INTEGRATED CONTROL OF CEREAL APHIDS/BARLEY YELLOW DWARF VIRUS.

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"From winter, plague and pestilence, good Lord deliver us."

Thomas Nashe 1567-1601.

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ABSTRACT

The cereal aphids Rhopalosiphum padi (L.) and Sitobion avenae (F.) cause spread of Barley Yellow Dwarf Virus in autumn sown crops over the winter. Control is achieved by correctly timed insecticide applications, commonly synthetic pyrethroids. Polyphagous predators contribute to the natural control of these aphids.

A field investigation into the effects of deltamethrin on polyphagous predators, using barriered plots, showed that natural control may be reduced due to the reduction in numbers of predators over the winter. Also, spring populations, which limit the growth of summer populations of aphids, may be reduced as larvae are most affected.

The field dispersal of apterous R. padi was simulated in a computer simulation model based on changes in distribution along crop rows, and found to be between 0.6 - 1.3 m day . Analysis of leaves, using ELISA, confirmed spread of virus in the crop, with a maximum in January. A damage code based on symptom expression in the crop was devised, but was of use only as a guide to infection.

Dispersal was observed by release of apterous R. padi in the centre of nineteen $1m^2$ experimental plots of wheat. Dispersal showed a step-like relationship with mean daily temperature and an "activity threshold" at 7-9 ^{o}C. Dispersal rates were much less than those obtained from commercial fields, possibly due to density-dependent mortality.

Experiments in controlled environment rooms showed that apterae moved greater distances at temperatures above the "activity threshold", but other factors were involved.

Observation of individual R. padi showed that apterae were capable of walking 0.7m hour at $11^{o} \pm 2^{o}C$.

The implications of all the results on improving forecasting and integrated control of cereal aphids and BYDV are discussed.

CONTENTS

CHAPTER ONE

INTRODUCTION

CHAPTER ONE INTRODUCTION

Cereal aphids are currently one of the most serious agricultural pests in the United Kingdom, due to their potential for direct damage to the crop, transmission of virus diseases and the difficulties of effective control measures.

Despite extensive research over the last fifteen years , some critical aspects of their biology are unknown, for example, the overwintering behaviour of viruliferous aphids, and the importance of polyphagous predators in their natural control.

These unknown areas are vital to the development of effective integrated control of cereal aphids, which is increasingly becoming the current aim of applied agricultural research.

The main purpose of this chapter is to provide an introduction to the cereal crop, the invertebrate fauna (cereal aphids and polyphagous predators), and the virus disease Barley Yellow Dwarf Virus which causes problems in autumn sown cereals. Current methods of aphid control in the autumn are reviewed. A summary of cereal aphid research is included, and the approach and place of the present study defined.

Part One Cereal growing in the U.K.

a) A short history.

Two hundred years ago Britain was a net exporter of wheat. At the trough of the farming depression between the wars, we were only 16% self sufficient. Today,we are again net exporters. In the 17th Century,the relatively low population of around 12 million was easily supported by the agricultural output, but after this, the

decline in self sufficiency was due to rapid population growth, cheap imports, and a weak market.

However, British farming since the Second World War has been characterised by Government intervention brought about initially by the Agricultural Act of 1947, and rapid technical progress. Before this, (in the 1940's), mean wheat yields had only increased to around 2 tonnes per hectare.By 1960, yields increased to 3.2 tonnes/ha and now are 7.7 tonnes/ha.

Probably the first significant technical advance in cereal production was the improvement in weed control in the early 1950's, followed by the introduction of better varieties in the mid 1950's, the greater use of fertilizers, and the introduction of minimal cultivation techniques.

As research and development have progressed, growers have been able to improve pest and disease control, use resistant, better yielding varieties, improve the precision of fertilizer application, and reduce losses in harvesting and storage of grain. Field sizes have increased to allow the more efficient use of complex machinery. Perhaps,of most significance has been the steady growth in the understanding of the needs of crops and the importance of timeliness in growing operations (Britton 1967, Butler 1983).

Figure 1.1 shows the relative importance, in terms of area, of oats, barley and wheat in the U.K. since 1940. The area of oats grown since 1945 has declined largely as a result of the virtual absence of farm horses now, and also because other markets are so limited. They do still persist on higher steeper land, with more acid soils and heavy rain (e.g. Scotland). The area of barley has increased at the expense of oats. In the 1980's in the U.K. the area

of barley marginally exceeds that of wheat (1984 wheat area 1.939 million ha, Barley 1.978 million ha) which has increased more steadily (Anon 1985).

Barley is marketed for malting, compounding into animal feeds and is also exported. Until recently, British wheat was only suitable for milling for lower grade baking and animal feeds and this contributed to barley's more widespread hectareage. However, due to world agricultural economics (e.g the USSR now import large quantities of wheat) and improvements in production, wheat is now the most profitable cereal cash crop. Indeed, with EEC subsidies and protection of farm prices there has been a 50% increase in production over the 1970's. Unfortunately, utilization has only increased by 5%, which has led to cereal surpluses and the famous EEC "grain mountains" (Butler 1983).

b) Cereal growing today.

Simplified, specialized growing systems, involving direct drilling, shallow cultivations, pest and disease management programmes (e.g. packages such as "Crop Watch"), the development of growth regulators, efficient fertilizers, selective herbicides and guaranteed prices have led to an increase in cereal growing and yields across the U.K. It has been incorporated into a variety of cropping/rotation systems, depending on soil and grower's choice. For example, cereal with a break crop of grass is common in Devon and Cornwall, whilst some growers on the thinner, chalky soils of Buckinghamshire use a break crop of peas or beans. Continuous monoculture of cereals is also common, although barley is more suited to this type of growing system, as there is no risk of the development of take-all.

Pesticide use has changed dramatically in cereal growing in recent years, and treatments have increased from an average of three to more than five for a single growing season, and the area of application has doubled between 1977 and 1982 (Carter 1984).

Cereal growers are now in danger of being "hoisted by their own petard" (Butler 1983), as production of cereals has reached a level where the cost of support policies is being questioned. As well as pressure to reduce the costs of support, there is pressure from those who do not wish to see the countryside so intensively farmed, and pressure from developed and now, developing countries, for modifications to the EEC export and import policies. All this is at a time when the costs of cereal production are remaining fairly steady. Indeed, the costs of Nitrogen fertilizers have actually fallen, from £120 to £95 a tonne (delivered to the farm) (Weeks pers. comm.).

The systems employed in growing cereals are being scrutinized to ensure that they are sustainable at economic costs of production, especially when they start to rise again, and to satisfy public concern over the environment. Therefore, whilst there is nothing new about integrated control methods, British agriculture seems to be entering a period when understanding and using them is becoming increasingly important to meet economic and environmental needs (Attwood 1985). The research aims of Applied Biologists and Environmentalists are becoming more widely accepted amongst the "conservative" farming industry.

Consequently, to improve precision of insecticide use, there is an increase in demand for precise, high quality advice on spray selection and timing at minimum cost. Indeed, essentially research based models of pest growth and development produced

for summer aphids are now being incorporated into larger more complex computer packages for advisory use that include fertilizer, herbicide, fungicide and fertilizer advice (Wratten, Holt and Watt 1984). A good European example of a computer-based pest and disease management system in use is EPIPRE, which has operated in the Netherlands since 1978. EPIPRE has been well documented (Reinink 1984, Rabbinge and Rijsdijk 1983), and relies on individual grower's records. Whilst use of EPIPRE does not increase yields, growers who follow the EPIPRE recommendations strictly tend to spray less frequently and use less chemical per spray (Reinink 1984).

Hopefully, such computer-based models will be extended to include background information, finances, warning signals about pests and diseases etc, and will enable growers to be better informed.

c) Growing techniques.

The majority of cereal crops today are sown in autumn/early winter instead of spring, owing principally to the larger yields and ease in cultivation techniques.

Sowing occurs within a range of dates, although recent research in Derbyshire has shown the physiological optimum sowing date for maximum tillering, duration of parenthesis development and ear density at harvest to be before 23rd September (Green, Furmston and Ivins 1985, Green and Ivins 1985). Such early sowing is not always possible, due to weather and farming operations, and sometimes crops are not sown until November. No similar research work has been conducted in South West England (location of the project). The yield benefit from early sowing must also be balanced

against infestation by viruliferous aphids and possible costs of the two pyrethroid sprays recommended for eary crops (ADAS).

In South West England, where cereal growing is frequently part of a dairy farming system, cereals are often sown into ploughed-in grass swards. This also increased the likelihood of BYDV infection from viruliferous aphids living on the grass and surviving ploughing, so insecticide application in this case is essential (Bassett pers. comm.). Chapter 3,1 outlines the growing regime employed at one of the sites used in this project, Anthony Estate Farm, and is typical of modern cereal crop management.

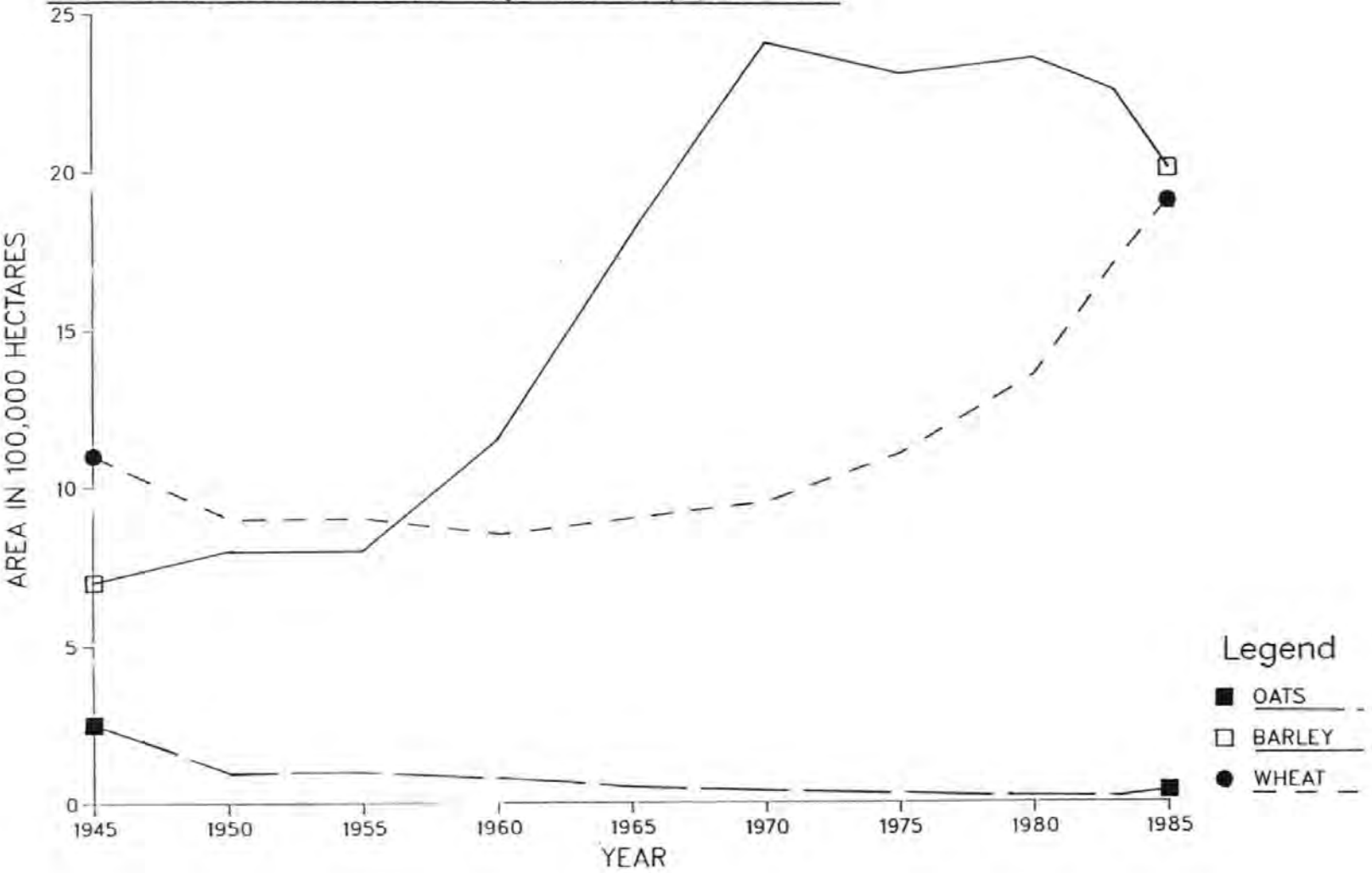
Once the crop is harvested, straw disposal is usually decided by factors other than pest, disease or weed control, and can be a problem. If livestock are kept, or a good market available, then straw is baled and removed from the field. Until recently, in most other cases the straw was burned, but this is becoming an increasingly unpopular practice.

After straw disposal, stubble "cleaning" before the next crop is important to reduce weed populations and the risk of disease and pests such as of viruliferous aphids carry-over on cereal volunteers.

The ultimate yield of the crop is dependent on the weather, which in turn determines which pest and disease combination causes most problems to cereal growers. For example, wet moist springs encourage leaf diseases, especially Septoria, but also encourage polyphagous predator populations of the cereal aphids which cause direct feeding damage to the ripening grains in the summer. The probability of an outbreak has been shown to be reduced in these situations (Powell, Dewar, Wilding and Dean 1983). The relationships between cereal aphids and weather

Figure 1.1

Areas of the three main cereal crops in the UK, 1945 - 1985.



have been the subject of much research, and answers are not always clear-cut (see Part 6).

d) Integrated Control.

Crop protection by integrated control can be defined as the use of a range of cultural methods such as crop rotation and cultivation, a selection of agrochemicals best suited to a particular cropping system, and the use of biological methods such as the introduction of natural enemies. These are incorporated into an overall programme which exploits the strengths and compensates for the weaknesses of the different components. Undue reliance on control methods which have adverse effects on wildlife and environmental health is avoided (Attwood 1985). In planning the overall strategy, any aspect of the husbandry techniques used that affect pest, disease or weed incidence should be included. In broad terms, integrated control aims for prevention, or containment of problems at levels where the value of any yield loss will be less than the cost of the control, i.e. the economic threshold.

For aphids, Cultural methods of control include the sowing of varieties resistant to diseases, late sowing to avoid viruliferous aphid attack, and the maintenance of hedges. Hedgerows provide overwintering sites for polyphagous predators (Sotherton 1984, 1985, Coombes and Sotherton 1986), and whilst polyphagous predators are not capable alone of preventing rapid population development in the spring, they, in conjunction with aphid specific predators, parasitoids and fungal diseases have been shown in simulation modelling to play an important part in limiting aphid outbreaks (Carter and Sotherton 1983). Full preventetive spraying is unlikely to be cost effective (especially since aphid outbreaks do

not occur every year Watt 1983). It is also undesirable as it encourages resistance, and is becoming environmentally unacceptable.

However, much work remains to be done in establishing threshold levels for pests other than summer cereal aphids. It is difficult to predict when an organism should be controlled, the extent to which its populations will develop, and the effect on yield. The level of control also is dependent upon the importance of the crop as a commodity on the farm and to the national economy.

An integrated control programme including both chemical and cultural techniques is desirable if the most ecological control methods for pests, diseases and weeds are to be achieved. Further, full cost-effectiveness will be maintained only if the balance between chemical and cultural control is adjusted, where necessary, to suit changing price structures within the farming industry.

Part Two Cereal aphids

The general biology and pest status of cereal aphids has been reviewed by Vickerman and Wratten (1979), Carter, Mclean, Watt and Dixon (1980) and Carter (1984). The introduction below relates to topics covered in this thesis. It,therefore,concentrates on the biology and ecology of cereal aphids in autumn and winter, and how this influences the problem of the introduction and spread of the virus disease BYDV in cereal crops.

a) Identification and Pest status.

Of the 40 or more aphid (Homoptera: Aphididae) species associated with Gramineae in Europe (Vickerman and Wratten 1979), only seven occur on cereal crops in Britain :-

Macrosiphum (Sitobion) avenae (F)- English grain aphid

Metopolophum dirhodum (Wlk.)- rose grain aphid

Rhopalosiphum padi (L) - birdcherry oat aphid

Macrosiphum (Sitobion) fragariae (Wlk.)- blackberry grass aphid

Metopolophum festucae (Theo.)- grass aphid

Rhopalosiphum insertum (Wlk.) - apple grass aphid

Rhopalosiphum maidis (Fitch) - corn leaf aphid

These can be identified by standard keys e.g. Stroyan (1972), Blackman (1974a), Blackman and Eastop (1984). Of these seven, only the first three are pests on cereals, though the others are potential grass pests. R. maidis is a more serious pest on maize and is not an important pest in this country. However, aphids are only pests in "outbreak" years (e.g.the M. dirhodum year of 1979) (Watt 1983).

Aphid feeding by S. avenae and M. dirhodum causes damage to cereals in summer directly by removing sap and indirectly due to the production of honeydew, which encourages the growth of fungi,

thereby reducing the light available for photosynthesis (Verjken 1979, Wratten 1975). The position of feeding - i.e developing grains, flagleaf, or lower leaves has been shown to affect grain quality by lowering the nitrogen content (Wratten 1978). Actual yield losses attributable to aphid feeding vary (George 1974, 1975, George and Gair 1979, Lee, Stevens, Stokes and Wratten 1981, Lowe 1974, Rabbinge and Mantel 1981, Verjiken 1979, Wratten, Holt and Watt, 1984) but may be as high as 42% (Kolbe 1969).

Limited evidence in the literature could be found of aphid feeding by R. padi causing direct damage to cereals in the autumn. They, and S. avenae do cause indirect damage by transmission of Barley Yellow Dwarf Virus (BYDV) (Plumb 1983).

b) Overwintering Biology

The terminology used follows that of Hille Ris Lambers (1966) and Blackman (1974a).

The life cycles and reproductive strategies of all three cereal aphid species have been thoroughly investigated and documented recently, and have been excellently summarized by researchers such as Hand (1982), Leather (1980), Watson (1983) and Williams (1980).

Aphids are either monoecious (living on one host plant) e.g. S. avenae on Gramineae, or heteroecious (alternating between a primary woody host and a secondary host) e.g. R. padi alternates between Gramineae and Prunus padus (L.) (the birdcherry) (Dixon 1977, Rogerson 1947). They are all capable of anholocyclic reproduction (reproducing viviparously and parthenogenetically on the Graminaeae) or holocyclic reproduction which involves production of sexual morphs and the production of eggs. Holocyclic reproduction occurs on the woody primary hosts.

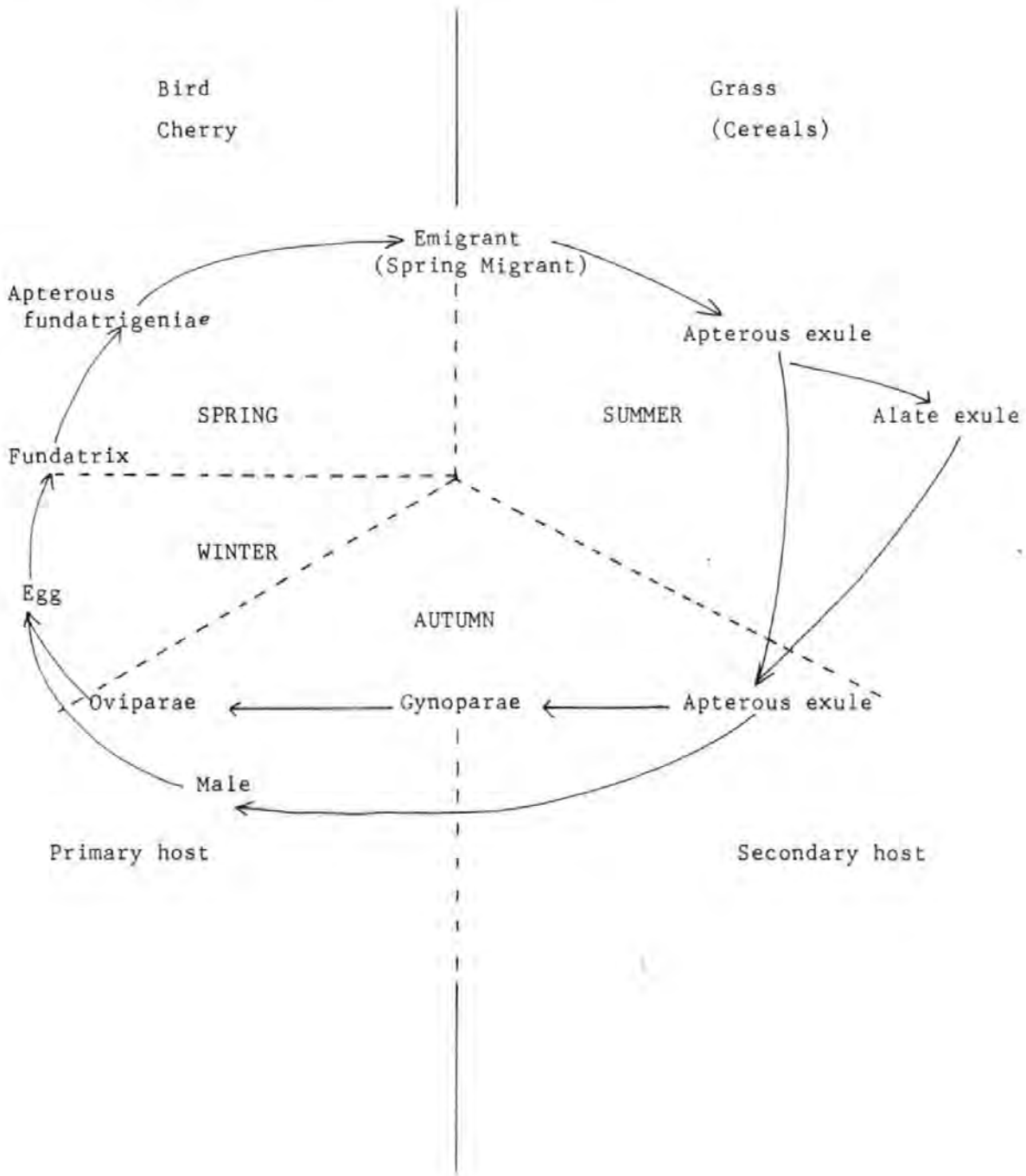
Fig. 1.2 shows a typical heteroecious aphid holocyclic life cycle. Usually, as is the case with M.dirhodum the viviparae (asexually reproducing females) occur on the secondary host during the summer and are known as "exules" or "alienicolae" and, as adults, become wingless apterae or winged "alatae". Alate exules are usually produced when colonies become crowded and the host plant becomes less suitable as a food source (often as a result of heavy aphid infestation) (Blackman 1974a). They are usually less fecund than apterae, but enable escape from unfavourable situations and the colonization of fresh host plants. In the autumn, the colonies of exules produce alate "gynoparae" and alate males in response to short daylength (Blackman 1974a), the males later than the gynoparae.

The gynoparae migrate from the secondary to the primary hosts, where they give birth by parthenogenesis to sexual egglaying females called "oviparae". The males also fly here and mate with these females, which then lay eggs. The eggs remain in diapause until early spring when apterous parthenogenetic "fundatricies" hatch from them. These feed on buds and new leaves and initiate colonies, "fundatrigeniae", on the primary host, which may be alate or apterous. Winged fundatrigeniae, sometimes known as spring migrants or emigrants, fly to create the first colonies on the secondary hosts.

All three important cereal aphid species can survive the winter as eggs, (which are more cold-hardy than viviparae) (Williams 1984), when following the holocyclic life cycle. However, they are potentially all capable of anholocyclic overwintering , but it is more common in S. avenae and R. padi. It is this ability which enables these species to exploit the increasing reservoirs of

Figure 1.2

Holocyclic Life Cycle of R. padi (from Dixon, 1978)



secondary hosts present as autumn sown cereals. No migration between primary and secondary hosts is required. However, this strategy is only possible in areas of mild winters (e.g.Southern England), but it has led in particular to viruliferous aphids spreading BYDV in crops in these areas (see part 3) in the autumn and winter months (Kendall and Smith 1981, Plumb 1983).

Virtually all the research to date is based upon the need for data to aid prediction of summer outbreaks and, therefore, has concentrated on population growth and development, and factors influencing mortality and the "switching" of life cycle strategy from anholocyclic to holocyclic according to weather factors such as low temperature (Williams 1984).

Overwintering of Sitobion avenae

The only direct evidence of holocyclic overwintering occurring in the U.K. is from limited observations made in S.E. Scotland (Turl 1980), and the three eggs found in Hand's work (1982) in a large scale investigation of overwintering sites. Other workers report the decline of S. avenae populations over the winter on continually monitored populations artificially established on pots of seedlings (Smith 1981, Watson 1983), and in the field (this project).

Indirect evidence for the occurrence of anholocyclic and holocyclic overwintering has been accumulated (Dean 1974a, 1978, Singer, Smith, Kendall, March, Mathias and Halfacree 1976, Watt 1979b). Dean (1974a) conducted experiments with artificial colonies on pots of cereal seedlings and concluded that S. avenae could overwinter viviparously and that it was largely or completely anholocyclic in S. England. In an extensive nationwide survey George (1974)

concluded that overwintering viviparae were concentrated in South West England because the weather is milder, and the more advanced crops provided shelter. Hand (1982) confirmed the presence of viviparae, and therefore anholocyclical overwintering on grasses and cereals sampled over three winters in Hampshire. Kendall and Smith (pers.comm) confirm this in Cornwall, Devon, Avon and Somerset.

In the USA Greene (1966) and Wallis and Turner (1972) recorded winter finds of apterous S. avenae in Oregon and Washington State respectively, although in the latter case, the aphids were found in an unusually warm microclimate produced by warm spring weather. In coastal areas of Canada with warm winters S. avenae apterae have also been found (Adams and Drew 1964, Forbes 1962). In the Netherlands, S. avenae was also found to overwinter successfully anholocyclically, (Hand and Hand 1986).

Overwintering of Rhopalosiphum padi

There are many records of holocyclic overwintering of R. padi on birdcherry (P. padus) in the U.K., (Dixon 1971, Gair 1953, Leather 1980, 1981b, Turl 1980), and in Finland (Leather and Lehti 1981), where P. padus is common and winters are very much colder. P. padus occurs naturally in Northern England, Wales and Scotland, reaching as far south as Gloucester (Clapham, Tutin and Warburg 1968). In Southern England it is only ever present due to ornamental planting. This scarcity led to the suggestion by Carter et al. (1980) that low summer populations of R. padi in Southern England are a result of little anholocyclic overwintering. Work at Long Ashton Research Station (Kendall pers. comm.), and by A'Brook (1974a), George (1974), Hand (1982) and Turl (1980) shows that R. padi is present throughout the autumn and winter. By early

spring, numbers are very low in cereals (Hand 1982, Hand and Hand 1986), which is possibly due to the viviparae being less suited in some way to winter survival, as was found by Dean (1974a) at Rothamstead, Leather (1980b) in East Anglia and Williams (1984) in Hampshire. They were shown to die out, eventually, due to adverse weather conditions. This evidence supports Carter's idea. The presence of R. padi on graminaceous hosts may only be a method of overwinter survival by this species, and may not significantly contribute to the next generation. "Oversummering" by R. padi in Southern England is little known, but the eventual autumn migrations to cereals are assumed to originate in graminaceous hosts (Vickerman and Wratten 1980). More research is necessary to decide if a true, anholocyclic life cycle is possible. It has been reported in France (Dedryver 1978) and in North America at Oregon (Greene 1966), New Brunswick (Adams and Drew 1964a) and in British Columbia (Forbes 1962). Certainly for the leaf feeding R. padi, ripening, senescing cereal crops do not make attractive host plants, so other crops such as permanent grassland need to be surveyed.

c) Autumn Migrations of Cereal aphids

The Autumn immigration of S. avenae and R. padi into cereal crops is either via long distance migrations or possibily short flights from adjacent hedgerows or other crops, (Vickerman and Wratten 1979). Aphid migrations, factors influencing initiation and the principles of infestation have been well documented (Dixon 1985, Johnson 1962, Kennedy and Thomas, 1974, Walters and Dixon 1982, 1983, 1984). However, the cycles of migration of European aphids are less predictable than the formal descriptions of life histories imply, largely due to the complex, mosaic environment of maritime

Europe (Taylor 1983). The establishment of the Rothamstead Insect Survey in 1964, and its extension across Europe in the voluntary co-operative venture EURAPHID has established large scale mapping of spatial trends in population density of most migrant aphid species. The data collected has led to predictions of timing and size of aphid migrations, which are disseminated via the "Aphid Bulletin" to ADAS advisors and crop consultants in this country (Taylor 1983, Woiwood and Tatchell 1984). Autumn cereal aphid migrations occur from September to mid October.

d) Overwintering Biology and Barley Yellow Dwarf Virus

The presence of R. padi in cereal crops in the early autumn and winter is largely responsible for the associated presence of the damaging BYDV. If overwintering viviparously leads to population losses due to the mortality caused by adverse weather conditions, these can be balanced against the nutritional benefits of virus infection demonstrated by Dixon (1978) and Olupomi (1981), which may enhance survival in the field.

The apterous progeny of immigrating alates, some viruliferous, establish colonies of aphids in cereal fields. This leads to an aggregated, contagious distribution within fields. These colonies will be referred to as "patches" throughout this project. As the aphids feed, they acquire the virus from their host plants. As the growing season progresses, the apterous aphids maintain these colonies, but also disperse by walking amongst the surrounding areas of crop, so the resultant distribution is less aggregated, tending towards evenness (Kendall and Smith 1983, Plumb and Thresh 1983). This process is called "secondary spread" of the apterae, and if the aphids are viruliferous, it results in patches of BYDV in the crop of a size related to the extent of movement of

these apterae between host plants.

Very little evidence was found in the literature on the inter-plant movement of apterous aphids on crops. Dean (1973) studied the spread of apterous S. avenae and M. dirhodum from artificially infested plants in cereal fields in June and July, and found that "patches" rarely persisted for longer than a few days. The dispersal of Myzus persicae(Sulzer) on brassicae and soil has been studied in detail (Ferrar 1967, Harrington and Cheng Xia-niam 1983, Jepson and Green 1982). M. persicae movement was reduced by high surface wetness and low temperature on the winter host brassicae plants, but the temperature was not specified. In the laboratory, first instar S. avenae nymphs are incapable of moving below -1 ^{o}C. Larger nymphs are completely immobilized at -4 ^{o}C, and at 3 ^{o}C all aphids are capable of movement (Smith 1981).

e) Control of cereal aphids and Barley Yellow Dwarf Virus. Recommendations

ADAS recommendations for control of autumn aphid infestations, and the concomitant spread of BYDV depend upon sowing date, the history of virus incidence in the location of the crop and the proportion of viruliferous alates caught in the local Rothamstead Insect Survey traps- he Infectivity Index determined by Plumb (1983).

The sprays recommended for effective Autumn insecticide use are synthetic pyrethroids. Optimum time for spraying has been found to be the last week in October and the first week in November (Kendall and Smith 1983, Petri 1981). However, for very early drilled crops, growers do apply sprays earlier, and may even apply two in a very high risk area such as South West England. Synthetic pyrethroids are more persistant than systemic organophorus compounds

such as dimethoate, so timing is less critical. This is an important point from a practical viewpoint, since weather often prevents access to crops in the Autumn.

Synthetic Pyrethroids.

The main commercially available synthetic pyrethroids in widespread use are deltamethrin, cypermethrin (two isomers are available), permethrin and fenvalerate. Photostable synthetic pyrethroids have been derived from natural pyrethrins occurring in pyrethrum flowers - Chrysanthemum anerariaefolium (Treviranus) as a result of over thirty years pioneering structure-activity research work by Elliot and his co-workers (Janes 1984, Elliot 1985). A wide range of synthetic pyrethroids exist today, with a range of insecticidal and acaricidal properties, and some species specificity favouring beneficial insects. They are contact insecticides, although the exact site of action is unknown, and possess a high toxicity to insects and a low toxicity to mammals, (LD50 mg.Kg -1 insects, =1; rats > 8000) (Elliot and Janes 1983). Mammals are able to metabolize synthetic pyrethroids at least 100 times faster than DDT, with a half life of 2 hours. Application rates are very low as compared with organochlorines, e.g. for control of cereal aphids, deltamethrin application rate is 7.5g a.i./ha as opposed to 244g a.i./ha for dimethon-S-methyl .Synthetic pyrethroids break down in the soil twenty times quicker than DDT (2 hours' half life as opposed to 17 days (Briggs 1985) and appear to cause little environmental contamination. Unfortunately, the acute toxicity of pyrethroids shows the following selectivity: insects > fish=amphibia >> mammals >> birds, and so broad scale application of synthetic pyrethroids where large areas of water could also be sprayed are not recommended. This is because aquatic animals in contaminated water

become intoxicated by ingestion, respiration and contact. Therefore the susceptibility of fish to deltamethrin is very high : in ppb the LC50 is 0.86 for Cyprinus carpio(L.)

and 0.50 for Salmo gairdenen(Richardson).

However, the rapid recovery of aquatic faunal numbers observed after spraying in Canada and also parts of Africa is thought to offset the detrimental environmental effects (Boquet and L'Hotellier 1985, Kingsbury and Kreitzweiser 1985).

Whilst the synthetic pyrethroids are,without question, a new and extremely important generation of insecticides possessing a number of significant advantages over the previously widely used chemical groups, prophylactic spraying and widespread use could well lead to the development of resistance in some species. Indeed, over 70 insect pest species have now been reported as resistant, including key pests already resistant to other compounds (Farnham 1985). Their long-term effects on the environment are also little known, although there is some indication of the detrimental effects to beneficial natural enemies of cereal aphids in the Autumn and Winter (Matcham and Hawkes 1985, Chapter 2).

Rationale of control

Generally, all winter cereals drilled before mid October are at risk, particularly winter barley. In high risk areas of the U.K., i.e.the South West, parts of the South and the coastal regions of Suffolk, Norfolk and Essex, spraying early winter sown barley ADAS recommends as routine. A routine spray on winter wheat is not recommended unless in a high risk area, and aphids are found. This extends to barley sown after the end of September (Carter 1984). In addition, Kendall, Smith and Bassett (pers. comm.) have shown that

crops following grass leys can become badly infected with BYDV, but they can be safeguarded by spraying the ley with Paraquat 10 days before drilling where minimal cultivations are used. This is to kill the plants on which the aphids survive.

In France, spraying decisions are based upon decision matrices which contain information on viruliferous autumn migrant aphids, the presence of volunteer cereals, the increase in number of plants infested with aphids and their estimated duration and temperature. (Lescar 1984).

Although control of cereal aphids and BYDV will essentially continue with chemical sprays, improvements in forecasting (see part 5) and plant breeding for resistance, (such as the new variety announced by NIAB Anon.1986) will hopefully lead to less insurance prophylactic spraying and associated risks of the development of resistance. If these are recognized, crop monitoring will increase. Thus growers will be encouraged to assess problems as they occur.

Part Three Barley Yellow Dwarf Virus.

Identification.

The disease of Gramineae now known as Barley Yellow Dwarf Virus is probably ancient, but it was not until 1951 that the cause was identified as an aphid transmitted virus disease of small grain cereals. It is an all-embracing name for diseases with similar symptoms and effects caused by persistently aphid-transmitted viruses only some of which are serologically related. Recent evidence suggests that the disease is caused only by some of a continuous overlapping range of luteo-viruses (Plumb 1983).

Until recently, the only practical method of diagnosing BYDV was by transmission to indicator plants using aphids. The development of typical symptoms (Chapter 3) was considered diagnostic. More recently, Enzyme-Linked Immunosorbent Assay (ELISA) and Serologically Specific Electron Microscopy (SSEM) has greatly increased the speed of diagnosis and the number of samples that can be handled.

Five isolates from BYDV infected plants have been identified by their relative vector specificity and their effects in the host. They are designated by the initial letters of their principal vector.

1. RPV Transmitted specifically by R.padi.
2. RMV Transmitted specifically by R.maidis.
3. MAV Transmitted specifically by S. avenae.
4. SGV Transmitted specifically by Schizaphis graminum.(Rondani).
5. PAV transmitted specifically by R.padi and S.avenae.

However, there are 23 known aphid vectors of BYDV isolates (A'Brook 1981a). Not all of these occur together in any one country and no virus isolate has been tested using all aphids. Therefore, the

classification above is locally and epidemiologically useful, but not necessarily universally applicable.

Effects on crops.

Barley Yellow Dwarf Virus affects barley, wheat, oats and rye. It affects the vascular tissue in the plant, causing tyloses to form in xylem elements, the phloem cells to die or degenerate, and callose to accumulate on the phloem sieve plates (Gill and Chong 1975, 1976, 1981). Whilst discoloration and chlorosis of the leaves (yellow in barley, reddish yellow in wheat and purplish red in oats) are the most used symptoms in recognition and quantification of BYDV in crops (see introduction Chapter 3.3), others, brought about by infection, are twisting of leaf blades, death of the apical shoot, leaf edge serration, severe dwarfing of the plants, increases in tillering and up to 90% reduction in yield (Greaves 1981). These effects are most pronounced if crops are infected early in the autumn for autumn sown cereals (Kendall pers. comm.), and this is the greatest problem in autumn sown crops (Gair 1981). Milder isolates of BYDV also decrease yield, but their effects are less well described. Infection at the seedling stage could be offset by favourable environmental conditions such as soil fertility. Also, damage caused directly by aphids or indirectly by other cereal diseases may be affected by virus infection of the host plant.

Effects on aphids.

Although BYDV does not multiply in its vector hosts, a complex relationship exists between the virus and its vector host (see next section). Olupomi (1981) showed that aphids on BYDV infected host plants were larger, reproduced earlier and produced more progeny than those on "healthy" plants. As R. padi is a leaf feeder, the increased

tillering and protein accumulation in infected host plants may be of benefit.

Epidemiology.

Viruses have two ecological survival mechanisms:-

1. Methods of perennation between seasons.
2. Methods of spread within a site within a season.

Barley Yellow Dwarf Virus has effective methods of both types (Harrison 1981).

Most species of the Gramineae are susceptible to one or more strains (Plumb 1983). The increasing trend for autumn sown cereals, late harvesting of cereals such as maize, and the ploughing-in of grass swards and cereal stubble, all perpetuate BYDV in its host plants. When climatic conditions favour aphid migrations between sites (i.e spring and autumn) and the subsequent spread of the progeny within the crop over winter, BYDV spreads between and within sites easily. Therefore it is a consistently prevalent virus.

BYDV is transmitted to its vector by an acquisition feed of a few hours. It is a circulative virus, remaining in the body fluids of the aphids, but not replicating. When the aphid feeds again, it is transmitted to a new host plant. The viviparous progeny of the vector aphid acquire the virus on feeding and do not lose it by ecdysis. Aphids arising from overwintering eggs on the woody primary hosts (e.g. Prunus padus for R. padi) are only virus vectors once they have fed on infected tissue. Virus is not transmitted via the eggs. Viviparous progeny are as efficient as adults at acquiring and transmitting BYDV, and all morphological forms are capable of BYDV transmission.

All aspects of vector biology affect their ability to

transmit BYDV. Of most epidemiological significance is whether a species alternates between graminaceous or other hosts and the timing and size of its migratory flights. As the life cycles of all BYDV vectors are so well adapted to the exploitation of cereal crops (Part 2) it is not surprising that BYDV is a major problem to autumn cereal growers, especially in high risk areas of the U.K. e.g. in South West England. The severity of the problem does depend upon the number of initial viruliferous aphids present in the area, and the extent of the secondary spread by the apterous progeny.

Part Four Polyphagous Predators.

Polyphagous predators are important natural enemies in agroecosystems as they feed on a wide variety of pest species. The potential of the taxonomic groups, Carabidae and Staphylinidae, in particular have been widely recognised (Coaker and Williams 1963, Edwards et al.1979, 1984, Penney 1966, Sunderland and Vickerman 1980, Wratten et al.1984). The Aranea, Dermapterae, Opiliones, Pseudoscorpionida Chilopoda and Acari may have a lesser role (Crook and Sunderland 1984, Dean 1974, Edwards et al.1979).

In fact, a non-specialist feeder of any species has potential value as a natural control agent, because it is able to persist in crops during periods of low pest densities. It is also present, therefore, during pest immigration and population development. The potential value of a polyphagous predator varies according to the degree of synchronization with each pest species (Sunderland 1975).

It is only really in the last decade that the role of polyphagous predators in restricting aphid population growth in cereals has been fully appreciated (Powell et al. 1983). They have become the subject of much research at Rothamsted, Southampton and Newcastle in the U.K., summarized by Edwards et al.(1979), Sunderland and Vickerman (1980), , Wratten, Bryan, Coombes and Sopp (1984). Their importance has led to the incorporation of "natural enemies" into Carter's within season model of population dynamics (explained in Part 2) (Wratten 1983).

In the field, Bryan and Wratten (1984) showed aggregation at high aphid densities by some Carabidae and Staphylinidae. Sunderland and Vickerman (1980) showed the proportions of individual carabid species containing aphid remains increased with aphid density, though the form of the relationship varied between species.

For example, 30% of the diet of Notiophilus biguttatus (F.) constituted aphids when densities increased from 1000 to 9999 per patch. In a simulation model of aphid population growth in the spring, Carter and Sotherton (1983) showed that, in the absence of predation, summer aphid outbreaks could be reached even with low initial densities. Including the potentially most useful predators (according to the predation index of Sunderland and Vickerman 1980)- Agonum dorsale, Demetrias atricapillus (L.) and Tachyporus sp. showed that with a low starting density and little immigration, an aphid outbreak could be prevented.

More basic knowledge is required about the effects of polyphagous predators (including confirmation that some do actually eat aphids). Chiverton (1984) obtained significant negative correlations between aphid and predator numbers. Sunderland and Vickerman (1980) produced a predator ranking score of 13 species of Carabidae, Staphylinidae and one Dermaptera based on aphid presence in the gut. Work is currently in progress at Glasshouse Crops Research Institute using ELISA techniques to study predation on aphids (Crook and Sunderland 1984, Sopp pers. comm.).

However, much of the work on the role of polyphagous predators is based on the cereal aphid populations that cause summer outbreaks. Little has been done on polyphagous predators over the earlier parts of the autumn sown cereal growing season when aphids spread BYDV. Jones (1976, 1979) published results of research into the composition, abundance and reproductive activity of common Carabidae in winter wheat, and found that some migrate to the crop in the autumn, whereas others live there permanently.

Sotherton (1984,1985) studied the distribution and abundance of predatory arthropods overwintering on farmland, and suggested that maintenance of field boundaries (preferably either grassy strips or clipped hedgerows on raised grass banks) could be of great benefit to maintain populations of polyphagous predators.

Biology and Ecology of Polyphagous predators.

Carabidae

Of the 40,000 species of Carabidae, 350 are found in the U.K. It was realised in the 1950's that their opportunist predatory habits made them an important group to study (Lovei 1984). The Carabidae are the dominant group of polyphagous predators, and a concise interpretation and synthesis of all the accumulated literature on Carabidae (e.g. Coaker and Williams 1963, Jones 1976, Mitchell, 1963 and Penney, 1966) was produced by Thiele (1979).In fact, of all the species of Carabidae, the basic fauna of agricultural land across N.Europe from Belo-Russia to England is surprisingly homogenous. Twenty six of the species found in the arable areas were encountered in at least one third of the regions investigated and include: Pterostichus vulgaris (L.), Harpalus rufipes (Degeer), Harpalus aeneus (F.), Agonum dorsale (Pont), Agonum muelleri (Herbst), Bembidion lampros (Herbst) and Trechus quadristriatus (Schrk). All these are efficient colonizers of the regularly disrupted agroecosystem, are capable of rapid reproduction (Lovei 1984), and in particular, H. rufipes, A. dorsale and B. lampros have been identified as cereal aphid predators (Sunderland and Vickerman 1980). The biology and ecology of these species have been studied in detail by Baker and Dunning (1975),

Jones (1979), Mitchell (1963b) and Lovei and Szentkiralyi (1984). Other cereal aphid predator species identified and studied include Amara aenea (Degeer), Amara plebeja(Gy.), Asaphidion flavipies(L.), Loricera pilicornis(F.), (Sunderland and Vickerman 1980), Nebria brevicollis (F.) (Penney 1966, Sunderland and Vickerman 1980), Pterostichus melanarius (Ill.) (Jones 1976,1979, Trittlevitz and Topp 1980), Pterostichus madidus (F.) (Luff 1974), and D. atricapillus (Sunderland and Vickerman 1980, Coombes pers. comm.).

Carabidae of agricultural fields have been shown to feed on a wide variety of prey, small mites and collembola, cabbage white butterfly eggs and larvae and wireworms (Coaker and Williams 1963, Edwards et. al. 1979 and Jones 1976). They also eat plant material. Capture is achieved by physical contact with prey items caught when foraging rather than by waiting in lairs. Of the cereal aphid predators already identified above, several are known climbers e.g. D. atricapulus (which is also not caught in pitfall traps), N. brevicollis, N. bigguttatus, T. quadristriatus, A. flavipes, B. lampros, Pterostichus melanarius and A. dorsale were also found in the plant layer (Vickerman and Sunderland 1975). However, B. lampros and H. rufipes have also been observed climbing and feeding on aphids, but it was concluded this behaviour was not important in their feeding and ecology by Lovei and Szentkiralyi (1984), and that A. dorsale rarely climbs.

Adult N. brevicollis prefer prey items up to 4mm in length (Penney 1966) and,therefore,its main prey is Collembola, although it does eat aphids and small spiders.

The physiological state of the Carabidae has also been shown to influence predation rate. For example, Baker and Dunning

(1975) found non-gravid B. lampros females ate more aphids in sugar beet fields than gravid ones. Some are strong fliers e.g. A. aeneus, others are capable of flight and rarely fly e.g. B. lampros and T. quadristriatus (Mitchell 1963).

Little is known about the nutrition of the larvae as, unlike the adult Carabidae who digest internally, (which permits identification of food items) they only ingest liquids. Therefore, feeding experiments have to be conducted. Luff (1974) found that larvae of P. madidus will eat aphids occasionally (86% of the times they were presented) and are entirely carnivorous. Also, Penney (1966) found that N. brevicollis larvae are entirely carnivorous up to the third larval stage.

All Carabidae are essentially ground living species and most take aphids on the soil in agricultural fields (Brandl and Topp 1985). Sunshine and temperature have been shown to influence carabid populations (Jones 1976,1979). Physiological development is encouraged by favourable long term temperatures, whilst short term "weather" encourages activity. It is important to remember that pitfall catches reflect the interaction of these two factors. The larger species are able to withstand hot, dry weather much better than small species. Indeed, the pitfall catches of larger species were correlated with accumulated temperatures above the assumed activity threshold of 5 ^{O}C. However, hot dry summers have been shown to produce low fecundity in Carabidae (Greenslade 1964). This explains why larger species are more abundant in the summer in the U.K. and small species such as B. lampros are virtually absent from summer pitfall catches. Rainfall seems to have no effect on

Carabidae. In the field Carabidae spend much time in crevices and in spaces in the soil where the relative humidity rarely falls below 98%. Activity of Carabidae is influenced more by the need to feed than by rainfall and temperature (Jones 1976,1979). Thiele (1979) suggested that the annual rhythms and life cycles of Carabidae fall into one of five broad groups. However, most workers divide the Carabidae into two simpler groups :-

1. Spring breeders, which hibernate as adults only, with peaks in adult abundance in the spring and autumn.
2. Autumn breeders, which mainly hibernate as larvae, and exhibit a single peak in mid summer (July-August).

Alternatively, Wallin (1985) suggests a more suitable designation of adult or larval overwintering respectively for the two groups, based on breeding history.

In most species, an obligatory dormancy occurs somewhere during the cycle of development. Some species are capable of breeding in more than one year e.g. A. dorsale (Jones 1979).

Thus Carabidae are able to exploit prey in a number of different crops in the agroecosystem, with varying diurnal and seasonal rhythms which operate almost in a "shift system" in agricultural fields.

Staphylinidae

Of the 27,000 known species, there are nearly 1000 species of Staphylinidae in Britain (Chinery 1977), of which species of the genera Philonthus and Tachyporus have been identified present in agricultural fields (Dean 1974, Dicker 1944, Pietraszo and Declercq 1978, Sotherton 1984 and Topp and Trittlevitz 1980).

In particular,

Tachyporus chrysomelinus(Gravenhorst), Tachyporus hypnorum (Gravenhorst) and Tachyporus obtusus(Gravenhorst), Philonthus species, Stenus species and Xantholinus species adults and larvae have been identified as cereal aphid predators (Crook and Sunderland 1985, Kowalski 1982, Sunderland 1975).

Most Staphylinidae are scavengers or predators, mainly fluid feeders and are found in agricultural fields, and wherever there is dead or decaying matter. They are strong fliers, and so are often poorly represented in pitfall catches (Sunderland and Vickerman 1980). Earlier work on the life cycle of Staphylinidae is summarized by Kowalski (1982). Adults overwinter by hibernating and emerge to reproduce in May and June. Larvae are then active in the crop until August when a second peak of adults occurs, mostly the new generation engaged in feeding prior to hibernation. The larvae are not only surface active, but also climb plants to eat cereal aphids (Vickerman and Sunderland 1975). Weed infestation increases Tachyporus sp. larvae abundance (Powell et al. 1983). Thus the larvae may be important cereal aphid predators.
Philonthus decorus(Gravenhorst) adults were captured in autumn by Frank (1968) so it is clear that all stages of Staphylinidae could be important aphid predators.

Araneae

Over 30,000 Araneae species exist, feeding almost exclusively on insects. Little attention has been paid to their use in insect pest suppression. They have not received serious attention because, until relatively recently, little was known of their ecology, especially as it pertains to interactions with associated prey populations and other arthropod competitors (Foelix 1982,

Riechart and Lockley 1984).

However, Araneae species have been captured in agricultural fields in pitfall traps (Edwards et al. 1979, Matcham and Hawkes 1985, Nyffler and Benz 1982, Sotherton 1984). There are two broad groups of Araneae:-

1. Web spinning Agelenidae, Linyphiidae, Theridiidae, Araneida and Uloboridae.

2. Free living Theridiosomatidae, Clubionidae, Lycosidae and Salticidae.

All types, but particularly the Linyphiidae, are aphid predators (Crook and Sunderland 1984, Foelix 1982, Sunderland and Vickerman 1980, Vickerman and Sunderland 1975). In cereal fields, the composition of the Araneae community in the vegetation layer has been shown to consist of mainly orb web spinners, whilst those on the ground surface are mainly the free living types, but Linyphiidae, ground web spinners are also found (Nyffeler and Benz 1982, Sunderland pers. comm.).

The Araneae of cereals are very diverse and there are diverse family specific modes of movement and capture of prey. Aphids are captured when moving on plants, by encountering webs, and when walking on the soil by encountering vagabond or hunting spiders. The largest orbweb spiders are capable of catching 10/20 insects per day in cereal fields, and vagabond spiders only 1 insect per day (Neffler and Benz 1982).

However, as most Araneae are such generalists with respect to diet - for example, Linyphiid triangularis (L.) accepted 150 of 153 offered different species of prey and as populations never become very dense, their roles as potential biological control agents can only ever be in conjunction with other polyphagous predators

(Neffler and Benz 1982). Nevertheless, in cereals, when aphid populations are developing, spiders can adjust to the available food supply by eating more prey when it is abundant. They are also capable, due to their low metabolism, of surviving several months without food, for example when hibernating.

Araneae of the temperate zones can be put into one of five groups, based on their annual cycles or periods of maturation, although the exact life cycles have only been investigated for a few species. Some reach the adult stage in the autumn, but most overwinter as nymphs.

The winter active adult Araneae, chiefly the Linyphiidae, are potential predators of apterous R. padi, and are active at temperatures as low as -4 ^{o}C. They have been identified in field boundaries over the winter (Sotherton 1984).

Dermaptera

Only about 200 species of Dermaptera exist, of which only four occur in Britain. Forficula auricularia (L.) is a common inhabitant of agricultural land, and as a plant climber has been shown to be an aphid predator, especially at low densities (Sunderland and Vickerman 1980, Vickerman and Sunderland 1975). Female Forficula are active throughout the winter, and there is a high degree of maternal care throughout. Nymphs eventually emerge at the second instar stage, and are fed and tended by the mother to such as extent that family groups are seen in the spring (Chinery 1977). Whilst Vickerman and Sunderland (1980) summarized earlier work on Forficula and noted that nymphs were not such efficient plant climbers and aphid predators as the adults, no assessments of the potential impact of these family groups on developing summer

aphid populations were found in the literature. Clearly, surface active females in the autumn could have a similar role to Opiliones and Araneae in control of R.padi.

Opiliones and Pseudoscorpionida

200 Opiliones species and 1500 Pseudoscorpionida species are common in Britain (Snow 1971). No direct evidence of aphid predation could be found in the literature, but it is generally assumed that their presence in the epigeal fauna of cereal fields could contribute to the general potential of polyphagous predators as natural control agents of cereal aphid populations. (Edwards et al. 1979,1984).

Acari

Over 1600 species of Acari exist in Britain. Many are extremely catholic, and feed on a wide range of living and dead plants and animals. Whilst their presence in the surface 20-30mm of the soil is recognized in agricultural fields (Edwards et al. 1979). Pergamusus species and Crombidiidae have been shown to contain aphid remains (Crook and Sunderland 1984).

As their populations show a general increase in autumn and winter, they must exert some natural control of cereal aphids in the same way as Opilliones and Pseudoscorpionida.

Chilopoda

About 20 species of Chilopoda exist in Britain (Lewis 1981). They are known to be present in agricultural fields (Edwards et al. 1984), and Lithobus species in particular have been shown to contain aphid remains in woodlands (Lewis 1981) and in cereal fields (Crook and Sunderland 1984). Their preference for high humidity, low light intensity and even temperatures means they prefer field

boundaries and also increase in weedy areas (Lewis 1981). They are capable of living five or six years, and the increase in abundance in the spring and autumn could be important in the natural control of developing cereal aphid populations at this time.

Part Five Current Cereal Aphid Research in the U.K.

The majority of work on cereal aphids recently has concentrated into two broad areas :-

1. The establishment of relationships between aphid population levels, crop growth stage and yield loss in outbreaks of aphids in the summer, leading to the development of a short term economic threshold based forecast.

This has led to the subsequent investigation into the overwintering of these aphids, and developing a longterm forecast based on overwintering data. The aim is to eliminate prophylactic spraying, which could lead to the development of resistance etc.

2. Investigating the autumn migrations of aphids into autumn sown crops, attempting to predict subsequent Barley Yellow Dwarf Virus infection in the crop, and the development of an optimal spraying time for autumn control.

An important element of cereal aphid research today is concerned with the effective development of forecasting aphid damage to cereals (either direct, in summer outbreaks of S. avenae, or indirect in the autumn due to the spread of BYDV by R. padi or S. avenae. To further this aim, the Rothamstead Insect Survey (R.I.S.) was established, initially,to continually monitor changes in aphid distribution and abundance throughout the U.K. It uses a network of 12.2m high suction traps to assess the relevance of aphid migrations. The aim is the development of forecasting systems. Detailed summaries of the R.I.S. are found in Taylor (1973, 1980), Woiwood and Tatchell (1984).

As the life cycles of the different aphid species involved vary in different areas of the U.K., growers have tended to experience direct feeding damage or indirect virus infection, according to location. This has led to the polarization of research into the two broad areas based on location.

1. Spring and summer outbreaks

The infestation of cereals at damage causing levels by S.avenae has been occurring since at least 1968 (Vickerman and Wratten 1979, Carter et al. 1980). This damage has been researched in a comprehensive series of open field and field cage experiments aimed at establishing relationships between aphid population levels and crop growth stage and yield loss (George and Gair 1979, Lee, Stokes & Wratten 1981, Wratten 1978). These well established relationships are now widely accepted and form the basis for the ADAS recommendations for spraying when numbers are 5 per ear at flowering and increasing, to prevent a yield loss of approximately 12.5%. More recently, research at U.E.A. has led to the use of weather data to predict the size and timing of the spring migrations (Walters, Watson and Dixon 1983, Watson and Carter 1983). This work has been incorporated into simulation and prediction models developed by Carter at Rothamstead (Carter and Dixon 1981, Carter and Dewar 1983, Carter 1984), and also in the Netherlands (Carter, Dixon and Rabbinge 1982), where cooperation of growers has been established in the EPIPRE system (Rabbinge and Rijsdijki 1983). Recent overwintering work on S. avenae and M. dirhodum has concentrated on the effects of weather on cereal aphid numbers (Watson 1983), general ecological work on population growth, composition and development, (Smith 1981, Williams 1984), and overwintering sites and dispersal

(Hand 1982), in outbreak and non-outbreak years.

