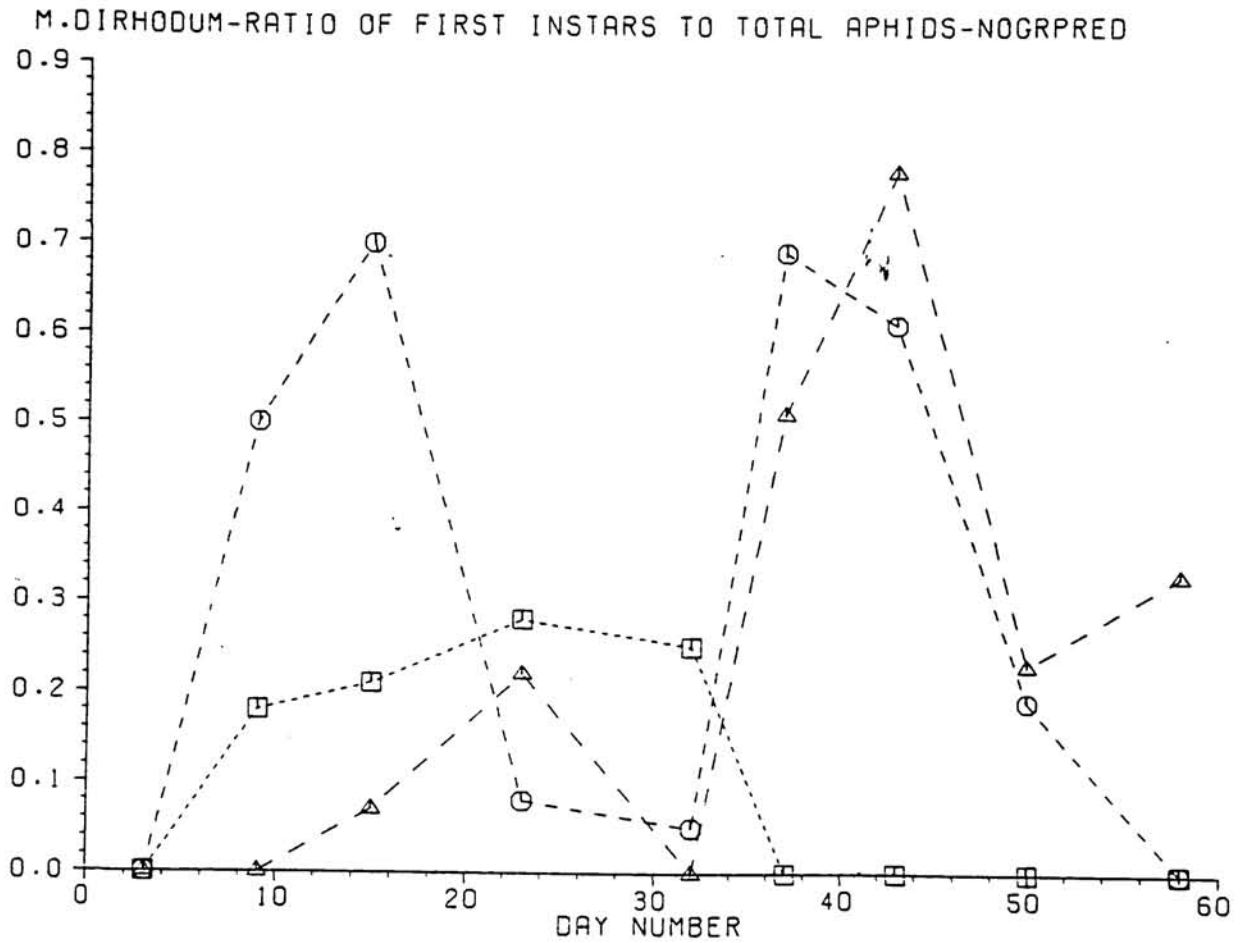
58

□ - SOWDATE 1

○ - SOWDATE 2

△ - SOWDATE 3

FIGURE 73:

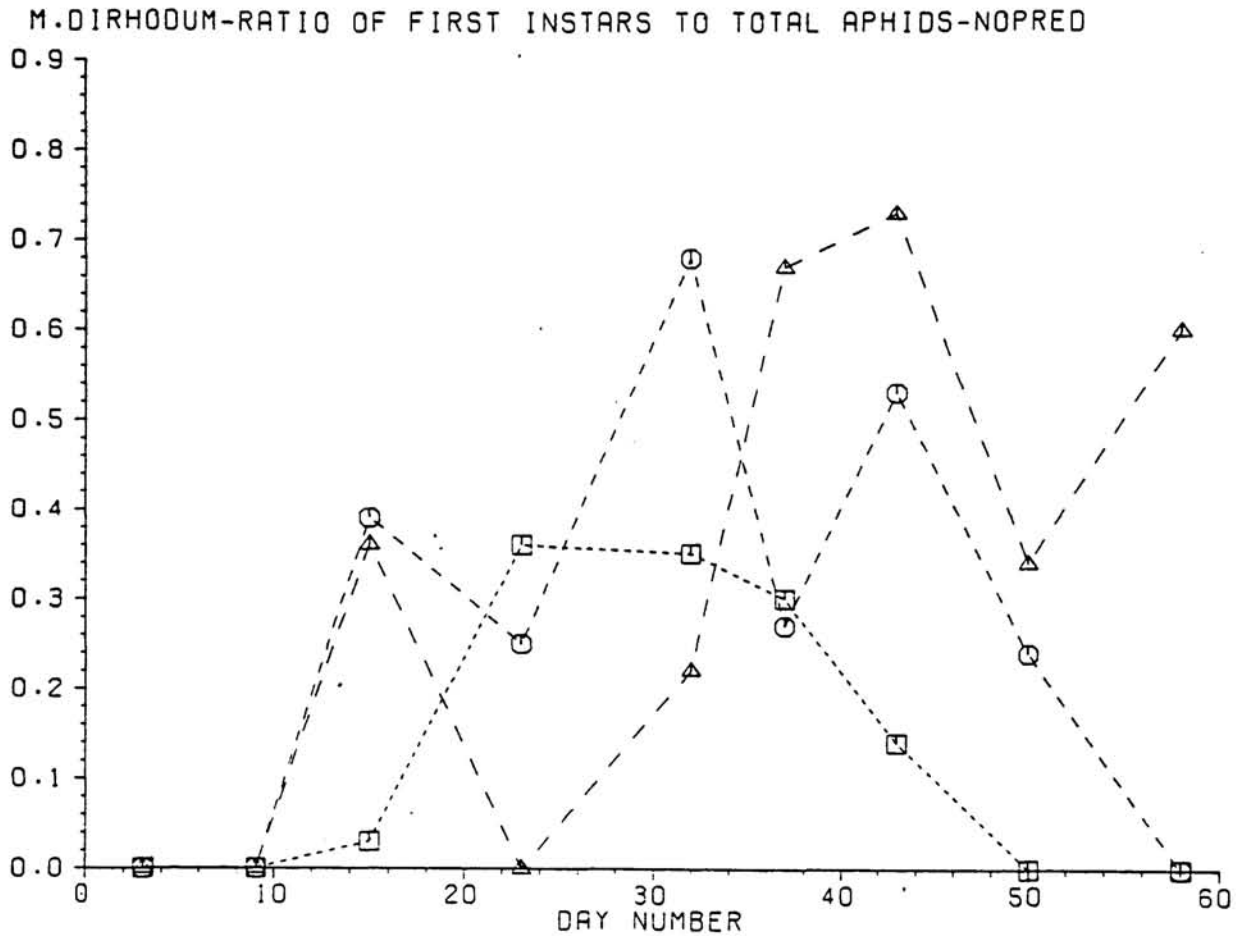
KEY

Assessment date	Day No.
-----------------	---------

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□	- SOWDATE 1
○	- SOWDATE 2
△	- SOWDATE 3

FIGURE 74 :

KEYAssessment
dateDay
No.:

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

TABLE 70 : Effect of crop age on *M. dirhodum* populations (first instar aphids) - summary of ANOVA[†].

[†] see text for guide to interpretation.

(A) Numbers per 100 tillers

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		‡	N.S.	N.S.	N.S.	N.S. [§]	*	**	**	**
Sow date	Main treatment comparisons									
1	1, 2 [†]					N.S.	N.S.	**	N.S.	N.S.
	2, 3					*	*	**	N.S.	N.S.
	1, 3					**	N.S.	**	**	N.S.
2	1, 2					N.S.	N.S.	**	N.S.	N.S.
	2, 3					N.S.	N.S.	N.S.	N.S.	N.S.
	1, 3					N.S.	N.S.	**	**	N.S.
3	1, 2					N.S.	N.S.	**	*	N.S.
	2, 3					**	N.S.	N.S.	N.S.	N.S.
	1, 3					*	N.S.	**	*	**

(B) Numbers per m²

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		‡	N.S.	N.S.	N.S.	N.S. [§]	**	**	**	**
Sow date	Main treatment comparisons									
1	1, 2					N.S.	N.S.	**	*	N.S.
	2, 3					N.S.	N.S.	*	N.S.	N.S.
	1, 3					*	N.S.	**	**	*
2	1, 2					N.S.	**	**	N.S.	N.S.
	2, 3					N.S.	N.S.	N.S.	N.S.	N.S.
	1, 3					N.S.	*	**	*	N.S.
3	1, 2					N.S.	N.S.	**	*	N.S.
	2, 3					**	N.S.	N.S.	N.S.	**
	1, 3					*	N.S.	**	**	**

(C) Ratio of first instars: total aphids

Date		7/6	13/6	19/6	27/6	6/7	11/7	17/7	24/7	3/8
F test for treatment effects		‡	N.S.	N.S.	N.S.	N.S.	**	**	**	**
Sow date	Main treatment comparisons									
1	1, 2							**	**	N.S.
	2, 3							**	N.S.	N.S.
	1, 3							**	*	N.S.
2	1, 2							**	N.S.	N.S.
	2, 3							N.S.	N.S.	N.S.
	1, 3							**	N.S.	N.S.
3	1, 2							**	N.S.	N.S.
	2, 3							*	N.S.	*
	1, 3							**	*	*

KEY

N.S. - not significant

* - significant ($p < .05$)

** - highly significant ($p < .01$)

[§] - significant interaction between main treatments and sow date.

‡ - too few aphids to analyse

proportion of these were deposited by apterae which were more numerous ($\bar{x} = 8.0$ compared to 0.0/100 tillers; Table 45).

Conversion of the data to numbers per M^2 made no difference to the pattern of nymph deposition in relation to sow date (Figures 60, 61 and 62) or to the results of statistical analysis (Table 69) indicating that the differential rates of nymph deposition on the 3 sow dates resulted from growth stage preferences rather than plant density effects.

On sow date 3, first instars formed a significantly greater proportion of total populations than on the earlier sowings (Figures 63, 64 and 65) ($p < .05$ on 24/7 and 3/8 (Table 69) and high rates of nymph deposition continued for a longer period of time.

Comparison between the fluctuations in alates and first instars, reveals a reasonably close positive relationship between the numbers of alates and the subsequent abundance of first instars (Figures 45 and 57; Figures 46 and 58; Figures 47 and 59), demonstrated most clearly on sow dates 2 and 3. This suggests as expected, that alates only settle and remain on the crop in large numbers when it is suitable for larviposition.

M. dirhodum (Figures 66, 67 and 68)

The pattern of successive exploitation of sow dates 1, 2 and 3 described for *S. avenae* was also shown by *M. dirhodum* although its occurrence on field plots was compressed into a shorter period of time. Around mid June, most first instars were deposited on sow date 1 (e.g. on 13/6, only 2 individuals were found on sow date 2 compared with 25 on sow date 1 (totals for all 3 main treatments)) (Figures 66 and 67). A subsequent decrease in numbers was accompanied by build up on sow dates 2 and 3. On the 'CONTROL' peak numbers (on 17/7) were significantly higher on sow date 3 than on 2 ($p < .01$) (Table 70), but the smaller differences on 'NOGRPRED' and 'NOPRED' did not attain statistical significance ($p = .05$).

As with *S. avenae*, an extended period of nymph deposition on 'NOPRED' (Figure 68) resulted in greatly increased overall populations by mid July (Figure 41). It is also noteworthy that substantially reduced rates of reproduction between 17/7 and 24/7 were followed by dramatic losses to the overall populations between 24/7 - 3/8, suggesting that variations in natality were a major source of population change (c.f. Southwood 1975).

Pattern of population change and the results of ANOVA were relatively unaffected by conversion of the data to 'numbers per M²' (Figures 69, 70 and 71; Table 70). Figures 72, 73 and 74 show that first instars made up a substantial proportion of total aphid populations, approaching 90% on 11/7 on sow date 3. The ratios of firsts : total aphids differed significantly between sow dates on 17/7 (Table 70), but on other occasions no sow date effects achieved significance.

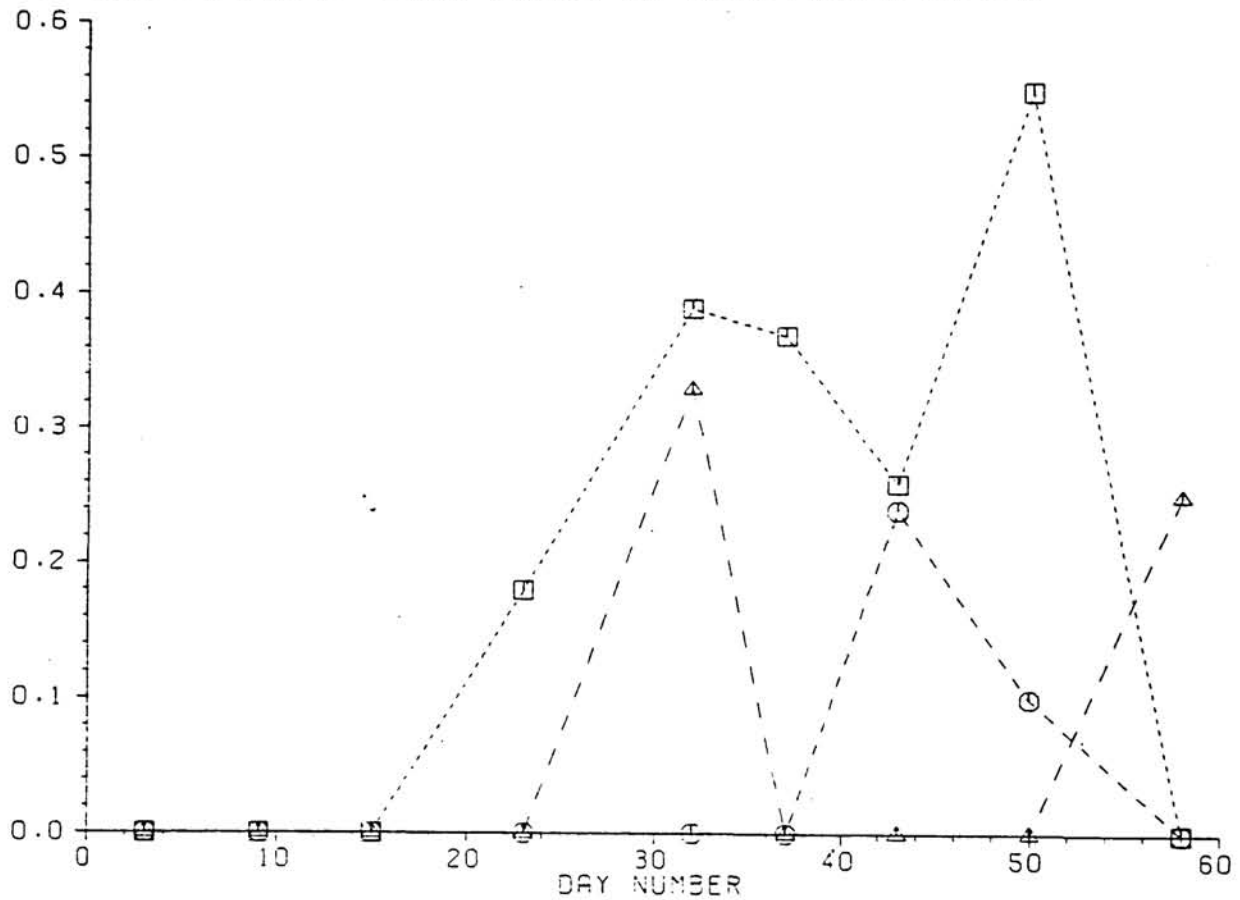
There was a clear positive relationship between numbers of alate and first instars (as was the case with *S. avenae*) indicating, as expected a correlation between alate settling and suitability of plants for reproduction. On sow date 1, very few alates (Figures 51, 52 and 53) appear to have deposited relatively large numbers of first instars (Figures 69, 70 and 71) suggesting that alates spent only short periods of time on these plants despite their suitability for reproduction.

3.3.2.4.4. Production of alates on the crop.

Fourth instar alates were extremely scarce on 'CONTROL' and 'NOGRPRED' treatments. Only *S. avenae* on 'NOPRED: sow date 1' occurred in 'countable' numbers (mean numbers/100 tillers reached a peak of 7.0 on 11/7; Table 47) probably because populations on this treatment were relatively dense and long lived (Figure 75, Tables 28 - 34). An increase in the proportion of alatiform : total fourth instars after 17/6 on sow date 1 was followed by a peak on 24/7 (Figure 75) which coincided with the overall

FIGURE 75 :

S.AVENAE-RATIO OF FORTH ALATES TO TOTAL FORTHS-NOPRED

KEYAssessment
dateDay
No.

7/6	3
13/6	9
19/6	15
27/6	23
6/7	32
11/7	37
17/7	43
24/7	50
3/8	58

□ - SOWDATE 1
 ○ - SOWDATE 2
 △ - SOWDATE 3

population collapse (Figure 41). Thus, on 'NOPRED' the sow date 1 population crash was induced partly by the production of alates while on 'CONTROL' and 'NOGRPRED', this potential cause of decline was not realised due to the earlier impact of predation.

3.3.2.5 Growth stage, nutrient levels and aphid attack.

The previous section described the differing patterns of aphid attack on crops sown at different times, and tested the significance of the results through analysis of variance. In this section, emphasis is placed on the possible causes of these differences. For this purpose, three phases of infestation have been distinguished - 'colonisation' 'development to peak populations' and 'population crash', and their timing related to crop growth stage and nutrient levels on the 3 sowings. The data for *S. avenae* is compared with nutrient levels in the ears of wheat plants and *M. dirhodum* compared with levels in the flag leaf. The programme of plant nutrient assays was designed to explain changes in *S. avenae* only - hence the emphasis on ears and flag leaves. It is not surprising, therefore that *S. avenae* abundance is better explained by these assays than *M. dirhodum*. Since the latter species feeds on the leaves at varying heights on the plants and lower leaves senesce during plant growth, aphid nutrition must vary considerably between colonies. A programme of plant analysis that took full account of these complications would involve too much work.

3.3.2.5.1 *S. avenae*

Colonisation

Rothamsted suction trap data (Table 24) show a similar level of *S. avenae* abundance over the 2 successive sampling periods 22/5 - 28/5 (7 individuals) and 29/5 - 4/6, (7 individuals,) yet alates only settled on the crop during the second period. Furthermore, the vast majority colonised and reproduced on sow date 1 (The mean (pooling main treatments)

number of first instars/100 tillers was 7.0 compared to 0.2 on sow date 2 and 0.1 on sow date 1: Table 42) suggesting discrimination by alates on the basis of crop growth stage. It appeared that the onset of 'heading' (G.S. 51-61) had elicited alate settling but this hypothesis was not confirmed by the results obtained on sow dates 2 and 3. On these crops, aphid attack began at an earlier stage - after 'pseudostem elongation' (G.S. 30) and colonisation seemingly continued later (up to 'watery ripe' (G.S. 71) on sow date 3 or 'early milk' on sow date 2 (G.S. 73)) - the continuing occurrence of alates was not associated with the appearance of fourth instar alates (Tables 42 - 50). These findings do not necessarily refute the hypothesis of growth stage discrimination because high levels of aphid aerial abundance, coupled with declining availability of optimal crops may have caused innate preference to wane. In other words, growth stage 30 became relatively attractive compared to the alternative crops available to the aphids. The importance of 'diminished preference' would have been enhanced in this experiment by the close proximity of old and young crops.

In retrospect, it is clear that the analysis of crop nutrient levels during colonisation may have helped explain growth stage discrimination by alates, but at the planning stages of the experiment, these analyses were intended mainly to throw light on the causes of population crashes. Sow date 2, however was analysed over the key growth stages, heading and flowering. Soluble nitrogen soared to exceptionally high levels on 16/7 (watery ripe) (Figure 77) and on 17/7 *S. avenae* alates (Figures 45, 46 and 47) and first instars (Figures 57, 58 and 59) were especially abundant on the crop (see Table below - compiling data from Tables 47, 48 and 49 and Figure 77).

	10/7	11/7	13/2	16/7	17/7	19/7	22/7	24/7	25/7
Mean no aphids/100 tillers on 'NOPRED' { Alates		4.0			4.0			1.0	
{ First instars		11.5			28.5			6.5	
Growth stage (Zadoks)	68			71			73		
Soluble N in the ear (% dry wt.)	.53		.68	1.05		.47	.70		0.64

Population development and peak populations.

All populations increased in size steadily after colonisation and nymph depositions. Peak populations coincided with similar growth stages on the 3 sow dates; late milk (G.S. 77) on sow date 1, early milk (G.S. 73) on sow dates 2 and 3. These peaks were also associated with high levels of soluble nitrogen (Figures 76, 77 and 78), soluble carbohydrate (Figures 79 and 80), and water (Figures 80, 81 and 82).

Population crash

Populations crashed soon after reaching their peaks despite continuing high levels of soluble nitrogen and carbohydrate. e.g. On 'NOPRED' mean numbers of *S. avenae*/100 tillers fell from 80.7 (11/7) to 77.3 (17/7) then to 22.3 (24/7 and finally to 0.3 (3/8) on sow date 1. On sow date 2 populations crashed from a peak of 118.0 (17/7) to 46.5 (24/7) then to 22.2 (3/8) (Tables 42-50). The production of alates on the crop accounts for some losses but the sudden nature of the crash points to mortality or dispersal of apterous morphs as the major causes of decline. On sow dates 1 and 2, the onset of population collapse was associated with decreasing water content of wheat ears (Figures 81 and 82). Possibly, a drop in turgor pressure reduced aphid ingestion rates resulting in restlessness and nutrient deficiencies. On sow date 3, population collapse could not be linked to changes in crop nutrient levels, or indeed to any other factor so the causes of decline must remain unexplained.

3.3.2.5.2. *M. dirhodum*

Colonisation

Although the sequential attack of sow dates 1, 2 and 3 indicated the possibility of growth stage discrimination, there was no obvious 'preferred' stage for colonisation and nymph deposition. On sow date 1, this coincided with the end of flowering (G.S. 69), high levels of

soluble carbohydrate (Figure 79) while on sow date 2 it was associated with inflorescence emergence (G.S. 50) and low levels of soluble nitrogen (Figure 77). Colonisation of sow date 3 came even earlier in the development of the crop, namely growth stage 41 (prebooting).

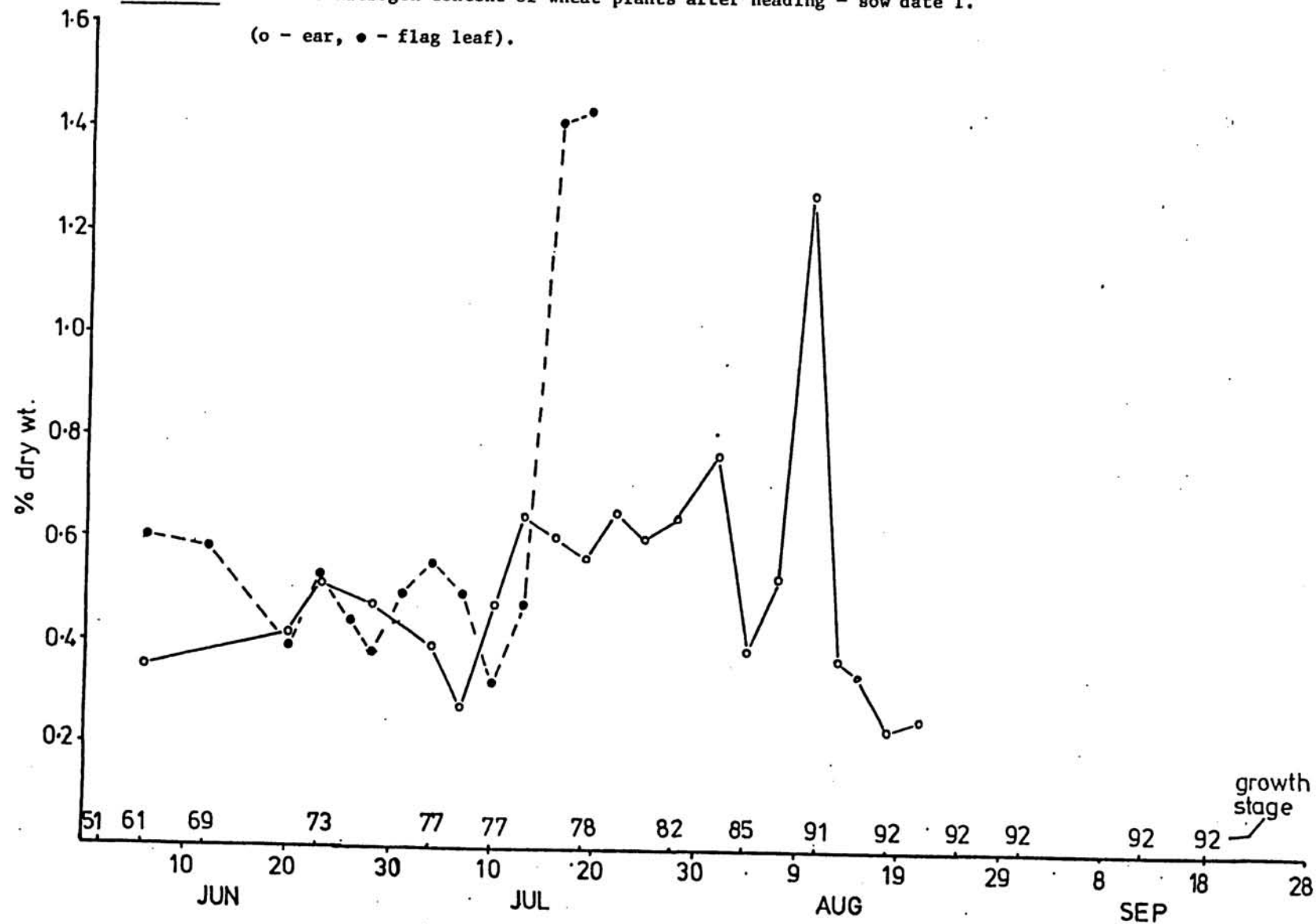
Population development and peak populations.

All populations built up steadily after colonisation but only on sow date 1 were the 2 phases; colonisation and build up distinct. On the later crops, alates continued to settle and deposit nymphs several weeks after the initial immigration. The large aerial populations (Tables 24 and 25) and lack of alternative crops at this time, were probable causes of this prolonged input to the crop. All populations reached their peaks (Figure 41) during the milky ripe stage : late milk (G.S. 77) in the case of sow date 1, early milk (G.S. 73) on sow dates 2 and 3. The peaks were associated with 'high levels' of soluble nitrogen (Figures 76, 77 and 78) and water (Figures 81, 82 and 83) but variable levels of soluble carbohydrate (Figures 79 and 80).

Population crash

Populations collapsed immediately after reaching peak numbers. Mean numbers/100 tillers on sow date 1 fell from 62.3 (6/7) to 46.7 (11/7) then to 13.7 (17/7). Population crashes were more sudden on the younger sowings - on sow date 2, a population of 163.5 (17/7) fell to 37.5 (24/7) and on sow date 3 numbers fell from a peak of 297.7 (17/7) to 65.3 (24.7) (Tables 52 - 59). Although soluble nitrogen levels fell on sow dates 2 and 3, they remained high during the crash on sow date 1. Soluble carbohydrate levels were variable and the water content of leaves did not change appreciably before and after the crashes (Figures 81, 82 and 83).

FIGURE 76: Soluble nitrogen content of wheat plants after heading - sow date 1.



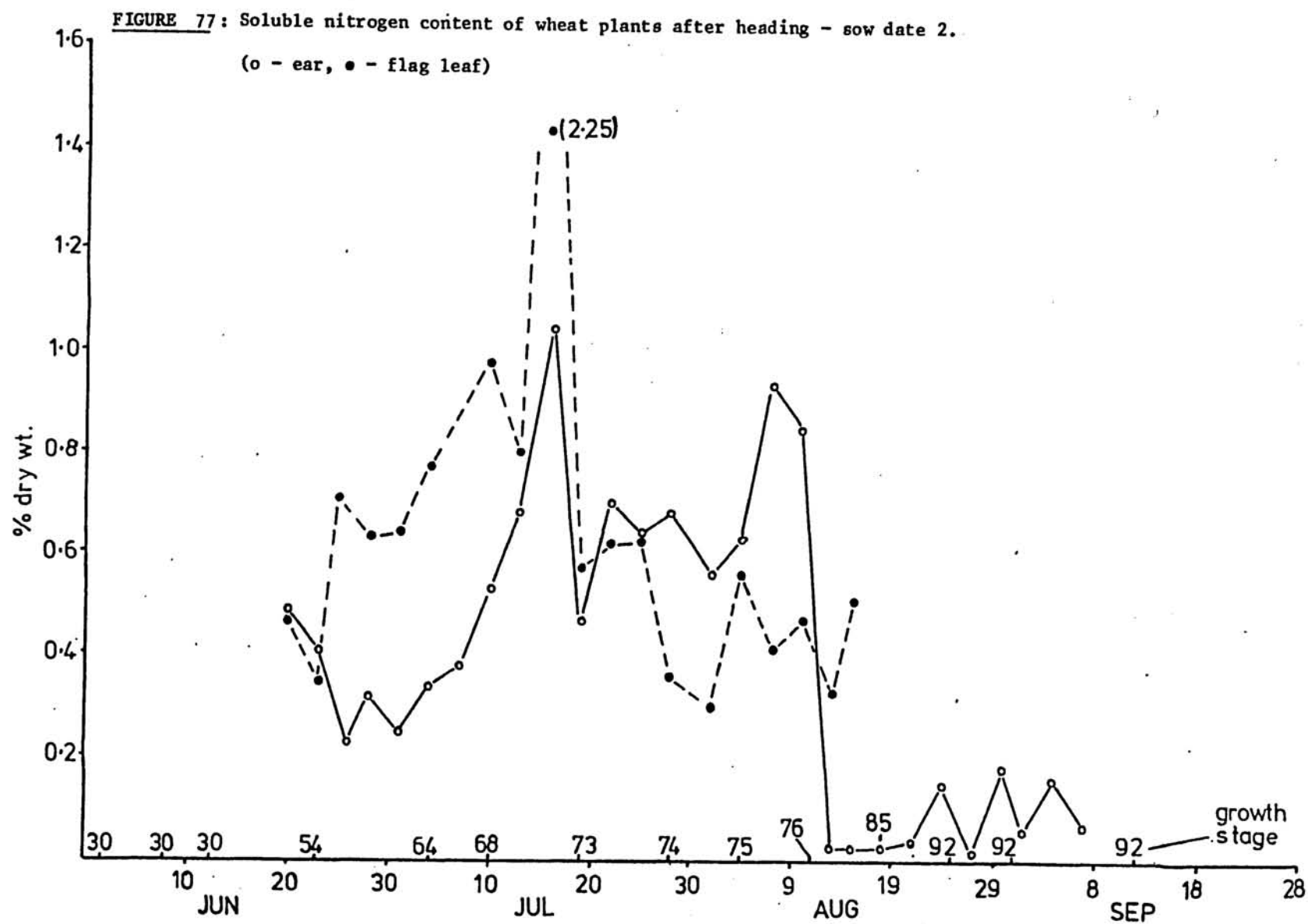
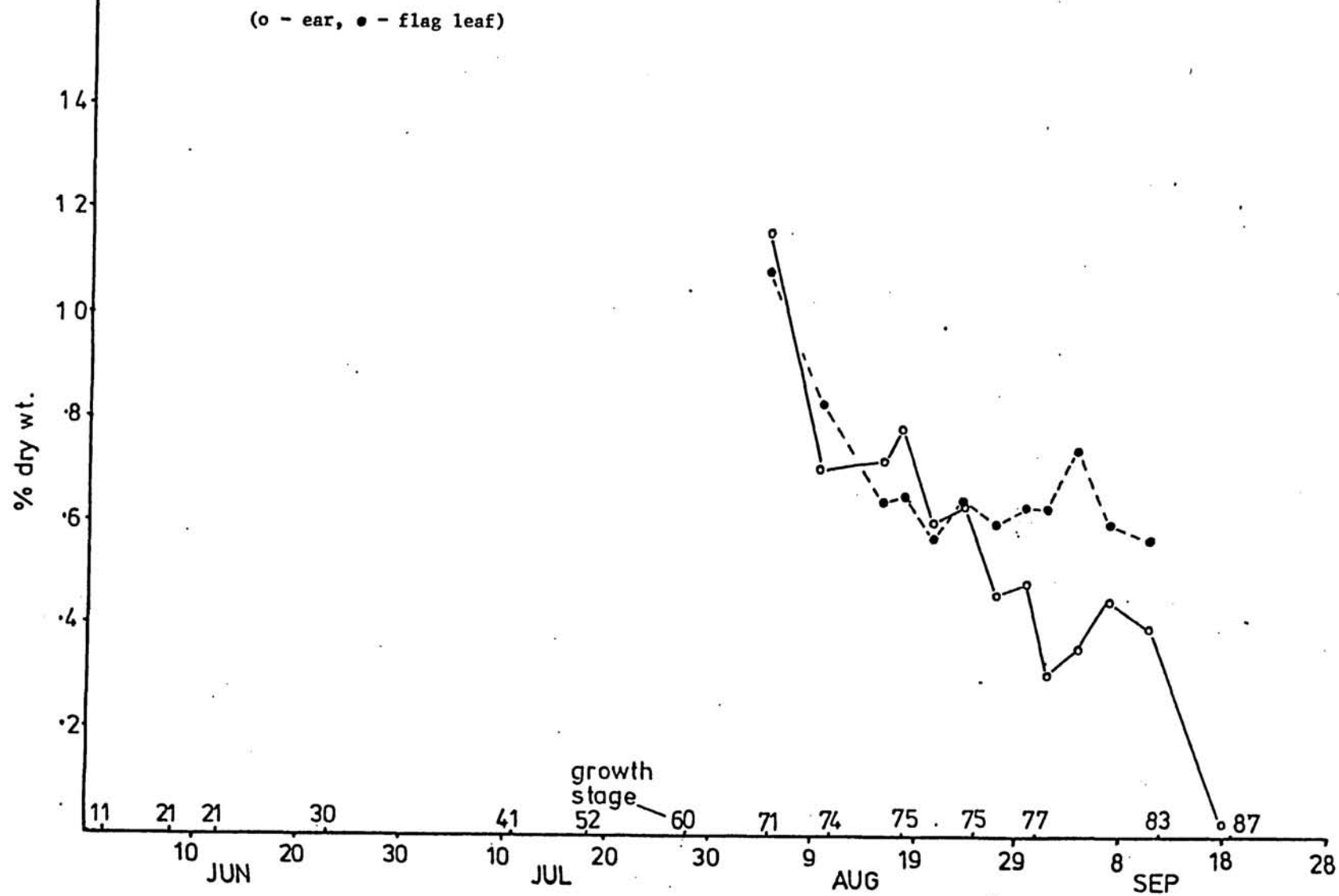
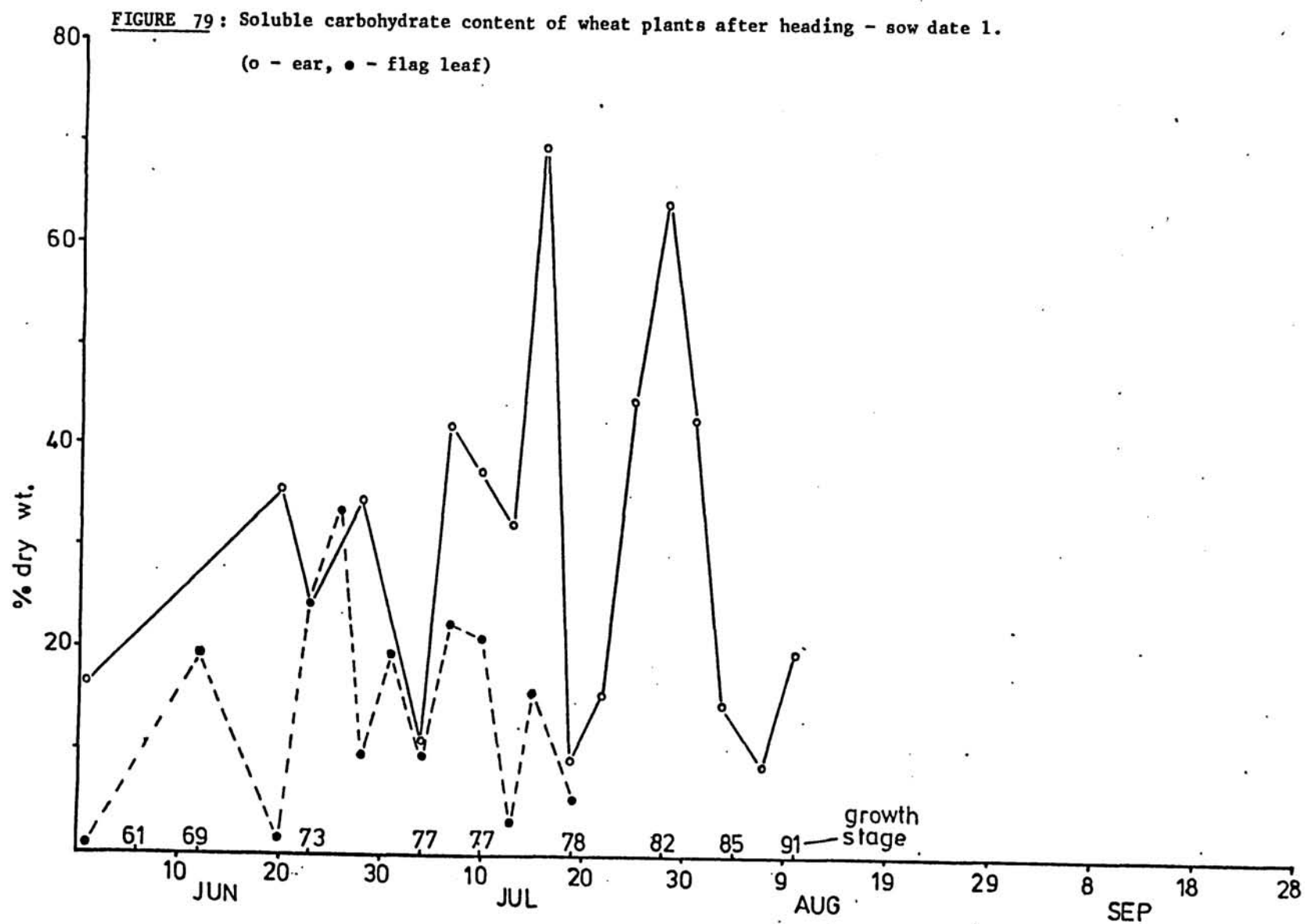
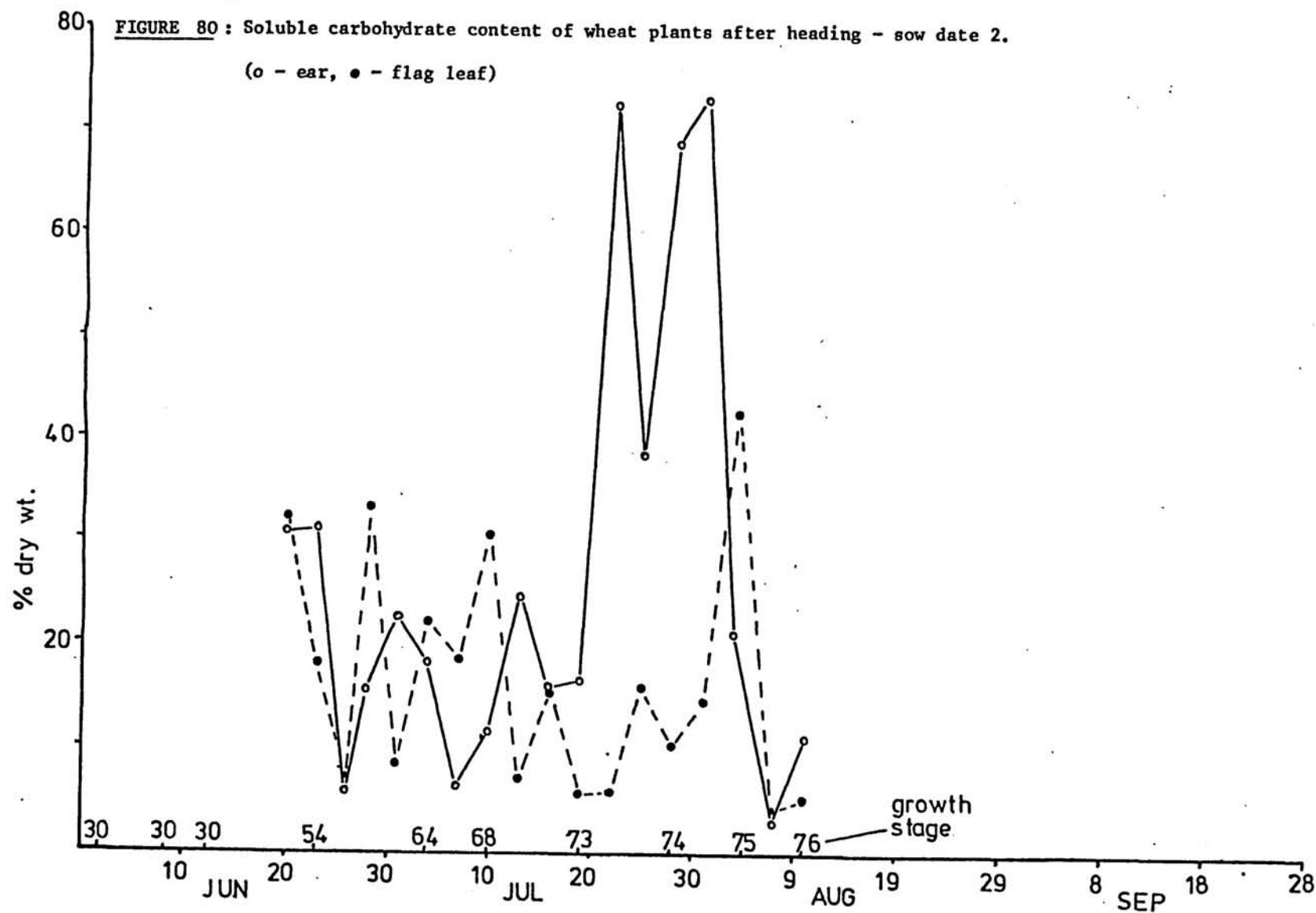
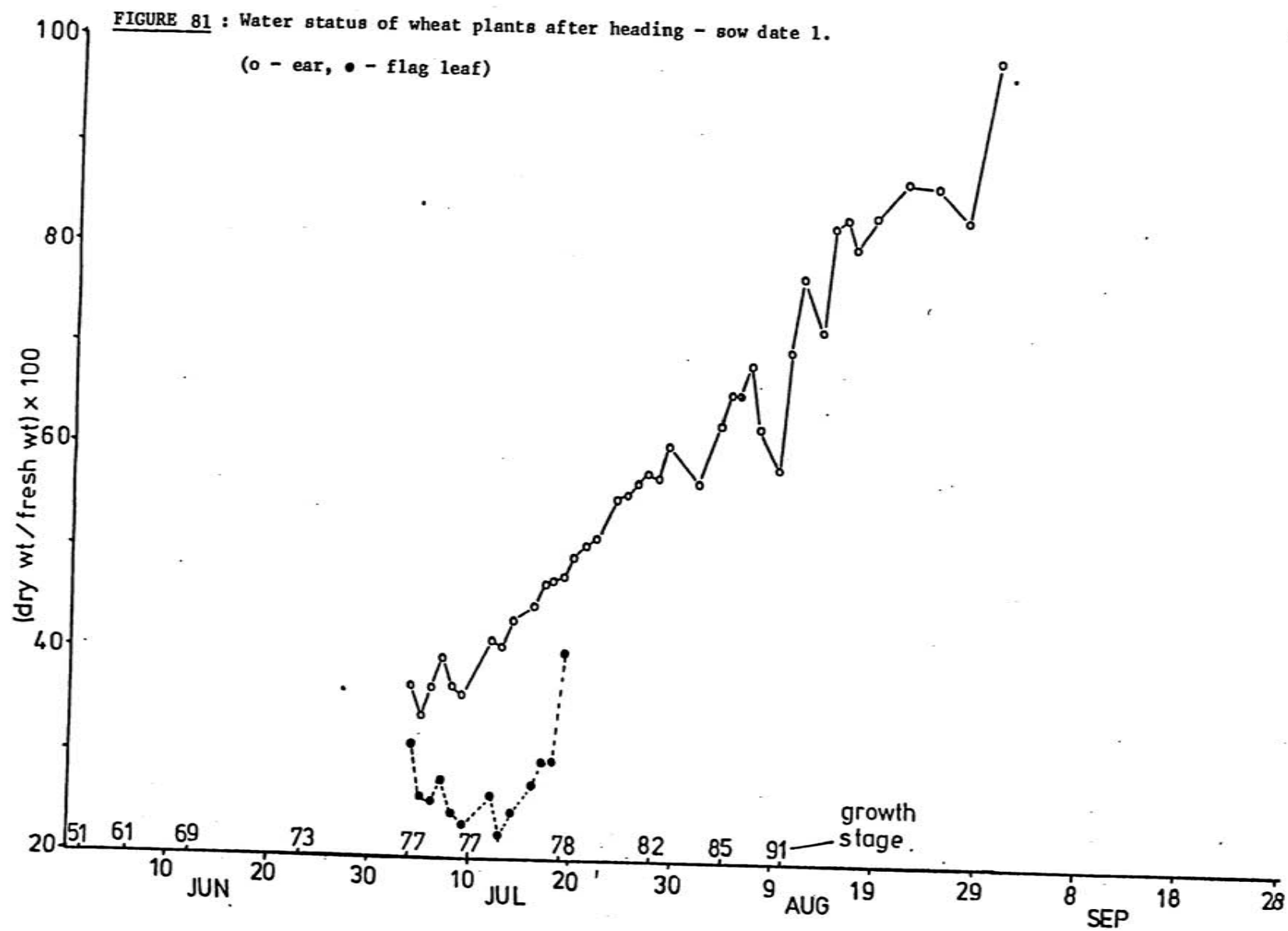