2. Autumn outbreaks and BYDV.

As the trend towards earlier sowing of autumn cereals continues (Carter 1984), so more cereal crops are present for colonization by winged aphid virus vectors migrating from grass, volunteers and other cereal crops such as late-harvested corn or maize (Hand 1982). The crops are at risk from September to November. Whilst the aphid feeding has been shown to cause some direct feeding damage (Mallott and Davey 1978), the most serious problem is not related to aphid numbers per se, but more related to the amount of virus these aphids are carrying. This is comparable to the minimal feeding damage caused by M. persicae on sugar beet and potatoes as compared with the damage due to sugarbeet yellows and the cost of obtaining uninfected seed potatoes (Gibson and Plumb 1977).

The Infectivity Index is used to provide regional ADAS guidelines as explained earlier (Carter 1984). However, it only provides an indication of the probable number of initial infection sources, and does not indicate the proportion of crop ultimately infected with virus. It is also only recorded at Rothamstead, Long Ashton and The Welsh Plant Breeding Station, so only provides an indication of disease incidence. Therefore, although incidence of disease can be forecast , improvements in the forecasting of the severity of disease outbreaks in high risk areas (e.g.South West England) are needed (Kendall and Smith 1983).

Kendall and Smith (pers. comm. and 1984), showed that the development of the aphid population in the crop, both during and after the invasion by migrants, and consequently much of the secondary spread, is very dependant on climatic factors such as

temperature and rainfall. It is little affected by the number of migrants. Indeed, Kendall and Smith (1983) found that migrant colonizing aphids infected >2% of plants in 1980-1982 and yet in 1981, plant infection had increased to >30% in early sown crops. This work is supported by Leather's work on the biology and ecology of R. padi (Leather 1980, Leather and Dixon 1981a and 1981b). Recent and current work at Long Ashton is concentrating on aphid infectivity, crop monitoring to predict local aphid population changes and virus spread and sources of aphids and virus (Kendall and Smith pers. comm. and 1984). Forecasting weather-dependent biological phenomena is extremely difficult, and more data is required of a basic nature over the winter months on cereal aphids. Although the effects of wind, low temperature and rainfall on population growth and development of S. avenae, (which is a virus vector) using shelter arrangements, clip-cages and "cold tolerant" aphids have been investigated (Smith, 1981, Watson 1983 and Williams, 1984), little field data is available on the principal virus vector R. padi, especially over the winter months. Whilst absolute microclimatic relationships between weather factors and aphid numbers are important for practical applications, any "risk factor" for biological events has to be based on standard, easily obtainable weather records. Although micro-climate recording devices are available to growers, they are by no means widespread (Burrage 1984).

A Royal Commission on Environmental Pollution (Anon. 1979) recommended that there should be an expansion of basic research on the factors determining the incidence of diseases and pests. This is particularly relevant to cereal aphids. Basic research, as well as

providing information to develop a forecasting scheme, may be directly applicable to integrated pest control.

Part six Aims of this project.

The general aim of this project was to investigate various aspects of the biology of the main BYDV virus vector, Rhopalosiphum padi over the autumn and winter, and certain aspects of its current control methods. This was with a view to providing information which would aid future control of this pest and develop our understanding of the overwintering period in cereal fields. The main aims may be defined more specifically as follows :-

Fieldwork in Wheat crops.

1. To investigate the distribution of apterous cereal aphids in commercial wheat crops, ascertain the most abundant species, and assess their movement in relation to climatic variables.

2. To demonstrate the occurrence of secondary spread and attempt to correlate overwintering presence of the two main virus vectors R. padi and S. avenae with severity of subsequent BYDV infection.

3. To estimate the density and activity of important ground living polyphagous predators (natural enemies) of cereal aphids over the winter, and to assess the effects of applications of a synthetic pyrethroid on their numbers.

Fieldwork in small outdoor plots of winter wheat.

To investigate apterous aphid movement by direct observation of the most common aphid species found in Section 1 , (i.e. R. padi), and attempt to quantify secondary spread in relation to climatic factors.

Laboratory work in controlled environments.

To examine the effects of temperature on :-

1. Movement rates of apterous R. padi.

2.The "disappearance" of apterae observed in small plots and in the field.

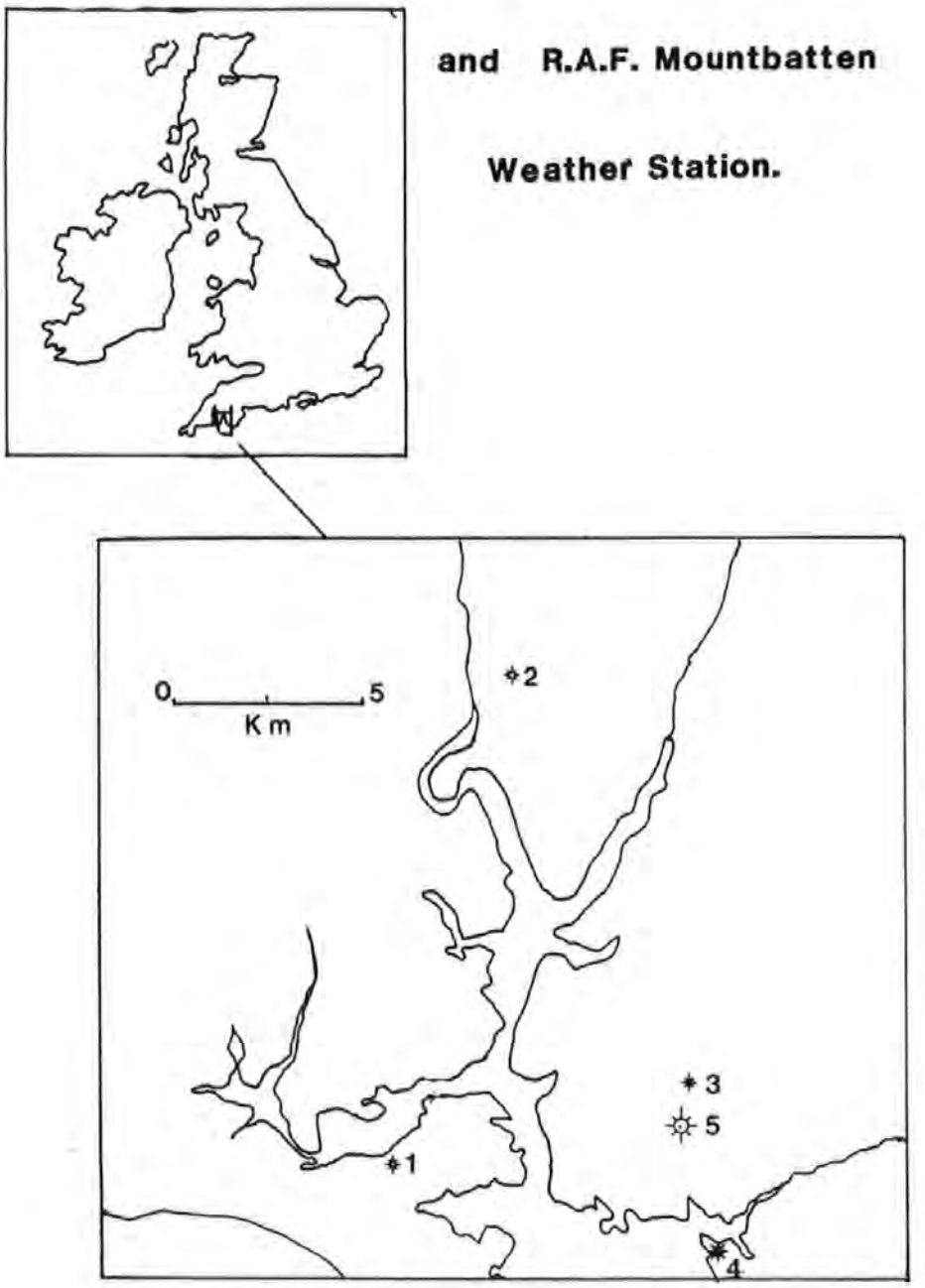
3. The nature of apterous aphid movement.

Computer simulation modelling.

1. To simulate dispersal rates of apterous aphids from the observed changing distributions in commercial wheat fields.

Therefore, the project aims to assess the role of overwintering movement of apterous cereal aphids in secondary spread. It also assesses the impact of a synthetic pyrethroid on polyphagous predators overwinter. Together these aspects may provide guidelines for the integrated control of BYDV.

Fig. 1.3 Location of field sites 1982-1985, and R.A.F. Mountbatten Weather Station.



✧1	Anthony Estate
✧2	Rumleigh
✧3	Skardon Place
✱4	RAF Mountbatten Weather station
☼5	Plymouth Polytechnic

CHAPTER TWO

POLYPHAGOUS PREDATORS IN WINTER WHEAT

2.1 Field assessment of the effects of deltamethrin, a synthetic pyrethroid on polyphagous predators in winter wheat

Introduction

Ground living polyphagous predators may be important in controlling populations of overwintering cereal aphids and the secondary spread of BYDV in the autumn. However, the application of insecticides before or during this period may have an adverse effect on natural control. There have been various instances where elimination of predators has resulted in increased pest attack (Wallace 1959, Klostermeyer and Rasmussen 1953, Wright 1962), but there have been relatively few studies into the effects in the field of insecticides on polyphagous predators (Edwards, Thornhill, Jones, Bater and Lofty 1984, Edwards and Thompson 1975, Matcham and Hawkes 1985, Powell, Dean and Bardner 1985). The widespread use of aphicides on crops could damage these natural enemy populations and so lead to a worsening of cereal aphid problems.

The commonest method used in field studies is pitfall trapping, a simple technique in which a container is sunk into the ground, flush with the soil. Surface active animals are captured on falling in. Extensive data is obtained on readily identifiable specimens. This method is particularly useful for study of the Carabidae, whose secretive habits make daytime searching and collecting tedious and inefficient (Durkis and Reeves 1982). Pitfall trapping is not without its limitations, and the methodology has been the subject of many articles and reviews over the last 20 years. Thomas and Sleeper (1977) suggested four sources of variation of capture success, the first due to biases caused by the intrinsic

properties of pitfall methodology. These non-random effects were noted in this investigation. Pitfall trapping should take into account the following (Kowalski 1974). :-

1. Traps should be placed uniformly in a grid pattern and numerous enough to minimize the effects of continuous trapping due to the proximity of vegetation, substrates or topographic features which affect dispersion of the animals at risk.
2. Traps should be of uniform size.
3. Distance between traps should be great enough to avoid disruption of normal behaviour or habitat.
4. Length of trapping period uniform.
5. Dry pitfalls remove the possibilities of repellancy or attractiveness due to preservatives (Luff 1975).
6. All traps should be placed in a homogeneous environment.

Southwood (1978) summarized the criticisms of earlier workers on pitfall trapping and concluded that "pitfall traps are of little value for the direct estimation of populations", mainly because they reflect activity. Also trap efficiency is species and habitat specific, depending upon prevailing and actual weather conditions (Luff 1975).

However, Baars (1979) summarized the work of ecologists such as Den Boer and Meyer and described his own work and suggests that satisfactory linear relationships between the mean densities in several habitats in different years, and the numbers of beetles trapped, can be obtained. With the help of continuous pitfall sampling, a reliable relative measure of the size of carabid populations can be obtained, and this is supported by Den Boer (1985). Thus when pitfall traps are in position for a long period of

time (ten months and eleven months in the case of this experiment), the effect of the limiting factors described above is minimised. A further point is that the selective trapping of diurnal or nocturnal species is avoided (Luff 1978). A randomized block design permits an assessment of relative numbers despite evidence to suggest the increased activity and, therefore, numbers caught in pitfall traps may not reflect the true picture (Chiverton pers.comm.). The experimental area used mirrored agricultural field conditions as close as possible, with an apparently homogeneous environment, reducing microclimate and vegetation differences to fulfil the criteria suggested above. The design of field experiments also presents problems. Although many polyphagous predators do not fly, they are extremely active and many can travel large distances (Edwards et al.1984). Hence, to assess the effects of pesticides in the field, plots must be either very large or be surrounded by a physical barrier. The latter choice was made in this experiment as it was most suitable in the conditions available.

2.2 Aims.

1. To assess the effects of a synthetic pyrethroid, deltamethrin, on polyphagous predator populations in winter wheat.
2. Make preliminary investigations on which timing of spray has most effect on population sizes.
3. To attempt to establish the longevity of any observed effects.
4. To establish if autumn spraying has any "knock-on" effects on summer aphid populations.
5. To discover the importance of position of pitfall traps within the plot.

2.3 Site Description.

In 1982-1983 and 1983-1984, an area of winter wheat (c.v.aquilla) was sown on a South facing slope at Rumleigh Experimental Station, (see Fig 1.3 for exact location) Grid Ref. SX 446683 (O. S. Sheet 261 Series M276). Sowing Dates were 29th October 1982, and 22nd September 1983.

2.4 The assessment of the effects of deltamethrin on polyphagous predators in winter wheat.

2.4.1. Materials and Methods

1. Treatments and plot design.

Each year, a randomized complete block design was used. Each subplot was surrounded by polythene barriers, 0.4m high dug into the soil to a depth of 0.15m using a rotovator, and supported by wires through 50mm square section posts (Plate 1). This design was similar to that used at Rothamsted Experimental Station (Edwards, Sunderland, and George 1979). The original 1mm diameter supporting wires were replaced following the destruction of the barriers in gales at the end of December 1982, with thicker 3mm diameter wire. This thicker wire was used in 1983-1984. Fig 2.1 shows the layout of the randomized blocks. Half of the subplots were sprayed with deltamethrin ("Decis" made by Roussel-Uclaf Ltd. France) using a knapsack sprayer, at the recommended rate of 7.5g a.i./Ha on the following dates.

Year 1 -Fences erected 22.12.82

18.1.83

24.4.83

24.6.83

Figure 2.1 Experimental plot design

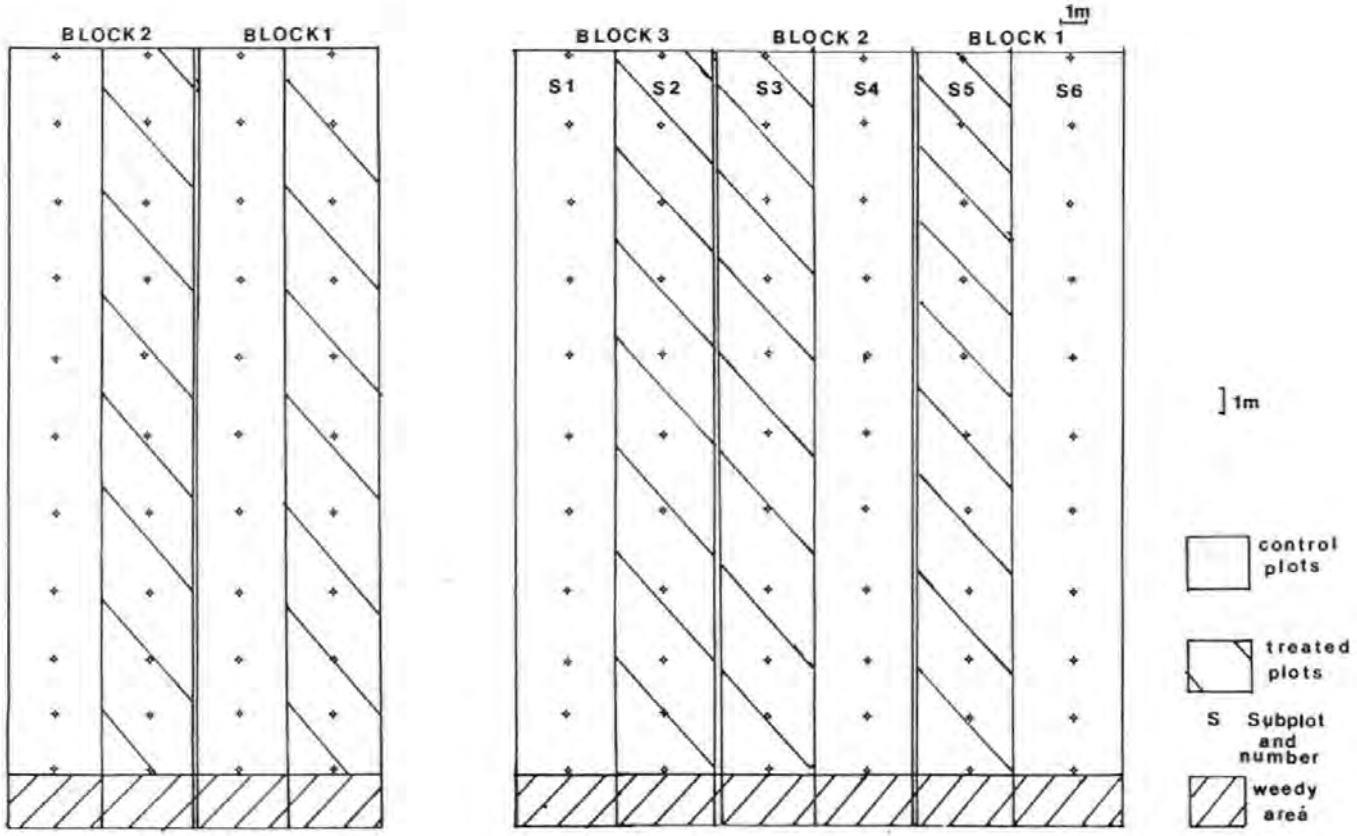


Plate 1 The barriered plots used to assess the effects of deltamethrin on polyphagous predators.

Year 2 -Fences erected 22.9.83

29.9.83

2.7.84

A 2m stretch of uncultivated grass and weeds in each subplot was included to provide an area of uncultivated ground which could provide shelter or overwintering sites (Sotherton 1984, 1985).

2. Sampling.

Pitfall traps were constructed from sawn-off milk bottles (80mm diameter), as shown in Fig. 2.2. These containers fulfilled important criteria suggested by authors :-

a) The edges were abrupt.

b) The traps were of sufficient depth to minimize possibilities of escapes.

c) Vertical sides facilitated removal of individuals.

d) Overhangs at the tops of the containers prevented the escape of any animals capable of climbing the vertical sides.

e) Replacements were readily available when breakages occurred (Thomas and Sleeper 1977).

Escape of captured insects was reduced by spraying of the inside of the traps with polytetra fluorethylene spray. Luff (1978) found glass the most effective material at reducing escapes. Two pieces of aluminium gauze of 1mm hole diameter were aligned at 45^{o} to each other across the bottom, secured by araldite and insulating tape around the sides of the bottles, enabling the traps to drain, and also preventing the escape of smaller carabids . Drainage was further enhanced by placing the traps in holes in the ground made with a crowbar to a depth of 0.4m and back filled with gravel (Fig.2·3)

Figure 2.2 Pitfall trap design

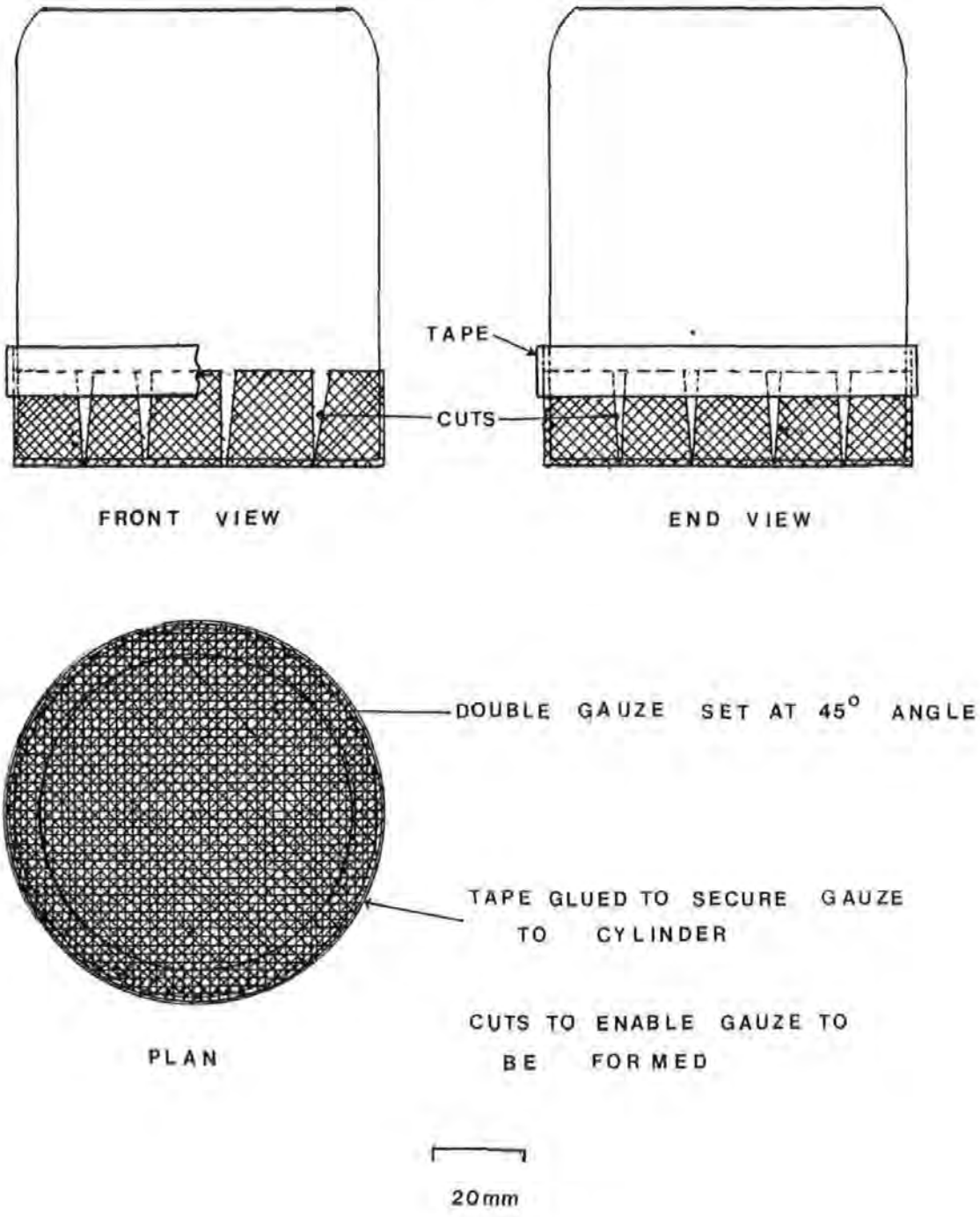


Figure 2.3 Positioning of pitfall trap in ground

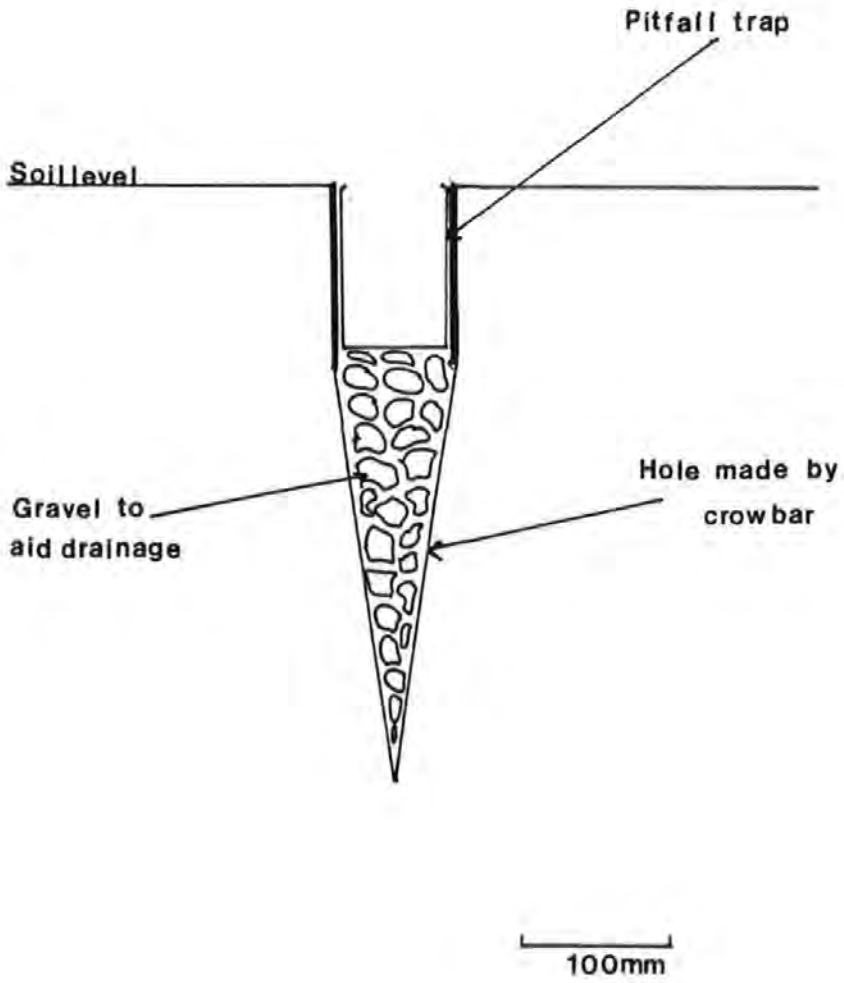


Plate 2 A pitfall trap in position.

The use of dry pitfalls enabled the re-release of live captured insects, and so prevented the sustained depletion of the polyphagous predator populations. Ten traps were positioned in the subplots at regular 3m intervals (Fig. 2.1 and Plate 2) and were emptied, using a spoon, at three, four or five or seven day intervals depending on the capture rate. All adult Carabidae were identified to species and other potential predators to taxonomic group (see Results). Recording continued for the entire two growing seasons, i.e. November-August 1982-1983, and September-August 1983-1984.

3. Analysis.

Any method of statistical analysis is based on several assumptions about the data. Analysis of variance (ANOVA) is most commonly used to investigate this type of data, and the assumptions basic to this are :-

1. The frequency distribution of the data is normal, and error terms are random and normally distributed.
2. Variances of the different samples are homogeneous with all errors arising from the same frequency curve.
3. Variances and means of the different samples are not correlated and are independent.
4. The main effects on the data collected are additive.

However, deviations from these assumptions are permissible, as the analysis is sufficiently robust.

Transformation of the data.

When data is not normally distributed, a transformation of the data is performed, where actual numbers are replaced by a function whose distribution is such that it normalizes the data and

stabilizes the variance (Southwood 1978).

From an ecological point of view, the dispersion pattern of individuals is seldom, if ever, normal, and so the variance is not independent of the mean. Their relationship has been shown by Taylor (Taylor 1984, Southwood 1978) to obey a power law which holds for a continuous series of distributions from regular through random to highly contagious (as in this experiment).

The relationship can be expressed by :-

$s^2 = a\bar{x}^b$ where constants

a = A sampling factor.

b = Index of aggregation.

In this experiment, a programme written in Fortran77 was used to calculate the mean and variance of the total catch per plot per sampling occasion and the value of b was found from fitting the equation by regression :-

$$\text{Log } s^2 = \text{Log}_{10} a + b\text{Log}_{10} \bar{x}$$

It can be shown that as variance varies with the mean in this way, the appropriate variance stabilizing transformation is :-

$z = x^p$

where z = transformed value

x = original raw number

p= 1-0.5b

If p=0, log transformations should be used, p=0.5 square roots.

The independence of the means and variances of the

transformed data was checked.

2.4.2. Results.

As insecticide was applied at different times in the two years, the data collected fall naturally into separate time periods. Species of adult Carabidae were caught, and classified according to size (Table 2.1). This produced three groups (large, medium and small Carabidae) & a fourth group, all Carabidae. All others were grouped as adult Staphylinidae, Araneae Carabid and Staphylinid larvae, and all were totalled to produce a group of all polyphagous predators. This was felt to produce the most useful division for analysis. Table 2.2 is an overall count of predators caught over the two years. No Dermaptera, Opiliones, Acari or Pseudoscorpionida were captured and too few Chilopoda to include in the totals. The faunal composition of the pitfall catches varied throughout the growing season (Fig. 2.6). Larvae were most abundant over the winter months whilst Araneaebecame more abundant in the spring. Numbers of adult Staphylinidae remained low (below 1 per sampling occasion) and variable throughout the two years. The large adult Carabidae catches were dominated by N. brevicollis in the autumn and P. cupreus from April to August.

P. melanarius and P. madidus were present in very low numbers over the winter, and were present in fewer numbers in the spring and summer. The medium adult Carabidae were uncommon in the winter, but dominated by A. aenea inthe spring, and found in large numbers in the summer. Small adult Carabidae were abundant in the autumn but very infrequently found at any other time, as Table 2.2 shows. Catches were dominated by T. quadristriatus in the autumn of 1982. All the species of Carabidae that were caught have been shown to

Table 2.1

Species and Size Classification of Adult Carabidae captured

Species	Length in mm	Size Class
Harpalus aeneus (F.)	8.5 - 12	Large (9 - 17 mm)
Nebria brevicollis (F.)	10 - 14	
Pterostichus cupreus (L.)	11 - 13.4	
Pterostichus madidus (F.)	13 - 17	
Pterostichus melanarius (Ill.)	12 - 18	
Pterostichus versicolor (Sturm)	9 - 12.2	
Harpalus rufipes (Gy.)	10 - 16.7	
Agonum dorsale (Pont)	6 - 8.2	
Loricera pilicornis (F.)	6 - 8.5	
Agonum mulleri (Herbst.)	7.2 - 9.5	Medium (6 - 8 mm)
Amara aenea (Degeer)	6.2 - 8.8	
Amara ovata (F.)	8 - 9.5	
Amara plebeja (Gy.)	6.3 - 7.8	
Bembidion lampros (Herbst.)	3 - 4.4	
Notiophilus biguttatus (F.)	5 - 5.9	Small (2 - 6 mm)
Trechus quadristriatus (Schrk.)	3.5 - 4	
Asaphidion flavipes (L.)	3.9 - 4.7	

Table 2.2

Polyphagous Predators caught in Pitfall Traps in Control and Treated Plots, 1982-83 and 1983-84

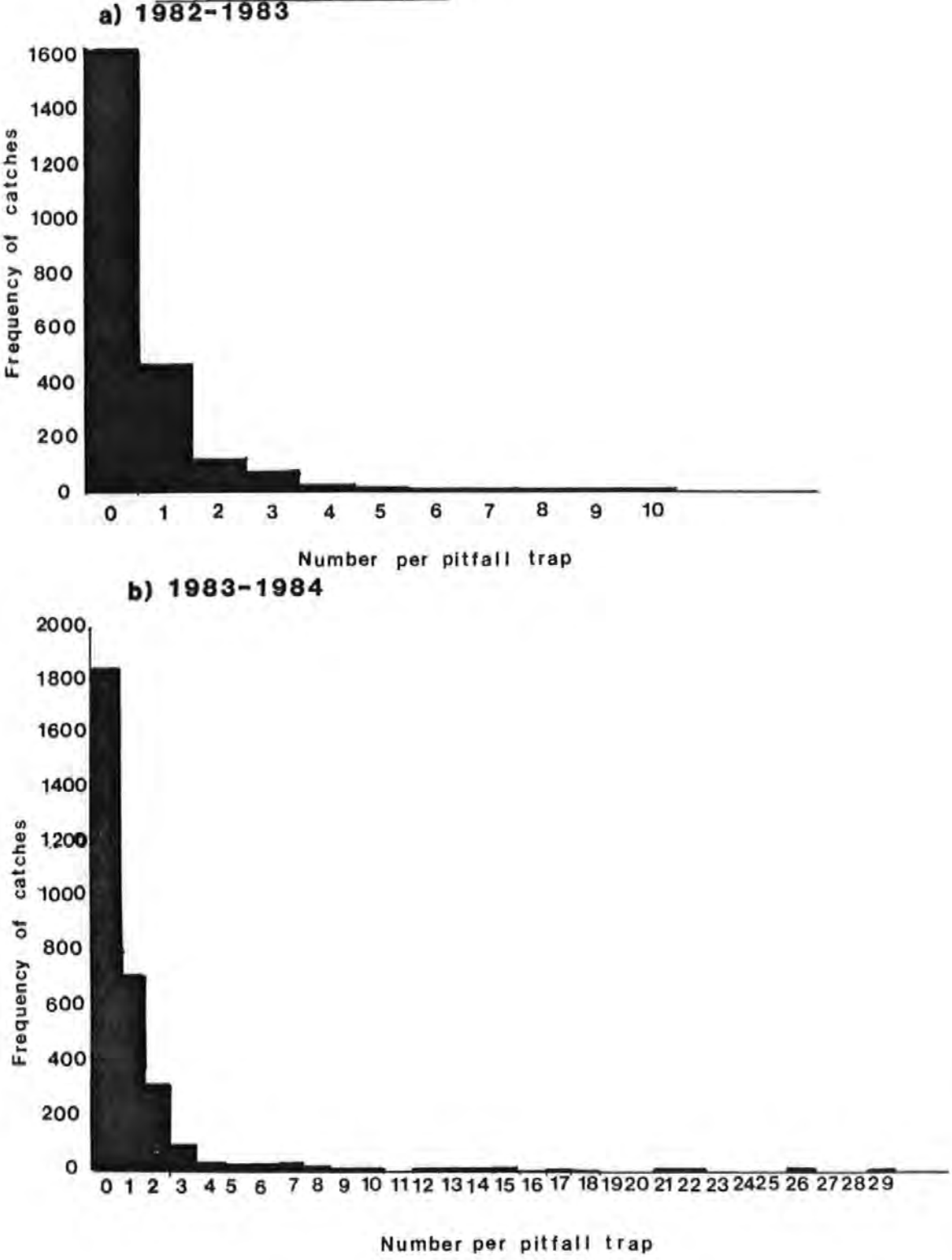
Predator Group	1982 - 83										1983 - 84			
	Nov 20th - Jan 18th		Jan 20th - Apr 21st		Apr 28th - Jun 29th		Jun 30th - Aug 5th		Oct 3rd - Apr 26th		Apr 30th - Jul 2nd		Jul 5th - Aug 20th	
	Control	To be Treated	Control	Treated	Control	Treated	Control	Treated	Control	Treated	Control	Treated	Control	Treated
Carabidae and Staphylinidae larvae	81	85	120	92	0	1	0	0	376	254	3	1	0	0
Adult Staphylinidae	6	5	9	11	9	12	4	1	25	23	33	21	7	1
Araneae	3	6	40	31	12	14	2	2	48	19	34	30	9	6
Large Carabidae	57	69	5	7	73	75	43	66	141	141	459	163	156	29
Medium Carabidae	1	3	2	3	63	66	26	46	36	40	301	297	77	44
Small Carabidae	45	40	0	2	3	6	1	0	59	47	5	8	1	0
Subtotal all Carabidae	103	112	7	12	137	147	70	112	236	228	765	468	234	73
All polyphagous predators	199	208	176	146	158	174	76	115	685	524	835	520	250	80

Table 2.1

Species and Size Classification of Adult Carabidae captured

Species	Length in mm	Size Class
Harpalus aeneus (F.)	8.5 - 12	Large (9 - 17 mm)
Nebria brevicollis (F.)	10 - 14	
Pterostichus cupreus (L.)	11 - 13.4	
Pterostichus madidus (F.)	13 - 17	
Pterostichus melanarius (Ill.)	12 - 18	
Pterostichus versicolor (Sturm)	9 - 12.2	
Harpalus rufipes (Gy.)	10 - 16.7	
Agonum dorsale (Pont)	6 - 8.2	
Loricera pilicornis (F.)	6 - 8.5	
Agonum mulleri (Herbst.)	7.2 - 9.5	Medium (6 - 8 mm)
Amara aenea (Degeer)	6.2 - 8.8	
Amara ovata (F.)	8 - 9.5	
Amara plebeja (Gy.)	6.3 - 7.8	
Bembidion lampros (Herbst.)	3 - 4.4	
Notiophilus biguttatus (F.)	5 - 5.9	Small (2 - 6 mm)
Trechus quadristriatus (Schrk.)	3.5 - 4	
Asaphidion flavipes (L.)	3.9 - 4.7	

Figure 2.4 Distribution of polyphagous predators per pitfall trap per 3 day sampling occasion



also added together to produce monthly total polyphagous predator catches, a table of data was produced which became far more meaningful to analyse. This is presented graphically in Figs. 2.5 a and b. As the number of sampling occasions per month was not constant, the mean catches per trapline per month were calculated, and then Taylor's power law was applied, as explained. The most appropriate transformations of the raw data were found, and the resultant means and variances of the transformed data were not significantly correlated (r^2=Ø.3Ø4 1982-1983, r^2=Ø.Ø16 1983-1984). A two-way analysis of variance was then performed on the mean monthly total polyphagous predator catch per pitfall trapline according to the linear model :-

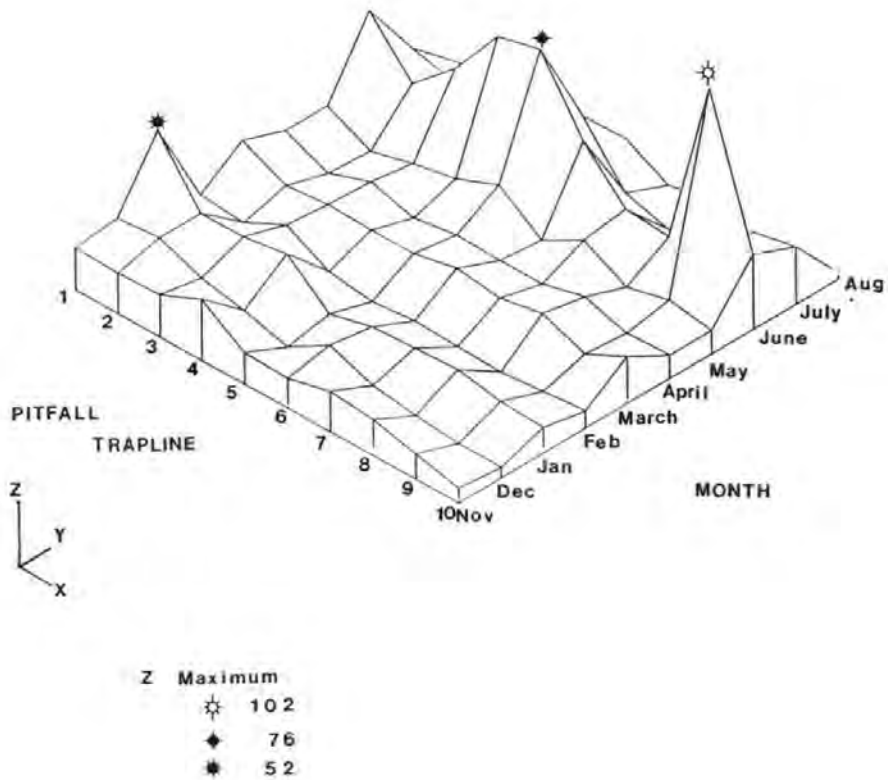
Mean monthly catch per trapline = mean catch + month + trap position + month.trap position + error.

The results are presented in Appendix 2A. In 1982-1983, month and trapline significantly contribute to the variation, whilst in 1983-1984, only month is significant. This could suggest "hot spots" existed in the plots of concentrations in predator distribution and activity, but because a Poisson distribution could be fitted to the data in Fig. 2.4., such high aggregation in the data is unlikely.

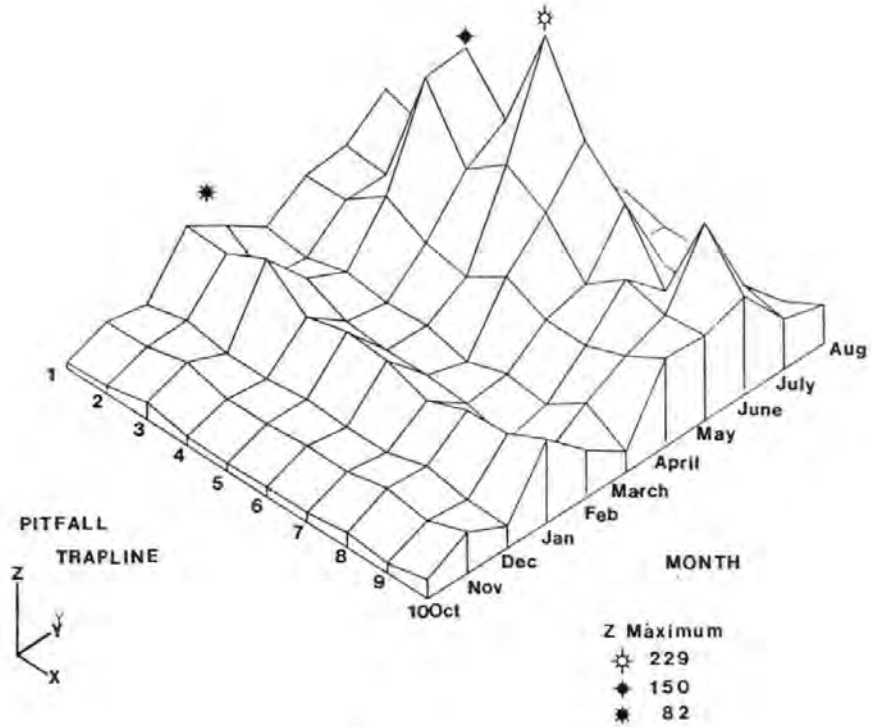
It is obvious that these individual pitfall catch records do not form a suitable basis for investigating the effects of insecticide applications, and so the raw data was first summed to produce a count for each plot per occasion, i.e. 4 for 1982-1983 and 6 for 1983-1984 (Appendicies 2C and 2D). All data was then corrected with respect to time to give a catch per three day constant time

Figure 2.5 Monthly total trap line catches

(a) 1982 - 1983



(b) 1983 - 1984



interval. The totals per occasion in the treated and untreated plots are shown for some taxonomic groups in Figs. 2.6 a and b. The points represent the numbers of polyphagous predators caught in 20 pitfall traps for 1982-1983 and 30 pitfall traps for 1983-1984. The data is tabulated in Table 2.3.

Transformation of the data

1. Treated and untreated plots were first checked separately, in accordance with assumption 2 of analysis of variance, using Minitab, as explained. The regression coefficients of the relationships obtained between the means and the variances were compared, using Student's t test tables to test for significant differences. Table 2.4 shows the b values (a measure of the aggregation of the population) obtained for the treated, untreated and pooled data. It can be seen from Table 2.3 that at certain times of the year, too few of certain taxonomic groups of predator were caught for an analysis of variance, and so Table 2.4 contains selected data for each group.

None of the b values of the treated and untreated data were significantly different at the 1% level, and so the data was pooled to calculate an appropriate transformation. The transformations were then checked by correlating the mean and variance of each per plot (treated and untreated) using a computer programme in Minitab. Unfortunately, some were still signifigantly correlated, and if these data were used, then the assumptions of the analysis of variance would be violated. Therefore, more powerful transformations were applied until mean and variance were not significantly correlated at the 1% level. The last two columns of Table 2.4 show

Table 2.3

Summary of Predator Catches over the Two Sampling Years

Year	Data Set	No. of Samples	Control		Insecticide treated	
			Sum	Mean Catch per occasion ± s.error	Sum	Mean Catch per occasion ± s.error
	1. All Polyphagous Predators					
1982 - 83	Pre-fence erection	18	130	7.21 ± 1.30	147	8.16 ± 0.54
	Pre-treatment	10	69	6.0 ± 1.23	63	6.26 ± 1.20
	Pooled pre-treatment	28	199	7.11 ± 0.93	208	7.48 ± 1.53
	Post 1st insecticide treatment	46	176	3.83 ± 0.40	146	3.33 ± 0.38
	Post 2nd insecticide treatment	24	160	6.68 ± 1.12	171	7.32 ± 1.52
	Post 3rd insecticide treatment	20	77	3.87 ± 0.70	115	5.71 ± 1.00
1983 - 84	Post 1st insecticide treatment	117	685	5.99 ± 0.59	524	4.54 ± 0.35
	Late post 1st insecticide treatment	39	835	21.50 ± 0.16	520	13.90 ± 2.13
	Post 2nd insecticide treatment	30	250	8.24 ± 1.23	80	2.71 ± 0.45
	2. Staphylinidae and Carabidae larvae					
1982 - 83	Pooled pre-treatment	28	81	2.89 ± 0.60	85	3.02 ± 0.57
	Post 1st insecticide treatment	46	120	2.61 ± 0.40	92	1.99 ± 0.34
	Post 2nd insecticide treatment	24	0	0 -	1	0.06 -
	Post 3rd insecticide treatment	10	0	0 -	0	0 -
1983 - 84	Post 1st insecticide treatment	117	376	3.22 ± 0.55	254	0.03 ± 0.01
	Late post 1st insecticide treatment	39	3	0.08 ± 0.04	1	0.03 ± 0.03
	Post 2nd insecticide treatment	30	0	0 -	0	0 -
	3. Staphylinidae					
1982 - 83	Pooled pre-treatment	28	6	0.20 ± 0.08	5	0.19 ± 0.08
	Post 1st insecticide treatment	46	9	0.08 ± 0.08	11	0.25 ± 0.06
	Post 2nd insecticide treatment	24	9	0.39 ± 0.13	12	0.49 ± 0.13
	Post 3rd insecticide treatment	20	4	0.20 ± 0.11	1	0.03 ± 0

1983 - 84	Post 1st insecticide treatment	117	25	0.21 ± 0.05	23	0.19 ± 0.04
	Late post 1st insecticide treatment	39	33	0.84 ± 0.15	21	0.53 ± 0.13
	Post 2nd insecticide treatment	30	7	0.25 ± 0.09	1	0.03 ± 0.03
	4. Araneae					
1982 - 83	Pooled pre-treatment	28	3	0.09 ± 0.06	6	0.22 ± 0.16
	Post 1st insecticide treatment	46	41	0.89 ± 0.21	31	0.68 ± 0.13
	Post 2nd insecticide treatment	24	12	0.48 ± 0.14	14	0.58 ± 0.15
	Post 3rd insecticide treatment	20	2	0.11 ± 0.06	2	0.09 ± 0.06
1983 - 84	Post 1st insecticide treatment	117	48	0.41 ± 0.15	19	0.16 ± 0.05
	Late post 1st insecticide treatment	39	34	0.87 ± 0.25	30	0.78 ± 0.24
	Post 2nd insecticide treatment	30	9	0.11 ± 0.11	6	0.19 ± 0.07
	5. Large Adult Carabidae					
1982 - 83	Pooled pre-treatment	28	57	± 0.47	69	2.45 ± 0.97
	Post 1st insecticide treatment	46	5	0.10 ± 0.05	7	0.16 ± 0.07
	Post 2nd insecticide treatment	24	73	2.98 ± 0.68	75	3.11 ± 0.68
	Post 3rd insecticide treatment	20	42	1.20 ± 0.42	66	3.32 ± 0.63
1983 - 84	Post 1st insecticide treatment	117	141	1.20 ± 0.17	141	1.21 ± 0.14
	Late post 1st insecticide treatment	39	459	11.8 ± 2.34	163	4.18 ± 0.71
	Post 2nd insecticide treatment	30	156	5.19 ± 0.83	29	0.96 ± 0.17
	6. Medium Adult Carabidae					
1982 - 83	Pooled pre-treatment	28	1	0.0 ± 0.05	3	0.05 ± 0.04
	Post 1st insecticide treatment	46	2	0.03 ± 0.03	3	0.07 ± 0.04
	Post 2nd insecticide treatment	24	63	2.53 ± 0.51	66	2.74 ± 0.77
	Post 3rd insecticide treatment	20	26	1.32 ± 0.35	46	2.29 ± 0.54

1983 - 84	Post 1st insecticide treatment	117	36	0.30 ± 0.10	40	0.33 ± 0.13
	Late post 1st insecticide treatment	39	301	7.72 ± 1.56	297	7.61 ± 1.40
	Post 2nd insecticide treatment	30	77	2.57 ± 0.56	44	1.47 ± 0.40

7. Small Adult Carabidae

1982 - 83	Pooled pre-treatment	28	45	1.6 ± 0.61	40	1.41 ± 0.49
	Post 1st insecticide treatment	46	0	0 -	2	0.05 ± 0.03
	Post 2nd insecticide treatment	24	3	0.14 ± 0.07	6	0.27 ± 0.09
	Post 3rd insecticide treatment	20	1	0.06 ± 0.04	0	0 -
1983 - 84	Post 1st insecticide treatment	117	59	0.50 ± 0.09	47	0.40 ± 0.09
	Late post 1st insecticide treatment	39	5	0.13 ± 0.06	8	0.12 ± 0.08
	Post 2nd insecticide treatment	30	1	0.03 ± 0.03	0	0 -

8. All Adult Carabidae

1982 - 83	Pooled pre-treatment	28	103	3.70 ± 0.88	112	4.0 ± 1.31
	Post 1st insecticide treatment	46	7	0.13 ± 0.07	13	0.28 ± 0.08
	Post 2nd insecticide treatment	24	137	5.65 ± 1.02	147	6.11 ± 1.41
	Post 3rd insecticide treatment	20	70	3.48 ± 0.59	112	5.61 ± 0.99
1983 - 84	Post 1st insecticide treatment	117	235	2.01 ± 0.25	228	1.95 ± 0.22
	Late post 2nd insecticide treatment	39	765	19.60 ± 3.60	468	11.90 ± 1.89
	Post 2nd insecticide treatment	30	234	7.46 ± 1.22	73	2.17 ± 0.45

Note: Number of Samples = Number of Occasions
2 plots for 1982/83 in both treatments
3 plots for 1983/84 in both treatments

these data sets.

At some times in both years, it was decided that sufficient numbers permitted investigation into the effects of deltamethrin on individual carabid species, and so Table 2.4 includes these. If the raw data means and variances were not significantly correlated for the unpooled data, then pooling was done first. Use of Taylor's power law is inappropriate for data of this kind. Also, low means and variance values are produced in many cases. Taylor's power law is not 100% efficient with means below 4 and variances below 2 (Taylor 1984). The data is variable according to time and spatial distribution, and in some cases the standard error of the b value found was very large. It can be seen that even when the most powerful data transformation (Log_{10} (N+1)) was used in some cases, the mean and variances of the data remains significantly correlated.

However, as analysis of variance is such a robust method of statistical analysis, it was felt that this was still the most appropriate method to use, but conclusions must be drawn in the light of a mean and variance relationship.

The model.

The linear additive model used for a Genstat programme was:-

Catch(per plot)= mean + block + treatment + time

+ treatment.time + error.

Thus the sources of variation are two types :-

1.Treatment effects -the sources of variation in which the investigation is primarily interested, i.e. deltamethrin treatment and its effect over time.

2. Block effects -the sources of variation which influences the

** = 5% significant
*** = 1% significant

Table 2.4 The Results of Application of Taylor's Power Law to the Data

Predator Group and Data Set	Control b	Control s.error of b	Treated b	Treated s.error of b	Pooled b	Pooled s.error of b	Correlation Coefficient of Means and Variances (r) after first transformation	If r significant, second transformation used	Correlation Coefficient of Means and Variances after 2nd transformation
(1) All Polyphagous predators 1982 - 83	1	0.44	1.72	0.338	1.57	0.45	0.667 **	$\sqrt{\ }$	0.085
Pre-fence erection									
Pre-treatment	Raw data Mean and Variance independent				1.04	2.031	0.218		
Pooled pre-treatment	1.11	0.586	1.46	0.395	1.49	0.459	0.623 **	$\sqrt{\ }$	0.011
Post 1st insecticide treatment	1.45	0.431	1.05	0.392	1.43	0.343	0.425 **	None better	
Post 2nd insecticide treatment	2.19	0.572	0.052	0.546	1.57	0.276	0.485		
Post 3rd insecticide treatment	Raw data Mean and Variance independent				0.739	0.739	0.299		
1983 - 84									
Post 1st insecticide treatment	1.64	0.288	0.996	0.203	1.39	0.211	0.429 ***	None better	
Late post 1st insecticide treatment	2.28	0.113	1.7	0.255	1.97	0.114	0.922	$\text{Log}(n+1)_{10}$	0.708 **
Post 2nd insecticide treatment	2.48	0.427	1.9	0.265	1.91	0.219	0.981	$\text{Log}(n+1)_{10}$	0.24
(2) Carabidae and Staphylinidae larvae Pre-treatment pooled	1.24	0.396	1.22	0.329	1.21	0.283	0.283		
1982 - 83 Post 1st insecticide treatment	0.856	0.276	0.892	0.392	0.987	0.201	0.141		
1983 - 84 Post 1st insecticide treatment	1.41	0.13	1.26	0.207	1.44	0.084	0.275		
3) Staphylinidae 1982 - 83 Post 1st insecticide treatment	1.18	0.534	2	0	1.26	0.223	0.628 ***	None better	
Post 2nd insecticide treatment	-0.69	1.188	-0.833	0.881	0.643	0.487	0.048	-	-
1983 - 84 Post 1st insecticide treatment	1.38	0.221	1.33	0.224	1.33	0.127	0.676 ***	None better	
4) Araneae 1982 - 83									
Post 1st insecticide treatment	0.804	0.315	0.843	0.253	1.12	0.205	0.223		
Post 2nd insecticide treatment	1.32	0.523	0.997	0.343	1.12	0.258	0.042		
1983 - 84									

** = 5% significant
*** = 1% significant

Predator Group and Data Set	Control		Treated		Pooled		Correlation Coefficient of Means and Variances (r) after first transformation	If r significant, second transformation used	Correlation Coefficient of Means and Variances after 2nd transformation
	b	s.error of b	b	s.error of b	b	s.error of b			
Late Post 1st insecticide treatment	2.13	0.241	1.73	0.176	1.99	0.217	0.583		
Post 2nd insecticide treatment	1.66	0.379	2	0	1.44	0.325	0.763 ***	None better	
(5) Large Carabidae									
1982 - 83									
Pooled pre-treatment	1.230	0.200	1.770	0.272	1.79	0.204	0.924 ***	Log_{10} (n + 1)	0.562 **
Post 1st insecticide treatment	1.000	0	2.000	0	1.230	0.209	0.764	None better	
Post 2nd insecticide treatment	Mean and Variance of Raw Data independent				1.490	0.330	0.571		
Post 3rd Insecticide treatment	0.493	0.871	1.740	1.410	0.242	0.592	0.026		
1983 - 84									
Post 1st Insecticide treatment	1.610	0.122	1.170	0.145	1.440	0.118	0.640 ***	None better	
Late post 1st insecticide treatment	2.070	0.077	1.800	0.197	2.080	0.074	0.065		
Post 2nd insecticide treatment	1.670	0.488	0.832	0.310	1.670	0.308	0.703	Log_{10} (n+1)	0.271
(6) Medium Carabidae									
1982 - 83									
Post 2nd Insecticide treatment	1.27	0.274	0.888	0.636	1.050	0.221	0.571		
Post 3rd Insecticide treatment	Mean and Variance of Raw Data independent				0.878	0.748	0.226		
1983 - 84									
Post 1st Insecticide treatment	1.070	0.385	1.360	0.305	1.210	0.192	0.035		
Late post 1st insecticide treatment	2.020	0.210	1.690	0.160	1.860	0.170	0.689		
Post 2nd Insecticide treatment	2.350	0.663	1.520	0.232	1.530	0.912	-0.174		
(7) Small Carabidae									
1982 - 83									
Pre-treatment pooled	1.500	0.385	1.350	0.535	1.310	0.304	0.006		
1983 - 84									
Post 1st Insecticide treatment	1.300	0.150	1.600	0.138	1.400	0.113	0.503 ***	None better	
Late post 1st insecticide treatment	2.070	0.766	1.850	0.630	1.920	0.228	0.990 **	$\sqrt{}$	0.929 ***

** = 5% significant
*** = 1% significant

Predator Group and Data Set	Control b	Control s.error of b	Treated b	Treated s.error of b	Pooled b	Pooled s.error of b	Correlation Coefficient of Means and Variances (r) after first transformation	If r significant, second transformation used	Correlation Coefficient of Means and Variances after 2nd transformation
(8) All Carabidae 1982 - 83									
Pre-treatment pooled	1.460	0.190	1.770	0.285	1.650	0.240	0.728 ***	√	0.320
Post 1st Insecticide treatment					1.060	0.207	0.799 ***	√	0.766 **
Post 2nd Insecticide treatment	Mean and Variance of Raw Data independent				1.400	0.213	0.582	√	0.038
Post 3rd Insecticide treatment					0.634	0.858	0.223		
1983 - 84									
Post 1st Insecticide treatment	1.430	0.176	1.280	0.164	1.300	0.139	0.355	$\log_{10}(n+1)$	0.328
Late post 1st insecticide treatment	2.170	0.118	1.320	0.311	2.060	0.124	0.029		
Post 2nd Insecticide treatment	2.050	0.230	1.770	0.293	1.970	0.171	0.737 **	$\log_{10}(n+1)$	0.516
Nebria brevicollis 1983 - 84									
Post 1st Insecticide treatment					1.450	0.090	0.050		
Trechus quadristriatus 1983 - 84									
Post 1st Insecticide treatment					1.470	0.118	0.806 **	None better	
Pterostichus cupreus 1982 - 83									
Post 2nd Insecticide treatment	1.960	0.242	-2.580	0	1.610	0.079	0.048		
Post 3rd Insecticide treatment					0.971	0.822	0.348		
1983 - 84									
Late post 1st insecticide treatment	2.070	0.070	1.770	0.725	2.060	0.072	0.224		
Amara aenea 1982 - 83									
Post 2nd Insecticide treatment	1.470	0.551	1.090	0.567	1.340	0.172	0.583		
Post 3rd Insecticide treatment					0.920	0.607	0.200		
1983 - 84									
Late post Insecticide treatment	2.160	0.219	1.680	1.160	1.900	0.179	0.755 ***	$\log_{10}(n+1)$	0.742 **

Table 2.5

Summary of the Analyses of Variance

Data Set	Source of Variation: Block	Decis Treatment	Time	Time/Treatment Interaction
1982-83 Pre-treatment			All poly predators ***	
Post 1st insecticide treatment	Large Carabidae **		Carabidae and Staphylinidae larvae ** All poly *** Large Carabidae **	
Post 2nd insecticide treatment	Large Carabidae *** Medium Carabidae ***	Amara aenea *	All poly predators *** Large Carabidae *** Pterostichus cupreus *** Amara aenea ***	
Post 3rd insecticide treatment	All poly predators ** All Carabidae **	All Carabidae * Amara aenea * Medium Carabidae ***		
1983-84 Post 1st insecticide treatment	Trechus quadristriatus ** All poly predators *** Large Carabidae *** All Carabidae *** Nebria brevicollis ***	Carabidae and Staphylinidae larvae * All predators *** Araneae ***	Large Carabidae *** Medium Carabidae *** Small Carabidae *** Carabidae and Staphylinidae larvae *** Trechus quadristriatus *** Nebria brevicollis *** Amara aene ***	Nebria brevicollis *
Late Post 1st insecticide treatment	All Carabidae ***	All poly predators * Medium Carabidae ** All Carabidae ** Amara aenea **	Medium Carabidae *** All Carabidae *** Amara aenea ***	Small Carabidae * Amara aenea *
Post 2nd insecticide treatment	Large Carabidae ** All poly predators ***	All Carabidae * Medium Carabidae ** All poly predators *** Large Carabidae ***	Medium Carabidae ***	

Significance: * = 10%
** = 5%
*** = 1%
_____ * Means and Variances correlated

treatment effects, i.e. environmental variation, and referring to the effects of environmental variation.