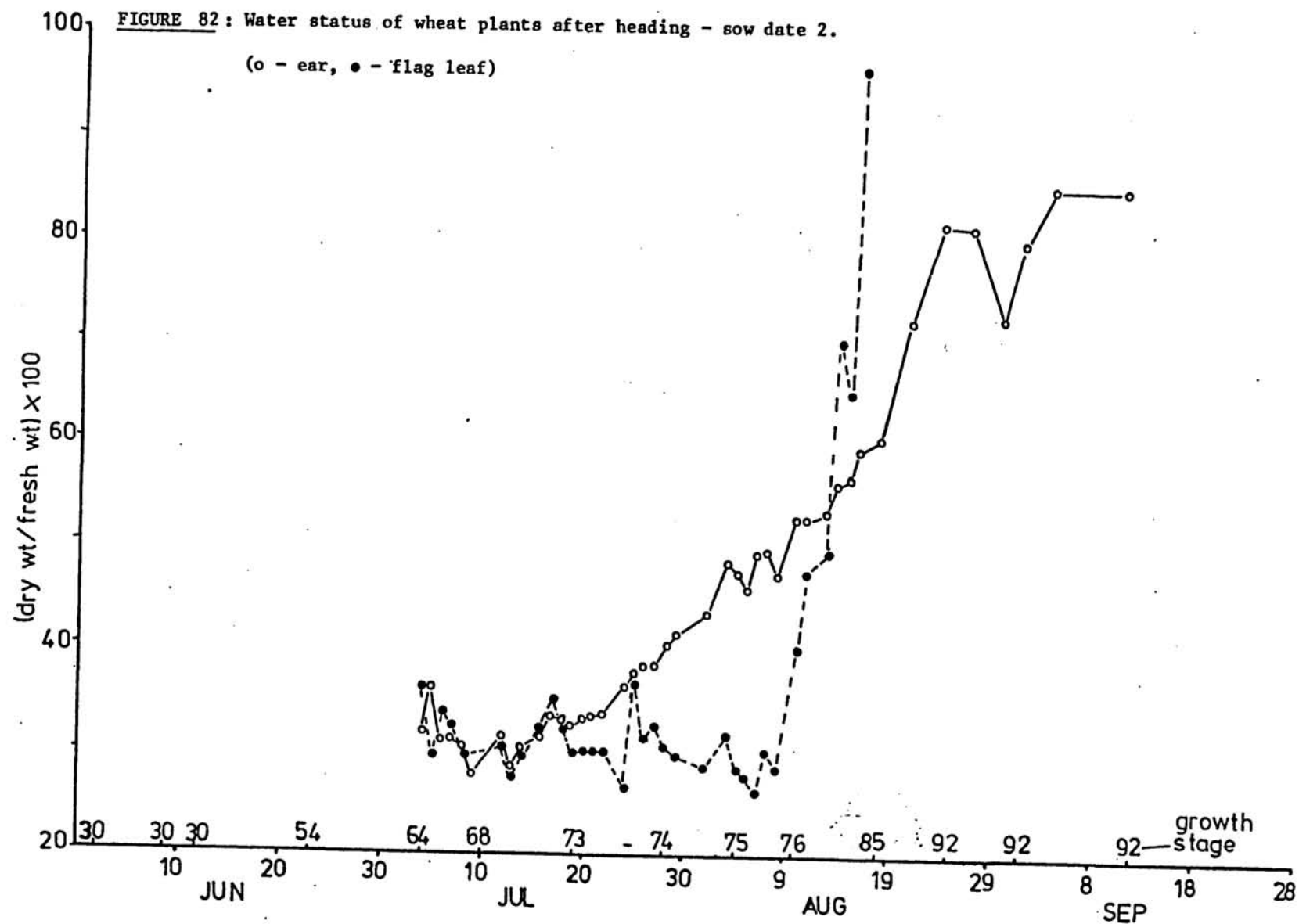
FIGURE 78 : Soluble nitrogen content of wheat plants after heading - sow date 3.

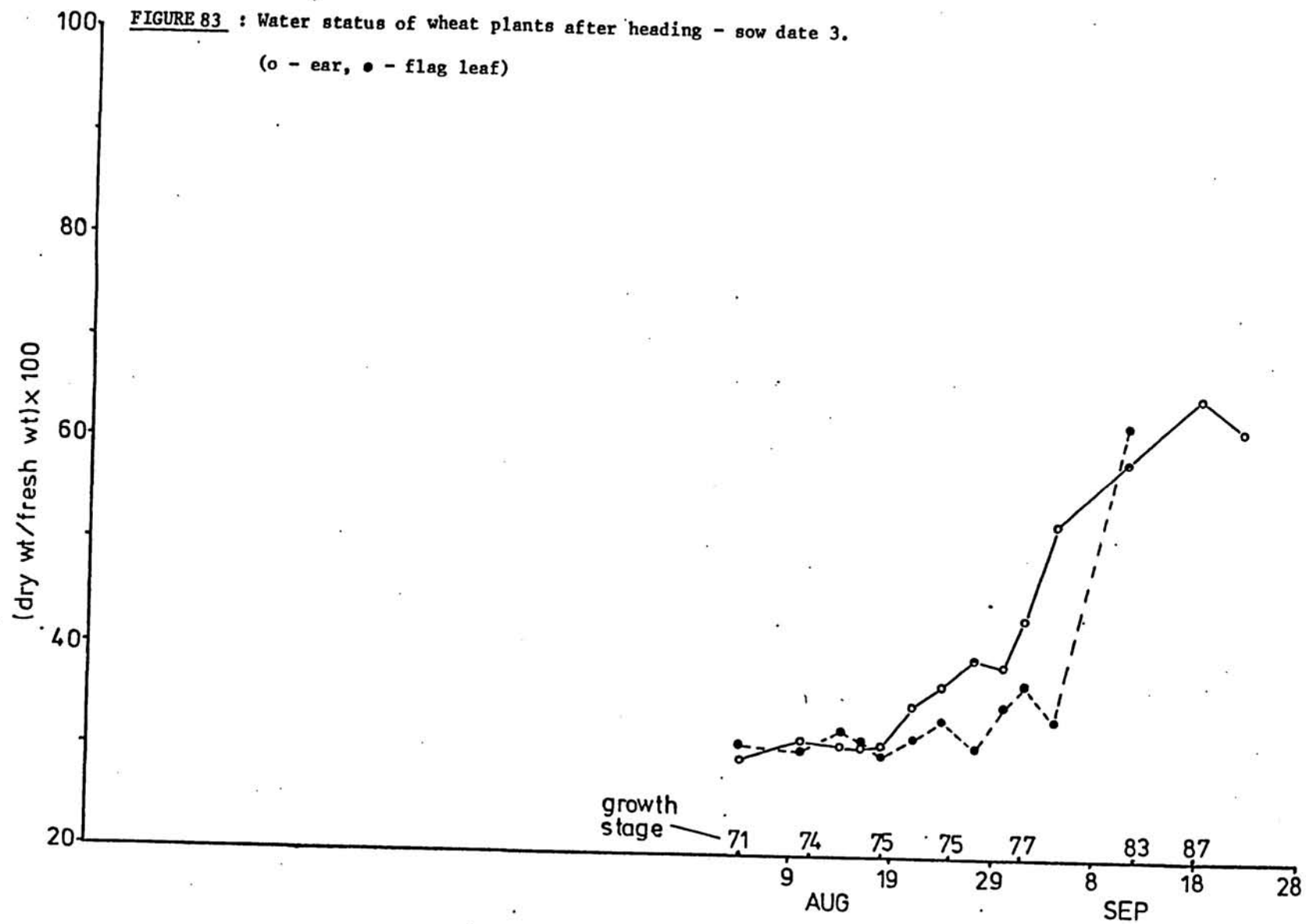












3.4 GENERAL DISCUSSION

3.4.1 APPRAISAL OF METHODS

The insecticidal check method (Debach 1946) proved to be a valuable tool in the assessment of predator impact. Applications of 'fonofos' and 'methiocarb' to barrier bordered plots achieved approximately 90% kill of ground beetles (Section 3.3.2.2). Similar methods have been used by other workers (Edwards and Steed, 1979; Edwards *et al*, 1979). Although there were indications of a direct detrimental effect on aphids infesting the later sown plots shortly after application, these effects were not sustained and on sow date 1 no effect was detected. The risk of direct effects would almost certainly have been reduced if 'fonofos' had been incorporated into the soil prior to, or during seed drilling. This was impractical, however because plots needed to be kept accessible to machinery until after the completion of the third sowing.

'Carbaryl' applications were made with limited expectations of success, (but see Meier, 1966) yet substantial depletion of syrphid larvae appears to have resulted (Section 3.3.2.2.). Syrphid egg counts differed little between treatments inferring that death occurred upon contact with toxic residues following egg hatch. 'Mummy' counts also differed little between treatments suggesting effective recolonization of sprayed plots and tolerance to residual deposits of carbaryl. (Morton (1977) and Cartwright (1979) reached similar conclusions with respect to orchard natural enemies and insecticidal spray deposits).

The simultaneous study of populations on crops sown at different times, provided a powerful technique for assessing the role of crop growth stage (Section 3.3.2.4). In essence, the method established 'crop growth stage' as an experimental variable whose effects could be distinguished from those due to factors that were uniform over the study site, such as weather and the aerial abundance of aphids. Predation

was initially expected to be one of these factors but, in the event predator impact at any one time differed considerably between sow dates. This was because syrphids normally oviposit in response to the presence of prey, hence sequential colonization of the crops by aphids was followed by sequential colonization by syrphids.

One drawback to the split plot experimental design (Section 3.3.1.1.) was the close proximity of different aged crops. Aphids could readily move from aging plants as they became unsuitable and infest adjacent plots. These interactions between plots probably contributed to the apparent waning of 'growth stage discrimination' shown by alates colonizing later sowings.

3.4.2. RELEVANCE OF THE RESULTS TO THE ECOLOGY AND PEST STATUS OF CEREAL APHID

3.4.2.1 The Value of Ground-based Predators.

During the present experiment, ground beetle predation was a negligible cause of cereal aphid mortality (Section 3.3.2.3.1), but unqualified extension of this conclusion to other cereal aphid populations would not be justified at this stage. First, predator effectiveness may have been atypical due to particular features of the habitat at Silwood Park (e.g. abundance of alternative prey). Secondly, exclusion treatments were established in late May meaning that potential predator impact earlier in the year was untested. Edwards *et al* (1979) have shown that whereas exclusion of ground beetles in March and April can lead to much larger aphid populations, this is less likely to occur when exclusion is delayed until May and June.

Results described in Chapter 2 also indicate negligible importance of ground predation over the winter months November - March, so considering all the results contained in this thesis, and those of Edwards *et al*, 1979, April - May would appear to be a critical period per ground beetle impact.

A thorough appraisal of the role of ground beetle predation would depend on a knowledge of the relative importance of overwintered and spring migrant aphids to the overall abundance on the crop during summer. At present, this information is lacking but there seems little doubt that, during outbreak years (e.g. 1976) summer immigrants form the main source of the attack. In these situations, ground beetle predation would be unlikely to limit population build up so other control measures would be required. Nevertheless, the conservation of these predators is to be recommended, both for the continued suppression of overwintered cereal aphids and for their likely contribution to the mortality of other cereal feeding arthropods.

3.4.2.2 The Value of 'aerial' predators

Predator exclusion by carbaryl applications prolonged crop infestations by *S. avenae* and *M. dirhodum* and in the latter species resulted in larger peak populations (Section 3.3.2.3.2). The foregoing discussion attributes these differences to predation by syrphid larvae on unsprayed plots giving quantitative support to the earlier observations on syrphid impact by Dean (1974d, 1975), Jones (1979b) and others. Similar quantitative studies using exclusion cages in 1976 in Sussex, U.K. also resulted in considerably larger aphid populations on plots that were free of 'aphid specific' predators - mainly syrphids and coccinellids (Sunderland and Vickerman, in press, cited by Vickerman and Wratten, 1979). Carillo (1973) working on barley in Chile, found that *M. dirhodum* populations 'resurged' more quickly after insecticide treatment than untreated populations. He attributed this partly to insecticidal kill of syrphids (also see Zuniga and Suzuki, 1970).

Van Emden (1966) provided an early conceptual framework for the consideration of predator effectiveness. He distinguished 3 major features of a predator - prey system that would influence predator effectiveness: voracity, synchronisation, and prey rate of reproduction. In the present

study, syrphid voracity appeared to outstrip the aphids' rate of increase, especially in the case of *M. dirhodum*. There is little doubt, therefore that syrphids were 'ecologically effective' predators. Nevertheless, poor synchrony between aphid build up and syrphid impact (as observed in the present study and noted by Dean (1975)) allows rapid population growth to occur for several weeks after colonisation. In *S. avenae*, this typically occurs between 'heading' and 'milky ripe' when (a) aphid rates of increase reach their peak (Watt, 1979; Verijken, 1979) and (b) greatest yield loss can occur (George, 1974). Hence, poor synchrony usually limits the 'economic effectiveness' of syrphids in cereals.

Problems of predator - prey synchrony justify the use of aphicides to control serious attacks by cereal aphids, but the use of specific materials is basically preferable. From the farmer's viewpoint, specific materials are likely to result in prolonged pest suppression due to the conservation of natural enemies. It may be possible to further enhance natural enemy impact by delaying sprays of specific materials until after the immigration of natural enemies - predator : aphid ratios are usually higher after pirimicarb sprays (Gough and Wilkinson, 1979). From the national viewpoint, specific materials are to be recommended on the grounds that their use should help maintain high regional populations of beneficial insects which might contribute to the suppression of cereal aphids (and other pests) in subsequent seasons (possibly increasing the number of 'non-aphid years' (McLean *et al*, 1977)).

3.4.2.3 Influence of crop growth stage and nutrient status.

The timing of aphid colonization differed greatly between crops sown in autumn, early spring and late spring. This was found to be more closely related to crop growth stage than the aerial abundance of aphids. 'Growth stage preference' was most obvious in *S. avenae* which colonized crops between 'heading' and 'watery ripe' growth stages. Experiments

reported in Chapter 4 provided evidence of 'pre heading' preference in *M. dirhodum*. This however, is not supported in the present work where the aphid was first recorded on the oldest crop after heading. It is possible that this infestation may have been initiated earlier but that these aphids were overlooked on 7/6 due to their cryptic colour and low feeding sites. Late in the season, *S. avenae* discrimination decayed somewhat, probably due to the increasing size of aerial populations, the absence of 'optimal' crops and the close proximity of aging and young crops. Sow date 2 was the only crop subjected to nutrient analysis over the heading stage.

The results show that exceptionally high levels of soluble nitrogen were accompanied by increased colonization by *S. avenae* at the 'watery ripe' growth stage. (Section 3.3.2.5).

This does not necessarily infer that high soluble nitrogen levels directly induced the alates to alight, stay and deposit nymphs. The metabolic events that elevated nitrogen levels probably caused changes in the concentrations of numerous untested plant constituents, any of which might be the behavioural cue influencing the aphids. It is also conceivable, that a nitrogen flush could coincide with a key change in the appearance of the plants, to which aphids might directly respond. Nevertheless, the mounting evidence on the role of nitrogen in the ecology of phytophagous insects argues strongly in favour of its relevance to cereal aphids.

In sucking insects, nitrogen (especially in the form of nutritionally useful amino acids) is considered to be a major limiting food resource to growth and development (Southwood 1973; Kennedy 1953; McNeill and Southwood, 1978; Lawton and McNeill, 1979; Dixon 1970, 1973). In addition, the feeding patterns and host plant shifts of some species have been explained in terms of the optimal exploitation of plant nitrogen resources

(McNeill and Southwood, 1978; Dixon, 1973). There is surprisingly little published work on the relationship between cereal aphids and plant nutrient levels. Verijken (1975) found positive correlations between levels of nitrogen fertiliser and the 'performance' of *S. avenae* in the laboratory, although in the field, nitrogen dressings 'hardly affected' *S. avenae*. In this context, it is significant that Watt (1979) recorded highest rates of reproduction and survival of *S. avenae* on oats after flowering. At this stage, wheat ears become an important 'nutrient sink' (Kennedy 1958) as the grains begin to fill and it appears that *S. avenae* exploits this by its ear feeding habit.

'Growth stage discrimination' may help explain the time lag between appearance of alates in Rothamsted suction traps and their arrival on the crop (Taylor 1974, George 1974) as well as the poor correlation between trap numbers and the abundance of colonist, in field counts (Dean 1973b, 1974a). It seems reasonable to suppose that crop colonization might depend on (a) suitable flight conditions coupled with (b) optimal crop growth stage. The inclusion of both these factors in a simple model may well result in improved short term predictions of *S. avenae* attack.

The pattern of sequential attack by *M. dirhodum* was less readily attributable to growth stage or crop nutrient levels (Section 3.3.2.5.2). Perhaps this is because these populations are spread between leaves of widely differing age which in turn differ widely in their nutrient status. As a result, the population as a whole may be 'buffered' from the effects of drastic physiological changes in individual parts of the host plant.

Fourth instar alates only occurred in significant numbers in the case of *S. avenae* on carbaryl treated, autumn sown plots where they were found late in the season (Section 3.3.2.4.4). This observation

implies:

- (a) that alate production potentially contributed to population decline but only late in the season. In the natural population (i.e. the CONTROL plots), this potential impact was pre-empted by an earlier decline caused by syrphid predation.*
- (b) that alate production was not triggered primarily by factors that were constant over the experimental site such as weather and photo-period. Instead, the high population densities and declining conditions of plants on sow date 1 - NOPRED were probably the most important stimuli.

Alate production in the Spruce aphid (*Elatobium abietinum* Walker) has been attributed to changes in leaf nitrogen and/or alterations in the amino acid composition of the sap (Carter and Cole, 1977; Parry, 1974). Similarly, Verijken (1979) found that increasing levels of nitrogen fertilizer reduced alate production in *S. avenae*. In the present work however, no clear correlation emerged between soluble nitrogen levels and alate production, although the possible importance of altered amino acid composition was not tested.

Aphid population peaks were associated with the milky ripe stage and high levels of soluble nitrogen, soluble carbohydrate levels did not change in a consistent manner on the 3 sowings but a consistent decrease in the water content of wheat ears may have induced the decline in *S. avenae* populations. (Section 2.3.2.5.1). The effect of host plant water stress has been the subject of some controversy in the past (Kennedy 1958). In the first place, plant physiological 'stress' including drought is known to result in hydrolysis leading to higher levels of 'available' nitrogen. On the other hand, water shortage would reduce the phloem pressure of the plant tissues resulting in slower aphid feeding rates and reduced performance. The studies of Mittler, for example (1954) showed that water shortage could drastically reduce aphid

* Carter *et al.* (1980) also concluded that host plant deterioration could not fully account for the collapse of a field population of *S. avenae*.

(*Tuberolachaus Salignus* (Gmelin)) feeding rates and induce restlessness.

Similarly, Wearing and Van Emden (1967) demonstrated that aphids feeding on pressurised artificial diets 'performed' better than unpressured 'controls'. Aphid species react differently to 'stressed' host plants (Wearing and Van Emden 1967), possibly due to differences in their dependence on phloem pressure for food uptake, (Wearing, 1966).

Changes in food quality experienced by *M. dirhodum* feeding on leaves were less synchronized than for *S. avenae* on the ears. Senescence of lower leaves occurs throughout the growth of wheat plants, forcing the dispersal of some colonies, while others on younger leaves continue to feed and reproduce.

Once the plants reached the milky ripe stage however, the leaves senesced at a greatly increased rate resulting in a relatively sudden population crash on plots where syrphid exclusion had prevented an earlier collapse.

CHAPTER 4

FURTHER STUDIES ON THE RELATIONSHIP BETWEEN CROP
GROWTH STAGE AND APHID ATTACK

CHAPTER 4

FURTHER STUDIES ON THE RELATIONSHIP BETWEEN CROP
GROWTH STAGE AND APHID ATTACK4.1 INTRODUCTION

A large number of descriptive cereal aphid studies have reported spectacular population outbreaks and crashes. (e.g. Jones, 1979b; Carter, *et al*, 1978; Dean 1973a; Dean and Luuring 1970; McLean *et al*, 1977.) Most workers have attempted to explain these occurrences, but this has normally been tackled by a correlation approach (e.g. Jones, 1979b). Unfortunately many separate ecological changes occur during outbreaks and crashes obscuring the true causes of observed events. Outbreaks normally occur soon after aerial populations of cereal aphids begin to increase, when temperatures are increasing and after crops enter the heading stage. Crashes are often associated with peak levels of predators, parasites and disease as well as marked changes in the physiology of the host plant.

The studies described in this chapter were concerned with the role of crop growth stage in determining colonisation (defined as alate settling and nymph deposition) and population collapse. Most of the experiments involved the comparison of aphid attack on plants at a range of growth stages in a field situation. Results were compared with those obtained on large plots of wheat sown in autumn, early spring and late spring. The results of the latter experiments are described more fully in Chapter 3.

4.2 MATERIALS AND METHODS.

4.2.1 APHID ATTACK ON SEQUENTIALLY SOWN POTTED WHEAT

Each week during the spring and summer 1977 - 1978, spring wheat seeds (c.v. Sicca, 2 plants per pot after thinning) were sown in 20 plant pots (diameter : 12.5cm) containing compost. The pots were placed in a line outside the glasshouse adjacent to earlier sown plants. Rows of pots were kept close together and arranged in ascending order of age - a layout considered preferable to a randomised design on the grounds that tall plants could obscure the presence of small plants to colonizing alates. In 1978, the plants were divided into 2 replicate batches, the first facing west - east, the second east - west. This represented an attempt to overcome the effects of possible directional colonization. In the event, no appreciable directional effects were observed so data were pooled for tabular and graphical presentation.

Before an aphid census, each group of plants was classified according to growth stage (Zadoks *et al*, 1974) then every tiller examined and aphids counted. On the later sown plants, tiller development was asynchronous so only those conforming to the recorded growth stage were included in the count. Because numbers of tillers varied between groups of plants, all data were expressed as 'No. per 100 tillers'. In 1977, 4 categories of aphid morph were distinguished; instars 1 and 2, 3 and 4, apterae and alatae. In 1978, aphids were simply recorded as alates and progeny.

In 1978, all plants were cleared of aphids 7 days before counting so that resulting infestations could be attributable to alate aphids colonizing plants of defined growth stage over a finite period of time. This was simply achieved by applications of the short persistence aphicide 'pirimicarb' (25% wettable powder).

4.2.2 APHID ATTACK ON SEQUENTIALLY SOWN WHEAT IN SILWOOD BOTTOM.

The layout of sequentially sown wheat plots has already been described in detail in Chapter 2 (Section 2.4.2) (Figure 11). Experimental 'blocks' were sown with 3 row plots of wheat at intervals through the autumn, winter and spring to produce a range of crop growth stages during the main period of aphid attack - summer 1978.

Before an aphid census, each plot was classified according to plant growth stage (Zadoks *et al*, 1974), 50 tillers selected at random from the central row and numbers of aphids recorded (separate counts for all instars). On 9/6 and 10/7, all 4 replicates were assessed but on 21/6, the large number of aphids and shortage of time necessitated a restricted assessment on replicate 1 only.

4.2.3 STUDIES ON GROWTH STAGE DISCRIMINATION IN THE LABORATORY.

Selection by alate *S. avenae* for wheat of differing growth stage was investigated in an aphid flight chamber (Figure 84) maintained in a 20° C.T. room. Ears or leaves of the plants were protruded through 2cm holes in the base of the chamber enabling plant heights to be standardized independent of growth stages. The chamber was illuminated by 4 fluorescent strip lights placed 5cm above the roof. Holes were sealed with 'Plasticine' prior to the release of alates which were collected from standard cultures maintained on wheat seedlings at 20°C. (A full description of the standard cultures is given in Section 2.2.1.1). Approximately 150 individuals were used for each experimental 'run' (= replicate) but only a small proportion of these settled on the test plants. Releases were made into the centre of the chamber from 'Fluon' coated beakers. Alates could only leave this beaker by flight - usually by climbing and take off from glass rods fixed vertically in the beakers with 'Plasticine'.

Numbers of alates and progeny were recorded after 1 and 3 days and the experiment was replicated 'in time' on 5 occasions using fresh plants placed in a new randomized arrangement.

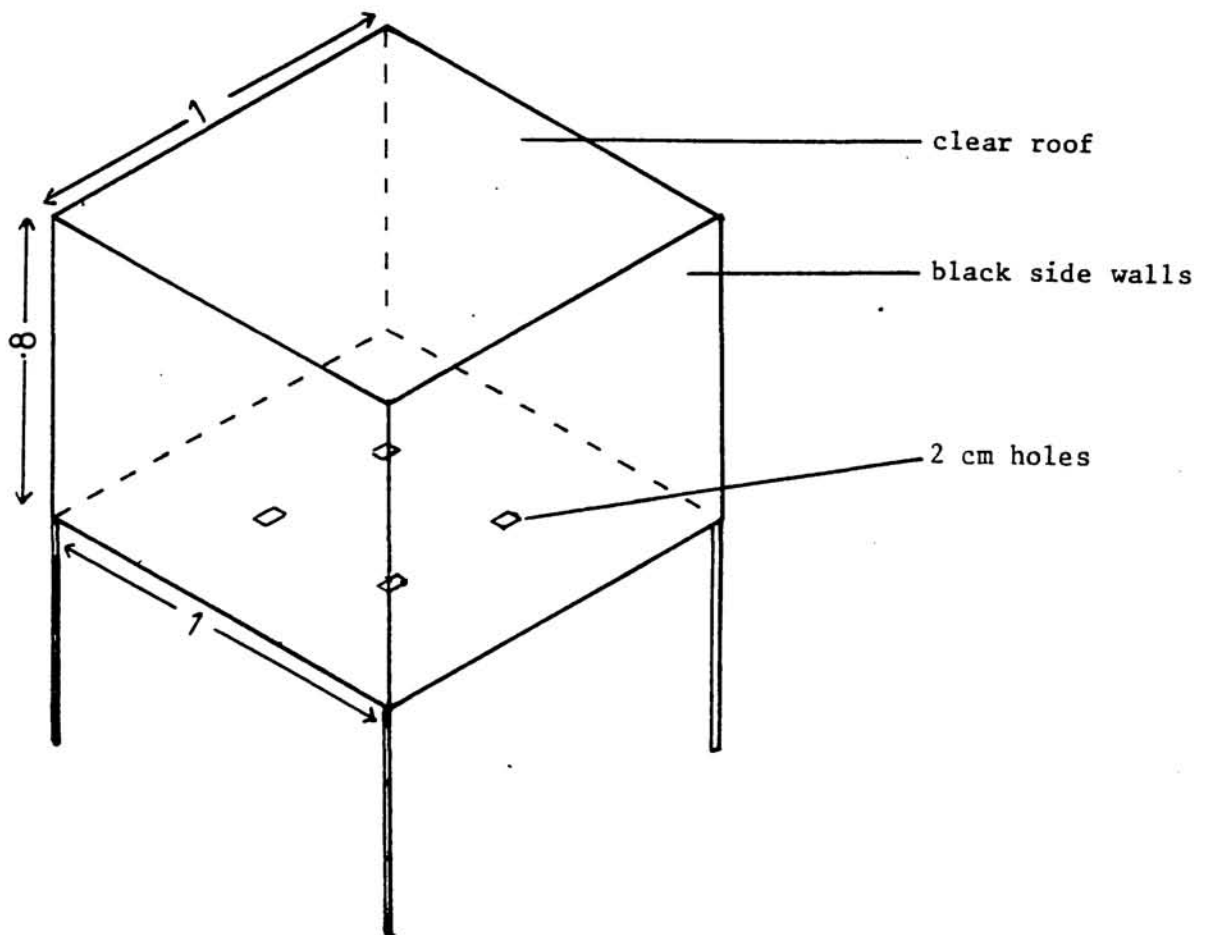


FIGURE 84 : Flight chamber used to study growth stage discrimination by *S. avenae*.

NB - dimensions in metres.

4.3 RESULTS AND DISCUSSION

4.3.1 OVERALL APHID ATTACK IN RELATION TO GROWTH STAGE.

4.3.1.1. Sequentially sown potted wheat 1977

S. avenae

In 1977, *S. avenae* was most abundant on wheat at the 'watery ripe' growth stage (Table 71). To a large extent this was a reflection of 'current crop suitability' to colonists since the population comprised largely alates and first instars. However, the presence of apterae indicates that earlier immigrants made some contribution to the total numbers. In contrast, remarkably few individuals were found on 'pre-heading' growth stages (Table 71). The results also show that plants that had reached the 'milky ripe' growth stage supported relatively few aphids, for which are two main explanations. First, a previously large population may have 'crashed' prior to the aphid census or secondly, very few aphids ever developed on the crop - possibly due to a lack of coincidence between suitable growth stage and abundant aerial populations.

M. dirhodum

M. dirhodum's distribution was the converse of *S. avenae*'s; most being found on 'pre-heading' plants and fewest on 'post heading' tillers (Table 71). Due to the presence of both alates and apterae in the population, the previous remarks on difficulties of interpretation apply equally for *M. dirhodum*.

4.3.1.2 Sequentially sown wheat in Silwood Bottom.

S. avenae

On all 3 occasions, aphids were scarce in the 'pre-heading' crops and relatively abundant on plants between 'late inflorescence emergence' and 'end of anthesis' (Table 72). There was a close positive relationship between aphid abundance and the percentage of tillers infested. There were too few sowings to thoroughly test the possibility of discrimination within the range 'late inflorescence emergence - end of anthesis', and where 2 growth stages in this range occurred together.

TABLE 71 : Numbers of aphids (per 100 tillers) infesting sequentially sown potted wheat - 22/7/77.

Growth Stage* Instar	<i>S. avenae</i>							<i>M. dirhodum</i>						
	21	30	30	35	35	71	75	21	30	30	35	35	71	75
1, 2	4	4	0	2	0	28	12	102	152	62	66	4	0	0
3, 4	0	0	0	0	0	24	2	18	12	30	2	2	0	0
AP	0	0	0	0	0	12	0	2	2	2	0	0	0	0
AL	0	0	0	0	2	16	4	4	6	6	10	8	0	0
TOTAL	4	4	0	2	2	80	18	126	172	100	78	14	0	0

* Zadoks decimal code (Zadoks *et al.*, 1974): 20-29, tillering; 30-39, stem elongation; 40-49, booting; 50-59, inflorescence emergence; 60-69, anthesis; 70-79, milk development. (See appendix for further details)

TABLE 72 : Numbers of *S. avenae* (per 50 tillers) infesting sequentially sown wheat in Silwood Bottom in relation to growth stage.