Table 2.5 is a summary of all the partial variance (F) ratios obtained by using the model, and Appendix 2B shows the programme used and the analysis of variance tables produced. Table 2.5 summarizes the results.

Interpretation of all results.

This is divided into data set. All the graphs in Figs. 2.6. reflect the temporal variation in activity and presence in the crop of the different polyphagous predator groups. In practically all the cases, the numbers caught in the treated and control plots follow the same pattern, but clearly many environmental variables influence the distribution of the catches. Consideration of such factors are beyond the scope of this investigation, but it is thought that changes in temperature and rainfall may explain the underlying trends.

1982-1983

1. Pre-treatment

In all the groups, no significantly different numbers were caught in the areas to become treated and control, and this suggests that the environment was homogeneous.

2. Post 1st insecticide treatment January- April

In this period, no significant differences between the numbers of any group in the treated and control areas existed, although 17% less total polyphagous predators, 22% less Araneae and 23% less larvae were found in the treated than in the control plots. The increase in Araneae numbers in the control plots up to a peak in

Figure 2.6 (a)

Total polyphagous predator catches 1982 - 1983.

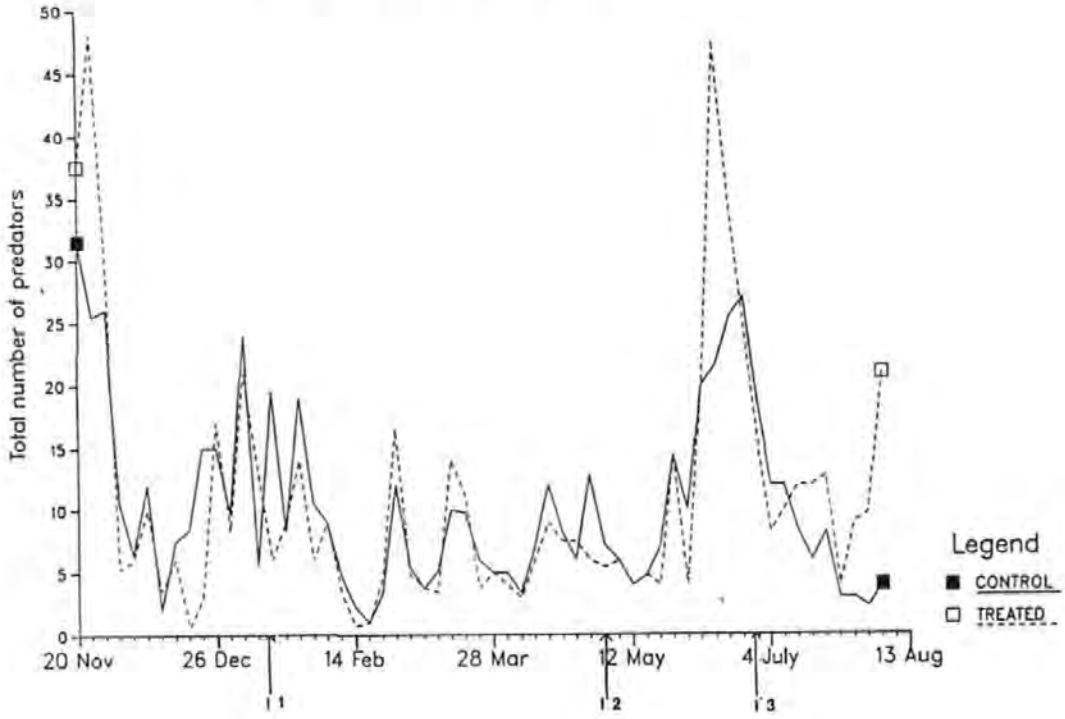
Each data point represents the sum of the catch corrected to 3 day standard trapping interval per 20 pitfall traps per treatment.

I1 = 1st insecticide application

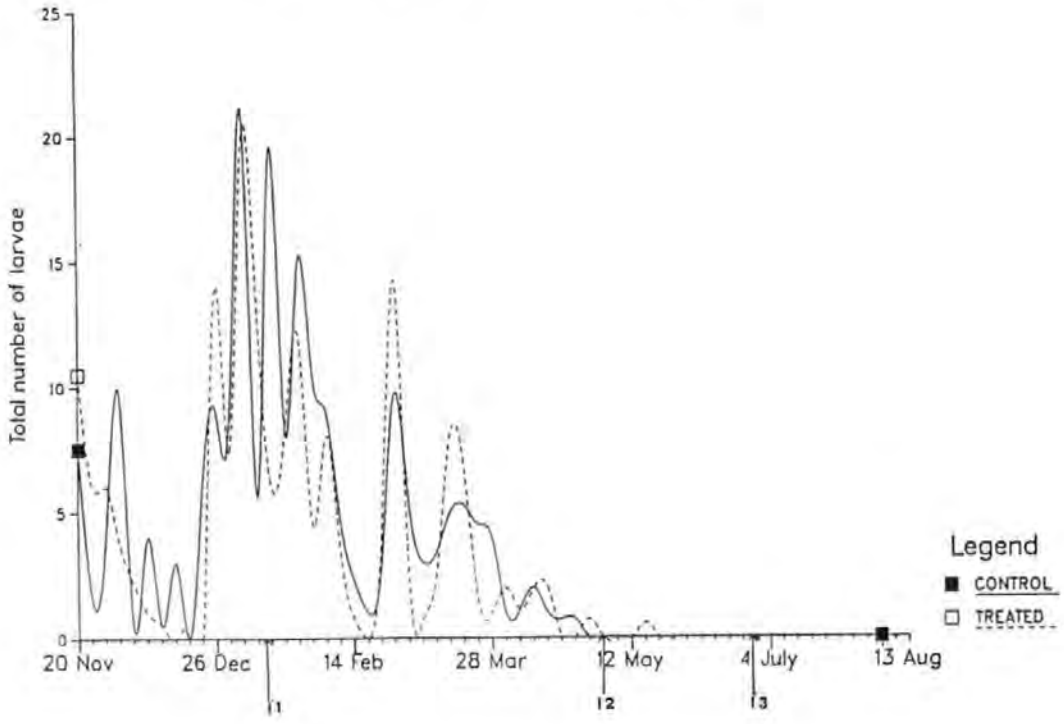
I2 = 2nd insecticide application

I3 = 3rd insecticide application

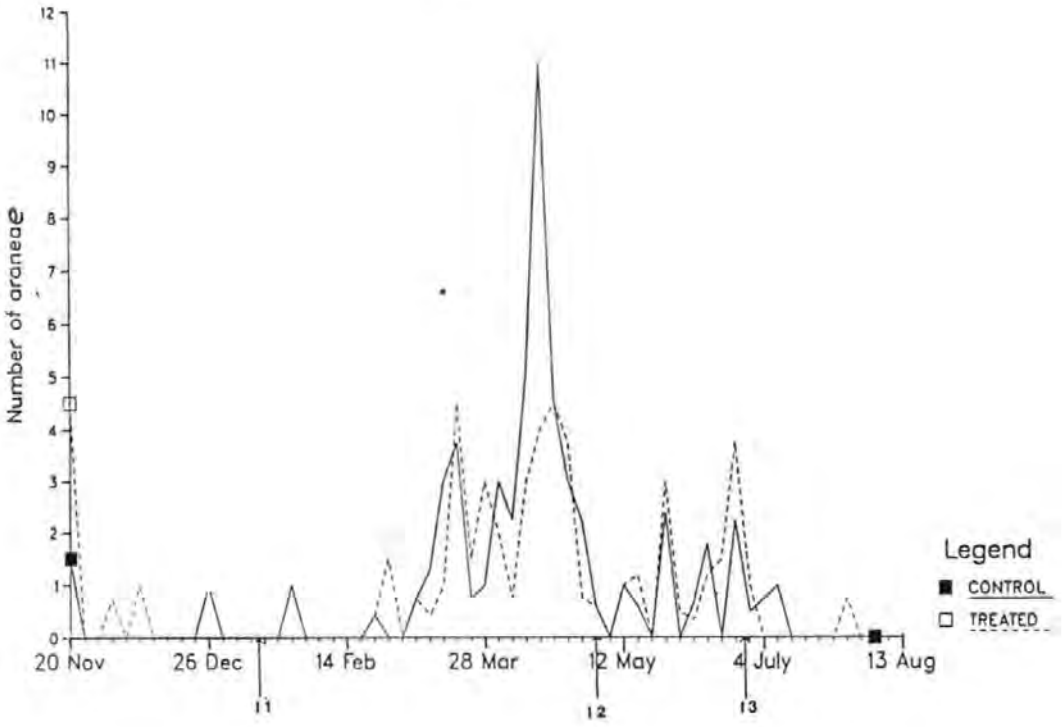
All polyphagous predators



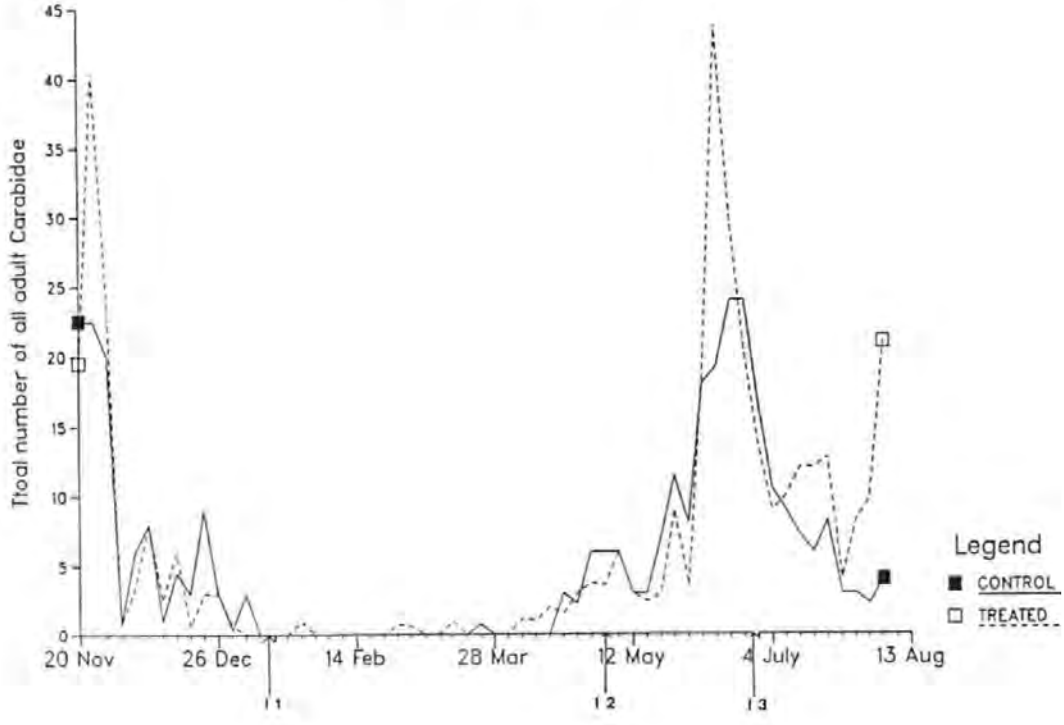
Carabidae and Staphylinidae larvae



Araneae



All adult Carabidae



mid April was not mirrored in the control plots, where numbers remained constant.

3. Post 2nd insecticide treatment April-June.

In this period, there was an overall increase in the treated areas in polyphagous predators of 7%, which can be explained by the sudden increase in the treated areas on occasion 47 in mid-June. This is due to an increase in the numbers of large and medium adult Carabidae - chiefly the species P. cupreus and A. aenea. However, although across the time period numbers of all groups are virtually equal, deltamethrin had a significant effect on A. aenea numbers. No larvae were found in any plots, and Araneae and Staphylinidae numbers were low and variable.

4. Post 3rd. insecticide treatment June -August.

In this period, 44% significantly more medium adult Carabidae and 35% more adult Carabidae in total were found in the treated plots, but the second difference was only slightly significant (10% level). Araneae numbers were equal in treated and control plots, and Staphylinidae numbers were low, variable and not significantly different.

1983-1984

1. Post 1st. insecticide treatment October-April.

In this period, there was a 24% reduction in total polyphagous predator numbers, and 60% reduction of Araneae (both 1% level significance) in the treated plots. Larvae numbers were reduced by 32% (significant at the 10% level in the ANOVA). The peaks in total numbers of predators caught in mid January and at the end of April are due to peaks in Larvae and Araneae respectively. The

results of the ANOVA for large and small Carabidae must be considered in the light of the knowledge that the means and variances are correlated (at the 1% significance level). These categories are dominated by the species N. brevicollis and T. quadristriatus repectively.

Significant block effects existed for these two species. The time/deltamethrin interaction for N. brevicollis was significant at the 5% level, suggesting that the effect of deltamethrin was not time constant. The peak time of Carabidae activity was November, apparent in both treated and control areas, though somewhat reduced in the former (Fig. 2.6b.).

2. Late post 1st insecticide April-June.

From April to July the total number of polyphagous predators caught in treated plots was reduced by 38%. Such a large reduction is mirrored in the large adult Carabidae with reductions of 64% for large, 38% for medium, and 39% overall for all Carabidae (Fig. 2.6.b).

The large and medium Carabidae groups were dominated by the species P. cupreus and A. aenea respectively. ANOVA shows a 5% significant reduction in numbers due to deltamethrin treatment for all Carabidae, medium Carabidae and A. aenea (though the latter two data sets have significantly correlated means and variances). ANOVA of all polyphagous predator numbers only show a 10% significant reduction, but here, too, the mean and variance are not independent. It is interesting to see that the deltamethrin /time interaction was significant for small Carabidae (chiefly B. lampros and A. aenea).

Figure 2.6 (b)

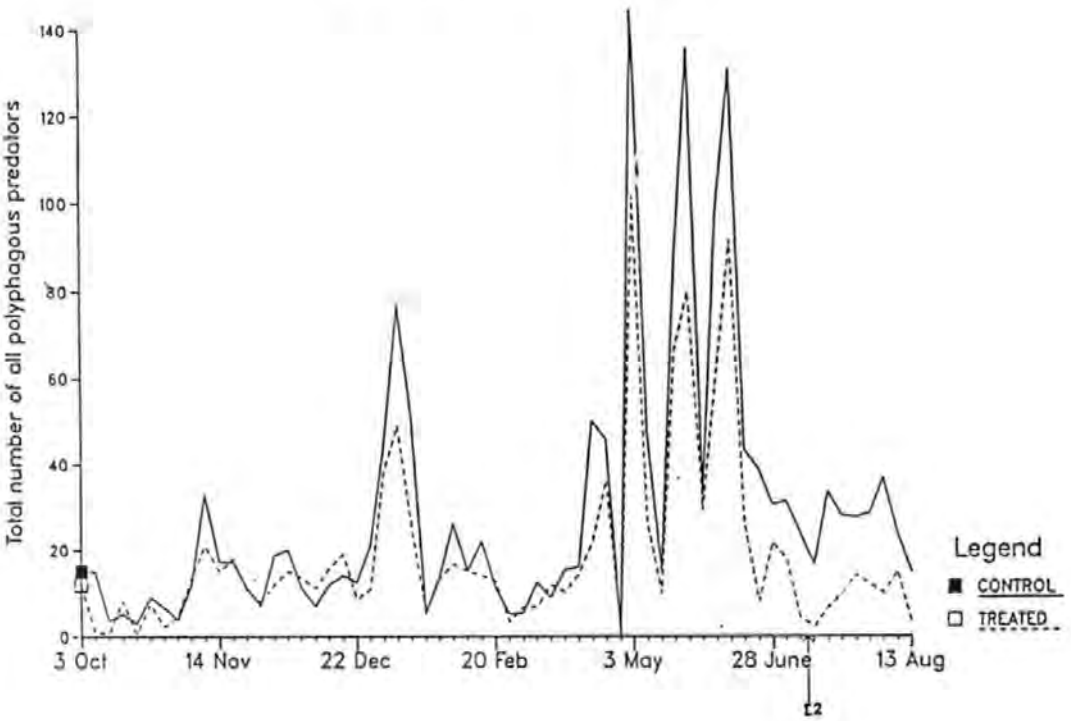
Total polyphagous predator catches, 1983 - 1984.

Each data point represents the sum of the catch corrected to 3 day standard trapping interval per 30 pitfall traps per treatment.

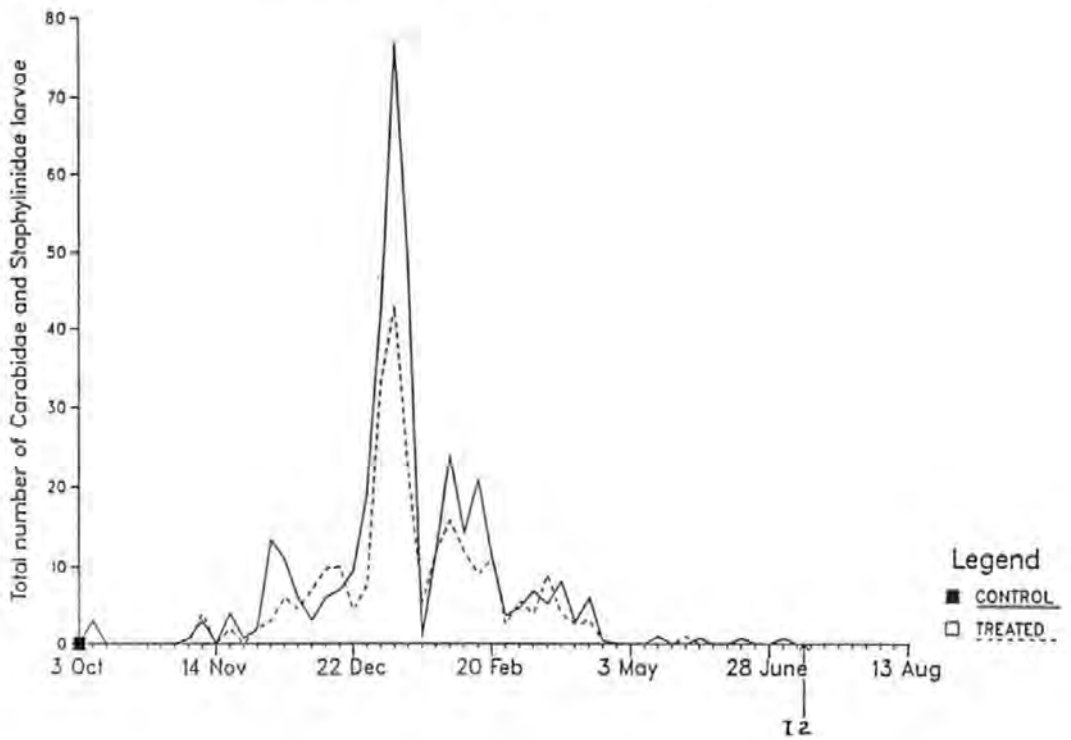
1st insecticide application 29 September 1983.

I2 = 2nd insecticide application.

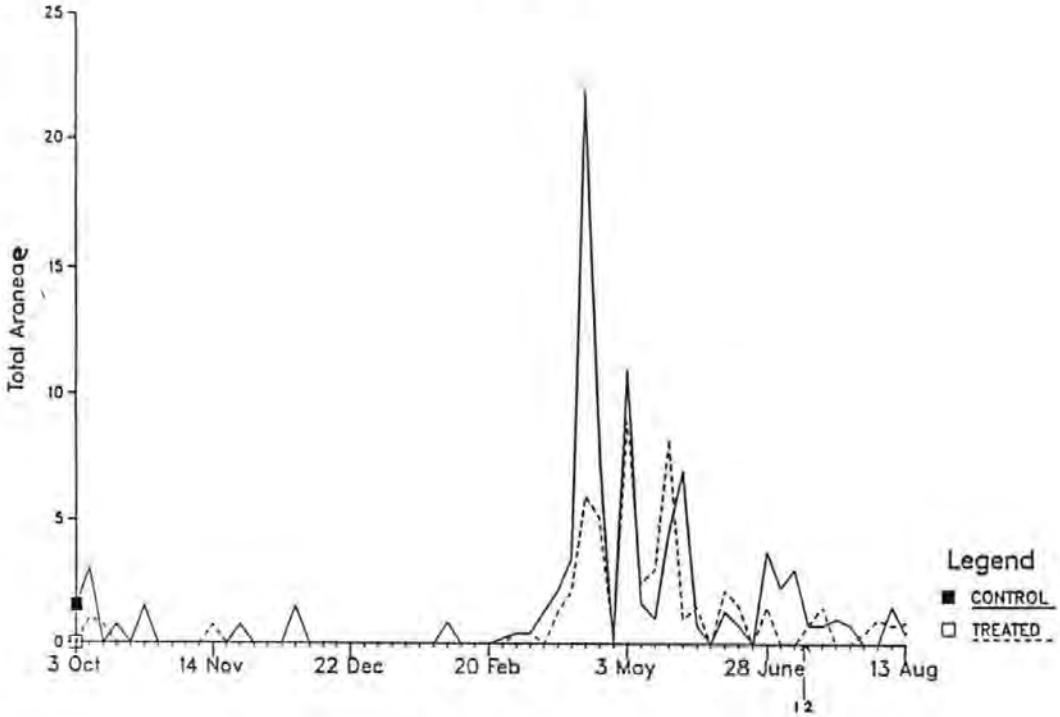
All polyphagous predators



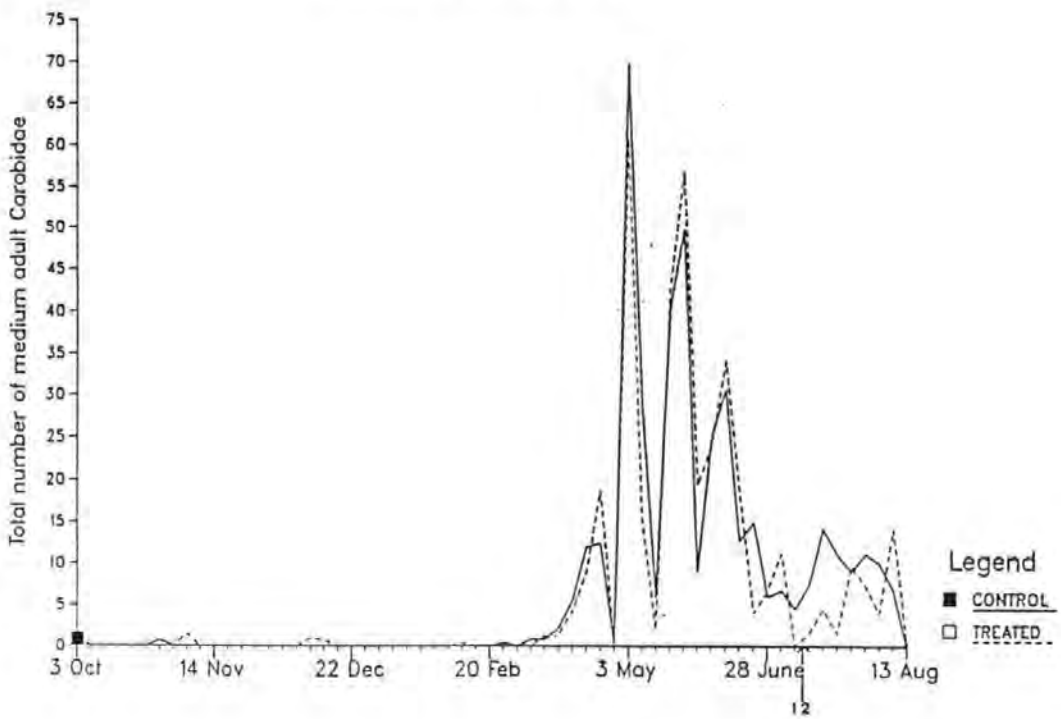
Carabidae and Staphylinidae larvae



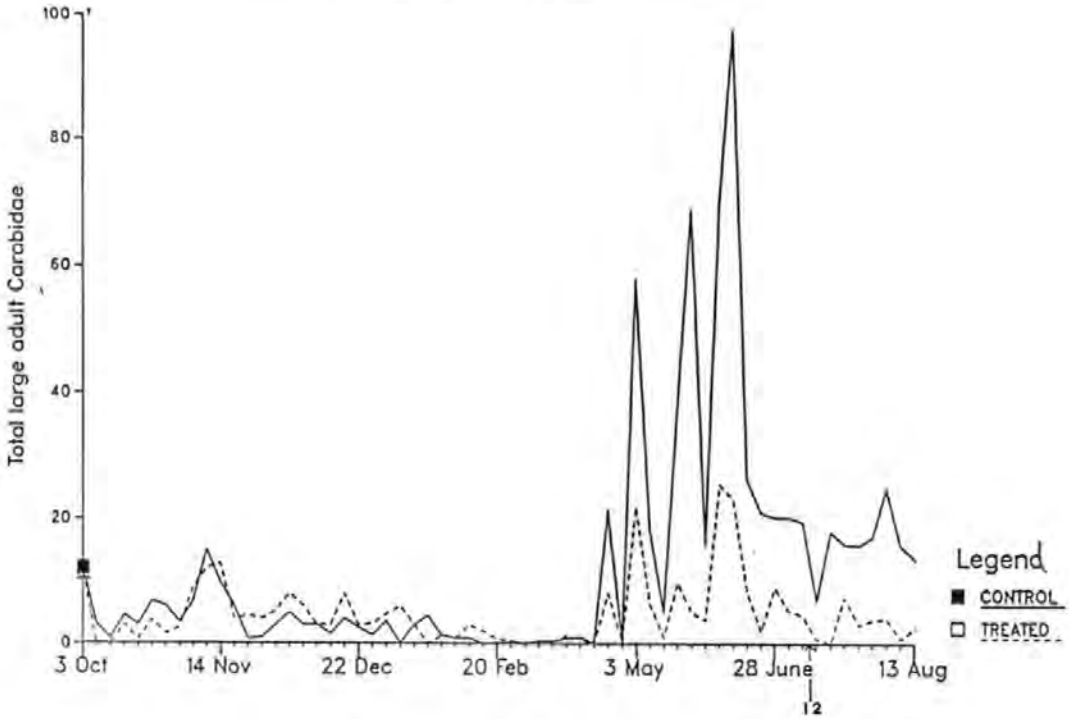
Araneae



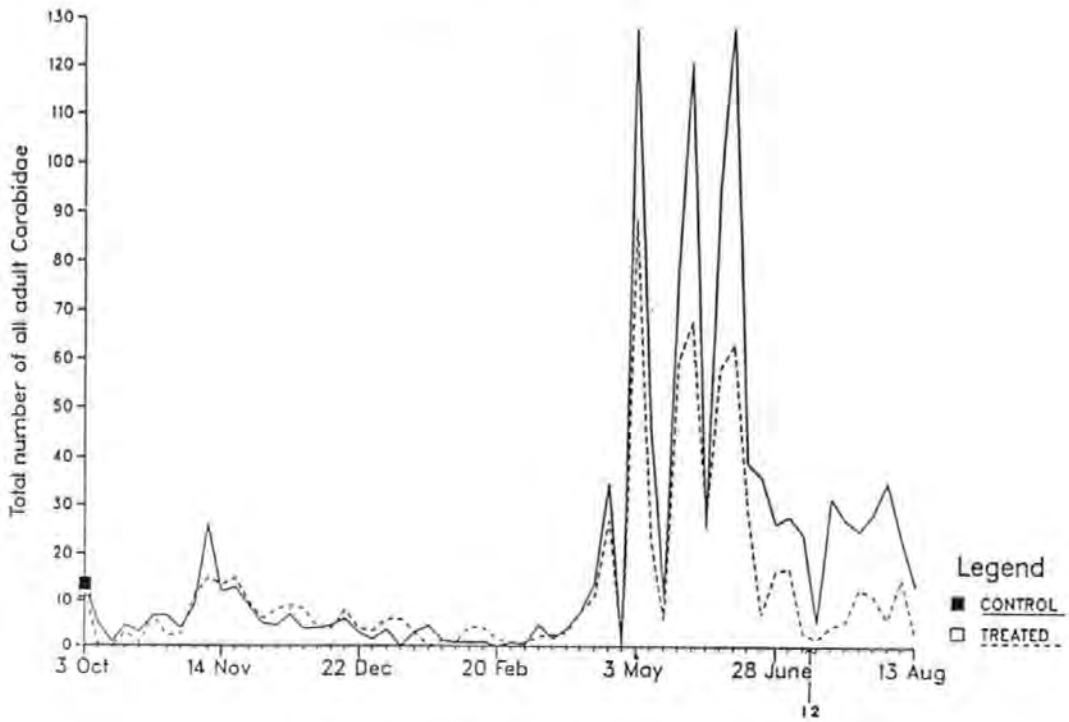
Medium adult Carabidae



Large adult Carabidae



All adult Carabidae



3. Post insecticide treatment July-August.

All predator groups were reduced in deltamethrin treated areas :- all predators 68% less (1% level significant), Araneae 33% less, Staphylinidae 86% less, large Carabidae 81% less (1% level significance), medium Carabidae 43% less (5% level significance), all Carabidae 69% less (10% level significance). In the large Carabidae group, this reduction continues on from April -July. In the medium Carabidae, an immediate reduction in numbers is followed by a gradual increase until early August.

Staphylinidae numbers remained very low in the treated, but increased slightly in the control plots.

Medium term effects. (i.e.over one growing season)

These are difficult to assess over the two sampling years. Figs. 2.6 a and b show that there is no general immediate reduction in numbers followed by a gradual increase. In 1982-1983, on 12 occasions the total number of individuals caught is greater in the treated areas!

However, the reduction in numbers lasted 61 days following the January spraying when all numbers are considered, 9 days in the case of larvae, 28 days for Araneae following the April spraying, and 14 days when all Carabidae are considered. In 1983-1984, an overall reduction in numbers in the treated areas is apparent throughout the whole growing season, as, apart from the one occasion 19 days after spraying, the deltamethrin appears to have reduced total numbers markedly, with only 2 occasions when more polyphagous predators were caught in the treated plots. The greatest effect on total numbers is seen in the catches following summer spraying. This pattern is also seen in the larvae and adult Carabidae (all) catches, greater

catches in treated areas only occuring on 5 and 12 occasions respectively. Araneaenumbers were low from October until late March, when the increase was reduced in size in the treated plots. No overall pattern for Staphylinidae adult catches emerge.

2.5 Mark, release and recapture of N. brevicollis.

2.5.1 Aims.

This investigation was included for three reasons :-

1. To check the efficiency of the barriers at preventing passage of polyphagous predators.

2. To estimate activity (by following individually marked beetles), and mortality of winter surface active polyphagous predators.

3. As an absolute method of estimation of population size. In practice, the only suitable species present in sufficient numbers was found to be the adult Carabid, N. brevicollis, so only this species was used.

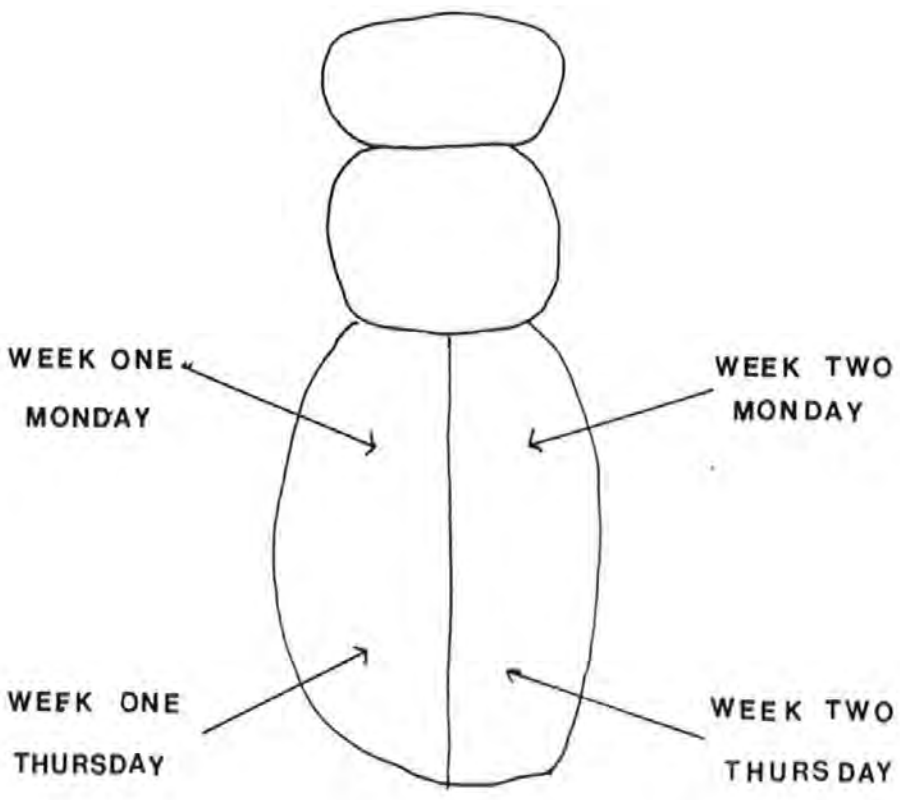
2.5.2Materials and Methods.

All adult N. brevicollis caught throughout the seven week time period between 3rd November and 1st December, were marked on the elytra using a fine paint brush, with the colour and location codes according to the scheme in Fig. 2.7. The beetles were kept immobile by holding the thorax in a strip of plasticine, in a plastic tray, and the Humbrol paint was allowed to dry before release in the centre of the source subplot. Marking in the field reduced handling and sampling time to a minimum. One colour was used for two weeks. Mark and recapture experiments are mostly based on the Lincoln Index, which makes the following assumptions (Southwood 1978):-

1. Marked animals are unaffected by the mark, and the marks are not

Figure 2.7

Location of colours used to mark adult Nebria brevicollis in the Mark-Recapture experiment.



lost.

2. Marked animals become completely mixed in the population.

3. The population is sampled randomly with respect to its marked status. :-

a) All individuals of the age classes and sexes are sampled in the proportion in which they occur.

b) All individuals are equally available for capture, irrespective of their position in the habitat or of the marks they carry.

4. Sampling is at discrete intervals and sample taking time must be small when compared with the total.

5. The population is a closed one.

6. No births/deaths occur in the sampling time (this can be allowed for by calculation).

7. Capture 1 or more times does not effect an animals subsequent recapture chances.

8. The probability of any animal surviving through the period is not affected by its age at the start.

Southwood (1978) reviews all the mark and recapture methods that have been developed for use in situations where individuals have been marked and recaptured more than once. All have their relative advantages and disadvantages. The Jolly- Seber method was the most suitable in this case (Begon 1979). The adult N. brevicollis found are likely to be at the same stage in their life history and approximately the same age, and the method has been used successfully in the past for this species (Greenslade 1964, Luff 1982). The Jolly-Seber method is usually reliable when 9% or more of the population is sampled, and this is thought to be the case when considering Carabidae inside barriered plots.

Table 2.6

Data (mhi) from Mark - Release - Recapture

Weekly Catch Date and week (beginning of week)		Captured	Released	Time of Release Marks j						
				1	2	3	4	5	6	7
		n_i	r_i	Recaptured Marks Mij						
30.10.83	1	-	19							
7.11.83	2	48	48	5						
14.11.83	3	29	29	2	17					
21.11.83	4	12	12	1	5	5				
28.11.83	5	22	22	2	6	5	5			
5.12.83	6	19	19	2	4	4	0	6		
12.12.83	7	17	17	0	1	2	1	6	3	
19.12.83	8	12	12	0	1	2	0	2	5	0
26.12.83	9	Not Sampled								
2. 1.84	10	19	-	1	0	1	0	5	6	0
9. 1.84	11	21	-	0	0	0	3	6	3	0
16. 1.84	12	11	-	0	0	0	0	0	4	0
23. 1.84	13	2	-	0	1	0	0	0	0	0
30. 1.84	14	6	-	1	0	0	0	1	1	0
6. 2.84	15	4	-	2	0	0	1	0	0	0
13. 3.84	16	8	-	2	1	0	1	0	0	0
20. 3.84	17	1	-	0	0	0	0	0	0	0
27. 3.84	18	Not Sampled								
5. 3.84	19	2	-	0	1	0	0	0	1	0
12. 3.84	20	0	-	0	0	0	0	0	0	0
19. 3.84	21	2	-	1	0	0	0	0	1	0
26. 3.84	22	2	-	0	0	0	0	1	1	0
2. 4.84	23	2	-	0	0	0	1	0	0	0

Marking continued until (and including) week beginning 19.12.84

However, as the results show, in individual plots, the total numbers of N. brevicollis adults captured over the entire seven week period of marking and the 5 month period of recapture were too low to provide a population estimate for each plot or even treatment. Therefore, an estimate of the population based on all catches across the experimental area will be performed.

The Jolly-Seber method of population estimate.

In this, only the most recent mark is noted. All previous marks are ignored. Each marked individual in the day "i" sample contributes only 1 mark (its most recent) to the total. The data obtained are set in Table 2.6 (Begon 1979), where the following additional assumptions apply :-

a) Every animal in the population whether marked or unmarked has the same probability, p_i (=1-q) of being caught in the ith sample, given that it is alive and in the population when the sample is taken.

b) Every marked animal has the same probability ϕ of surviving, from the ith to the (i+1)th sample and of being in the population at the time of the i+1 sample, given that it is alive and in the population immediately after the ith release (i=1,2,....s-1).

c) Every animal caught in the ith sample has the same probability, v_i, of being returned to the population.

d) Marked animals do not lose their marks, and all marks are reported on recovery.

e) All samples are instantaneous, i.e. sampling time is negligible, and each release is made immediately after the sample.

In table 2.6,

i= trapping event

n_i = number(total) caught in the ith sample .

R_i = number of marked animals released after the ith sample.

r_i = number of animals released after the ith sample which are subsequently recaptured.

m_i = number of marked animals caught in the ith sample.

mh_i = number caught in the ith sample last caught in the hth sample.

Z_i' = number of animals caught before the ith sample which were not caught in the ith sample, but were caught subsequently.

y_i = number of animals marked and released on day i, and caught again subsequently.

Such that

$$Z_{(i+1)} - Z_i = r_i \quad m_{(i+1)}$$

The estimates of M_i, p_i, N_i, ϕ_i, B_i and the standard errors were calculated from a modification of Jolly's method after Seber(1973) according to Begon (1979). m_i, r_i, y_i, and z_i, can be observed directly from the data and therefore the following equations can be used :-

1) $\hat{M}_i$, Estimate of the total number of marked animals in the population $= m_i + \frac{z_i r_i}{y_i}$

2) $\hat{N}_i$, Estimate of the total number of animals in the population $= \frac{\hat{M}_i (n_i + 1)}{(m_i + 1)}$

3) $\hat{\phi}_i$, Probability that an animal alive at release of ith sample will survive untill time of i+1 sample $= \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + r_i}$

Table 2.7

Transformed Data from Mark-Release-Recapture

Day_i (week)	r_i	m_i	y_i	z_i
1	19	-	12	-
2	48	5	34	7
3	29	19	18	22
4	12	11	6	29
5	22	18	14	17
6	19	16	8	15
7	17	13	0	10
8	12	10	-	0

Table 2.8

Final Estimates from Mark-Release-Recapture

i	$\hat{M}_i$	ρ_i	$\hat{N}_i$	s.error $\hat{N}_i$	$\hat{B}_i$	s.error $\hat{B}_i$	ϕ_i	s.error ϕ_i
1	-	-	-	-	-	-	-	-
2	14.88	0.10	22.72	3.19	1.34	7.62	0.94	0.13
3	54.44	0.66	59.39	8.82	-4.20	13.01	1.07	0.31
4	69.00	0.92	84.33	23.70	30.44	7.19	0.64	0.19
5	44.71	0.82	53.09	6.84	-3.21	15.62	1.05	0.79
6	51.63	0.84	67.50	16.82	51.50	1.88	0.24	0.22
7	13.00	0.77	15.60	0.63	-	-	-	-
$\bar{x}$	41.27	0.68	50.44		15.17		0.79	

4) $\hat{B}_i$, Estimate of number of new animals joining the population between t_i and $t_{(i+1)}$ are alive at $t_{(i+1)}$ $= \hat{N}_i - \hat{\phi}_i N_i$

5) p_i, Proportion of the population captured $= \frac{m_i}{n_i}$

It was decided to only use data from the first eight weeks of sampling as too few individuals were caught (a mean of 5-7 per week) for the remaining three months, for accurate population estimates.

2.5.3 Results

As can be seen from Table 2.8, the population estimates varies in response to change in the estimate of the number of marked animals in the population (M_i). This is itself dependent upon the captures, recaptures and distribution of the capture history of marked individuals, according to equation 1. Thus an accurate estimate will be produced when captures and recaptures are high. The mean value for the total population in the entire experimental plot is 50.44, which, if the area of the experimental crop is taken as $690m^2$, indicated a population density of N.brevicollis of 0.07 per m^2. This may seem rather low, but activity of adults is rather low in the autumn. In fact, only 159 individuals were captured in total -an average of 19.88 per week during the experiment, or 0.33 per trap. If each of the 60 traps is assumed to operate over a similar area, then the effective area of each trap is $11.5m^2$. However, this could be an overestimate and consequently the density of N.brevicollis could be underestimated. It is also interesting to see that from the population estimates obtained, most

Table 2.9

The Movements of N. brevicollis Individuals crossing Sub-Plot Boundaries

Occasion (some pooled)	Sub-Plot (number as in Figure 2.1) 1	2	3	4	5	6	Total No. of Travellers Caught	m_i	Proportion marked individuals 'travellers'
1							0	-	
2					1(6) [1] b	1(5) [1] a	2	5	0.400
3	1(6) [2] m		1(2) [1] l			[1(6) [2] a]	2	19	0.105
4	1(5) [2] p				1(1) [1] c		2	12	0.167
5	1(5) [1] o [1(6) [3] m] 1(6) [2] n				[1(1) [4] c] 1(1) [4] d	[1(6) [3] a] 1(5) [2] b	4	18	0.222
6						1(2) [5] e	1	16	0.063
7	1(2) [6] q			1(1) [4] g	[1(1) [4] c]	[1(2) [5] e]	2	16	0.125
8			1(1) [6] i		1(4) [2] f	[1(5) [3] b]	2	10	0.200
(no new marks)					1(6) [6] g				
10	[1(6) [2] n]		[1(1) [6] i]		[1(4) [2] f]		0	13	0.000
11					[1(4) [2] f]		0	12	0.000
12			[1(1) [6] i] 1(2) [5] k		[1(6) [6] g]		1	4	0.250
13 and 14 (pooled)			1(1) [3] j		1(3) [6] h		2	3	0.667
15 and 19 (pooled)			[1(1) [3] j]	1(1) [4] g			1	2	0.500

Key [ ] = week of most recent mark ( ) = sub-plot mark given a - q = individual beetle

[ ] = these beetles not used in calculation of proportion of travellers

of the population appears to have been marked ! This could be due to the marking method causing the beetles' activity to change and be more suceptible to capture.

The fluctuations in the week to week populations are probably due to activity. When insects are active, their probability of capture and the effective area of sampling are increased. However, this should not affect the estimation of the population size if intermixing of the marked animals had occurred. As recording continued, it became obvious that individuals which had been given marks specific to a plot and occasion had crossed the internal barriers, or possibly they could have escaped across an external barrier and then re-entered a different plot. Table 2.9 traces the movements of these individuals and also shows the proportion of marked individuals captured on each sampling day carrying a mark of a different plot (travellers/m_i). The "body" of Table 2,9 is the number of individuals with i, their origin for the first capture plot shown in parentheses, and the subsequent previous capture plot on successive capture occasions. The marking scheme used enables an observation of individuals' movements, and these are shown also in the table by the letters a-q adjacent to the individuals. In some cases, they stayed in the same subplot for the duration of the experiment (e.g. f). In other cases, they moved from plot to plot (e.g. b).

However, if the individual stays in a subplot, it becomes incorporated into the "fixed" population of that subplot, and is not included in "travelling" population estimates, and the subplot origin code (6) becomes the same as the "moved into" subplot. These are represented as ( ) in the table. 17 individuals were found to

travel, five were captured three times in different plots from their original, five two times, and seven one time. Thus, of the 159 individuals marked in total, 13% crossed one or more barrier during the experiment, with a mean 18% of beetles marked per sampling occasion being "travellers".

One of the underlying assumptions to this method is that an animal once emigrating does not return. However, because 13% of all marked beetles were shown to cross barriers, and possibly external barriers, this last assumption may be unrealistic. The estimations of B show a net gain of individuals, with a mean value of 15.17, which tends to suggest a general immigration into the plots. This could be possibly be due to late emergence of N. brevicollis adults. A more appropriate method of analysis is not available.

Other methods of absolute estimates that could have been used include soil core sampling and D-vac sampling. However, N. brevicollis is a surface active nocturnal carabid, and also as it had not been captured in very large numbers, the latter method was thought inappropriate. Some soil cores were taken in December 1983, but contained no individuals.

Mark and recapture was really the only method of population estimation which enabled the efficiency of the barriers to be investigated, and therefore its inherent disadvantages had to be accepted.

2.6 Assessment of yields at Rumleigh.

Synthetic pyrethroids have been shown to produce a yield gain (Kendall et al. 1982). It was felt desirable to measure the yield of the wheat crop each year. When the % moisture content of the grain was found to be 20% by weight, random samples of wheat

Table 2.10

Yield of Crop at Rumleigh per 100 tillers

Year	Block	Yield in Grammes		$\bar{x}$ Yield	
		Treated	Control	Treated	Control
1982/83	1	25.74	22.91	23.92	22.45
	2	22·10	21·99		
1983/84	1	14.93	13.48	16.26	13.96
	2	15.99	15.13		
	3	17.87	13.28		

were taken from each plot and the resultant yields are shown in Table 2.10. An ANOVA was performed on the data using Minitab, and the results are shown in Appendix 2.E. No significant difference in yields of treated and control plots in either year was found, so in this investigation, no yield benefit due to deltamethrin application could be seen. Any possible effects it may have had were undoubtedly masked by other contributing factors. In 1983, BYDV was virtually absent in the crop. In 1984, 18% of tillers counted exhibited BYDV symptoms in the treated plots, and 28% in the control plots (as assessed by the method explained in Chapter 3).

2.7 Summer Population counts of S. avenae and M. dirhodum.

In each summer, estimates of the aphid populations in each plot were taken in June to establish if any significant differences existed in the development of populations in the treated and control areas.

Materials and Methods

1982-1983

Five metre sections of row were randomly selected, two per treatment, and marked with 1.5 m bamboo poles at either end. Along all rows, every tiller was examined, and the position on the tiller (flag leaf of ear), species and life stage of each individual aphid was recorded on June 9th, 14th, 20th and 30th (following spraying). All tillers were between growth stage 10.1-10.5 (Large 1954) throughout sampling.

Results

On June 9th and 14th, aphids were found on the flag leaf

Figure 2.8 Sitobion avenae counts June 1983, totals per treatment

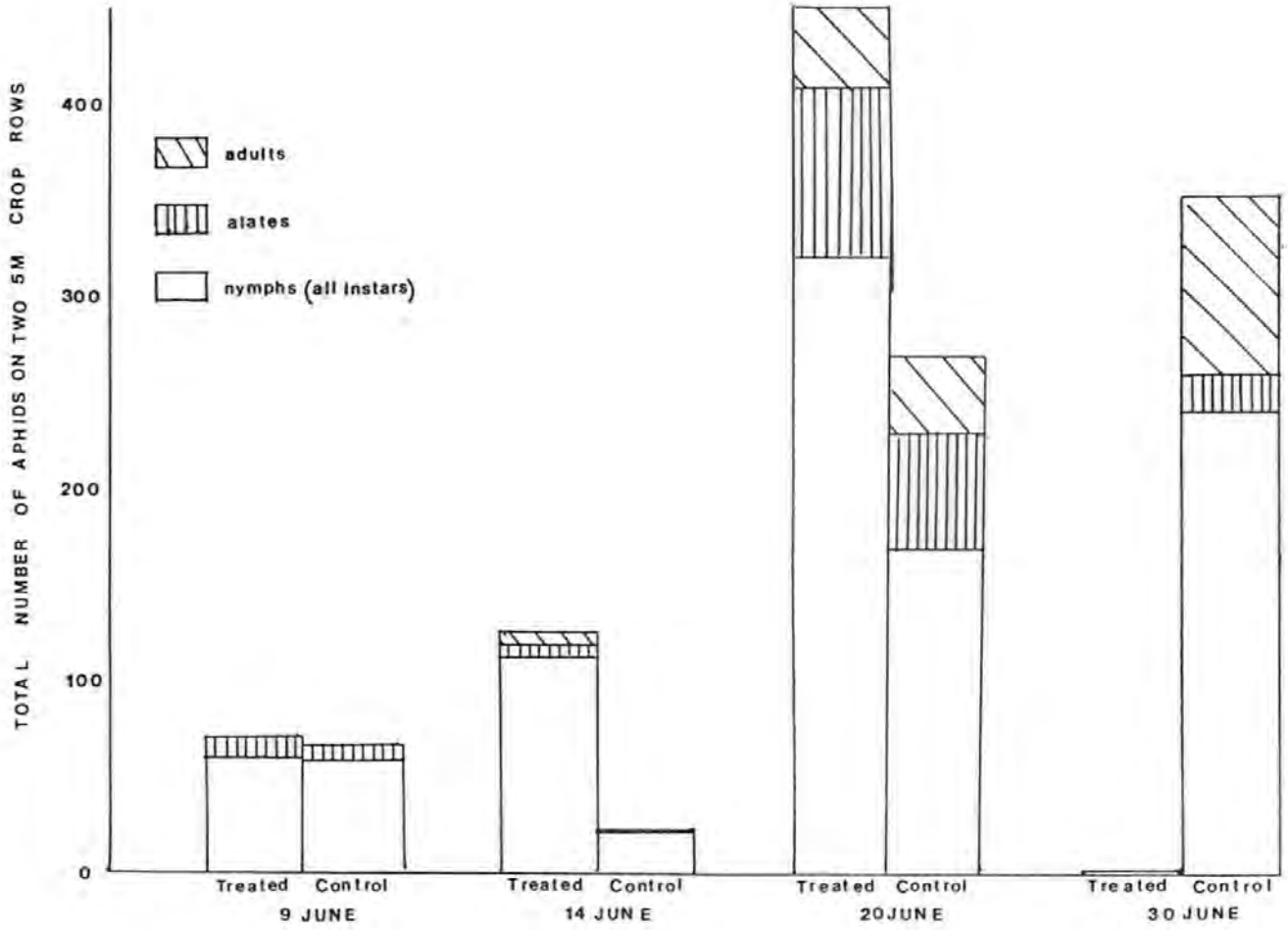
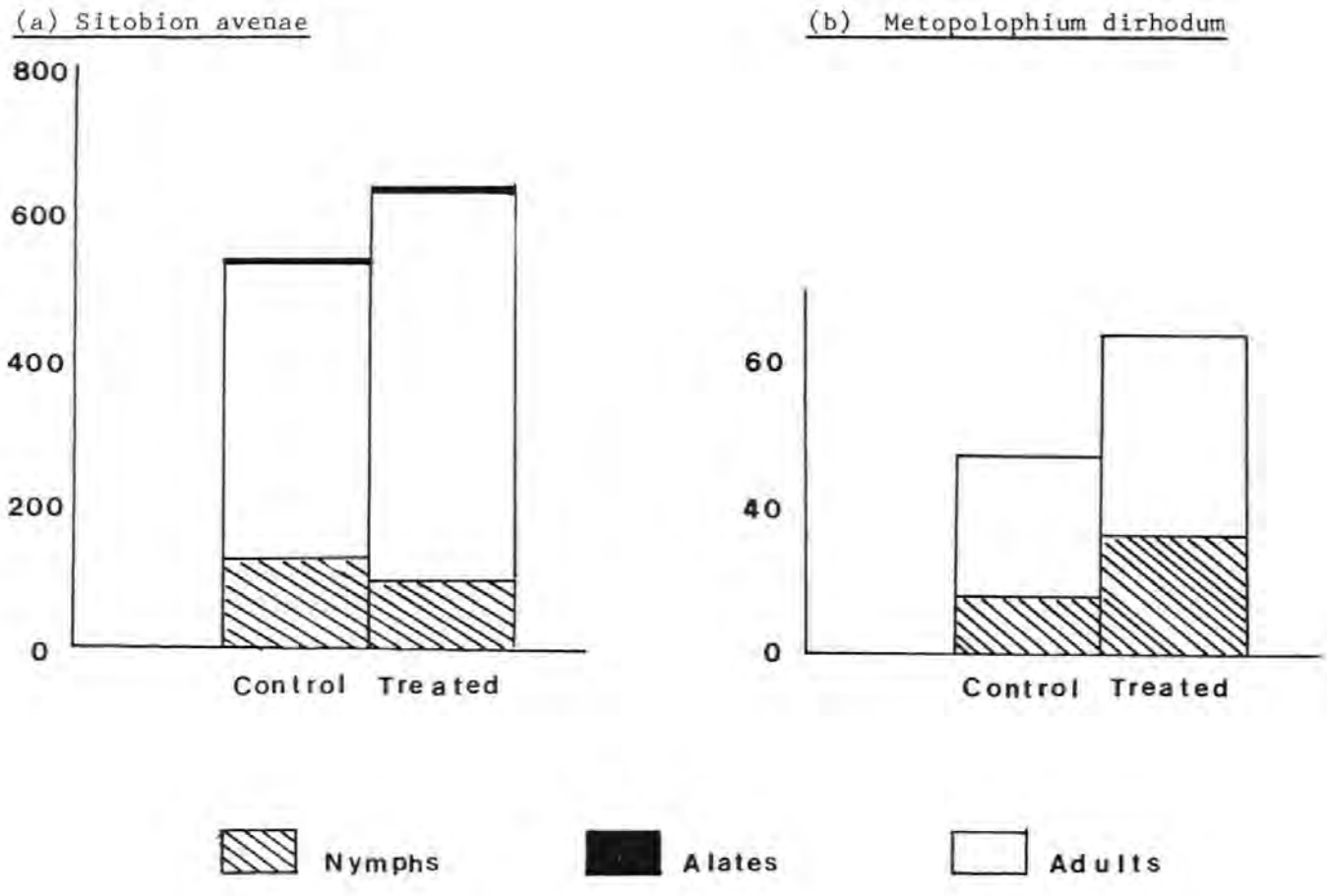


Figure 2.9 Total population counts June 1984 in treated and control plots



and on the ears, but by 20th June, all were only on the ears. Some aphid mummies were found on the tillers. It can be seen from Fig 2.8 that the population follows the same development pattern in all plots, viz alates arrive, reproduce, and the resultant progeny mainly develop into apterae. Too little data was collected for statistical analysis. However, it can be seen from Fig. 2.8 that more aphids of all stages were found in the treated as compared to the control plots, despite the fact that numbers of polyphagous predators captured in both treated and control plots were not significantly different.

1983-1984

One count of aphid populations was taken from 50 randomly sampled tillers per plot, giving 150 tillers per treatment, on 21st June 1984 (Fig. 2.9), S. avenae and M. dirhodum aphids were found, but too few of the latter for statistical analysis. A binomial distribution was found to be the best fit to the data, and a logit analysis was performed. A general linear model with binomial errors was fitted to the data using the statistical package GLIM. This allowed for the large number of tillers scored with no aphids on them. However, no significant differences in the numbers of alates, adults and nymphs between treated and control plots could be found.

The sizes of the aphid colonies were extremely variable (Fig. 2.10.). Clearly, some block and treatment interactions were acting on the populations in the different plots, perhaps making certain plants or plots more attractive to invading aphids. More infested tillers were found in the control plots than in the treated plots, but it is the occasional large colony found in the treated plots which contributes to the large number of aphids found here.

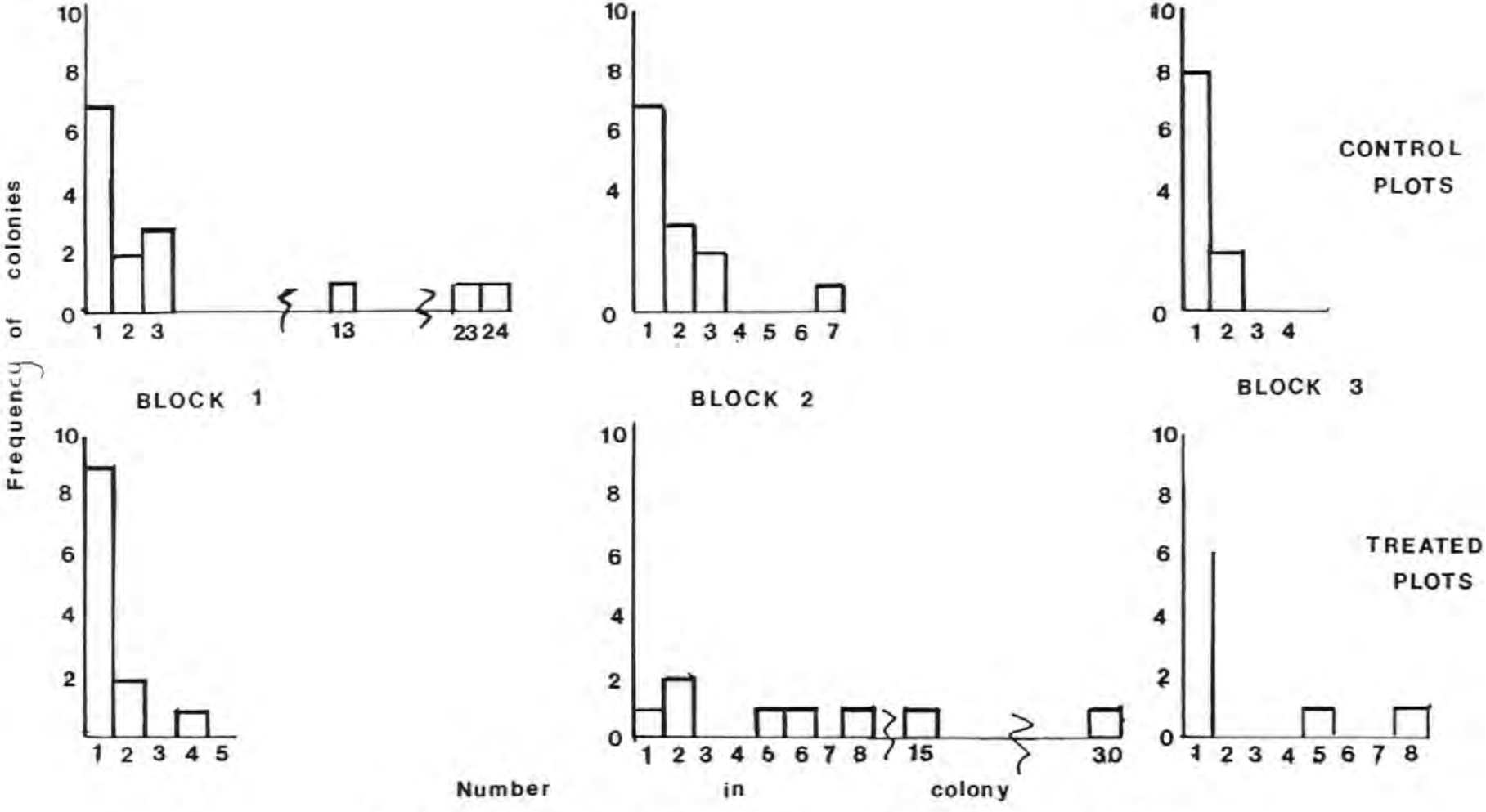


Fig.2.10 Sizes of adult S. avenae colonies 1984.

2.8 Discussion.

The implications of the results must take into account several considerations. The extreme variability of the sizes of the trap catches observed must partly reflect activity differences. The effects of activity on pitfall trapping has been investigated for adult Carabidae (Baars 1979, Den Boer 1985, Greenslade 1964) (see Introduction). Trap catches also depend upon environmental variables, chiefly temperature but not rainfall, although in very wet conditions catches are very small (Jones 1976, 1979). It has also been suggested by Chiverton (1984) and Sotherton (1983) that insecticide application increases predator activity because prey populations are reduced. This is thought to lead to the "recovery" of predator populations in the short-term that has been observed in insecticide trials. In this experiment, such a significant short-term increase was seen in medium adult Carabidae numbers in the treated plots following the June aphicide spray in 1983. In 1983-1984 numbers remained lower for several months in the treated plots, and this was most marked from April-June with a reduction of 39% for all Carabidae. These results illustrate that it may be useful to continue the use of pitfall traps for the entire growing season to investigate the effects of insecticide applications on polyphagous predators. Also the effects may be underestimated, if insecticide activates natural enemies. However, pitfall trapping is not a suitable technique for sampling all polyphagous predators. The summer larvae of the spring breeding Carabidae such as *A. dorsale*, *B. lampros*, *P. melanarius* and the *Harpalus* species are not surface active, and are not caught in pitfall traps, as the results show.

Some species such as D. atricapillus, N. biguttatus, some Araneae and Staphylinidae avoid pitfall traps (Williams 1962). This could explain why Staphylinidae numbers were continuously low throughout the trapping periods, as Baker and Dunning found in cereal fields (1975). Although the absence of summer surface active larvae of Tachyporus species, (as found by Kowalski (1982) in cereal fields), could suggest that the populations of Staphylinidae species were low in the experimental wheat plots.

Some within-trap predation was observed. Sunderland (1975) observed Carabidae eating Linyphiidae and Philonthus species and Chilopodae will eat any other insects met if hungry (Lewis 1981). N. brevicollis will eat small Araneae (Penney 1966), and P. melanarius has also been identified as a predator in pitfall traps (Mitchell 1963). As pitfall traps were emptied every three or four days when predator abundance was at its highest, in the summer, the effects of within-trap predation were reduced.

The mark and recapture experiment showed that the barriers were not completely efficient in preventing intermingling between subplots, as indicated by N. brevicollis adults between November -March 1983-1984. No similar evidence could be found in the literature. This suggests that the reduction in polyphagous predator numbers caused by deltamethrin may have been underestimated.

The results show a changing faunal composition of the pitfall traps which reflect individual species of Carabidae life cycles and phenology identified by previous workers. For example, the autumn and winter domination of catches by adult N. brevicollis has been shown in winter wheat and fallow. (Jones 1976,1979).

Although larvae were not identified to species, it is reasonable to assume from life history studies (Penney 1966) that the peak larvae catches obtained in January were due to N. brevicollis, as they lay eggs in November, whilst larvae catches in autumn could be due to P. madidus, as Jones (1979) observed these egg laying from August to October. In the autumn, P. melanarius, H. rufipes and H. anaeus were also found in small numbers, having developed from summer larvae. In general, the larger Carabidae (generally spring breeders) are more able to withstand the hotter summer temperatures, and do not suffer risk of desiccation and so are caught more in April-September. N. brevicollis is similar to the smaller Carabidae in its heat tolerance, and this is why it goes into summer aestivation parapause (Thiele 1979), reappearing in September along with T. quadristriatus and B. lampros. In mild winters, Jones (1979) found N. biguttatus active in winter wheat crops, which the results in this investigation confirm. A. dorsale emerges in April or May having overwintered as pupae, and lay eggs. A few individuals emerge in late September and early October, and they are capable of breeding for two years (Sotherton pers. comm., Jones 1979).

As has already been explained in Chapter one, the presence of all other groups of polyphagous predator is constant over the whole growing season, but with continual changes in the constituent species. The spatial distribution of polyphagous predators within agricultural fields and in relation to type of boundary has been investigated over the last decade, but only in any detail for Carabidae and Staphylinidae. Jones (1976) suggested that forest originating Carabidae species such as N. brevicollis are found in greater numbers near hedges than in the centre of wheat fields in

the Autumn, whilst in species such as P. melanarius no influence of pitfall trap position relative to a hedge could be found. Wallin (1985) found in Sweden that B. lampros moved from field edges into the centre of cereal fields early season, and P. cupreus found in August and September were emerging within the field. Hedges per se were found by Desender (1982) not to have much influence on the spatial distribution of Carabidae in fields, but Sotherton (1985) found significantly more D. atricapillus and B. lampros along hedge banks than along any other boundary type overwinter. Lovei (1984) and Lovei and Szentkiralyi (1984) found,in Hungary,no striking evidence to suggest field edges supported more Carabidae and a more diverse community than the centres of agricultural fields. Baker and Dunning (1975) also found in the U.K. In sugar beet fields that the trap location had slight, but mostly significant effects on the numbers of Carabidae trapped. However, no soil samples were taken, so the numbers of Carabidae may have been underestimated.

Desender (1982) showed that grassy strips along the cereal field boundaries had an important hibernation function for crop field and spring breeding Carabidae in Belgium. The density, which was sometimes as high as 900 per m^2, was correlated with the mean depth of the soil layer. Adult Staphylinidae have also been shown to hibernate in grassy strips along field boundaries (D'Hustler and Desender 1984) in Belgium,and in grassy strips, hedge banks and shelter belts in the U.K. (Sotherton 1984, 1985). The buffering of temperature fluctuations due to a dense vegetation, deep sod layer and a well developed litter layer make grassy strips suitable as an overwintering site.

Wallin (1985) summarized all the recent work, and suggests that habitats such as shelter belts, grassy strips, hedges and hedgebanks closely adjacent to arable fields play an important role during the life cycle of many field-inhabiting Carabidae and Staphylinidae, especially spring breeders hibernating as adults.

However, in this investigation, no evidence was found to support these theories. No significant movement out into the plots from the grassy strip was found (Figs. 2.5 a and b) at the time of emergence of spring breeders. This may be because the fences were erected in 1982-1983 well into the autumn, when all spring breeders would have gone into hibernation, and the barriered areas of grass/weeds were too small to support large populations. Also, in 1983-1984, when barriers were erected in September, this was not seen either. Previous work has been conducted in large agricultural fields and, given the relative mobility of adult Carabidae, the plots may have been too small to show any effects of the uncultivated area.

The results obtained in this investigation have bearing on two main areas :-

1. The effects of deltamethrin spraying overwinter.

It can be assumed that any polyphagous predators active over the winter period will feed to a greater or lesser degree on apterous R. padi, and therefore exert a natural control on the concomitant spread of BYDV. Although N. brevicollis adults have not been shown to be such active aphid predators by Sunderland and Vickerman (1980), these investigations were carried out in June and July, when other more active climbing

spring breeding Carabidae such as A. dorsale were present.

The early application of deltamethrin is recommended for early sown winter crops (M.A.F.F. Anon), and a significant reduction in the total number of polyphagous predator numbers from October -April was seen in 1983-1984. The barely significant reduction in larvae numbers over the same time would probably be greater if insecticide application was October/November (when most farmers spray), because larvae are much more abundant then. From the population estimates for N. brevicollis obtained in November and December, the general level of Carabidae populations in the plots would appear low at 0.07 per m^2 with a mean survival rate of 0.803. Other workers have produced estimates at higher densities e.g. 0.6-0.9 per m^2 in June -September (Jones 1976), 0.1 per m^2 in beech litter plots (Greenslade 1964). No estimates could be found for N. brevicollis in winter in the literature. Winter predation on aphids also may be greater by non-pitfall captured groups such as Araneae, and this has not been assessed.

2. The effects of deltamethrin spraying in spring and summer.

As already discussed, insecticide spraying in April appeared to increase predator numbers in 1982-1983. However, in 1983-1984, no second spray was added at this time, and significant reductions in all polyphagous predator numbers, medium and all adult Carabidae and A. aeneus were seen. (Although the variances and means of the latter three were not independent). These reductions are not easy to explain. Perhaps they could be due to spray killing the spring breeding adult Carabidae in the autumn just at the beginning of hibernation, or maybe the insecticide was effective in killing

pupae and eggs of species such as A. dorsale. No evidence was found in the literature to support these ideas. It is also not due to the "knock-on "effect of the reductions in January seen in the larvae populations, which may at first seem an explanation, since only autumn breeders' larvae, in particular N. brevicollis are active then (Kowalski pers. comm.). It is probably most likely a result of the killing of the overwintering R. padi populations in the sprayed areas i.e.removal of prey, with resultant death of polyphagous predators. However, Carter and Sotherton (1983) and Chiverton (1984) demonstrated that this lack of prey produced increased activity, and therefore pitfall catches would increase, as happened in the previous year. If the barriers are not 100% efficient, perhaps predators moved out of the sprayed plots and artificially increased predator populations in the control plots. This explanation seems reasonable when the polyphagous predators in question are considered, especially A. aeneae, a strong flyer and P. cupreus, a climber.

In 1982-1983, significantly more S. avenae were found in the treated plots as compared with the control plots , over the month of June. It has been suggested that natural enemies have a role in controlling summer outbreaks of S. avenae (Carter and Dixon 1981), but a mild spring is essential for the development of the natural enemy populations. The results obtained in this investigation agree with this, since the control exerted by polyphagous predators was obviously removed by spraying in April. However, there were sixteen more polyphagous predators captured in the treated plots than the control plots! This could possibily be

explained by movement between plots across barriers, or possibly by assuming an increase in activity immediately following spraying due to the direct effects of the insecticide and also removing any R. padi left in the crop. However, the increase in numbers is due to a dramatic increase in Carabidae numbers (Fig. 2.6 a.) in June, chiefly A. aeneq. This could be due to adults flying into the crop or across from the control areas as a response to the increased population of S. avenae present in the sprayed plots.

In 1983-1984, more S. avenae and M. dirhodum were found in the treated than in the control plots, but these were not significant differences, and there were more infested tillers found in the control than in the treated plots. Also, analysis of the data revealed that definite conclusions are difficult to draw from the results, and that more samples would have made interpretation easier, due to the aggregated distribution of aphid populations. However, the development of different sized colonies in the treated and untreated plots (Fig. 2.10) may be a result of different polyphagous predator feeding strategies, which could be a result of inter and intra specific competition within plots.

Certain medium sized Carabidae have been shown to be capable of aggregation in patches of high prey densities (Bryan and Wratten 1984), and in this investigation significantly less were caught in the treated plots. Therefore,the aphid distributions found could be a result of a combination of ecological factors due to the environment, polyphagous predator response, polyphagous predator species composition and also behavioural factors such as competition for aphid food resources. The complex effects of deltamethrin application on polyphagous predators on summer population

development of S. avenae and M. dirhodum are impossible to isolate in this investigation.

The yields of the crops in both years were not significantly increased in the treated plots, despite 28% of sampled tillers exhibiting BYDV symptoms in the control plots, indicating some BYDV incidence. However, insecticide application is just one small contributing factor to the yield, and its effects may be masked by other factors.

2.9 Conclusions

1. Autumn spraying may reduce the size of the populations of Carabidae and Staphylinidae in the spring by killing the larvae in the autumn and winter.

2. Natural control of aphids by polyphagous predators in winter may be reduced.

3. The reduction in polyphagous predator populations caused by autumn spraying may reduce the natural control of the development of aphid populations in spring and summer, but the effects are complex and not easily understood.

2.10 Suggestions for further work.

A repeat investigation should include

1. Identification of all autumn and winter pitfall catches to species, including larvae, to establish if carnivorous Araneae are present and the composition of the Carabidae and Staphylinidae larvae fauna.

2. Investigation into the predation of larvae and N. brevicollis on apterous aphids present in the crop in winter.

3. Aphid counts to be carried out from October- April in treated and control plots to establish population development rates.

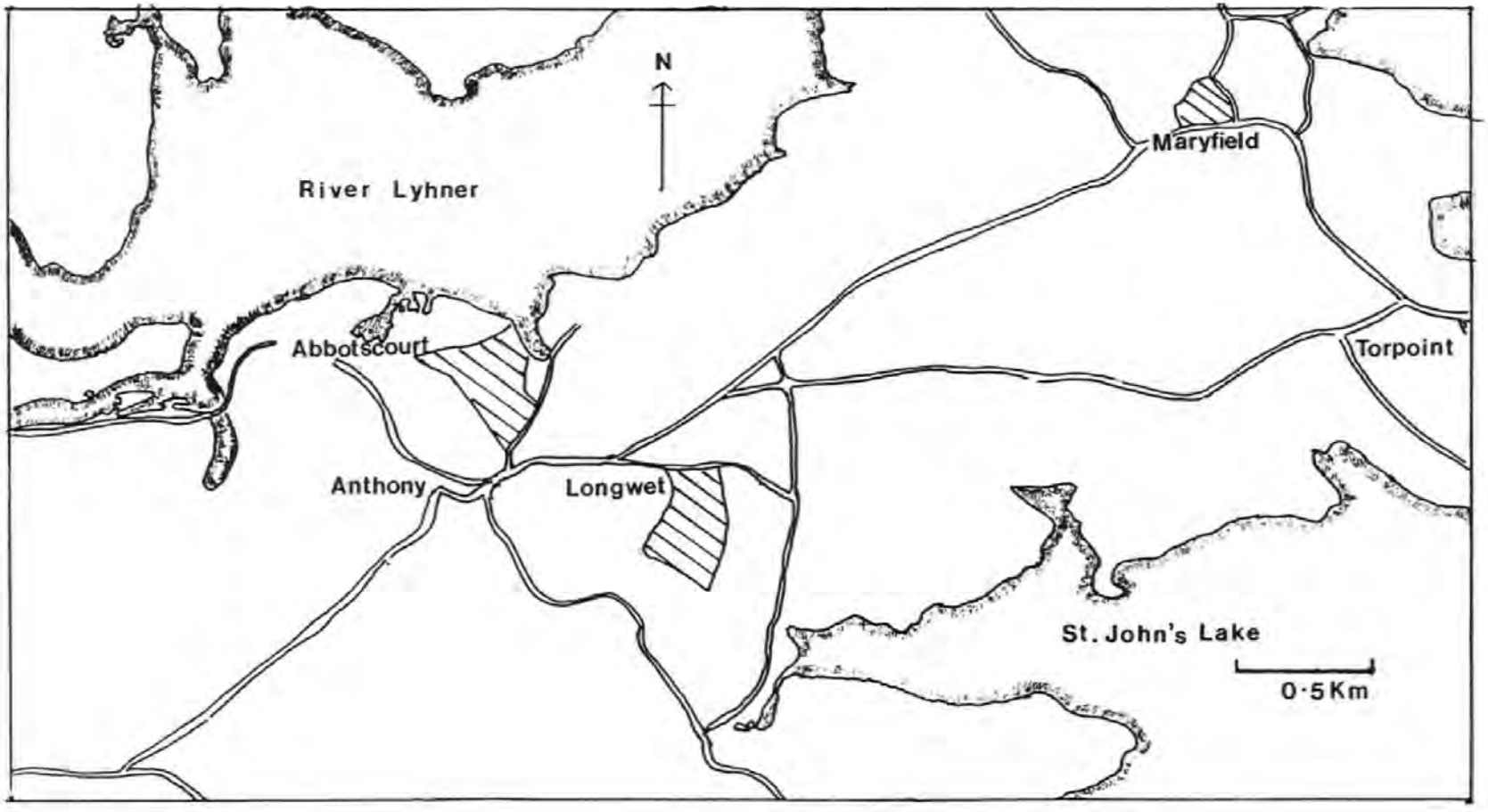
4. Further investigations into the efficiency of the barriers to prevent escapes.

5. More detailed and extensive aphid population counts to be made in the summer to investigate the medium-term effects of deltamethrin application more thoroughly.

CHAPTER THREE

BARLEY YELLOW DWARF VIRUS IN WINTER WHEAT

Figure 3.1 Location of fields used for sampling of apterous cereal aphids 1983 - 1985



3.1 Site description

All fieldwork was carried out on Anthony Estate Farm in S. E. Cornwall. The farm covers 458.3ha from Torpoint to Tregantle (5.6Km) (Fig. 3.1), and is devoted to dairy and cereals. 248 ha (56%) of the area is currently in cereals (12 ha oats, 133 ha winter barley and 103 ha winter wheat).

Table 3.1 shows the crops grown on Anthony Estate Farm for the seasons when fieldwork was conducted. Two crop rotation systems are in existence :-

1. In the dairy farming area, grass is used as a break crop for three years, followed by two winter wheat crops and then two winter barley crops.
2. In the arable farming area, winter oats or oilseed rape is used as a break crop. On the better land, this is followed by two winter wheat crops and two winter barley crops. On the lighter land, this is followed by one winter wheat crop and three winter barley crops.

Figure 3.1 shows the location of the fields used, and Table 3.2 shows the cropping and husbandry history of the fields used. Appendix 3.1 shows the functions of the sprays used.

1. Maryfield 1982-1983.

This 2.8 ha field was sown with winter wheat, c.v.Hobbit (soft endosperm) on 7th November 1982 at a rate of 188.25 Kg/ha.

2. Abbotscourt 1983-1984.

This 14.8 ha field was sown with winter wheat, c.v.Rapier (soft endosperm) on 20th September 1983 at a rate of 188.25 Kg/ha.

3. Longwet 1984-1984.

This 8.4 ha field was sown with winter wheat, c.v. Avalon

Table 3.1

Crops at Anthony Estate Farm

Crop -Area in hectares

Growing Season	Oats	Spring Barley	Winter Barley	Winter Wheat
1984/85	17	-	121	126
1983/84	5	89	51	121
1982/83	12	7	56	103

Table 3.2(a)

Previous Crop History of Fields Used

Field and Year of Sampling		Previous 3 years to Sampling	Crops
Maryfield	1983	1979 - 80	Grass
		1980 - 81	Grass
		1981 - 82	Grass
Abbotscourt	1983 - 84	1980 - 81	Winter Barley
		1981 - 82	Winter Barley
		1982 - 83	Peas
Longwet	1984 - 85	1981 - 82	Winter Wheat
		1982 - 83	Winter Barley
		1983 - 84	Peas (manured)

Table 3.2b

Cropping Husbandry of Fields used in Field Sampling

Field	Year	Date	Fertiliser or Sprays applied	
			Common Name	Scientific Name
Maryfield	1	10.11.82	Tribunyl	Methabenzthiazurone
		1. 4.83	Bavistim	Carbendazim)
			CMPP	Mecoprop) Tank Mix
			Oxytrilcm	Toxynil)
		16. 4.83	Cycocel	Chlormequatchlorine) Tank
			Bayleton	Triademethon) Mix
		1. 6.83	Bayleton	Triademethon) Tank
			Captofol	) Mix
Abbotscourt	2	27. 9.83	Stomp	Pendimethalin
		25.10.83	Sumicidin	Fenvalerate
		18. 2.84	Nitrogen	-
		14. 3.84	Cycocel	See Above)
			Calyxin	Triademethon) Tank
			Bavistim	See Above) Mix
		20. 3.84	Nitrogen	-
		17. 4.84	Nitrogen	-
		9. 5.84	Cycocel	See Above
		9. 6.84	Cycocel	See Above
Longwet	3	29. 9.84	Stomp	See Above
		11.11.84	Cypermethrin	Cypermethrin
		20. 2.85	Avenge (½ rate)	Diphenzoquot methylsulphate
		28. 2.85	Nitrogen	
		9. 4.85	Nitrogen	
		15. 4.85	Bravo	Chorothalonil) Tank
			Bavistim	See Above) Mix
		30. 4.85	Nitrogen	
		6. 6.85	Bravo	See Above) Tank
			Corbel	Fenpropimorph) Mix
		29. 6.85	Bayleton	See Above) Tank
			Cycocel	See Above) Mix

(hard endosperm) on 24th September 1984.

Yields over the three years for each field were 7.9 (6.74), 6.7 (5.83) and 6.92 (5.85) tonnes per hectare respectively. Average yields across the whole farm are shown in parentheses following the figures. The yields are greater in each sampled field. This could be because all the wheat crops are first time crops following fallow (Maryfield), or a pea crop (Abbotscourt and Longwet).

3.2. Aims.

1. To attempt to correlate Barley Yellow Dwarf Virus symptom expression in a commercial crop with important crop characteristics such as yield and height.
2. To correlate aphid presence with BYDV presence in the crop.
3. To demonstrate secondary spread of BYDV using enzyme-linked immunosorbent assay (ELISA).

3.3 Detection of virus symptoms in the field, yield assessments, and correlation with aphid presence.

3.3.1 Introduction.

Barley Yellow Dwarf Virus is brought into crops in the autumn by alate immigrant cereal aphids, chiefly R. padi and S.avenae. The proportion of crops ultimately infected with BYDV depends not only on the primary infection by these alates, but also on the subsequent spread of the virus within the crop during the late autumn and early winter by the apterous offspring. This is called "secondary spread" of virus, and is itself dependant upon the changing apterous aphid distribution in cereal crops overwinter.

In the field, symptoms of BYDV infection are most apparent in late spring, when patches of infected plants can be seen (Plates 3a and b). The sizes of these patches vary within and between years,

Plate 3a A patch of BYDV in wheat (Maryfield, June 1983)

Plate 3b The patchy distribution of BYDV (Maryfield, June 1983)

according to crop and location.

In May and June, the infected leaves turn bronze-red in wheat, bright yellow in barley and reddish-purple in oats (Doodson and Saunders 1970a). Quantification in the field is usually by means of assessing the percentage of crop showing symptoms per $1m^2$ of crop sampled in May (Kendall and Smith 1981).

Although scales of damage have been produced for April and May use based on leaf discolouration, intensity of discolouration and tiller heights (Doodson and Saunders 1970b), and for May/June use based on whole plot appearance (Watson and Mulligan 1960), no scales could be found based on individual plants. This detail was neccessary if an attempt to correlate aphid presence over the winter with virus presence was to be made.

However, many factors cause stress in plants, which result in discolouration in leaves, decrease in yield, leaf curling and strap leafing (Greaves 1981), and also symptom expression is dependent upon the crop cultivar, growth stage at infection, environmental conditions, and the virus strain involved. Any symptom-based damage scale can only be a guide to BYDV presence.

3.3.2 Materials and Methods

1. Damage code

It was decided to devise a damage code based on the reddening of the leaves, because this is the most severe form of symptom expression. The code is presented in Table 3.3 and Plates 4a-h. Clement, Lister and Foster (1985) suggested that leaf reddening was the best guide of virus infection in Indiana.

Plate 4 . illustration of BYDV Damage Code

a) 2

b) 3

c) 4

d) 5

Plate 4 continued

e) 6

f) 7

g) 8

h) 9

2. Sampling the crop.

In June in years one and two, every crop row sampled in Chapter 4, Section 4.3, was sampled as follows :-
One hundred tillers at 100mm regular intervals along the crop rows were scored according to the BYDV damage code in Table 3.3. Any other tillers between these showing symptoms of classes 6-9 were also recorded, along with their position along the row to the nearest 10mm and height. All the tillers were marked with short green garden ties. The day before commercial harvest, i.e. in July in year one and August in year two, the ripe head of wheat was cut from each marked tiller, individually labelled, the garden tie was removed, and the samples were taken to the laboratory.

Weighing and sorting

The grains were separated from the chaff using a mechanical seed sorting device developed by Dr. K. Thompson at Plymouth Polytechnic. This uses an electric motor to blow air from under the wheat sample held in a plastic container. The chaff is blown up through a perspex tube to a collection point, and the grains of wheat remain in the bottom container. The grains were counted and then weighed on a Sartorius balance to 10mg accuracy, to produce an individual ear yield corresponding to a commercial yield taken from the field at 20% moisture content per weight. It was assumed that all tillers' grains contained the same amount of water.

Sampling for aphid presence

This is fully described in Chapter 4, section 4.3.

Table 3.3

The BYDV Damage Code

Code	Colour	% leaf discolouration from tip to bottom
1	Green	0
2	Yellowing	1 - 25
3	Yellowing	25 - 50
4	Yellowing	50 - 75
5	Yellowing	75 - 100
6	Reddening	1 - 25
7	Reddening	25 - 50
8	Reddening	50 - 75
9	Reddening	75 - 100

Table 3.4

Distribution of Scored Tillers in the Damage Code Classes

Year and Date of Scoring	Total No. of Tillers	Class 2		3		4		5		6		7		8		9	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1 19.6.83	984	577	58	53	5	3	1.2	33	3.3	120	12.2	90	9	57	5.8	20	2
2 26.6.83	1042	484	46	297	28.5	112	10.7	70	6.7	40	3.8	11	1	50	0.04	0	0

3.3.3 Results.

BYDV Damage assessment

Table 3.4 summarizes the codes obtained in each year. At Maryfield, 53% of all tillers' flag leaves were infected with rust, 0.005% with Septoria, and 3% with both, so the effects of BYDV may have been compounded. At Abbotscourt, only 4% were infected with Septoria leaf diseases.

Further analysis of the results.

The two years' data were analysed seperately, due to the different crop varieties, fields and climatic conditions existing in 1983 and 1984. Model 1 regression analysis was used to attempt to explain and predict the relationship between BYDV damage code and :-

1. Height of tiller.
2. Number of grains per tiller.
3. Yield per tiller.

No evidence was found in the literature to suggest that BYDV has any effect on the amount of chaff (non grain material) in ears of wheat, so this relationship was not investigated. Model 1 regression analysis is suitable for this type of data because the code is a discontinuous variable (Sokal and Rohlf 1981). However, for all three regressions for both years, very little variation was explained in the regression analysis. At Maryfield, 0.1% for code and tiller height, 5.4% for code and number of grains, and 1.6% for code and yield. At Abbotscourt, the regression explained 3.4%, 0.1% and 0.1%of the variation respectively.

Correlation of BYDV damage code, yield and height of tillers with aphid presence.

Although little of the variation in tiller height and yield was found to be explained by the BYDV damage code, it was decided to investigate the relationships between these three crop variables and aphid presence overwinter to discover if any predictions were possible.

The yields, heights and BYDV damage codes were summed over each 1m section of the 10m sampled crop rows to produce a single value for each variable (of the tillers sampled every 100mm only). The number of alates, adults and 2nd-4th instar nymphs (both forms of the 4th instar nymphs) of the species R.padi and S.avenae found per 1m section of the same 10m sampled crop rows were then totalled over three overwintering time periods :-

1. October- December
2. January- March
3. October- March

i.e. 1. and 3. at Abbotscourt and Longwet fields only, as Maryfield was only sampled for period 2. Alates were included, as they are potentially the initial source of infection, whilst 1st instar nymphs were not included as field observations showed that these do not contribute to spread, but tend to remain stationary. The end of March was chosen as a final date, as it has been shown by Kendall & Smith (1984) that infection with virus as late in the growing season as April has little effect on the plants and the resultant yield of the crop.

The aphid counts obtained are presented in Appendix 3A,1-3.

Table 3.5

Results of the Application of Taylor's Power Law on the Aphid Count Data

Data Sets	Species and Time Period	No. of Points h	Correlation of Mean and Variance	b Value	st.error of b	Correlation of Mean and Variance of Transformed Data
Maryfield Abbotscourt Longwet	Sitobion avenae (all 3 years)	41 (see note)	0.849	1.37 p=0.315	0.270	0.120
Maryfield Abbotscourt Longwet	Rhopalosiphum padi (all 3 years)	41 (see note)	0.933	1.17 p=0.415	0.672	0.018
Maryfield	All aphids Jan - Mar	10	0.944	0.763 p=0.6185	0.256	- 0.944 **
Abbotscourt	All aphids Oct - Dec	10	0.470	0.828 p=0.586	0.738	0.655
	All aphids Jan - Mar	6	0.854	1.75 p=0.125	0.836	- 0.702
	All aphids Oct - Mar	6	0.847	1.60 p=0.2	0.477	- 0.702
Longwet	All aphids Oct - Dec	3				
	All aphids Jan - Mar	3	0.325	0.726 p=0.637	0.150	0.017
	All aphids Oct - Mar	3				

* = 5% ** = 1%

Note: Maryfield sampled all rows Jan - Mar = 10 points
Abbotscourt sampled all rows Oct - Dec = 10
Abbotscourt sampled 6 rows Jan - Mar = 6
∴ Abbotscourt sampled all winter, only 6 rows = 6
Longwet sampled all rows Oct - Dec = 3
Longwet sampled all rows Jan - Mar = 3
Longwet sampled all rows all winter = 3

Total number of row sampling occasions = 41

They were then corrected with respect to the number of sampling occasions each row was visited. Taylor's Power Law was then applied to the mean and variance of the number of each species per 1m section of row (as explained in Chapter Two). As Taylor's Power Law is species specific, a relationship for the mean and variance (and hence the transformation) was obtained from pooling time periods and also across the three sampling years, for each species. Table 3.5 shows the number of mean and variance points involved for each species, and the transformations used.The transformed data was then correlated with the crop characteristics of :-

1. Yield per 1m section of row. (all 3 years).
2.Height per 1m section of crop row (all three years).
3. BYDV damage code per 1m section of row (years 1 and 2).

As fifty four correlation tests were performed in total, 2.7 would be significant by chance alone at the 5% level. Therefore, the 1% level was chosen as that at which a correlation obtained was designated significant. Table 3.6 shows the correlations obtained, and Fig. 3.2 shows the only relationship significant at the 1% level.

Maryfield

In all cases, no relationships were even weakly correlated.

Abbotscourt

Weak correlations significant at the 5% level were found for R.padi numbers from October-December, and October-March and tiller height and for both species from October- December. A stronger correlation betwen BYDV code and S.avenae numbers from October- December significant at the 1% level was found, with a weak correlation significant at the 5% level between BYDV code and

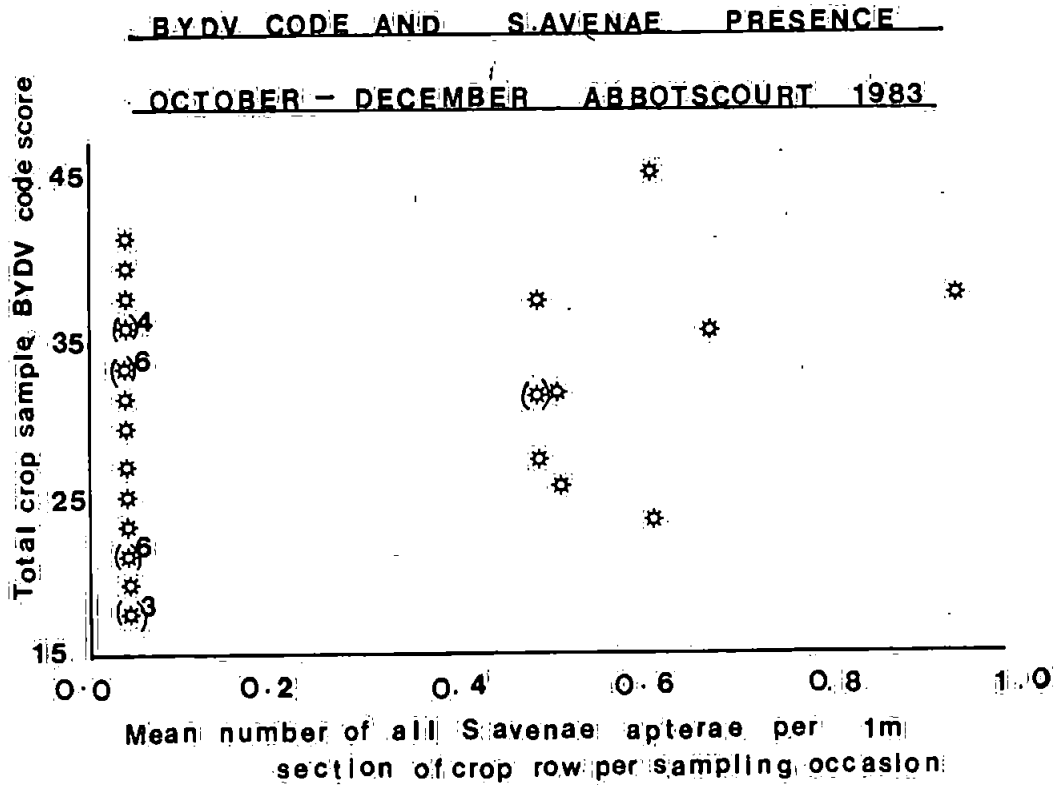
Table 3.6

Summary of Relationships between Aphid Numbers and Crop Characteristics as shown by r, the correlation coefficient

Data Set	Crop Character-istic	October - December			January - March			October - March (all winter)		
		S. avenae	R padi	All Aphids	S. avenae	R. padi	All Aphids	S. avenae	R. padi	All Aphids
Mary-field 1982 - 83	BYDV Code		n/a		ns	ns	ns		n/a	
	Tiller height		n/a		ns	ns	ns		n/a	
	Yield		n/a		ns	ns	ns		n/a	
Abbots-court 1983 - 84	BYDV Code	- 0.306 ***	ns	ns	ns	0.252 **	ns	ns	ns	ns
	Tiller height	ns	0.248 **	0.232 **	ns	ns	ns	ns	0.264 **	ns
	Yield	ns	ns	ns	ns	ns	ns	ns	ns	ns
Longwet 1984 - 85	Tiller height	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Yield	ns	ns	ns	ns	ns	ns	ns	ns	ns

ns = not significant ** = r significant at 5% level *** = r significant at 1% level

Figure 3.2


BYDV CODE AND S.AVENAE PRESENCE
OCTOBER – DECEMBER ABBOTSCOURT 1983
Total crop sample BYDV code score
45
35
25
15
0·0
0·2
0·4
0·6
0·8
1·0
Mean number of all S.avenae apterae per 1m section of crop row per sampling occasion

R. padi numbers from January- March.

Longwet

In all cases, no relationships were even weakly correlated.

The lack of significant correlations obtained between aphid numbers and crop characteristics is likely to indicate that numbers of aphids present in the sampled crop rows in all three years were below an unknown economic threshold level. As the summer aphid presence economic threshold for spraying is 5 or more per tiller at the onset of flowering, it is reasonable to assume that the numbers found in the sampled fields are low (Appendix 3A).

The lack of significant correlations obtained between BYDV damage code and crop characteristics indicates that virus presence was also likely to be low at Anthony in the sampled fields. However, patches of BYDV were seen at Maryfield and Abbotscourt (Plate 3a and 3b) and some samples sent to Long Ashton Research Station for ELISA analysis confirmed the presence of virus along the sampled crop rows at Maryfield.

3.4 The use of ELISA (Enzyme Linked Immunosorbent Assay) to detect Barley Yellow Dwarf Virus in leaves collected at Longwet field, Anthony 1984-1985, and the subsequent correlation with aphid spread and crop characteristics.

3.4.1 Introduction

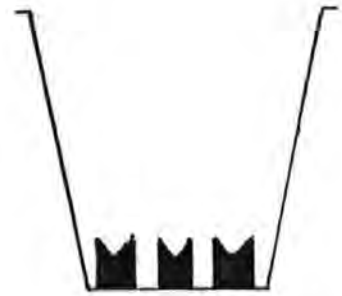
The BYDV presence code developed in Chapter 3, section 3.3 had been shown to be inadequate at describing the presence of virus in the crop, and so it was decided to use a method which was independent of field symptom expression, and could be used throughout the sampling period. The use of transmission tests, where aphids are maintained on test plants for a few days and the plants left to grow on to symptom expression was not suitable, due to:-

1. Availability of time.
2. Symptom expression had been shown to be inconsistent with disease presence.
3. The monitoring of secondary spread of apterous aphids would be difficult, if aphids were removed from the field at each sampling occasion !

As ELISA has been used successfully for BYDV detection by workers at Long Ashton (Kendall pers. comm) and at East Malling Research Station (Clarke pers. comm.), (although it is being superceded at the latter establishment), and the technique is quick, specific and easily standardized with a limited budget, it was decided to use ELISA to detect virus at Longwet field over 1984-1985. The basis of the enzyme linked immunosorbent assay was pioneered by Engvall and his colleagues, and by Vari, Weemen and Schuurs (Voller, Bidwell and Bartlett 1979). It is almost as

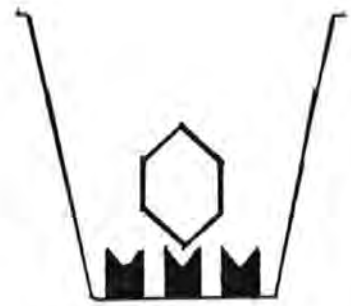
Figure 3.3 The principle of the ELISA technique

1. Specific antibody adsorbed to plate



Wash

2. Add test sample containing virus



Wash

3. Add enzyme-labelled specific antibody

Wash

4. Add enzyme substrate

Colour intensity $\propto$ virus concentration

sensitive as radio-immune assay because soluble antigens or antibodies are linked to insoluble solid phases in such a way to retain their immunological component. It is independent of the ratio of antibody to antigen and so once the appropriate concentrations for the antibody preparations are ascertained, they are applicable for detecting viruses at all concentrations. Although ELISA is used in quantitative investigations (Clark and Adams 1977), its use here was purely qualitative. In this investigation, the "double antibody sandwich" form of ELISA was used, as it has been found to be the most suitable for plant viruses (Clark 1977).

In this method, (Fig 3.3) virus in the test sample is selectively trapped and immobilized by specific antibody adsorbed onto a solid surface (polystyrene microtitre plates) (Voller et. al. 1979). Trapped virus is then reacted with further specific antibody to which an enzyme has been linked. After washing, enzyme labelled antibody that has complexed with the trapped virus is detected colorimetrically by adding phosphate enzyme substrate.

The ELISA technique is widely used in agricultural research. Within four years of its introduction, it became the test of choice for the diagnosis and epidemiology of a wide range of plant pathogens. Adequate sensitivity is essential to detect very low levels of infecting virus e.g. 0.01 ng cucumber mosaic virus in ml^{-1} plant suspension. More commonly, 1-100 ng ml^{-1} is detectable e.g. lettuce mosaic virus at 10 ng ml^{-1} and BYDV at about 30 ng ml^{-1}. (Voller et al. 1979). It can also be used to differentiate between closely related viruses e.g. B and F strain BYDV.

More recently, ELISA has been used to detect pathogens in insect vectors, aphid remains in polyphagous predators (Chiverton

1984, Loveii, Sopp and Sunderland pers. comms.) and the virus itself in aphid vectors (Plumb 1983).

The B strain is the severe form of the virus, more readily transmitted by R.padi and F is the mild strain, more readily transmitted by S. avenae, though the two are by no means mutually exclusive (Lyons pers. comm.). These strains were originally designated by Plumb (1974).

Practical Aspects.

1. Only those polystyrene microtitre plates which had been checked by the manufacturer were used. This ensured that antigen uptake onto the surface was uniform across the plates, as Voller et al. (1980) showed that performance is dependent upon the affinity of the protein antigen for the solid phase.

2. Washing between stages was essential, and the wetting agent, Tween 20 was used to prevent post-coating adsorption of protein to the well surface.

3. Test samples were added to duplicate wells to increase sensitivity.

4. Interpretation of results can be quantitative. However, as the actual absorbance values obtained were low as compared with other workers (Voller et al. 1980),but by no means too low to be due to experimental error, it was decided to restrict interpretation to simple presence or absence.

3.4.2 Materials and Methods.

Appendix 3B lists the components and the concentrations of the buffer solutions and the reagents.

1. Preparation of controls.

a) Negatives. (i.e. leaves known to be virus free).

A constant supply of three week old wheat plants c.v.aquilla was available from a glasshouse (for cultivation details see Chapter 4, section 4.5) and these had no contact with cereal aphids and so were virus free.

b) Positives. (i.e. leaves containing virus).

At first, Long Ashton Research Station provided some leaves from a viruliferous aphid culture and these were used. Later, some viruliferous aphids were obtained from the same source, and a viruliferous cereal aphid culture was established. (practical details see Chapter 4, section 4.5). Leaves were taken from the plants in this and were used to provide the positive controls.

2. Extraction of test samples.

Deep frozen leaf samples collected at Anthony from October 1984 to March 1985 were thawed, a small batch at a time, weighed on a Sartorius microbalance, cut up, and placed in labelled Bijoux glass jars with an appropriate volume of PBS-tween solution to give a 1:1000 dilution by weight. The leaves were then ground up using a M.S.E. overhead micro homogeniser (which was rinsed thoroughly between samples in distilled water and dried to prevent contamination), and allowed to stand for an hour to settle out. The resultant liquid test samples were pipetted into labelled micro centrifuge tubes and subsequently spun for 3 minutes in a high speed M.S.E. micro centrifuge at 13,000 r.p.m. The samples were stored in the refrigerator at 4 ^{o}C until they were needed. 50 samples were extracted in this manner per day.

3. ELISA Technique.

The best conditions for this virus-antiserum system were developed by Clark and Adams at East Malling Research Station, and are routinely followed in the below manner by Lyons at Long Ashton Research Station. New glasswear was used at each separate stage of the technique. It was first treated with a silicon wash Dimethyldichlorosilane solution c.a. 2% in 1.1.1.Trichloroethane, and allowed to dry in an oven. The principle of the ELISA technique is shown in Fig 3.3. It was found that stages 1 and 2 fitted into Day 1, and stages 3 and 4 into day 2. All pipetting was done using 3 Jencoms variable volume Finnpipettes, two single pipettes 5-50 µl and 50-250 µl, and one 150-250µl eight track multichannel pipette. The correct sized sterile disposal tips were used with each and plastic reservoirs for the reagents where appropriate. Purified globulin and conjugated enzyme-labelled γ globulin was supplied by Dr. M. Clark at East Malling Research Station for B and F strains of BYDV, and was kept at all times at 4 ^{o} C. All glassware, reagent reservoirs and 96 flat bottomed well microtitre plates (supplied by Nunc Ltd.) were colour coded according to BYDV strain, and kept separate.

a) Coating

B and F strain purified γglobulin was added to coating buffer in separate coated glass beakers, to produce 1 in 1000 dilutions, and shaken for at least one minute to disperse the antibody. In practice, 15 µl of antibody in 15 mls of coating buffer was found sufficient to coat all 96 wells of a micro-titre plate. 200 ul of each specific antibody solution was added to each well, using the multichannel pipette, the plate was covered with cling

film, and then incubated for 3 hours at 30 ^{o} C. The plate was then washed by flooding the wells with 10% PBS-Tween, left for three minutes, this was repeated three times. It was then shaken vigorously in the air, blotted dry on paper towel and covered with fresh cling film. It was found to be most convenient to coat enough plates for a whole week of ELISA analysis on Mondays (i.e. 20 plates in total) and then store plates in a deep freeze at -10 ^{o}C until required.

b) Addition of the test samples

200 ul aliquots of 25 test samples were then added to duplicate wells in each coated microtitre plate along with full concentration positive, half concentration positive (1:2000) and negative samples. The outermost wells were not used for test samples, as they are known to produce inaccurate results due to the plate construction (Clark and Adams 1977, Lyons pers. comm.). The plates were then covered with cling film and left at 4^{o}C overnight.

c) Addition of Enzyme labelled specific antibody.

The plates were washed as in a) and purified enzyme labelled γ globulin was added to PBS-tween in coated glass beakers in a similar manner as the coating antibody to produce an enzyme labelled antibody suspension for both B and F strain of BYDV. 200 µl aliquots of each were then added to each well, covered with cling film, and incubated at 30^{o} C for 5 hours.

d) Addition of enzyme substrate.

The plates were washed three times as in a). 16 tablets of phosphatase substrate supplied by Sigma chemicals were dissolved in 120 mls of substrate buffer by shaking. This was found to be adequate for four microtitre plates. 250 µl aliquots were added to

each well, using the multi-channel pipette, and the plates were incubated at room temperature, uncovered for 2 hours.

e) Stopping the reaction and assessment.

The plates were placed on a microtitre plate shaker, and 50 µl of 3m NaOH was added to groups of eight wells simultaneously, using the multichannel pipette. The shaking was essential to prevent layering. A Dynatech microelisa reader was used to read and record the absorbance of each individual well at 405 nm. The intensity of the yellow colour that develops is proportional to virus concentration of the sample.

3.4.3 Results.

1. Sample extraction

It was found that 0.8 ml was the minimum volume of liquid on which the M.S.E. overhead homogeniser could operate. Consequently some of the early autumn leaf samples were too small to be extracted singly. To overcome this problem, small leaves were combined in the following scheme, with some loss of precision.

1. Leaves of the same plant.
2. Leaves of plants at distances along the row within 0.01m of each other.
3. Leaves of plants at distances along the row within 1m blocks e.g.0-0.99, 1-1.99 etc.

32% of all ELISA samples analysed were pooled according to 2. and 1.6% according to 3. Some samples were also diluted to produce a half concentration extract if sample combination was only enough to produce a volume of 0.4 ml. In the subsequent analysis of the results of the ELISA, samples, rather than leaves are used to assess

secondary spread, thereby eliminating complications arising from attempting to decide which leaf in the pooled sample contained the virus. This level of accuracy is sufficient for the illustrative aims of the investigation in this Chapter.

2. The ELISA Technique

The technique was first checked with known positives verified by Lyons at Long Ashton Research Station, until reproducable, positive results were obtained. The following problems were encountered :-

a) Occasionally, as Table 3.7 shows, a batch of microtitre plates were responsible for complete failure of any test solutions and controls to produce a colour change. Plates supplied by Numc (Lyons pers. comm.) proved to be the most satisfactory.

b) The controls produced different absorbance valuation on each plate, and also the half concentration known positive samples never had an absorbance reading of exactly half of the known positive control. It was therefore decided to interpret the results with reference to the individual plates only, with no attempt to compare absorbance values between plates.

The results of ELISA can be used in the following ways :-

1. To show the temporal variation in the overall proportion of leaf samples containing BYDV (Fig. 3.4).

2. To demonstrate the spread of both virus strains and each virus strain along the sampled crop rows (Fig. 3.5).

3. To quantify this spread, and correlate it with the simultaneous aphid spread along the sampled crop rows.

4. To attempt to correlate virus presence with resultant yield in 1985.

1. Temporal variation

Figure 3.4 shows that the overall proportion of ELISA samples from all rows containing either or both strains of BYDV increased over the winter of 1984-1985 to a maximum of 100% in January (110 days after initial sampling). It is reasonable to assume therefore that all aphids sampled were virus vectors. After this date, interpretation is difficult due to a low incidence of positive samples obtained from 1 March, which could be due to either sampling technique malfunction or a true non-appearance of virus, and this is why Fig. 3.4 shows a pecked line between the last two points. Table 3.7 below shows the total number of samples used for the ELISA on each occasion for each row. Gaps correspond to dates when sampling of the individual rows did not occur.

2. Spread of virus along sampled crop rows.

This is best shown graphically, with reference to each strain, and each crop row (Fig. 3.5). In all three rows, virus presence remained patchy until mid December, when presence was fairly widespread across all rows. In all rows most virus was present in January and February(88-100% of all samples) but this reduced to 50-60% by the end of February/beginning of March, when aphid numbers were low following the severe cold of February 1985. The following points can be seen from the graphs :-

In Row 2, the F strain of virus was far more widespread in February than the B strain, but this position was reversed in mid December.

In Row 3, more F strain was present in the leaf samples at the end of March than the B strain.

Table 3.7 Total Number of Leaf Samples, ELISA Samples and Number of Samples containing either or both BYDV Strain (B or F) for Each Crop Row

ROW 1

Date	Occasion Number	Total Number of Leaf Samples	Total Number of ELISA Samples	Number of Samples with either or both B + F Strains	% Samples Containing BYDV
12.10	1	0	0		
19	2	5	3	0	0
22	3	5	5	0	0
25	4	8	4	1	25
29	5	6	4	1	25
2.11	6	15	12	1	8.3
5	7	13	4	0	
9	8	17	8	4	50
12	9	31	20	4	20
16	10				
19	11	42	31	3	9.7
23	12	40	25	1	4
26	13	37	19	1	5.3
30.11	14	63	33	3	9.1
3.12	15				
7.12	16	102	65	17	26.2
11	17	70	39	17	43.6
21	18				
24	19				
31	20				
14.1.85	21	47	26	23	88.5
21	22				
25	23				
28	24	35	27	27	100
1.2	25				
4	26	43	31	28	90.3
8	27				
18	28	8	6	3	50
22	29				
1.3	30				
4	31	13	Lost due to experimental area		
25	32	15	13	8	6.1
28	33				
Grand Totals		585	387	146	
Number of Occasions		21			

ROW 2

Date	Occasion Number	Total Number of Leaf Samples	Total Number of ELISA Samples	Number of Samples with either or both B + F Strains	% Samples Containing BYDV
12.10.84	1	1	1	0	0
19	2	6	4	1	25
22	3	1	1	0	0
25	4	2	1	0	0
29	5	5	3	0	0
2.11	6	10	9	2	22.2
5	7	13	5	0	0
9	8	15	7	2	28.6
12	9				
16	10	22	6	1	16.7
19	11	14	8	0	0
23	12				
26	13	27	14	8	57.1
30.11	14				
3.12	15	56	21 (31 lost)	9	33.3
7	16				
11	17	46	24	13	54.2
21	18	82	50	43	86
24	19				
31.12	20	73	55	23	41.8
14.1.85	21				
21	22	48	36	23	63.9
25	23				
28	24				
1.2	25	36	29	27	93.1
4	26				
8	27	9	8	8	100
18	28				
22	29				
1.3	30	4	4	0	0
4	31	4	4	0	0
25	32				
28	33	5	5	2	40
Grand Totals		478	295	162	
Number of Occasions		21			

ROW 3

Date	Occasion Number	Total Number of Leaf Samples	Total Number of ELISA Samples	Number of Samples with either or both B + F Strains	% Samples Containing BYDV
12.10.84	1	3	3	0	0
19	2	13	9	0	
22	3	1	1	0	0
25	4	11	8	0	0
29.10	5	7	6	2	33
2.11	6				
5	7	5	5	0	0
9	8	4	1	0	0
12	9				
16	10				
19	11	11	5	5	100
23	12				
26	13	21			
30.11	14				
3.12	15	27	19	12	63.2
7	16				
11	17	42	40	13	32.5
21	18				
24	19	53	33	6	18.2
31.12	20				
14.1.85	21				
21	22				
25	23	36	25	21	84
28	24				
1.2	25				
4	26				
8	27	9	9	9	100
18	28				
22	29				
1.3	30	6	6	0	0
4	31				
25	32				
28	33	6	5	4	80
Grand Totals		258	186	76	
Number of Occasions		16			

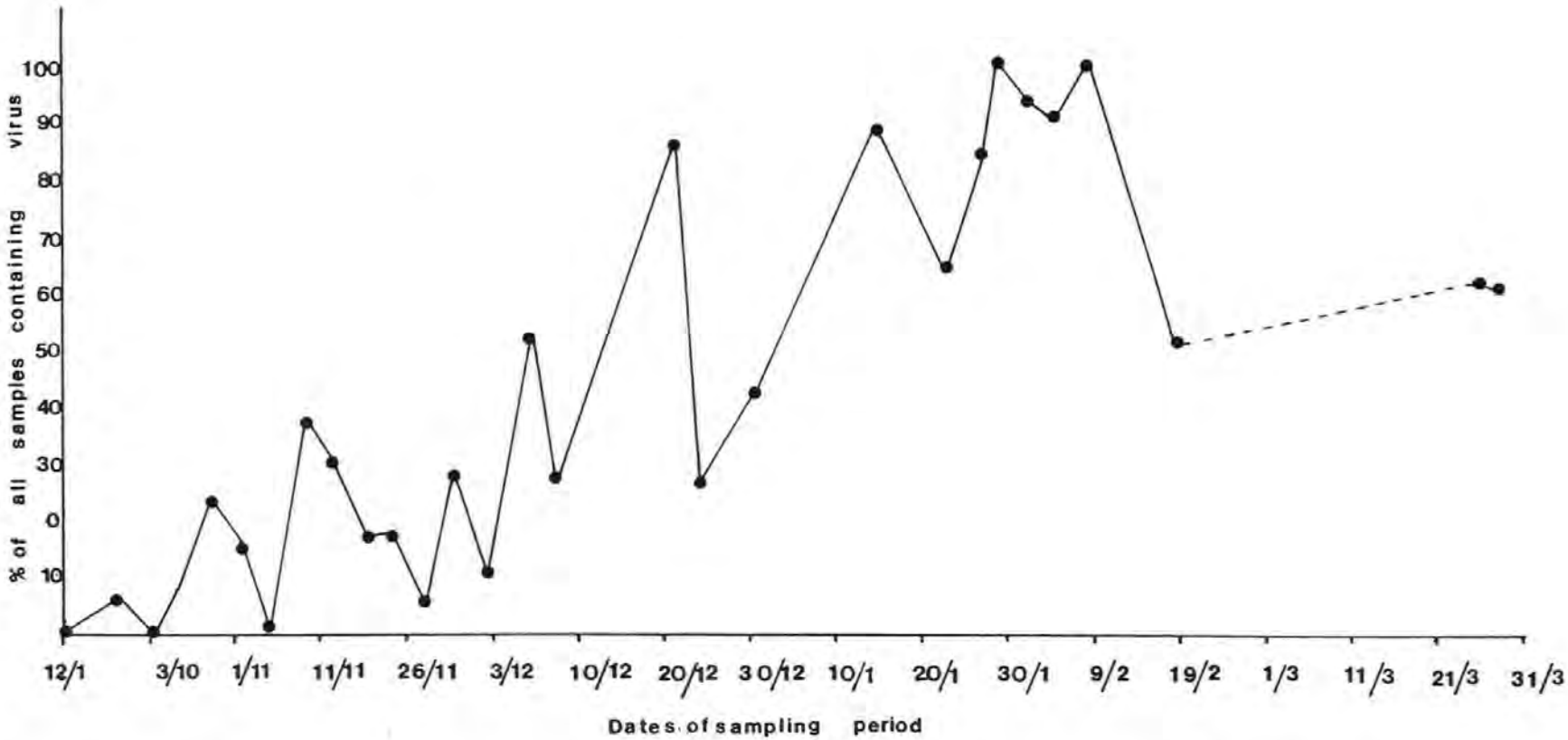


Figure 3.4 The percentage of ELISA samples containing virus (either B or F strain, or both) at Longwet field, Anthony, 1984 - 1985

3. Quantification of spread and correlation with aphid numbers and spread.

The numbers of positive BYDV containing samples, as shown with ELISA for each strain and all virus strains, were totalled per 1m section of the 10m sampled crop rows, for the three overwintering time periods used for aphid numbers. These sample totals were then corrected for number of sampling occasions per time period and correlated with the transformed aphid counts already obtained in Section 3.3 using Minitab. Table 3.8 shows the correlations obtained and Fig 3.6 shows the most significant relationships.