		9/6							21/6 [†]							10/7						
Sow date* Ref.		1	2	3	4	5	6A	6B	1	2	3	4	5	6A	6B	1	2	3	4	5	6A	6B
Growth stage [‡]		69	69	69	56	30	11	11	73	73	71	71	57	30	30	77	76	76	73	69	39	58
REPLICATE 1	1			6					9	0	9		23		4		1			5	10	5
	2			10	2				5	3	5	8	5		8	1	1		2	1	3	8
	3			9					9	6	2	7	3		1			1	2	1	2	3
	4 (AP)			9					2	11	1	4	3		1				2			1
	4 (AL)										1				1							
	AP		1	1	1				2		6	2	6		1		1	1	1	1	3	4
	AL			1											1				1			1
TOTAL		0	1	36	3	0	0	2	27	20	24	21	40	3	14	3	3	2	6	10	18	22
% INFESTED TILLERS		0	2	10	4	0	0	4	16	28	20	20	14	6	10	6	6	4	12	14	10	24
REPLICATE 2	1	6	2	1												5				13		22
	2		1	1	2											2				24	2	27
	3					1										21				8		3
	4 (AP)															8				1		
	4 (AL)															7				1		1
	AP				1	1										1				8		11
	AL			1	1											1				7		2
TOTAL		6	3	3	4	2	0	0	12	0	1	3	81	5	66	12	0	1	3	81	5	66
% INFESTED TILLERS		2	2	6	6	4	0	0	14	0	2	6	46	8	38	14	0	2	6	46	8	38
REPLICATE 3	1		35	1												1	1				2	19
	2	2	21		2														1	6	2	10
	3			1															1	4		2
	4 (AP)	1		5																5		2
	4 (AL)																	1				
	AP	2	11														1			2		5
	AL			1													1					6
TOTAL		5	67	8	2	0	0	0	1	1	1	4	18	7	44	1	1	1	4	18	7	44
% INFESTED TILLERS		6	20	6	2	0	0	0	2	2	2	6	20	12	28	2	2	2	6	20	12	28
REPLICATE 4	1			2														3		27	12	46
	2		1	7															1	20		19
	3			5																15	3	3
	4 (AP)	1	4																	7		3
	4 (AL)																					7
	AP			1																4	3	6
	AL																		2	2		3
TOTAL		1	5	15	0	0	0	0	1	0	4	1	75	19	87	1	0	4	1	75	19	87
% INFESTED TILLERS		2	6	6	0	0	0	0	2	0	2	2	26	16	44	2	0	2	2	26	16	44
MEANS	TOTAL	3	19.0	13.5	2.3	0.5	0.0	0.5	27.0	20.0	24.0	21.0	40.0	3.0	14.0	4.3	1.0	2.0	3.5	43.5	12.3	54.3
	% INFESTED TILLERS	2.5	7.5	7.0	3.0	1.0	0.0	1.0	16.0	28.0	20.0	20.0	14.0	6.0	10.0	6.0	2.0	2.5	6.5	26.5	11.5	33.5

* Winter wheat (c.v. Maris kinsman) sow dates: 1 - 14/9, 2 - 30/9, 3 - 14/10, 4 - 11/11, 5 - 9/3, 6A - 11/5
Spring wheat (c.v. Sicca) sow date : 6B - 11/5

[‡] Zadoks decimal code (Zadoks et al., 1974) 10-19, seedling growth; 20-29, tillering; 30-39, stem elongation; 40-49, booting; 50-59, inflorescence emergence; 60-69, anthesis; 70-79, milk development (see appendix for further details)

[†] only replicate 1 counted

the direction of alate preference was not consistent. Thus, on 9/6, more aphids were found on 'end of anthesis' than on ' $\frac{3}{4}$ inflorescence emergence' whereas on 10/7, there were fewer aphids on 'end of anthesis' than 'inflorescence emergence complete'. This anomaly may have arisen because of the combination of high levels of aphid abundance and scarcity of suitable plants which perhaps resulted in a decline in preference.

On 9/6, sow dates 1, 2 and 3 were all classified as G.S.69 ('anthesis complete') but their rank in aphid attack differed between replicates possibly due to gradients in soil fertility or aphid colonization.

The relatively large numbers of aphids found on 9/6 on replicate 1, sow date 3 declined slightly by 21/6 when the plants reached the 'watery ripe' stage. The decline was associated with greater numbers of apterae and an increased proportion of infested tillers. By 10/7 when the wheat was 'medium ripe', the population had collapsed. Considering the results of concurrent field studies on an adjacent study site (Section 3.3.2) it seems probable that this population crash resulted from syrphid predation rather than changes in nutritional quality of the plants.

Finally, the hypothesis of a 'post-heading' preference was further supported by the heavy attack on 10/7 on sow date 6B compared with 6A. Although sown at the same time, 6B - the spring variety was beginning to 'come into ear' on 10/7 whereas 6A - the winter variety had not reached the 'booting' growth stage.

M. dirhodum

On 10/7, *M. dirhodum* was found predominantly on the younger crops (Table 73) but the hypothesis of 'pre-heading preference' was apparently contradicted by other results. First, on 10/7, more aphids occurred on 6B - a 'post-heading' crop, than on 6A - a 'pre-heading' crop (Table 73).

TABLE 73 : Numbers of *M. dirhodum* (per 100 tillers) infesting sequentially sown wheat in Silwood Bottom in relation to growth stage.

		9/6							21/6 [†]							10/7						
Sow date* Ref.		1	2	3	4	5	6A	6B	1	2	3	4	5	6A	6B	1	2	3	4	5	6A	6B
Growth stage [‡]		69	69	69	56	30	11	11	73	73	71	71	57	30	30	77	76	76	73	69	39	58
REPLICATE 1	1	1								25	16	12									9	12
	2	2	2	3					3	52	11	2				1				3	9	
	3	3		3					5	33	5	9								2		
	4 (AP)								3	10		11								9		4
	4 (AL)								1													
	AP	6			1	1				1	3	3								2		5
	AL										1		1							1		2
TOTAL		12	2	6	1	1	0	0	12	121	36	35	1	0	0	1	0	0	1	26	32	
% INFESTED TILLERS		6	4	2	2	2	0	0	14	30	10	22	2	0	0	0	0	0	2	16	20	
REPLICATE 2	1	10	4			8										4			1		3	12
	2					2										1				9	1	
	3				3																	
	4 (AP)	4																				
	4 (AL)																			2		1
	AP	2																				
	AL					1																
TOTAL		16	4	0	3	11	0	0								5	0	0	1	0	14	13
% INFESTED TILLERS		4	2	0	2	6	0	0								4	0	0	2	0	2	2
REPLICATE 3	1			5												7			4		10	14
	2																					4
	3		5			5	2															5
	4 (AP)		1			3																
	4 (AL)					3																
	AP																					
	AL																					
TOTAL		0	6	5	11	2	0	0								8	0	0	6	0	3	28
% INFESTED TILLERS		0	4	2	2	2	0	0								2	0	0	4	0	0	12
REPLICATE 4	1																	7	6		10	27
	2																				4	4
	3																				1	10
	4 (AP)																				1	8
	4 (AL)																				1	6
	AP			1				1										1		2	7	1
	AL																					
TOTAL		0	0	1	0	0	1	0								1	0	8	6	0	18	63
% INFESTED TILLERS		0	0	2	0	0	2	0								2	0	2	2	0	10	16
MEANS	TOTAL	7.0	3.0	3.0	3.8	3.5	0.3	0.0	12.0	121.0	36.0	35.0	1.0	0.0	0.0	3.8	0.0	2.0	3.3	0.3	15.3	34.0
	% INFESTED TILLERS	1.8	2.5	6.0	1.5	2.5	0.5	0.0	14.0	30.0	10.0	22.0	2.0	0.0	0.0	2.0	0.0	0.5	2.0	0.5	7.0	12.5

* Winter wheat (c.v. Maris kinsman) sow dates: 1 - 14/9, 2 - 30/9, 3 - 14/10, 4 - 11/11, 5 - 9/3, 6A - 11/5
 Spring wheat (c.v. Sicca) sow date: 6B - 11/5

[‡] Zadoks decimal code (Zadoks *et al.*, 1974) 10-19, seedling growth; 20-29, tillering; 30-39, stem elongation; 40-49, booting; 50-59, inflorescence emergence; 60-69, anthesis; 70-79, milk development (see appendix for further details)

[†] only replicate 1 counted

Secondly, on 9/6 and 21/6 largest populations occurred on the older 'post-heading' crops (Table 73). In both these cases there is evidence that the populations were not newly founded by colonizing alates and that initial attack may have been associated with 'pre-heading' growth stages. In the first case, heading had only recently occurred and the aphid instar distribution was fairly 'well spread'. In the second, much of the nymph deposition could be attributed to apterae. For example, on 9/6, sow date 1, a total of 28 aphids included 8 apterae but no alates.

4.3.1.3 General Remarks.

The relationship between aphid numbers and crop growth stage provides some useful indications of differential attack by aphids, but abundance inevitably results from factors other than current crop suitability. For example, an inherently susceptible growth stage may escape attack if the aerial abundance of aphids is low. Alternatively, large populations may be found on 'unsuitable' plants due to colonization and build up over earlier, more 'suitable' growth stages. To overcome these difficulties, subsequent experiments investigated alate settling and colonization in relation to growth stage over short periods of time. This eliminated these confounding effects of population build up and variable alate abundance.

4.3.2 COLONIZATION AND NYMPH DEPOSITION IN RELATION TO GROWTH STAGE.

4.3.2.1 Sequentially sown potted wheat 1978.

Two separate 'runs' of the experiment provided overwhelming support for the hypotheses of 'pre-heading preference' in *M. dirhodum* and 'post-heading preference' in *S. avenae* (Table 74, Figures 85 and 86). Abundance of newly deposited nymphs varied according to growth stage more clearly than did alate numbers - presumably because alates are more mobile and are bound to be found on unsuitable plants during test feeds. In addition to the remarkable preference switch occurring between pre and post heading, the results identify stages of maximal preference

TABLE 74 : Numbers of alates (per 100 tillers) infesting sequentially sown potted wheat* in relation to growth stage.

18/7/78				27/7/78			
Growth stage		<i>S. avenae</i>	<i>M. dirhodum</i>	Growth stage		<i>S. avenae</i>	<i>M. dirhodum</i>
Description	Code†			Description	Code†		
Stem elongation	33	3.7	74.1	Stem elongation	34	0.0	32.3
"	37	8.5	44.7	"	35	8.3	14.6
Booting	44	6.8	59.1	Booting	45	9.8	11.8
"	48	12.2	36.6	Heading	58	41.7	11.1
Heading	59	34.8	0.0	Flowering	68	69.7	3.0
Flowering	68	50.0	0.0	↑ Watery	70	31.7	4.9
"	68	66.7	14.3	"	71	25.9	3.7
"	69	53.6	14.3	M i l k	72	28.6	10.7
† M Watery	70	36.4	8.2	"	73	32.3	9.7
i Early milk	72	61.9	23.8	"	73	23.1	3.9
k " "	72	84.2	15.8	"	73	28.6	23.8
d " "	73	18.2	13.6	l Mid milk	74	40.9	0.0
e " "	73	30.0	15.0	"	75	40.9	0.0
v " "	74	21.1	5.3	"	75	44.4	0.0
e l Mid milk	75	100.0	37.5	"	76	58.3	0.0
l " "	75	27.8	0.0	Late milk	77	28.6	0.0
p " "	76	42.1	10.5	"	77	75.0	0.0
m " "				↓ " "			
e " "							
n " "							
t " "							
↓ Late milk							

* plants cleared of aphids 1 week before counts using 'pirimicarb' aphicide

† Zadoks et al (1974)

FIGURE 85 : Numbers of nymphs infesting sequentially sown potted wheat* - 27/7/78.

* plants cleared of aphids 1 week before counting using 'pirimicarb' aphicide.

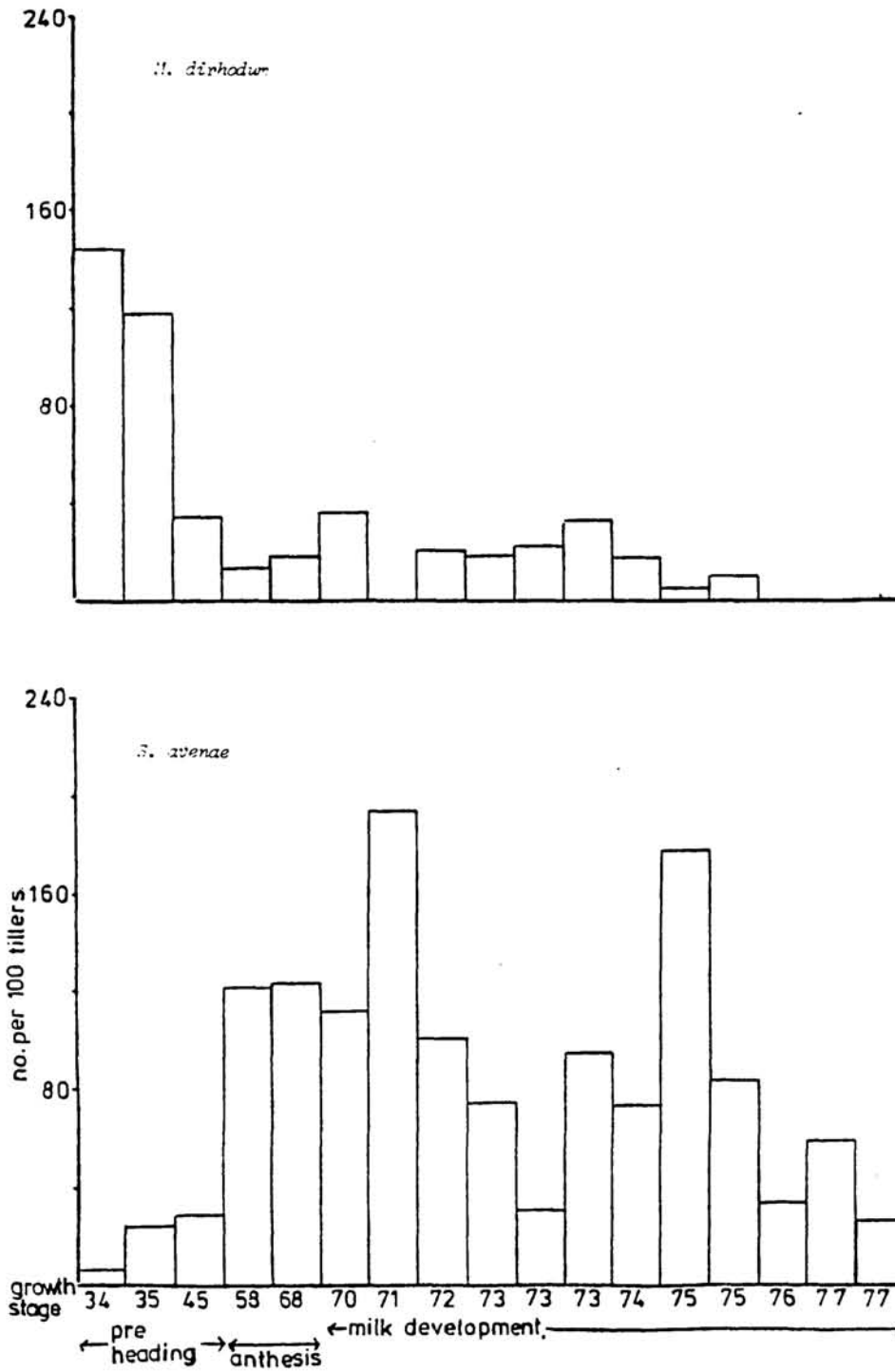
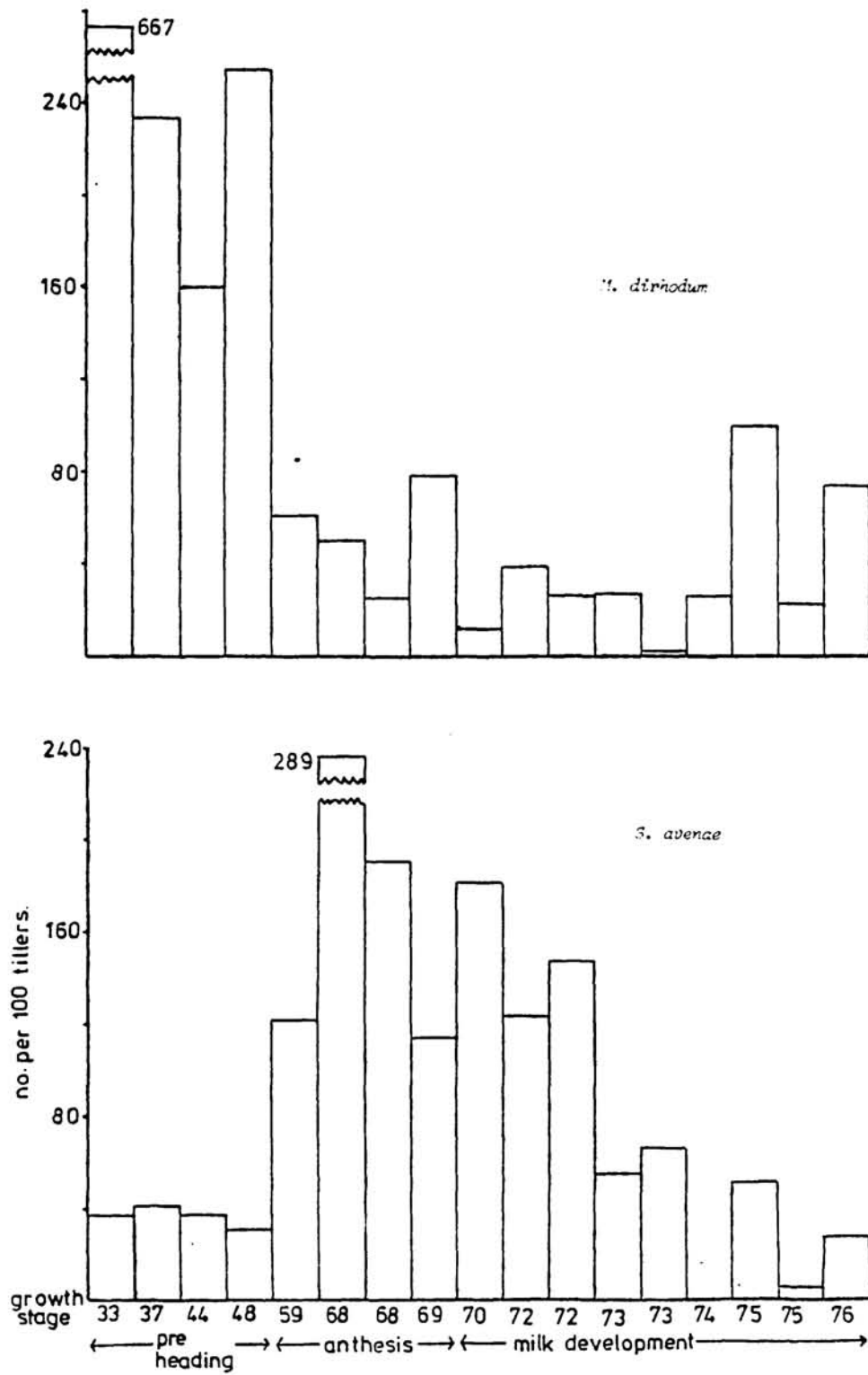


FIGURE 86 : Numbers of nymphs infesting sequentially sown potted wheat* - 18/7/78.

* plants cleared of aphids 1 week before counting using 'pirimicarb' aphicide.



within these broad phases of plant growth (Figures 85 and 86). For example, on 18/7, *M. dirhodum* deposited substantially more nymphs on the youngest plants tested (G.S.30 - 'pseudo stem erection') than on plants just one week older (G.S.37 - 'flag leaf just visible'). On the same occasion, considerably more *S. avenae* nymphs were deposited on plants reaching the end of flowering than on plants one week older or younger. The notable feature of this result is that the older plants seemed visually indistinguishable from the 'preferred' plants implying that similar numbers of alatae might be landing but that chemical differences, e.g. in amino acid composition, affected whether they staged and reproduced. Similar results were obtained on the second 'run' of the experiment. *M. dirhodum* nymphs again occurred predominantly on the youngest plants but *S. avenae* nymphs were most numerous on 'watery ripe' instead of 'end of flowering' wheat. Nevertheless these nymphs could have been deposited several days previously when the plants were at the end of flowering. Indeed the results in Table 4 show that alates had already become more numerous on 'flowering' than on 'watery ripe' plants.

4.3.2.2 Studies on growth stage discrimination in the laboratory.

(Table 75, Figure 87).

As in the previous experiment, differences between growth stages were greater in terms of 'numbers of newly deposited nymphs' than 'number of alates'. During the first few hours of each experiment, many aphids took to flight but few settled on the test plants. After 24 hours some plants had been colonized but alates were fairly evenly spread between the 4 growth stages (Figure 87A). Nevertheless, discrimination between these stages was already apparent in terms of nymph deposition (Figure 87C) with over 90% of the nymphs occurring on the 2 youngest growth stages. After 3 days, alates were more clearly aggregated on the youngest growth stage. (Figure 87B) although the distribution of nymphs had become slightly more even (Figure 87D).

FIGURE 87 : Growth stage discrimination by *S. avenae* in a laboratory flight chamber - distribution of alates and progeny on wheat at 4 growth stages. (A - alates after 1 day, B - alates after 3 days, C - nymphs after 1 day, D - nymphs after 3 days)

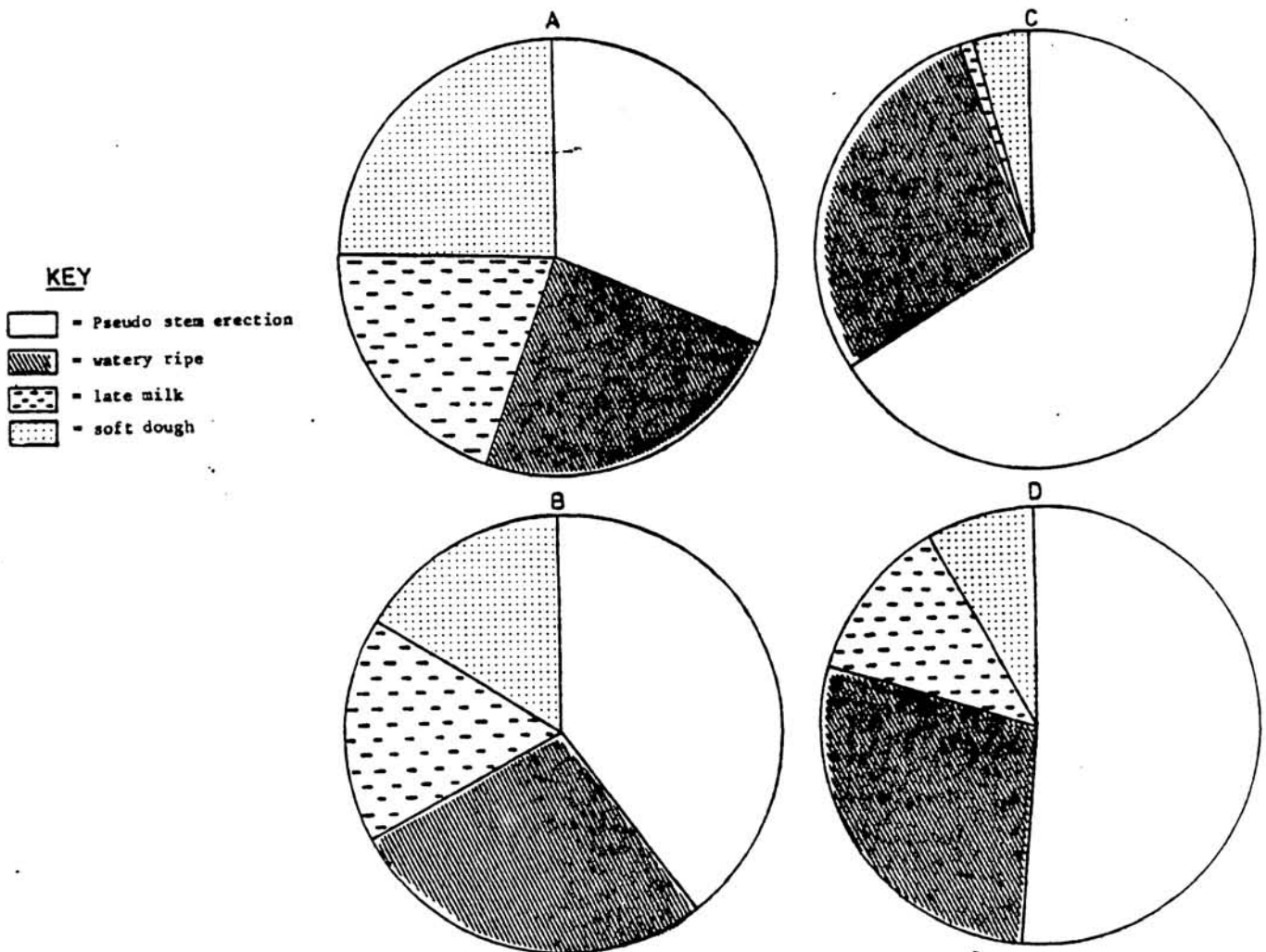


TABLE 75 : Growth stage discrimination of alates released into a laboratory flight chamber - raw data.

Growth stage		Replicate	ALATE SETTLING				NYMPH DEPOSITION			
Description	Code*		1 Day		3 Days		1 Day		3 Days	
			No. settled	No./total no. settled	No. settled	No./total no. settled	No. deposited	No./total no. deposited	No. deposited	No./total no. deposited
Pseudo stem	30	1	19	.16	24	.23	5	.71	29	.44
		2	23	.39	31	.44	16	.70	73	.54
		3	29	.25	39	.38	7	.30	52	.41
		4	20	.37	26	.46	6	1.00	45	.58
		5	58	.41	56	.50	14	.74	54	.60
Watery ripe	71	1	22	.19	20	.20	2	.29	17	.26
		2	9	.15	14	.20	7	.30	34	.25
		3	42	.37	40	.38	10	.43	49	.39
		4	16	.30	15	.26	0	0	22	.29
		5	29	.21	30	.30	5	.26	14	.24
Late milk	77	1	24	.21	11	.11	0	0	3	.05
		2	8	.14	11	.16	0	0	9	.07
		3	10	.09	23	.22	1	.04	25	.20
		4	17	.31	14	.25	0	0	10	.13
		5	36	.26	26	.14	0	0	7	.17
Soft dough	85	1	54	.45	48	.46	0	0	17	.26
		2	19	.32	15	.21	0	0	19	.14
		3	34	.30	2	.02	5	.22	1	.01
		4	1	.02	2	.04	0	0	0	.00
		5	18	.13	12	.06	0	0	0	.00

* Zadoks *et al* (1974)

The relative non-preference for wheat at 'late milk' and 'soft dough' growth stages compared with 'watery ripe' supports earlier observations on field plots (Section 3.3.2.4) and potted wheat plants (Figures 85 and 86), where little recolonization of crops occurred after the early milky ripe stage. In this experiment, fewer alates settled on these plants (Table 5) and these deposited fewer nymphs both in terms of absolute numbers (Figure 87) and numbers per 'settled' alate ($\bar{x}$ = .42 on G.S.85; .63 on G.S.77; 1.29 on G.S.71 and 1.52 on G.S.30 after 5 days). The apparent preference for the pre-heading plants (G.S.30) however is less easily reconciled with earlier conclusions but 4 possible explanations are suggested.

- (I) Alates reared on seedlings under constant conditions may be less discriminating than field aphids. Perhaps changing environmental conditions during the spring contribute to the development of discrimination behaviour in the field.
- (II) Test leaves may have constituted a larger surface area of 'acceptable' host tissue than test ears. Although leaves were trimmed to make them comparable in size to the ears, this was entirely subjective.
- (III) The presence of *M. dirhodum* on 'pre-heading' plants may elicit non-preference by *S. avenae*. Ecologically, this would represent avoidance of interspecific competition by the latter species.
- (IV) In the field, growth stage discrimination may occur in 2 stages. First the selection of tall plants, then the rejection of plants at, or beyond the 'milky ripe' stage. In the laboratory, standardisation of plant heights would have eliminated discrimination between vegetative and 'watery ripe' crops.

4.4 GENERAL DISCUSSION.

The studies reported in this chapter show important effects of crop growth stage on colonization by alate cereal aphids, *M. dirhodum* preferring 'pre-heading' plants especially at the end of flowering.

These conclusions are in general accordance with those reached in Chapter 3 where aphid attack was compared on large plots sown during autumn, early spring and late spring (Section 3.3.2.4). In these studies, aphid abundance was related to crop nutritional status and when the heaviest colonization of sow date 2 by *S. avenae* was observed, plants were between 'flowering' and 'milk development' growth stages, and soluble nitrogen levels extremely high. (Section 3.3.2.5.1). It seems probable, therefore that *S. avenae* alates may respond to high soluble nitrogen levels by depositing nymphs. Way (1967) showed that alate *Aphis fabae* (Scop) selectively colonized field beans with solid heads of unexpanded flower buds in preference to plants at earlier or later growth stages. This helped to explain the year to year differences in attack on crops sown in March, April and May when related to the varying predominance of primary and secondary migration.

The pattern of aphid attack during the year follows a complex pattern, shaped by aerial abundance of aphids and plant suitability. Although there are important regional and yearly differences, the basic pattern is as follows. Early sown cereals run the risk of attack by all species as seedlings during the autumn. At this time, *R. padi* may be more abundant than at any other time of the year (Section 2.4). Although plants can probably compensate for direct feeding damage incurred during autumn, greatest yield loss results from the introduction of barley yellow dwarf virus (B.Y.D.V.) into the crop (Plumb, 1977). In the spring, the developing plants are primarily 'at risk' to attack

by *M. dirhodum* but as the crop reaches anthesis, *S. avenae* is much more likely to colonize, but this risk declines after 'early milky ripe'. (Section 4.3.2.1). *S. avenae* and *M. dirhodum* populations can continue to develop on plants after they have become relatively unattractive to reproducing alates, but after 'late milky ripe' a plant induced population crash is inevitable. (Section 3.3.2.4 and Section 3.3.2.5 and Watt (1979)).

Overall aphid abundance in relation to growth stage is a function, not only of colonisation by alates but also of rates of population development. The latter has been studied on oats by Watt (1979) who found that although *M. dirhodum* rates of increase changed little during crop development, the fecundity of *S. avenae* apterae soared once ears became available. After late milky ripe, fecundity and survival both declined. The coincidence between high alate attractiveness and suitability for population development is a 'formula' for possible outbreaks. The practical relevance of this is obvious but its importance is further enhanced by the fact that yield reduction can be most serious between these growth stages. George (1974) considered that aphid feeding prior to grain filling had little effect on yield. He also showed (George, 1978) that aphid control at the 'milky ripe' growth stage increased yield by just 2% compared to 11% when sprayed at flowering, suggesting minimal effects on yields of infestations at this time.

When the potential for aphid attack, build up and damage all reach their peak over a narrow range of crop growth stages, it is likely that losses will vary considerably between years mainly due to fluctuations in the aerial abundance of aphids during this critical period.

This inherent instability in numbers of *S. avenae* hinders their suppression by natural enemies, mainly due to problems of asynchrony between pest attack and natural enemy impact (Section 1.5.2 and Van Emden,

1966). Predator exclusion experiments during summer (Section 3.3.2.3) for example showed significant impact of syrphids on aphid abundance but lateness of its effect meant that it could not be considered to be 'economic impact'. In this situation 'general' predators such as carabids and staphylinids might be 'effective' natural enemies if they readily 'switched' from alternative prey to cereal aphids once they exceeded the damage threshold. Although recent experiments have convincingly demonstrated ground beetle effectiveness during March and April (Edwards and Steed, 1979; Edwards *et al.*, 1979), no such effect has been shown during May and the remaining summer months (Edwards *et al.*, 1979; Chapter 3) when outbreaks due to mass migrations can occur. It appears then that although predation certainly reduces regional aphid populations and possibly limits numbers on crops during the spring, other control measures are required for effective crop protection in outbreak situations.

Growth stage discrimination by alates demonstrated in this chapter may point the way to an improved approach to control through plant breeding. At present varietal susceptibility is often assessed on the basis of the performance (Adams and Van Emden 1972) of apterae placed on plants at the seedling stage (Dean 1973c; Elamin, 1975 and Adams and Drew 1964b), yet the marked preference of *S. avenae* for feeding on ears (Latteur, 1971, 1976) means that these results could be misleading. (Watt, 1979). Lowe (1978) has attempted to screen cereal cultivars on the basis of 'performance' of apterae placed on the ears but discrepancies in test cultivar growth stages have obscured the underlying differences in aphid susceptibilities. On the basis of the present findings (Section 3.3.2.4 and 4.3.2), it is proposed that 'alate non-preference' would be a powerful form of resistance to aphid attack in the field. The aphid flight chamber used to study discrimination in the laboratory (Section 4.3.2.2) might be modified for the purposes of

initial screening. Later trials would need to investigate the stability of 'non-preference' resistance (Painter, 1951) in situations where aphids were denied a choice of plants.

Chemical control measures directed against the direct losses caused by *S. avenae* will clearly be most effective when timed to coincide with the end of flowering, when the crop is at greatest risk. This recommendation is already given in the U.K. (George, 1974) for cereal aphid control. In the present studies, the observation that few *S. avenae* colonized plants after the 'early milk' stage* implies that short persistence aphicides applied around the time of flowering should be as effective for the control of *S. avenae* as persistent ones. It would appear in general therefore that the short persistence properties of 'pirimicarb' should not limit its efficacy for cereal aphid control in the summer. Furthermore, its use should prove beneficial due to its merits of intrinsic specificity (Proctor and Baranyovits, 1969) (see Chapter 3).

The studies on the relationship between cereal aphid populations and crop growth stage, described in this thesis usefully extend our understanding of cereal aphid ecology, and could perhaps help towards improved forecastings of pest attack. Several workers have reported poor correlations between the catches of cereal aphids in Rothamsted suction traps and field populations. Taylor (1974, 1977) and George (1974) considered the timing of alate arrival in traps and on the crop while Dean (1973b, 1974a) focussed on the relative abundance of cereal aphids. He found that out of 10 years when cereals were heavily infested, there were only 3 when trap catches were higher than average. The conclusions of the present work are that crop colonization is not only a function of the aerial abundance of aphids but also of the crop growth stage. Forecasting might, therefore be improved by considering both these factors.

* Carter *et al* (1980) reported that *S. avenae* continued to arrive after flowering in small plots cleared of aphids using pirimicarb.

CHAPTER 5

INTEGRATED PEST MANAGEMENT (IPM): PRACTICAL IMPORTANCE IN WORLD AGRICULTURE,
FUTURE DEVELOPMENTS AND PROSPECTS FOR IPM OF CEREAL PESTS IN THE U.K.

CHAPTER 5INTEGRATED PEST MANAGEMENT (IPM): PRACTICAL IMPORTANCE IN WORLD AGRICULTURE,
FUTURE DEVELOPMENTS AND PROSPECTS FOR IPM OF CEREAL PESTS IN THE U.K.5.1 INTRODUCTION

The object of this chapter is to assess critically the practical impact of the integrated control concept in agriculture; to consider the technical scope for improved crop protection in cereals in the light of recent research findings (emphasising those obtained in the present work); and to develop a 'plan of action' for the implementation of integrated control in cereals.

'Integrated control' and 'cereal crop protection' are both subjects of considerable interest and controversy at present and the discussion that follows inevitably reflects a personal viewpoint and bias.

5.2 THE RELEVANCE OF INTEGRATED CONTROL TO WORLD AGRICULTURE5.2.1 Introduction

Today, the integrated control concept forms the basis of the scientific approach to pest control. Since Stern *et al* (1959) defined the approach as 'applied pest control which combines and integrates biological and chemical control' there has been a proliferation of research activity devoted to non-chemical methods. University and college courses have increasingly emphasised integrated control, and many text books have reviewed the concepts and methods involved and the successes achieved (e.g. Huffaker and Messenger 1976). Despite this, the scale of its influence in world agriculture has not been sufficiently discussed in the literature.

5.2.2 Historical Background to Pest Control

In his transition from hunter/nomad to farmer, Neolithic man must have consciously or unconsciously used two main criteria for his selection of plants for domestication. The first was agronomic suitability.

Plants needed to be easy to grow and capable of producing sufficient 'yield' to justify agricultural effort. In most climatic regions, harvested produce and crop seeds needed to store well, and the interval between planting and harvesting needed to be as short as possible. (The delay between input of effort and reward must have constituted a major psychological/cultural barrier to the initiation of agriculture). The second criterion was palatability to man and his domesticated animals. The plants fulfilling these requirements were taxonomically varied but most shared important features of their ecology. In general, they were associated with disturbed habitats where evolutionary pressure had placed a 'premium' on rapid growth, high seed production and short generation times. These attributes were crucial rather than competitive ability and susceptibility to pests and diseases. In contrast to plants from undisturbed habitats, they tended to possess low levels of secondary plant substances involved in preventing pest and disease attack. Instead, they often escaped attack 'though being out of phase with pests in time and space.' Plant domestication involved the cultivation of these plants on a relatively large scale, sometimes growing the same plants year after year on a single plot. Thus monoculture weakened some ecological escape mechanisms possessed by these plants in nature. In ecological terms (Feeny, 1976), unapparent plants were made artificially apparent. It was not surprising that relatively high levels of pest damage sometimes followed, at any rate when this process was taken to extremes as in some modern agriculture.

According to Coppel and Mertins (1976) Man's early active attempts to reduce pests included hand removal of phytophagous insects (Bottrell and Adkisson 1977), spraying the crop with insecticidal plant extracts and even natural enemy introductions. Over a longer time scale, some problems were unwittingly solved. First, crops adapted in response to the new pressures imposed by agriculture resulting in higher levels of

natural resistance. Secondly early farmers tried a variety of growing techniques (sowing dates, plant spacings, crop mixtures etc), all with effects, often unconscious on pest damage (Perrin 1977) until yield was optimised. Crop species that were especially susceptible to attack were never established or were abandoned in some regions.

By the 1930's, agriculture had undergone a number of revolutions but crop protection still depended on the complementary use of all these trial and error methods. It would be naive to suppose their achievements were satisfactory. Indeed, the enthusiasm with which D.D.T. was welcomed in the 1940's (Horsfall 1965, Wigglesworth, 1976) is a reflection of the inadequacy of traditional methods. The attributes guaranteeing D.D.T.'s astonishing success were its high efficacy against a broad spectrum of insect pests, low cost, low mammalian toxicity, simple manufacture and chemical stability. Its widespread use was to greatly increase crop yields and decrease incidence of some major vector-borne diseases, but also to initiate a process of self-perpetuating dependence on pesticides that has been referred to as "addiction" by De Bach (1974).

Opinions are divided on the nature of pesticide addiction. It may, as De Bach implies involve the unquestioning use of chemical control despite spiralling costs rendering them non cost effective - a blinkered attitude cultivated by ruthless sales pressure from pesticide salesmen. At the other extreme, addiction may represent an unwillingness to abandon high yields easily achieved with pesticides or demanding pesticides as security for the high cost of capital inputs. Two major drawbacks to chemical control of insect pests arose within ten years of D.D.T.'s introduction (Ripper, 1956). The first was the selection of resistant pest strains (Brown 1974, 1977; Georgiou 1972; Margham 1975) the second was the destruction of insect natural enemies which

enabled unrestrained resurgence of target organisms after spraying. Furthermore, some previously insignificant species became major pests in the absence of natural checks to their population increase. The best documented of these case is the fruit tree red spider mite, *Panonychus ulmi* Koch. (Coaker, 1977; Kirby, 1973; McMurtry *et al*, 1970; Ripper, 1956). Other important 'new' pests are citrus scale insects (De Bach, 1974), bollworms in cotton (Lingren *et al*, 1968; Ridgeway *et al*, 1967; Bottrell and Adkisson, 1977) and coffee leaf miners (*Leucoptera* spp) (Le Pelley, 1968; Bess, 1958). In the last 20 years numerous authors have elaborated on the shortcomings of pesticides (e.g. Douthett & Smith, 1971; Smith & Van den Bosch, 1967; Smith, 1970; Newsom, 1970) and the overall impression conveyed by the scientific literature was that they would shortly become obsolete as primary agents of pest control and therefore research effort needed to be concentrated on non-chemical methods. The publication of Rachael Carson's 'Silent Spring' was, however a more significant landmark in the history of pesticides. The widespread public concern that it aroused prompted governments to respond by introducing more stringent regulatory procedures for pesticides and by shifting research funds away from pesticides.

Other modern means of maximizing crop yields were increasing the status of pests. Crop cultivars, selected for high yield as for the "Green Revolution" were often highly susceptible to pests and disease (Anon, 1974; Dahlberg 1979). Extending the scale of monocultures and the frequency of cropping in a season were also exacerbating pest problems (Southwood and Way 1970). Many observers felt that whenever a single method was employed to remove a single limitation to yield, failure was inevitable due to unforeseen repercussions elsewhere in the agroecosystem. Recognition of these complexities lead to an ecological approach to pest control. It was felt that ecologists would view crop protection as an

exercise in applied ecology and as such would draw on a wider range of methods to control pests, blended with care to minimize undesirable side effects.