It was decided to only look at relationships within time periods, since correlations across time periods (e.g. B virus strain October-December and R. padi numbers January-March would be meaningless). The correlations show that in Longwet field the virus vectors were R. padi. It would be unreasonable to suggest that the maximum rate of virus spread must be at the same rate as apterous aphid spread (Chapter 4, Section 4.3).

4. Correlations of virus presence with crop characteristics.

The sample totals obtained for each 1m section of row in Section 3.3 were correlated with the heights of tillers and yields of the 1m sections using Minitab. Table 3.9 shows the correlations obtained. As would be expected, the relationships between virus presence, tiller height and yield are largely negative and only very weak if positive. However, the only significant relationship (at the 5% level) is between F strain virus and tiller height. These results confirm those obtained in Section 3.3, and suggest that the level of virus and aphids in Longwet fields between October 1984 and

Table 3.8

Summary of Relationships between Aphid Numbers and BYDV Presence as shown by ELISA at Longwet

A October - December

BYDV Strain	Aphid Count Sitobion avenae	Rhopalosiphum padi
B	0.013	0.363 **
F	- 0.206	0.418 **
B + F	- 0.122	0.433 **

B January - March

BYDV Strain	Aphid Count Sitobion avenae	Rhopalosiphum padi
B	- 0.054	0.586 ***
F	0.117	0.717 ***
B + F	0.054	0.853 ***

C October - March

BYDV Strain	Aphid Count Sitobion avenae	Rhopalosiphum padi
B	0.152	0.568 ***
F	- 0.083	0.278
B + F	- 0.020	0.589 ***

*** = significant at the 1% level

** = significant at the 5% level

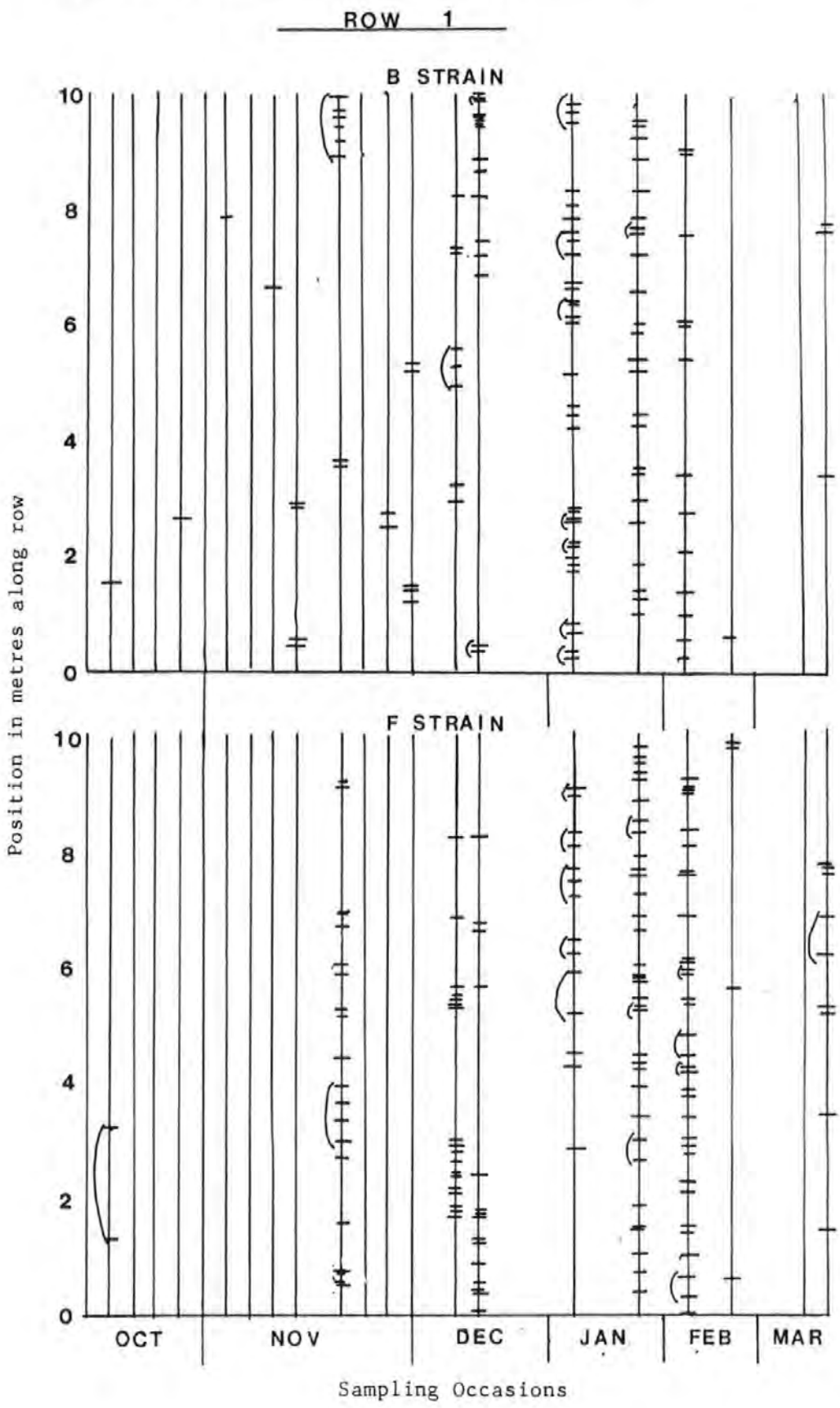
Table 3.9

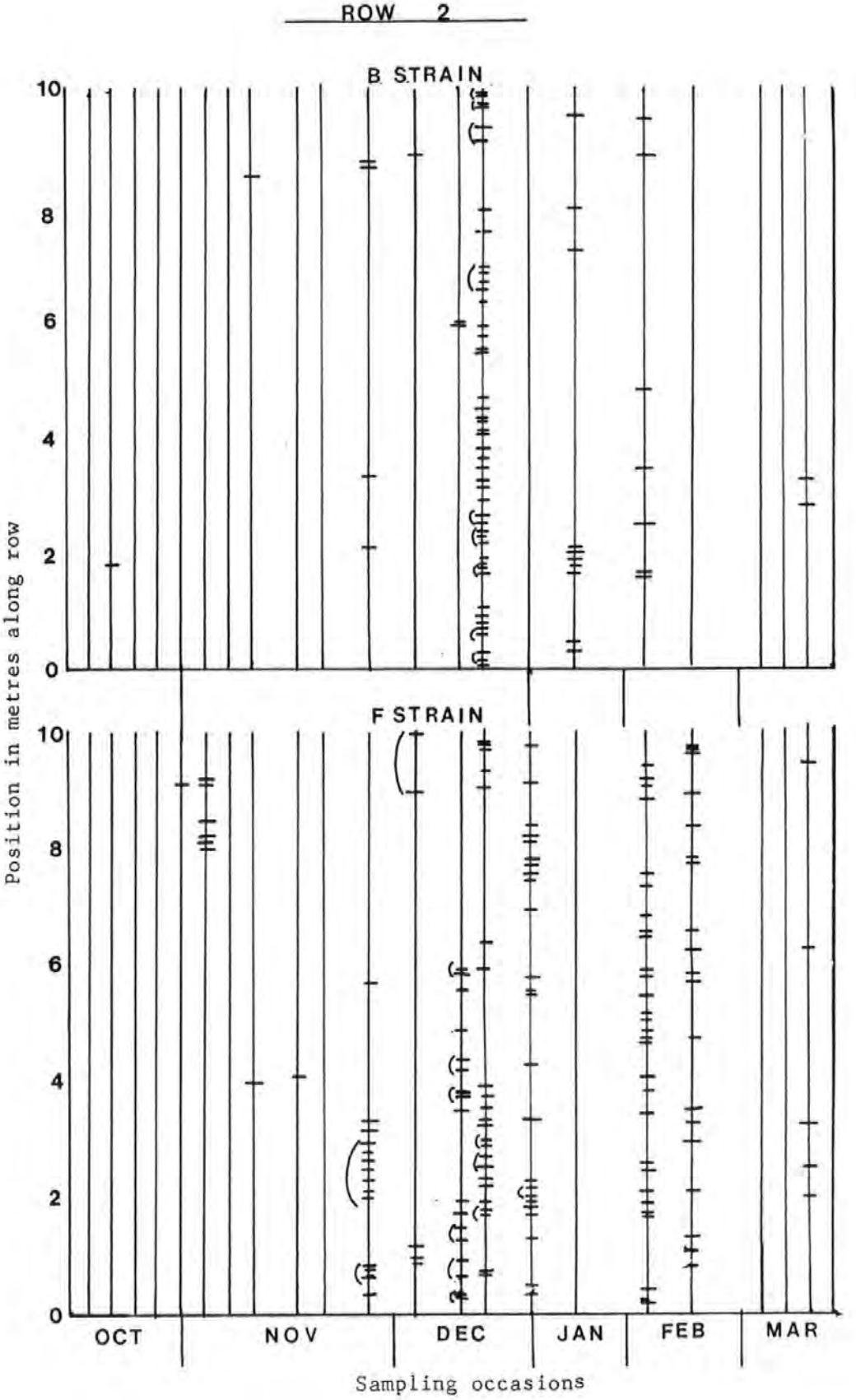
Summary of the Relationships between BYDV Presence and Crop Characters

Crop Characters	BYDV Presence and Strain								
	Oct - Dec			Jan - Mar			Oct - Mar		
	B	F	B + F	B	F	B + F	B	F	B + F
Height (50m of 10 tillers)	-0.034	-0.229	-0.159	-0.166	-0.162	-0.207	-0.154	-0.450 **	-0.200
Yield (50m of 10 tillers)	-0.044	0.039	0.045	-0.105	-0.209	-0.207	-0.030	-0.323	-0.200

** = significant at 5% level

Figure 3.5 The spread of virus, as sampled by ELISA, along sampled crop rows October - March 1984 - 1985




ROW 2
B STRAIN
F STRAIN
Position in metres along row
10
8
6
4
2
0
OCT
NOV
DEC
JAN
FEB
MAR
Sampling occasions

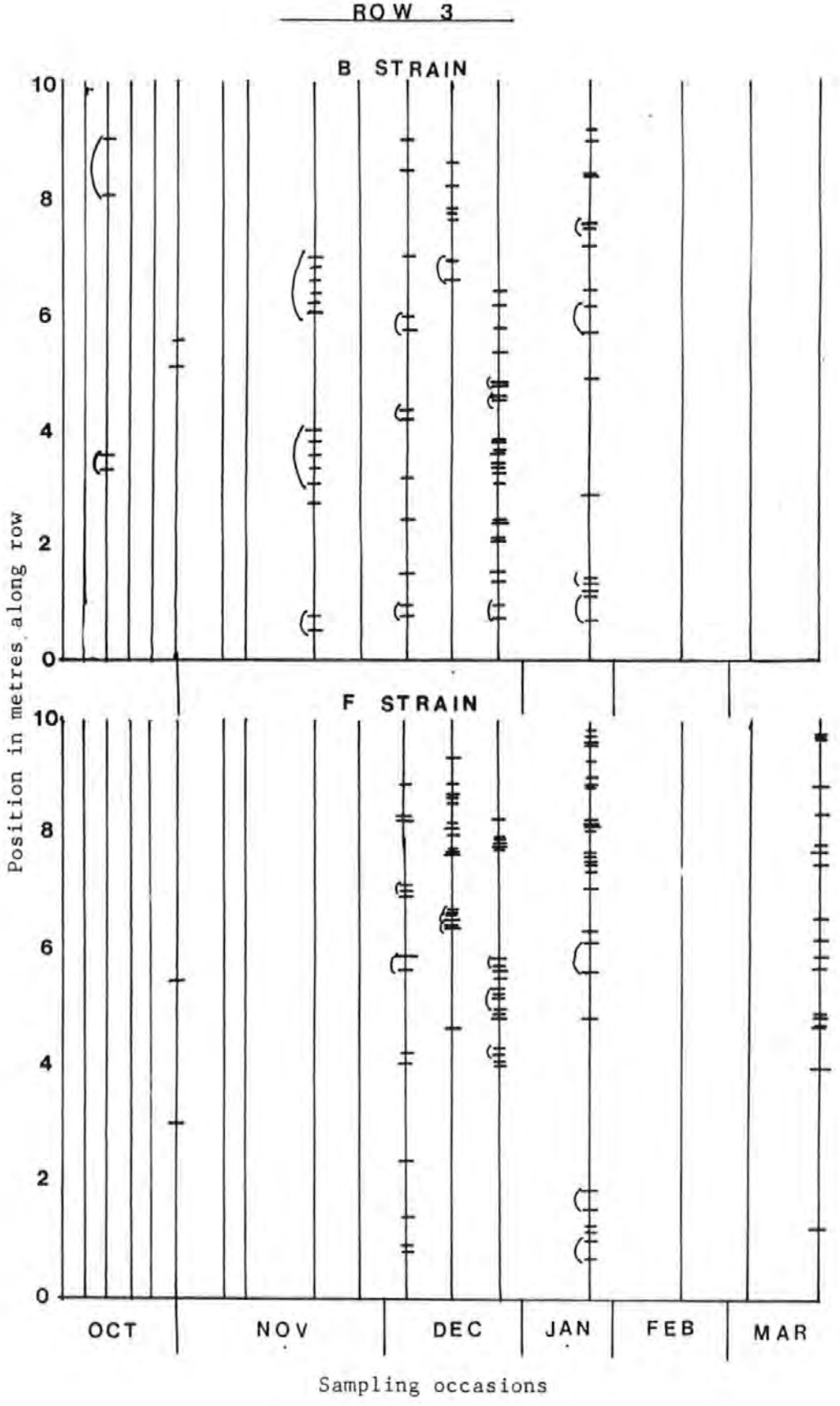
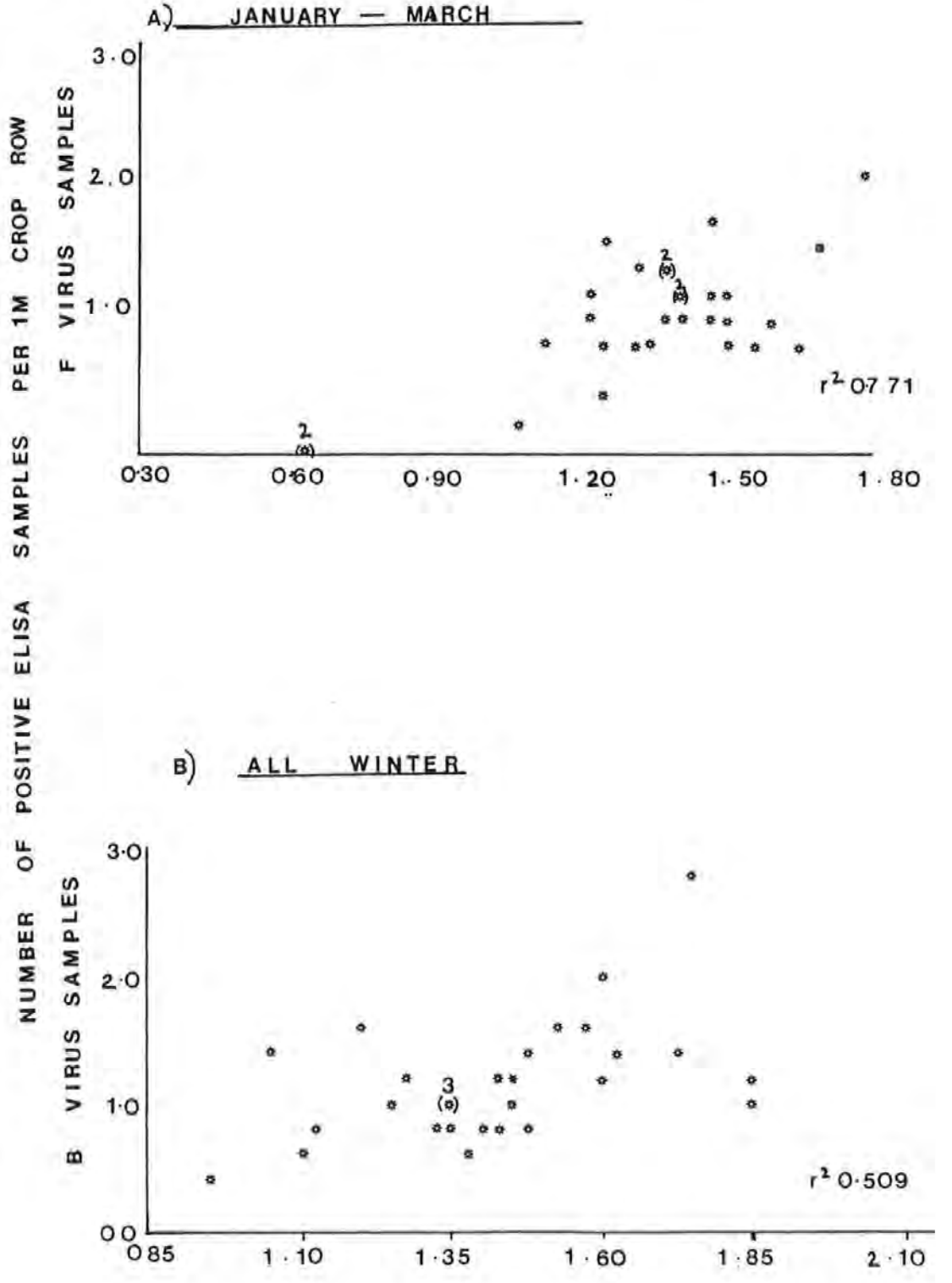

ROW 3
B STRAIN
F STRAIN
Position in metres along row
10
8
6
4
2
0
OCT
NOV
DEC
JAN
FEB
MAR
Sampling occasions

Figure 3.6

Relationship between aphid numbers and ELISA results



March 1985 was too low to have a large effect on yield.

3.5 Discussion.

1. Barley Yellow Dwarf Virus and Aphid presence.

Given that the BYDV damage code devised in this project could only ever be a guide to aphid presence, and the variability of symptom expression in infected crop plants, the aphid presence and code relationships could not be precise. A further complication is the use of different winter wheat varieties in the three different fields in the three sampling years, a factor beyond the control of the project. It would seem from the results obtained that BYDV damage code was so variable that yield and tiller height could not be predicted. The levels of densities of S. avenae and R. padi found were probably too low to exert much effect amongst the mass of variables, biotic and abiotic, that affect crop yield (although R. padi feeding can effect yield, Mallott and Davey 1978). There could have been insufficient damage at higher codes to reduce yields. Some trends do emerge from the data from Abbotscourt. Despite the fact that BYDV damage code does not adequately describe differences in yields and tiller heights, it must, because of its very nature, represent a measure of virus presence. The significant correlation with BYDV damage code and S.avenae presence from October- December suggests that S.avenae was the most important virus vector for producing symptom expression in the crop, and it exerted its effects in the Autumn, which agrees with Gair (1981), Kendall and Smith (1982, 1983). Plumb, Gutteridge, Hubband and Lennon (1984) reported a low Infectivity Index for autumn 1983, but what infection did occur in the U.K. was due to S.avenae in the North

Midlands and South Yorkshire, and infective S.avenae were found at Starcross (Plumb, Gutteridge and Lennon 1983). On Anthony Estate farm, numbers of aphids, particularly R. padi reached high levels on adjacent fields of winter barley of up to 500m $^{-2}$ in November (Lambden pers. comm.).

The R. padi presence in Autumn 1983 at Abbotscourt, although only at densities around 200m^{-2} could have affected yield by causing some feeding damage. Alternatively, the strain of virus they were carrying did not produce recognizable symptoms, which is why there was no correlation with BYDV code. In Autumn 1984, the Infectivity Index was similar to Autumn 1983 (Plumb et al. 1984). As the crop was sampled for virus presence using ELISA throughout the 1984-1985 sampling period, the BYDV code was not used at Longwet. Also, it had been shown to be of little value in assessing virus in the crop. As no significant relationships were found between aphid numbers and tiller height and yield it must be assumed that the densities at which R. padi and S. avenae were present in 1984-1985 were below the damage threshold. However, the amount of virus they brought to the crop did reduce the tiller height.

The results obtained by analysis of the leaves using ELISA confirm that secondary spread had occurred and by January all R. padi individuals appeared to be virus vectors. The late sowing date in 1982 meant that Maryfield did not receive any aphicide, so the results obtained in Section 3.3 can be applied to the whole field, and therefore it is with some confidence that the results suggest aphid densities must have been below economic threshold levels. However, this is not to suggest that a later sowing date exerts a yield benefit, due to avoidance of aphid infestations,

because Maryfield was unique of the three fields used. It had only recently been ploughed, and so the higher yield reflects a variety of factors. Unfortunately, at Abbotscourt and Longwet, the yields obtained from the farm records applied to the whole field, and whilst no aphid presence/yield relationships were found along the sampled crop rows, this should not be extended to include the whole field, as all yield measurements were taken inside the unsprayed areas set aside by the grower. An additional complication is the yield benefit accrued by the autumn application of synthetic pyrethroid (Kendall and Smith 1982).

2. Role of overwintering movement of apterous cereal aphids in secondary spread of BYDV.

The results of the ELISA analysis of Section 3.4, where infection was found to occur in 80-90% of all leaf samples demonstrate that movement until January of apterous cereal aphids is central to secondary spread of BYDV. From January- March the correlation between R. padi presence and both strains of virus was highly significant. This suggests that aphids found after January acquire virus from infected crops, but could also suggest that viruliferous aphids were more cold hardy. No evidence was found in the literature to support or reject this idea. However, samples taken towards the end of February (after a very cold spell when sampling was not carried out due to extremely adverse weather conditions), contained far less virus, so interpretation of this "end of winter period" results is difficult. The virus has been shown to persist in cereal plants from autumn inoculation until June using ELISA in wheat and oats in Indiana (Clement, Lister and Foster

1986), but at low levels and little R. padi overwintering occurred. Nevertheless, virus is capable of persisting for many months in crop plants so the observed drop in % of leaves infected could be due to experimental error. Distribution of virus within cereal plants has been shown to be limited to the phloem, parenchyma companion cells and sieve elements (Gill amd Chong 1975). Although BYDV is capable of spread to other leaves in 6-12 hours, virus may not spread to all leaves in an infected plant (Matthews 1981). The apparent reduction in % of infected leaves could be a reflection of virus distribution within the sampled plant.

Virus transmission is not a simple process. The results obtained from sampling in commercial wheat crops have confirmed some assumptions about secondary spread of BYDV, and have provided some evidence of the process. However, they have also illustrated some of the difficulties of virus work, mainly due to symptoms becoming apparent only in the following spring after initial infestation, and also the unreliability of the use of symptom expression to quantify virus presence.

3.6 Conclusions.

1. BYDV was present at different levels in all three fields sampled at Anthony Estate farm in 1982-1983, 1883-1984 and 1984-1985.
2. A BYDV damage code based on symptoms and devised in this project was of limited value in predicting yield.
3. Secondary spread of apterous aphids, particularly R. padi and the concomitant spread of BYDV was demonstrated at Longwet field in 1984-1985 by ELISA. Infection was shown to be present in 90% of leaf samples taken along the sampled crop rows by January.
4. Aphid numbers at Anthony Estate farm over the winter appeared to

have no significant effect on the yields of the crops in the unsprayed areas and in an unsprayed field, so aphid presence in all three years was probably below an economic threshold.

CHAPTER FOUR

DISPERSAL OF *RHOPALOSIPHIUM PADI* IN WINTER WHEAT

4.1 Introduction.

a) Dispersal and migration.

The study of dispersal and migration of insect pests is essential to the development of integrated pest control. As late as 1972, Headley has been quoted as saying that "Agricultural pest control is still handled as though pests were immobile" (Stinner, Barfield and Dohse 1983). However, Clark, Jones and Holling (1978) state that movement studies have progressed from an earlier preoccupation with statistical problems of pattern description, to the present treatment of movement as an ecological process on the same order as predation or reproduction. Stinner et al. (1983) hope that studying movement as a component-structured process will lead to substantial improvements in theory and experimentation.

Most animals move about to seek food or mates, to avoid predation or for some other reason. Whatever the objective, their success in achieving those objectives affects their survival or reproductive rate. Thus the population dynamics of a species may depend on its movement patterns, and one cannot be completely understood without the other (Jones 1977).

The definition of insect movement is itself a matter of some controversy (Stinner et al. 1983). Southwood (1978) defines any movement away from an aggregation as dispersal. If dispersal involves long distance "straightened out" movements, in which individuals are temporarily inhibited from responding to vegetative stimuli, then it is termed migration. If successful, migration takes the organism to a new habitat (Kennedy 1961, Southwood 1978). Only some species of insects exhibit migratory behaviour (Southwood 1978)

and thus there is a variation in the innate tendancies of species to disperse. The term trivial dispersal is applied to short meandering movements limited to within a habitat, in which individuals exhibit appetitive behaviour.

The process of dispersal is thought to be density dependant by some authors (Hargrove 1981, Taylor and Taylor 1977, Taylor, Woiwood and Perry 1978 and Taylor 1980), but not by others (Hanski 1982).

In this thesis, the term dispersal will be used to describe all movements of apterous aphids within cereal crops between plants, either plant-plant or plant-soil-plant, and thus refers to within-habitat movement. The term migration is used to describe the movement between cereal crops by alate aphids at different times of the year.

b) Methods of studying dispersal in invertebrates and other animals.

Over the last fifteen years, a variety of experimental methods have been used to study dispersal. It is studied in two main ways.

1. Release of marked individuals at a central release point, and subsequently recapturing them at set distances from the release point, in traps. Dispersal estimates are then based on averaging distances at which recaptures are made and on mathematical descriptions of the numbers caught in the traps. These descriptions tend to fall into two main groups of empirical relationship, and are all summarized by Southwood (1978). For example, this approach was used by Hawkes (1969, 1972) who marked cabbage root flies, Delia radicum(L.), with radio-active Phosphorus, Rogers (1977) who

marked tsetse flies, Glossina fuscipes(Westwood) with oil paint, and Kareiva (1982) who marked flea beetles, Phyllotreta crucifera(L) and Phyllotera striolata(L.).

2. Tracking marked individuals,or observing un-marked individuals.

An extension of this approach is to release marked individuals and then continually monitor their distances from the release point, using telemetry. These distances are then used to calculate dispersal estimates rather than set trapping distances. One of the earliest and most comprehensive studies was by Siniff and Jessen (1969) who monitored the movement of red fox Vulpes fulva, snowshoe hare Lepus americana and raccoon Procyron lotor using radio transmitters. Stevens (1982) studied adult white fringed weevils, Graphognathus leucoloma (Boheman), by tagging them radio-actively. Jones (1977a and b) directly observed the search behaviour of adult cabbage butterflies Pieris rapae(L.) and also 3 caterpillar species P.rapae, Plusiacali californica(Speyer) and Plutella maculipennis (Curt.).

Tracking/observational experiments on dispersal take one or two forms.

a) A fixed time interval is used in the recording, and the duration, speed and angles of movement between each point in time are recorded. This method is used when tracking throughout the periods of movement is not possible.

b) All behavioural events are recorded for all individuals and then used in an attempt to understand behaviour underlying dispersal. For example, Jones (1977a) was able to collect data on the movement patterns of caterpillars and adult cabbage butterflies. This data

was used to develop an understanding of egg laying movement in adults. It was also used to ascertain that caterpillars exhibit increasingly directional movement as their hunger increases.

Whichever method of investigating dispersal is used, a relatively recent development is the subsequent computer simulation of animal movement. Simulation allows the testing of theories of dispersal, allows quantitative predictions to be made which can lead to field experiments, and has been useful in studies of the evolution of migration. It can also be employed in the estimation of dispersal rates.

Simulation models involve two different types of variable :-

1. If fixed time intervals were used, the variables for the model are duration, speed, and angles of movement between each point (Siniff and Jessen (1969, Zaluchi and Kitchen 1982). The latter study was based on movement of a prosobranch gastropod, Polinices incei (Phillippi), which leaves a track in sand.
2. If all behavioural events were recorded then these determine the variables used for the model. For example, Jones (1977) used head turning and turning, for caterpillar behaviour, whilst Hawkes, Patton and Coaker (1978) used flight direction, flight length and length of inactivity between flights as the variables.

Simulations of mark-release experiments using central release points of individuals have been conducted using homogeneous and heterogeneous environments to assess dispersal in each, and are available for a variety of animals and experimental situations. For example, Shigesada's (1982) model (based on Morista's work) of ant lions, Glenduroides japonicus(L.) used a release point in an

homogeneous field, at the centre.

Rogers (1977), modelled dispersal of Tsetse fly, G. fuscipes in which flies were recaptured in a series of decagonal "flyrounds" around a natural concentration of flies (the release point). A random-walk was assumed. He used a variety of constant step lengths per day and then compared observed field results with those simulated. He was then able to estimate the dispersal rate in terms of the distance moved per day.

4.2 Rationale of the methods of study of dispersal used in this project.

The study of aphid dispersal has concentrated on aphid migrations and distribution changes e.g. via the Rothamstead Insect Survey (Taylor and Taylor 1979), and is outlined in the introduction.

It was decided to approach the study of apterous aphid dispersal initially in commercial fields, and then in increasingly controlled experiments to develop an understanding of the process. Preliminary attempts at marking individual apterae showed this approach to be unsuitable, due to high mortality rates induced by fluorescent dusts and nail varnish and ecdyses of nymphs.

As field sampling essentially measured the temporal and spatial changes of distribution (Section 4.3), then the first approach was to use these to locate "patches" of apterae and to assess dispersal from these along sampled crop rows.

It was decided to use a simple simulation model, with a range of constant step lengths per day in a random-walk type process, to find the best estimate of field dispersal rates.

Investigating dispersal in 3 dimensions from a central

release point in an homogeneous habitat in which predators were excluded, was felt to be the most appropriate method available to investigate dispersal in more detail.

Dispersal was estimated by calculating the mean of the distance dispersed by individuals found in "distance classes" from the release point. This was simple, and avoided the use of traps.

These experiments were then followed by releasing apterae in small trays of cereals in controlled environment rooms. This enabled an assessment of the effects of temperature on dispersal to be made, without the complications of other factors.

Tracking individuals on the soil in the laboratory permitted a detailed study of dispersal of apterous R. padi, without the influence of host plant presence. A fixed time interval was used and the step length, angle of turn and direction of movement between these fixed points was recorded.

4.3 The use of the distribution of cereal aphids in commercial crops to assess dispersal.

4.3.1 Introduction.

The data collected in this experiment provides general information on the presence and relative abundance of all three cereal aphids, R. padi, S. avenae and M. dirhodum over the winter.

Taylor and Taylor (1979) used the changing distributions of alates caught in the Rothamstead Insect Survey traps to assess dispersal by aphids in migration across the U.K. Whilst the scale of this investigation is much smaller, the principles are the same.

4.3.2 Aims

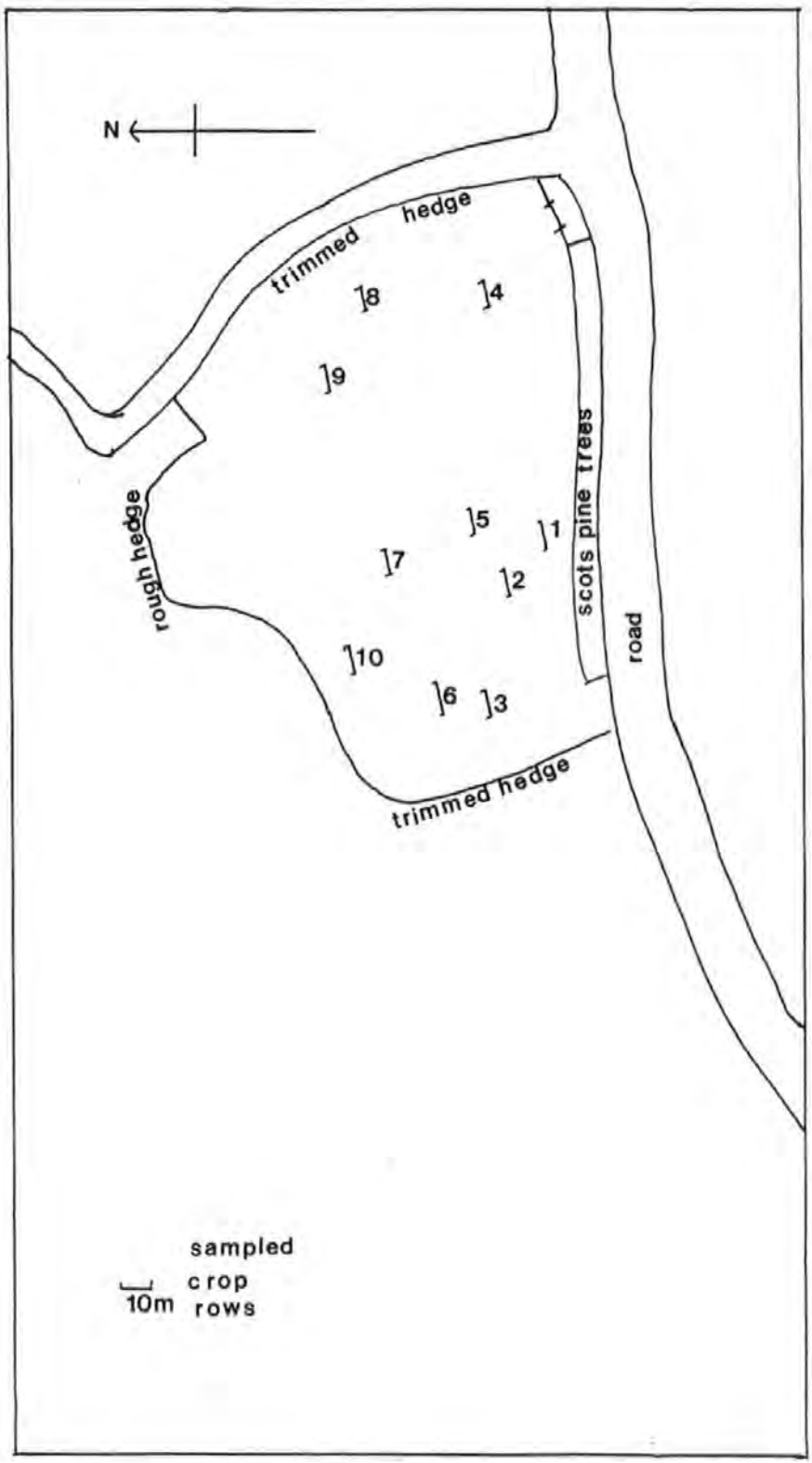
1. To assess the presence and abundance of cereal aphids between years and within years in commercial wheat crops.
2. To use the spatial and temporal changes in distribution to assess dispersal by apterous aphids.

4.3.3 Materials and Methods.

Fieldwork continued at Anthony Estate Farm over the three growing seasons, and is summarized in Table 4.1 (see Chapter 3, Section 3.1 for site description). Fig. 4.1 shows the location of these fields on the farm. In each year a number of crop rows were randomly selected for study, in areas of the fields determined by the farmer. Figs.4.2 a-c show the exact locations of these rows. Random number tables were used to generate the number of paces to walk in North-South and East-West directions to locate the ends of rows to be sampled. All rows were at least two tram lines (approx 30m) from field boundaries to avoid edge effects. The rows were marked at either end with white glass-fibre rods (5mm diameter),

Figure 4.1 Distribution of sampled crop rows in the fields used

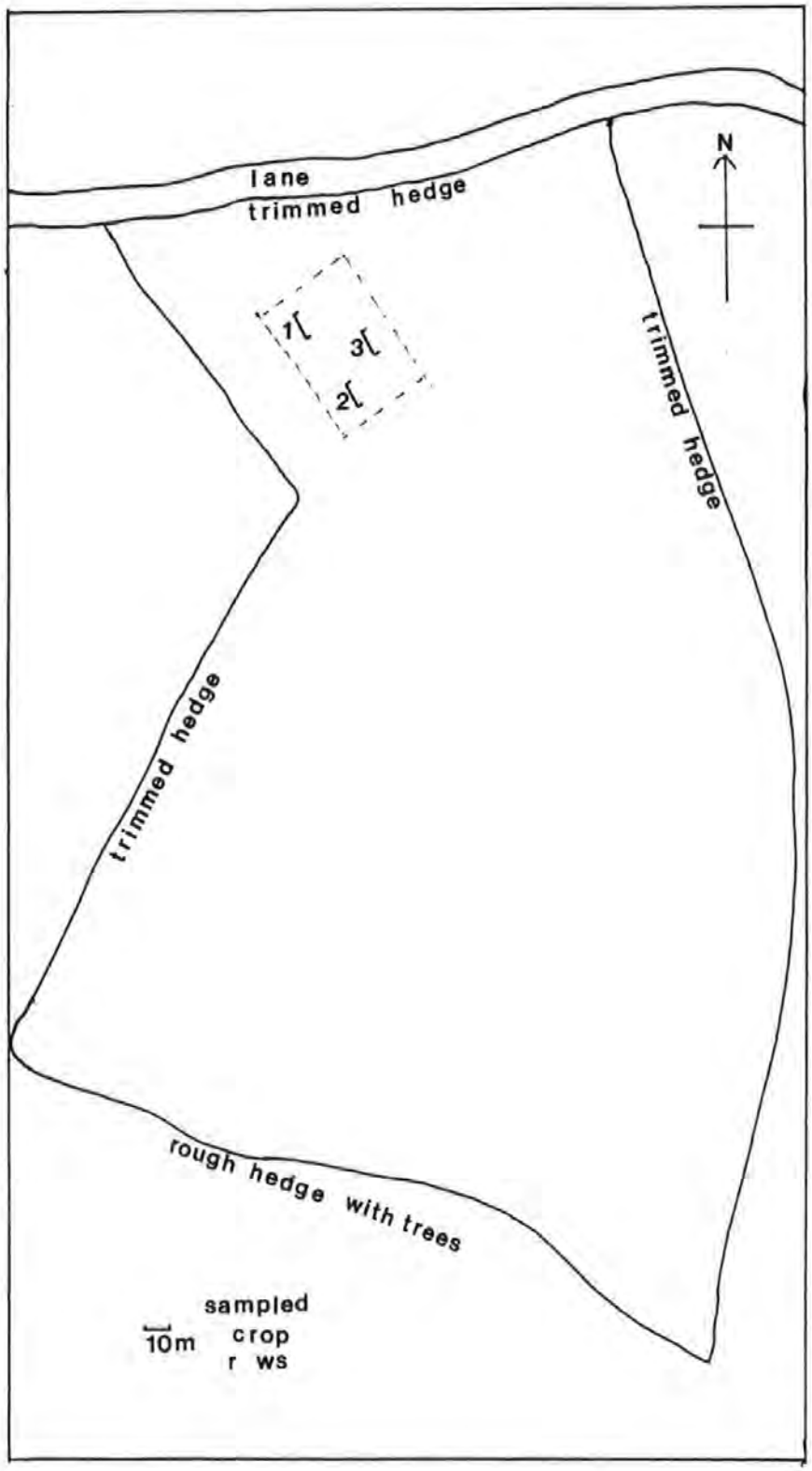
(a) Maryfield 1983



all field unsprayed

SCALE 1:2500

(c) Longwet 1984 - 1985



(b) Abbotscourt 1983 - 1984

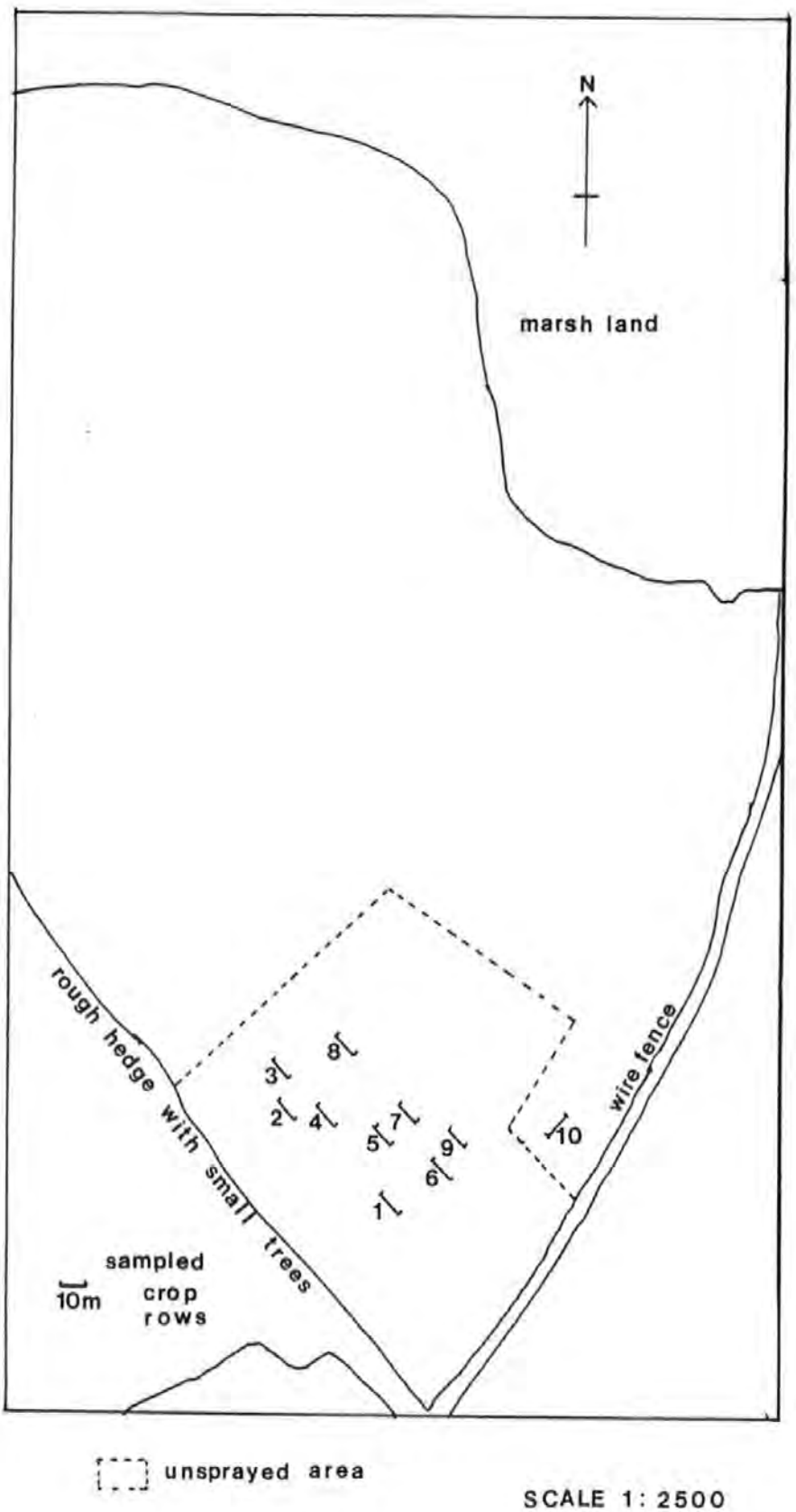


Table 4.1

Summary of Field Sampling

Year	Field	Sampling Occasions	Time Periods Aphids found in Crop		
			R. padi	S. avenae	M. dirhodum
1983	Maryfield	21 25.1.83 - 30.6.83	25.1.83 - 25.5.83	1.3.83 - 14.6.83	22.3.83 - 7.6.83
1983 - 1984	Abbotscourt	39 10.10.83 - 31.5.84	10.10.83 - 31.5.84	4.11.83 - 31.5.84	10.10.83 - 22.11.83 30.3.84 - 31.5.84
1984 - 1985	Longwet	33 12.10.84 - 31.3.85	12.10.84 - 31.3.85	12.10.84 - 11.12.84 14.1.85 - 1.3.85	None Found

which permitted all farming operations to proceed unhindered.

Sampling.

In each year, a tape measure was first secured at each end of the row and run alongside the soil adjacent to the row. Each row was then sampled by kneeling on the soil adjacent to the row and closely inspecting each tiller. The position to the nearest 10mm, life cycle stage, morph and species of every aphid found was recorded by two workers (one at either end of the row). Sampling efficiency was checked by each person searching the same section of row on two rows, on four occasions. Comparison of records confirmed 100% agreement.

In year three, any aphids found were carefully transferred to an adjacent leaf and the source leaf was placed in an appropriately labelled plastic bag for subsequent analysis using ELISA (Chapter 3, Section 3.4) and deepfrozen. In years one and two, 10 rows were originally sampled, but in year two this was reduced to 5 rows due to time constraints. In year three, 3 rows were sampled in total. Sampling of all rows continued every 3-4-7 days throughout.

Weather records

Weather records were obtained where necessary from R.A.F.Mountbatten Metereological Station (See Fig. 1.3 for location), 9 km East of Anthony Estate.

4.3.4. Results

Practical aspects and observations

1. Although external factors rarely interfered with sampling, fieldwork was not considered practicable when snow covered the ground, in storms or heavy rain.

2. Due to the constant trampling of rows adjacent to one side of

the sampled crop rows, a different microclimate undoubtedly developed along this side, but it was not possible to measure the effect of this.

3. By the end of November, growth of the crop was such that overlapping of the leaves occurred across adjacent crop rows. The tillers became "bushy" and sampling took considerably longer. Obviously movement of apterae across rows via leaf bridges could now occur.

4. On very windy days in the winter (>20 m.p.h. winds), aphids were found at the base of leaves, in the centre of the plants.

5. When there was frost on the ground and on the leaves, and the previous night temperature had been -5 ^{o}C (e.g. 20.1.84), the few aphids found appeared to be dead. This agrees with Williams (1984), who suggests that below -5 ^{o}C, mortality occurs.

6. M. dirhodum adults were easily dislodged.

7. M. dirhodum nymphs collect on the midribs of cereal leaves.

8. Continual removal of leaves throughout the growing season from the rows sampled 1984-1985 did not appear to adversely affect the crop. It appeared to be the same height as the rest of the crop in the field (although this was not tested statistically).

9. In late winter/early spring of 1984 the weather was very dry. Over all the farm the wheat leaf tips developed reddening. This was not taken to be an early appearance of BYDV since the reddening was completely uniform, and also seen in other wheat crops in Devon.

10. First instar nymphs were difficult to find singly (length 1mm), and were most often found in groups of three or more on the underside of leaves.

11. The densities of aphids found by sampling in this way were very similar to those found by other workers (Kendall pers. comm, Hand 1982).

12. A low level of parasitism was observed in all three years (<1% aphids found were mummies).

Table 4.1 shows the presence of the three main cereal aphid species on the wheat crops sampled. Appendix 3 summarizes the data collected over the three years of sampling.

Maryfield was not sprayed with aphicide as the crop was late sown (Section 3.2), whilst large numbers of R. padi found in barley on the farm (up to 30 per tiller at Abbotscourt), together with ADAS recommendations for this and the following year resulted in aphicide applications in November in both fields except in the experimental area.

R. padi was consistently found in most abundance over the three years. As most data was therefore available on this species, it was decided to concentrate investigations into the nature of the movement of R. padi. Also, it is the most common BYDV vector.

As field sampling continued during the course of the project, it became obvious that not every sampled crop row yielded enough data for subsequent analysis. To aid decision as to which crop rows to use for further analysis, the following preliminary steps were taken :-

1. First instar nymphs were eliminated from aphid counts. They had been observed to occur mainly in stationary groups of three or more, feeding, which could tend to make distributions appear more contagious, and create "illusionary" patches of aphids.

2. The most appropriate life cycle stages to reflect aphid

Figure 4.2

Distribution of R. padi Adults, Alates and 2nd - 4th Instar Nymphs along sampled Crop Rows at Abbotscourt, 1983 - 1984, and Longwet, 1984 - 1985

x axis = months

y axis = section of row, ie

1 = 0 - 0.99 m

2 = 1 - 1.99 m

3 = 2 - 2.99 m

4 = 3 - 3.99 m

5 = 4 - 4.99 m

6 = 5 - 5.99 m

7 = 6 - 6.99 m

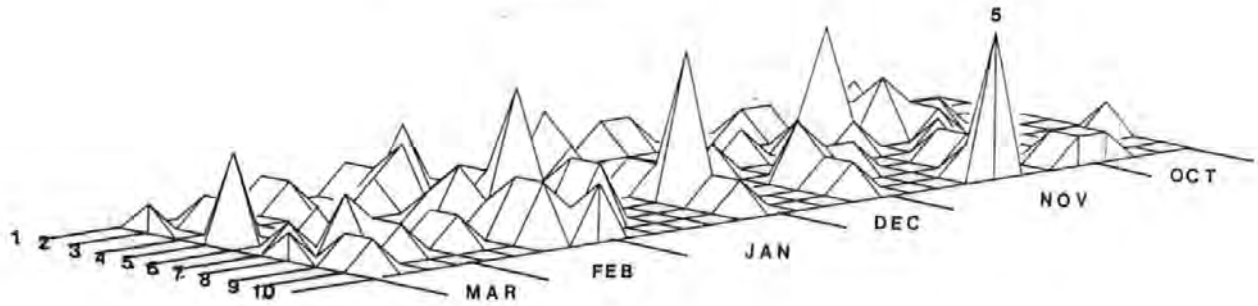
8 = 7 - 7.99 m

9 = 8 - 8.99 m

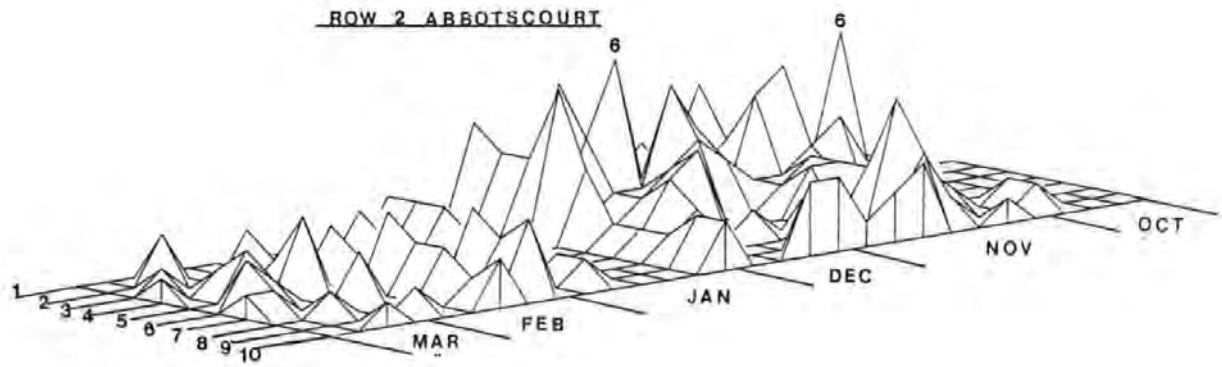
10 = 9 - 10 m

z axis numbers refer to peaks on each graph.

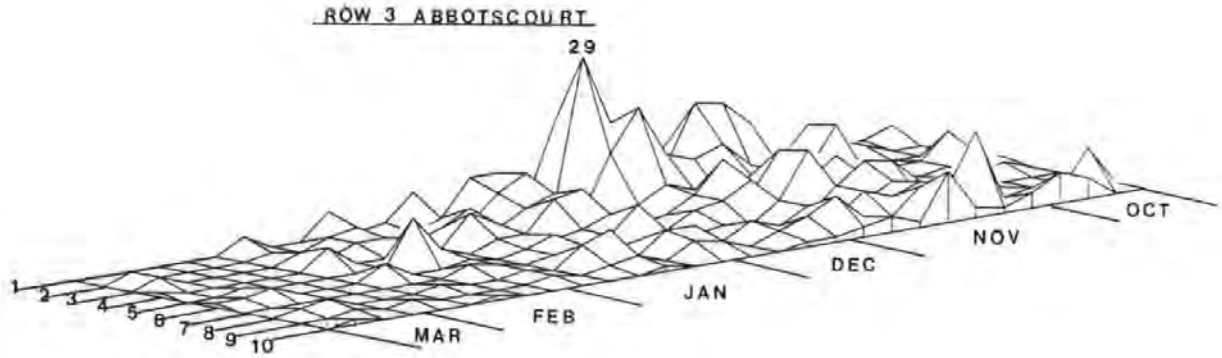
ROW 1 ABBOTSCOURT

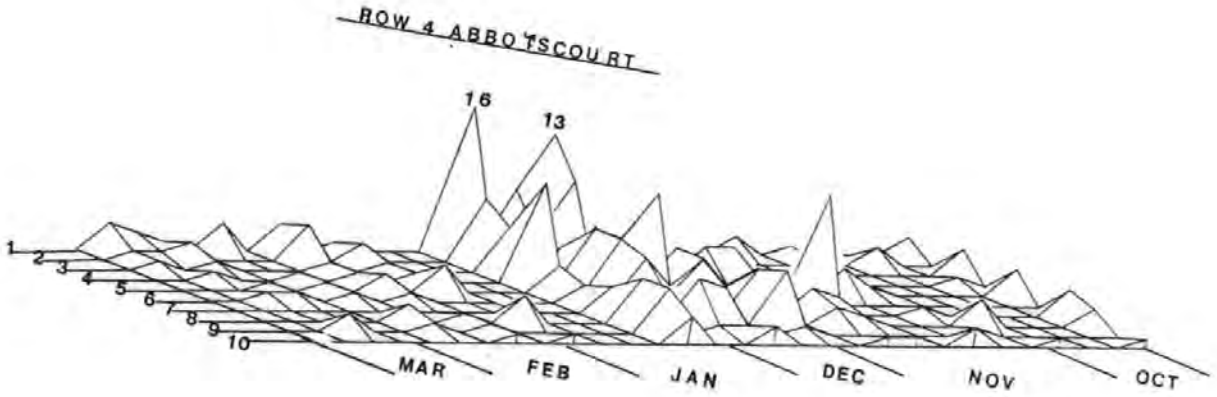


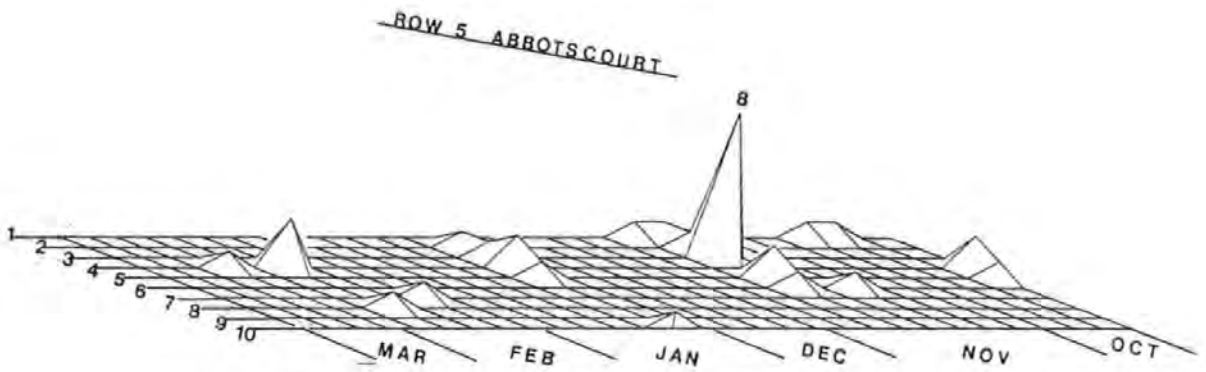
ROW 2 ABBOTSCOURT



ROW 3 ABBOTSCOURT




ROW 4 ABBOTSCOURT
16
13
1
2
3
4
5
6
7
8
9
10
MAR
FEB
JAN
DEC
NOV
OCT


ROW 5 ABBOTSCOURT
8
1
2
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4
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8
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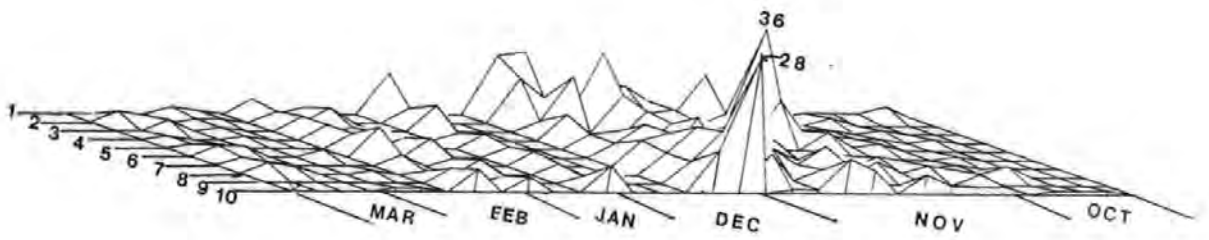
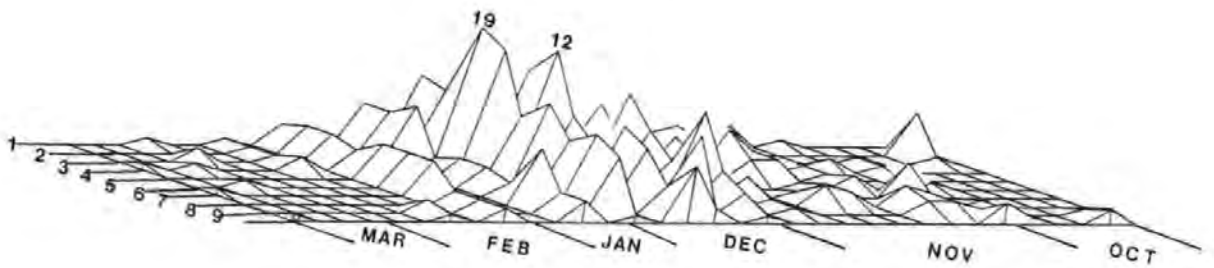
10
MAR
FEB
JAN
DEC
NOV
OCT

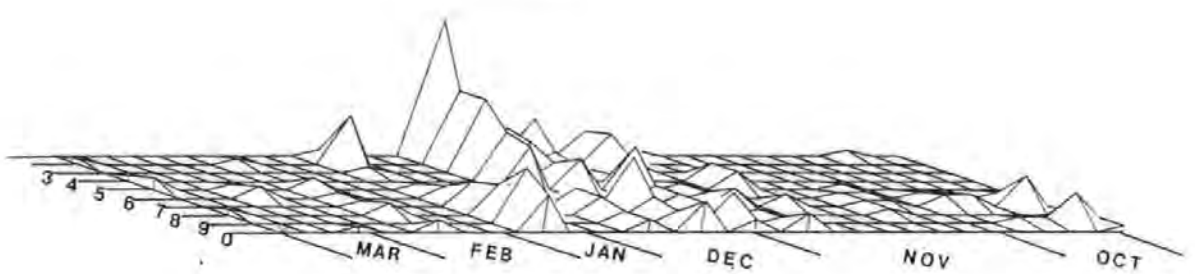
ROW 1 LONGWET



ROW 2 LONGWET



ROW 3 LONGWET



population movements and secondary spread, generally, were alates (the initial sources of infection), adults, second-fourth instar and fourth alatiform instar nymphs.

The numbers of these stages found in each 1m section of each 10m sampled crop row (0-0.99m, 1-1.99m etc.) were totalled for each sampling occasion and plotted on 3 dimensional graphs (Figs. 4.2. a-b). Although Maryfield was regularly sampled in year one, with such low numbers of R. padi (maximum 5 aphids per 1m section of row on 10 March 1983), further investigation of secondary spread at Maryfield was impossible. However, the data did confirm the contagious or "patchy" distribution of R. padi aphids in the cereal crop, and also illustrates that reproduction occurs in S. avenae and R. padi throughout the winter (Smith 1981). In year 2 at Abbotscourt, rows 2-4 appeared to contain enough data (Fig. 4.2). In year three at Longwet, rows 1 and 2 had possibilities for October-March, and Row 3 for October- December (Fig. 4.2.a). The three dimensional plots serve to confirm the initial contagious distribution of R. padi individuals along cereal rows, which may tend towards uniformity as the winter continues.

The original distribution data (unpooled) was used to identify "patches" of aphids, and first instar nymphs were included (as they do form the initial source). A variety of methods were used to investigate apterous aphid dispersal along rows 2-4 at Abbotscourt and rows 1-3 at Longwet.

The use of sequential histograms

Figs. 4.3a & b are examples of periods within the sampling programmes at Abbotscourt and Longwet when patches of aphids were seen to develop and then disperse along the sampled crop row. The histograms were drawn for every occasion for every row, but examples only are presented here. The plots did reveal a number of points relevant to interpretation of the data :-

a) Alate inclusion did not aid patch identification. In many cases, single alates were not followed later by colonies of first instar nymphs in the same plant position, and also their locations may be the result of disturbance due to sampling technique.

b) R. padi individuals have been shown to move into the soil at low temperatures, and to move vertically to the tops of tillers at higher temperatures on sunny days (Bassett pers. comm.), so it is possible that some underground movement may occur along crop rows. The observed movement of R. padi in commercial crops could be a product of a variety of types of movement (along rows, underground, across leaf bridges etc.).

However, some conclusions can be drawn about the aggregated distributions of apterous R. padi as patches of aphids, and the subsequent spread of the apterae along the rows.

Abbotscourt 1983-1984

Row 2

On this row, aphid distribution was consistently aggregated into two broad areas until 17th February, when distribution became more uniform.

Figure 4.3(a)

Sequential histograms of R.padi individuals on row 3 at Abbotscourt

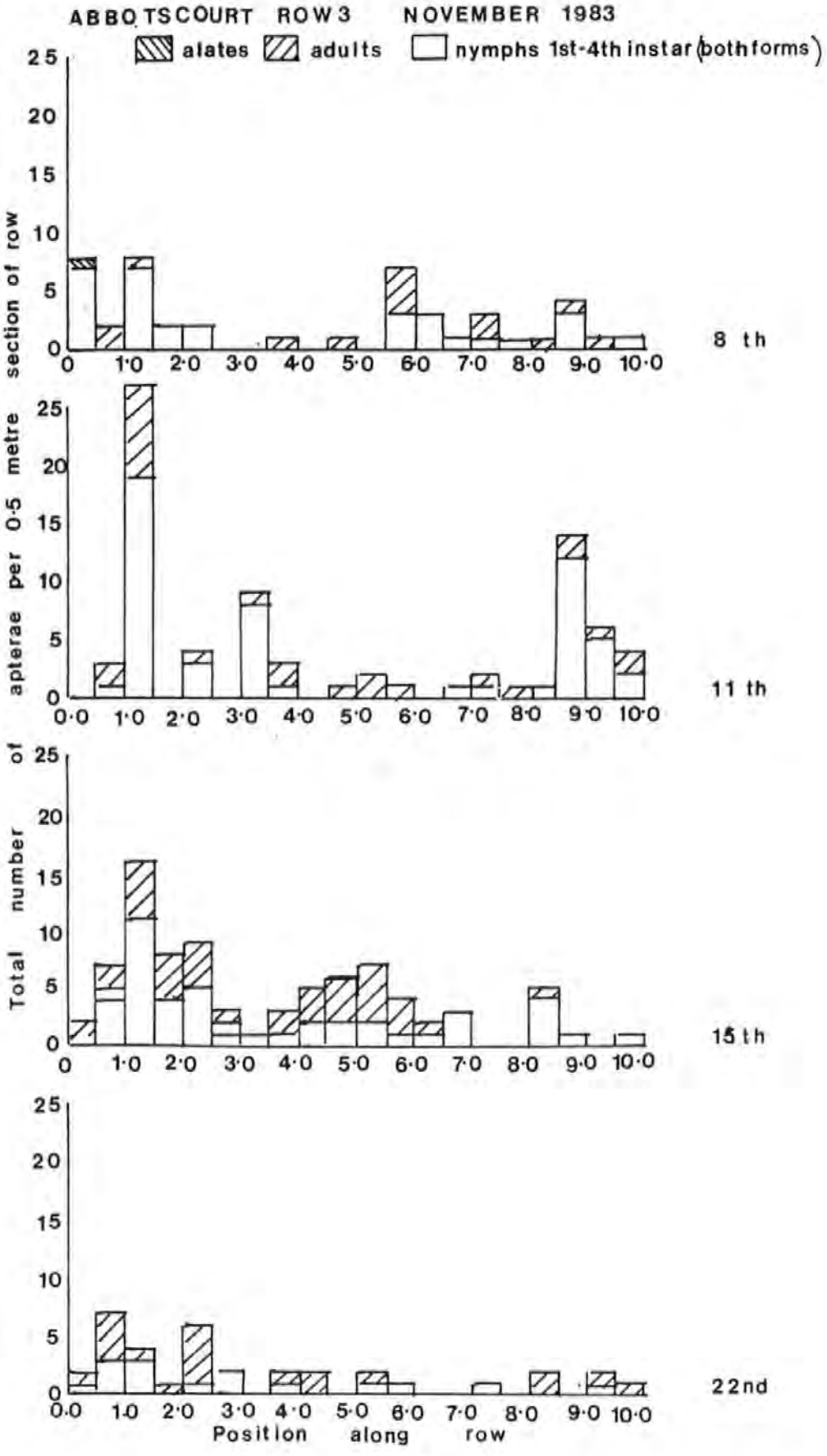
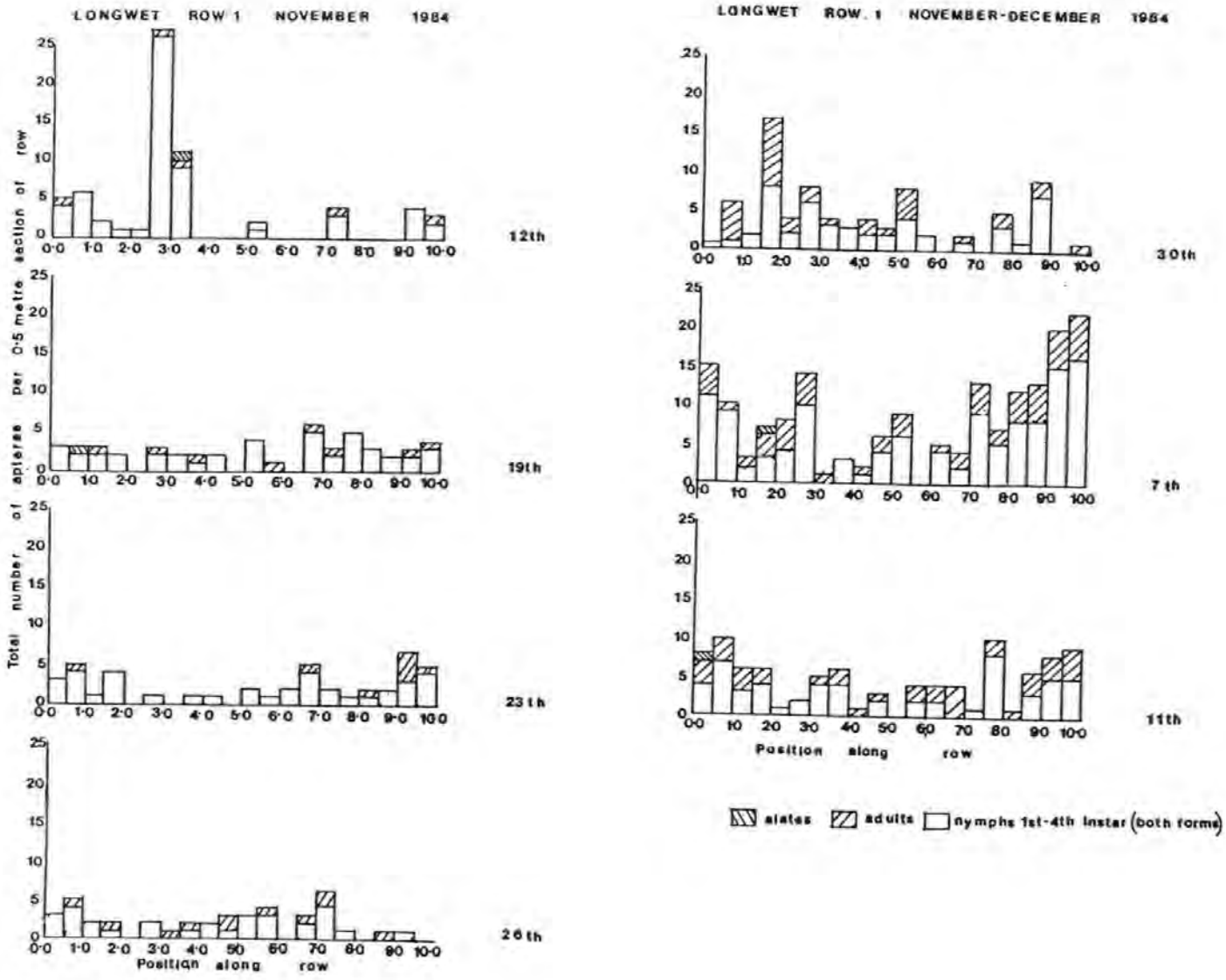


Figure 4.3 (b) Sequential histograms of R.padi individuals on row 1 at Longwet



Row 3

This provided most data. Fig. 4.3a illustrates the development of a patch in the 0-2m section of row from 8th-22nd November. By 27th December (occasion 15) the distribution of apterae was far less aggregated and had tended towards uniformity. A further patch developed and dispersed from 27th April -15th May.

Row 4

On 16th December, three broad patches of apterae could be identified, 0-2m, 2.75-6m and 6.5-10m, which had dispersed into a more uniform distribution by 27th December.

Longwet 1984-1985

Row 1

This row provided most data. Between 2nd and 5th November, 28 first instar nymphs disappeared from the 8.5-9.5m section of row, and this could be due to predation. Aphid distribution remained aggregated into patches of varying sizes throughout November and early December, as Fig. 4.3b shows. By January though, this distribution was far more uniform. The distribution remained fairly uniform until the end of March, with slight aggregations around the 1.5-3.5m and the 8-10m section.

Row 2

Aphid numbers on this row remained very low throughout the sampling period (Appendix 3A). On 3rd December, four weak aphid aggregations could be seen across the row, which had become more uniform by 31st December.

Row 3

On this row aphids were found in low numbers in isolated

groups until 26th November (occasion 13) when patches were seen to develop in the 0-5m and 8-10m sections of row. These persisted until 25th January (occasion 23). After this time, numbers remained really low until the end of sampling.

In all three rows at Longwet, the aphid populations were visibly reduced following the severe winter of January-March 1985. Although this inevitably reduced the sampling programme achieved at this time, the data collected reflects the processes of mortality occurring in the field to R. padi.

Table 4.2 summarizes the possible patches of 10 or more aphids in total identified by visual interpretation of the sequential histograms, and states their persistence over time. It was decided to investigate the development and spread of these patches in greater detail to increase understanding by the following methods.

1. The use of probability paper.

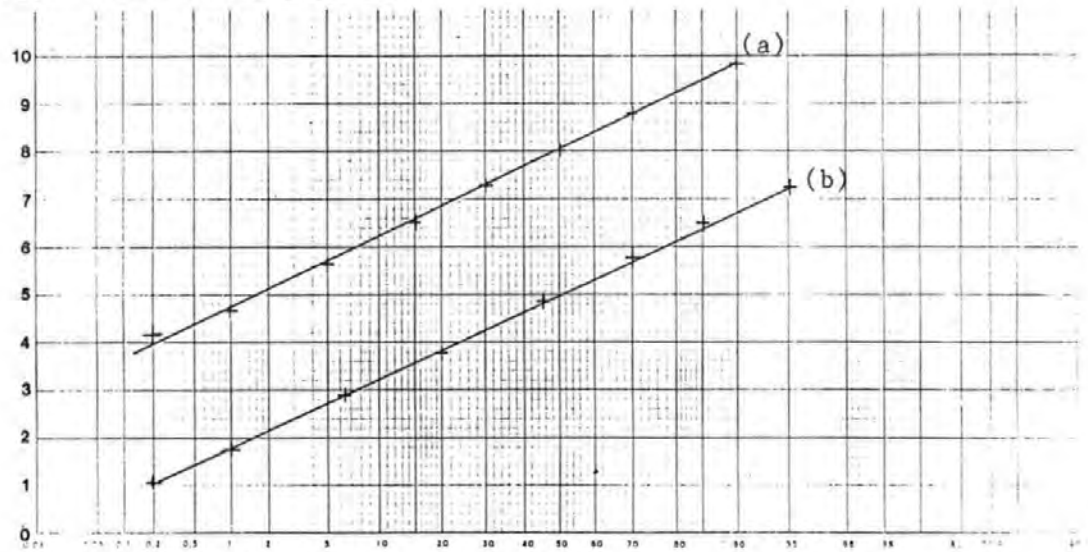
Probability paper tests the normality and uniformity of a set of samples, and reveals any polymodality in the data (Southwood 1978). In this investigation, it is being used to ascertain the distribution of apterous aphids along sampled crop rows, to identify the development of aphid aggregations into patches, and to follow the temporal progress of these patches. Cumulative percentages of total aphids present are plotted against distance along the row. If the distribution was random or regular along the row, then a sigmoid curve would be produced -Fig. 4.4b.

If the distribution was normally distributed, with the mode half way along the row, then a straight line would be produced, with

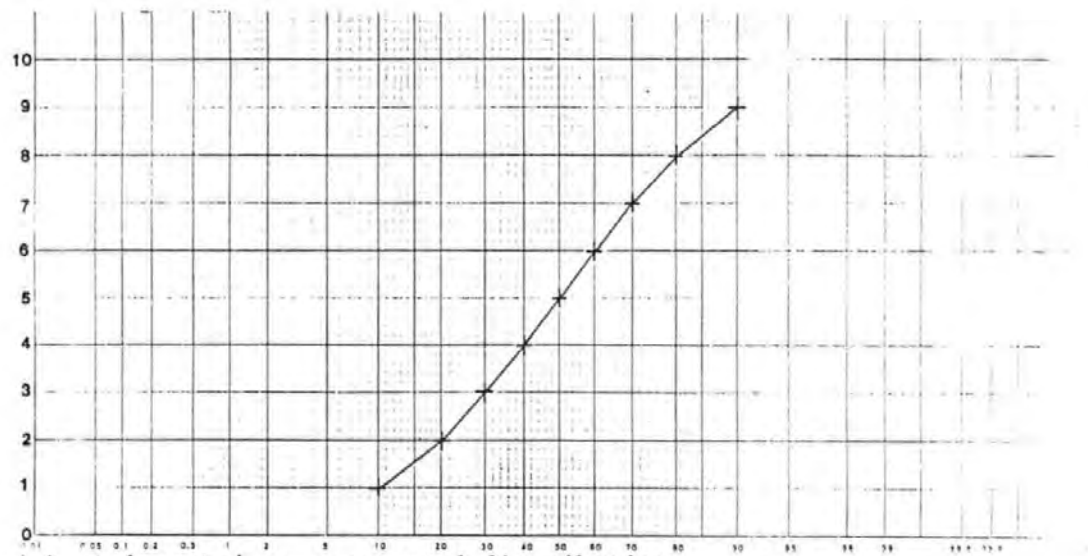
Figure 4.4

Examples of different distributions on probability paper

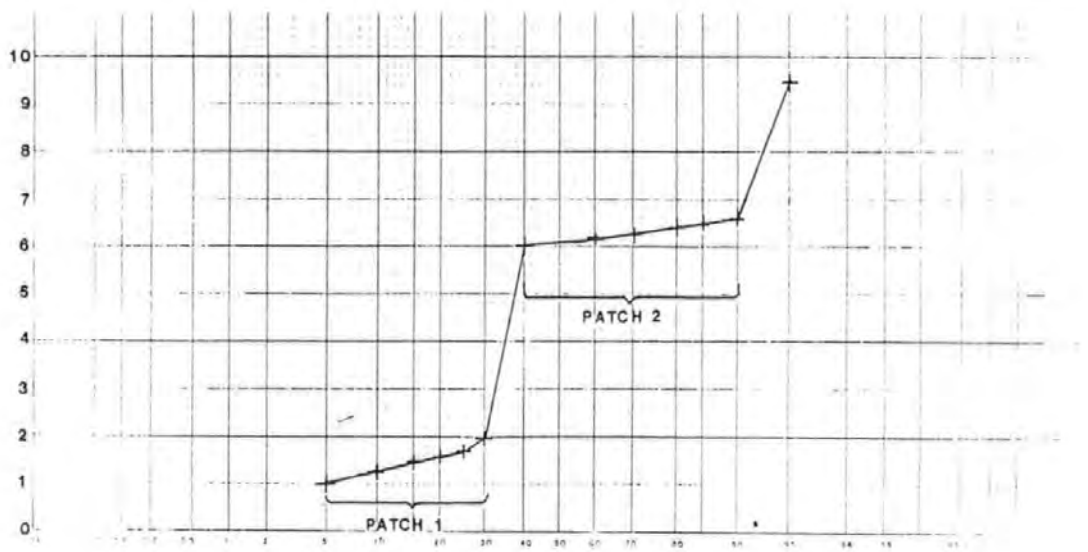
(a) A random distribution



(b) A normal distribution



(c) A 'patchy' or aggregated distribution



the mean at the 50% mark (line a, Fig. 4.4a.). If the mode was at 8m along the row, then line b would be produced.

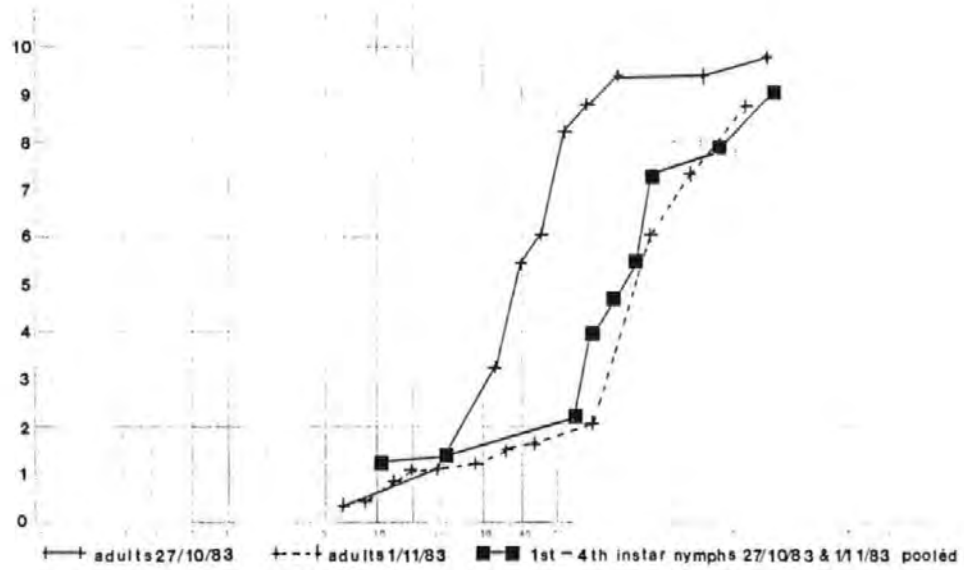
If the distribution was concentrated into one or more "patches", then a more complex curve would be produced. -Fig. 4.4c. The more horizontal sections of the plot correspond to patches in which aphids are normally distributed. The gradient of the slope of these sections is related to degree of aggregation.The more aggregated, the lower the gradient. In Fig. 4.4c, the near vertical sections of the curve correspond to a section of crop row where the distribution is more uniform or where aphids are absent.

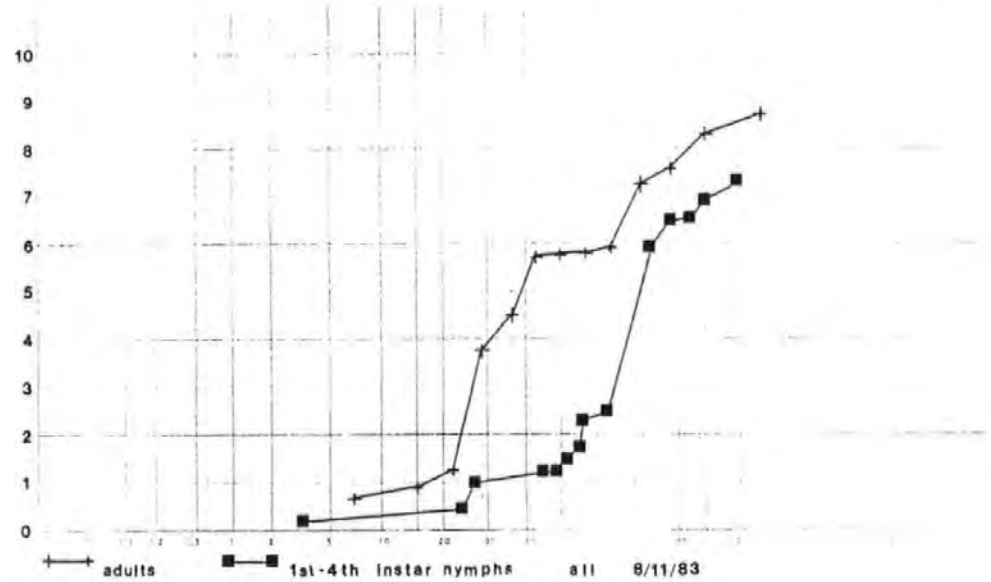
Therefore, if cumulative percentage of aphids is plotted against position along the row for each sampling occasion of each row, then the shape of the resultant plots should reveal the location and size of patches of aphids along the row. If the shape of the probability plot alters with time to a more uniform distribution, as in Fig. 4.4a, then spread of apterae along the row is assumed to have occured.

Plots were produced for each life stage of R. padi for the rows identified in 1 above, as containing potential patches for subsequent analysis. Life stages were treated separately as there was no justification for combining them, as distributions are undoubtedly different. Preliminary plots showed that at least eight positions were necessary to produce a meaningful probability plot. Therefore it was decided to pool individuals across sampling occasions where numbers were low. This was felt to be acceptable in some months when the distribution along the row clearly had been seen from the sequential histograms to remain very similar, but not when it had obviously changed. A selection of the probability plots

Figure 4.5

Distributions along row 3 at Abbotscourt 27 October - 27 December 1983





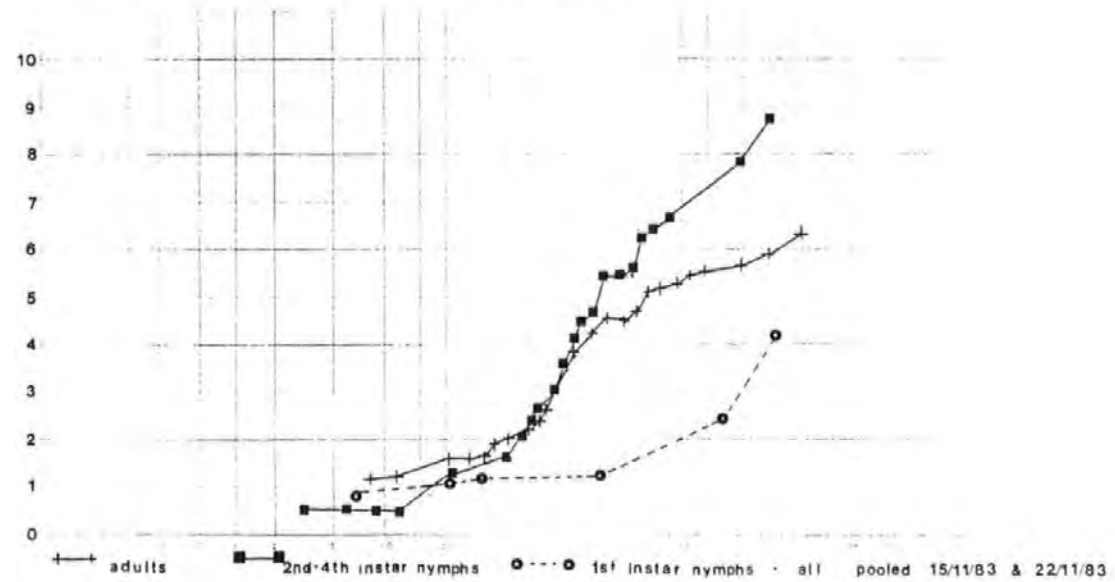


Table 4.2

Visual Identification of apterous R padi 'patches' from Sequential Histogram

Field	Row	Original Extent in m.	Final Extent in m.	Duration in Time	Patch Number
Abbotscourt	2	2 - 4.5 m	0 - 5 m	1 November - 13 December (sampling occasions 5 - 13)	1
	3	0 - 2.5 m	0 - 5 m	1 November - 27 December (sampling occasions 5 - 15)	2
	3	1.5 - 4.5 m	0 - 5 m	18 April - 15 May (sampling occasions 32 - 38)	3
	4	0 - 2 m 2.75 - 6 m 6.5 - 10 m	0 - 10 m	16 December - 10 January (sampling occasions 14 - 17	4
Longwet	1	2.5 - 3.5 m	Difficult to define	12 November - 16 November (sampling occasions 9 - 11)	5
		8 - 10 m	5.5 - 10 m	16 November - 14 January (sampling occasions 11 - 21)	
		1.5 - 2.5 m	1.5 - 3.5 m	16 November - 14 January (sampling occasions 11 - 21'	
	3	0 - 3 m	0 - 3 m	26 November - 25 January (sampling occasions 13 - 23)	6
		6 - 10 m	4.8 - 10 m	11 December - 25 January (sampling occasions 17 - 23	

obtained for the selected rows are presented in Fig . 4.5.

Fig. 4.5 shows the development of a patch in the 0-5m section of row 3 at Abbotscourt, from sampling occasion 5-15, with similar distributions for adults and 1-4th instar nymphs. On occasion 11, sufficient 1st instar nymphs were found to permit a probability plot on their own, and 80% of all individuals were found in this section. By occasion 15, distribution was more uniform.

Use of the probability plots confirmed the contagious distribution of R. padi apterae in the cereal fields sampled in 1983-1984 and 1984-1985, and suggested that the patches numbered in the last column of Table 4.2 merit further investigation.

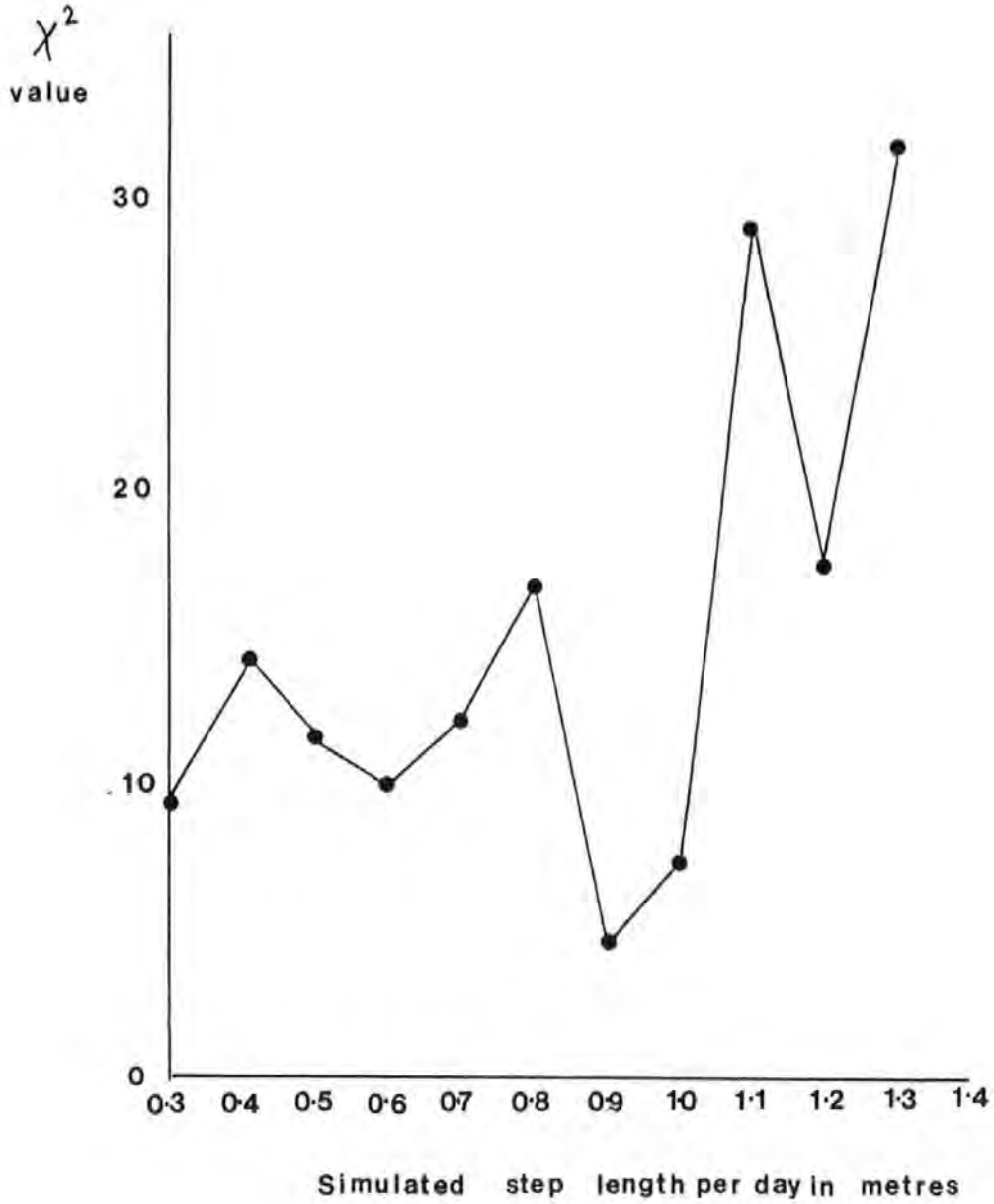
2. Simulation modelling of apterous aphid movement.

To attempt to estimate aphid dispersal rates, a simple computer simulation model written in Fortran77 was used. The model makes the following assumptions :-

1. Mortality or disappearance from the sampled crop rows is density independent. If it were density dependent then dispersal would be overestimated (see discussion).
2. There is a constant movement rate, i.e. step length per day.
3. Adults and the 2nd -4th instar nymphs have the same step length.
4. First instars present at the start of a simulation run are available to disperse on the 5th day and are then included in the total number of dispersing adults and other larger instar nymphs as dispersing agents. For simulations of less than 5 days, first instars were not included in the final totals for analysis. This is based upon field observations obtained in Section 4.5, where individual colonies of newly deposited first instar nymphs were seen to develop into second instars after five days in November- December

Figure 4.6

χ^2 values obtained in the simulation run on row 1 Longwet, 23 - 26 November 1984



at Skardon Place.

5. All movements are described by a random-walk process.

The distribution of aphids along the sampled crop row had to be clearly aggregated into a patch at the start of the simulation.

The computer program, and an example of the output obtained are in Appendix 4A. Each clearly identified patch, obvious in interpretation of the earlier methods (Table 4.2), was divided into its constituent sampling occasions and twelve simulations were run on each period using a range of step lengths between 0.1 and 1.4m per day. The program moved aphids from the initial observed distribution to produce a final distribution.

The "goodness of fit" of each simulated final distribution was then tested with that obtained by field sampling using a Chi-squared test. This was based on numbers of aphids per 1m section of row and the expected numbers for comparisons were the model outputs. Thus Chi-squared values were produced for each step length for each distribution, the lowest Chi-squared values corresponding to the most likely step length of the aphids. Fig. 4.6 illustrates this graphically. To further refine dispersal estimates, 10 simulations of the step length per day that produced the lower Chi-squared values were subsequently run and compared, as above, before the dispersal rates in Table 4.3 were arrived at.

The dispersal rates varied throughout the sampling time periods, from 0.1m/day on Row 1 at Abbotscourt from 2nd-13th December, to 1.4m/day on Row 3 at Longwet from 3rd-11th December.

However, in two data sets, the distributions obtained by running 10 simulations based on the step lengths that originally

Table 4.3

Summary of the Step Lengths per day produced by Simulation Modelling

Data Set	Patch No.	Row	Period of Time of Simulation	Step Length per day (m)	Value	Significance at 1% level	No. of Simulations
Abbots-court	1	2	2 Dec - 13 Dec	0.1	0.73		32
	2	3	1 Nov - 4 Nov	0.8	2.59		42
			8 Nov - 11 Nov	0.6	0.87		42
			11 Nov - 15 Nov	1.3	7.95		42
			15 Nov - 22 Nov	1.1	2.91		42
			22 Nov - 29 Nov	0.9	4.02		42
			29 Nov - 2 Dec	0.5	9.83		42
			2 Dec - 13 Dec	1.1	9.42		42
			13 Dec - 27 Dec	0.5	2.69		42
	3		18 Apr - 15 May	1.0	0.10		32
	4		16 Dec - 27 Jan	0.9	4.44		42
Longwet	5	1	12 Nov - 19 Nov	1.3	20.55	*	42
			23 Nov - 26 Nov	0.9	7.01		42
			14 Dec - 12 Jan	1.1	2.73		42
	6	3	26 Nov - 3 Dec	1.3	4.48		42
			3 Dec - 11 Dec	1.3	4.48		42
			11 Dec - 24 Dec	0.6	64.68	*	42
			24 Dec - 25 Jan	1.1	25.59	*	42

Mean Step Length per day = 0.893 metres

(standard error $\pm$ 0.089)

gave the lower Chi-squared values were significantly different at the 1% level. They are marked with a * in Table 4.3.

On Row 3 at Longwet from 24th December-25th January, dispersal must have occurred, as numbers were much reduced, but not one step length produced a distribution statistically similar to the observed field data. Increasing the step length per day to higher than 1.4m did not improve the "fit" either. This simulation was omitted.

The simulation model, was successful in fitting the observed data in 83% of the cases used, from sampling at Abbotscourt and Longwet.

An attempt to relate the dispersal rates to major environmental variables was made. The variables chosen should be easily obtained by growers, which is an important consideration if this work is to have any practical applications.

The variables chosen were calculated over each period for which a simulation run produced an estimate of dispersal rate. e.g. Row 2 Abbotscourt, 2nd-13 th December 1983.

The variables were :-

1. Mean daily air temperature.
2. Mean daily grass minimum temperature.
3. Lowest grass minimum temperature.
4. Mean daily rainfall.
5. Mean daily windspeed.
6. Mean daily relative humidity.
7. Maximum daily rainfall.

Because of the differences in topography between R.A.F. Mountbatten and Anthony (Fig 1.3), it was felt that the highest gust

of wind experienced at Mountbatten was probably not a reflection of that experienced at Anthony, so this was not included.

Grass minumum temperature was included as it was felt to be the most accurate representation of the temperature actually experienced by the aphids (Hand 1982, Williams 1984). It has also been shown (Williams 1984) that below $-5^{o}C$, aphid mortality is induced. Maximum daily rainfall was also included to attempt to isolate mortality. The relationships were assessed by correlation using MINITAB, but unfortunately, no environmental variable was significantly correlated with dispersal rates (Appendix 4D).

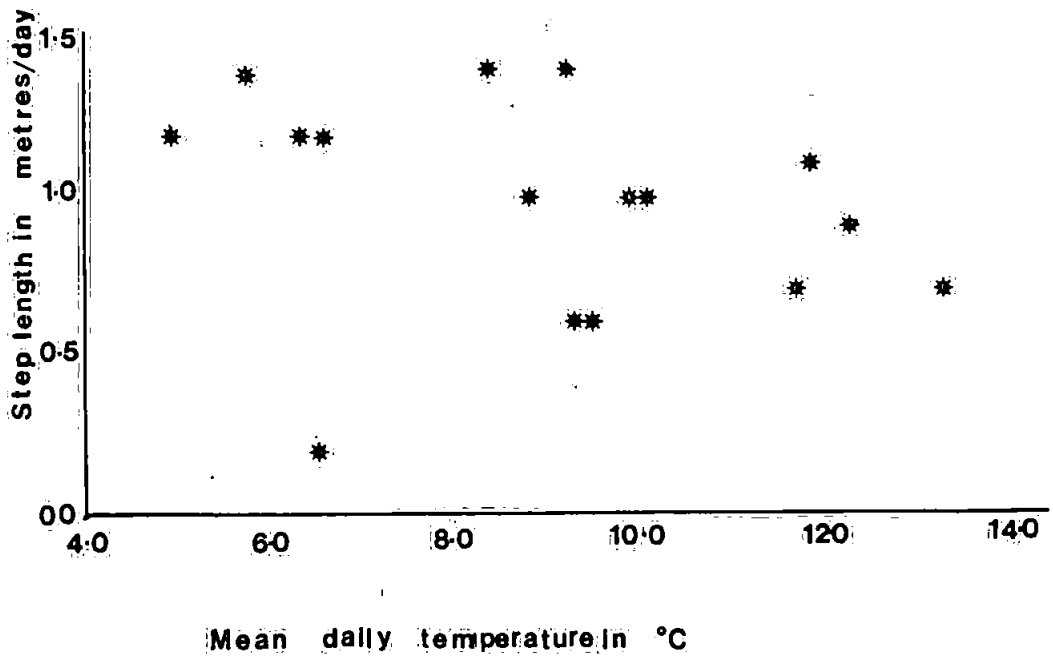
There was little variation in dispersal rate, with a mean of 0.89m per day. The results suggest that in the field, over the late autumn and winter, although temperature and other climatic factors were very variable, there was no significant effect on dispersal rate. i.e. until 25th January 1984, and 27th January 1985).

The effects of mean daily temperature (Fig. 4.7) can be explained in relation to an activity temperature threshold. In invertebrates, some functions such as flight or movement are only possible when temperature is above a certain "threshold" level. Once this threshold is exceeded, and they are moving, further increases in temperature do not appreciably affect or improve their movement. Indeed, excessive heat may inhibit any movement. This is well documented in insects (Lewis and Taylor 1974), and in cereal aphids in particular for take-off thresholds (Walters and Dixon 1982, 1983, 1984). However, there is very little field evidence on walking of insects (Section 4.5).

Given the range of dispersal rates estimated using the simulation model, it is assumed that although mean daily grass

Figure 4.7

Relationship between simulated mean dispersal rate per day and mean daily temperature



minimum temperatures were occasionally very low, i.e. -8.7° C and probably inhibited movement (Section 4.5), on the whole temperatures must have been above the "threshold" for apterous R. padi dispersal. The one exception is the estimate of 0.1m/day for Abbotscourt, Row 2 from 2-13th December, when the mean daily air temperature was 6.6 °C. Also, at Rumleigh (Section 4.5) apterous R. padi were observed to remain stationary when air temperatures did not rise above 2 °C, and such low air temperatures were not reached in either field at Anthony over the time of the simulations.

4.3.4 Discussion

Presence and abundance between years and within years.

The presence of R.padi on the crops in all three sampling seasons confirms its ability to overwinter anholocyclically and agrees with the conclusions of A'Brook (1974) George (1974), Hand (1982), Kendall (1981,1983), and Turl (1980).

S.avenae was present at Maryfield and Abbotscourt throughout the sampling seasons, but was absent at Longwet between December and January. This absence is difficult to explain. One possible reason could be that some holocyclic overwintering was occurring, as found by Hand (1982). However, this could not be verified, as S. avenae individuals, when present, were not identified to sexual morphs, and no eggs were found.
Densities of S.avenae were consistently low, at Longwet after mid November (i.e.2 or 3 per 10m row) and given the aggregated distribution in cereal fields, it is reasonable to assume that this lack of S.avenae was no more than an artifact of the method of sampling.

The presence of M. dirhodum in the spring at Maryfield and

Abbotscourt was as expected, and individuals were undoubtedly the progeny of the fundatricies of the spring migrations from holocyclically overwintering clones. This agrees with the findings of Hand (1982) and Williams (1984). However, as no M.dirhodum were found throughout the winter, there is no evidence to suggest total anholocyclic overwintering as found by Dean (1973), Singer et al. (1976) and Turl (1980). Nevertheless, the presence of M.dirhodum adult and nymph apterae at Abbotscourt in October and November must indicate some anholocyclic ity. Hand (1982) found M. dirhodum in maize, mature grassland and in non crop vegetation until December. At Abbotscourt, the previous crop had been peas. Therefore it is conceivable that the M.dirhodum could have survived on volunteer cereals or grass weeds over the summer until November, (especially as no herbicides were applied against Monocotyledenous weeds). The crop was sown early, and their presence in the crop was just at the end of their lifecycle on cereals. This was not repeated at Longwet however, which had a similar cropping history.

Of the three species, R.padi was consistently the most abundant over the three sampling periods. However, numbers declined over the winter, as mortality factors exerted their effects, as found by Hand (1982), Hand and Hand (1986), Leather (1980), Smith (1981), Watson (1983), and Williams (1984), even though these workers showed R. padi to be the least "hardy". Although it is interesting to explore reasons why populations of R. padi decline steadily after January, it is not really relevant to the scope of this project, which is primarily concerned with the movements of apterae before this date, as it is in autumn and early winter that the most damaging spread by BYDV to winter cereal crops occurs.

Also, the effects of climatic factors such as rain, wind, low temperatures etc. are density independent, and so the distributions of apterous aphids will not be altered appreciably.

The distribution of all three aphid species across the fields sampled confirmed an aggregated spatial pattern. Some sampled rows were consistently good "aphid" rows, e.g. Row 3 at Abbotscourt and Row 1 at Longwet, whilst others were abandoned (Rows 6-10 at Abbotscourt), due to the paucity of aphids found.

2. Apterous aphid movement.

The three dimensional plots, the sequential histograms and probability paper plots used in this section, all enabled the distribution and abundance of apterous R. padi to be assessed graphically, and led to the suggested "patches" to be used for further investigation. A follow-on step to this was the use of a simple computer simulation model to estimate dispersal rate. It was a random-walk type model and could only be applied to aphid aggregations. However, the model was an aid to interpretation of the process of dispersal in cereal fields by apterae, and defines movement in the simplest terms. A statistical test was used to assess the "goodness of fit" of the model output. Only those dispersal rates that produced distributions similar to field distribution were used.

Secondary spread has been demonstrated along the cereal rows sampled. Any estimation can only be tentative however, since the field situation is very complex.

Three types of factor must influence the dispersal rates obtained, and should be considered at this stage :-

1. Climatic factors

As explained in Section 4.5, temperature is probably the most important environmental variable for aphids (Hand 1982). It acts directly on activity, development, reproduction and mortality (Williams 1984), and also indirectly by affecting host plant growth rates and physiology, activity of predators and parasites, and the virulence of pathogens.

As Hand (1982) showed, climatic variables are difficult to interpret singly. Adverse weather conditions such as snow and cold are just as detrimental to aphid populations as a combination of high winds, gales and very heavy rain, though the actual effects may be different (e.g. melting snow may drown aphids, whilst high winds knock them off the plants possibly causing physical damage).

Longwet field was far more exposed to the prevailing Southwest to West winds than Abbotscourt field, but Abbotscourt was North facing and frost took longer to clear on winter mornings. These inter-site differences may be important.

Short bursts of sunshine have been shown to stimulate reproduction in R. padi (Smith 1981), but subsequent development rates may be very slow due to very cold temperatures.

Numbers of aphids may appear low, and therefore secondary spread may have appeared to have ceased along a crop row simply because the previous night temperature had been low enough to induce movement into the soil (if this actually does occur, see Section 4.6) (Bassett pers. comm.).

It is important to remember that any climatic variables are likely to exert their effects in a density independent manner

2. Host plant factors

BYDV presence in plants has been shown to produce larger viruliferous individuals (Olupomi 1981), which may be capable of dispersal over larger distances. Crop nutrition and quality may not have been uniform across the crop, either due to heterogeneity in the field (soil, fertilizer etc.). This could explain the very different dispersal rates obtained at Abbotscourt over the same time period of simulation on Rows 2 and 3 between 2nd- 13th December (Table 4.4).

3. Natural enemies.

Simulation modelling produced rather large dispersal estimates as compared with laboratory studies. The effects of natural enemies on dispersal were not investigated. The investigation at Rumleigh Experimental Station (Chapter 2) revealed that surface- active polyphagous predators are present on wheat crops in autumn and early winter. Indeed, Staphylinidae were observed at Abbotscourt in November climbing plants and on the ground. It would be reasonable to assume that some of the losses in aphid populations were due to predation. If mortality were density-dependent, this could result in the removal of the centre of a "patch" between sampling occasions and the consequent misinterpretation of the later distributions. There is some evidence to suggest that some polyphagous predators exert mortality in a density-dependent manner (Bryan and Wratten 1984). It is reasonable to assume that the winter present polyphagous predators act in the same manner.

However, the presence of polyphagous predators could result

in increased dispersal of apterae, and therefore increase secondary spread of BYDV by inducing them to release alarm pheromones, as found bt Roitberg, Myers and Frazer (1977) in pea aphids. These aphids tended to disperse more after disturbance by Coccinelidae.

Field observations suggest that most movement occurs around the late morning/mid-day. This may be a response to temperature, but moving at this time of day may also enable avoidance of many nocturnally active polyphagous predators (Vickerman and Sunderland 1975, Williams 1959).

In reality, the field situation is a result of the complex interaction between all these factors and the aphid behaviour. For example, heavy rain and strong winds at night could dislodge aphids, and lead to an increased level of dispersal and predation.

Further fieldwork was obviously necessary. The experiments in Section 4.4 were therefore designed to study apterous aphid dispersal in more controlled environments, where fewer interacting factors existed.

If the range of step lengths produced by simulation are not overestimates, it would appear that apterae are very mobile. Dean (1973) found that apterae of S. avenae and M. dirhodum rarely remained on tillers of spring barley and oats longer than about two days, whilst colonies persisted for about a week. His experiments led to mean diplacement estimates for apterae dispersing from artificial colonies of Ø.6-Ø.8m /day. These are clearly similar to those observed here for R. padi, but again, predators could have influenced results.

Greaves et al. (1983) found that BYDV patches of "foci" in winter cereal fields varied between 1-6m in diameter. Unfortunately,

no aerial photographs of the fields used for sampling in this project were available, so no measures of patch diameters were made but they were erved to be of a variable size. Whilst dispersal rates were obtained by simulation and by direct observation (up to 0.3m in 2 days) in Sections 4.3 and 4.4 such a range of dispersal rates could account for the variability in BYDV patch size. However, virus transmission is not a simple process. The results obtained from sampling in commercial wheat crops have confirmed some assumptions about secondary spread of BYDV, and have provided some evidence of the process. They have also illustrated the difficulties of overwintering fieldwork (aside from the adverse weather conditions for the research workers!):-

1. Low densities of aphids found per 10m crop row per sampling occasion.
2. Virus symptom expression not visible until the following late spring, so there is no evidence of dispersal available at an early stage.
3. Achieving the balance between the sampling programme most suited to the aims of the research and the method of sampling achieved within the constraints of the requirements for commercial crops.
4. The sampling method used only enabled movements to be studied in one dimension along crop rows. Studying movements across rows within a commercial wheat crop was not possible, due to the amount of trampling of the crop in a square around quadrats that would be necessary.

However, some conclusions are able to be drawn from the results, and several suggestions for further work can be made.

4.3.5 Conclusions

1. R. padi, M. dirhodum and S. avenae were all present at various times between October and May on winter wheat crops at Anthony Estate farm in 1983, 1983-1984, and 1984-1985.

2. The dispersal rate of R. padi was simulated in a simple computer simulation model, and was found to be between 0.1m and 1.3m per day.

3. The variability in dispersal rates was not significantly correlated with the weather factors tested.

4.3.6 Suggestions for further work.

Field investigations in unsprayed areas of commercial wheat crops in the autumn should continue, and should include :-

1. A simultaneous assessment of the activity of polyphagous predators by pitfall trapping, and D-Vac extraction to establish densities.

2. Subsequent examination of the gut contents of the predators , and the use of ELISA techniques (e.g. Chambers and Sunderland 1984) to establish if predation on aphids is occurring.

3. Sampling over a wide area over the winter months to locate developing patches of aphids along sections of rows, and then close observation of those individuals over 24 hour periods (using infra-red light at night) to establish if :-

a) Density-dependent mortality due to predators occurs.

b) The time of peak activity in the field over the winter.

c) The extent of vertical movements, if any, into the soil.

4.4 The release of apterous R. padi in small experimental plots of winter wheat (c.v. aquilla) to estimate dispersal rates by regular observation.

4.4.1 Introduction

Aphids collected in commercial wheat fields were used for all experiments to eliminate potential artifacts or anomalies produced by the use of colonies acclimatised to long day photoperiods and the warmer temperatures associated with laboratory cultures (Southwood 1978).

The timing of the experiments in years 1 and 2 (January-March) was determined in an attempt to facilitate isolation of an activity threshold in field conditions. Temperatures in late winter have been shown in Section 4.3 likely to be below such a threshold. Experiments conducted in November- December were likely to be above the activity threshold.

4.4.2 Aims.

1. To study dispersal of apterous R.padi under field conditions in a more detailed manner than in Section 4.3.
2. To develop the understanding of dispersal of R.padi, interplant and across rows of winter wheat.
3. To identify those factors which have most effect on dispersal.
4. To estimate dispersal from release of apterae into an "empty" environment.

4.4.3 Site descriptions

Experimental work in this Section was carried out on a total of twenty $1m^2$ plots of winter wheat (c.v.aquilla) over two winters :- 1983-1984 and 1984-1985. The plots were situated at Skardon Place

Plate 5 Small scale $1m^2$ plots of winter wheat (Skardon Place, 1984)

experimental garden in years one and two, and at Rumleigh experimental station in year two.

Skardon Place Grid Ref 481552 O.S. Sheet 261 Series M276.

This is a 0.1ha walled garden containing ornamental shrubs, trees, three glasshouses and situated 0.75km North of the Polytechnic. Plate 4 shows the experimental plots used. They were separated by paving slabs, surrounded by Clematis hedge on one side and Cryptomeria, Forsythia, Hebe deutzia and Leylandii cypress ornamental bushes on the other. Two plots had to be sited under a 6m high apple tree.

Rumleigh Experimental Station Grid Ref 446683 O.S.Sheet 261 Series M276.

General introduction see Chapter 2. The $50m^2$ experimental area used for the $1m^2$ plots of winter wheat was on a North facing gentle slope surrounded by grass paths. The metereological station is 25m to the North of the plots.