It was against this background that the term 'integrated control' was introduced (Stern *et al*, 1959). Certainly the practice was not new, but the concept was explicitly defined for the first time.

5.2.3 The Impact of Integrated Control in World Agriculture

It is extremely difficult to gauge the practical impact of integrated control in agriculture. Most published accounts have stressed the potential of the approach and a few apparently outstanding successes. (Van den Bosch and Messenger, 1973; Apple and Smith, 1976; Huffaker and Messenger, 1976; Metcalf and Luckman, 1975:*) In contrast little attention has been paid to failures and the difficulties posed by the integrated control approach (Way, 1977b). Furthermore, success stories are difficult to interpret purely on the basis of technical achievement. Farmer acceptance is the 'acid test' of new agricultural methods but the scale of adoption of programmes is rarely mentioned. Furthermore, sometimes successes continue to be quoted long after limited programmes had been abandoned in practice (e.g. strip cropping or intercropping of alfalfa especially to limit *Lygus hesperus* migrations into cotton (M.J. Way. pers. comm.)).

Most integrated control programmes are based on the maxim that in all crops natural enemies should be conserved yet many workers have noted that their effectiveness in the majority of crops often falls short of that found in tree crops (e.g. De Bach, 1974). Numerous authors have discussed this (Lloyd, 1960; Newsom, 1970; Ridgeway, 1972; Hansberry, 1968; Ehler and Van den Bosch, 1974) including Southwood (1977) who examined the successes achieved in classical biological

* also; Smith and Pimentel 1978; Brader, 1979; Rabb and Guthrie, 1970; Van Emden, 1974 and National Academy of Sciences 1969.

control in relation to agroecosystem stability. He noted that successes were predominantly associated with tree crops such as citrus, coconuts etc. In contrast, natural enemy releases had rarely achieved 'complete' success in annual crops. (Table 76). It is also noteworthy that problems associated with natural enemy destruction (new pests and resurgence) usually arise in more stable agroecosystems. Tree crops such as coconuts, apples and citrus are of considerable local economic importance, but their contribution to the world's food supply (especially the poorer nations) is secondary to that of annual crops, especially small grains.

Very recently, the United States 'Office of Technological Assessment' (OTA) (OTA, 1979; Hoch, 1979) has conducted an exhaustive review of current pest control practices in the United States and of the potential for new approaches. Detailed reports were prepared for each of seven cropping systems and separate committees reviewed the Federal constraints to improved crop protection and the effects of introducing U.S. technology to the developing world.

The conclusions of this major study contrast sharply with the impression conveyed by biological control and integrated control textbooks also produced in the U.S. First, it is clear that foliar applied conventional pesticides are the major means of controlling virtually all the arthropod pests in most of the cropping systems - wheat, corn, soybeans, apple, potato and California vegetables. Secondly 'alternative' approaches are only of secondary importance in most crops, the exceptions being in Texas where in sorghum sowing date manipulation is widely used and in cotton natural enemies help to control many of the pests.

In view of these findings, the key question must be : why has integrated pest management (IPM) failed to replace pesticide dependence

TABLE 76 Cases of biological control of insects by imported natural enemies grouped according to habitat characters (on r - K continuum); based on the analysis of Table 12 of De Bach (1964).

(Reproduced from Southwood, 1977b)

Habitat type	All cases		Cases graded 'Complete Control'	
	No.	% total	No.	% total
r-end				
Cereals and forage crops (wheat, lucerne, etc).	6	4	0	0
Vegetables (tomatoes asparagus, taro, etc).	21	14	0	0
Sugar cane, cotton, pasture	19	12	2	8
Trees (citrus, coconut, oak, olive, grape, etc)	107	70	23	92
K-end				

as the principle approach to controlling arthropod pests and can more widespread implementation be expected in the near future? In this regard, the OTA (1979) concluded:

'We project that the implementation of IPM in crop protection in the United States will proceed slowly over the next 15 years unless much greater inputs are made at the National and State levels. The major obstacle to faster adoption is the lack of demonstrated feasible IPM systems. This is due to a number of factors, but lack of information on the basic biology of pests and crops, lack of established economic thresholds, cost/benefit analyses of IPM programmes, and the primitive state of predictive modelling and agroecosystem analysis are the most important.'

This conclusion also conflicts with the impression conveyed by the biological control/integrated control literature which has tended to dwell on isolated success stories instead of analysing the obstacles to IPM implementation in general and in specific crop situations (Way, 1977b). It also refutes the forcefully expressed view of Van den Bosch (1978) that practical IPM programmes already exist but that their widespread implementation has been prevented by a 'conspiracy' ultimately maintained by pesticide manufacturers, apparently anxious not to lose sales to alternative approaches. Corbet and Smith, 1976 have also recognised the severely limited scale of IPM success but have urged the need for strong support from the public and legislators. Their view implies that IPM programmes rarely pass the acid test of farmer acceptance when pesticides remain a viable option.

Another useful approach to assessing the impact of integrated control is to consider its effect on the pesticide business. The integrated control approach demands that pesticides should only be used in relation to defined need and that placement and timing of applications should optimise kill of target species with minimal effects on other

organisms. Such 'rational' pesticide usage should retard the development of resistance (Corbett, 1979) and reduce the risk of side effects (resurgence, new pests, wildlife destruction and pollution). The development and use of intrinsically selective insecticides has been repeatedly advocated in the literature. Obviously, if these principles were closely adhered to in agriculture, pesticide manufacturers would have needed to radically change their screening objectives and overall style of business. A fall in the overall volume of sales, coupled with the shift towards careful usage of existing chemicals would encourage firms to provide an overall pest control service. In addition, considerable 'development effort' would be devoted to integrating existing chemicals into integrated control programmes by careful attention to 'ecological selectivity'. (timing and placement) (Newsom *et al*, 1976). There would be a greatly increased need for skilled technical support at all stages of product development and sales. Intrinsically selective materials including virus's and pheromones would be developed to satisfy the demands of integrated control and effort in this area would overwhelm attempts to develop broad spectrum materials.

In reality none of these changes have occurred. The overall volume of sales continues to increase (Graham Bryce 1979; Anon, 1979c) and there appears to be little commercial advantage in specificity, not only because markets for selective materials are relatively small, but because farmers often face a complex of pests. Indeed the highly acclaimed selective properties of the aphicide pirimicarb have not guaranteed overwhelming world wide commercial success. This is because cheaper broad spectrum materials still provide good control. The willingness of farmers to pay a little more for selectivity has been governed mainly by the strength of support provided by agricultural

extension services. Today, specificity is likely to be regarded more as a drawback in practice than an advantage.

There are some markets that are so large that development of a specific material is justified but screening techniques are not geared to the discovery of specific rather than broad spectrum materials. In this context, it is noteworthy that the recent development of synthetic pyrethroids utilised structure-activity studies to optimise properties of persistence against a broad spectrum of insect pests. (Elliot 1976).

Although major changes in chemical crop protection materials and application methods are foreseen (Graham Bryce 1979; Brauholtz, 1977) involving improved molecular design and management of pesticide use, the overall expectation is one of increasing demand for more or less conventional pesticides (Corbett 1978). According to Roberts (1975) the main reasons for future growth will be the increased importance of cash crops and the need for crop protection 'packages' to accompany releases of high yielding crop varieties in the developing world. The F.A.O. Panel of Experts recently concluded that a substantial increase in pesticide usage would be the most practical means of crop losses in the developing world.

5.2.4 Reasons for the Restricted Impact of Integrated Control

The failure of the integrated control approach to dominate crop protection requires careful explanation. How is it that pesticides have continued to be widely used in view of their widely publicised shortcomings? Why have the exciting novel approaches failed to live up to the hopes of early proponents and why has the integrated control approach failed to achieve acceptance with farmers? An understanding of the answers to these questions is essential to improve the direction

of pure and applied research and the proper allocation of funds. I believe that they are largely answered in terms of:

- (i) The convenience of pesticides.
- (ii) The limited geographical range of resistant strains and the availability of new pesticides to replace those rendered ineffective by resistance.
- (iii) Major drawbacks to alternative methods.

5.2.4.1 Convenience of Pesticides

The convenience aspect requires little explanation. Pesticides are simple to use, reasonably dependable and can often be applied on a curative basis. Hence the farmer only needs to worry about actual problems arising in a particular season. Preventative methods of pest suppression such as mixed cropping may require extra effort by the farmer to deal with a range of potential pests, some of which might never arrive. Their use in routine spray programmes may be 'mindless' (Way, 1978) but may be an invaluable aid to smooth running of a farm business. This aspect has been vividly discussed by Scott (1979) for the case of pest control in top fruit in the U.K. He has noted that crop protection decisions form only a small fraction of the 'constant stream of management decisions the farm owners must take' and it is for this reason that there is a 'necessity for farm operations to be as simple as possible if the owners are to retain the day - to - day control on which the success of their businesses probably depend. It is therefore necessary to plan a routine spray programme using as few chemicals as possible'

5.2.4.2 Limited Geographical Range of Resistance and the Availability of Replacement Chemicals

Statistics on pesticide resistance appear alarming. Georghiou and Taylor (1977c) for example, reported that 364 arthropod species

had developed resistance to insecticides. However resistant strains are often confined to a small part of a pest's geographical range (Reynolds 1977). Furthermore, the high profitability of pesticides has encouraged the development of new products to replace those made obsolete by resistance. Hence farmers have rarely needed to consider alternative methods. The prospects for the future are much more alarming considering the falling rate of new pesticide introductions (Goring, 1977; Lewis 1977) set against the accelerating rate of resistance development, its expanding geographical scale and the increasing phenomenon of multiple resistance (Georghiou and Taylor, 1977c). Comins (1978) considered that it is "increasingly likely that the development of pesticide resistance by arthropod pests will outpace the development of new chemical agents and render crops completely vulnerable", a view also implied by Hueth and Regev (1974), Conway and Comins (1979) and Southwood (1977, 1979). (NB resistance often remains in a population even when selection pressure is removed; Matthews (1979)). Nobody can accurately predict the pesticide industry's prospects of keeping pace with resistance by finding new chemicals (Casida, 1978) but a number of undesirable side effects of following such a course can be envisaged.

(I) Multiresistant strains tend to possess high levels of 'background resistance' conferring high levels of tolerance even to entirely novel pesticides. Multiresistant strains of *Spodoptera littoralis* in Egypt were substantially more tolerant to newly introduced 'permethrin' than susceptible strains. (Fullbrook and Holden, 1979; Sawicki, 1979, 1980).

(II) All other things being equal, new pesticides will cost more than their superceded counterparts. This arises firstly from the ever increasing costs of pesticide evaluation, development, registration and marketing and secondly from the sharp increase in farmer 'bearable price' that accompanies the decline in effectiveness of competitive compounds.

(III) There is little doubt that manufacturers will continue to devote high resources to discovering insecticide replacements for the major markets, such as bollworms in cotton, and in these areas innovation may well keep pace with resistance. Markets, less severely affected by resistance may benefit from a surplus of suitable materials as a 'spin off' from the cotton 'treadmill'. Minor markets where resistance is a serious problem may however reach the situation in which pesticides become obsolete either because development of appropriate chemicals is commercially unattractive or else because costs of registration are too high. An example is that of glasshouse crops (Rudd Jones 1973, Hussey 1973). In such areas there is a well defined need for an increased emphasis on integrated control and possibly for public sector support of pest control development costs.

One of the most alarming trends in pest control recently has been the apparent decline in research activity on the part of manufacturers in response to increasing development costs. Lewis (1977) and others have drawn attention to the falling rate of new insecticide introductions over recent years. Prohibitive costs of satisfying registration requirements are cited as a primary cause of this trend, especially with respect to the Environmental Protection Agency (E.P.A.) in the United States (Anon, 1978). Similar claims have been made in the field of pharmaceuticals (Steward and Wibberly, 1980). Some authors have suggested that regulatory legislation has become so stringent, that it creates more problems than it has solved. Djerassi *et al*, (1974) proposed that changes at the regulatory level should carry a 'research impact statement' (Djerassi 1973) in which legislators are obliged to assess possible adverse effects of legal changes on research activity. The philosophy behind this was that safety could not be regarded as an absolute criterion. If the prospects of discovering new drugs and pesticides were jeopardised by unduly rigorous statutes, the net effect

for the community could be distinctly adverse. Criticism has been levelled not only at the costs of complying with individual governments' regulations but at the lack of harmonisation between authorities (Edson, 1973; Wright, 1973), even within the E.E.C. Wright (1973) listed more than 20 official bodies involved in registration procedures for pesticides in Western Europe. Reinforcing this view, Matthews (1979) stated that 'the search for new chemical groups which are toxicologically and environmentally acceptable should be fostered rather than restricted by new legislation.' Djerassi *et al*, (1974) were particularly concerned with the prohibitive costs of supplying adequate data on pheromone safety to satisfy E.P.A. requirements. They argued that by applying criteria developed for conventional pesticides, the E.P.A. were acting against the interests of improved pest control. These allegations emphasise the role of the public sector in shaping the 'innovative climate' for improved crop protection and apply to 'minor market' and 'selective' insecticides as well as the more novel 'biorational' materials; insect growth regulators and pheromones.

5.2.4.3 Major Drawbacks to Alternative Methods

Not enough attention has been paid to the limitations of new approaches in pest control. The summary compiled below represents an attempt to rectify this. Although not exhaustive, it attempts to highlight some of the reasons why these methods have not been major 'panaceas' for pest problems. This is not to question their undoubted value in some specific and possibly highly important situations. It is the 'art' of integrated control to devise the optimal blend of methods for satisfactory control in a given situation. Furthermore many of the key drawbacks that are included are commercial or managerial in character indicating that, should pesticides become obsolete, other methods could prove practical. It is simply the case at present that cheap broad spectrum materials still provide good control in very many

situations so obviating the need for more difficult alternatives to be considered.

The most important conclusion from the summary is that despite the impressive technical potential of alternative methods, they have rarely been able to compete with conventional pesticides on the basis of effectiveness, convenience, cost and compatibility with intensive agricultural methods. The question of compatibility merits further consideration at this point in view of the emphasis placed on it by proponents of integrated control. 'Biorational' materials (Djerassi *et al*, 1974) and natural enemies (De Bach, 1974) suppress pest populations with minimal adverse effects on beneficial organisms. Resistant crop cultivars may actually enhance the impact of other pest mortality factors (Pathak, 1975; Russell, 1979). Insects may be more restless exposing more to predation and adverse weather; rates of increase are depressed enhancing natural enemy impact (Lawton and McNeill, 1979; Starks *et al*, 1972; Wyatt, 1970; Van Emden, 1978); individuals may be more susceptible to insecticides (Kea *et al* 1978) sometimes due to their reduced body size (Raman, 1977). Experience has shown that these merits of ecological compatibility have not been of notable importance to the farmer. He has been more concerned with agronomic compatibility - after all, pest control is not his only requirement for growing crops successfully. Pesticides, by virtue of this quality have earned a major place in crop protection.

PRACTICAL LIMITATIONS OF ALTERNATIVES TO CONVENTIONAL PESTICIDES - SUMMARY

The objective of this summary is to indicate the reasons why alternative methods have failed to have a substantial and widespread effect on crop protection practices. The fact that these methods have already been successfully employed in particular situations is fully recognised. Furthermore, some of the techniques might increase considerably in significance depending on technical innovation, legislative changes or most importantly, reduced viability (due to rising costs or resistance) of conventional pesticides which are currently preferred on the grounds of 'convenience' and 'agronomic compatibility'.

* Disadvantages of high specificity

(a) Crops are usually infested by more than one significant pest so techniques that control complexes of insects and mites are usually required. If each pest is controlled with specific materials, there may be benefits in terms of reduced incidence of secondary pests but the farmer may find he needs to employ a number of techniques to do the job of a single broad spectrum insecticide: This is likely to involve an increase in time, effort and cost.

(b) Commercial organisations involved in pest control justifiably regard specific techniques of pest control as commercially unviable apart from a few exceptional 'problem areas' such as mosquito control in California. First, the high cost of developing and marketing new techniques can only be justified for relatively large markets but markets for 'specifics' are inevitably relatively small. Secondly, the number of markets for 'specifics' is smaller than might be expected, either because farmers value the capacity of broad spectrum insecticides to control pests of minor or occasional importance or because such a product can be used on their other crops. Thirdly, demand for specific materials is bound to fluctuate between seasons more than for broad spectrum materials hampering the management of finance and product supply.

+ Incomplete control of pests

Techniques that give only moderate control of pests are likely to be unacceptable while conventional pesticides remain effective. There are four reasons for this: (a) The economic thresholds associated with some pests are exceedingly low, e.g. virus vectors, pests causing 'cosmetic' damage to the harvested product and pests of crops intended for processing (their occurrence in the product is regarded legally as contamination). (b) If substantial numbers of pests survive, these may increase to potentially damaging populations sooner after treatment than after a highly effective 'clean up' treatment. (c) Familiarity with highly effective pesticides has led farmers to aim for 'clean' crops. (d) Many countries base their pest control recommendations on the results of straightforward experiments designed to test the effectiveness, in terms of 'percent kill' of pesticides. As long as conventional materials remain effective, they are likely to perform well in these tests.

1. PARASITES AND PREDATORS

a) Natural Control

(I) Magnitude and timing of impact unpredictable except in some perennial tree and bush crop situations.

b) Classical biological control

(I) Successful in 'introduced' crops where pests have hitherto been isolated from natural enemies but satisfactory levels of natural enemy effectiveness are normally restricted to perennial crops especially tree and bush crops (Southwood 1978).

c) Inundative release

(I) Usually technically complex except in enclosed environments such as glasshouses (Scopes, 1975).

(II) Commercially unattractive - patent protection difficult, high costs of production, disadvantages of specificity * short 'shelf life' of living organisms hence difficulties in coping with fluctuating demand.

d) General limitations

(I) Incompatible with the need for broad spectrum pesticides to control other pests in a complex (unless, of course non-chemical methods can be found for these pests or else insecticide resistant natural enemies can be used. (Croft, 1976)).

(II) Control incomplete *

(III) Harassment of vectors by natural enemies can increase dispersal (Tamaki *et al.*, 1970, Roitberg and Myers 1978) and hence the role of virus spread (Roitberg and Myers, 1978, Roitberg *et al.* 1979).

(IV) Carter (1973) has suggested that parasites may directly transmit virus following the discovery that aphid honeydew (an important food for parasites) can be a highly infective virus source (Richardson and Sylvester 1965).

(V) Some predators can sometimes be injurious to crops if they require plant food to supplement a predominantly arthropod diet (e.g. earwigs and predacious bugs in orchards).

2. RESISTANT CULTIVARS

(I) Characters for resistance must not conflict with other components of optimal agronomic/commercial performance

(II) Characters conferring resistance to one pest may lead to increased susceptibility to another (Beck and Maxwell 1976) e.g. the trego character in cotton impacts resistance to boll weevil but susceptibility to *Lygus* bugs (Lincoln *et al.*, 1971).

(III) Screening difficulties, e.g. biotype variability and long R and D time (Beck and Maxwell, 1976).

(IV) Resistance breaking biotypes (Russell, 1978; 1979; Dunn, 1978) although probably less of a problem with 'horizontal resistance' (Vander Plank, 1963).

3. CULTURAL CONTROL
 - (I) Host free seasons, crop rotation and habitat diversification conflict with the benefits of monoculture.
 - (II) Particular cultural operations (sowing, ploughing etc) that are ideal for crop protection may be sub optimal for overall crop production.
 - (III) Control may be incomplete +
 - (IV) High levels of crop protection especially difficult to achieve where complexes of pests are present.
 4. MULTIPLE CROPPING
 - (I) Highly valuable to subsistence farmers where crop protection benefits can supplement 'spread of risk' advantages of multiple cropping. To the developed farmer, advantages of simplicity outweigh the drawbacks associated with pest damage.
 - (II) Control may be incomplete. +
 5. PATHOGENS
 - a) Local inoculation, natural spread
 - (I) Epidemiology poorly understood.
 - (II) Rapid spread may depend on high population levels.
 - (III) Little or no evidence of spread of multiplication of pathogens used against annual crop pests.
 - b) Inundation
 - (I) Poor chemical/light stability (currently being overcome by formulation).
 - (II) Disadvantages of high specificity.*
 - c) General Limitations
 - (I) In the past, uncertain patent status of living organisms has discouraged commercial exploitation - probably not a limitation in the future (Anon 1979a).
 - (II) In the U.S.A., fears that insect pathogens could mutate to harmful biotypes have prompted the Environmental Protection Agency (E.P.A.) to impose more stringent regulatory requirements than for conventional pesticides. Following a recent review by the E.P.A. (Baker, 1979), these procedures have now been simplified (Hardwick 1980). However, until now these obstacles, together with the small market potential of pathogens has discouraged commercial exploitation (Djerassi *et al*, 1974).

(III) Control often incomplete + e.g. *Bacillus thuringiensis* against cotton bollworms (Bull *et al*, 1979).
 6. HORMONES (Ruscoe 1975)
 - (I) Subject to cross resistance induced by conventional pesticides.
 - (II) Contrary to the expectations of early proponents (Williams 1967) hormones can select strains with specific resistance.
 - (III) Since effectiveness is dependent on insect life stage, a long residual life is required but hormones are inherently short in persistence.
 - (IV) Crop protection delayed until moulting.
 - (V) Disadvantages of high specificity. *
 - (VI) Too specific for markets to justify cost of commercial development.
- N.B. - some of these objections do not apply to the more recently developed growth disrupters (e.g. diflubenzuron).
7. PHEROMONES
 - (I) In the case of 'the confusion technique', already mated female immigrants may be unaffected and initiate an attack.
 - (II) High cost relative to conventional pesticides.
 - (III) Short persistence (might be overcome by formulation e.g. 'Hercon' laminated plastic or 'Conrel' hollow fibre dispensers (Baker 1979)).
 - (IV) Resistance possible (Brown, 1974).
 - (V) Disadvantages of high specificity. *
 - (VI) In the past, uncertain patent status has limited commercial development - probably not a problem in the future.
 - (VII) E.P.A. regulatory requirements have been 'at least as severe' as for conventional pesticides (Djerassi *et al*, 1974). This has very recently been reviewed by the E.P.A. (Baker, 1979) and registration procedures have now been simplified (Hardwick, 1980). There is unlikely to be any need for registration for mass trapping techniques (Baker, 1979).
 - (VIII) Level of control attainable has hitherto been incomplete. +

5.3 FUTURE DEVELOPMENTS IN CROP PROTECTION

5.3.1 Ecological compatibility versus agronomic compatibility.

There is little doubt that compatible combinations of pest control measures will offer the most satisfactory long term solution to pest problems. This is the conventional wisdom of the integrated control approach. However, to gain widespread farmer acceptance, the pest control package needs to be closely integrated to the overall crop production system (agronomic compatibility). This additional constraint needs to be incorporated into control programmes from the early stages of their development rather than appearing as an insurmountable stumbling block after a particular technical means of pest control has been developed. For example research effort devoted to natural enemy introductions will be fruitless if farmers depend on broad spectrum materials to control another pest in a complex.

5.3.2 Selective Pesticide Applications

Selectivity of pesticide applications has been a long standing 'keynote' of integrated control (Ripper *et al*, 1951; Croft and Brown 1975). Intrinsically selective materials are technically inadequate in situations where complexes of pests are present, and the inevitably small size of their markets makes them commercially less attractive than broad spectrum materials. In addition, the probability of discovering compounds with a predetermined, narrow range of activity must be relatively less. (Usterstenhofer, 1970). It is astonishing, therefore that more research has not been devoted to methods of obtaining 'ecological selectivity'. Some established practices already achieve this requirement through manipulation of timing, placement and release rate (e.g. seed treatments [placement], winter washes [timing] and granules [rate of release and placement]) (Graham Bryce, 1979). These methods, however were devised with objectives other than selectivity such as natural enemy conservation in mind. 'Aldicarb',

for instance is applied exclusively as a granule formulation to overcome the otherwise prohibitive toxic risk to operators. Winter washes make use of materials that would be phytotoxic if used in the summer. Seed treatments are simply an effective means of maximizing delivery of toxicant to seed and seedling pests. Similarly, microencapsulation formulations have primarily been developed to enhance the persistence of foliar applied pesticides so it has been fortuitous that increased selectivity towards chewing insects has incidentally been obtained.

There is much more scope to improve ecological selectivity (Ripper *et al*, 1951; Graham Bryce, 1977;*) by imaginative formulation and application (e.g. Meyer and Luckmann, 1970)* but this will only follow from more widespread proof and recognition of the practical value of natural enemy conservation. For cereal aphid control, C.D.A. (controlled droplet application) methods of application in cereals restrict pesticide deposits to the uppermost parts of wheat plants enabling good control of *Sitotia avenae* feeding on the ears (Pickin, 1978) without impaction on predacious syrphid larvae nesting low down the plants during daytime. Electrostatic or electrodynamic charging of droplets (Matthews, 1979; Coffee 1979) might enable insecticides to be applied to seedling stage infestations of cereal aphids with minimal spray contact with the soil. These techniques should be a powerful means of improving the environmental safety of otherwise broad spectrum pyrethroids which have been proved outstandingly effective for this purpose (Horellou and Evans, 1979). Optimal droplet sizes/distributions for insect mortality may well differ between leaf feeding pests and natural enemies, offering scope for manipulation to improve selectivity. Surprisingly fast rates of natural enemy colonization of sprayed orchards (Morton, 1977; Cartwright, 1979) suggest that survival could

* also see Van den Bosch and Stern (1962).

be increased by strip spraying. Alternate strips could be sprayed on day 1 and the remaining strips sprayed several days later (c.f. Matthews, 1979). Good survival of some natural enemies compared with pests would result from their higher levels of mobility coupled with the fact that treated foliage is not consumed, sparing them the 'stomach poison' effects of pesticides (c.f. Cartwright, 1979). The approach has recently been tested in an orchard in the U.K. (Cartwright, 1979) but its greatest potential probably lies in crops where parasites are the 'key' natural enemies, (parasites are mostly highly mobile) as is the case with the coffee leaf miner (Bess, 1958; Le Pelley, 1968).

Weed scientists have exercised extraordinary ingenuity in the selective usage of broad spectrum herbicides. The recirculating sprayer, the carpet applicator, the rope wick applicator and the Stoneville wiper (Robinson, 1978; Fawcett, 1980) are imaginative means of restricting the placement of chemicals and there is no reason why a similar approach could not be used to improve placement of insecticides to spare beneficial insects.

5.3.3 Secondary plant chemicals : prospect of selectivity against phytophagous insects.

Perhaps the most exciting long term developments in crop protection will stem from recent findings on the role of secondary plant chemicals in limiting pest attack (Chapman, 1974; Beck and Reese, 1977; Harborne 1977; Kogan, 1977; Bernays and Chapman, 1976; 1978; Lawton & McNeill 1979). Secondary plant substances comprise a diverse group of chemical types, but for the purpose of this discussion, they are best classified on a functional basis.

1. Volatile repellents and attractants, e.g. allyl isothiocyanate.
2. Antifeedants, e.g. alkaloids, monoterpenes, triterpenes.
3. Digestibility reducing compounds, e.g. tannins and resins.
4. Toxins, e.g. cyanide, glucosinolates, alkaloids.

The significance of these chemicals to crop protection is two fold. First, their possible use when applied to crops as sprays; secondly their incorporation into new crop cultivars by plant breeding.

The work of Visser and Ave (1978) is one example of the role of plant volatiles in host plant location by phytophagous insects. His work has shown that plant colonization by the Colorado beetle (*Leptinotarsa decemlineata*) depends on precise concentrations and isomer ratios of several distinct attractants. Surely mechanisms of this level of complexity invite disruption for crop protection? Workers at the Centre for Overseas Pest Research, London have recently tested compounds that totally block antennal response (E. Bernays, *pers. comm.*). Volatile deterrents have important practical advantages for pest control. They could be applied in the form of capsules designed to control release rates according to the chemical's intrinsic volatility, crop microclimate and geographical location. Furthermore, contact with the foliage would not necessarily be required, so compounds otherwise unsuitable on the grounds of phytotoxicity or residue problems might become viable. It is likely that formulations currently being developed to control pheromone release could be used in this context (e.g. Conrel's hollow fibres for controlled vapour release (Brooks *et al*, 1977, 1979)).

Antifeedants and oviposition inhibitors have attracted intermittent research interest (e.g. Gill and Lewis, 1971; Ruscoe, 1972; Jacobson *et al*, 1978) but there has been no attempt to improve active molecules by analogue synthesis coupled with structure-activity relationship studies. This approach has proved invaluable in the development of drugs and some pesticides (Moorefield, 1965; Sagers, 1977; Metcalf, 1977; Elliot, 1976; Ford, 1979) and will be essential if 'evolved plant defenses' are to be used as 'leads' for the synthesis of new crop protection agents. The

fact that volatile deterrents have not been exploited to date can be explained in terms of the lack of this approach, coupled with the fact that pesticide manufacturers' 'screens' are geared to the detection of straightforward 'kill' by candidate materials. This is astonishing because theoretically chemicals possessing these properties are the ideal crop protection agents, preventing damage from a broad range of phytophagous insects with no direct effects on natural enemies. These idealized properties might not always be achieved. Shoonhoven and Jermy (1977) for example, discussing the antifeedant activity of plant extracts, state that the 'taxonomic' spectrum of activity is surprisingly narrow. However, they cite the following exceptions - allyl arylesters, organotin (Ascher, 1979; Ascher *et al* 1978) and copper compounds, and azadaractin (Griffiths *et al*, 1978). Some of the objectives facing the synthetic chemist can already be defined.

- (I) Minimization of phytotoxicity.
- (II) Minimization of antifeedant/toxic effects on mammals.
- (III) Optimization of chemical stability.
- (IV) Achievement of relatively broad spectrum activity on phytophagous insects.
- (V) Systemic activity (more important than for pesticides because insects may leave treated foliage, survive and colonise new growth (Gill and Lewis, 1971)).

The insecticidal effects of plant toxins have been extensively catalogued (Jacobson, 1975) and some, such as derris and pyrethrum have achieved widespread use as insecticides (Metcalf, 1977). Again however, the full potential of this source of insecticide 'leads' can only be realized by a programme of testing and analogue synthesis. The successes achieved in the development of photostable pyrethroids endorses the value of such an approach (Elliot 1977, 1978; Ruscoe, 1979; 1980). Now,

close attention needs to be paid to the potential of other plant extracts that can be used against insects.

Since secondary plant chemicals evolved in response to the dual pressures of pest and disease attack, it is likely that some compounds possess dual effects against both kinds of organism. It is also noteworthy that recent knowledge relating to allelopathy may guide future developments in weed control (Putman and Duke, 1978).

Knowledge of the relationship between secondary plant chemicals and insect attack may contribute to the production of resistant crop cultivars. Where secondary chemicals are recognized as a major determinant of pest attack (Dunn, 1978) these chemicals could be used as initial indicators of resistance in candidate cultivars thereby reducing R and D times and some of the practical difficulties involved in screening (Lowe, 1978). Raman *et al* (1979) for example have recently suggested screening glycoalkaloid levels in potatoes as an indicator of likely aphid resistance. A more radical development would follow from new breeding techniques (Silcock and Burne, 1980) that enable plant breeders to introduce genes into crops from unrelated plant taxa opening up a virtually infinite gene pool on which to draw for sources of resistance.

For centuries, plants evolved in disturbed habitats have been grown as crops in monocultures increasing their 'apparency' to phytophagous insects. The discussion above leads to the conclusion that in future, secondary chemicals from 'naturally' apparent plants (e.g. tree crops) may be introduced to crop plants to provide appropriate protection from pests.

5.3.4 The Resistance Problem.

The discussion so far has been concerned with the prospect of achieving selectivity in crop protection with consequent benefits in

terms of avoiding problems of resurgence and 'new' pests. Attention is now focussed on the possibility of alleviating the pesticide resistance problem. The first important point to make is that resistance to intrinsically selective or selectively applied materials is likely to develop more slowly than to broad spectrum applications in circumstances where resistant individuals suffer heavy losses to the surviving natural enemies*(Proctor & Baranyovits, 1969; Knipling, 1979). Field counts often show greatly increased 'natural enemy : pest' ratios following applications of selective materials. (Gough and Wilkinson, 1979). Survivors of conventional broad spectrum sprays are able to build up rapidly in the absence of natural enemies and of potentially competitive phytophagous insects. The population is descended both from resistant individuals and those which were simply missed by the spray but subsequent applications of pesticide to control 'resurged' populations increase the overall level of resistance in the population.

An alternative approach is one of modifying pesticide usage to delay the onset of resistance. Spraying in relation to economic thresholds is part of this approach, already encompassed in the principles of integrated control. Much more controversial, have been the methods proposed explicitly for alleviation of the resistance problem, in particular the alternation or mixing of pesticides with negatively correlated modes of action. Conway and Comins (1979) have concluded from their resistance model that "resistance to both compounds A and B will occur more or less at the same time whether A is used in mixture with B or is alternated with B or is used subsequent to resistance developing to B." Like the conclusions of any model, this statement can only be interpreted in the light of the assumptions used in its construction, although they are supported by the experimental findings of Brown (1971). On the other hand Matthews (1979), attributes the

* Oppenoorth (1976), however has argued on biochemical grounds that specific compounds are more vulnerable to development of resistance than broad spectrum materials..

prolonged susceptibility of African cotton bollworms in part to alternating use of carbaryl and DDT, Conway and Comins (1979) emphasise that their conclusions "break down if the resistance gene is recessive or if resistance is polyfactorial, with each individual gene conferring no advantage". Unfortunately the genetic basis of resistance is usually elucidated a long time after a pesticide has failed to provide good control in the field so categorical recommendations on spray regimes cannot be made. There has also been lengthy debate over the question of high kill or low kill as a means of slowing resistance. Views on this remain polarised but it seems reasonably certain that sprays should ideally be applied at a sufficiently high rate to kill all heterozygote resistant individuals that come into contact with the spray (Wood, 1981). This effectively renders the gene recessive since heterozygotes have no selective advantage over the susceptible individuals and this has the effect of slowing resistance. (Taylor & Georgiou 1979). In practice however, it is virtually impossible to determine this ideal application rate, firstly because the tolerance factor possessed by the heterozygotes is unlikely to be known before spraying; secondly, because optimal strength spray deposits always decay to sub optimal concentrations; and thirdly because spray distributions are never uniform.

The question of optimising application rates is often raised once resistance is suspected in the field, but by then it may be too late. At first sight, it would seem logical to raise rates to maintain kill of heterozygotes (c.f. foregoing discussion) but by this stage important genetic changes are likely to have occurred making this the worst strategy. It appears that during the period of successful pesticide use, subtle genetic changes occur that

complement the effect of the resistance gene itself.

Resistance genes per se can be harmful to an organism leading in the absence of insecticide to a reduction in fitness (Bishop, 1980, 1981). Hence, the evolution of individuals that possess resistance without undue loss of fitness may involve the selection of 'modifier' genes to offset the major gene's harmful effect, (Bishop 1981). 'Modifier' genes may also lead to an increase in the level of intrinsic dominance of the resistance gene (Davidson, 1981) further accelerating selection rates. Secondary resistance mechanisms may also be selected which in combination with the primary mechanism could confer greatly increased levels of resistance. Hence once resistance reaches a detectable level in the field, drastic genetic changes are likely to have already occurred making choice of control strategy still more complicated. Furthermore, at this stage homozygous resistant individuals are likely to occur in small, though significant numbers so further high strength sprays may only serve to select and 'fix' these highly resistant insects in the population. After this phase, withdrawal of the pesticide will not usually cause the population to revert to the susceptible state (Brown, 1977).

There are additional means of slowing resistance that have been examined theoretically such as allowing pests to survive in unsprayed refugia (Georghiou and Taylor, 1977 a, b; Comins, 1977a; Wood 1981); spray mosaics (Curtis *et al* 1978); mass release of susceptible insects (Curtis 1981); use of short persistence insecticides (Georghiou 1972, Brown 1974); eradication of resistance 'foci' (Curtis 1981; Sawick, 1980) and spraying only as required. These proposals have not however been adopted because their value has not been demonstrated experimentally and because many of these strategies conflict with the goal of high level pest control.

In some parts of the world, workers have devised spray schedules to counter resistance simply on the basis of intuition. Sometimes this intuition may be ill founded as in the case of Thai vegetables where mixtures and alternations are widely used on an *ad hoc* basis. (A Kohli - *pers. comm*). In other cases intuitively devised programmes have been carefully planned and may in fact retard resistance. In Swaziland, for example acaricides have been applied to cotton on a rotation basis. The cotton growing area was divided into four sectors, each using a different acaricide at any one time (Duncombe, 1973; N. Morton *pers. comm*). A similar practice has been adopted for *Spodoptera littoralis* control in Egypt (Proctor *pers. comm*) and has further been proposed for anopheline mosquito control (Curtis *et al* 1978). These workers initiated such programmes in response to urgent local need, not to the desire for basic knowledge. It would seem prudent to seek this basic data through field experimentation as a matter of the utmost priority. Field experiments would need to be conducted on a large scale and over a long period of time with the result that they would be relatively costly. Nevertheless, work is justified on the grounds of the paramount importance of the resistance problem, highlighted by the cases of bollworms and *Spodoptera* spp. on cotton (Reynolds, 1977), *Plutella* spp. on vegetables, aphids on hops (Muir, 1979) and mites in glasshouses and on top fruit (Way, 1978).

5.4 PROSPECT FOR INTEGRATED CONTROL IN CEREALS

5.4.1 Contribution of the present studies to improved control of Cereal Aphids.

The present research was concerned with the basic ecology of cereal aphids but many of the findings on cereal aphid ecology may be relevant to the formulation of improved control strategies. The purpose of this section is to summarize the practical significance

of the results and to recommend further work where appropriate.

(i) Alate *R. padi* infesting early sown wheat seedlings in the autumn occurred in the highest numbers on the youngest plants. The individuals on these plants deposited more nymphs and survival was better than on the two older sowing (Section 5.4). This capacity of alate discrimination could be exploited in plant breeding. At present 'antibiosis' has been the main property sought in breeding programmes (e.g. Elamin, 1975, 1976; Lowe 1978) yet non-preference would clearly be a powerful means of preventing attack and consequent virus losses. Similarly, repellancy to alates would be a valuable property of crop protection chemicals used to control aphids. It is noteworthy that Horellou and Evans (1979) attribute the spectacular levels of BYDV control achieved with 'permethrin' partly to repellancy properties (Ruscoe 1977, 1979; Highwood, 1979) contributing to its superiority over the selective aphicide 'pirimicarb' (Evans, *pers. comm*).

These observations underline the merits of late autumn sowings to avoid the high rise of attack during September and October (Plumb, 1977); however other problems are created by this practice (see below). In any case there is a clear potential for the development of medium and short range forecasting schemes; the former being based on *R. padi* densities on summer crops; the latter involving aerial densities, proportion of viriliferous individuals and sowing date of particular crops.

(ii) Observations on the overwintering survival of aphids on potted cereals and supplementary experiments using artificial wind, showed that wind, especially gusty wind was a major factor accounting for the mortality of virginoparous aphids on cereals. Short periods of very low temperature (down to about -10°C) did not reduce aphid numbers

except in 1978-1979 when newly exposed aphids experienced low temperature and heavy dew in combination. Nevertheless, prolonged periods of cold were associated with a steady decline in aphid populations. *S. avenae* and *M. dirhodum* were both capable of reproduction during the winter months given short periods of favourable weather. *M. dirhodum* appeared to have a lower temperature threshold for reproduction than *S. avenae* resulting in substantial population build up in experimental shelters. Attempts to forecast survival of cereal aphids during winter should therefore take into account wind speed and gustiness, the intensity and duration of low temperature, the occurrence of dew and the duration of temperatures suitable for aphid reproduction.