4.4.4 Materials and Methods.

1. Insect cultures.

Two insect cultures were maintained in the open air, one at Skardon Place and one at Rumleigh. Twelve seedlings of winter wheat (c.v.aquilla) were grown in 70x70mm square plastic pots in Levington's Universal Compost in a glasshouse maintained at 23^{o} C under daylight. Three weeks after sowing at Growth Stage 3.14 on the Zadoks scale, (Zadoks, Chang and Konzak 1974) they were transplanted to 70x70mm square plastic pots in garden soil, watered regularly and left to become established. They were then transplanted to the insect cages which were a modification of the culture cages used at Long Ashton Research Station. The cage dimensions were

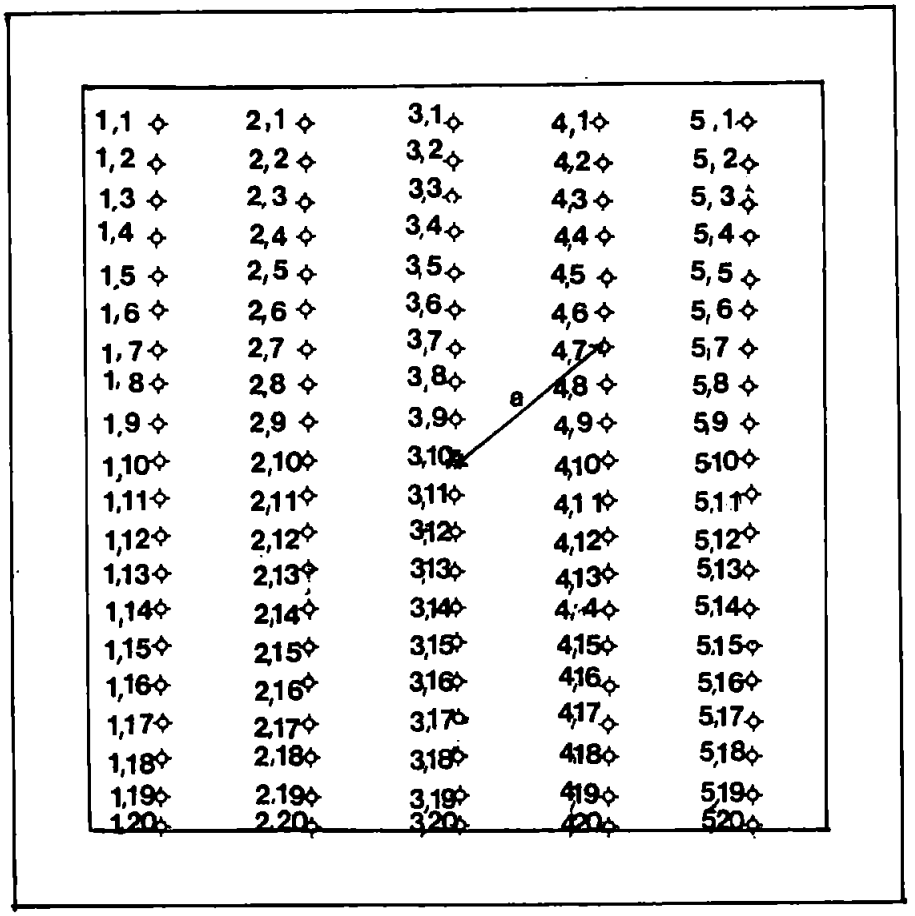
510mmx380mmx680mm, with 200x43mm wooden frames. Tops and sides were 200 μ nylon mesh (which prevents escape of 1st instar nymphs) (supplied by Simon Ltd) glued to the wood with Evostick and varnished with yacht varnish (supplied by International Paints). The bases consisted of 3mm solid perspex to which the wooden frames were screwed. These were pushed into the soil, and the cages were kept steady with bricks placed on the top frames. Access to the interior was by means of a front opening surrounded by Velcro and the front panel of mesh was edged by Velcro, providing a sealed unit. (Plate 5). Apterous R.padi were collected at Anthony early in the sampling season in Abbotscourt and Longwet field and individually placed, using a fine camel hair brush (Vanden 1972), on individual two leafed oat seedlings (c.v. Perianth) for one day (grown in 150mm diameter round plastic pots in Levington's Universal Potting Compost). They were then removed and kept sep rate on individual plants in individual "cages" in an $11^{o} \pm 2^{o}C$ room until symptoms of BYDV could be detected in the test plants, in which case any responsible aphids were killed (This is the standard transmission test used at Agricultural Research Stations). The remaining aviruliferous "wild" R.padi were transferred as above to the wheat plants in the 70x70mm square plastic pots in the insect cages. The cultures were then left to become established into colonies of at least 20 apterae per plant. The plants grew at the same rate as those in the experimental plots. Watering of the culture plants was carried out when necessary.

2. Experimental Plot Design.

In both years, winter wheat (c.v.aquilla) was sown in the plots so as to provide five rows of 20 plants, i.e. 100 plants

Figure 4.8

Plan view of $1m^2$ plot of winter wheat (c.v. aquilla) showing distance measured for dispersal estimates



◇ plant

X release point

a a typical distance dispersed

1,1etc code number of plants

200mm

arranged as in Fig 4.8, which also shows the numbering scheme used for each individual plant.

Each plot was surrounded by 110mm plastic "square section" guttering 100mm width and 50mm deep, joined by corner pieces, as plate 4 shows. This guttering was dug into the ground and carefully adjusted level with the soil surface. These gutters prevented the passage of walking polyphagous predators into the experimental plots. They were filled with water containing detergent. In 1985 at Rumleigh fluorescent circular yellow water traps were also placed amongst the crop rows, to attract any aerial predators and parasites such as Syriphidae.

At Skardon Place in 1983, six plots were sown on 24th of September, and in 1984, six were sown at Skardon Place and eight at Rumleigh Experimental Station on 18th September.

3. Experimental procedure.

a) Preparation of the plots.

Ten days before the start of the experiment, the plot was sprayed with aphox, a quick acting contact insecticide, at a rate of 0.14Kg a.i ha $^{-1}$. This was to remove any naturally occurring infesting aphids of all species. On the day of release, the plot was also hand-searched and any aphids present that had escaped insecticide were removed. Plant 3,10, at the centre of the experimental plot was removed, and a hole dug of sufficient size to allow a 70mm square plastic pot to sit in the soil with the top edge flush with the soil surface.

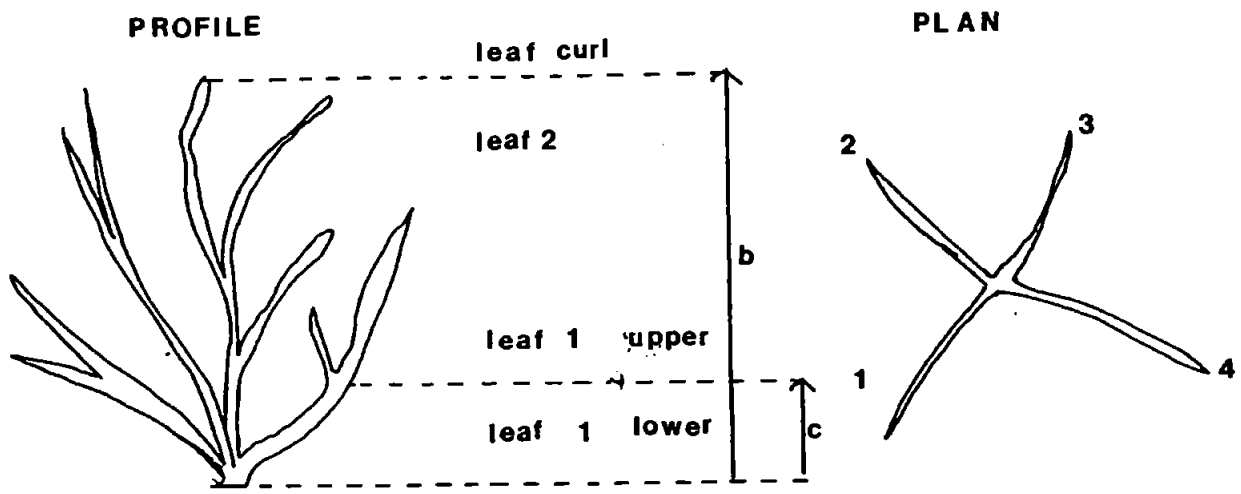
b) Sampling.

Day 1. -late afternoon or early morning

A plant was taken from the insect culture. The exact

Figure 4.9

Three dimensional location recording scheme for apterae distributed throughout the plot



b height of plant

c height of leaf 1 etc.

1-4 : Tiller number

all tillers labelled clock wise

"leaf curl": Youngest leaf

positions of all the aphids on this were recorded as below, and the plant was placed in position 3,10 in the plot.

Day 2.0900 hrs - Day 4 dusk.

Every hour during the hours of daylight the rows were hand-searched and aphids' positions were recorded according to the scheme shown in Fig 4.9 i.e. plant number, individual tiller number, leaf number, and position on the leaf, either upper or lower.

Day 4 1600-1700 hrs daylight permitting, or day 5 0900 hrs.

Aphids' final positions (in three dimensions) were recorded and they were removed using a fine camel-hair paint brush, and returned to the outdoor aphid culture. The following heights and distances were recorded from plants on which aphids had been found during the experiment.

1) Direct distance from centre of release point to centre of plant ("a" in Fig 4.8).

2) Height of all tillers from ground level ("b" in Fig 4.9).

3) Height of individual leaves ("c" in Fig 4.9).

4. Environmental monitoring.

Skardon Place

a) Year one

1. Daily maximum and minimum temperatures were recorded using a maximum/minimum thermometer positioned 1m above the ground on a sheltered wooden board adjacent to the experimental plots.

2. Daily grass minimum temperatures were obtained from R.A.F. Mountbatten Weather Station, 3km South East of Skardon Place (Fig 1.3).

3. Daily rainfall was obtained from a standard raingauge set into the soil adjacent to the plots.

4. Duration of rainfall was obtained from a tilting siphon raingauge (borrowed from Bristol Metereological office.) set into the soil adjacent to the plots.

b) Year two. Autumn.

All the above environmental variables were recorded. Some limited hourly temperatures were obtained from a max/min thermometer used for 1. above for experiments 2S3 and 2S3N, and 2S4 and 2S4N (See summary Table 4.5).

Rumleigh

Year two Winter

Environmental variables 2.- 4. were recorded at the Meterological Station 50m North of the experimental plots. Daily maximum and minimum temperatures were recorded from the inside of a standard Stevenson screen 1.5m above ground level.

In some experiments (Table 4.4) hourly temperatures were recorded using a Model D Grant temperature with three probes positioned:

(a) In the crop canopy. The probe was positioned inside a cover constructed of three 200mm plant pot saucers bolted together to leave an airflow gap between each. The interior surfaces were painted matt black, and the exterior surfaces with gloss white paint. The cover enabled the true crop canopy temperature to be recorded independent of direct sunlight (Cochran pers. comm).

(b) Below the soil surface. The probe was positioned horizontally and covered with 15mm of soil.

(c) In the soil. The probe was positioned vertically in the soil to a depth of 100mm to produce an integration of the soil temperature

to this depth. Observations at Skardon Place (experiments 1S1-1S5 and 2S1-2S4N) showed that aphids tended to move less distances when the leaves were wet or in rain. Therefore in the winter experiments in 1985, a "surface wetness" recorder was used, built at the polytechnic to a design developed at Long Ashton Research Station by Huband (pers.comm.), which uses a D.C supply from a mains transformer to record the duration of the presence of water droplets on artificial "cereal leaves".

The artificial leaf probes were pieces of leaf-shaped semi-conductors mounted on wooden sticks. These records were achieved by means of measures of the resistance generated on the semi-conductor, which was linked in to a Rikadenka chart recorder housed in a nearby garage.It was calibrated at the start of every run to read maximum when the "leaf" was covered with water droplets, and minimum when completely dry.

4.4.5 Results

Practical aspects and observations

1. In experiment 1S5, a naturally occurring apterous R.padi aphid colony was found on plant 3,1 and so only half of the plot was used for further analysis.

2. During sampling, occasionally, individuals were knocked from the plants. They were carefully returned with a fine camel-hair brush, but the effects of this experience on their subsequent behaviour is unknown.

3. It was also recognized that disturbance to the aphids by the sampling method may be of some importance in influencing the distributions obtained. Two experiments were conducted

simultaneously with a "normal" run in which distribution was only sampled at the final sampling occasion.

4. In very windy conditions (>20 m. p. h.) aphid colonies were positioned in the centre of the experimental plots at 0900 hrs on Day 1, rather than in the late afternoon the previous day. This was due to the heavy overnight losses experienced in windy conditions in preliminary investigations.

General observations.

Table 4.4 summarizes the experiments conducted and the level of environmental monitoring achieved.

1. A general increase in numbers of aphids found in mid-morning each day of sampling.

2. The most favoured positions for apterae at 0900 hrs or 1000hrs were on the undersides of leaves, or in the centre of the youngest and longest leaves at the top of each tiller. This was also seen by McPherson and Brann (1983, Pike and Schnaffner (1985), Smith (1981) and Watson (1983).

3. 1st, 2nd and 3rd instar nymphs were seen to be the most stationary life cycle stages, remaining in the same position on leaves at the hourly sampling occasions for up to 2 days. The aphids could of course also be moving away from the aggregations and returning between sampling occasions, but field observations cannot confirm or dispute this.

4. The total numbers of aphids decreased in all experiments. Fig 4.10 is an example of the numbers of aphids found at hourly intervals up to 68 hours after initial release.

Estimation of mean distance dispersed.

The plants in the experimental plot were each assigned to

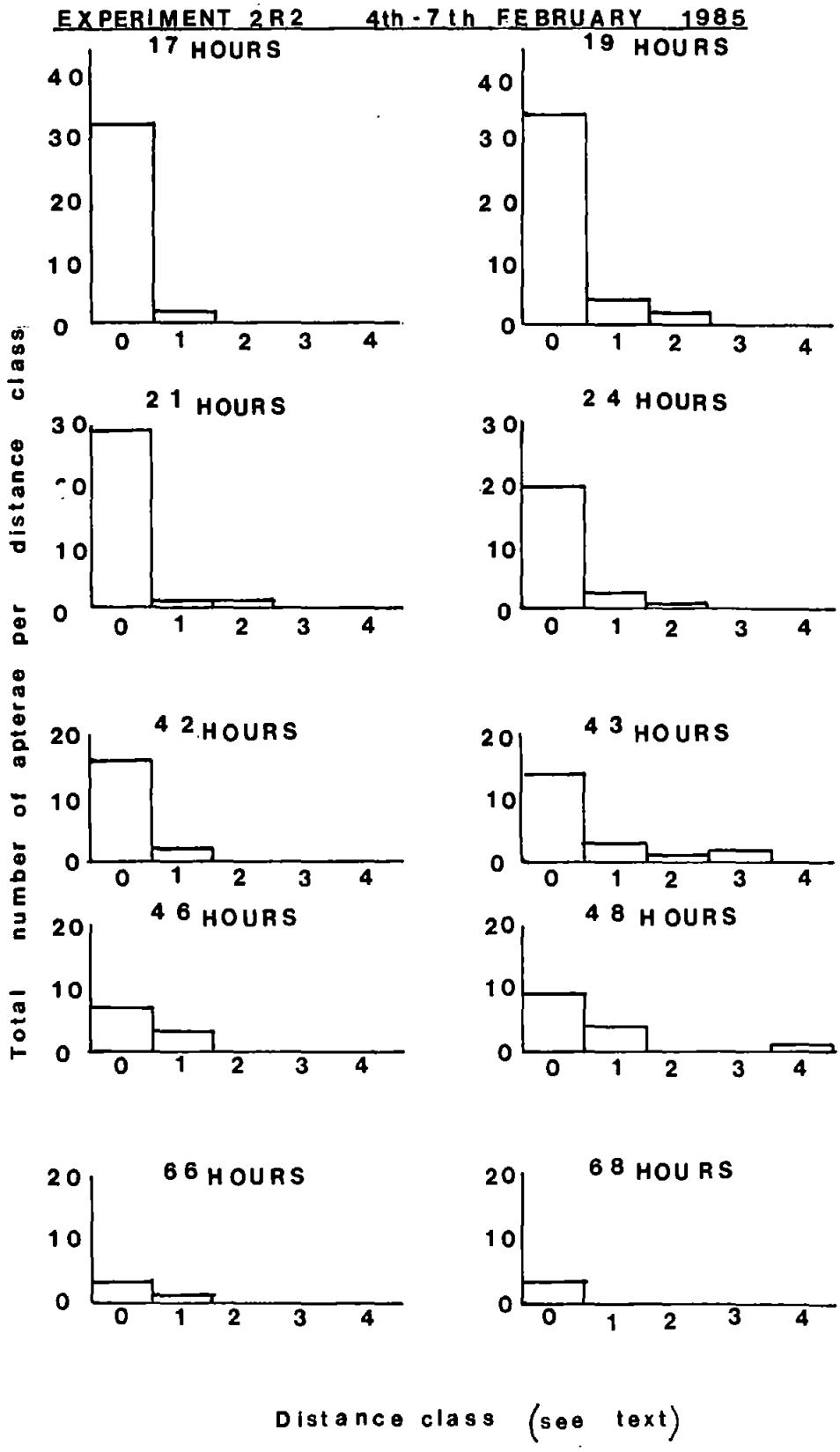
Table 4.4

Summary of Experiments on $1m^2$ Plots

Date and Time of Release	Duration of Hourly Distribution Records	Temperature Records Fh = all expt. hourly Ph = part expt. hourly	Rainfall Date	Hours of Rainfall	Aphids released Adults	Nymphs	Total	Duration of Experiment in Hours	Notes	Name of Experiment
(a) Skardon Place 1984										
17 Jan 1330	1330 17 Jan 1430 19 Jan	Daily max/min at site	18 Jan 19 Jan	5.75 3.0	30	30	60	48	Preliminary experiment	1S1
26 Jan 0930	1030 26 Jan 1000 28 Jan	Daily max/min at site	26 Jan	2.33	2	28	30	50	Observations at 90-minute intervals	1S2
7 Feb 1445	1000 8 Feb 1100 11 Feb	Daily max/min at site	7 Feb 8 Feb	0.17 0.33	3	41	44	91		1S3
21 Feb 1500	1000 22 Feb 1200 25 Feb	Daily max/min at site	22 Feb 23 Feb	0.25 0.58	0	40	40	93		1S4
6 Mar 1530	0900 7 Mar 1700 9 Mar	Daily max/min at site + Ph	-	-	5	50	55	73	Only use half of distribution data due to natural colony	1S5
(b) Skardon Place 1984										
5 Nov 1500	1000 6 Nov 1600 8 Nov	Daily max/min at RAF Mountbatten	6 Nov 7 Nov 8 Nov	1.25 5.75 7.50	15	42	57	55		2S1
12 Nov 1500	1000 13 Nov 1500 16 Nov	Daily max/min at RAF Mountbatten	13 Nov 14 Nov 15 Nov 16 Nov	3.5 16.83 3.75 0.33	4	45	50	102		2S2
26 Nov 1530	0900 27 Nov 1500 29 Nov	Daily max/min at site + Ph	27 Nov 28 Nov 29 Nov	4.25 4.67 4.17	1	36	37	62		2S3
26 Nov 1530	0900 27 Nov 1500 29 Nov	Daily max/min at site + Ph	27 Nov 28 Nov 29 Nov	4.25 4.67 4.17	5	15	20	62	Experiment to check sampling method - no 'disturbance'	2S3N
3 Dec 1530	0900 4 Dec 1600 6 Dec	Daily max/min at site + Ph	4 Dec 5 Dec	0.33 6.42	3	31	34	72		2S4
	0900 4 Dec 1600 6 Dec	Daily max/min at site + Ph	4 Dec 5 Dec	0.33 6.42	1	23	24	72	Experiment to check sampling method - no 'disturbance'	2S4N
(c) Rumleigh 1985										
28 Jan 1500	0900 29 Jan 1600 30 Jan	Daily max/min at site (screen)	28 Jan	5.5	10	16	26	48	At release, four adults on soil	2R1
4 Feb 1530	0900 5 Feb 1600 7 Feb	Daily max/min at site (screen) + Fh	7 Feb	3.08	19	27	46	72	At release, two adults and nine nymphs on soil	2R2
11 Feb 1530	0900 12 Feb 1600 14 Feb	Daily max/min at site (screen) + Ph	-	-	17	48	65	72	At release, two adults and three nymphs on soil	2R3
18 Feb 1530	0900 19 Feb 1600 21 Feb	Daily max/min at site (screen)	-	-	12	24	48	72	Ice crystals on plant on 19 Feb	2R4
24 Feb 1600	0900 25 Feb 1300 28 Feb	Daily max/min at site (screen) + Ph	25 Feb 26 Feb	0.08 0.25	14	28	42	90	At release, three nymphs on soil	2R5
5 Mar 0900	1000 5 Mar 1300 9 Mar	Daily max/min at site (screen) + Ph	5 Mar 6 Mar	10.25 6.75	26	159	185	75	At release, two adults and five nymphs on soil	2R6
12 Mar 1530	0900 13 Mar 1400 15 Mar	Daily max/min at site (screen) + Ph	-	-	20	67	87	53	Adults total includes four alates	2R7
20 Mar 0900	1000 20 Mar 1500 22 Mar	Daily max/min at site (screen) + Ph	-	-	10	21	31	54		2R8
26 Mar 0900	0900 26 Mar 1600 28 Mar	Daily max/min at site	-	-	29	350	379	79	At release, four adults and two nymphs on soil at Skardon Place	2S9

Figure 4.10

The numbers of aphids found per hour at Rumleigh, 4th - 7th February 1985



distance class based on their direct distance from the central release plant 3,10. The aphids found at the hourly sampling occasions were then also assigned to distance classes shown below, and the mean distance dispersed by the apterae for each hour was calculated on the basis of the mean distance from release point for each distance class.

Class 1 Release point.

Class 2 50-94 mm from release point

Class 3 95-154mm from release point

Class 4 155-254mm from release point

Class 5 255-354mm from release point

Class 6 355-454mm from release point

Class 7 455-650mm from release point

However, as numbers of aphids found decreased so rapidly after 48 hours in most experiments (Fig. 4.10), few estimates of dispersal are calculated after this time. In some cases it was neccessary to pool hourly records to obtain sufficient data for an estimation of the mean distance dispersed to be made. Table 4.5 and Fig. 4.11 summarizes dispersal rates obtained for selected time periods after release.

Summary of all individual experiments.

Fig .4.11 illustrates the results obtained for some experiments in which mean dispersal distances for selected hours after release can be calculated. Although interpretation of the graphs may lead to overall trends being identified, a close inspection of the numbers of aphids involved and the environmental variables pertinent to each individual experiment (as above) does reveal 2 trends in the data.

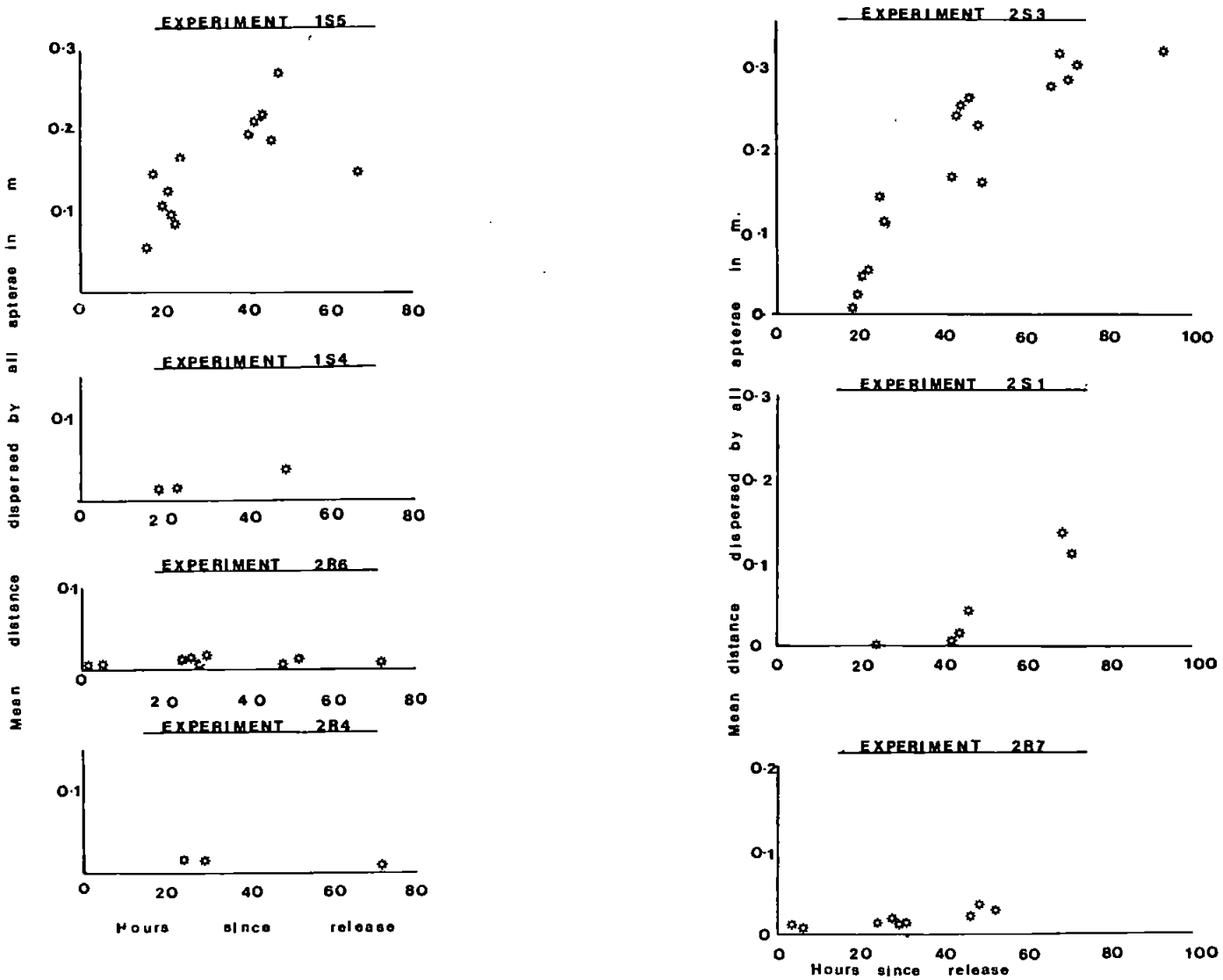


Figure 4.11 Hourly mean distances dispersed for selected experiments

Key * = a.m. release
- = no estimates possible (due to disappearance or lack of sufficient aphids)
R = RAF Mountbatten records

Table 4.5

Summary of Environmental Variables and Mean Distance dispersed by Apterous R. padi in Release Experiments

(a) 48 Hours After Start

EXPT	Mean Distance Dispersed (in cm)	Disappearance in %	Rainfall Duration Hours	Rainfall Amount mm	Mean Daily Temperature in °C	Mean Grass Minimum Temperature in °C	Artificial Leaf Hours 'dry'	Artificial Leaf Hours 'wet'
1S1	-	100						
1S2	-	80						
1S3	4.67	89	0.50	0.30	8.60	5.30		
1S4	1.93	78	0.83	2.55	6.50	2.20		
1S5	28.91	67	0.00	0.00	8.40	1.10		
2S1	2.74	51	1.75	2.80	8.70R	5.30		
2S2	33.78	70	17.75	14.58	8.10R	2.80		
2S3	22.73	68	7.92	10.70	9.10	5.30		
2S4	1.48	61	3.92	8.60	8.60	5.80		
2R1	2.73	88	14.75	10.40	8.90	0.90	3	22
2R2	4.16	70	2.00	0.80	8.90	3.50	39	1
2R3	0.00	62	0.00	0.00	-1.30	-5.70	48	0
2R4	1.08	30	0.00	0.00	2.90	-8.80	41	3
2R5	2.05	79	0.25	0.10	6.90	-1.60	31	8
2R6*	0.45	50	17.00	14.20	7.80	2.20		
2R7	3.51	70	0.00	0.00	3.50	-7.50		
2R8*	4.50	93	0.00	0.00	2.30	-4.50	29	1
2S9*	2.57	77	0.00	0.00	6.40	1.90		

(b) 72 Hours After Start

1S1	-	-						
1S2	-	-						
1S3	2.33	94	0.50	0.30	7.60	1.50		
1S4	3.06	91	0.83	2.55	6.40	1.30		
1S5	24.86	80	0.00	0.00	7.50	-1.30		
2S1	9.81	79	13.50	23.91	9.50	6.80		
2S2	27.25	71	24.08	23.65	7.30	1.40		
2S3	35.75	81	13.08	15.80	10.20	6.70		
2S4	5.04	85	6.45	10.50	8.00	4.50		
2R1	-	-						
2R2	0.00	93	12.42	1.40	9.60	4.90	51	1
2R3	0.00	62	0.00	0.00	-0.90	-8.70	72	0
2R4	0.88	43	0.00	0.00	3.10	-6.40	62	3
2R5	0.00	93	0.25	0.10	7.10	-1.90	36	26
2R6	0.75	65	17.00	14.20	6.70	-1.10		
2R7	-	-						
2R8	-	-						
2S9	2.50	89	0.00	0.00	6.50	0.10		

1. The overall disappearance of the aphids present on the original release plant. This loss was investigated graphically (Fig. 4.12), and shows an exponential decline in every case, i.e a linear relationship if $\log_{10}$ number of aphids is plotted against time.

2. In some experiments (2R3, 2R4 and 2R5) the number of aphids found following a cold night was very low at 0900h, but increased at 1000h and 1100h. This, combined with the presence of apterae observed on the soil surface is evidence of the movement of apterous R. padi into the soil when night temperatures are low.

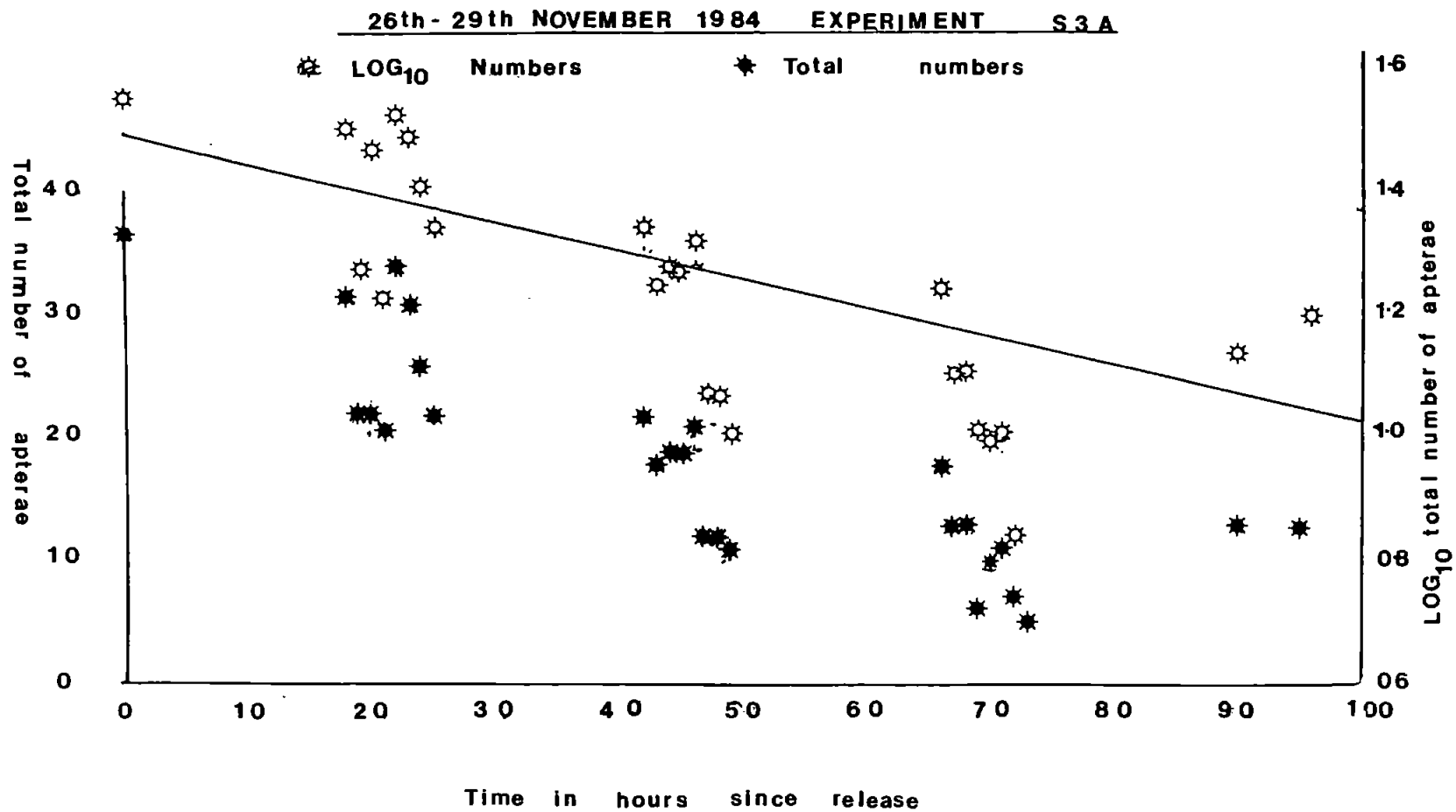
Further analysis of the results.

The mean distance dispersed for each experiment was obtained for two time periods after release, 48 and 72 hours, either by direct calculation from distance classes, (Appendix 4E), or from the relationships shown in Fig 4.11. Standard environmental variables were also calculated from the metereological data recorded for these two time periods, and the amount of disappearance of aphids from the release point was calculated.

This is summarized in Table 4.5. Mean daily temperatures was calculated from the max./min. thermometer at Skardon Place, and the daily max./min. temperatures recorded at Rumleigh Metereological Station. Although Williams (1984) has outlined the problems associated with the use of such records, it was felt best to use these since the Grant temperature Recorder did not produce complete records for all experiments.

However, in two experiments at Skardon Place in November-December, the max./min. records were not available, and so records taken at R.A.F. Mountbatten were used instead.

Figure 4.12 The decline in total number of aphids present on a $1m^2$ plot of winter wheat (c.v. aquilla) 26 - 29 November 1984



Model 1 regression analysis was used to assess the relationships using MINITAB, after 48 and 72 hours between mean distance dispersed and the following :-

1. Disappearance of aphids (expressed as %).
2. Mean daily temperature.
3. Hours of rainfall.
4. Amount of rainfall.
5. Mean grass minimum temperature.

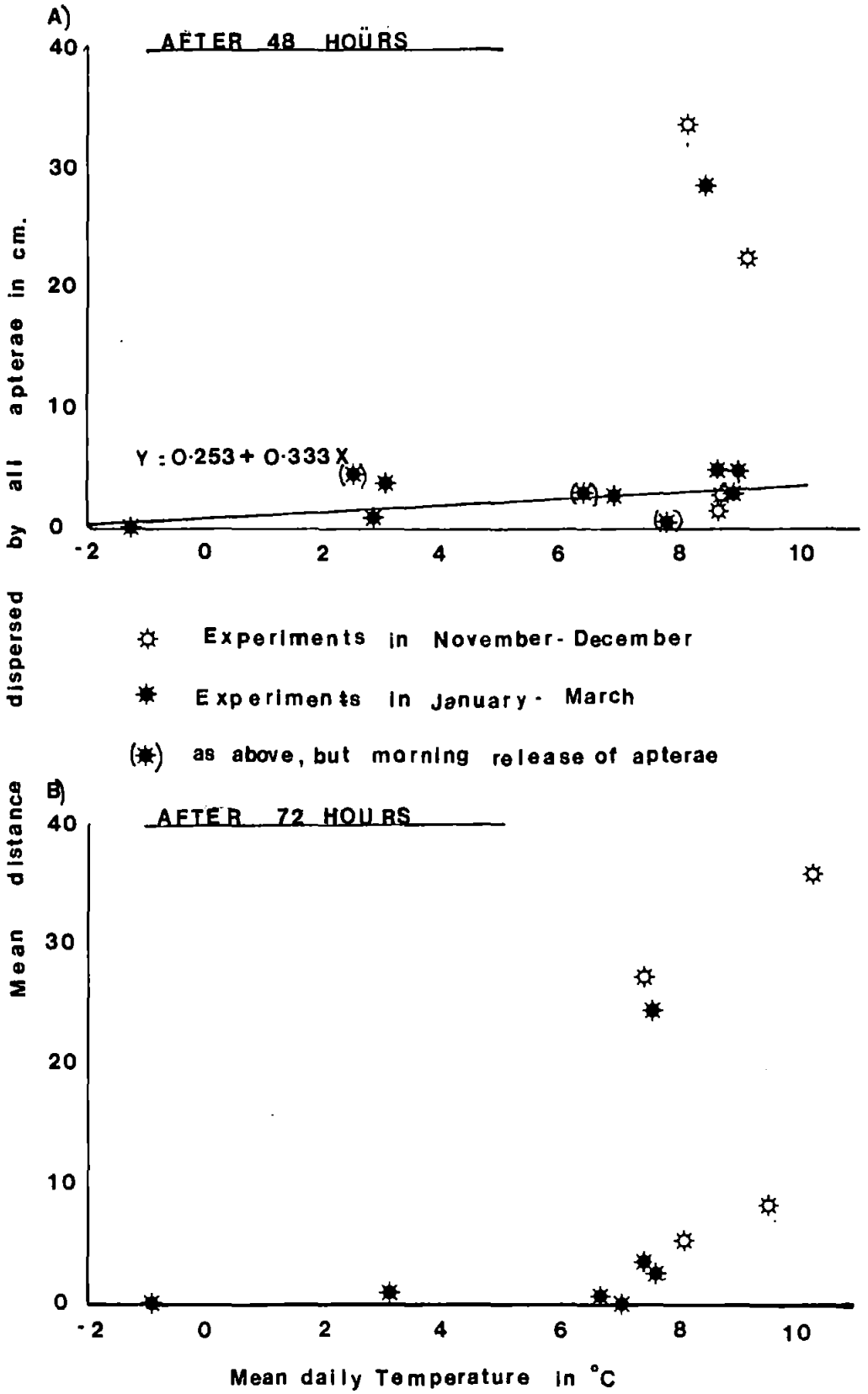
It was found that none of the linear regressions obtained could satisfactorily explain the variation in the data, and that a multiple regression involving all the environmental variables could only explain 12.55% of the variation (r^2 value corrected for degrees of freedom).

However, Fig. 4.13 illustrates the relationship obtained for 48 and 72 hours mean dispersal distances and mean daily temperature, and this suggests an "activity threshold" for apterous R. padi as around 7-9° C, which agrees with the results of apterae movement generated by a simple simulation model in Section 4.3.

It would seem that movement in apterous R. padi is induced at around 8° C by an unknown random stimulus, but in some experiments the apterae clearly did not respond to this stimulus and dispersed less. Inspection of the "artificial leaf" records of duration of leaf wetness revealed that although leaves are obviously wettened in periods of rain, they also remain wet for several hours following dew (e.g. in 2R4, no rain fell at all, and yet leaves were very wet for 3 of the 48 hours), and so it was decided to look at dispersal rate of apterae and environmental variables for those

Figure 4.13

Relationship between temperature and mean distance dispersed in $1m^2$ experimental plots



experiments where records of "leaf wetness" were available, to attempt to discover if this was the stimulus suggested above.

Hours of wetness were defined as hours when the surface "wetness" recorder produced values of 9 or above (on a scale of 1-10), and "dryness" as hours when the recorder produced values of 3 or below (on a scale of 1-10).

Fig. 4.14 shows the relationships between wetness and dispersal which do not suggest any consistent results. The only useful relationship is between mean daily temperature and dispersal rate regressed against dispersal rate, when 81% of the variation (for mean daily temperature below 8°C) was explained, and the equation fitting the data was :-

mean dispersal rate = 0.253+ 0.333 Mean daily temperature.

This is the line drawn in on Fig. 4.13 a.

However, it must be seen from these relationships that duration of leaf wetness or dryness is not the unknown stimulus producing movement in apterae in some cases around a threshold, and not in others.

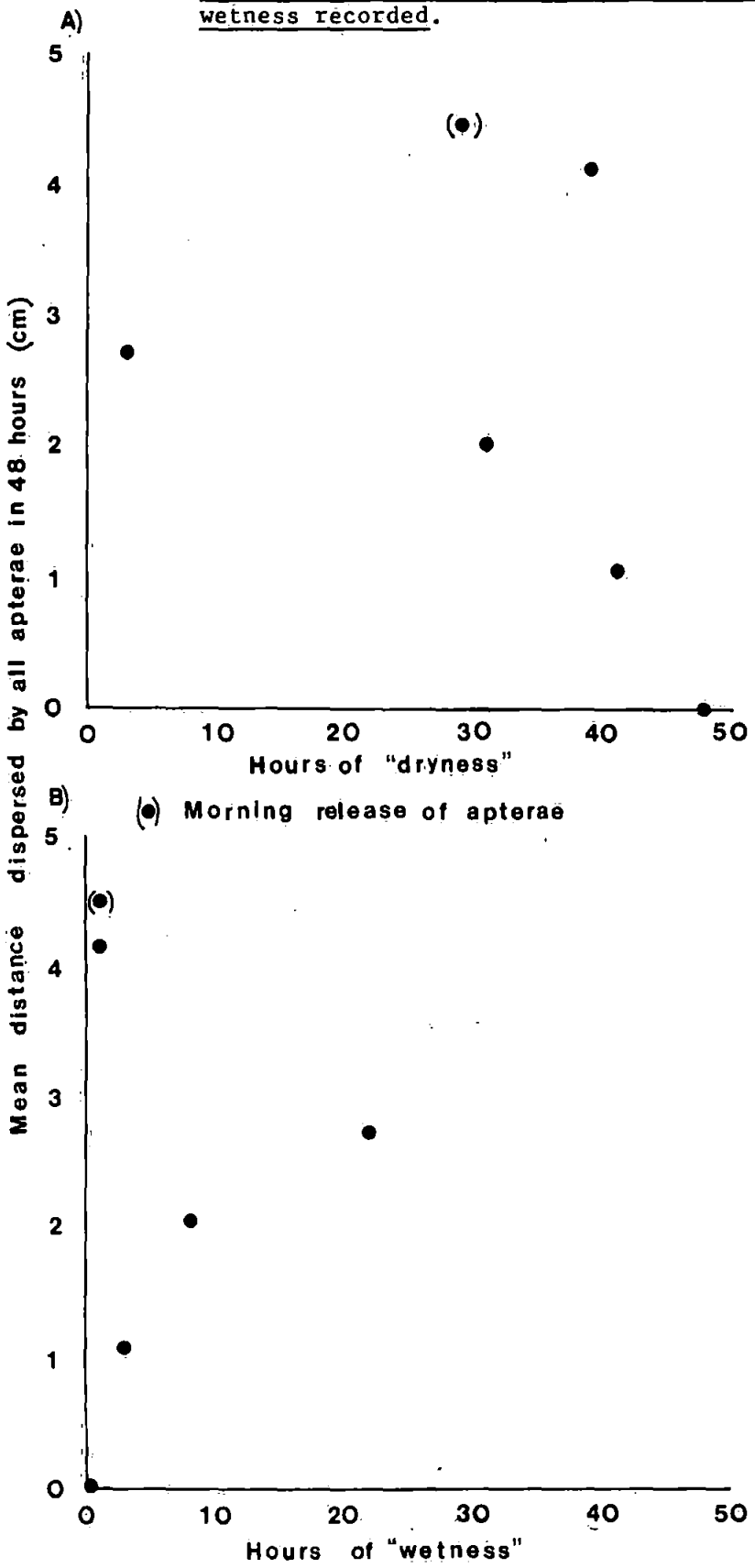
These dispersal experiments also enabled other aspects of R. padi behaviour to be investigated:-

1. Observed development Rates.

At Skardon Place in year two, several groups of first instar nymphs were observed being deposited at the beginning of the experimental runs, and five days later these nymphs had developed into 2nd instar nymphs, some discarded cuticles were also seen in some cases.

At Rumleigh in experiment 2R6, 9 first instar nymphs present at the release on 5th March 1985 had developed into second instar nymphs by 1300 on 6th March, and the discarded cuticles were

Figure 4.14 The relationships between mean distance dispersed after 48 hours, (A) hours of 'dryness' and (B) hours of 'wetness' of the leaves as produced by the surface wetness recorded.



also observed.

Even through the coldest weather, apterae were observed at Rumleigh depositing nymphs, and nymphal development continued. However, when colonies released at the start of experiments already contained first instar nymphs, the length of time spent in that stage could not be assessed, since their exact date of birth was not known.

2. The variation in vertical distribution of apterae.

This is fully described in Section 4.7.

4.4.6 Discussion.

The results obtained suggest that there is a temperature threshold at around 7-9^{o}C, at which some unknown random stimulus initiates movement in some apterous R. padi at some times of the year, but not in others. Little movement occurs in January-February. In 1984, there were only 2 days at this time when mean daily temperature was above 9^{o} and 9 days in 1985. Mean dispersal distances calculated are lower than those obtained by simulation modelling of dispersal from changes in distribution in commercial fields. These latter rates could be a result of density-dependent mortality caused by surface active polyphagous predators "eating out" the centre of patches (see discussion Section 4.3). Alternatively, the dispersal rates obtained from the 1m^{2} plots could be underestimates if apterae were able to escape outside the barriers of the plots, a point also suggested by Nakamura and Ohgushi (1983) in their assessment of dispersal experiments. Also, these simulated dispersal rates were over periods of 4 or more days, when unknown factors could exert their influence between sampling occasions.

Although field collected aviruliferous "wild" R. padi were

used in all experiments, the differences in dispersal rates obtained could be simply due to the amount of cold-acclimatization the aphids received prior to the experiment. However, if the three sets of experiments are considered separately, the same phenomenon of some movement in some experiments and not in others still occurs.

At colder temperatures (daily mean -2 to 7°C), very little apterous movement occurs. This was observed by Pike and Schaffner (1985) in Washington State U.S.A., where if daily mean temperatures approach or drop below freezing, R. padi activity ended in November, and there was a decline in numbers. Hurst (1966), Watson, Heathcote, Lauckner and Sowray (1975) observed that severity of virus in sugarbeet is lower following harsh winters due to the decrease in numbers.

At colder temperatures, the host plants themselves are also under more stress, photosynthesis will be reduced, and so if apterae are successively living and feeding on an adequate plant, there is little inducement to move. Alternatively, apterae could be stimulated to move, due to unsuitability of the hostplant.

At lower temperatures Wellings and Dixon (1983) showed that Drepanosiphum platanoides(Schr.), the sycamore aphid was stressed if it did not have a period of cold acclimatization. This is because the increased body size developed by living in warmer conditions led to increased maintenance costs and so it is reasonable to assume that a cold spell in winter would likewise stress apterous R. padi and reduce movement.

As there was no relationship between grass minimum temperature (which is a truer representation of the actual temperature experienced at night Hand 1982, Williams 1984), and

dispersal rate, it is likely that a short exposure to extreme cold conditions has no effect on R. padi apterae. Evinhuis (1968) found this when exposing nymphs of the apple grass aphid R insertum (Wlk.) to -7.5° C for 24 hours. However, such low temperatures could have induced mortality as Williams (1984) found that the LT50 for R. padi in January was around -7.8°C, and in 5 of the experiments at Rumleigh, 1985, the mean grass minimum temperatures were below 0 °C.

However, daily mean temperature was calculated using the standard thermometers inside a 1.2m Stevenson Screen at Rumleigh (temperature recorders were unreliable). If the relationship calculated by Hand (1982) and Williams (1984) is used to correct the daily maximum and minimum temperatures recorded at Rumleigh, for example, then the daily mean temperature is slightly reduced (from 12.6 °C over 3 days in Experiment 2R2, to 12.52°C). This is because screen thermometers tend to overestimate minimum and underestimate maximum temperatures in the crop canopy. The correction is probably too fine to have a large effect on activity threshold estimates.

It would seem that R. padi is similar to many temperate species in exhibiting a temperature threshold, and findings can be compared with those of other insect species. For example, White and Franklin (1976) found that newly emerged southern pine beetles, Dendroctonus frontalis (Zimm.) only just became active at 9°C. (They are capable of flying in forests at lower temperatures than this however, as the bark in which they live is warmed by the sun). Wiktelus (1981) showed that R. padi has a seasonally variable migration flight threshold (16-17°C in the spring, 13-14°C in the summer, and 9-10°C in the autumn.

Wilson (1970) found that the sand dune inhabiting species of Cicindela formose generose (L.) and Cicindela lepida (L.) did not move until the air temperature reached 12 °C. Guppy (1982) found that flight activity in northern June beetle, Phyllophaga fusca (Froulich), and the common June beetle Phyllophaga anxiia (Le Conte) occurred in mid May after a threshold of accumulated 156 day degrees above 5-6°C since 1 April. Also, when the soil temperature reached 10 °C, flight activity started 12-45 minutes after sunset. However, if the air temperature, whilst the beetles were in flight, dropped ~~below~~ 10°C they did not return to the soil, but only fed. At 5 °C or below, individuals fell from trees as low temperature eventually inhibited activity. Smith (1981) found that at 3 °C S .avenae apterae were capable of walking, and at -4°C, larger instars became completely immobilized.

Mortality in experiments 2R3 and 2R4 (or possibly stress induced lethargy, as very little dispersal was seen) could have been induced by ice crystals forming on the body surface, or by nucleation of ice particles around the gut contents (Williams 1984). However, temperature, whilst important in controlling the overall movement of R. padi, is clearly not responsible in isolation, since at the same temperatures some move and some do not. Variation in temperature or daily range could be important.

Rainfall duration and amount and wind gustiness and amount have all been investigated with specific reference to overwintering survival of cereal aphids (Smith 1981, Watson 1983), but only in passing in relation to movement of apterae. Interpretation of results was also compounded by losses at the start of experiments, of up to 60%, when aphids were placed in the field (Smith 1981). However, protection

from wind and rain increased survival in the plants in Smith's experiments, and this was attributed to the feeding habits of R. padi being in sheltered positions on the leaves.

Watson (1983) found that rainfall knocked apterous S. avenae from the crop, but that it was unlikely that rainfall was directly responsible for aphid mortality. Pearson (1980) found that aphid populations were not reduced following heavy rain and high winds, presumably because the aphids sheltered. Wallin and Loonan (1980) found that the severity of BYDV decreased when there was heavy rainfall, due to increased mortality. Watson (1983) assessed the effect of rainfall and temperature on activity of S. avenae by basing activity as a measure of the number of individuals caught in sticky traps on the ground. 26% of all individuals were found on the ground and activity was significantly related to temperature and rainfall, but not the wind in one year, whilst in the second year, 29% of all individuals were found on the ground, but activity was not significantly related to temperature, rainfall or wind.

The combined effects of rainfall and wind on cereal aphid population survival, reproduction and dispersal are obviously not clear. In field investigations correlations between mortality and different weather factors depend upon the weather experienced at the time of the natural decline in numbers of cereal aphid populations over the winter (Watson 1983).

Certainly, at higher temperatures, more dispersal does occur than at lower temperatures by apterous R. padi, but in the experiments conducted in this Section, duration and amount of rainfall and the duration of time the leaf surfaces remained wet or dry did not appear to encourage or

restrict dispersal.

Other environmental factors which could have aided dispersal by apterous R. padi which were not investigated were wind direction and gustiness. Field observations did show that on windy days (i.e. >20 m.p.h. winds), apterae were always found in more sheltered places on plants, so wind per se may not increase dispersal. Indeed, of the three experiments where substantial dispersal was observed, one was conducted in a very still week in March 1984, at Skardon Place, which would imply that gusts of wind did not increase dispersal.

The stimulus that induces movement could be a combination of environmental factors, operating at different times and in different ways on apterous populations of R. padi and their dispersal.

Day and night conditions may act separately on aphids (Smith 1981, Turl 1980, Watson 1983). Frost, poor nutrition due to the host plants being stressed due to cold, lack of water and wind may combine to induce aphids to remain stationary and disperse little,or, alternatively induce movement, and the effect of seasonality must also be considered (Wiktelus 1981). During daylight hours, a warm sunny day could induce apterae to move onto less wind sheltered leaf surfaces, and invoke movement if the temperature rose above the activity threshold. A gust of wind could then knock apterae from the plant, under these conditions and lead to increasing dispersal. Equally well a short shower of rain could do the same. No direct evidence of these events was observed however.

A further complicating factor in understanding the results

of the experiments conducted, is the amount of disappearance of individuals from the arenas . Although dispersal could not be related to the disappearance over the course of the experiments, disappearance was the most overriding feature. As the disappearance was found to occur at an exponential rate, in all experiments, there was no evidence to suggest predation or density-dependent mortality, so it would be reasonable to assume that mortality was density-independent, as observed by Smith (1981, Watson (1983) and Williams (1984), or that apterae were moving into the soil.

Investigations in Section 4.6 reveal that apterae move with a high degree of directionality. This could result in individuals walking completely out of the arena without encountering a plant, and then reaching the water barrier and drowning. This is not likely to be a major cause of disappearance.

Disappearance is not lower in the experiments conducted in November-December (when it was thought that temperatures would be above the activity threshold), than in those conducted in January-March, so it is not a seasonal response in R. padi populations.

It can be concluded that dispersal of apterous R. padi in cereal crops is not a simple process. It involves the interaction of a range of environmental factors, host plant factors and intrinsic aphid factors. On some occasions, movement is induced, and in some it is not.

Dispersal has been studied in conditions similar as possible to the field in these experiments. Traps were not used, but classes of distance, akin to the "fly rounds" used by Rogers (1977)

in his studies of Tsetse fly, instead. Stevens (1982) suggested that insects in dispersal experiments may not behave in the same way as indigenous wild populations. Pre-treatment of the apterous R. padi used in these experiments was negligible. Behaviour was not disrupted by marking. However, the colonies of apterae established on the central release plants used were far more dense than those ever observed in the field, but requirements for sufficient numbers for dispersal estimates necessitated this, and the effects on behaviour of the apterae are unknown. Field observations showed that individuals seemed to cluster together under leaves and in the youngest "leaf curls" for long periods of time.

From the results obtained, it would seem that apterous R. padi, although capable of moving distances of up to Ø.3m in 48 hours, are not always induced to do so under field conditions. This stimulus could be environmental or hostplant induced.

4.4.7 Conclusions.

1. The mean distances dispersed after 48 and 72 hours were extremely variable.

2. The variation in mean distance dispersed was found not to be significantly correlated to any measured environmental variable except temperature.

3. Dispersal occurred in some experiments, but not in others at a mean daily temperature (as measured by a sheltered max./min. thermometer or in a standard Stevenson screen) of between 7-9 ^{o} C.

5. It is suggested that there is an activity threshold at around 7-9^{o}C.

6. Much disappearance from the experimental plots occurred, which was

exponential with respect to time.

7. Most apterous aphids remained at the release plant.

8. No evidence exists to suggest that any density-dependent mortality occurred.

9. Apterae were observed walking on the soil surface in a highly directional manner.

10. Dispersal from the central release point is adequately described by a "random-walk" process, as numbers at the release point increased at certain times of the day.

4.4.8Suggestions for further work.

1. Execution of more experiments in an identical design, but with increased environmental monitoring, to include :-

a) Daily sunshine.

b) Mean daily wind speed at the site.

c) 24 hour crop canopy temperature records.

2. 24 hour observations of apterae distribution and movement using infra red light in hours of darkness, to ascertain if the stimulus to movement acts at night, and discover if nocturnal activity produces disappearance.

4.5 The release of apterous R.padi in small plots of winter wheat in controlled environments to investigate dispersal in constant temperatures.

4.5.1 Introduction.

From the results obtained in the dispersal experiments on outdoor experimental plots of winter wheat, it became apparent that more experiments were necessary in controlled environments. It was hoped that the removal of confusing influences of rainfall and wind on dispersal of apterae would lead to a clearer insight into the effects of temperature, and may confirm if the disappearance obtained in the field experiments in Section 4.4 was due to movement into the soil.

4.5.2 Aims of this investigation.

1. Investigate the disappearance of the apterae over the course of dispersal experiments.
2. Attempt to quantify the temperature that induces the movement of apterae into the soil.

4.5.3 General materials and Methods.

All wheat plants used were c.v. aquilla, and all growth stages used are Zadoks growth stages. The glasshouse at Skardon Place was maintained at 23°C, with a natural daylight regime.

4.5.3a. The insect culture.

Transmission tests to establish virus free aphids for use in all experiments were first performed - as explained in section 4.4.4.1. The virus free apterae, and any progeny were then transferred to individual oat seedlings (c.v. Peniarth) growing in Levington's Universal potting compost in 820mm square plastic pots.

Oats were found to be the best plant on which to culture R.padi. A 70mm diameter glass sleeve covered at one end with 200μ diameter nylon mesh, secured with insulation tape was then placed over the plant, and pushed into the compost to a depth of 10mm.

These "minicultures" were then placed in a 11 $^{o}\pm$ 2 ^{o}C controlled environment room with a 16hr daylight cycle on a metal sand filled tray which was kept moist by watering three times a week. These conditions are used at Long Ashton Research Station (Chinn pers. comm.) to induce reproduction in R.padi at an increased rate.