(iii) Incidental field observations during winter indicated surprisingly high levels of parasite activity during winter and early spring (also found by G.P. Vickerman (*pers. comm*)). Short periods of warm, sunny weather were seemingly sufficient to induce searching. Parasite releases during spring might be a highly effective means of limiting the build up of large populations in the summer. At this time aphids are few compared to the rest of the year enabling high parasite : host ratios to be achieved. In addition search success at this time is probably high relative to the reproductive rates of the aphids, due to sub optimal plant suitability (Section 4.4) as well as to low temperatures. Aphid hosts and parasites are both easily reared and 'mummies' can be stored under refrigeration until needed. Against this is the sheer scale of a rearing programme necessary even for a small country such as the U.K. Nevertheless, this should not deter 'feasibility studies' from being carried out.

(iv) Syrphid predation had a substantial impact on *S. avenae* and *M. dirhodum* populations during summer. Although clearly 'ecologically effective', the impact came too late to be 'economically effective',

cereal yields being relatively insensitive to feeding losses after the milky ripe growth stage (Wratten *et al* 1979). Although this conclusion can probably be applied generally to the cereal aphid situation in the U.K. where crop 'heading' often marks the onset of attack, it may not hold in other parts of the world (e.g. France, S. Africa, Brasil, Argentina and Chile) where infestations build up over a much longer period (leaf feeding species such as *M. dirhodum* and *S. graminum* are more important in these countries). There, the pattern of attack suggests that predators and parasites could be highly 'economically effective' because the time lag between attack and natural enemy impact would be short compared to the total duration of the infestation. In these circumstances, farmers might find that a single spray of a selective material could ensure prolonged aphid control due to the impact of 'conserved' natural enemies whereas multiple sprays of a broad spectrum material would be required.

Vickerman and Sunderland (1977) showed that the broad spectrum material, dimethoate drastically reduced populations of Syrphidae and other natural enemies in cereals. Furthermore, studies by Carrillo (1973) and others (Zuniga and Suzuki, 1970) demonstrated rapid resurgence of cereal aphid populations following broad spectrum sprays - but not after application of the specific aphicide pirimicarb. If experiments can demonstrate prolonged control with pirimicarb and this obviates the need for multiple sprays, 'pirimicarb' would become cost-competitive to the farmer. At present, conventional broad spectrum materials are frequently preferred outside the U.K. on the grounds of low costs. In this context it is noteworthy that field populations of syrphid larvae have normally been unaffected by pirimicarb applications (Gough and Wilkinson, 1979) despite intrinsic toxicity of the material (Proctor and Baranyovits, 1969). This apparent contradiction can be

resolved on the basis of (a) minimal contact of spray with syrphid larvae resting low down the plants during daytime (Vickerman and Sunderland 1974) (b) short persistence of pirimicarb (i.e. spray deposits could fall to sublethal levels before syrphid larvae commence searching after dark) (c) low inherent toxicity of deposits compared to direct sprays (unknown at present). Pickin (1978) has shown that C.D.A. (controlled droplet application) in wheat results in spray deposition being largely confined to the uppermost parts of plants. The use of these methods should minimise lethal effects of broad spectrum materials on syrphid larvae resting low down the plants during daytime. Mortality of ground beetles might also be avoided (conventional sprays can be detrimental (Vickerman and Sunderland, 1977) due to excessive run off onto the soil (>80%; Courshee, 1960)). In some countries aerial CDA applications are commonplace giving the benefits of high work rates and water conservation as well as the possible bonus of sparing syrphid larvae. One adverse feature of failing to penetrate the crop canopy is the reduced effectiveness against leaf feeding species such as *R. padi*, *M. dirhodum* and *S. graminum*. Indeed it is possible that sprays applied in recent years to control *S. avenae* on the ears have had a more destructive effect on cereal aphid natural enemies than on *M. dirhodum*, possibly explaining the latter's considerable importance in 1979 (Schaefer *et al* 1979) when scarcity of natural enemies undoubtedly permitted very rapid aphid build up in favourable weather conditions.

Numerous factors other than pesticide usage potentially influence syrphid impact. The abundance of adults might easily be boosted by the presence of flowering weeds in the crop or close proximity to floral rich hedgerows. (Van Emden, 1965). There is little doubt, however that farmers currently place an overwhelming priority on

efficient weed control and large field size. Perhaps food sprays (Rabb *et al*, 1976) would be a more agronomically compatible means of increasing the attractiveness of crops to aphid predators.

(v) Aphid performance varies considerably in relation to growth stage of the crop. In the case of *S. avenae* plants become highly attractive to colonizing alates around the flowering - watery ripe stage (Sections 4.4 and 3.3.2.4) and high levels of suitability for reproduction are maintained into the milky ripe stage. (Watt, 1979). This phase of crop growth is also particularly sensitive to yield loss (George, 1974; Wratten *et al*, 1979) so control activities directed towards the prevention of direct feeding losses should be focused on these growth stages. Timely sprays are most easily achieved by C.D.A. methods (Matthews, 1977; 1979) being less restricted by weather and soil conditions (Linke, 1978; Adams, 1978).

Crop growth stage should also be an important component of forecasting schemes operating at the farmer level. It seems likely that aphid attack depends on crop growth stage and the aerial abundance of aphids (in turn a function of weather and population size). Inclusion of the 'growth stage factor' may well rectify the hitherto poor performance of Rothamsted suction trap data in predicting the timing and abundance of aphids in the field (Vickerman and Wratten, 1979).

The discriminatory abilities of aphids may also be exploitable by plant breeding. Non-preference resistance operating at the heading - watery ripe growth stages would be a powerful means of reducing aphid attack during the summer or winter wheat. As already mentioned most workers have been concerned with 'antibiosis resistance.

5.4.2 Relationship between cereal aphid control and other pest control activities.

It is clear from the foregoing discussion that considerable scope exists for improved control of cereal aphids but these proposals need to be placed firmly in perspective. Adoption of pest control measures is governed by a complex of factors of which 'technical merit' is just one. The farmer most readily accepts methods that are compatible with other pest, disease and weed control activities and in general with his crop production technology. To take one simple example, notably reduced levels of nitrogen fertilizer applications would probably reduce pest attack but this benefit would not compensate for the substantial loss in yield due to poor plant nutrition.

Table 77 illustrates the difficulty in devising 'all purpose' cultural control measures for animal pests of cereals in the U.K. Cultivation, crop rotation and sowing date can all be manipulated to suppress individual pests but often this will exacerbate problems from another pest. Thus early autumn sowings reduce wheat bulb fly, slug and leather jacket losses but increase the risk of attack by fruit fly and aphids. *R. padi* is a particularly important species of aphid in the autumn, partly due to its abundance at that time and partly because of its role as a vector of the 'severe' strain of barley yellow dwarf virus (B.Y.D.V.). Cultivation and crop rotation can be used to reduce wireworm, saddle gall midge and cereal leaf beetle problems but this is likely to increase wheat bulb fly losses.

TABLE 77 Influence of cultural practices on invertebrate pest problems in cereals (From Jones and Jones, 1974; Edwards, 1975 and Perrin, 1978).

	OPTIMUM CULTURAL PRACTICES		
	CULTIVATION	ROTATION	SOW DATE
Wheat bulb fly <i>Delia coarctata</i>	-	-	Early Autumn or Spring.
Frit fly <i>Oscinella frit</i>	-	?	Late Autumn
Wireworms <i>Agriotes</i> spp	+	+	?
Slugs <i>Agriolimax reticulatus</i>	+	-	Early Autumn or Spring
Saddle gall midge <i>Haplodiplosis equestris</i>	+	+	Autumn or Early Spring
Aphids <i>S. avenae</i> , <i>M. dirhodum</i> , <i>R. padi</i>	?	?	Late Autumn and Early Spring
Nematodes <i>Heterodera avenae</i>	?	-	?
Cereal Leaf Beetle <i>Oulema melanopa</i>	+	+	?
Cutworms <i>Agrotis</i> spp etc.	-	-	Early Autumn
Leatherjackets <i>Tipula</i> spp	+	-	Early Autumn

Individual farmers rarely face the full range of pests listed in Table 77 so, normally control is simplified. Wireworms, for example are chiefly a pest on newly cultivated land of which there is very little in the U.K.; Frit fly damage is mainly confined to oats and maize - both minor cereal crops in the U.K.; and saddle gall midge and cereal leaf beetle are relatively very localised, occasional pests (Jones and Jones, 1974).

Much more serious difficulties are presented by the adverse effect of disease and weed control on aphid problems.

(I) Fungicides may reduce the natural controls acting on cereal aphids (Potts and Vickerman, 1974) as a result of:

- a) Direct kill of predators (e.g. 'benomyl' is toxic to insects).
- b) Deprivation of fungal food for *Tachyporus* spp (Staphylinidae).

These predators have been regarded as important in reducing cereal aphid populations (Potts and Vickerman, 1974; Potts, 1977). They benefit from both fungal and aphid food for completion of their life cycle.

- c) Toxicity to cereal aphid pathogens (*Entomophthora* spp) (Zimmerman, 1976; Fritz, 1976; Wilding *et al*, 1979).

(II) Some fungicides, such as 'tridemorph' increase aphid reproductive rates (Sagenmuller, 1977) (others, such as 'benomyl' and 'carbendazim' are however toxic to cereal aphids (Vickerman 1977b)).

(III) Weed control eliminates refuges used by ground beetles (Speight and Lawton, 1976; Perrin, 1978; Vickerman and Wratten, 1979; Jones 1979a). Vickerman (1974) has noted that grass weed herbicide applications were associated with higher numbers of cereal aphids. He has also found more aphids on 'monoculture' spring barley than on crops undersown with grass legume mixtures (Vickerman, 1978).

5.4.3 Relationship between crop protection and the overall production system and crop economics.

The growing trend towards maximization of yield in cereals (Way, 1978) has produced important changes in the crop production system. A number of these changes are likely to have directly affected cereal aphid numbers. Furthermore, their dependence on increased pesticide inputs could (a) exacerbate the aphid problem (see above) and (b) lead to routine aphicide applications regardless of economic thresholds. Some of the effects of yield maximization on the status of pests can be summarised as follows:-

(I) High yielding cereal growing systems state that the crop needs to be drilled early enough to become well established before the winter. Whittles (1977) believes that "it is important to drill as early as possible (from mid-September)." He readily accepts that this creates problems but recommends the use of pesticides to protect the crop.

"This will inevitably produce disease problems in the winter, and these should be controlled with the appropriate fungicides, as soon as possible in the winter"

Early sowings also increase problems due to some aphids and weeds. Aphid infestations at this time are particularly alarming. *R. padi* is commonly the predominant species, capable of infecting the crop with the 'severe' strain of the 'B.Y.D.V.'. (Plumb, 1974). Virus losses can be considerable; Bayon and Ayrault (1977) recorded losses of 2 - 3.5 t/ha on winter barley in France. Effective control of these aphids is best achieved with 'permethrin' due to its repellent/antifeedant activity (Ruscoe, 1977; Highwood, 1979) and negative temperature - activity relationship (Horellou and Evans, 1979). However, conventional high volume applications of permethrin are likely

to be detrimental to beneficial soil fauna.

Weeds, like the crop are capable of vigorous growth before winter so control measures are essential in early sown crops (J. Elliot, 1978; Holroyd 1978).

(II) Low plant densities are a feature of high yielding wheat programmes - achieved at present by low seed rates and minimal tillering cultivars, but in the future also by means of plant growth regulators (Daybell, 1980; Seddon, 1980b). The overall trend is towards 'drilling to a stand', (Way 1978), an approach which depends on ensuring the survival of virtually every seed. Reduced plant densities may have both deleterious and beneficial effects.

Deleterious effects

- a) Less compensation for pest damage (Bardner and Fletcher, 1974).
- b) Possibility of increased pest attack. (Adesiyun (1978) found that on low density stands of cereals, frit fly densities were reduced on a 'per unit area' basis, but 'numbers per tiller' were increased.).
- c) Reduced ability to 'out compete' weeds.
- d) Less shearing action between leaves caused by wind increasing the overwintering survival of anholocyclic aphids. (Section 2.7.1.5).

Beneficial effects

- a) Slower development of disease epidemics (e.g. mildew and yellow rust (Burdon, 1978)).
- b) Virus transmission by aphids may be reduced. Aphids infesting low density cereal stands are less likely to be dislodged (Section 2.5.3.8) and less likely to relocate a suitable host plant. Against this is the possibility that dislodged aphids would, on average move a greater distance before finding a new plant, so increasing the spread of virus across the field. The net effect of plant density on virus damage is difficult to predict since

it depends not only on apterous survival and movement but also on rates of alate colonization.

(III) High yielding cereal systems involve the application of considerably increased quantities of nitrogen fertilizer. Aphid populations generally build up more rapidly under these conditions (Auclair, 1963; Van Emden *et al.*, 1969; Mackauer and Way, 1976) and the increasing world-wide importance of aphids has been attributed, in part to increased fertilizer useage (Baranyovits, 1973). More work needs to be done on cereal aphids but in a preliminary study, Verijken (1975, 1979) found that aphid performance in the laboratory was boosted when high levels on nitrogen were applied. This was not confirmed in the field but experiments conducted in the present research indicated a positive relationship between alate colonization and soluble nitrogen levels in wheat plants (Section 3.3.2.5.).

It should be clear from the foregoing discussion that control measures directed against cereal aphids need to be carefully integrated into a programme for the control of all cereal pests, diseases and weeds and moreover, should be compatible with the overall crop production system. Progress towards integrated control will depend on promising research findings, being further evaluated in large scale 'development trials' followed by farmer 'demonstrations'. At each stage, techniques should be evaluated on the basis of economic and practical suitability as well as technical merit. This approach will ensure that the resulting integrated control programme should be sufficiently acceptable to farmers to supercede pesticide dependance. Of course the question of 'economic suitability' is no simple matter. Many authors have recognised that the benefits of integrated control over pesticide reliance are felt over a wider geographical and time

scale than can be assessed at the individual farmer level. This broad approach has been adopted to compare optimal strategies for pesticide usage in relation to the risk of resistance development (e.g. for cattle ticks; Sutherst *et al* 1979; Sutherst and Comins, 1979; and for alfalfa weevils, Gutierrez *et al*, 1979)). Similarly, Hueth and Regev, (1974) regarded insect susceptibility to insecticides as a non-renewable resource that should be conserved by regional policies - a view that has been reaffirmed by Southwood (1979). If this broad view could be extended to include in an economic model the cost of treating 'secondary pests', 'resurgent populations', and the value of wildlife, the costs of alternative pest control strategies could be compared on a regional basis. At the farmer level, crop value is a major factor governing the approach to pest control.

'Insurance' applications of pesticides are much more likely to appear justified in the high value, intensive crops such as cotton, vegetables and top fruit than in extensive crops such as forage grass. In this context it is significant that cereals in western Europe have steadily been changing from an extensive to an intensive crop.

Way and Cammell (1979) have examined the economics of cereal growing in Europe and concluded that, to a large extent inflated grain prices are responsible for the spiralling agrochemical inputs. In view of the fact that cereal surpluses are anticipated in the near future, Way and Cammell (1979) recommend emphasis on 'optimal' rather than 'maximal' yields with greater emphasis on 'quality' and the use of insecticides in relation to forecasting and crop monitoring. A particularly disturbing aspect of cereal growing economics highlighted by Way and Cammell (1979) is that "the farm price of the cereal crop tends to be adjusted to cover the cost of inputs which encourages the advocates of high yields regardless of the cost". Under these circumstances cost-benefit analyses are almost bound to favour heavy

pesticide usage. The first step towards integrated control must be a return to realistic pricing of the crop enabling alternative control methods to be selected on the basis of actual cost effectiveness.

5.5 RECOMMENDATIONS

The technical recommendations listed below are based on the assumption that there will be a return to realistic cereal pricing, but that pesticides will maintain a prominent place in cereal growing. Realistic pricing could lead to some reduction in inputs but in this context, pesticides would probably be the last elements to be withdrawn unless spectacular developments in plant breeding occur. This is because their use can be justified on the grounds that energy costs of pesticides are small compared to the energy returns they provide (increased yield) (Green, 1979). Moreover, their cost can be so low compared to their potential benefits (Southwood, 1979) that their use is almost bound to be indiscriminate. If a return to realistic pricing was coupled with substantial increases in fossil fuel prices, cereal production technology would undoubtedly change but because 85% of the total energy consumption in agriculture is in the form of fuel and fertilizers (Green, 1979), these elements are likely to be the prime areas for economy. Pesticides, on the other hand are likely to be used more economically in future due to improved application techniques such as electrostatic (Matthews, 1979) and electrodynamic (Coffee, 1979) spraying.

Recommendations towards integrated control are divided into two phases: the first being attainable with existing technology; the second depending on further technical advances. Foremost among these will be the development of new cultivars capable of vigorous growth during autumn, obviating the need to drill early to maximise yield.

5.5.1 Progress towards integrated control in the short term

Farmer recommendations.

1. Apply summer aphicides with careful attention to economic thresholds (George and Gair, 1980) and the precise growth stage of the crop (Section 4.4: Wratten *et al*, 1979).
2. Use selective aphicides to control spring and summer aphid populations except rarely where non-aphid pests need to be controlled (e.g. saddle gall midge and cereal leaf beetle etc). At present, there is no simple alternative to conventional insecticides for these pests.
3. Use selective aphicides to control autumn attacks by *R. padi* (at present pyrethroids are likely to come into use (Horellou and Evans, 1979)).
4. Avoid prophylactic treatments. Increase the practicality of eradicant sprays by:
 - (a) using tramlines (improving access to the crop)
 - (b) paying attention to warnings in the farming press:
 - (c) using C.D.A. methods of application to increase work rates and the number of days suitable for spraying (Adams, 1978) (also desirable to minimise environmental pollution (RCEP, 1979)).
5. Direct drill to reduce wheat bulb fly attack (Edwards, 1975).

Research recommendations

1. Assess the impact of a wide range of herbicides, fungicides, insecticides and plant growth regulators used in cereals on beneficial organisms by means of laboratory and field studies.
2. Monitor potential pests (e.g. mites, thrips, saddle gall midge) that may become important due to widespread pesticide usage. Bardner *et al* (1979) reported larger thrip populations on plots treated with fonofos granules.

3. Monitor pesticide resistance before control failures are reported.
4. Evaluate the effects on aphids of cultivar diversification employed for disease control (Barrett, 1978; Wolfe, 1978; Burdon, 1978; Perrin, 1978; Priestley, 1979).
5. Provide information on aphid resistance in the N.I.A.B. catalogue of recommended cereal varieties, (detailed information on disease resistance is already included).
6. Screen existing cereal varieties for resistance to pests and diseases in the autumn. (Seedling resistance to aphids has already been tested by Elamin (1975); Comeau and Dubec (1978) have screened out varieties for virus tolerance and a virus tolerant cultivar of barley (c.v. Corade) has recently been bred in the U.K. (Seddon, 1980a)).
7. Develop improved methods of slug control. Slugs cause serious damage on heavy soils and their numbers are increased by 'direct drilling' (Edwards, 1975). Methods requiring further evaluation include:
 - (a) seed treatments with molluscicides or repellents (Scott *et al*, 1977).
 - (b) 'in row' applications of molluscicide granules. This treatment would probably need to be restricted to parts of the field that were particularly at risk due to the potential high cost.

5.5.2 Progress towards integrated control in the long term.

1. Develop new varieties capable of vigorous growth in October.

2. Drill late to escape disease and aphid attacks (Plumb, 1977).
3. Test the economic and technical feasibility of spring releases of parasites for biological control of cereal aphids. (Summer parasite releases have already proved partially successful in the control of sorghum aphids (Starks *et al*, 1976)).
4. Develop aphid resistant cultivars. The following mechanisms of resistance would all be relevant to crop protection but these need to be tested for both seedling and post-flowering stages.
 - (a) Antibiosis - slowing population development.
 - (b) Non-preference-reducing the numbers of initial colonists.
 - (c) Virus tolerance.

A number of workers have noted varietal differences in levels of aphid attack. Lloyd (1979), for example noted that in 1977 "c.v. Kador consistantly received very few colonists - the same occurred in 1978 with c.v. Sentry." Further work is needed to check the reproducibility of these observations.*

5. Develop controlled droplet application (C.D.A.) methods in cereals. The advantages of these techniques are being increasingly recognised for herbicides (Linke, 1978) although "published work with insecticides and fungicides is still rather limited" (Linke, 1978). Pickin (1978) reported good control of *S. avenae* by C.D.A. using 'pirimicarb', but further work using tractor mounted equipment is required. There is little doubt that electrodynamic methods of application (Coffee, 1979) offer the greatest potential benefits, in terms of efficacy, economy, versitility, simplicity, safety and lack of contamination.
6. Establish economic thresholds for barley yellow dwarf virus (B.Y.D.V.)

* Aphid resistance in cv Kador has recently been confirmed by Starks *et al* (1980) and Lowe (1980) and H.F. Van Emden has suggested that ancient wheat varieties provide a source of resistance genes (Long, 1980).

damage. Decide whether the superior control of vectors attainable with permethrin compared with pirimicarb is worthwhile in terms of yield considering its potentially harmful effects on natural enemies.

7. Continue pursuit of short term objectives.

5.6 EPILOGUE

This chapter has set out to draw together conclusions of the present research, relate them to existing knowledge and propose recommendations. These have been formulated against a background of rapid change in the technology of cereal production and an awareness of the overall objectives of integrated pest control in agriculture. The discussion is perhaps best concluded by considering the gap between the 'potential' for integrated control and its realisation in practice; and the capability of research to help bridge the gap.

Numerous excellent text books pay homage to the potential of integrated control and its widespread acceptance in 'academic' and 'official' sectors. Crop protection in some countries adheres closely to its principles but this has generally been the result of 'bad experiences' rather than 'enlightened foresight.' Today, the risks of overreliance on chemical control are as serious as they have ever been. Synthetic pyrethroids have given a new 'lease of life' to chemical control and although they represent an important 'step forward' in terms of efficacy and mammalian safety, they will rapidly lead to the emergence of resistant strains. Problems created by the aggravation of secondary pests already limit the use of pyrethroids in some situations so they have not displaced the need for integrated pest control even in the short term.

In the U.K., farmers, advisors and research workers have a more

'enlightened' attitude than in most parts of the world yet 'the pesticide treadmill' has recently got underway in cereals. This clearly underlines the attraction of pesticides in terms of convenience and compatibility with the crop production system. This fact should never be overlooked by research workers and there is no room for prejudice against pesticides. Furthermore, they should not be regarded as any less 'scientifically respectable' than the so called 'biological methods' of pest suppression. Improved management of pesticide usage is probably the most important objective of crop protection research in the future. Placement and timing of applications may be manipulated to improve the survival of natural enemies; other management strategies may help to retard the development of pesticide resistance. Unfortunately, these 'key research areas' are not well supported by industry at present and little interest is apparent in the public sector. Nevertheless, it is the approach of the experimental ecologist that will be most useful in realizing these objectives.

One of the intentions of this chapter has been to highlight the overwhelming need for pest control measures to be integrated, not only with each other but also with disease and weed control activities and the overall crop production system. There is a clear need for multidisciplinary teams of workers to cooperate in developing compatible methods for use in agriculture. This has already happened in the U.K. in the case of the A.D.A.S./M.A.F.F. integrated control programme for orchards but this approach needs to be much more widespread on other crops. The maintenance of a high scientific standards in agricultural research is absolutely vital but the fragmented nature of research funding and the demands of scientific publication can often be antagonistic to collaboration between workers.

Research on the cereal aphid problem in the U.K. reflects this

picture of high scientific standards but an absence of overall direction. It is unfortunate that there is no central body responsible for acting on recommendations as presented in this thesis. There seems little doubt that pesticides will become increasingly used in cereals despite the growth in research knowledge needed to support a move towards integrated control. It is likely, however that if chemical control's cost effectiveness diminishes, due to realistic pricing, resistance etc., there will be an inescapable need for an integrated control approach in the future and this knowledge will then prove useful.

SUMMARY

SUMMARY

1. Cereal aphids (mainly *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi* are pests of increasing importance in the U.K. and other temperate countries. Until recently, investigations into their field ecology have been predominantly 'descriptive' surveys concerned with the patterns of population build up and decline on crops in the summer.
2. Attempts to relate these data to the aerial abundance of aphids, the numbers of natural enemies, weather, crop growth stage and various components of farmer practice have indicated some of the possible factors influencing aphid abundance, but their relative importance in quantitative terms has remained poorly understood.
3. In nature, a large number of biological and environmental factors act upon populations but because these often occur simultaneously, their individual effects are best assessed by the use of experimental methods in the field. In the present research, this approach has been applied to the study of several 'key' aspects of cereal aphid ecology that have been relatively poorly understood, namely overwintering, natural enemy impact and the effects of crop growth stage on aphid populations.
4. During two winters, replicated experiments were carried out at Silwood Park, Ascot, U.K. using virginoparous cereal aphids artificially infested onto potted wheat seedlings placed in the field. Large, well ventilated shelters were used to protect some populations from rain alone, or wind and rain combined. Physical barriers and insecticidal exclusion methods protected some populations from ground predators. By

comparing the size of these differently treated populations at frequent intervals it was possible to assess the relative importance of various mortality factors.

In addition, by relating the changes in abundance between counts to meteorological data, it was possible to indicate weather factors that influenced, or equally important did not influence aphid numbers.

5. During the first winter (25/11/77 - 20/3/78) three 'treatments' were compared using *S. avenae* and *M. dirhodum*; 'exposed', 'wind and rain protected' and 'wind, rain and ground predator protected'.

5a. No consistent differences were found between the latter two treatments suggesting that predation was a negligible cause of mortality. Before extending this conclusion to the field, it needs to be stressed first that the impact of predators could be greater in other locations and secondly that their possible importance before late November and after late March was untested in the experiment. Other recent studies have established that ground beetle predation in the spring can reduce the size of summer populations in certain habitats.

5b. Exposed populations of *S. avenae* and *M. dirhodum* declined steadily during the winter, losses being associated especially with high winds. Survivors were often found in sheltered niches on the plant such as leaf whorls, leaf bases and beside transverse folds in leaves bent over by the wind. Populations protected from wind and rain survived significantly ($p < .05$) better than exposed ones; *S. avenae* declined, but at a much slower rate while *M. dirhodum* actually increased during the winter. Surprisingly, periods of potentially adverse low temperature (sub zero °C) did not cause sudden losses of either species.

5c. Very short periods (i.e. hours) of warm weather in mid winter

enabled reproduction to occur in both species especially *M. dirhodum*. On these occasions, daily mean temperatures were commonly lower than 5°C, the often used approximate temperature threshold for temperate insect multiplication. Clearly the use of this threshold in a cereal aphid population model would be misleading, unless a reduced time scale was used (e.g. half hourly mean temperatures).

It is concluded that the ability to reproduce at relatively low temperatures contributes significantly to the overall capability of the aphids to survive through the winter because it can help offset winter mortality.

5d. Short periods of warm weather were also important to parasite activity. Adult parasites (*Aphidius* spp.) were observed searching plants for aphids throughout the winter and parasitism was an important cause of mortality in March.

6. From this first season of overwintering studies, it seemed that wind and rain was a major cause of overwintering mortality and that cold alone did not have an immediate lethal effect. The main objectives of the next season's work using *S. avenae* only were first, to investigate the separate effects of wind and rain, and secondly to study further the steady decline in *S. avenae* numbers that had been observed on wind and rain protected plants. The latter was relevant because in the 1977 - 1978 experiment, three main factors could have caused the steady decline, namely competition from *M. dirhodum* which overran the plants originally intended for *S. avenae*; wind, which was reduced - not eliminated by the shelters; and possibly deleterious chronic rather than acute effects of temperature.

In an experiment undertaken from 27/11/79 with *S. avenae* significant

improvements were made to the shelter design and experimental layout, and the aphids were counted more frequently.

6a. 'Exposed' and 'rain protected' populations both declined at a similar steady rate during the winter. Losses were notably high immediately after *S. avenae* introduction to the field, probably because some occupied exposed feeding sites from which they could readily be dislodged by wind. Populations protected from rain and wind survived significantly ($p < .05$) better. Clearly, wind was a prime factor governing the survival of virginoparous *S. avenae*.

6b. Sometimes dead aphids were found on the plants after periods of severe cold (e.g. below -10°C) but these never outnumbered those surviving. Moreover the rate of population decline was not notably higher during harsh periods compared with relatively mild spells. This evidence indicates that temperatures as low as -10°C do not have what could be termed a 'catastrophic' effect on *S. avenae* populations. Nevertheless, the fact that populations protected from both wind and rain did decline during the winter requires explanation. Low temperature was the only obvious potential cause of mortality acting on these populations (the possible role of ground based predators (December - March) had been discounted by the previous experiment). It was proposed, therefore that temperature might have contributed to the gradual decline in *S. avenae* population by acting in subtle ways, e.g. (i) by preventing reproduction that would otherwise enable aphids to offset losses from other causes; (ii) by preventing feeding, leading to starvation or dessication; (iii) by damaging host plants forcing aphids to search for new feeding sites; and (iv) by directly killing aphids involving the severity and also duration of freezing temperatures.

7. During the 1977 - 1978 winter, natural infestations of *R. padi* and *S. avenae* were monitored on winter wheat. This involved frequent observations of individual colonies on marked seedlings.

7a. The results supported the conclusions of shelter experiments already discussed. That is, high wind was often associated with sudden aphid losses, rain was unimportant and low temperature had no clear acute adverse effect. It was also found that both species were more abundant on young plants (Feekes g.s.1) than on older ones (Feekes g.s.3).

7b. In addition, these studies provided a picture of population development on a colony by colony basis. First, this enabled some components of overall 'performance' (e.g. alate resting times, number of nymphs deposited per plant, nymphal rates of development, nymphal survival etc.), to be estimated. Secondly, it highlighted the considerable variation in 'performance' that exists between colonies in the field.

8. In order to study the relationship between wind and overwintering mortality in greater depth, a range of simple tests were carried out mostly using artificial wind and artificially infested pots of seedlings.

8a. The proportion of *S. avenae* dislodged increased with increased windspeed but also if the wind was gusty rather than steady, if the aphids were large rather than small and if they were feeding on terminal rather than basal parts of the plants. This evidence indicated that the shearing action between leaves moving in the wind dislodges more aphids than the physical impact of wind itself.

8b. The knowledge that terminal feeding renders an aphid more susceptible to wind action helped to explain why in a separate experiment, *S. avenae*

(which feeds terminally) suffered heavier losses than *M. dirhodum* and *R. padi* (which feed basally). It also helped to explain why in field shelter experiments, *S. avenae* survived poorly during the winter compared to *M. dirhodum* (5b. and 5c. above).

8c. Further simple experiments investigated the possibility that prolonged wind might kill aphids by enhancing the chilling effect of low temperature. In the first experiment, no aphids died until they had been exposed to freezing natural winds for more than 1 - 2 hours. The second experiment indicated that wind in combination with low temperature was potentially important because it could directly damage plants forcing aphids to move off in search of new feeding sites.

9. Other 'chronic' means by which wind could possibly increase mortality include (i) restriction of aphids to sheltered niches that may be nutritionally inadequate and (ii) enhancing dessication especially if low temperature prevented feeding. Neither of these possibilities were tested experimentally.

10. Field studies on summer populations were concerned with the relative importance of various factors determining the abundance of cereal aphids.

10a. In 1977 a replicated experiment was set up to obtain weekly measurements of a large number of these factors, namely immigration, crop suitability, parasitism, disease, mortality due to ground based predators, mortality due to aerial predators, and wind and rain. Unfortunately, the experiment was not a success due to the use of 'introduced' plants, disturbance of artificially infested aphids during transfer to the field, small plot size and the low densities of aphids and natural enemies in 1977. Ways in which these problems can be overcome are discussed and it is proposed that applied appropriately the approach could have widespread application

in the field study of insect pest ecology.

11. An experiment from late May to August 1978 investigated the effects of fewer factors using large field plots of winter wheat. Physical and insecticidal exclusion methods were used to compare three main treatments on large square 'main' plots; namely, 'control', 'no ground predators' and 'no predators' (= ground and aerial predators). These main treatments were replicated three times and within each main plot there were three sowings (29/9/77, 10/3/78 and 11/5/78) giving three distinct growth stages making nine treatments in total.

11a. Comparison between the sizes of aphid populations on the nine treatments showed that ground based natural enemies had no effect on aphid numbers whereas syrphid flies caused *S. avenae* and *M. dirhodum* populations to collapse, pre-empting a later fall induced by deteriorating plant quality. Syrphid predation also resulted in *M. dirhodum* peak populations being reduced. The suddenness and magnitude of the Syrphid induced population crash was surprising especially considering the small numbers of eggs and larvae found in daytime searches but this may be explained in terms of (i) well known difficulties involved in estimating Syrphid populations, (ii) the dramatic increase in Syrphid voracity that follows the final larval moult coupled with (iii) the synchronous development of the Syrphid population.

Although the experiment provided a clear, quantitative demonstration of Syrphid impact, this probably came too late to reduce yield loss.

11b. The exact nature of the plant induced 'crash' was not determined by the experiment although notable numbers of fourth instar alates occurred only on plots that had been kept free of all predators (NB this only applied to *S. avenae* on sowdate 1., very few fourth instar alate *M. dirhodum* were recorded).

11c. Similar patterns of aphid colonization, build up and decline occurred on the three sowings but the timing of these phases was more closely linked to crop growth stage than to calendar time, especially in *S. avenae*. Thus, as the summer progressed, each sowing in turn became preferred demonstrating a powerful influence of crop growth stage on aphid populations.

12. Supplementary experiments were carried out to investigate the influence of crop growth stage in greater depth. They were especially concerned with its effect on colonisation by alates. They mainly involved the use of rows of test wheat plants representing a wide range of growth stages, placed outdoors exposed to natural immigration by alate aphids.

12a. *M. dirhodum* consistently deposited far more nymphs on 'pre-heading' plants compared with older ones whereas *S. avenae* preferred 'headed' plants. Even within 'headed' plants, these alates clearly discriminated between different growth stages. 'Flowering' - 'watery ripe' plants were the most attractive growth stages.

12b. The plant physiological basis of crop suitability was not investigated in great detail. Assays of soluble nitrogen, soluble carbohydrate and water content were mainly carried out to throw light on the causes of plant induced population crashes. The period of aphid colonization was only covered in the case of the intermediate sowing where high levels of soluble nitrogen in the ear coincided with arrival exceptional numbers of alates and deposition of first instar *S. avenae*. The assays failed to give a clear indication of the causes of the plant induced population crash.

12c. Although the innate preference for particular crop growth stages

was probably exaggerated in the experiment due to easy choice, it is proposed that crop growth stage is a major factor determining colonization in the field.

13. A critical appraisal is made of the practical impact of the integrated control concept in agriculture and possible future developments in crop protection discussed (the practical merits of chemical control, selective use of pesticides, secondary plant chemical derivatives for use in crop protection, solutions to the pesticide resistance problem).

Against this background, ways in which cereal aphid control might be improved are suggested, based on recent research findings, especially those contained in the present thesis. Because aphid control cannot be considered separately from other pest, disease and weed control activities, these suggestions are presented in the form of recommendations for integrated control of all kinds of pest. A series of short term recommendations emphasising the 'rational' use and selection of pesticides are considered to be practical using currently available technology. Implementation of long term proposals depends on certain technical advances, especially in the field of plant breeding.

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PLATE 1 Shelter used to protect pots of infested wheat seedlings from wind and rain: Winter 1978-1979



PLATE 2 Experimental layout: shelter experiments 1978-1979



PLATE 3 Pot of wheat seedlings sheltered from wind and rain
covered by drifted snow in January 1979



PLATE 4 Polythene barriers used to exclude ground predators from plots of winter wheat

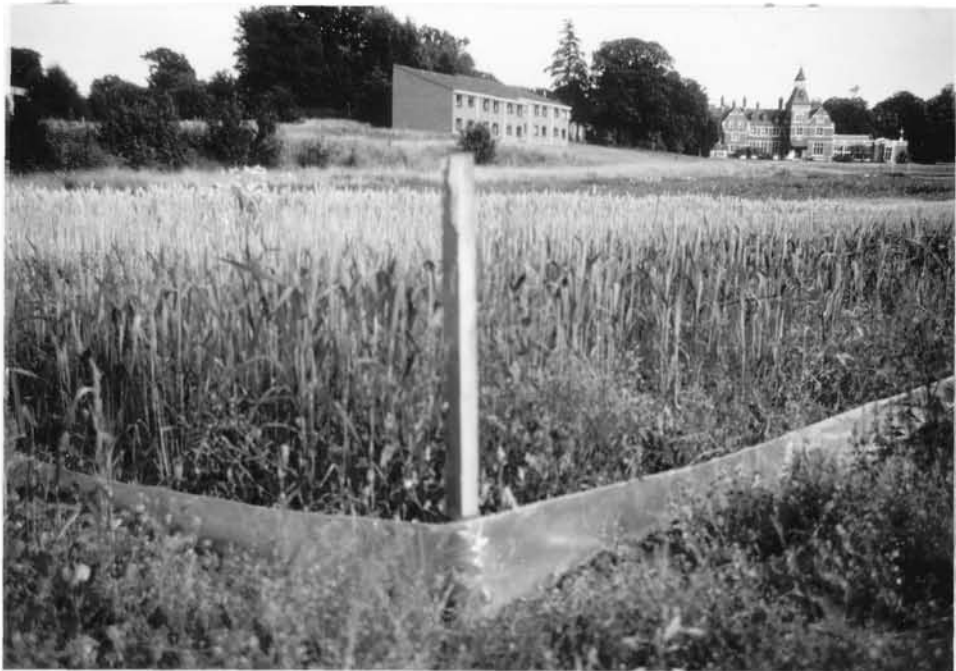


PLATE 5 General view of the experimental site used to study the effect of predators and crop sow date on aphid populations



GENSTAT V MARK 4.01
(C)1977 LAWES AGRICULTURAL TRUST (ROTHAMSTED EXPERIMENTAL STATION)

```

1 #REFE#INIA
2          ##WINTER 1977-78 S.AVENAE ##
3
4 #UNIT#612
5 #NAME#PHOTLEV=EXPOSED,NOWINRAI,NOWINPRE
6 #FACT#ROWS=3=4(1...3)
7 #FACT#COLS=4=(1...4)3
8 #FACT#SHELTER#PHOTLEV=1,1,1,1,2,3,3,2,3,2,2,3
9 #DEAD/S#COUNT,COUNT10
10 #PRIN/P#ROWS,COLS,SHELTER,COUNT10,COUNT10.0
11 #CALC#COUNT=LOG(COUNT+1)
12 #CALC#COUNT10=LOG(COUNT10)
13 #LOC#COLS/ROWS
14 #TREA#SHELTER
15 #COVA#COUNT10
16 #ANOVA#COUNT
17 #UN#

```

```

COUNT 0 MNMINMAX      20.1667      10.0000      65.0000      12 VALUES      0 MISSING **
COUNT10 0 MNMINMAX      39.0000      16.0000     102.0000      12 VALUES      0 MISSING

```

ROWS	COLS	SHELTER	COUNT10	COUNT
1	1	EXPOSED	31	10
1	2	EXPOSED	25	12
1	3	EXPOSED	45	17
1	4	EXPOSED	41	13
2	1	NOWINRAI	24	11
2	2	NOWINPRE	38	17
2	3	NOWINPRE	16	19
2	4	NOWINRAI	37	31
3	1	NOWINPRE	31	10
3	2	NOWINRAI	42	13
3	3	NOWINRAI	36	16
3	4	NOWINPRE	102	65

APPENDIX 1 : Computer programme used for analysis of variance on total aphid numbers - overwintering experiment 1977 - 78.

GENSTAT V MARK 4.01
(C)1977 LAWES AGRICULTURAL TRUST (ROTHAMSTED EXPERIMENTAL STATION)

```

1 #EFFECT#INTA
2
3 #INTER 1977-78 M.DIRHODUM ##
4 #INTERVAL ANALYSIS ##
5 #OCCASION 1 ##
6 #UNIT#12
7 #NAME#PROTLEV=EXPOSED,NOWINRAI,NOWINPRE
8 #FACT#ROWS=3=4(1...3)
9 #FACT#COLS=4=(1...4)3
10 #FACT#SHELTER#PROTLEV=1,1,1,1,2,3,3,2,3,2,2,3
11 #EAD/S#COUNT1,COUNT2
12 #CALC#COUNT3=LOG(COUNT1+1)
13 #CALC#COUNT4=LOG(COUNT2+1)
14 #CALC#COUNT5=COUNT3-COUNT4
15 #PRINT#ROWS,COLS,SHELTER,COUNT1,COUNT3,COUNT2,COUNT4,COUNT5$10,3
16 #LOC#COLS/ROWS
17 #TREAT#SHELTER
18 #ANOVA#COUNTS
19 #END#

```

```

COUNT1 0 MINMAX 46.3333 13.0000 126.0000 12 VALUES 0 MISSING
COUNT2 0 MINMAX 28.8333 8.0000 74.0000 12 VALUES 0 MISSING

```

ROWS	COLS	SHELTER	COUNT1	COUNT3	COUNT2	COUNT4	COUNT5
1	1	EXPOSED	14.000	2.639	8.000	2.147	0.442
1	2	EXPOSED	35.000	3.584	20.000	3.045	0.539
1	3	EXPOSED	37.000	3.526	18.000	2.944	0.582
1	4	EXPOSED	32.000	3.497	27.000	3.332	0.164
2	1	NOWINRAI	54.000	4.078	78.000	4.359	-0.272
2	2	NOWINPRE	33.000	3.526	25.000	3.258	0.268
2	3	NOWINPRE	44.000	3.784	17.000	2.890	0.894
2	4	NOWINRAI	51.000	3.951	29.000	3.401	0.550
3	1	NOWINPRE	54.000	4.007	34.000	3.555	0.452
3	2	NOWINRAI	33.000	3.526	14.000	2.704	0.814
3	3	NOWINRAI	45.000	3.929	16.000	2.833	0.995
3	4	NOWINPRE	125.000	4.844	60.000	4.111	0.713

APPENDIX 2: Computer programme used for analysis of variance on rates of change between counts - overwintering experiment 1977-78

GENSTAT V MARK 4.01
(C)1977 LAWES AGRICULTURAL TRUST (ROTHAMSTED EXPERIMENTAL STATION)

```

1  *DEFINITIONS
2
3
4  *UNIT#515
5  *NAME#PROTLEV=EXPOSED,NORAIN,NOWINRAI
6  *FACT#ROWS*3=5(1...3)
7  *COLS*5=(1...5)3
8  *SHELTER*PROTLEV=2,1,3,2,1,1,3,2,3,2,3,2,1,1,3
9  *READ/S#COUNT1,COUNT2
10 *CALC#COUNT3=LOG(COUNT1+1)
11 *CALC#COUNT4=LOG(COUNT2+1)
12 *CALC#COUNT5=COUNT3-COUNT4
13 *PRINT#ROWS,COLS,SHELTER,COUNT1,COUNT3,COUNT2,COUNT4,COUNT5*10.3
14 *!LOC#COLS/ROWS
15 *TREA#SHELTER
16 *ANOVA#COUNT4,COUNT5
17 *RUN#

```

```

COUNT1 0  MNMINMAX      30.4667      13.0000      49.0000      15  VALUES      0 MISSING
COUNT2 0  MNMINMAX      29.6667      15.0000      53.0000      15  VALUES      0 MISSING

```

ROWS	COLS	SHELTER	COUNT1	COUNT3	COUNT2	COUNT4	COUNT5
1	1	NORAIN	32.000	3.497	20.000	3.045	0.452
1	2	EXPOSED	24.000	3.367	19.000	2.906	0.372
1	3	NOWINRAI	34.000	3.555	30.000	3.611	-0.056
1	4	NORAIN	35.000	3.584	33.000	3.526	0.057
1	5	EXPOSED	23.000	3.178	22.000	3.175	0.043
2	1	EXPOSED	13.000	2.639	15.000	2.773	-0.134
2	2	NOWINRAI	43.000	3.912	53.000	3.989	-0.077
2	3	NORAIN	30.000	3.011	41.000	3.738	-0.127
2	4	NOWINRAI	23.000	3.367	38.000	3.664	-0.296
2	5	NORAIN	24.000	3.367	24.000	3.219	0.145
3	1	NOWINRAI	45.000	3.829	42.000	3.761	0.067
3	2	NORAIN	37.000	3.638	30.000	3.611	0.027
3	3	EXPOSED	18.000	2.944	18.000	2.944	0.000
3	4	EXPOSED	21.000	3.091	15.000	2.773	0.318
3	5	NOWINRAI	30.000	3.434	33.000	3.526	-0.092

APPENDIX 3 : Computer programme used for analysis of variance on (a) total aphid numbers and (b) rates of change between counts - overwintering experiment 1978 - 79.

APPENDIX 4 : Computer programme used to perform ANOVA on aphid counts -
summer 1978 experiment.

```

1  "PEFE"SUMMER
2  "%%DIRHODUM 13/6/78 COMPARISON WITH SPRAYED ZONE"
3
4  "C1=FIRSTINSTARS"
5  "C2=SECOND INSTARS"
6  "C3=THIRD INSTARS"
7  "C4=FOURTH INSTAR APTERA"
8  "C5=FOURTH INSTAR ALATES"
9  "C6=ADULT APTERA"
10 "C7=ADULT ALATES"
11 "C8=TOTAL APHIDS/100 TILLERS"
12 "C9=RATIO OF FIRST INSTARS/ TOTAL APHIDS"
13 "C10=RATIO OF FOURTH ALATES/TOTAL FOURTHS"
14 "C11=RATIO OF ALATES/TOTAL APHIDS"
15 "C20=LOG (TOTAL APHIDS+1) PER 100 TILLERS"
16 "C21=LOG (TOTAL ALATES+1) PER 100 TILLERS"
17 "C22=ARCSIN PROPORTION OF FIRSTS"
18 "C23=ARCSIN PROPORTION OF ALATE FOURTHS"
19 "C24=ARCSIN PROPORTION OF ALATES/TOTAL"
20 "C32=LOG(TOTAL APHIDS+1) PERIMETER SQUARED"
21 "C33=LOG(ALATES+1) PER 1 METRE SQUARED"
22 "C40 =LOG FIRSTS/100 TILLERS"
23 "C41=NO. FIRSTS/ METRE SQUARED"
24 "C42=LOG FIRSTS/METRE SQUARED"
25 "UNIT"527
26 "SCAL"51=5.30
27 "SCAL"52=3.82
28 "SCAL"53=3.42
29 "NAME"ILEV=CONTROL,BUGHPRED,BUGPRED
30 "FACT"COLSS3=(3(1...3))3
31 "FACT"ROWSS3=9(1...3)
32 "FACT"SONDATS3=1,2,3,3,1,2,3,2,1,1,2,3,2,1,3,3,1,2,2,1,3,2,3,1
33 "FACT"INSSILEV=3(1,2,3,3,1,2,2,3,1)
34 "FACT"SUBPS3=(1...3)9
35 "HEAD/S"C1,C2,C3,C4,C5,C6,C7
36 "BLOCK"(ROWS*COLS)/SUBP
37 "TREA"INS+SONDAT
38 "CALC"C8=C1+C2+C3+C4+C5+C6+C7
39 "CALC/ZDZ=ZERO"C9=C1/C8
40 "CALC/ZDZ=ZERO"C10=C5/(C4+C5)
41 "CALC/ZDZ=ZERO"C11=C7/C9
42 "CALC"C20=LOG(C8+1)
43 "CALC"C21=LOG(C7+1)
44 "REST"C8SSONDAT=1
45 "CALC"C30=C8*51
46 "REST"C8SSONDAT=2
47 "CALC"C30=C8*52
48 "REST"C8SSONDAT=3
49 "CALC"C30=C8*53
50 "REST"C8
51 "REST"C7SSONDAT=1
52 "CALC"C31=C7*51
53 "REST"C7SSONDAT=2
54 "CALC"C31=C7*52
55 "REST"C7SSONDAT=3
56 "CALC"C31=C7*53
57 "REST"C7
58 "REST"C1SSONDAT1
59 "CALC"C41=C1*51
60 "REST"C1SSONDAT2
61 "CALC"C41=C1*52
62 "REST"C1SSONDAT3
63 "CALC"C41=C1*53
64 "REST"C1
65 "CALC"C32=LOG(C30+1)
66 "CALC"C33=LOG(C31+1)
67 "CALC"C40=LOG(C1+1)
68 "CALC"C42=LOG(C41+1)
69 "PRIN/P"ROWS,COLS,SUBP,INS,SONDAT,C1,C2,C3,C4,C5,C6,C7,C8S9,0
70 "PRIN/P"INS,SONDAT,C8,C20,C30,C32,C7,C21,C31,C33S10,3
71 "PRIN/P"INS,SONDAT,C1,C40,C41,C42,C9S10,3
72 "PRIN/P"INS,SONDAT,C10,C11S10,3
73 "ANOVA"C20,C32,C21,C33,C11,C40,C42,C9,C10
74 "RUN"

```

APPENDIX 5 : Computer programme used to perform ANOVA on 'percentage infested tillers' - summer 1978 experiment.

```

1  "REFE"PCENTINF
2
3  ""ANALYSIS OF PERCENT INFESTED TILLERS SUMMER 1978 ""
4  "" 13/6/78 S.AVENAE SPRAYED ""
5  "" 13/6/78 S.AVENAE UNSPRAYED ""
6  "" 13/6/78 M.DIRRHODUM SPRAYED ""
7  "" 13/6/78 M.DIRRHODUM UNSPRAYED ""
8  "" 19/6/78 S.AVENAE SPRAYED ""
9  "" 19/6/78 S.AVENAE UNSPRAYED ""
10 "" 19/6/78 M.DIRRHODUM SPRAYED ""
11 "" 19/6/78 M.DIRRHODUM UNSPRAYED ""
12 "" 6/7/78 S.AVENAE SPRAYED ""
13 "" 6/7/78 S.AVENAE UNSPRAYED ""
14 "" 6/7/78 M.DIRRHODUM SPRAYED ""
15 "" 6/7/78 M.DIRRHODUM UNSPRAYED ""
16 "" 11/7/78 S.AVENAE SPRAYED ""
17 "" 11/7/78 S.AVENAE UNSPRAYED ""
18 "" 11/7/78 M.DIRRHODUM SPRAYED ""
19 "" 11/7/78 M.DIRRHODUM UNSPRAYED ""
20 "" 17/7/78 S.AVENAE SPRAYED ""
21 "" 17/7/78 S.AVENAE UNSPRAYED ""
22 "" 17/7/78 M.DIRRHODUM SPRAYED ""
23 "" 17/7/78 M.DIRRHODUM UNSPRAYED ""
24 "" 24/7/78 S.AVENAE SPRAYED ""
25 "" 24/7/78 S.AVENAE UNSPRAYED ""
26 "" 24/7/78 M.DIRRHODUM SPRAYED ""
27 "" 24/7/78 M.DIRRHODUM UNSPRAYED ""
28 "UNIT"527
29 "NAME"ILEV=CONTROL,NOGRPREO,NUPREO
30 "FACT"SUHPS3=(1...3)9
31 "FACT"INSSILEV=3(1,2,3,3,1,2,2,3,1)
32 "FACT"SONDATS3=1,2,3,3,1,2,3,2,1,1,2,3,2,1,3,2,1,3,3,1,2,2,1,3,2,3,1
33 "FACT"ROXSS3=9(1...3)
34 "FACT"COLSS3=(3(1...3))3
35 "READ/S"C1,C2,C3,C4,C5,C6,C7,C8,C9,C10,C11,C12,C13,C14,C15,C16,C17,C18,
36 C19,C20,C21,C22,C23,C24
37 "BLOCK"(ROW*COLS)/SUHP
38 "JREA"INS*SONDAT
39 "CALC"C31=ARCSIN(SQRT(C1/100))
40 "CALC"C32=ARCSIN(SQRT(C2/100))
41 "CALC"C33=ARCSIN(SQRT(C3/100))
42 "CALC"C34=ARCSIN(SQRT(C4/100))
43 "CALC"C35=ARCSIN(SQRT(C5/100))
44 "CALC"C36=ARCSIN(SQRT(C6/100))
45 "CALC"C37=ARCSIN(SQRT(C7/100))
46 "CALC"C38=ARCSIN(SQRT(C8/100))
47 "CALC"C39=ARCSIN(SQRT(C9/100))
48 "CALC"C40=ARCSIN(SQRT(C10/100))
49 "CALC"C41=ARCSIN(SQRT(C11/100))
50 "CALC"C42=ARCSIN(SQRT(C12/100))
51 "CALC"C43=ARCSIN(SQRT(C13/100))
52 "CALC"C44=ARCSIN(SQRT(C14/100))
53 "CALC"C45=ARCSIN(SQRT(C15/100))
54 "CALC"C46=ARCSIN(SQRT(C16/100))
55 "CALC"C47=ARCSIN(SQRT(C17/100))
56 "CALC"C48=ARCSIN(SQRT(C18/100))
57 "CALC"C49=ARCSIN(SQRT(C19/100))
58 "CALC"C50=ARCSIN(SQRT(C20/100))
59 "CALC"C51=ARCSIN(SQRT(C21/100))
60 "CALC"C52=ARCSIN(SQRT(C22/100))
61 "CALC"C53=ARCSIN(SQRT(C23/100))
62 "CALC"C54=ARCSIN(SQRT(C24/100))
63 "PRIN/P"ROWS,COLS,SUHP,INS,SONDAT,C1,C2,C3,C4,C5,C6,C7,C8,C9,C10,C11,
64 C12,C13,C14,C15,C16,C17,C18,C19,C20,C21,C22,C23,C2459.0
65 "ANOVA"C31,C32,C33,C34,C35,C36,C37,C38,C39,C40,C41,C42,C43,C44,C45,C46,C47,C48,
66 C49,C50,C51,C52,C53,C54
67 "RUN"

```

APPENDIX 6 : Computer programme used to perform ANOVA on natural enemy counts - summer 1978 experiment.

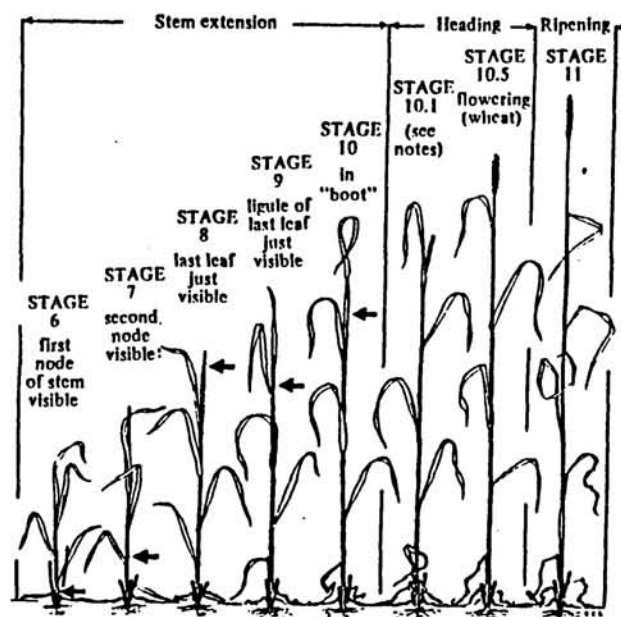
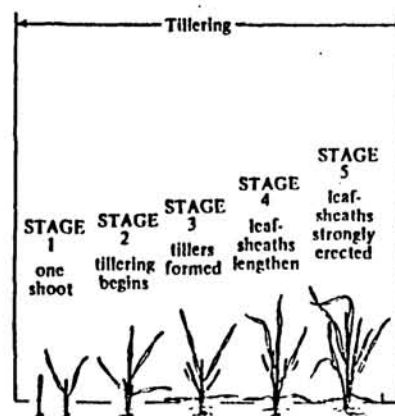
```

"REFR" NATENEM
"NATURAL ENEMIES" 6/7/78 SPRAYED"" "RAY SMITH FKT 315"
      "INCLUDES CORRECTED CALCULATION OF ARC SIN TRANSFORMATION"
"C1...C7=S.AVENAE"
"CH...C14=M.DIRHODUE"
"C20=TOTAL APHIDS PER 100 TILLERS"
"C15=MUMMIES,C25=LOG MUMMIES+1"
"C16=SYRPHID EGGS,C26=LOG SYRPHID EGGS +1"
"C17=DISEASE ,C27=LOG DISEASE+1"
"C30=MUMMIES/TOTAL APHIDS"
"C31=SYRPHID EGGS/TOTAL APHIDS EXCLUDING INDIVIDUALS AFFECTED BY DISEASE"
"C32=DISEASE/TOTAL APHIDS"
"C40=ARCSIN PROPORTION OF MUMMIES"
"C41=ARCSIN PROPORTION OF DISEASE"
"UNIT" S27
"NAME" 1LEV=CONTROL,UNEXPOSED,EXPOSED
"FACT" CULSS3=(3(1...3))3
"FACT" ROWSS3=9(1...3)
"FACT" SUBDATS3=1,2,3,3,1,2,3,2,1,1,2,3,2,1,3,2,1,3,3,1,2,2,1,3,2,3,1
"FACT" INSS1LEV=3(1,2,3,3,1,2,2,3,1)
"FACT" SUBPS3=(1...3)4
"READ/S" C1,C2,C3,C4,C5,C6,C7,CH,C9,C10,C11,C12,C13,C14,C15,C16,C17
"BLOCK" (ROWS*COLS)/SUBP
"AREA" INS*SUBDAT
"CALC" C20=C1+C2+C3+C4+C5+C6+C7+C8+C9+C10+C11+C12+C13+C14
"CALC" C25=LOG(C15+1)
"CALC" C26=LOG(C16+1)
"CALC" C27=LOG(C17+1)
"CALC/ZDZ=ZERO" C30=C15/(C20+C15)
"CALC/ZDZ=ZERO" C31=C16/C20
"CALC/ZDZ=ZERO" C32=C17/(C20+C17)
"CALC" C40=ARCSIN(SQR(C30))
"CALC" C41=ARCSIN(SQR(C32))
"PRINT/P" ROWS,COLS,SUBP,INS,SUBDAT,C1,C2,C3,C4,C5,C6,C7,CH,C9,C10,C12,C13,
C14,C20$9.0
"PRINT/P" INS,SUBDAT,C20,C15,C25,C16,C26,C17,C27$10.3
"PRINT/P" INS,SUBDAT,C30,C40,C31,C32,C41$10.3
"ANOVA" C25,C40,C26,C31,C27,C40
"END"

```

Second of two cards

Growth Stages in Wheat • Oats • Rye and Barley Key No. 1-1



From EAR EMERGENCE

STAGE

- 10.1 First ears just visible
(Awns just showing in barley, ear escaping through split of sheath in wheat or oats)
- 10.2 ¼ of heading process completed
- 10.3 ½ of heading process completed
- 10.4 ¾ of heading process completed
- 10.5 All ears out of sheath
(for wheat)
- 10.5.1 Beginning of flowering
- 10.5.2 Flowering complete to top of ear
- 10.5.3 Flowering over at base of ear
- 10.5.4 Flowering over, kernel watery ripe
- 11.1 Milky ripe
- 11.2 Mealy ripe, contents of kernel soft but dry
- 11.3 Kernel hard (difficult to divide by thumb nail)
- 11.4 Ripe for cutting. Straw dead

PLANT PATHOLOGY LABORATORY
HARPENDEN, HERTS

Ministry of Agriculture, Fisheries and Food
(Publications), Tolcarne Drive, Pinner, Middlesex HA5 2DT

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Decimal Code for the Growth Stages of Cereals

Key No. 1-2

Notes:

- i Principal growth stages 5 and 6 distinguish between non-synchronous and synchronous crops. A non-synchronous crop is one in which the degree of inflorescence-emergence or anthesis varies between plants and is represented by even codes 50 - 68. A synchronous crop is one in which all plants exhibit inflorescence-emergence or anthesis to the same degree and is represented by the odd codes 51 - 69.
- ii Different codes may be used concurrently e.g. (a) in a seedling crop with 3 leaves, a main stem and one tiller, codes both for leaf number (code 13) and for tiller number (code 21) are applicable, (b) in a crop where plants have, on average, a main stem, 4 tillers and the 1st node detectable, codes for tiller number (24) and stem elongation (31) are applicable. Concurrent codes should be recorded unless the low-ranking code is difficult to determine in which case it is advisable to use only the high-ranking code.

Table 1

A decimal code for the growth stages of cereals.
Principal growth stages.

1-digit code	Description
0	Germination
1	Seedling growth
2	Tillering
3	Stem elongation
4	Booting
5	Inflorescence emergence
6	Anthesis
7	Milk development
8	Dough development
9	Ripening
T	Transplanting and recovery (rice only)

Table 2

A decimal code for the growth stages of cereals.
Secondary growth stages.

2-digit code	General description	Feekes' scale	Additional remarks on wheat, barley, rye, and oats
<i>Germination</i>			
00	Dry seed		
01	Start of Imbibition		
02	—		
03	Imbibition complete		
04	—		
05	Radicle emerged from caryopsis		
06	—		
07	Coleoptile emerged from caryopsis		
08	—		
09	Leaf just at coleoptile tip		
<i>Seedling growth</i>			
10	First leaf through coleoptile	1	On main shoot. A leaf is expanded when the next leaf is visible emerging through the leaf sheath
11	First leaf unfolded 1)		
12	2 leaves unfolded		
13	3 leaves unfolded		
14	4 leaves unfolded		
15	5 leaves unfolded		
16	6 leaves unfolded		
17	7 leaves unfolded		
18	8 leaves unfolded		
19	9 or more leaves unfolded		
<i>Tillering</i>			
20	Main shoot only	2	This section to be used to supplement records from other sections of the table: "concurrent codes".
21	Main shoot and 1 tiller		
22	Main shoot and 2 tillers		
23	Main shoot and 3 tillers		
24	Main shoot and 4 tillers		
25	Main shoot and 5 tillers		
26	Main shoot and 6 tillers		
27	Main shoot and 7 tillers		
28	Main shoot and 8 tillers		
29	Main shoot and 9 or more tillers		

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Table 2 (continued)
A decimal code for the growth stages of cereals.
Secondary growth stages.

2-digit code	General description	Feekes' scale	Additional remarks on wheat, barley, rye and oats
<i>Stem elongation</i>			
30	Pseudo stem erection 2)	4-5	In rice: Vegetative lag phase
31	1st node detectable	6 7	Jointing stage
32	2nd node detectable		
33	3rd node detectable	8	Above-crown nodes
34	4th node detectable		
35	5th node detectable		
36	6th node detectable		
37	Flag leaf just visible	8	
38	—		
39	Flag leaf ligule/collar just visible	9	Pre-boot stage. In rice: Opposite auricle stage
<i>Booting</i>			
40	—		
41	Flag leaf sheath extending		Little enlargement of the inflorescence, early boot stage
42	—		
43	Boots just visibly swollen		Mid-boot stage
44	—		
45	Boots swollen	10	Late-boot stage
46	—		
47	Flag leaf sheath opening		
48	—		
49	First awns visible		In awned forms only
<i>Inflorescence emergence</i>			
50	First spikelet of inflorescence just visible	[N]	N = non-synchronous crops. S = synchronous crops. See text.
51	—	[S]	
52	1/4 of inflorescence emerged	[N]	
53	—	[S]	
54	1/2 of inflorescence emerged	[N]	
55	—	[S]	
56	3/4 of inflorescence emerged	[N]	
57	—	[S]	
58	Emergence of inflorescence completed	[N]	
59	—	[S]	

Table 2 (continued)
A decimal code for the growth stages of cereals.
Secondary growth stages.

2-digit code	General description	Feekes' scale	Additional remarks on wheat, barley, rye and oats
<i>Anthesis</i>			
60	Beginning of anthesis	[N S]	10.51 Not easily detectable in barley. In rice: Usually immediately following heading
61			
62			
63	Anthesis half-way	[N S]	
64			
65			
66	Anthesis complete	[N S]	
67			
68			
69			
<i>Milk development</i>			
70	—	10.54	Increase in solids of liquid endosperm notable when crushing the caryopsis between fingers
71	Caryopsis watery ripe		
72	—		
73	Early milk	11.1	
74	—		
75	Medium milk		
76	—	11.2	
77	Late milk		
78	—		
79	—		
<i>Dough development</i>			
80	—	11.2	Finger nail impression not held
81	—		
82	—		
83	Early dough		Finger nail impression held, inflorescence losing chlorophyll
84	—		
85	Soft dough		
86	—		
87	Hard dough		
88	—		
89	—		

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Table 2 (continued)

A decimal code for the growth stages of cereals.
Secondary growth stages.

2-digit code	General description	Feekes' scale	Additional remarks on wheat, barley, rye, and oats
<i>Ripening</i>			
90	—		In rice: Terminal spikelets ripened. In rice: 50% of spikelets ripened
91	Caryopsis hard (difficult to divide by thumb-nail) 3)	11.3	
92	Caryopsis hard (can no longer be dented by thumb-nail) 4)	11.4	In rice: Over 90% of spikelets ripened 5)
93	Caryopsis loosening in daytime		
94	Over-ripe, straw dead and collapsing		
95	Seed dormant		
96	Viable seed giving 50% germination		
97	Seed not dormant		
98	Secondary dormancy induced		
99	Secondary dormancy lost		
<i>Transplanting and recovery (rice only)</i>			
T1	Uprooting of seedlings		
T2	—		
T3	Rooting		
T4	—		
T5	—		
T6	—		
T7	Recovery of shoot		
T8	—		
T9	Resumption of vegetative growth		

Notes to Table 2

- 1 Stage of seeding inoculation with rust in the greenhouse.
- 2 Only applicable to cereals with a prostrate or semi-prostrate early growth habit.
- 3 Ripeness for binder (ca 16% water content). Chlorophyll of inflorescence largely lost.
- 4 Ripeness for combine harvester (< 16% water content).
- 5 Optimum harvest time.

Reference:

Zadoks, J. C., Chang, T. T. and Konzak, C. F. (1974)
A decimal code for the growth stages of cereals.
Weed Res., 14(6), 415-421

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TABLE 28

RAW DATA-"ON PLANT" COUNTS OF MUMMIES, SYRPHID EGGS AND DISEASED APHIDS (100 FIL. S) - 77

TREAT SOW DAT ROW COL SUBP MUM S/EGG DIS

CONTROL	1	1	1	1	0	5	0
CONTROL	1	2	2	2	0	8	0
CONTROL	1	3	3	3	3	1	0
MEAN					1.0	4.7	0.0

CONTROL	2	1	1	2	1	1	0
CONTROL	2	2	2	1	2	0	0
CONTROL	2	3	3	1	*	*	*
MEAN					1.5	0.5	0.0

CONTROL	3	1	1	3	0	0	0
CONTROL	3	2	2	3	2	0	0
CONTROL	3	3	3	2	0	0	0
MEAN					0.7	0.0	0.0

NOGRPRD	1	1	2	2	1	1	0
NOGRPRD	1	2	3	2	0	0	0
NOGRPRD	1	3	1	2	0	0	0
MEAN					0.3	0.3	0.0

NOGRPRD	2	1	2	3	1	1	0
NOGRPRD	2	2	3	1	1	0	0
NOGRPRD	2	3	1	3	0	1	0
MEAN					0.7	0.7	0.0

NOGRPRD	3	1	2	1	0	0	0
NOGRPRD	3	2	3	3	0	0	0
NOGRPRD	3	3	1	1	0	0	0
MEAN					0.0	0.0	0.0

NOPRED	1	1	3	3	0	0	0
NOPRED	1	2	1	1	0	8	0
NOPRED	1	3	2	2	0	9	0
MEAN					0.0	5.7	0.0

NOPRED	2	1	3	2	1	0	0
NOPRED	2	2	1	2	0	0	0
NOPRED	2	3	2	1	*	*	*
MEAN					0.5	0.0	0.0

NOPRED	3	1	3	1	1	0	0
NOPRED	3	2	1	3	1	0	0
NOPRED	3	3	2	3	0	0	0
MEAN					0.7	0.0	0.0

NOPRED	1	1	3	3	1	4	0
NOPRED	1	2	1	1	0	0	0
NOPRED	1	3	2	2	0	0	0
MEAN					0.3	1.3	0.0

NOPRED	2	1	3	2	0	0	0
NOPRED	2	2	1	2	0	0	0
NOPRED	2	3	2	1	*	*	*
MEAN					0.0	0.0	0.0

NOPRED	3	1	3	1	0	0	0
NOPRED	3	2	1	3	0	0	0
NOPRED	3	3	2	3	0	0	0
MEAN					0.0	0.0	0.0

".....SPRAYED ZONE....."

".....UNSPRAYED ZONE....."

TABLE 29

RAW DATA-"ON PLANT" COUNTS OF HUMMIES, SYRPHID EGGS AND DISEASED APHIDS(100 TIL.S) -13/6

TREAT SOWDAT ROW COL SUBP HUM S/EGG DIS

CONTROL	1	1	1	1	5	15	6
CONTROL	1	2	2	2	3	1	0
CONTROL	1	3	3	3	1	0	2
MEAN					3.0	5.3	2.7

CONTROL	2	1	1	2	1	0	2
CONTROL	2	2	2	1	4	1	0
CONTROL	2	3	3	1	*	*	*
MEAN					2.5	0.5	1.0

CONTROL	3	1	1	3	1	0	0
CONTROL	3	2	2	3	0	0	0
CONTROL	3	3	3	2	0	0	0
MEAN					0.3	0.0	0.0

NOGRPREP	1	1	2	2	3	21	0
NOGRPREP	1	2	3	2	0	4	0
NOGRPREP	1	3	1	2	0	3	0
MEAN					1.0	9.3	0.0

NOGRPREP	2	1	2	3	7	4	0
NOGRPREP	2	2	3	1	3	1	0
NOGRPREP	2	3	1	3	1	0	0
MEAN					3.7	1.7	0.0

NOGRPREP	3	1	2	1	0	8	0
NOGRPREP	3	2	3	3	1	0	0
NOGRPREP	3	3	1	1	0	0	0
MEAN					0.3	2.7	0.0

NOPRED	1	1	3	3	0	0	0
NOPRED	1	2	1	1	2	10	0
NOPRED	1	3	2	2	0	10	2
MEAN					0.7	6.7	0.7

NOPRED	2	1	3	2	0	0	0
NOPRED	2	2	1	2	0	0	0
NOPRED	2	3	2	1	*	*	*
MEAN					0.0	0.0	0.0

NOPRED	3	1	3	1	1	0	0
NOPRED	3	2	1	3	0	0	0
NOPRED	3	3	2	3	0	0	0
MEAN					0.3	0.0	0.0

NOPRED	1	1	3	3	4	3	2
NOPRED	1	2	1	1	0	0	0
NOPRED	1	3	2	2	1	0	0
MEAN					1.7	1.0	0.7

NOPRED	2	1	3	2	3	13	0
NOPRED	2	2	1	2	1	0	0
NOPRED	2	3	2	1	*	*	*
MEAN					2.0	6.5	0.0

NOPRED	3	1	3	1	1	0	0
NOPRED	3	2	1	3	0	0	0
NOPRED	3	3	2	3	1	0	0
MEAN					0.7	0.0	0.0

".....SPRAYED ZONE....."

".....UNSPRAYED ZONE....."

TABLE 30

RAW DATA-"ON PLANT" COUNTS OF MURRIES, SYRPHID EGGS AND DISEASED APHIDS (100 TILLS)-1976

TREAT SUBDAT ROW COL SUBP' HUM S/EGG DIS

".....SPRAYED ZONE....."	CONTROL	1	1	1	1	0	0	0
	CONTROL	1	2	2	2	7	15	0
	CONTROL	1	3	3	3	2	0	0
	MEAN					3.0	5.0	0.0
	CONTROL	2	1	1	2	0	0	0
	CONTROL	2	2	2	1	0	0	0
	CONTROL	2	3	3	1	*	*	*
	MEAN					0.0	0.0	0.0
	CONTROL	3	1	1	3	0	1	0
	CONTROL	3	2	2	3	2	0	0
	CONTROL	3	3	3	2	1	0	0
	MEAN					1.0	0.3	0.0
".....UNSPRAYED ZONE....."	NOGRPRE	1	1	2	2	0	1	0
	NOGRPRE	1	2	3	2	2	11	0
	NOGRPRE	1	3	1	2	0	0	0
	MEAN					0.7	4.0	0.0
	NOGRPRE	2	1	2	3	0	11	0
	NOGRPRE	2	2	3	1	2	2	0
	NOGRPRE	2	3	1	3	1	2	0
	MEAN					1.0	5.0	0.0
	NOGRPRE	3	1	2	1	0	0	0
	NOGRPRE	3	2	3	3	0	2	0
	NOGRPRE	3	3	1	1	0	0	0
	MEAN					0.0	0.7	0.0
".....TREATMENT ZONE....."	NOPRED	1	1	3	3	0	5	0
	NOPRED	1	2	1	1	2	2	0
	NOPRED	1	3	2	2	0	10	0
	MEAN					0.7	5.7	0.0
	NOPRED	2	1	3	2	0	0	0
	NOPRED	2	2	1	2	0	16	0
	NOPRED	2	3	2	1	*	*	*
	MEAN					0.0	8.0	0.0
	NOPRED	3	1	3	1	2	0	1
	NOPRED	3	2	1	3	2	3	0
	NOPRED	3	3	2	3	1	0	0
	MEAN					1.7	1.0	0.3
".....TREATMENT ZONE....."	NOPRED	1	1	3	3	1	0	0
	NOPRED	1	2	1	1	1	3	0
	NOPRED	1	3	2	2	0	9	0
	MEAN					0.7	4.0	0.0
	NOPRED	2	1	3	2	0	0	0
	NOPRED	2	2	1	2	0	0	0
	NOPRED	2	3	2	1	*	*	*
	MEAN					0.0	0.0	0.0
	NOPRED	3	1	3	1	0	0	0
	NOPRED	3	2	1	3	0	0	0
	NOPRED	3	3	2	3	0	0	0
	MEAN					0.0	0.0	0.0

TABLE 31

RAW DATA-"ON PLANT" COUNTS OF MUMMIES, STYRPID EGGS AND DISEASED APHIDS (100 TIL.S) - 6/7

TREAT SODAT ROW COL SUBP NUM S/EGG DIS

CONTROL	1	1	1	1	5	0	4
CONTROL	1	2	2	2	5	0	1
CONTROL	1	3	3	3	3	1	0
MEAN					4.3	0.3	1.7

CONTROL	2	1	1	2	1	0	0
CONTROL	2	2	2	1	4	0	0
CONTROL	2	3	3	1	*	*	*
MEAN					2.5	0.0	0.0

CONTROL	3	1	1	3	8	0	1
CONTROL	3	2	2	3	7	0	0
CONTROL	3	3	3	2	0	0	0
MEAN					5.0	0.0	0.3

NOGRPRE	1	1	2	2	5	0	0
NOGRPRE	1	2	3	2	9	0	2
NOGRPRE	1	3	1	2	3	0	0
MEAN					5.7	0.0	0.7

NOGRPRE	2	1	2	3	4	0	0
NOGRPRE	2	2	3	1	1	0	0
NOGRPRE	2	3	1	3	2	0	0
MEAN					2.3	0.0	0.0

NOGRPRE	3	1	2	1	0	0	0
NOGRPRE	3	2	3	3	2	11	0
NOGRPRE	3	3	1	1	0	0	0
MEAN					0.7	3.7	0.0

NOPRED	1	1	3	3	10	0	4
NOPRED	1	2	1	1	8	8	2
NOPRED	1	3	2	2	11	0	0
MEAN					9.7	2.7	2.0

NOPRED	2	1	3	2	1	0	1
NOPRED	2	2	1	2	5	0	0
NOPRED	2	3	2	1	*	*	*
MEAN					3.0	0.0	0.5

NOPRED	3	1	3	1	3	0	0
NOPRED	3	2	1	3	0	0	0
NOPRED	3	3	2	3	3	0	0
MEAN					2.0	0.0	0.0

NOPRED	1	1	3	3	15	0	4
NOPRED	1	2	1	1	12	4	2
NOPRED	1	3	2	2	11	5	0
MEAN					12.7	3.0	2.0

NOPRED	2	1	3	2	3	0	1
NOPRED	2	2	1	2	4	9	0
NOPRED	2	3	2	1	*	*	*
MEAN					3.5	4.5	0.5

NOPRED	3	1	3	1	1	0	0
NOPRED	3	2	1	3	0	0	0
NOPRED	3	3	2	3	0	0	0
MEAN					0.3	0.0	0.0

".....SPRAYED ZONE....."

".....UNSPRAYED ZONE....."

TABLE 32

RAW DATA-"IN PLANT" COUNTS OF ADULTS, STYPPID EGGS AND DISEASED APHIDS (100 YLD. 5) - 11/

TREAT SUBDAT ROW COL SUBP SUM S/EGG GAS

".....SPRAYED ZONE....."	CONTROL	1	1	1	1	0	0	1
	CONTROL	1	2	2	2	4	0	0
	CONTROL	1	3	3	3	10	0	3
	MEAN					4.7	0.0	1.3
	CONTROL	2	1	1	2	1	0	5
	CONTROL	2	2	2	1	7	1	0
	CONTROL	2	3	3	1	*	*	*
	MEAN					4.0	0.5	2.5
	CONTROL	3	1	1	3	9	0	1
	CONTROL	3	2	2	3	6	3	1
	CONTROL	3	3	3	2	1	0	0
	MEAN					5.3	1.0	0.7
".....SPRAYED ZONE....."	NOGRPEED	1	1	2	2	3	0	0
	NOGRPEED	1	2	3	2	11	0	0
	NOGRPEED	1	3	1	2	2	0	0
	MEAN					5.3	0.0	0.0
	NOGRPEED	2	1	2	3	7	0	1
	NOGRPEED	2	2	3	1	1	0	3
	NOGRPEED	2	3	1	3	5	0	1
	MEAN					4.3	0.0	1.7
	NOGRPEED	3	1	2	1	1	0	0
	NOGRPEED	3	2	3	3	0	0	1
	NOGRPEED	3	3	1	1	1	0	0
	MEAN					0.7	0.0	0.3
".....SPRAYED ZONE....."	NOPEED	1	1	3	3	4	0	3
	NOPEED	1	2	1	1	11	3	0
	NOPEED	1	3	2	2	0	0	0
	MEAN					5.0	1.0	1.0
	NOPEED	2	1	3	2	4	0	4
	NOPEED	2	2	1	2	3	0	2
	NOPEED	2	3	2	1	*	*	*
	MEAN					3.5	0.0	3.0
	NOPEED	3	1	3	1	1	0	0
	NOPEED	3	2	1	3	0	0	0
	NOPEED	3	3	2	3	1	0	0
	MEAN					0.7	0.0	0.0
".....SPRAYED ZONE....."	NOPEED	1	1	3	3	10	0	0
	NOPEED	1	2	1	1	4	0	1
	NOPEED	1	3	2	2	5	0	0
	MEAN					6.3	0.0	0.3
	NOPEED	2	1	3	2	1	0	2
	NOPEED	2	2	1	2	2	0	0
	NOPEED	2	3	2	1	*	*	*
	MEAN					1.5	0.0	1.0
	NOPEED	3	1	3	1	1	0	0
	NOPEED	3	2	1	3	0	0	0
	NOPEED	3	3	2	3	6	0	2
	MEAN					2.3	0.0	0.7

TABLE 33

RAW DATA--"ON PLANT" COUNTS OF MUMMIES, SYRPHID EGGS AND DISEASED APHIDS (100 TIL. 5) - 17/7

TREAT SOW DAT ROW COL SHEP MUM S/EGG DIS

CONTROL	1	1	1	1	0	0	0
CONTROL	1	2	2	2	5	0	0
CONTROL	1	3	3	3	3	0	0
MEAN					2.7	0.0	0.0

CONTROL	2	1	1	2	0	0	0
CONTROL	2	2	2	1	11	1	0
CONTROL	2	3	3	1	*	*	*
MEAN					5.5	0.5	0.0

CONTROL	3	1	1	3	2	0	0
CONTROL	3	2	2	3	3	0	0
CONTROL	3	3	3	2	2	0	0
MEAN					2.3	0.0	0.0

NOGRFPED	1	1	2	2	0	0	0
NOGRFPED	1	2	3	2	1	0	0
NOGRFPED	1	3	1	2	4	0	0
MEAN					1.7	0.0	0.0

NOGRFPED	2	1	2	3	2	0	1
NOGRFPED	2	2	3	1	3	2	0
NOGRFPED	2	3	1	3	11	0	0
MEAN					5.3	0.7	0.3

NOGRFPED	3	1	2	1	1	0	0
NOGRFPED	3	2	3	3	0	0	0
NOGRFPED	3	3	1	1	1	0	0
MEAN					0.7	0.0	0.0

NOPRED	1	1	3	3	8	0	0
NOPRED	1	2	1	1	14	0	0
NOPRED	1	3	2	2	2	0	1
MEAN					8.0	0.0	0.3

NOPRED	2	1	3	2	5	0	0
NOPRED	2	2	1	2	16	34	2
NOPRED	2	3	2	1	*	*	*
MEAN					10.5	17.0	1.0

NOPRED	3	1	3	1	0	0	0
NOPRED	3	2	1	3	5	0	0
NOPRED	3	3	2	3	8	0	0
MEAN					4.3	0.0	0.0

NOPRED	1	1	3	3	0	0	0
NOPRED	1	2	1	1	8	0	0
NOPRED	1	3	2	2	0	0	0
MEAN					2.7	0.0	0.0

NOPRED	2	1	3	2	0	0	0
NOPRED	2	2	1	2	12	0	0
NOPRED	2	3	2	1	*	*	*
MEAN					6.0	0.0	0.0

NOPRED	3	1	3	1	1	0	0
NOPRED	3	2	1	3	0	0	0
NOPRED	3	3	2	3	*	*	*
MEAN					0.5	0.0	0.0

TABLE 34

RAW DATA-"ON PLANT" COUNTS OF HONEYEES, SYRPHID EGGS AND DISEASED APHIDS (100 TILLS) - 24/7

TREAT SO/DAT ROW COL SUBP SUM S/EGG DIS

CONTROL	1	1	1	1	0	0	0
CONTROL	1	2	2	2	4	0	1
CONTROL	1	3	3	3	0	0	0
MEAN					1.3	0.0	0.3

CONTROL	2	1	1	2	2	0	0
CONTROL	2	2	2	1	20	6	4
CONTROL	2	3	3	1	*	*	*
MEAN					11.0	3.0	2.0

CONTROL	3	1	1	3	7	0	1
CONTROL	3	2	2	3	5	3	0
CONTROL	3	3	3	2	2	0	0
MEAN					4.7	1.0	0.3

NOGRPEED	1	1	2	2	0	0	0
NOGRPEED	1	2	3	2	3	0	0
NOGRPEED	1	3	1	2	12	0	0
MEAN					5.0	0.0	0.0

NOGRPEED	2	1	2	3	9	0	0
NOGRPEED	2	2	3	1	23	8	1
NOGRPEED	2	3	1	3	28	3	13
MEAN					20.0	3.7	4.7

NOGRPEED	3	1	2	1	3	0	0
NOGRPEED	3	2	3	3	1	3	0
NOGRPEED	3	3	1	1	4	0	1
MEAN					2.7	1.0	0.3

NOPRED	1	1	3	3	6	0	0
NOPRED	1	2	1	1	21	0	0
NOPRED	1	3	2	2	7	0	0
MEAN					11.3	0.0	0.0

NOPRED	2	1	3	2	17	0	4
NOPRED	2	2	1	2	17	0	0
NOPRED	2	3	2	1	*	*	*
MEAN					17.0	0.0	2.0

NOPRED	3	1	3	1	1	0	0
NOPRED	3	2	1	3	1	2	1
NOPRED	3	3	2	3	9	0	0
MEAN					3.7	0.7	0.3

NOPRED	1	1	3	3	2	0	1
NOPRED	1	2	1	1	8	0	0
NOPRED	1	3	2	2	*	0	0
MEAN					5.0	0.0	0.3

NOPRED	2	1	3	2	9	0	0
NOPRED	2	2	1	2	35	0	0
NOPRED	2	3	2	1	0	*	*
MEAN					14.7	0.0	0.0

NOPRED	3	1	3	1	4	0	0
NOPRED	3	2	1	3	2	17	3
NOPRED	3	3	2	3	0	0	0
MEAN					2.0	5.7	1.0

TABLE 35

RAW DATA-"ON PLANT" COUNTS OF NUBMIES, STAPHID EGGS AND DISEASED APHIDS(100 TIL.S) — 3/8

TREAT SOG DAT ROW COL SUBP SUM S/EGG DIS

CONTROL	1	1	1	1	0	0	0
CONTROL	1	2	2	2	1	0	0
CONTROL	1	3	3	3	0	0	0
MEAN					0.3	0.0	0.0

CONTROL	2	1	1	2	8	0	0
CONTROL	2	2	2	1	13	0	0
CONTROL	2	3	3	1	*	*	*
MEAN					10.5	0.0	0.0

CONTROL	3	1	1	3	5	0	0
CONTROL	3	2	2	3	3	0	0
CONTROL	3	3	3	2	2	0	0
MEAN					3.3	0.0	0.0

NOGRPREP	1	1	2	2	2	0	0
NOGRPREP	1	2	3	2	0	0	0
NOGRPREP	1	3	1	2	0	0	0
MEAN					0.7	0.0	0.0

NOGRPREP	2	1	2	3	10	0	0
NOGRPREP	2	2	3	1	21	0	2
NOGRPREP	2	3	1	3	12	0	1
MEAN					14.3	0.0	1.0

NOGRPREP	3	1	2	1	6	0	0
NOGRPREP	3	2	3	3	6	6	4
NOGRPREP	3	3	1	1	5	0	10
MEAN					5.7	2.0	4.7

NOFPRED	1	1	3	3	0	0	0
NOFPRED	1	2	1	1	7	0	0
NOFPRED	1	3	2	2	0	0	0
MEAN					2.3	0.0	0.0

NOFPRED	2	1	3	2	19	0	0
NOFPRED	2	2	1	2	62	5	4
NOFPRED	2	3	2	1	*	*	*
MEAN					40.5	2.5	2.0

NOFPRED	3	1	3	1	6	0	1
NOFPRED	3	2	1	3	10	16	4
NOFPRED	3	3	2	3	11	0	1
MEAN					9.0	5.3	2.0

NOFPRED	1	1	3	3	1	0	0
NOFPRED	1	2	1	1	0	0	0
NOFPRED	1	3	2	2	0	0	0
MEAN					0.3	0.0	0.0

NOFPRED	2	1	3	2	0	3	0
NOFPRED	2	2	1	2	31	0	2
NOFPRED	2	3	2	1	*	*	*
MEAN					15.5	1.5	1.0

NOFPRED	3	1	3	1	0	0	0
NOFPRED	3	2	1	3	1	4	16
NOFPRED	3	3	2	3	8	0	0
MEAN					3.0	1.3	4.7

TABLE 42

RAW DATA-NO. APHIDS PER 100 TILLERS.-S.AVENAE 7/6

TREAT	SUBS	ROW	COL	SUBP	1	2	3	4(4P)	4(4L)	AP	AL	TOT
CONTROL	1	1	1	1	11	9	0	8	0	1	4	33
CONTROL	1	2	2	2	8	3	9	1	0	3	3	24
CONTROL	1	3	3	3	8	4	1	0	0	1	1	13
MEAN					8.3	5.3	1.7	3.0	0.0	1.7	2.7	22.7
CONTROL	2	1	1	2	0	4	4	0	0	1	1	16
CONTROL	2	2	2	1	0	0	0	0	0	1	2	3
CONTROL	2	3	3	1	0	0	0	0	0	0	0	0
MEAN					0.0	2.0	2.0	3.0	0.0	1.0	1.5	9.5
CONTROL	3	1	1	3	0	0	0	1	0	1	0	2
CONTROL	3	2	2	3	0	0	0	0	0	0	1	1
CONTROL	3	3	3	2	0	0	0	0	0	0	3	3
MEAN					0.0	0.0	0.0	0.3	0.0	0.3	1.3	2.0
NOGRFED	1	1	2	2	13	10	3	9	0	1	5	41
NOGRFED	1	2	3	2	0	3	5	1	0	4	3	16
NOGRFED	1	3	1	2	4	4	0	0	0	6	3	17
MEAN					5.7	5.7	2.7	3.3	0.0	3.7	3.7	24.7
NOGRFED	2	1	2	3	1	0	0	0	0	1	1	3
NOGRFED	2	2	3	1	0	0	0	0	0	0	0	0
NOGRFED	2	3	1	3	1	0	0	2	0	2	0	5
MEAN					0.7	0.0	0.0	0.7	0.0	1.0	0.3	2.7
NOGRFED	3	1	2	1	1	0	0	1	0	0	1	3
NOGRFED	3	2	3	3	0	0	0	0	0	0	0	0
NOGRFED	3	3	1	1	0	0	0	0	0	0	0	0
MEAN					0.3	0.0	0.0	0.3	0.0	0.0	0.3	1.0
NOFRED	1	1	3	3	7	2	0	0	0	1	4	20
NOFRED	1	2	1	1	8	0	0	0	0	1	1	10
NOFRED	1	3	2	2	6	5	3	1	0	1	1	17
MEAN					7.0	2.3	3.0	0.3	0.0	1.0	2.0	15.7
NOFRED	2	1	3	2	0	0	0	0	0	0	0	0
NOFRED	2	2	1	2	0	2	0	0	0	0	0	2
NOFRED	2	3	2	1	0	0	0	0	0	0	0	0
MEAN					0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0
NOFRED	3	1	3	1	0	0	0	0	0	1	0	1
NOFRED	3	2	1	3	0	0	1	0	0	0	0	1
NOFRED	3	3	2	3	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.3	0.0	0.0	0.3	1.0	0.7
NOFRED	1	1	3	3	6	1	1	2	0	0	1	11
NOFRED	1	2	1	1	0	3	0	0	0	0	0	3
NOFRED	1	3	2	2	7	9	0	1	0	1	1	24
MEAN					4.3	4.3	2.3	1.0	0.0	0.0	0.7	12.7
NOFRED	2	1	3	2	0	1	0	0	0	1	0	2
NOFRED	2	2	1	2	0	0	2	0	0	0	2	4
NOFRED	2	3	2	1	0	0	0	0	0	0	0	0
MEAN					0.0	0.5	1.0	0.0	0.0	0.5	1.0	3.0
NOFRED	3	1	3	1	0	0	0	0	0	0	0	0
NOFRED	3	2	1	3	0	0	0	0	0	0	0	0
NOFRED	3	3	2	3	0	0	1	5	0	0	0	6
MEAN					0.0	0.0	0.3	1.7	0.0	0.0	0.0	2.0

TABLE 43

RAW DATA-NO. APHIDS PER 100 TILLERS.-S.AVENAE 13/6

TREAT	SUNDAI	ROW	CON	SUBP	1	2	3	4(4P)	4(4G)	4P	4G	TOT
CONTROL	1	1	1	1	9	3	1	2	0	1	1	8
CONTROL	1	2	2	2	7	15	5	15	0	9	1	52
CONTROL	1	3	3	3	10	5	9	0	0	8	0	32
MEAN					5.7	7.7	5.0	5.7	0.0	6.0	0.7	30.7
CONTROL	2	1	1	2	0	1	0	0	0	1	1	3
CONTROL	2	2	2	1	10	2	4	6	0	7	2	28
CONTROL	2	3	3	1	*	*	*	*	*	*	*	*
MEAN					5.0	1.5	2.0	3.0	0.0	1.5	1.5	14.5
CONTROL	3	1	1	3	3	0	0	0	0	0	0	3
CONTROL	3	2	2	3	0	0	0	1	0	0	0	1
CONTROL	3	3	3	2	0	0	0	0	0	0	0	0
MEAN					1.0	0.0	0.0	0.3	0.0	0.0	0.0	1.3
NOGRPED	1	1	2	2	0	2	3	0	0	0	1	6
NOGRPED	1	2	3	2	9	2	5	3	1	6	0	26
NOGRPED	1	3	1	2	4	0	*	0	0	3	2	19
MEAN					4.3	1.3	4.0	3.0	0.3	3.0	1.0	17.0
NOGRPED	2	1	2	3	0	1	0	0	0	3	0	4
NOGRPED	2	2	3	1	7	1	0	2	0	0	3	13
NOGRPED	2	3	1	3	0	0	0	2	0	1	1	10
MEAN					4.3	0.7	0.0	1.3	0.0	1.3	1.3	4.0
NOGRPED	3	1	2	1	1	0	0	0	0	0	1	2
NOGRPED	3	2	3	3	5	1	0	0	0	1	0	7
NOGRPED	3	3	1	1	0	0	0	0	0	0	0	0
MEAN					2.0	0.3	0.0	0.0	0.0	0.3	0.3	3.0
NOGRPED	1	1	3	3	1	0	0	0	0	1	1	3
NOGRPED	1	2	1	1	0	10	7	3	0	4	1	31
NOGRPED	1	3	2	2	2	2	1	1	0	1	1	8
MEAN					3.0	4.0	2.7	1.3	0.0	2.0	1.0	14.0
NOGRPED	2	1	3	2	0	3	0	1	0	0	1	5
NOGRPED	2	2	1	2	5	2	1	0	0	0	0	8
NOGRPED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					2.5	2.5	0.5	0.5	0.0	0.0	0.5	6.5
NOGRPED	3	1	3	1	0	0	0	0	0	0	0	0
NOGRPED	3	2	1	3	0	0	2	1	0	0	1	4
NOGRPED	3	3	2	3	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.7	0.3	0.0	0.0	0.3	1.3
NOGRPED	1	1	3	3	0	0	0	0	0	1	0	1
NOGRPED	1	2	1	1	1	1	0	0	0	2	1	4
NOGRPED	1	3	2	2	3	2	0	0	0	1	1	7
MEAN					1.3	1.0	0.0	0.0	0.0	0.7	1.0	4.0
NOGRPED	2	1	3	2	0	1	0	0	0	1	0	2
NOGRPED	2	2	1	2	0	0	3	1	0	0	2	6
NOGRPED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					0.0	0.5	1.5	0.5	0.0	0.5	1.0	4.0
NOGRPED	3	1	3	1	0	0	0	0	0	1	0	1
NOGRPED	3	2	1	3	0	1	0	0	0	0	0	1
NOGRPED	3	3	2	3	0	0	1	0	0	0	0	1
MEAN					0.0	0.3	0.3	0.0	0.0	0.3	0.0	1.0

TABLE 44

RAW DATA-NO. APHIDS PER 100 TILLERS.-S.AVENAE 1976

TREAT	SQUAT	ROW	COL	SUMP	1	2	3	4(AP)	4(AT)	AP	AL	TOT
CONTROL	1	1	1	1	9	3	6	3	0	0	0	12
CONTROL	1	2	2	2	28	33	21	4	0	0	2	100
CONTROL	1	3	3	3	3	19	22	7	0	5	0	56
MEAN					10.3	18.3	16.3	5.0	0.0	4.3	0.7	38.0
CONTROL	2	1	1	2	5	16	3	0	0	3	0	27
CONTROL	2	2	2	1	7	16	7	0	0	0	0	30
CONTROL	2	3	3	1	*	*	*	*	*	*	*	*
MEAN					6.0	16.0	5.0	0.0	0.0	1.5	0.0	26.5
CONTROL	3	1	1	3	0	2	1	0	0	1	0	4
CONTROL	3	2	2	3	1	1	0	1	0	0	0	3
CONTROL	3	3	3	2	0	1	0	0	1	1	0	3
MEAN					0.3	1.3	0.3	0.3	0.3	0.7	0.0	3.3
NUGRPPED	1	1	2	2	0	2	1	0	0	1	0	4
NUGRPPED	1	2	3	2	16	16	16	7	0	9	1	65
NUGRPPED	1	3	1	2	18	14	4	6	0	5	2	49
MEAN					11.3	10.7	7.0	4.3	0.0	5.0	1.0	39.3
NUGRPPED	2	1	2	3	0	0	0	1	0	0	0	1
NUGRPPED	2	2	3	1	11	21	6	0	0	2	3	37
NUGRPPED	2	3	1	3	16	7	2	0	0	3	5	33
MEAN					9.0	9.3	0.7	0.3	0.0	1.7	2.7	23.7
NUGRPPED	3	1	2	1	0	6	0	0	0	0	0	6
NUGRPPED	3	2	3	3	0	0	6	0	0	0	0	0
NUGRPPED	3	3	1	1	9	0	0	0	0	1	1	11
MEAN					3.0	2.0	0.0	0.0	0.0	0.3	0.3	5.7
NUGRPPED	1	1	3	3	1	0	6	0	0	3	3	7
NUGRPPED	1	2	1	1	2	15	10	3	0	5	5	40
NUGRPPED	1	3	2	2	1	3	6	2	0	2	2	16
MEAN					1.3	6.0	5.3	1.7	0.0	3.3	3.3	21.0
NUGRPPED	2	1	3	2	0	5	1	0	0	0	0	6
NUGRPPED	2	2	1	2	6	11	2	3	0	0	0	22
NUGRPPED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					3.0	7.0	1.5	1.5	0.0	0.0	0.0	14.0
NUGRPPED	3	1	3	1	0	0	0	0	0	1	1	2
NUGRPPED	3	2	1	3	5	0	0	0	0	0	0	5
NUGRPPED	3	3	2	3	0	6	0	0	0	0	0	0
MEAN					1.7	0.0	0.0	0.0	0.0	0.3	0.3	2.3
NUGRPPED	1	1	3	3	0	8	3	0	0	2	0	13
NUGRPPED	1	2	1	1	17	13	3	5	0	6	3	47
NUGRPPED	1	3	2	2	5	0	1	0	0	5	0	11
MEAN					7.3	7.0	2.3	1.7	0.0	4.3	1.0	23.7
NUGRPPED	2	1	3	2	1	0	1	0	0	2	0	4
NUGRPPED	2	2	1	2	8	2	0	1	0	0	3	14
NUGRPPED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					4.5	1.0	0.5	0.5	0.0	1.0	1.5	9.0
NUGRPPED	3	1	3	1	3	0	0	0	0	0	0	3
NUGRPPED	3	2	1	3	0	0	0	0	0	0	1	1
NUGRPPED	3	3	2	3	1	0	0	0	0	0	0	1
MEAN					1.3	0.0	0.0	0.0	0.0	0.0	0.3	1.7

RAW DATA-NO. APHIDS PER 100 TILLERS.-S.AVENAE 27/6

REPEAT	SOUND	ROW	CID	SUMP	1	2	3	4 (AV)	4 (AD)	AP	AD	TOT
CONTROL	1	1	1	1	16	2	2	2	0	12	2	19
CONTROL	1	2	2	2	10	24	13	15	0	11	1	74
CONTROL	1	3	3	3	15	12	11	1	5	11	0	75
MEAN					13.7	15.0	10.7	9.0	1.7	11.3	1.0	59.3
CONTROL	2	1	1	2	4	1	2	1	0	3	2	13
CONTROL	2	2	2	1	7	13	14	0	1	2	2	39
CONTROL	2	3	3	1	*	*	*	*	*	*	*	*
MEAN					5.3	7.0	9.0	0.5	0.5	2.3	2.0	20.0
CONTROL	3	1	1	3	0	0	1	0	0	0	0	1
CONTROL	3	2	2	3	16	6	0	0	0	3	2	29
CONTROL	3	3	3	2	4	0	0	0	0	0	1	5
MEAN					7.3	2.0	0.3	0.0	0.0	1.0	1.0	11.7
NOGRADED	1	1	2	2	0	1	3	1	0	1	1	7
NOGRADED	1	2	3	2	9	10	6	2	0	3	1	30
NOGRADED	1	3	1	2	22	14	6	9	2	5	1	59
MEAN					10.0	9.3	5.0	4.0	0.7	3.0	1.0	32.0
NOGRADED	2	1	2	3	9	0	4	1	1	2	0	16
NOGRADED	2	2	3	1	5	11	7	0	1	0	7	34
NOGRADED	2	3	1	3	18	13	7	4	0	2	2	40
MEAN					11.3	8.0	6.0	1.7	0.7	1.3	3.0	32.0
NOGRADED	3	1	2	1	0	0	0	0	0	0	0	0
NOGRADED	3	2	3	3	0	0	0	0	0	0	3	3
NOGRADED	3	3	1	1	2	0	0	0	0	0	3	5
MEAN					0.7	0.0	0.0	0.0	0.0	0.0	2.0	2.7
NOGRADED	1	1	3	3	11	8	3	5	2	8	0	37
NOGRADED	1	2	1	1	21	4	7	3	1	3	2	41
NOGRADED	1	3	2	2	3	0	4	4	0	13	1	25
MEAN					11.7	4.0	4.7	4.0	1.0	6.0	1.0	34.3
NOGRADED	2	1	3	2	0	0	0	0	0	0	2	2
NOGRADED	2	2	1	2	10	0	2	1	0	0	0	36
NOGRADED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					3.5	3.0	1.0	0.5	0.0	0.0	5.0	19.0
NOGRADED	3	1	3	1	4	0	0	0	0	0	0	4
NOGRADED	3	2	1	3	0	0	0	0	0	0	0	0
NOGRADED	3	3	2	3	0	0	0	0	0	0	0	0
MEAN					1.3	0.0	0.0	0.0	0.0	0.0	0.0	1.3
NOGRADED	1	1	3	3	8	16	15	0	5	21	4	69
NOGRADED	1	2	1	1	11	8	4	5	0	2	0	30
NOGRADED	1	3	2	2	7	13	6	3	0	3	0	32
MEAN					8.7	12.3	8.3	2.7	1.7	8.7	1.3	43.7
NOGRADED	2	1	3	2	1	0	0	0	0	0	2	3
NOGRADED	2	2	1	2	16	15	15	11	0	2	2	61
NOGRADED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					8.5	7.5	7.5	5.5	0.0	1.0	2.0	32.0
NOGRADED	3	1	3	1	1	0	0	1	0	1	0	3
NOGRADED	3	2	1	3	0	0	0	0	0	0	0	0
NOGRADED	3	3	2	3	0	0	0	0	0	0	0	0
MEAN					0.3	0.0	0.0	0.3	0.0	0.3	0.0	1.0

TABLE 46

RAW DATA=NO. APHIDS PER 100 TILLERS.-S. AVEAEE 6/7

TREAT	SURF	ROW	COL	SNIP	1	2	3	4(AP)	4(AL)	AP	AL	TOT
CONTROL	1	1	1	1	2	4	3	0	0	3	0	12
CONTROL	1	2	2	2	0	1	1	0	0	3	1	5
CONTROL	1	3	3	3	4	3	0	1	0	14	0	38
MEAN					3.3	2.7	3.3	2.3	0.0	6.7	0.0	18.3
CONTROL	2	1	1	2	0	4	4	1	0	0	1	10
CONTROL	2	2	2	1	3	3	2	1	0	2	2	16
CONTROL	2	3	3	1	8	8	8	8	8	8	8	8
MEAN					1.3	3.3	3.0	2.5	0.0	4.0	1.5	16.0
CONTROL	3	1	1	3	0	0	2	0	0	0	0	2
CONTROL	3	2	2	3	19	5	6	0	0	2	3	35
CONTROL	3	3	3	7	3	1	0	2	0	0	0	6
MEAN					7.3	2.0	2.7	0.7	0.0	0.7	1.0	14.3
HOPPED	1	1	2	2	0	0	2	0	0	0	0	2
HOPPED	1	2	3	2	2	18	1	0	3	2	0	26
HOPPED	1	3	1	2	0	5	0	1	0	1	0	7
MEAN					0.7	7.7	1.0	0.3	1.0	1.0	0.0	11.7
HOPPED	2	1	2	3	12	1	0	0	1	3	2	21
HOPPED	2	2	3	1	19	14	15	11	9	2	3	88
HOPPED	2	3	1	3	3	5	17	0	6	1	2	28
MEAN					11.3	8.0	13.3	3.7	0.3	2.0	2.3	31.0
HOPPED	3	1	2	1	4	3	1	0	1	1	0	10
HOPPED	3	2	3	3	0	3	0	0	0	0	0	3
HOPPED	3	3	1	1	0	0	0	0	0	0	0	0
MEAN					1.3	2.0	0.3	0.0	0.3	0.3	0.0	4.3
HOPPED	1	1	3	3	12	10	4	4	2	15	1	57
HOPPED	1	2	1	1	13	3	9	2	4	9	0	49
HOPPED	1	3	2	2	34	15	16	9	4	6	4	98
MEAN					19.7	9.3	11.3	6.3	3.3	10.0	1.7	81.7
HOPPED	2	1	3	2	11	7	5	3	0	5	1	32
HOPPED	2	2	1	2	7	13	16	12	0	2	1	49
HOPPED	2	3	2	1	8	8	8	8	8	8	8	8
MEAN					4.0	10.0	9.5	7.5	0.0	3.5	1.0	40.5
HOPPED	3	1	3	1	2	0	0	0	0	0	0	2
HOPPED	3	2	1	3	0	0	0	0	1	0	0	1
HOPPED	3	3	2	3	10	8	4	4	0	1	3	30
MEAN					4.0	2.7	1.3	1.3	0.3	0.3	1.0	11.3
NOPPED	1	1	3	3	7	0	7	1	3	13	0	31
NOPPED	1	2	1	1	8	7	8	6	1	3	0	33
NOPPED	1	3	2	2	4	4	6	2	2	2	2	22
MEAN					6.3	3.7	7.0	3.0	2.0	6.0	0.7	28.7
NOPPED	2	1	3	2	11	0	0	0	2	0	0	13
NOPPED	2	2	1	2	13	5	3	0	0	4	1	26
NOPPED	2	3	2	1	8	8	8	8	8	8	8	8
MEAN					12.0	2.5	1.5	0.0	1.0	2.0	0.5	19.5
NOPPED	3	1	3	1	1	0	0	0	0	2	0	3
NOPPED	3	2	1	3	0	3	0	0	0	0	0	3
NOPPED	3	3	2	3	0	0	0	0	0	0	0	0
MEAN					0.3	1.0	0.0	0.0	0.0	0.7	0.0	2.0

TABLE 47

RAW DATA=40. APHIDS PER 100 TILLERS.-S.AVENAE 11/7

TREAT	SUBPLOT	ROW	COL	SUBP	1	2	3	4(AP)	4(AL)	AP	AL	TOT
CONTROL	1	1	1	1	0	0	1	2	0	1	0	4
CONTROL	1	2	2	2	1	0	0	0	0	1	0	2
CONTROL	1	3	3	3	1	1	5	7	0	2	0	16
MEAN					0.7	0.3	2.0	3.0	0.0	1.3	0.0	7.3
CONTROL	2	1	1	2	9	13	13	8	0	18	0	59
CONTROL	2	2	2	1	14	14	11	15	0	5	3	65
CONTROL	2	3	3	1	*	*	*	*	*	*	*	*
MEAN					11.5	13.5	12.0	10.5	0.0	13.0	1.5	62.0
CONTROL	3	1	1	3	7	0	0	1	0	3	1	12
CONTROL	3	2	2	3	7	1	0	0	0	0	2	10
CONTROL	3	3	3	2	12	2	0	0	0	2	2	18
MEAN					7.7	1.0	0.0	0.3	0.0	3.7	1.7	15.3
NUGRPPED	1	1	2	2	0	1	0	0	0	0	1	2
NUGRPPED	1	2	3	2	1	2	0	0	0	2	1	6
NUGRPPED	1	3	1	2	2	0	2	0	0	1	0	11
MEAN					1.0	3.0	0.7	0.0	0.0	1.0	0.7	6.3
NUGRPPED	2	1	2	3	7	2	3	1	0	7	2	22
NUGRPPED	2	2	3	1	30	31	3	3	0	8	18	93
NUGRPPED	2	3	1	3	3	2	22	11	0	13	0	51
MEAN					13.3	11.7	9.3	5.0	0.0	9.3	6.7	55.3
NUGRPPED	3	1	2	1	1	0	0	0	0	0	0	1
NUGRPPED	3	2	3	3	0	0	0	0	0	0	2	2
NUGRPPED	3	3	1	1	5	0	0	0	0	0	2	10
MEAN					3.0	0.0	0.0	0.0	0.0	0.0	1.3	4.3
NOPPED	1	1	3	3	24	18	13	18	1	14	2	90
NOPPED	1	2	1	1	12	14	12	8	8	11	1	64
NOPPED	1	3	2	2	13	11	31	12	12	5	4	84
MEAN					16.3	14.3	18.7	12.0	7.0	10.0	2.3	70.7
NOPPED	2	1	3	2	3	4	6	4	0	4	2	27
NOPPED	2	2	1	2	20	12	9	9	0	5	0	64
NOPPED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					11.5	10.0	7.5	6.5	0.0	6.0	4.0	45.5
NOPPED	3	1	3	1	0	3	1	0	0	0	1	5
NOPPED	3	2	1	3	0	0	0	0	0	0	0	0
NOPPED	3	3	2	3	14	0	0	0	0	2	2	18
MEAN					4.7	1.0	0.3	0.0	0.0	0.7	1.0	7.7
NOPPED	1	1	3	3	1	1	0	0	0	1	0	3
NOPPED	1	2	1	1	18	11	10	1	0	5	1	46
NOPPED	1	3	2	2	0	0	1	0	0	0	0	1
MEAN					6.3	4.0	3.7	0.3	0.0	2.0	0.3	16.7
NOPPED	2	1	3	2	1	0	3	0	0	11	1	16
NOPPED	2	2	1	2	25	13	12	16	0	3	5	74
NOPPED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					13.0	6.5	7.5	8.0	0.0	7.0	3.0	45.0
NOPPED	3	1	3	1	0	0	0	0	0	2	0	2
NOPPED	3	2	1	3	5	1	0	1	0	0	2	9
NOPPED	3	3	2	3	11	2	0	1	2	0	5	21
MEAN					5.3	1.0	0.0	0.7	0.7	0.7	2.3	10.7

TABLE 48

RAW DATA-NO. APHIDS PER 100 TILLERS.-S.AVENAE 17/7

TREAT	SO	DO	AT	ROW	COL	SUBP	1	2	3	4(AP)	4(AL)	AP	AL	TOT
CONTROL	1	1	1	1	1	1	0	0	0	0	0	0	0	0
CONTROL	1	2	2	2	2	2	0	1	0	0	0	0	2	3
CONTROL	1	3	3	3	3	3	0	0	0	0	0	0	0	0
MEAN							0.0	0.3	0.0	0.0	0.0	0.0	0.7	1.0
CONTROL	2	1	1	2	1	1	9	2	0	3	0	5	2	21
CONTROL	2	2	2	2	2	2	37	32	14	13	0	10	5	114
CONTROL	2	3	3	3	3	3	*	*	*	*	1	*	*	*
MEAN							23.0	17.0	7.0	6.0	1.5	7.5	3.5	67.5
CONTROL	3	1	1	3	1	1	11	2	2	0	0	4	1	20
CONTROL	3	2	2	3	2	2	35	16	9	0	0	1	17	79
CONTROL	3	3	3	3	3	3	5	0	0	2	0	1	5	14
MEAN							17.0	6.0	3.7	0.7	0.0	2.0	4.0	37.3
NOGPPED	1	1	2	2	1	1	0	0	0	0	0	0	1	1
NOGPPED	1	2	3	2	2	2	4	16	3	0	0	0	3	26
NOGPPED	1	3	1	2	2	2	3	1	1	0	0	0	1	6
MEAN							2.3	5.7	1.3	0.0	0.0	0.0	1.7	11.0
NOGPPED	2	1	2	3	1	1	11	1	4	9	0	2	4	31
NOGPPED	2	2	3	3	2	2	65	31	46	31	0	20	10	209
NOGPPED	2	3	1	3	3	3	0	0	0	4	0	0	3	19
MEAN							25.3	10.7	17.3	14.7	2.7	10.0	5.7	66.3
NOGPPED	3	1	2	1	1	1	9	6	0	0	0	0	2	17
NOGPPED	3	2	3	3	2	2	19	0	0	1	0	0	7	27
NOGPPED	3	3	1	1	1	1	4	2	1	0	1	0	6	13
MEAN							10.7	2.7	0.3	0.3	0.0	0.0	5.0	19.0
NOGPPED	1	1	3	3	1	1	14	32	25	4	0	15	2	97
NOGPPED	1	2	1	1	1	1	15	31	27	4	0	5	4	99
NOGPPED	1	3	2	2	2	2	10	3	11	2	0	3	7	36
MEAN							13.0	22.0	21.0	4.7	3.0	7.7	6.0	77.3
NOGPPED	2	1	3	2	2	2	3	2	6	10	0	2	2	32
NOGPPED	2	2	1	2	2	2	54	54	32	39	0	16	6	204
NOGPPED	2	3	2	1	1	1	*	*	*	*	1	*	*	*
MEAN							24.5	28.0	19.0	24.5	5.0	9.0	4.0	116.0
NOGPPED	3	1	3	1	1	1	5	0	0	0	0	0	1	6
NOGPPED	3	2	1	3	2	2	11	17	1	0	0	0	4	33
NOGPPED	3	3	2	3	3	3	56	8	2	0	0	4	14	44
MEAN							24.0	4.3	1.0	0.0	0.0	1.3	6.3	41.0
NOGPPED	1	1	3	3	1	1	0	1	1	0	0	1	0	3
NOGPPED	1	2	1	1	1	1	19	16	6	1	4	5	3	54
NOGPPED	1	3	2	2	2	2	0	0	0	0	0	0	0	0
MEAN							6.3	5.7	2.3	0.3	1.3	2.0	1.0	19.0
NOGPPED	2	1	3	2	2	2	1	0	2	1	0	5	1	10
NOGPPED	2	2	1	2	2	2	9	26	22	17	10	4	10	98
NOGPPED	2	3	2	1	1	1	*	*	*	*	*	*	*	*
MEAN							5.0	13.0	12.0	9.0	5.0	4.5	5.5	54.0
NOGPPED	3	1	3	1	1	1	5	0	0	0	0	0	0	5
NOGPPED	3	2	1	3	2	2	16	3	0	0	0	2	2	23
NOGPPED	3	3	2	3	3	3	*	*	*	*	*	*	*	*
MEAN							10.5	1.5	0.0	0.0	0.0	1.0	1.0	14.0

TABLE 49

RAW DATA-NO. APHIDS PER 100 TILLERS.-S. AVEHAIE 24/7

TREAT	SURDAT	ROW	COL	SUBP	1	2	3	4(2P)	4(2.7)	AF	AL	TOT
CONTROL	1	1	1	1	0	0	0	0	0	0	0	0
CONTROL	1	2	2	2	1	1	3	3	1	3	9	9
CONTROL	1	3	3	3	0	7	0	0	0	0	0	7
MEAN					0.3	2.7	1.0	1.0	0.0	0.3	0.0	5.3
CONTROL	2	1	1	2	2	3	2	3	1	0	1	14
CONTROL	2	2	2	1	10	11	14	11	1	0	3	54
CONTROL	2	3	3	1	*	*	*	*	1	*	*	*
MEAN					9.0	7.0	6.0	7.0	2.0	3.0	0.3	30.3
CONTROL	3	1	1	3	3	0	2	1	1	0	2	4
CONTROL	3	2	2	3	11	10	0	0	1	2	5	26
CONTROL	3	3	3	2	16	6	2	3	1	3	3	33
MEAN					10.0	5.3	1.3	1.3	0.0	1.7	3.3	23.0
NUGREENED	1	1	2	2	1	1	1	0	1	1	0	4
NUGREENED	1	2	3	2	2	4	3	3	1	1	1	14
NUGREENED	1	3	1	2	0	2	11	0	1	1	0	21
MEAN					3.0	2.3	5.0	1.0	0.3	1.0	0.3	13.3
NUGREENED	2	1	2	3	7	0	3	1	1	7	1	14
NUGREENED	2	2	3	1	11	8	23	30	1	0	4	44
NUGREENED	2	3	1	3	9	10	7	10	1	7	4	53
MEAN					9.0	6.0	11.0	13.7	2.0	7.3	3.0	52.0
NUGREENED	3	1	2	1	8	0	0	2	1	1	0	11
NUGREENED	3	2	3	3	25	10	0	1	1	0	7	49
NUGREENED	3	3	1	1	64	50	33	21	1	4	24	202
MEAN					32.3	22.0	13.0	8.0	0.0	1.7	10.3	47.3
NUGREENED	1	1	3	3	1	8	1	0	1	0	1	12
NUGREENED	1	2	1	1	5	11	17	4	1	4	3	51
NUGREENED	1	3	2	2	2	9	0	0	1	0	2	4
MEAN					2.7	6.3	6.0	1.3	2.7	1.3	2.0	22.3
NUGREENED	2	1	3	2	3	6	4	8	1	4	0	27
NUGREENED	2	2	1	2	10	17	21	12	1	1	2	60
NUGREENED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					6.5	12.5	12.5	10.0	1.5	2.5	1.0	40.5
NUGREENED	3	1	3	1	6	2	1	0	1	2	3	14
NUGREENED	3	2	1	3	18	19	11	5	1	0	10	69
NUGREENED	3	3	2	3	40	9	2	3	1	1	4	63
MEAN					21.3	10.0	4.7	2.7	0.0	1.0	9.0	48.7
NOPRED	1	1	3	3	0	0	0	0	0	1	0	1
NOPRED	1	2	1	1	1	7	7	0	1	2	1	19
NOPRED	1	3	2	2	0	0	0	2	0	0	0	2
MEAN					0.3	2.3	2.3	0.7	0.3	1.0	0.3	7.3
NOPRED	2	1	3	2	0	0	0	1	0	0	0	1
NOPRED	2	2	1	2	23	16	14	10	2	0	7	72
NOPRED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					11.5	8.0	7.0	5.5	1.0	0.0	3.5	36.5
NOPRED	3	1	3	1	4	2	1	1	0	0	3	11
NOPRED	3	2	1	3	35	13	0	1	0	1	12	62
NOPRED	3	3	2	3	*	*	*	*	*	*	*	*
MEAN					19.5	7.5	0.5	1.0	0.0	0.5	7.5	36.5

TABLE 50

RAW DATA-NO. APHIDS PER 100 TILLERS.-S. AVENAE 3/8

	TRIAL	STAND	ROW	CUB	DATE	1	2	3	4 (AP)	4 (AL)	AP	AL	TOT
CONTROL	1	1	1	1		0	0	0	1	0	0	0	1
CONTROL	1	2	2	2		0	0	0	0	0	0	1	1
CONTROL	1	3	3	3		0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.0	0.3	0.0	0.0	0.3	0.7
CONTROL	2	1	1	2		0	0	0	0	0	0	2	2
CONTROL	2	2	2	1		0	1	0	0	0	0	0	1
CONTROL	2	3	3	1		*	*	*	*	*	*	*	*
MEAN						0.0	0.3	0.0	0.0	0.0	0.0	1.0	1.3
CONTROL	3	1	1	3		23	1	0	1	0	1	4	30
CONTROL	3	2	2	3		19	1	0	0	0	0	2	22
CONTROL	3	3	3	2		17	2	0	1	0	0	11	31
MEAN						19.7	1.3	0.0	0.7	0.0	0.3	5.7	27.7
NOGRPEED	1	1	2	2		0	0	0	0	0	0	0	0
NOGRPEED	1	2	3	2		0	0	0	0	0	0	0	0
NOGRPEED	1	3	1	2		0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOGRPEED	2	1	2	3		1	0	0	0	0	0	1	2
NOGRPEED	2	2	3	1		0	0	2	1	0	0	1	4
NOGRPEED	2	3	1	3		0	0	0	0	0	0	3	3
MEAN						0.3	0.0	0.7	0.3	0.0	0.0	1.7	3.0
NOGRPEED	3	1	2	1		27	3	0	0	0	0	10	41
NOGRPEED	3	2	3	3		13	7	2	0	0	0	27	49
NOGRPEED	3	3	1	1		29	1	0	0	0	0	14	44
MEAN						23.0	4.0	0.7	0.0	0.0	0.0	18.3	38.0
NOPEED	1	1	3	3		0	0	0	0	0	0	0	0
NOPEED	1	2	1	1		0	0	1	0	0	0	0	1
NOPEED	1	3	2	2		0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3
NOPEED	2	1	3	2		1	1	0	0	0	0	0	2
NOPEED	2	2	1	2		17	11	7	7	0	1	0	43
NOPEED	2	3	2	1		*	*	*	*	*	*	*	*
MEAN						7.0	6.0	3.5	3.5	0.0	0.5	0.0	22.5
NOPEED	3	1	3	1		14	5	7	0	0	0	11	37
NOPEED	3	2	1	3		132	50	13	1	3	0	31	246
NOPEED	3	3	2	3		25	10	5	1	0	0	21	62
MEAN						57.0	27.0	8.3	0.7	1.0	0.0	21.0	115.0
NOPRED	1	1	3	3		0	0	0	0	0	0	0	0
NOPRED	1	2	1	1		0	0	0	0	0	0	0	0
NOPRED	1	3	2	2		0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOPRED	2	1	3	2		0	0	0	0	0	0	1	1
NOPRED	2	2	1	2		3	1	0	0	0	2	5	11
NOPRED	2	3	2	1		*	*	*	*	*	*	*	*
MEAN						1.5	0.5	0.0	0.0	0.0	1.0	3.0	6.0
NOPRED	3	1	3	1		0	0	0	0	0	0	0	0
NOPRED	3	2	1	3		81	15	1	2	0	0	13	112
NOPRED	3	3	2	3		4	1	0	0	0	0	7	12
MEAN						28.3	5.3	0.3	0.7	0.0	0.0	6.7	41.3

.....ESTIMATED VALUE.....

RAW DATA-PERCENT INFESTED TILLERS-S AVERAGE

TREAT SOWDAT ROW COL SUBP 13/6 15/6 6/7 11/7 17/7 24/7

CONTROL	1	1	1	1	22	6	8	4	0	0
CONTROL	1	2	2	2	15	25	5	1	3	7
CONTROL	1	3	3	3	16	1	21	7	4	3
MEAN					17.7	10.7	11.3	4.0	2.3	3.3

CONTROL	2	1	1	2	9	5	9	10	9	9
CONTROL	2	2	2	1	16	6	12	25	34	29
CONTROL	2	3	3	1	*	*	*	*	*	*
MEAN					12.5	5.5	10.5	17.5	21.5	19.0

CONTROL	3	1	1	3	0	3	1	4	9	5
CONTROL	3	2	2	3	1	3	13	6	20	12
CONTROL	3	3	3	2	1	2	5	9	8	13
MEAN					0.7	2.7	6.3	6.3	12.3	10.0

NOGRPRD	1	1	2	2	5	6	2	2	2	3
NOGRPRD	1	2	3	2	11	15	0	4	16	10
NOGRPRD	1	3	1	2	10	15	3	5	6	13
MEAN					8.7	12.0	4.3	3.7	8.0	8.7

NOGRPRD	2	1	2	3	4	0	10	10	10	8
NOGRPRD	2	2	3	1	7	6	26	23	53	31
NOGRPRD	2	3	1	3	6	15	0	12	14	19
MEAN					5.7	7.0	12.0	15.0	25.7	19.3

NOGRPRD	3	1	2	1	0	1	2	1	4	7
NOGRPRD	3	2	3	3	4	0	2	2	14	23
NOGRPRD	3	3	1	1	0	4	9	5	8	53
MEAN					1.3	1.7	4.3	2.7	8.7	27.7

NOFRED	1	1	3	3	13	3	27	30	31	5
NOFRED	1	2	1	1	10	11	25	30	43	29
NOFRED	1	3	2	2	10	8	32	36	19	3
MEAN					11.0	7.3	28.0	32.0	31.0	12.3

NOFRED	2	1	3	2	2	3	9	12	16	12
NOFRED	2	2	1	2	5	14	16	25	46	31
NOFRED	2	3	2	1	*	*	*	*	*	*
MEAN					3.5	8.5	12.5	18.5	31.0	21.5

NOFRED	3	1	3	1	1	1	1	2	8	8
NOFRED	3	2	1	3	7	2	1	0	11	32
NOFRED	3	3	2	3	0	0	11	5	18	24
MEAN					2.7	1.0	4.3	2.3	12.3	21.3

NOFRED	1	1	3	3	26	3	9	2	3	3
NOFRED	1	2	1	1	5	15	19	20	18	14
NOFRED	1	3	2	2	12	6	14	1	0	1
MEAN					14.3	8.0	14.0	7.7	7.0	6.0

NOFRED	2	1	3	2	2	2	3	12	7	1
NOFRED	2	2	1	2	4	7	13	24	37	25
NOFRED	2	3	2	1	*	*	*	*	*	*
MEAN					3.0	4.5	8.0	18.0	22.0	13.0

NOFRED	3	1	3	1	0	2	1	2	7	9
NOFRED	3	2	1	3	1	0	3	5	14	29
NOFRED	3	3	2	3	0	2	9	8	*	10
MEAN					0.3	1.3	4.3	5.0	10.5	16.0

TABLE 52

RAW DATA-NO. APHIDS PER 100 TILLERS.-M.DIRRHODUM 13/6

TREAT	SUNDAT	ROW	COL	SURP	1	2	3	4(AP)	4(AL)	AP	AL	TOT
CONTROL	1	1	1	1	0	0	0	0	0	0	0	0
CONTROL	1	2	2	2	6	18	7	7	0	1	1	40
CONTROL	1	3	3	3	0	0	6	0	0	1	0	7
MEAN					2.0	6.0	3.3	2.3	0.0	0.7	0.3	15.7
CONTROL	2	1	1	2	0	0	0	0	0	1	0	1
CONTROL	2	2	2	1	0	0	0	0	0	0	0	0
CONTROL	2	3	3	1	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.5
CONTROL	3	1	1	3	0	0	0	0	0	0	0	0
CONTROL	3	2	2	3	0	0	1	1	0	1	0	3
CONTROL	3	3	3	2	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.3	0.3	0.0	0.3	0.0	1.0
NOGRPRD	1	1	2	2	0	0	0	1	0	0	0	1
NOGRPRD	1	2	3	2	7	23	16	9	0	0	0	55
NOGRPRD	1	3	1	2	12	8	3	3	0	4	0	30
MEAN					6.3	10.3	6.3	4.3	0.0	1.3	0.0	28.7
NOGRPRD	2	1	2	3	1	0	0	0	0	1	0	2
NOGRPRD	2	2	3	1	1	0	0	0	0	0	0	1
NOGRPRD	2	3	1	3	0	0	0	2	0	0	1	3
MEAN					0.7	0.0	0.0	0.7	0.0	0.3	0.3	2.0
NOGRPRD	3	1	2	1	0	0	1	0	0	0	0	1
NOGRPRD	3	2	3	3	0	0	0	0	0	0	0	0
NOGRPRD	3	3	1	1	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3
NOPRED	1	1	3	3	0	0	0	0	0	0	0	0
NOPRED	1	2	1	1	0	0	0	0	0	0	0	0
NOPRED	1	3	2	2	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOPRED	2	1	3	2	0	0	0	0	0	0	0	0
NOPRED	2	2	1	2	0	0	0	0	0	0	0	0
NOPRED	2	3	2	1	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOPRED	3	1	3	1	0	0	0	0	0	0	0	0
NOPRED	3	2	1	3	0	5	0	0	0	1	0	6
NOPRED	3	3	2	3	0	0	0	0	0	0	0	0
MEAN					0.0	1.7	0.0	0.0	0.0	0.3	0.0	2.0
NOPRED	1	1	3	3	0	0	1	0	0	0	0	1
NOPRED	1	2	1	1	0	0	5	4	0	1	0	10
NOPRED	1	3	2	2	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	2.0	1.3	0.0	0.3	0.0	3.7
NOPRED	2	1	3	2	0	0	0	0	0	0	0	0
NOPRED	2	2	1	2	0	0	0	0	0	0	0	0
NOPRED	2	3	2	1	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOPRED	3	1	3	1	0	2	0	0	0	1	1	4
NOPRED	3	2	1	3	0	0	0	0	0	1	0	1
NOPRED	3	3	2	3	0	1	0	0	2	0	0	1
MEAN					0.0	1.0	0.0	0.0	0.0	0.7	0.3	2.0

TABLE 53

RAW DATA-NO. APHIDS PER 100 TILLERS.-M. DIRHODUM 1976

TREAT	SOW	DATE	ROW	CUL	SURP	1	2	3	4(AP)	4(AL)	AP	AL	TOT
CONTROL	1	1	1	1	1	0	0	0	0	0	0	0	0
CONTROL	1	2	2	2	2	14	4	1	0	0	4	0	25
CONTROL	1	3	3	3	3	7	10	0	0	0	1	0	18
MEAN						7.0	4.7	0.3	0.0	0.0	2.3	0.0	14.3
CONTROL	2	1	1	2	2	0	0	0	0	0	0	0	0
CONTROL	2	2	2	1	1	0	0	0	0	0	0	0	0
CONTROL	2	3	3	1	1	*	*	*	*	*	*	*	*
MEAN						0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CONTROL	3	1	1	3	3	0	5	1	1	0	1	0	4
CONTROL	3	2	2	3	3	4	7	4	4	0	3	1	23
CONTROL	3	3	3	2	2	2	0	0	0	0	1	0	3
MEAN						2.0	4.0	1.7	1.7	0.0	1.7	0.3	11.3
NOGRPRD	1	1	2	2	2	0	0	0	0	0	0	0	0
NOGRPRD	1	2	3	2	2	21	21	8	0	3	0	0	53
NOGRPRD	1	3	1	2	2	4	3	7	2	0	1	0	17
MEAN						8.3	8.0	5.0	0.7	1.0	0.3	0.0	23.3
NOGRPRD	2	1	2	3	3	2	0	0	0	0	0	0	2
NOGRPRD	2	2	3	1	1	14	0	6	1	0	2	0	23
NOGRPRD	2	3	1	3	3	3	0	3	0	0	0	0	6
MEAN						6.3	0.0	3.0	0.3	0.0	0.7	0.0	10.3
NOGRPRD	3	1	2	1	1	2	3	0	0	1	3	0	4
NOGRPRD	3	2	3	3	3	0	2	1	0	0	0	0	3
NOGRPRD	3	3	1	1	1	0	0	0	0	0	0	0	0
MEAN						0.7	1.7	0.3	0.0	0.3	1.0	0.0	4.0
NOPRED	1	1	3	3	3	0	0	0	0	0	0	0	0
NOPRED	1	2	1	1	1	2	14	7	0	0	0	0	23
NOPRED	1	3	2	2	2	0	0	0	0	0	0	0	0
MEAN						0.7	4.7	2.3	0.0	0.0	0.0	0.0	7.7
NOPRED	2	1	3	2	2	11	0	0	0	0	1	2	14
NOPRED	2	2	1	2	2	0	2	2	0	0	1	0	5
NOPRED	2	3	2	1	1	*	*	*	*	*	*	*	*
MEAN						5.5	1.0	1.0	0.0	0.0	1.0	1.0	9.5
NOPRED	3	1	3	1	1	8	0	2	0	0	1	0	11
NOPRED	3	2	1	3	3	0	4	6	0	0	1	0	11
NOPRED	3	3	2	3	3	10	10	5	3	0	0	0	28
MEAN						6.0	1.7	4.3	1.0	0.0	0.7	0.0	16.7
NOPRED	1	1	3	3	3	0	0	0	0	0	1	0	13
NOPRED	1	2	1	1	1	1	1	4	1	0	1	0	8
NOPRED	1	3	2	2	2	0	5	5	0	0	0	0	16
MEAN						4.3	4.0	3.0	0.3	0.0	0.7	0.0	12.3
NOPRED	2	1	3	2	2	0	1	0	0	0	0	0	10
NOPRED	2	2	1	2	2	7	1	3	1	0	0	1	13
NOPRED	2	3	2	1	1	*	*	*	*	*	*	*	*
MEAN						5.0	1.0	1.5	0.5	0.0	0.0	0.5	11.5
NOPRED	3	1	3	1	1	0	0	0	0	1	2	2	5
NOPRED	3	2	1	3	3	4	2	0	0	0	1	0	7
NOPRED	3	3	2	3	3	5	10	2	1	0	2	0	20
MEAN						3.0	4.0	0.7	0.3	0.3	1.7	0.7	10.7

TABLE 54

RAW DATA-NO. APHIDS PER 100 TILLERS.-M. DIRRHODUM 27/6

TREAT	SOW DAT	ROW	COL	SURP	1	2	3	4(AP)	4(AL)	AP	AL	TOT
CONTROL	1	1	1	1	2	10	6	2	0	6	0	32
CONTROL	1	2	2	2	0	1	2	1	0	4	0	4
CONTROL	1	3	3	3	0	2	2	0	0	1	0	5
MEAN					0.7	6.3	3.3	1.0	0.0	3.7	0.0	15.0
CONTROL	2	1	1	2	2	0	1	1	0	2	2	4
CONTROL	2	2	2	1	14	4	2	2	0	1	0	23
CONTROL	2	3	3	1	*	*	*	*	*	*	*	*
MEAN					8.0	2.0	1.5	1.5	0.0	1.5	1.0	15.5
CONTROL	3	1	1	3	2	2	0	3	1	7	0	15
CONTROL	3	2	2	3	7	4	4	2	0	0	2	19
CONTROL	3	3	3	2	0	0	3	1	0	0	0	4
MEAN					3.0	2.0	2.3	2.0	0.3	2.3	0.7	12.7
NOGRPHED	1	1	2	2	10	4	0	0	0	3	0	17
NOGRPHED	1	2	3	2	6	14	0	2	0	3	0	25
NOGRPHED	1	3	1	2	0	0	0	0	0	0	0	0
MEAN					5.3	6.0	0.0	0.7	0.0	2.0	0.0	14.0
NOGRPHED	2	1	2	3	0	0	0	0	0	1	0	1
NOGRPHED	2	2	3	1	6	1	1	10	0	4	2	24
NOGRPHED	2	3	1	3	0	0	0	0	0	0	0	0
MEAN					2.0	0.3	0.3	3.3	0.0	1.7	0.7	8.3
NOGRPHED	3	1	2	1	0	0	0	0	0	0	0	0
NOGRPHED	3	2	3	3	0	0	0	0	0	0	0	0
NOGRPHED	3	3	1	1	2	0	0	0	0	1	0	3
MEAN					0.7	0.0	0.0	0.0	0.0	0.3	0.0	1.0
NOPRED	1	1	3	3	41	13	7	4	0	9	0	74
NOPRED	1	2	1	1	32	7	9	6	0	8	0	62
NOPRED	1	3	2	2	0	0	0	0	0	0	0	0
MEAN					24.3	6.7	5.3	3.3	0.0	5.7	0.0	45.3
NOPRED	2	1	3	2	0	0	0	0	0	0	0	0
NOPRED	2	2	1	2	8	3	0	0	0	2	3	16
NOPRED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					4.0	1.5	0.0	0.0	0.0	1.0	1.5	4.0
NOPRED	3	1	3	1	0	0	0	0	0	1	0	1
NOPRED	3	2	1	3	0	0	0	1	0	0	0	1
NOPRED	3	3	2	3	0	0	0	0	0	0	1	0
MEAN					0.0	0.0	0.0	0.3	0.0	0.3	0.0	0.7
NOPRED	1	1	3	3	17	4	3	1	0	6	0	30
NOPRED	1	2	1	1	2	2	1	0	0	0	2	12
NOPRED	1	3	2	2	1	3	3	0	0	1	1	7
MEAN					6.7	4.7	2.0	0.3	0.0	4.3	1.0	19.0
NOPRED	2	1	3	2	0	0	0	0	0	2	0	2
NOPRED	2	2	1	2	4	0	0	0	0	0	2	6
NOPRED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					2.0	0.0	0.0	0.0	0.0	1.0	1.0	4.0
NOPRED	3	1	3	1	0	2	0	0	0	0	0	2
NOPRED	3	2	1	3	0	1	0	0	0	0	0	1
NOPRED	3	3	2	3	5	0	0	0	0	0	1	6
MEAN					1.7	1.0	0.0	0.0	0.0	0.0	0.3	3.0

TABLE 55

RAW DATA-NO. APHIDS PER 100 TILLERS.-M.DIRHODUM 6/7

TREAT	SUNDAT	ROW	COL	SUMP	1	2	3	4(AP)	4(AL)	AP	AL	TOT
CONTROL	1	1	1	1	1	0	0	0	0	1	0	2
CONTROL	1	2	2	2	0	0	0	0	0	0	0	0
CONTROL	1	3	3	3	0	0	2	0	0	1	0	3
MEAN					0.3	0.0	0.7	0.0	0.0	0.7	0.0	1.7
CONTROL	2	1	1	2	0	8	0	0	0	1	0	9
CONTROL	2	2	2	1	5	6	4	3	0	1	0	19
CONTROL	2	3	3	1	*	*	*	*	*	*	*	*
MEAN					2.5	7.0	2.0	1.5	0.0	1.0	0.0	14.0
CONTROL	3	1	1	3	4	5	8	0	0	9	0	26
CONTROL	3	2	2	3	17	2	2	1	1	1	5	29
CONTROL	3	3	3	2	10	7	7	0	0	2	0	26
MEAN					10.3	4.7	5.7	0.3	0.3	4.0	1.7	27.0
NOGRPRD	1	1	2	2	3	1	4	0	0	1	3	12
NOGRPRD	1	2	3	2	3	0	0	0	0	2	1	6
NOGRPRD	1	3	1	2	0	0	0	0	0	0	0	0
MEAN					2.0	0.3	1.3	0.0	0.0	1.0	1.3	6.0
NOGRPRD	2	1	2	3	0	0	0	0	0	0	1	1
NOGRPRD	2	2	3	1	1	5	8	0	0	1	0	15
NOGRPRD	2	3	1	3	1	0	7	0	0	1	2	11
MEAN					0.7	1.7	5.0	0.0	0.0	0.7	1.0	9.0
NOGRPRD	3	1	2	1	0	0	0	1	0	3	0	4
NOGRPRD	3	2	3	3	0	0	0	0	0	0	0	0
NOGRPRD	3	3	1	1	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.3	0.0	1.0	0.0	1.3
NOPRD	1	1	3	3	19	20	8	0	0	8	1	56
NOPRD	1	2	1	1	11	15	8	5	0	0	4	43
NOPRD	1	3	2	2	39	31	9	2	0	5	2	88
MEAN					23.0	22.0	8.3	2.3	0.0	4.3	2.3	62.3
NOPRD	2	1	3	2	25	6	3	2	0	4	0	40
NOPRD	2	2	1	2	9	0	0	0	0	3	0	11
NOPRD	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					16.5	3.0	1.5	1.0	0.0	3.5	0.0	25.5
NOPRD	3	1	3	1	0	0	0	0	0	0	0	0
NOPRD	3	2	1	3	0	0	0	1	0	0	0	1
NOPRD	3	3	2	3	40	5	5	1	0	0	13	74
MEAN					15.3	1.7	1.7	0.7	0.0	0.0	4.3	23.7
NOPRD	1	1	3	3	10	9	1	0	0	8	1	29
NOPRD	1	2	1	1	13	2	0	0	0	0	0	15
NOPRD	1	3	2	2	0	0	0	0	0	0	0	0
MEAN					7.7	3.7	0.3	0.0	0.0	2.7	0.3	14.7
NOPRD	2	1	3	2	19	8	0	0	1	2	0	30
NOPRD	2	2	1	2	6	10	0	0	0	0	1	17
NOPRD	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					12.5	9.0	4.0	0.0	0.5	1.0	0.5	27.5
NOPRD	3	1	3	1	0	0	0	0	0	0	0	0
NOPRD	3	2	1	3	2	0	0	1	0	0	1	4
NOPRD	3	3	2	3	0	0	0	0	0	0	0	0
MEAN					0.7	0.0	0.0	0.3	0.0	0.0	0.3	1.3

TABLE 56

RAW DATA-NO. APHIDS PER 100 TILLERS.-M.DIRHOODUM 11/7

TREAT	SOW	DATE	ROW	CUL	SURP	1	2	3	4(AP)	4(AL)	AP	AL	TOT
CONTROL	1	1	1	1	1	0	0	0	0	0	0	0	0
CONTROL	1	2	2	2	2	5	0	0	0	0	0	1	6
CONTROL	1	3	3	3	3	12	0	0	0	0	1	0	13
MEAN						5.7	0.0	0.0	0.0	0.0	0.3	0.3	6.3
CONTROL	2	1	1	2	5	1	0	0	0	5	3	14	
CONTROL	2	2	2	1	20	4	11	4	0	0	0	0	31
CONTROL	2	3	3	1	*	*	*	*	*	*	*	*	*
MEAN					16.5	4.5	5.5	3.0	0.0	6.5	1.5	37.5	
CONTROL	3	1	1	3	25	0	0	0	0	0	1	26	
CONTROL	3	2	2	3	57	1	0	1	0	1	7	57	
CONTROL	3	3	3	2	12	0	0	0	1	4	1	18	
MEAN					31.3	0.3	0.0	0.3	0.3	1.7	3.0	37.0	
NOGRPRD	1	1	2	2	0	0	0	0	0	0	0	0	0
NOGRPRD	1	2	3	2	0	0	0	0	0	0	0	0	0
NOGRPRD	1	3	1	2	0	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOGRPRD	2	1	2	3	14	0	0	0	0	0	1	15	
NOGRPRD	2	2	3	1	17	0	0	4	0	1	5	31	
NOGRPRD	2	3	1	3	17	0	3	2	0	5	2	29	
MEAN					16.0	0.0	1.0	3.3	0.0	2.0	2.7	25.0	
NOGRPRD	3	1	2	1	0	0	3	0	0	2	1	6	
NOGRPRD	3	2	3	3	12	0	0	0	0	0	2	14	
NOGRPRD	3	3	1	1	53	2	10	1	0	1	3	78	
MEAN					21.7	0.7	7.0	0.3	0.0	1.0	2.0	32.7	
NOPRD	1	1	3	3	11	7	9	21	0	4	2	54	
NOPRD	1	2	1	1	9	2	17	28	0	1	1	58	
NOPRD	1	3	2	2	15	0	1	9	0	3	0	28	
MEAN					11.7	3.0	9.0	19.3	0.0	2.7	1.0	46.7	
NOPRD	2	1	3	2	13	20	24	6	0	12	1	76	
NOPRD	2	2	1	2	55	40	19	22	0	11	0	147	
NOPRD	2	3	2	1	*	*	*	*	*	*	*	*	
MEAN					34.0	30.0	21.5	14.0	0.0	11.5	0.5	111.5	
NOPRD	3	1	3	1	5	0	0	0	0	1	1	7	
NOPRD	3	2	1	3	4	3	0	0	0	0	0	7	
NOPRD	3	3	2	3	103	3	6	2	0	4	22	140	
MEAN					37.3	2.0	2.0	0.7	0.0	1.7	7.7	51.3	
NOPRD	1	1	3	3	1	4	0	0	0	5	0	10	
NOPRD	1	2	1	1	3	10	11	16	0	16	0	56	
NOPRD	1	3	2	2	0	0	0	0	0	0	0	0	
MEAN					1.3	4.7	3.7	5.3	0.0	7.0	0.0	22.0	
NOPRD	2	1	3	2	19	3	7	7	0	4	1	41	
NOPRD	2	2	1	2	30	1	0	0	0	0	3	34	
NOPRD	2	3	2	1	*	*	*	*	*	*	*	*	
MEAN					24.5	2.0	3.5	3.5	0.0	2.0	2.0	37.5	
NOPRD	3	1	3	1	0	0	0	1	0	0	0	7	
NOPRD	3	2	1	3	0	0	0	0	0	0	0	0	
NOPRD	3	3	2	3	125	5	2	1	0	1	18	152	
MEAN					46.3	1.7	0.7	0.7	0.0	0.3	6.0	55.7	

TABLE 57

RAW DATA-NO. APHIDS PER 100 TILLERS.-M. DIRHOODUM 17/7

TREAT	SOW	DATE	ROW	COL	SUBP	1	2	3	4(AP)	4(AL)	AP	AL	TOT
CONTROL	1	1	1	1	1	0	0	0	0	0	0	0	0
CONTROL	1	2	2	2	2	0	0	0	0	0	0	0	0
CONTROL	1	3	3	3	3	0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CONTROL	2	1	1	2	2	23	1	18	9	0	5	2	57
CONTROL	2	2	2	1	1	27	37	5	19	0	9	6	103
CONTROL	2	3	3	1	1	*	*	*	*	*	*	*	*
MEAN						25.0	19.0	11.5	13.5	0.0	7.0	4.0	80.0
CONTROL	3	1	1	3	3	109	38	6	3	0	4	13	173
CONTROL	3	2	2	3	3	273	52	8	1	0	3	16	363
CONTROL	3	3	3	2	2	67	1	4	1	0	2	5	80
MEAN						149.7	33.7	6.0	1.7	0.0	3.0	11.3	205.3
NOGRPRED	1	1	2	2	2	0	0	0	0	0	0	0	0
NOGRPRED	1	2	3	2	2	0	0	0	0	0	0	0	0
NOGRPRED	1	3	1	2	2	0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOGRPRED	2	1	2	3	3	21	7	0	10	0	12	4	54
NOGRPRED	2	2	3	1	1	51	14	3	0	0	4	14	116
NOGRPRED	2	3	1	3	3	54	10	3	0	0	0	6	73
MEAN						52.0	10.3	2.0	3.3	0.0	5.3	8.0	91.0
NOGRPRED	3	1	2	1	1	46	2	3	1	0	1	4	57
NOGRPRED	3	2	3	3	3	117	15	0	0	0	0	17	149
NOGRPRED	3	3	1	1	1	135	27	10	2	0	0	9	182
MEAN						99.3	14.7	4.3	1.0	0.0	0.3	9.7	129.3
NOPRED	1	1	3	3	3	4	0	0	6	0	3	0	13
NOPRED	1	2	1	1	1	3	5	9	3	3	4	1	28
NOPRED	1	3	2	2	2	0	0	0	0	0	0	0	0
MEAN						2.3	1.7	3.0	3.0	1.0	2.3	0.3	13.7
NOPRED	2	1	3	2	2	64	14	1	7	0	16	5	107
NOPRED	2	2	1	2	2	101	58	19	23	1	7	11	220
NOPRED	2	3	2	1	1	*	*	*	*	*	*	*	*
MEAN						82.5	36.0	10.0	15.0	0.5	11.5	8.0	163.5
NOPRED	3	1	3	1	1	55	8	1	1	0	1	8	74
NOPRED	3	2	1	3	3	201	47	21	7	0	0	17	293
NOPRED	3	3	2	3	3	404	70	12	4	0	8	28	526
MEAN						220.0	41.7	11.3	4.0	0.0	3.0	17.7	297.7
NOPRED	1	1	3	3	3	1	0	0	0	0	0	0	1
NOPRED	1	2	1	1	1	1	0	2	2	0	3	0	14
NOPRED	1	3	2	2	2	0	0	0	0	0	0	0	0
MEAN						0.7	2.0	0.7	0.7	0.0	1.0	0.0	5.0
NOPRED	2	1	3	2	2	34	8	5	0	0	0	3	50
NOPRED	2	2	1	2	2	84	20	11	2	0	3	11	131
NOPRED	2	3	2	1	1	*	*	*	*	*	*	*	*
MEAN						59.0	14.0	8.0	1.0	0.0	1.5	7.0	90.5
NOPRED	3	1	3	1	1	18	4	0	0	0	1	3	26
NOPRED	3	2	1	3	3	119	12	0	0	0	1	13	145
NOPRED	3	3	2	3	3	*	*	*	*	*	*	*	*
MEAN						64.5	8.0	0.0	0.0	0.0	1.0	5.0	45.5

TABLE 58

RAW DATA-NO. APHIDS PER 100 FILLERS.-M.DIRRHODUM 24/7

TREAT	SUM	DATE	ROW	CNL	SUBP	1	2	3	+(AP)	+(AL)	AP	AL	TOT
CONTROL	1	1	1	1	1	0	0	1	0	0	0	0	1
CONTROL	1	2	2	2	2	0	0	0	1	0	0	0	1
CONTROL	1	3	3	3	3	0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.7
CONTROL	2	1	1	2	1	8	1	0	0	0	1	1	11
CONTROL	2	2	2	1	1	7	0	0	1	0	0	2	22
CONTROL	2	3	3	1	1	*	*	*	*	*	*	*	*
MEAN						7.5	3.5	3.0	0.5	0.0	0.5	1.5	16.5
CONTROL	3	1	1	3	3	66	40	11	0	1	7	6	131
CONTROL	3	2	2	3	3	23	10	10	5	0	2	3	54
CONTROL	3	3	3	2	2	6	10	6	2	0	2	1	27
MEAN						31.7	22.0	9.0	2.3	0.3	3.7	3.3	72.3
NOGRPHED	1	1	2	2	2	0	0	0	0	0	0	0	0
NOGRPHED	1	2	3	2	2	0	0	0	0	0	0	0	0
NOGRPHED	1	3	1	2	2	0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOGRPHED	2	1	2	3	3	9	8	1	1	0	3	1	23
NOGRPHED	2	2	3	1	1	6	8	8	8	0	2	3	35
NOGRPHED	2	3	1	3	3	0	2	3	0	0	2	0	7
MEAN						5.0	6.0	4.0	3.0	0.0	2.3	1.3	21.7
NOGRPHED	3	1	2	1	1	0	14	6	0	0	2	1	23
NOGRPHED	3	2	3	3	3	19	19	17	5	0	2	1	63
NOGRPHED	3	3	1	1	1	59	44	28	21	0	0	1	153
MEAN						26.0	25.7	17.0	8.7	0.0	1.3	1.0	74.7
NOPRED	1	1	3	3	3	0	0	0	0	0	0	0	0
NOPRED	1	2	1	1	1	0	0	0	0	0	0	0	0
NOPRED	1	3	2	2	2	0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOPRED	2	1	3	2	2	12	5	13	6	0	1	0	37
NOPRED	2	2	1	2	2	0	15	9	4	0	3	1	38
NOPRED	2	3	2	1	1	*	*	*	*	*	*	*	*
MEAN						9.0	10.0	11.0	5.0	0.0	2.0	0.5	37.5
NOPRED	3	1	3	1	1	8	3	6	0	0	3	0	20
NOPRED	3	2	1	3	3	18	16	27	7	0	0	4	72
NOPRED	3	3	2	3	3	37	45	12	6	0	1	3	104
MEAN						21.0	21.3	15.0	4.3	0.0	1.3	2.3	65.3
NOPRED	1	1	3	3	3	0	0	0	0	0	0	0	0
NOPRED	1	2	1	1	1	0	0	1	0	0	0	0	1
NOPRED	1	3	2	2	2	0	0	0	0	0	0	0	0
MEAN						0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3
NOPRED	2	1	3	2	2	6	0	0	1	0	0	0	7
NOPRED	2	2	1	2	2	11	2	2	0	1	0	0	15
NOPRED	2	3	2	1	1	*	*	*	*	*	*	*	*
MEAN						8.5	1.0	1.0	0.5	0.5	0.0	0.0	11.5
NOPRED	3	1	3	1	1	3	0	4	0	0	1	1	9
NOPRED	3	2	1	3	3	25	15	12	3	0	0	4	54
NOPRED	3	3	2	3	3	*	*	*	*	*	*	*	*
MEAN						14.0	7.5	6.0	1.5	0.0	0.5	2.5	34.0

TABLE 59

RAW DATA-NO. APHIDS PER 100 TILLERS.-M. DIRHODUM 3/8

TREAT	SO-OAT	ROW	CUL	SUBP	1	2	3	4 (AP)	4 (AL)	AP	AL	TOT
CONTROL	1	1	1	1	0	0	0	0	0	0	0	0
CONTROL	1	2	2	2	0	0	0	0	0	0	0	0
CONTROL	1	3	3	3	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CONTROL	2	1	1	2	0	0	0	0	0	0	0	0
CONTROL	2	2	2	1	0	0	0	0	0	0	0	0
CONTROL	2	3	3	1	*	*	*	*	*	*	*	*
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CONTROL	3	1	1	3	1	0	0	0	0	1	0	2
CONTROL	3	2	2	3	4	0	0	0	0	0	0	4
CONTROL	3	3	3	2	0	0	0	0	0	0	0	0
MEAN					1.7	0.0	0.0	0.0	0.0	0.3	0.0	2.0
NOGRPHED	1	1	2	2	0	0	0	0	0	0	0	0
NOGRPHED	1	2	3	2	0	0	0	0	0	0	0	0
NOGRPHED	1	3	1	2	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOGRPHED	2	1	2	3	0	0	0	0	0	0	0	0
NOGRPHED	2	2	3	1	0	0	0	0	0	1	0	1
NOGRPHED	2	3	1	3	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.3
NOGRPHED	3	1	2	1	3	0	0	0	0	0	0	3
NOGRPHED	3	2	3	3	0	0	0	0	0	0	0	0
NOGRPHED	3	3	1	1	0	0	0	0	0	0	0	0
MEAN					1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
NOPRED	1	1	3	3	0	0	0	0	0	0	0	0
NOPRED	1	2	1	1	0	0	0	0	0	0	0	0
NOPRED	1	3	2	2	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOPRED	2	1	3	2	0	0	0	0	0	0	0	0
NOPRED	2	2	1	2	0	0	0	4	1	2	0	23
NOPRED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					0.0	4.0	4.0	2.0	0.5	1.0	0.0	11.5
NOPRED	3	1	3	1	10	1	0	0	0	2	0	13
NOPRED	3	2	1	3	2	2	1	0	0	1	2	4
NOPRED	3	3	2	3	17	0	0	0	0	4	1	22
MEAN					9.7	1.0	0.3	0.0	0.0	2.3	1.0	14.3
NOPRED	1	1	3	3	0	0	0	0	0	0	0	0
NOPRED	1	2	1	1	0	0	0	0	0	0	0	0
NOPRED	1	3	2	2	0	0	0	0	0	0	0	0
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOPRED	2	1	3	2	0	0	0	0	0	0	0	0
NOPRED	2	2	1	2	0	0	0	0	0	0	0	0
NOPRED	2	3	2	1	*	*	*	*	*	*	*	*
MEAN					0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NOPRED	3	1	3	1	0	0	0	0	0	2	0	2
NOPRED	3	2	1	3	0	1	2	0	0	0	0	3
NOPRED	3	3	2	3	3	0	0	0	0	0	0	3
MEAN					1.0	0.3	0.7	0.0	0.0	0.7	0.0	2.7

TABLE 60

RAW DATA-PERCENT INFESTED TILLERS-M. DIRKSDOM

TREAT	SUNDAT	ROW	COL	SUBP	13/6	19/6	6/7	11/7	17/7	24/7
CONTROL	1	1	1	1	6	0	1	0	0	0
CONTROL	1	2	2	2	6	6	0	1	0	2
CONTROL	1	3	3	3	2	4	2	1	0	0
MEAN					4.7	3.3	1.0	0.7	0.0	0.7
CONTROL	2	1	1	2	2	0	3	9	9	1
CONTROL	2	2	2	1	0	0	4	9	18	9
CONTROL	2	3	3	1	*	*	*	*	*	*
MEAN					1.0	0.0	3.5	9.0	13.5	5.0
CONTROL	3	1	1	3	10	4	8	11	34	35
CONTROL	3	2	2	3	2	12	8	16	63	28
CONTROL	3	3	3	2	4	3	2	7	22	16
MEAN					5.3	6.3	6.0	11.3	39.7	26.3
NOGRPEED	1	1	2	2	3	0	1	0	0	0
NOGRPEED	1	2	3	2	7	7	3	0	0	0
NOGRPEED	1	3	1	2	5	4	0	0	0	0
MEAN					5.0	3.7	1.3	0.0	0.0	0.0
NOGRPEED	2	1	2	3	1	2	1	3	13	8
NOGRPEED	2	2	3	1	1	4	4	9	33	12
NOGRPEED	2	3	1	3	3	1	4	7	16	6
MEAN					1.7	2.3	3.0	6.3	20.7	8.7
NOGRPEED	3	1	2	1	0	6	4	2	21	13
NOGRPEED	3	2	3	3	0	3	0	5	38	20
NOGRPEED	3	3	1	1	0	0	0	15	27	37
MEAN					0.0	3.0	1.3	7.3	28.7	23.3
NOPEED	1	1	3	3	15	0	8	12	3	0
NOPEED	1	2	1	1	0	4	7	5	7	0
NOPEED	1	3	2	2	0	0	8	5	0	0
MEAN					5.0	1.3	7.7	7.3	3.3	0.0
NOPEED	2	1	3	2	0	6	5	16	16	12
NOPEED	2	2	1	2	0	3	4	18	36	18
NOPEED	2	3	2	1	*	*	*	*	*	*
MEAN					0.0	4.5	4.5	17.0	26.0	15.0
NOPEED	3	1	3	1	1	4	0	2	16	6
NOPEED	3	2	1	3	1	5	1	4	43	28
NOPEED	3	3	2	3	1	12	23	31	68	40
MEAN					1.0	7.0	8.0	12.3	42.3	24.7
NOPEED	1	1	3	3	7	2	3	4	1	0
NOPEED	1	2	1	1	3	3	1	6	7	1
NOPEED	1	3	2	2	2	2	0	0	0	0
MEAN					4.0	2.3	1.3	3.3	2.7	0.3
NOPEED	2	1	3	2	0	5	2	7	12	2
NOPEED	2	2	1	2	3	4	2	7	29	3
NOPEED	2	3	2	1	*	*	*	*	*	*
MEAN					1.5	4.5	2.0	7.0	20.5	2.5
NOPEED	3	1	3	1	2	3	0	2	8	7
NOPEED	3	2	1	3	0	2	1	1	30	25
NOPEED	3	3	2	3	1	8	13	23	*	16
MEAN					1.0	4.3	4.7	12.0	19.0	16.0