After 10-14 days in these "minicultures", numbers increased by three to five times. The glass covers were removed and the aphid infested plants were transferred to an insect cage (Plate 6) identical to those used in the outdoor cultures in Section 4.4, situated in a 11$^{o}\pm$ 2 ^{o}C controlled environment room with a 10 hour daylight cycle, and standing in a metal sand-filled tray which was watered three times a week. Moist sand produces the optimum humidity for R.padi reproduction. Fresh oat plants (c.v. peniarth) G.S Stage 23 (Zadoks et al. 1974), grown in Levington's Universal potting compost in 100mm square plastic pots were added to the culture every week. These were grown at Skardon Place in the glasshouse.

Fresh batches of R.padi apterae were collected at Anthony every two to three months during the winter months.

For all the experiments in this section, individual wheat plants (cv.aquilla) grown in sieved garden soil in 700mm square plastic pots were placed in the insect cage for seven to ten days before experiments started, to become colonized with apterous

Plate 6 The standard insect cage.

R.padi. If after three days, no apterae had moved to the plants, then some were transferred using a fine camel-hair brush.

4.5.3b. Establishment of winter wheat (c.v.aquilla) arenas for dispersal experiments.

1) Cereal plants for dispersal estimates in 0.25m experimental arenas (4.5.A).

Each week, 40 individual winter wheat (c.v.aquilla) seeds were sown in 70mm square plastic pots in Levington's Universal potting compost and grown to the three tiller stage (G.Stage 23, Zadoks et al. 1974) in a glasshouse. This took two to three weeks. They were then transplanted into sieved garden soil in drilled plastic 500x500m trays (depth 80mm), to provide three rows of eight plants at 150mm row spacing, 50mm between plants, and watered. The central plant space of the central row was filled with an empty 70mm square plastic pot (Plate 7) to enable easy inclusion of a "source" R.padi culture (Plant 3,4). The arenas were established five days before experimentation commenced, were watered and then placed in the controlled environment room two days later, to permit acclimatization by the plants.

2) Cereal plants for experiments to investigate the effect of temperature on dispersal (4.5.B and 4.6).

Each week, wheat plants were grown as above, and then transplanted into sieved garden soil in plastic 370x220x650m trays, watered, and left for five days. The plants were arranged in two rows 200mm apart, of 5 plants, 50mm between the plants. The central plant position of one row was filled with an empty 70mm square plastic pot as above, and the acclimatization period was the same. The soil was surrounded by a 200mm high continuous fluon sprayed

Plate 7 $0.25m^2$ experimental arena used in controlled environment rooms.

transparent plastic barrier to prevent escape (Plate 8).

For the experiments in Section 4.6, the plastic trays were planted with two complete rows of wheat plants, 200mm apart.

4.5.A The release of apterous R.padi in 0.25m experimental plots of winter wheat in controlled environment rooms.

Experimental Methods.

1. Preparation. Day 1 0900h.

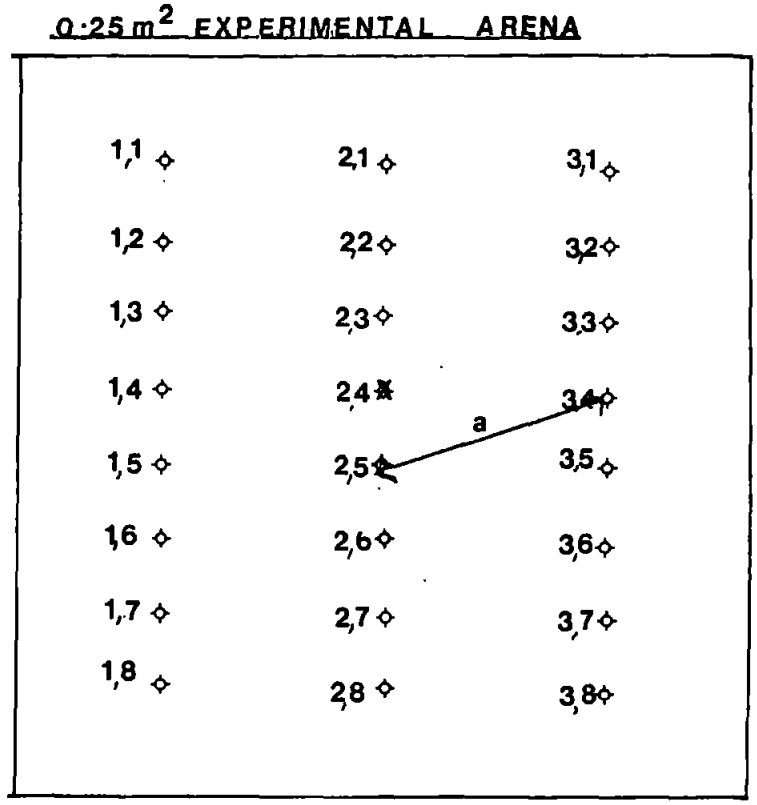
The central pot of the arena was removed and an individual plant which had become colonized with aphids in the insect culture (see 4.5.3a) was placed in the central hole, and the soil carefully made level across the edge of the plastic pot. The arena was then placed in the appropriate controlled environment room (either at 6^{o} or $11^{o}C$, ($\pm$ $2^{o}C$), with a 10 hour daylight cycle (to simulate winter conditions) provided by fluorescent lighting.

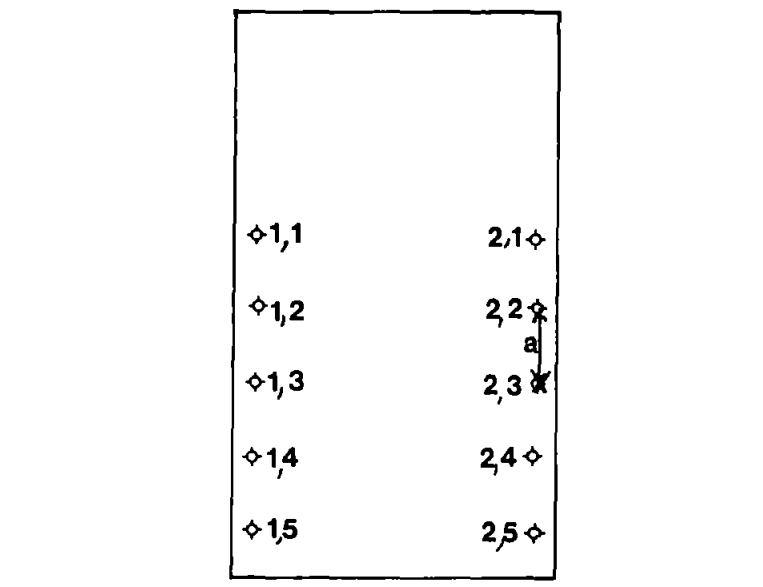
2. Sampling. Day 1 1000h Day 3 1700h.

Every hour, during the hours of daylight, the rows were handsearched, and aphids positions recorded according to the scheme explained in 4.4.4 and Figures 4.8 and 4.9. Then, at 0900hon day 4, the final positions were recorded, and the aphids were returned to the insect culture using a fine camel hair brush.

The soil was also searched according to the scheme outlined in 4.5B below. Two experiments were conducted as above without hourly searching to plot distribution of apterae at 11 $^{o}C\pm$ $2^{o}C$ to check if the sampling method had any effect on the estimates of dispersal. Fig. 4.15 shows the layout of the arenas used in the experiments.

Figure 4.15 Plan view of experimental arenas used in controlled environment experiments





a a typical distance dispersed

◇ X release plant

1,1etc code number of plants

100mm

Plate 8 The insulated box inside a deep-freeze.

4.5.B The release of apterousR.padi in seed trays of winter wheat in controlled environment rooms.

Experimental Methods.

The central pot of the arena was removed and an individual plant which had become colonized with aphids in the insect culture (see 4.5.3a) was placed in the central hole, and the soil carefully made level across the edge of the plastic pot. The arena was then placed in the appropriate controlled environment room, either at 6°or 11 °,(±2°C), with a 10 hour daylight cycle (to simulate winter conditions) for the hours of daylight. It was subsequently removed at the end of the day and placed in either a refrigerator (at 5°C), or inside an insulated wooden box inside a deepfreeze(at -4°C, reducing to -9°C by the end of the night), containing a Max/min thermometer simulate a hard night frost (Plate 7). Next morning at 0900h, the position, lifecycle stage and distance from the release plant of each aphid found was recorded. The aphids were removed from all plants in the usual way, the wheat plants were cut off to soil level, searched as a check and removed.

The soil filled tray, and its plastic barrier was then placed in the source controlled environment room, and left until thawed (3-4 hours). The soil was then transferred to six labelled plastic bags, according to location. Any aphids and all organic matter present in the soil were subsequently extracted by the standard technique of soil washing and floatation (Southwood 1978). Preliminary investigations with soil containing known numbers of apterae revealed a satisfactory recovery efficiency of 80-90%. 19 runs of these experiments were performed.

4.5.4. Results

The results of experiments conducted in 0.25m^2 trays and in seed trays with different overnight regimes are discussed here.

Observations

1. In all experiments, no live aphids were found in the soil.

2. In experiment 4 at 9°C (this temperature regime was produced due to a malfunction in the thermostat) first instar nymphs were deposited during the course of the experiment. Interpretation of numbers was made more difficult, as they developed into larger nymphs, and the final number of apterae was greater than the initial number !

3. In some experiments batches of first instar nymphs were laid and fourth instar alatiform nymphs developed overnight into alates.

4. Apterae were observed climbing across leaf bridges in the following experiments :-

Expt. 2. at 11°C between 1300h and 1500h from Plant 2,4 to 3,6.

Expt. 1. at 11 °C between 1200h and 1400h from plant 2,4 to 3,5.

5. In 78% of the experiments conducted with different overnight temperature regimes, 90% of the aphids released were recovered at the end of the experiments.

6. In three of the five experiments conducted to simulate late winter conditions, (Day temperature 5°C, night temperature of -4 °C, reducing to -9°C), apterae were found in the soil at the release plant. In two, apterae were found 7cm from the release point.

7. In three of the five experiments conducted to simulate severe overnight frosts (day temperature 11° ± 2°C and night temperature of -4°C, reducing to -9 °C), apterae were found in the soil at the release plant, but none in the soil around other plants. In four of

the five experiments, all aphids were found at the end of the experiment.

8. In four of the ten experiments mentioned in 4 and 5 above, 90% or more of the apterae at the end of the experiment were found at the release plant.

Analysis of the results.

A) Estimation of dispersal in 0.25m trays and in small trays in different overnight temperature regimes.

Appendix 4F summarizes the results of experiments 4.5.A. The plants in the experimental arenas were each assigned to a distance class, based on their direct distance from the central release plant 2,4 or 2,3 for the $0.25m^2$ trays and the seed tray experiments respectively. The mean distance dispersed by the apterae was then calculated in a similar manner to that already described in Section 4.4.

Distance classes were :-

Class 1 release point

Class 2 50-94mm from release point

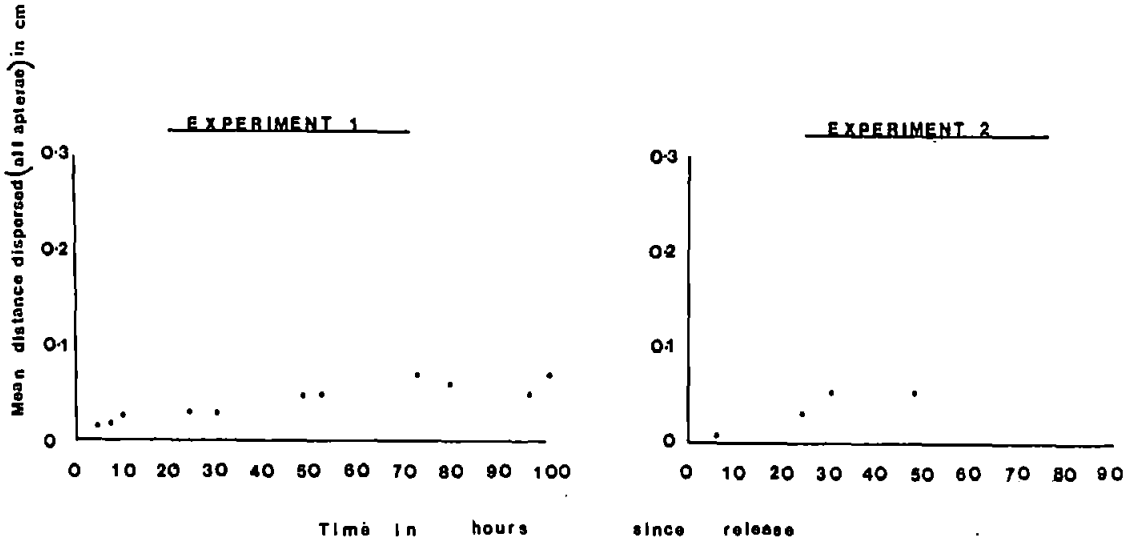
Class 3 95-154mm from release point

Table 4.6 summarizes the mean distances dispersed in the different temperature regimes used, and shows the distribution of apterae in the soil. The mean distances dispersed for some experiments are shown in Fig. 4.16.

The most obvious feature of these results is that the mean dispersal distances are all low, (even in the 11 $^{o}\pm2^{o}C$ controlled environment room) as compared with those shown in the outdoor $1m^2$ plots (Section 4.4) (Table 4.5). It was hoped that experiments

Figure 4.16 Hourly mean distances dispersed in controlled environment rooms

(A) Experiments at 6 ± 2°C



(B) Experiments at 11 ± 2°C

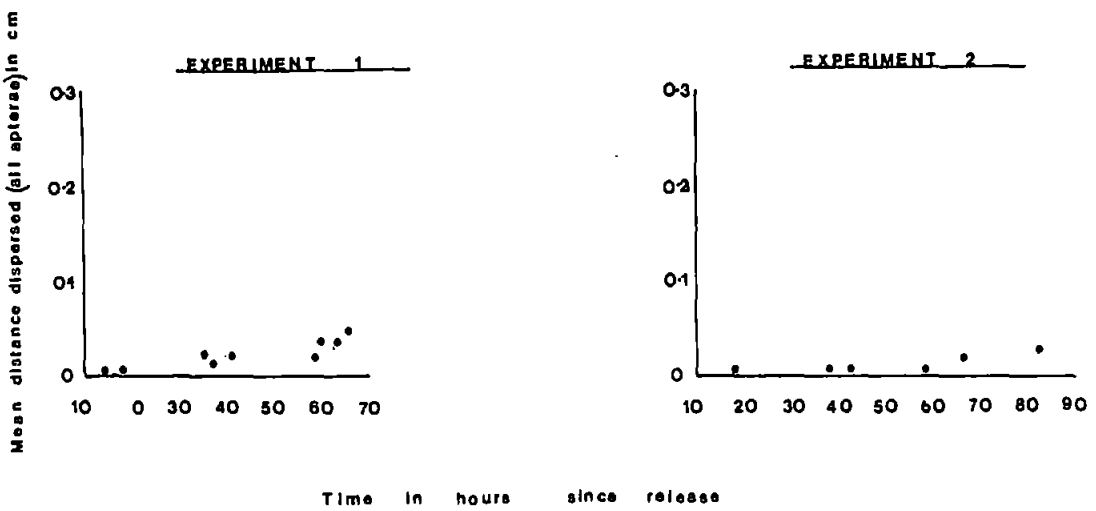


Table 4.6

Summary of Experiments to Investigate the Effect of Temperature on Dispersal

Experimental regime		Dispersal rate in cm			Disappearance in %			No. and Distribution of Apterae in Soil				Notes
		24h	48h	72h	24h	48h	72h	At release point	Class 1	Class 2	Class 3	
6° ± 2°C all time	(1)	1.47	1.83	5.4	45	48	34	7	1	0	3	In experiment 4, temperature rose to 9 - 11°C, and so these results are not included in calculation of mean dispersal estimates
	(2)	0.92	0.80	2.77	54	37	27	0	0	0	0	
	(3)	1.13	1.02	5.25	18	27	27	0	0	0	0	
	(4)	0.15		3.9	4	-	0	2	1	1	0	
	(5)	1.14	2.68	2.35	15	41	0	-	Not available		-	
	x	0.96	1.58									
	±	0.22	0.42									
11° ± 2°C all time	(1)	2.91	4.33	6.39	36	31	41	0	0	1	1	
	(2)	2.53	5.18	-	44	44		0	0	0	0	
	(3)	0.48	-	-	28			1	0	0	0	
	x	1.97	4.76									
	±	0.75	0.43									
11° ± 1°C all time	(1)	-	-	3.75			62		Not available			These are 'no disturbance' runs to check experimental procedure
	(2)	-	4.26	-		0			Not available			
6° ± 2°C Day -4°C Night (reducing to -9°C)	(1)	0.20			5			1	1	0	0	
	(2)	1.20			0			3	1	0	0	
	(3)	0.50			0			0	0	0	0	
	(4)	0.00			29			1	0	0	0	
	(5)	1.3			27			0	0	0	0	
	(6)	-			59			-	-	-	-	No soil search!
	x	0.64										
	±	0.26										
17° + 2° Day -4°C Night (reducing to -9°C)	(1)	1.0			0			0	0	0	0	
	(2)	1.20			9			0	0	0	0	
	(3)	0.00			0			4	0	0	0	
	(4)	2.68			0		Not	0	0	0	0	
	(5)	3.56			20		Applicable	0	0	0	2	
	x	1.69										
	±	0.63										
17° ± 2°C Day 5° + 1° Night	(1)	1.00			9			0	0	0	0	At night, put in refrigerator
	(2)	1.00			3			0	0	0	0	
	(3)	0.3			3			0	0	0	0	
	(4)	0			0			0	0	0	0	
	x	0.76										
	±	0.23										

- = Not calculated

conducted at $6^{o}\pm$ 2 ^{o}C would be below this. A Mann-Whitney U test showed the mean distances dispersed after 48 hours by apterae at the two temperatures in the $\emptyset.25m^2$ experimental trays to be significantly different.

B) Estimation of movement into the soil.

Appendix 4G details, and Table 4.6 summarizes, the experiments conducted with overnight temperatures of -4 ^{o}C, reducing to -9 ^{o}C, and 5 ^{o}C as explained in 4.5B.

It can be seen from Table 4.6 that more apterae were found in the soil in the $\emptyset.25m^2$ plot dispersal experiments at $6^{o}\pm$ 2^{o}C than at $11^{o}\pm$ 2^{o}C.

The majority of the apterae remains were found in the soil at the release point, as Table 4.6 shows, and it must be remembered that these aphids could have fallen from the plants and died, and therefore not represent positive movement by individuals.

However, as individuals have been observed in the field, and in the controlled environment rooms walking on the soil surface, it could be equally likely that the individuals were walking on the soil surface rather than burrowing into it.

4.5.6 Discussion.

It was hoped that the results obtained would provide some clear evidence for the existence of an "activity threshold" suggested by the field data collected in Sections 4.3 and 4.4, without the complications of the effects of wind and rain. Statistically significant differences in mean dispersal rates after 48 hours in the two temperatures were found.

The results obtained in experiments of 4.5B are rather

surprising. The mean dispersal rate obtained in the $11^{o}\pm^{o}C$ by day and the $5^{o}C$ by night regime would be expected to be higher than that for the $11^{o} \pm 2^{o}C$ by day and the $-4^{o}C$, reducing to $-9^{o}C$ by night, but it was not. This could be due to inherent variability in apterous R. padi. Three types of factor must influence the dispersal rates observed, and should be considered at this stage.

1. Experimental factors.

a) The lighting in the controlled environment rooms was always constant, there was no sunrise or sunset, and the effects of this on the aphids are unknown.

b) Escape from the $\emptyset.25m^{2}$ trays could have occurred. Aphids were observed on clothing and on the floor, and this could have led to underestimates of dispersal due to escapes.

c) Although the soil washing technique was proved to be 80-90% efficient at soil sampling, some individuals must have been lost from the experimental "system".

2. Host plant factors.

The nutrition and nutrient content of host plants grown in Levington's potting compost and reared inside a glasshouse is likely to be of superior quality to those grown in soil. Dispersal estimates in the controlled environment regimes may be lower than those of field, simply because there is no nutritional stimulus to move. This could override any environmental temperature factors.

3. Aphid factors.

The R. padi individuals used in all these experiments were of the same culture used for the experiments at Rumleigh in January-March 1985. It has already been shown in Section 4.4 that dispersal distances in these field experiments were low. Therefore

cold-acclimatization history of these apterae may well be the overriding influence on their behaviour. Dispersal is consequently low, even though the environmental temperature may be above an "activity" threshold. Thus an awareness of the climatic history of the apterae may be an important factor.

Whilst escape may be a factor, the disappearance rate of apterae from the experimental plot is lower than that obtained in the field experiments (mean 38%, s. error 3.2, as opposed to mean 69%, s. error 6.5 respectively). The disappearance calculations for the controlled environment experiments do include the aphids found in the soil, which the field estimates do not. Dispersal rate after 24, 48 and 72 hours in these experiments were not significantly correlated to disappearance.

All mean dispersal distances obtained were much lower than those obtained in the field, which could suggest that wind and rainfall increase movement of apterae, due to aphids being blown or washed from plants, and then climbing onto new plants. This was suggested by Smith (1981) and Watson (1983). The dispersal distances obtained could be underestimates, as apterae may have travelled further than the limits of the experimental arenas. However, in experiments conducted with different overnight temperature regimes, no escaped apterae were ever found inside the refrigerator or insulated box inside the deep-freeze, and so any escape could have happened during the day. Jepson (1983) found that apterous M. persicae were found to move frequently from leaf to leaf in controlled environments, but rate of movement was not related to temperature measured in thermal time.

Aphid remains were found in the soil at the end of the

experiments conducted in the controlled environment rooms. It cannot be stated whether this due to movement into the soil as a result of low temperatures, or to apterae dying and falling onto the soil surface from the plants, or from apterae walking on the surface.

In some experiments, apterae numbers were observed to increase in the middle of the day, and this was attributed to movement out of the soil. It could equally as well be attributed to individuals having left the release plant early in the morning, and returned at midday.

4.5.7 Conclusions

1. The dispersal rates of apterous R. padi have been calculated for $6^{o}\pm2^{o}C$ and $11^{o}\pm^{o}C$ controlled environment rooms, and shown to be greater in the latter.

2. Aphid remains were found in the soil in all temperature regimes, except in $11^{o}\pm 2\ ^{o}C$ by day and $5^{o}C$ at night.

3. The presence of aphid remains in the soil at the end of the experiments could not be attributed directly to movement by apterae into the soil.

4.5.8 Suggestion for further work.

1. Establishment of cereal plants in clear-sided narrow boxes of soil, with removable dark coverings, and the observation of colonies of R. padi established on these plants in controlled environments at $6^{o}\pm2^{o}C$ and at $11^{o}\pm2^{o}C$ over 24 hour periods using infra-red light at night. This would be to ascertain if diurnal movement patterns include movements into the soil.

2. Attempts to mark individual aphids need to be resumed, to establish movement patterns of individuals at different temperatures on and across plants.

3. Introduction of artificial rain and wind in a series of experiments identical to those conducted here to ascertain if they increase or reduce dispersal of apterous R. padi .

4.6 Investigations into the nature of dispersive movements of apterous R. padi by direct observations.

4.6.1 Introduction.

Movement in a variety of insects has been studied by direct observation (Hawkes 1969, Hawkes, Patton and Coaker 1976, Jones 1977, Newell 1986 and Rogers 1977). Very little work has been carried out on direct observation of apterous aphids.

Ferrar (1967) summarized earlier work on interplant movement of Myzus persicae(Sulzer), and stated that in general, the likelihood of walking of apterae away from a colony increased as unfavourable conditions (e.g. heat, wilting of plants, crowding, deterioration of host plants) increased.

Whilst the movement of apterae is either active (i.e. walking across leaf bridges or across the soil) or passive (i.e. being dislodged by some combination of environmental factors such as rain or wind, Ferrar 1967, Watson 1983), such movement results in dispersal of apterae, and ultimate spread of BYDV.

Investigation of the performance of apterous R. padi on the soil is essential for a more complete understanding of the field dispersal process. Any possible inhibitory effect of hostplant presence is removed in these experiments. Direct measurement of the movement of which individuals are capable is therefore possible.

4.6.2 Aims.

1. to determine the nature of movement on the soil by apterous R. padi and estimate dispersal rate in the absence of the host plant.
2. To determine the degree of turning and directionality of this

movement.

3. To investigate the behavioural stages involved in moving across the soil surface.

4.6.3 Experimental methods.

Each week, an experimental arena of ten plants was placed on a shelf in a controlled environment room at either $11^{o} \pm 2^{o}C$ or $6^{o} \pm 2^{o}C$. A clear plastic sheet was then clamped in position directly above the arena, and an acetate sheet placed on the top of this at the start of each observation of an individual.

Individual 4th instar nymphs or apterous adults (from the insect culture maintained at the same temperature) were then placed on the soil surface at the centre of the arena. Simultaneously, a stop watch was started, and two types of behaviour experiments were conducted. This is defined as "focal-animal" (continuous sampling by Altmann (1984).

a) The nature of behaviour on the soil surface.

the aphid was closely observed for ten minutes, and every type of behaviour exhibited, and the time of change in behaviour noted.

b) Directionality of movement.

Every 20 seconds, a mark was placed exactly above the aphid on the acetate sheet. This continued until the aphid reached a wheat plant stem, and the marks were numbered.

The distance between the marks was measured using a fine pair of dividers, and the true bearing of the direction between points measured on a 360^{o} compass rose using a protractor. The distances between the points and their bearings were then recorded on a BBC microcomputer.

4.6.4 Results.

The nature of aphid behaviour on the soil surface.

General observations.

1. On being placed on the soil surface, individuals spent a variable amount of time "orientating" before setting off to walk in a particular direction.

2. Crossing over gaps, often relatively large in aphid terms, always involved individuals first stretching across the gap with the front pair of legs, and then swinging the rest of the body and legs across and often down into the soil, and then climbing vertically before resuming soil surface movement.

3. Behaviour on stones on the soil surface became more "confused", with apterae often turning many times and crossing and recrossing the same spot.

4. Some nymphs and a few adults were observed burrowing into the soil.

5. Individuals varied in the length of time spent stationary at plant stems or leaves at the initial encounter; some climbed straight up the stems or onto the leaves, whilst others "deliberated", but no trend could be observed with regard to life stage or temperature.

Table 4.7 summarizes the total number of apterae observed in this experiment at each temperature. (The temperature was recorded in the constant environment room at the start of each 10 minute observation period). Observed behaviour was divided into 7 main categories, and then subdivided further.

Table 4.7

Numbers of R. padi observed at the Different Temperatures for 10 minutes each

Temperature in ^{o}C	Number of Apterae			Total Number
	Adults	4th instar Nymphs		
		Apterous	Alatiform	
5.3	4	5		9
6.5	19	6	2	27
9	4	2		6
10	10	15		25
11	7	12		19
				86

They were:-

1. Plant related activities

a) encountering plants.

b) walking on plants.

c) stationary on plants.

2. Walking on the soil surface in one of eight general directions decided by the observer, with North corresponding to away from the release point towards the artificial lights. These directions were:- NW, N, NE, E, SE, S, SW and W.

3. Burrowing into the soil.

4. "Orientating" or stationary on the soil surface.

5. Gap related activities, i.e. all types of observed behaviour - sensing, climbing, crossing, turning and recovering (after the crossing).

6. Stone related activities, i.e. all types of observed behaviour - sensing, climbing, crossing, turning and recovering (after the crossing).

7. Turning, but not walking on the soil surface, unrelated to gaps or stones.

Often aphids crossed a gap and immediately encountered a stone.

Table 4.8 summarizes the mean percentage of time spent by adults and 4th instar nymphs observed at the different temperatures. The results suggest that both adults and nymphs spend longer stationary on the soil surface at lower temperatures, always at the beginning of the observation period.

Although encountering and crossing gaps and stones took up

Table 4.8

The Percentage of Time Spent in Each Activity by Individuals at Different Temperatures

Temp. in °C	Plant Associated Behaviour				Walking - General Direction								Total Walking	Burrowing into Soil	Turning on Soil	Orientating on Soil	Encountering gaps	Obstacles Stones
	Encounter	Walk	Stop	Total	NW	N	NE	E	SE	S	SW	W						
(a) Adults																		
5.3				0.0	3.2	2.2	2.6	1.2	1.7	8.6	6.6	3	29.1		3.8	44.7	11.5	10.9
6.5	0.3	0.4	0.5	1.2	3.6	5.9	5.7	5.2	3.2	6.4	3.4	5.5	38.9	0.4	8.2	28.2	11.4	11.7
9	0.4	5.5	2.2	8.1	6.5	9.9	3.5	9.0	2.4	1.7	2.9	4.3	40.2		6.5	17.6	18.7	8.9
10	2.7	9.2	4.3	16.2	7.3	8.0	2.5	6.1	1.0	6.8	2.4	6.5	40.6		6.4	10.4	8.0	18.4
11	0.4	10.4	5.6	16.4	5.6	7.8	4.6	2.8	2.6	2.4	3.7	6.2	35.7		1.3	5.0	20.3	21.3
(b) Nymphs (4th instar apterous)																		
5.3				0.0	1.3	5.9	9.1	9.7	3.0	7.7	1.0	2.8	40.5	8.8	2.9	31.1	13.4	3.3
6.5	0.2	0.3		0.3	2.7	8.3	4.0	4.0	1.9	7.8	3.9	5.2	37.8	0.5	11.7	16.2	11.1	22.1
9				0.0	4.1	15.2	1.8	0.6	0	11.3	11.1	15.3	59.4		6.2	12.9	15.6	5.9
10	1.2	3.7	1.5	6.4	2.1	12.4	1.0	2.9	1.8	17.8	4.9	8.7	51.3		6.3	20.7	3.2	11.8
11	0.3	3.4	0.8	4.5	2.8	5.0	4.9	1.2	3.1	2.9	5.1	3.4	28.4	0.7	1.8	24.6	20.3	19.7
(c) Nymphs (4th instar alatiform)																		
6/7				0.0	5.4	8.9	1.4	4.2	5.4	1.0	0.0	5.6	31.9		13.3	12.3	17.3	25.2

time when apterae were being observed, they still maintained an overall directionality as individuals. Some did not walk in certain directions at all (Appendix 4H).

Further analysis.

It was decided to investigate the observed patterns of movement further to ascertain if populations of apterae walk in a random-walk type model (See introduction, Chapter 4).

It is reasonable to assume that the control of directionality in individuals is likely to be independent of temperature, and so all individuals were pooled to calculate the total amount of time spent walking in each direction. This is illustrated in Fig. 4.17, and it can be seen that this pooling emphasizes trends in the data.

Therefore, as individuals appear to be highly directional, it was decided to base analysis on the first direction of walking observed. Table 4.9 summarizes the results and the Chi-squared test performed.

The hypothesis was that a random-walk process is in operation on the R. padi population. Equal numbers of individuals will start to walk on the soil in each direction.

However, as can be seen from Table 4.9, the Chi-squared value was significant at the 1% level, which could lead to rejection of the hypothesis. This could be due to the effect of the light source on the movement of apterae, which could exert a positive phototactic response. If North is not included in the Chi-squared analysis, then the Chi-squared value produced is not significant. It is reasonable to assume therefore, that the apterae do exhibit a

Figure 4.17 Amount of time spent by individual R.padi individuals observed for 10 minute periods walking in each of eight compass directions (relative to the observer)

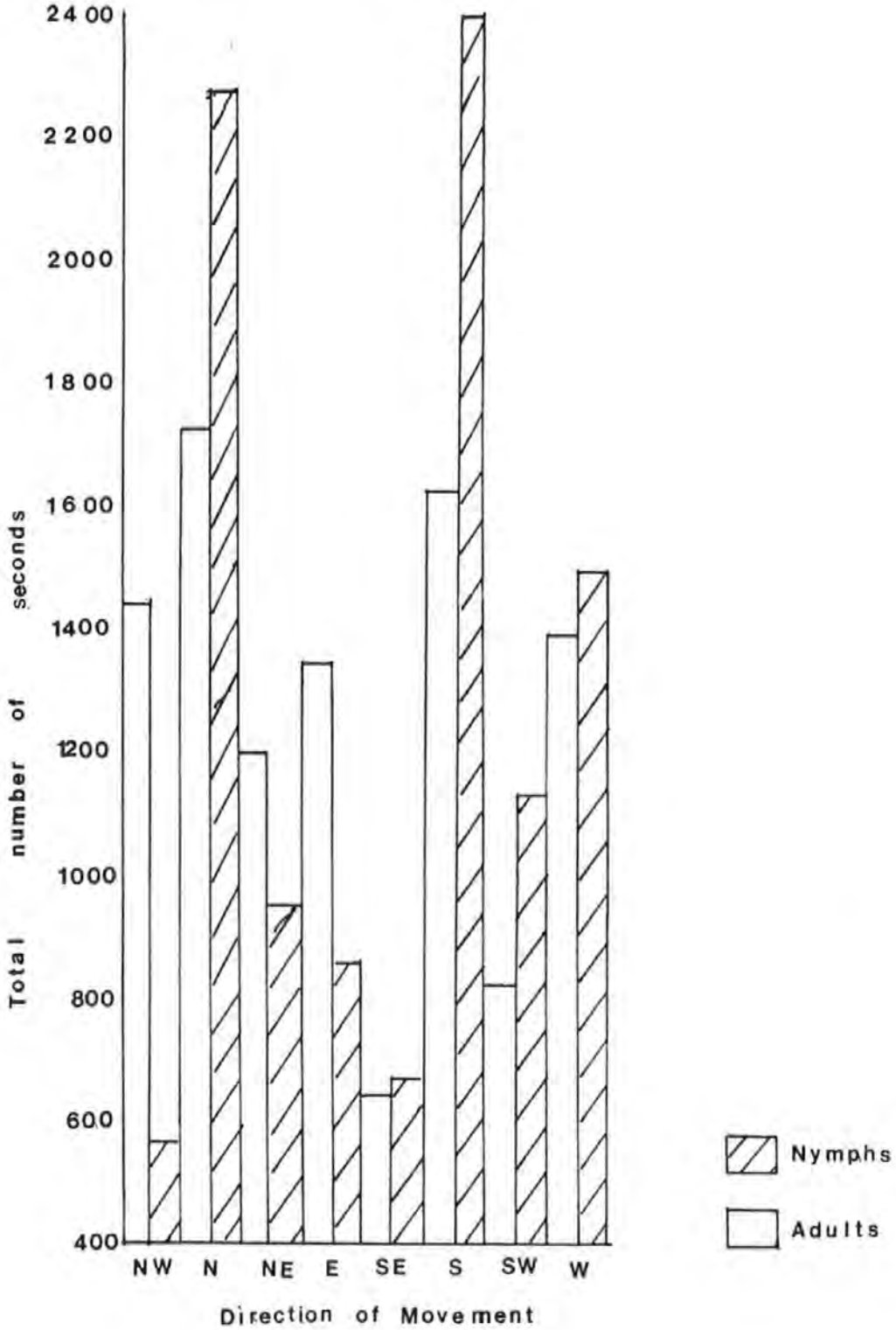


Table 4.9

Distribution of the First Direction walked by Apterous R.padi Individuals on the Soil Surface
(Adults, 4th instar alatiform and apterous nymphs pooled)

Direction on 8 compass points	Numbers of Individuals		
	Observed	Expected	
		all 8 directions	N. 7 directions
NW	10	10.5	8.71
N	23	10.5	
NE	9	10.5	8.71
E	8	10.5	8.71
SE	4	10.5	8.71
S	12	10.5	8.71
SW	9	10.5	8.71
W	9	10.5	8.71
χ^2 value		20.38 (1% significant)	4.07 (not significant)

NB 2 of the 86 observed aphids did not walk across the soil for the periods of observation.

random-walk type process in dispersal on the soil in the absence of a light.

b) Directionality of movement.

Whilst it is useful to know that movement on the soil surface is composed of a variety of different types, it is the overall direction of movement and distance travelled which is important for greater understanding of dispersal of apterous R. padi. Fig. 4.18 shows examples (to life size) of three tracks of individual apterae. Table 4.10 summarizes the number of apterae observed in each temperature, the total distance covered, number of turning movements and the mean angle of turn exhibited. These latter two calculations were made using a programme written in BBC Basic by Newell (pers. comm.), which commences with the second angle of turn after the first direction walked, and thus removes the bias due to walking towards the light. 50 individuals were observed in total, 25 at each temperature (6 $\pm$ 2°C and 11 $\pm$ 2°C), but only 24 and 19 records were usable respectively.

At the two temperatures the mean angles of turn for each individual were then used in a Mann-Whitney statistical test and found to be significantly different at the 5% level, so there was some evidence to suggest that apterae turn more at lower temperatures. There was also a significant difference in the mean distance displaced at the two different temperatures (2.7% level), but no significant difference between the mean step length between points at the different temperatures. The Mann-Whitney test for difference in the two populations of data recorded at the two temperatures was used because the data was not normally distributed.

Figure 4.18

Examples of tracks of individual apterae recorded at 6 ± 2°C (lifesize)

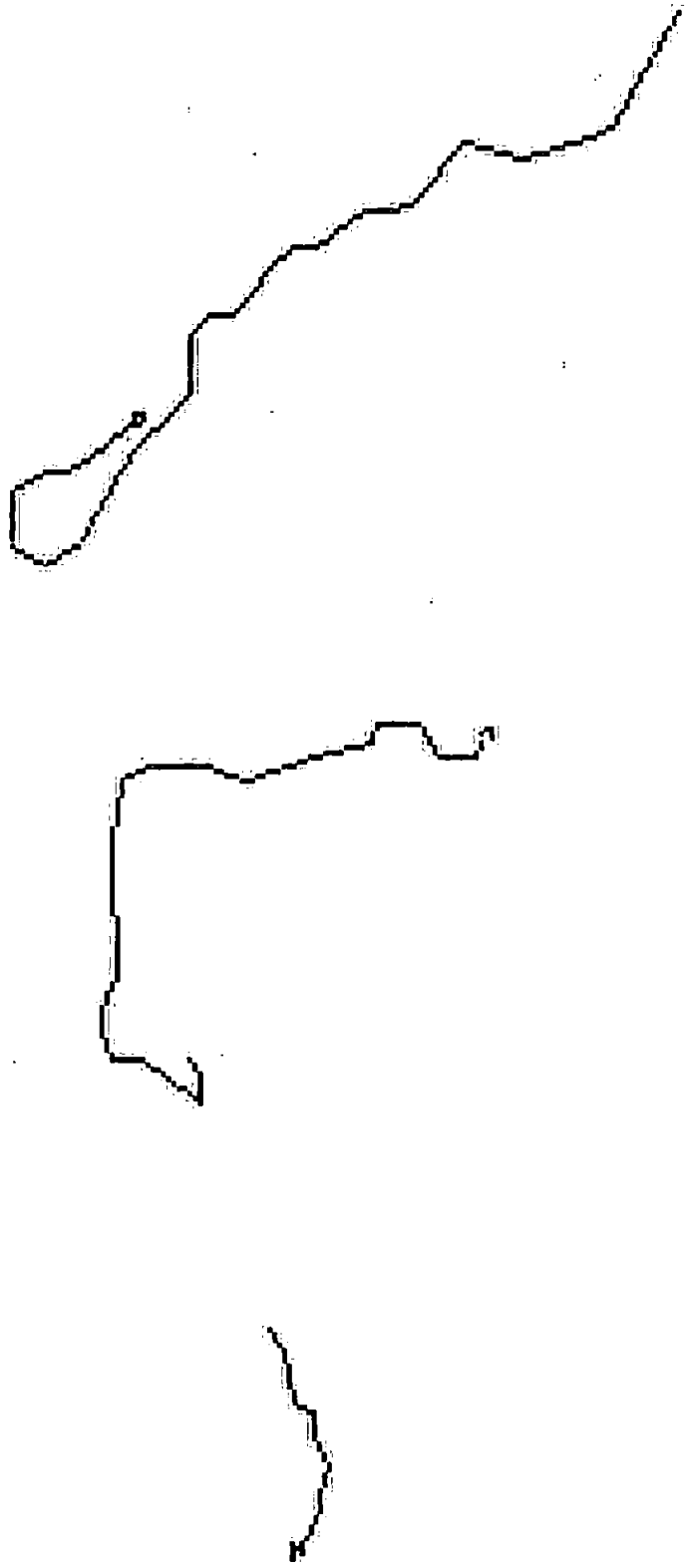


Table 4.10

Summary of the Mean Distance Walked, Mean Angle of Turn, and Number of Turns in each Class of Angle of Turn by individual R. padi (Adults, 4th instar alatiform and apterous Nymphs all pooled) in Controlled Environment Rooms

Temp. in °C	Mean Angle of Turn ± s.error	Mean Distance Travelled ± s.error	Mean Step Length ± s.error	Mean Number of Turns in Each Class in degrees ± s.error								
				0 - 20	21 - 40	41 - 60	61 - 80	81 - 100	101 - 120	121 - 140	141 - 160	161 - 180
11 ± 2	33.9 ± 3.2	95.9 ± 10.0	4.2 ± 0.4	7.5 ± 0.6	4.7 ± 0.6	4.2 ± 0.6	1.6 ± 0.3	0.5 ± 0.2	0.8 ± 0.2	0.4 ± 0.2	0.4 ± 0.2	0.1 ± 0.1
6 ± 2	42.8 ± 3.0	68.0 ± 9.4	2.9 ± 0.3	7.5 ± 1.0	3.3 ± 0.5	3.6 ± 0.6	2.0 ± 0.4	0.3 ± 0.1	0.65± 0.2	0.7 ± 0.2	0.2 ± 0.1	0.2 ± 0.1

Mean speeds for walking were 12.6mm per minute (±1.12) at 11°±° C, and 8.9mm per minute (± Ø.65) at 6° ± 2°C.

4.6.5 Discussion.

These results show that apterous R. padi exhibit a high degree of directionality in movement across the soil surface in controlled environment conditions and can reach speeds of Ø.76m an hour at 11°± 2° C, and Ø.54 m an hour at 6°± 2° C. The soil surface would not appear to be a barrier to R. padi dispersal, and tillers are easily located (Pearson 198Ø). Ferrar (1967) found that adult Myzus persicae could walk at Ø.72m an hour at 8°C on the soil surface (which is comparable) and also exhibited a high degree of directionality. These experiments also suggest that R.padi behaves similarly. This high degree of directionality and low angles of turn is likely to be advantageous for apterous R.padi inhabiting regularly spaced homogeneous host plants, since encounter with host plants is more likely than if the individuals exhibited a low degree of directionality with greater angles of turn, and spent long periods of time covering the same areas of ground. The observed distribution of angles of turn of individuals were not normally distributed, and this was found by Zaluchi and Kitching (1982) in their studies on a prosobranch gastropod. However, in the field apterae move in complex environments, where sensory imputs and environmental cues play a major role in the determination of the tracks of the animals. In these situations, it is difficult to distinguish between an animals basic or underlying movement pattern and movements due to animal/environment interaction. Field observations of apterae (Section 4.4) suggest that they could be

divided behaviourally into "walkers" and "sitters". A similar division was also seen in pea aphids, Acyrthosiphon pisum(L.), but the division was "runners" and "searchers" after dropping from the host plant (Roitberg and Myers 1979). If the "walkers" moved for only an hour in the middle of the day, when temperatures were above the "activity" threshold, at the speeds observed then movement at the rates simulated in Section 4.3 would be possible. The findings of this experiment also show that R. padi individuals can be active in the absence of a host plant in a controlled environment room at $6^{o}\pm 2^{o}C$.

4.6.6 Conclusions.

1. Apterous R. padi adults and 4th instar nymphs are able to walk on sieved garden soil at $6^{o} \pm 2^{o}C$ and $11^{o} \pm 2^{o}C$ in controlled environment rooms.

2. Adults spend more time motionless at the start of the release at lower temperatures, but this trend was not observed in the 4th instar nymphs.

3. Encounters with stones momentarily produced increases in the rate of turning of individuals, but did not affect the overall directionality of movement observed.

4. Some burrowing into the soil was observed at 6^{o} C in adults, and at $5^{o}C$ and $11^{o}C$ in 4th instar nymphs.

5. Individuals exhibited varied responses to initial encounters with plant stems and leaves.

6. There was a positive phototactic response to the lighting in the controlled environment, with 28% of all individuals commencing to walk in this direction.

7. If the variation in the data due to location of the light source

was removed, then the movement of apterous R. padi is random with respect to direction.

8. Individuals exhibit a high degree of directionality in walking on the soil, with mean angles of turn of 33.9° at 11°±2 °C and 42.8° at 6°± 2°C. The increase in angle of turn (and the concomitant decrease in directionality) observed at the lower temperature was significant at the 5 % level.

9. This difference is likely to be a behavioural response to temperature.

4.6.7 Suggestions for further work.

Observation of apterous R. padi in the following conditions :-

1. All life stages on the soil at the two different temperatures.
2. At lower temperatures on the soil.
3. On different types of soil in the laboratory.
4. In a similar manner in field conditions.
5. Walking across plants.

4.7 Investigation into the vertical movements of apterous R. padi on cereal plants in the field and in controlled environment rooms.

4.7.1 Introduction.

Direct observation of apterae in the field (Results, Section 4.4) showed that intra-leaf movement occurred throughout the daylight sampling hours. Individuals moved between leaves, into the sheltered, youngest leaf and also around the bases of the plants, during their "normal" periods of activity.

Observations in the field by other workers (Kendall and Bassett pers. comms) suggest that movement in a vertical direction may be related to temperature. More aphids have been observed nearer the top of plants on warmer days. Also, in experiments in Section 4.5, apterae were found in the soil, and it was hoped that the analysis of the data presented in this current Section may produce an insight into the time of day that this movement occurred.

Therefore, the three dimensional distribution data collected in Sections 4.4 and 4.5 was used to assess the changes in vertical distribution with time.

4.7.2 Aims.

1. To study dispersal of R. padi in a vertical plane in field conditions and in constant temperature rooms.
2. To ascertain any pattern in vertical movements of apterae.
3. To establish if any pattern is innate, or induced by environmental stimuli such as changing temperature.

4.7.3 Experimental Methods

The basic arrangements of the experimental arenas, insect cultures and sampling regimes used, are all explained in Sections 4.4.4 and 4.5.3. It was decided to use the aphid distribution data

collected from the field experiments in which daily, hourly, crop canopy, soil surface layers and the top 50mm soil temperature records were available, and for those experiments in the controlled environment rooms where temperature remained constant at either $11^{o} \pm 2^{o}$ C or $6^{o} \pm 2^{o}$ C. There were 5 field experiments which fitted this category (1S5, 2R2, 2R5, 2R6 and 2R7) and three at each controlled environment temperature.

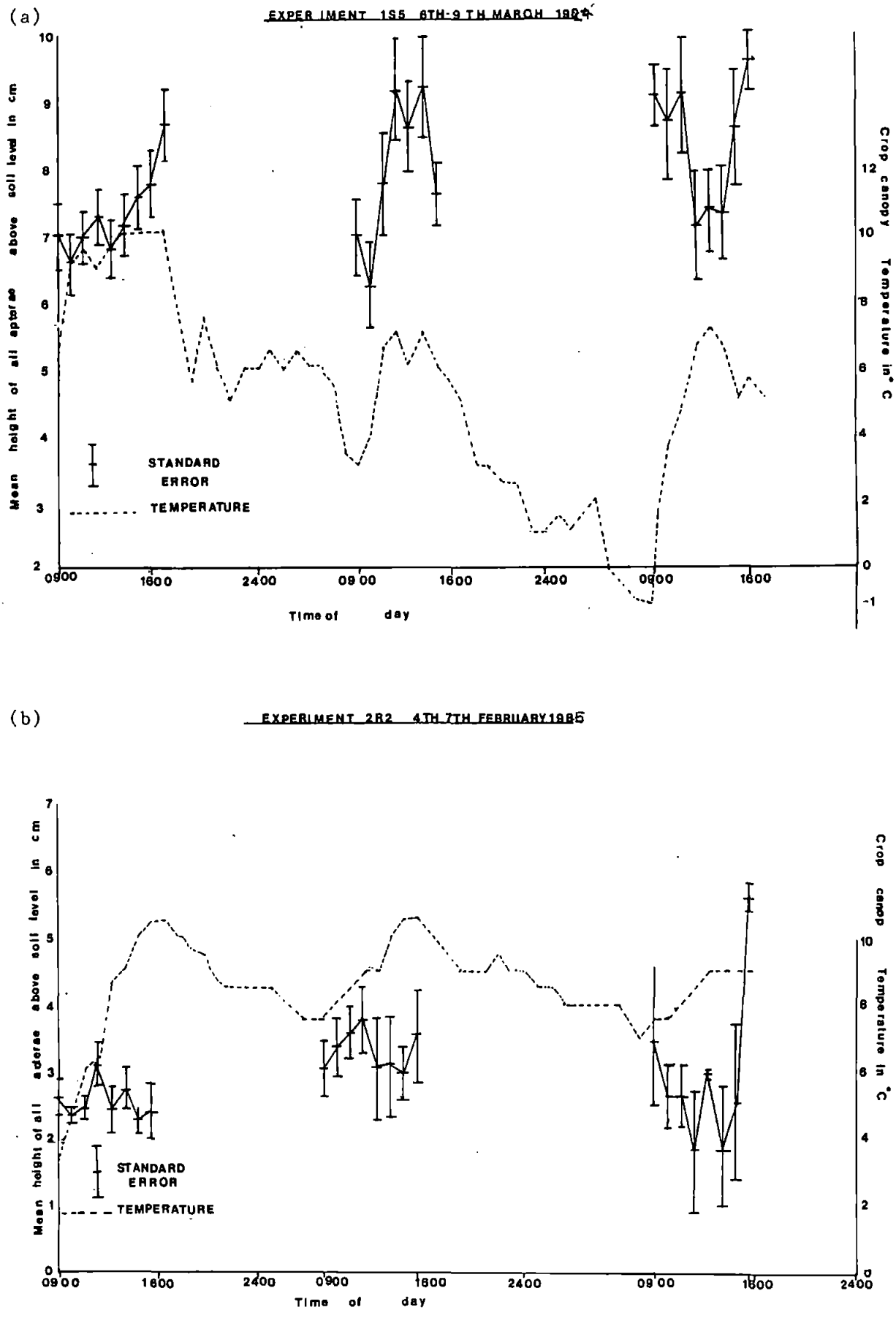
The mean height above soil level of all apterae was calculated for each hour of daylight observations for each experiment (Figs. 4.19a & b). In these calculations, apterae in the youngest leaves (the "leafcurl") were assumed to be at the height recorded for the total height of the stem in question. Whilst this undoubtedly will overestimate mean height, it was the best method available, and the only way of quantifying the heights of these particular apterae above the soil.

4.7.4 Results.

1. Field observations.

No overall diurnal pattern of movement emerges from the data presented in Figs. 4.19a & b. On day 1 in all experiments, there was an overall increase in the height of apterae above ground between 0900 and 1600 hr. It would also appear that daytime and overnight hourly crop canopy temperatures have little influence on height. Low night temperatures in experiment 1S5 between Day 2 and 3 did not appear to induce movement downward towards the soil (the mean height above soil level actually increases overnight here, and also in experiment 2R7). Indeed, in experiments 2R6 and 2R7, apterae appeared to remain stationary on the leaves from 1600 on Day 1 to 0900 on Day 2. These were generally found in sheltered positions on

Figure 4.19 To show the mean height above ground level of apterae during daylight hours



the plants (inside the youngest leaves, underneath second leaves or inside the leafsheath of the first leaf), so presumably the microclimate may be better for survival than burrowing into the soil. The soil itself was frozen anyway when these experiments were conducted.

It was decided to attempt to relate mean height above soil level of apterae with the following, (and if any correlations were obtained, use Model 1 regression analysis to describe the relationship mathematically):-

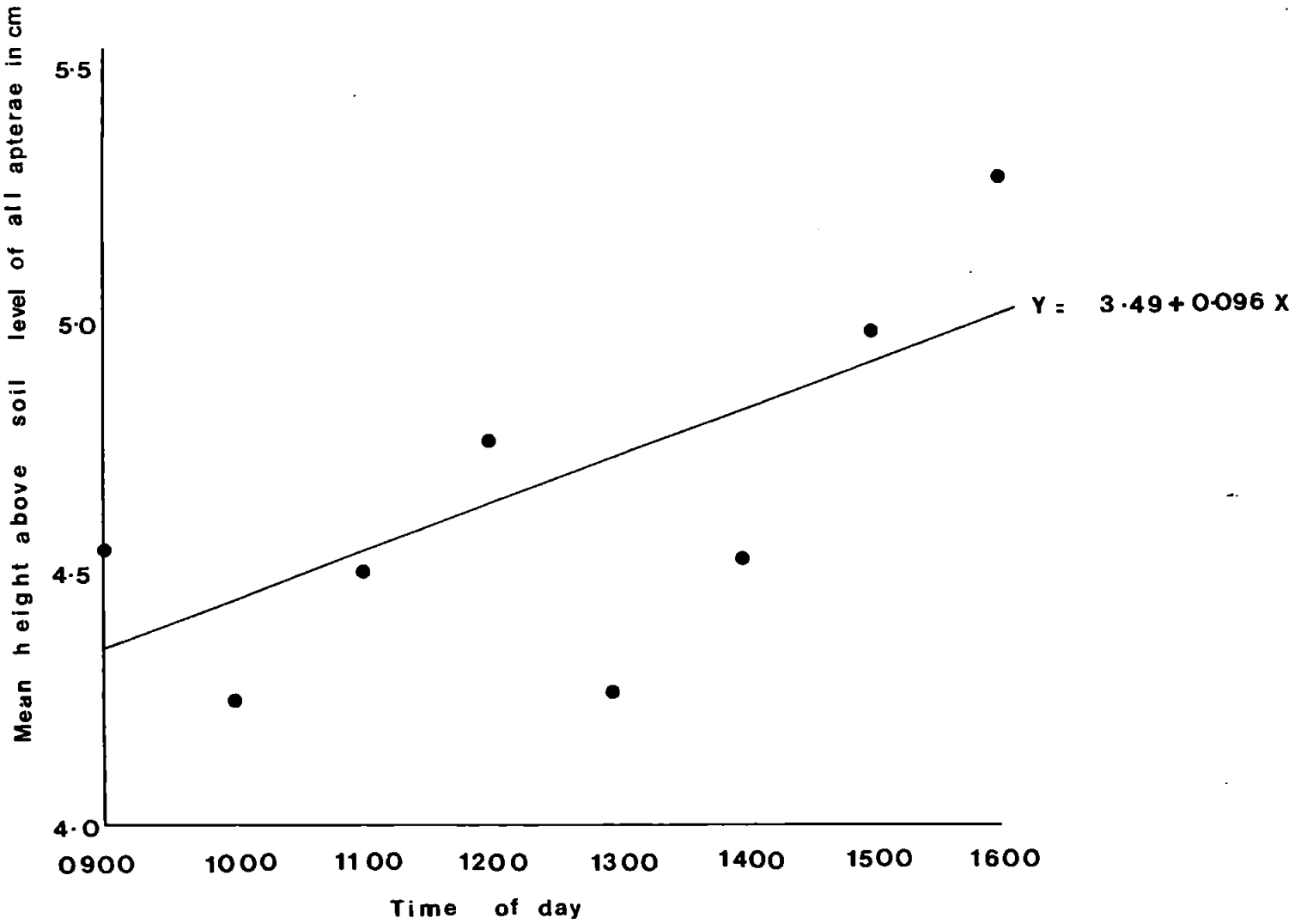
1. Temperature in the crop canopy.
2. Temperature in the surface layers of the soil.
3. Temperature in the top 50mm layer of the soil.

The only two experiments in which mean height above soil level was significantly correlated with any of these three variables were :- 1S5, mean height and crop canopy temperature, r^2 = -0.605, (1% level significant) and 2R5, mean height and soil surface temperature, r^2= 0.487 (1% level significant).

However, the temperature profiles and height distributions of the apterae for these two experiments were different, and were conducted in March 1984 and February 1985 respectively.

It was next decided to investigate the relationship between mean height above soil level of apterae and time of day, to discover if the changing vertical distribution of apterae is independent of temperature. The mean heights of apterae above soil level were calculated from pooling all data for each hour of daylight recording was made (i.e.0900h to 1600 h) and then plotted against time. A significant relationship between time of day and mean height above soil level was obtained (r^2= 0.717, significant at the 5% level),

Figure 4.20 Relationship between mean height above soil level of R.padi apterae and time of day in the field



and a regression analysis explained 41.7% of the variation (Fig 4.20).

The regression equation is

Mean height = 3.49 + 0.0966 time of day. The "t" value of the regression was just significant at the the 5% level, and so the results suggest a general upward movement of apterae on cereal plants between the hours of daylight.

2. Controlled environment room experiments.

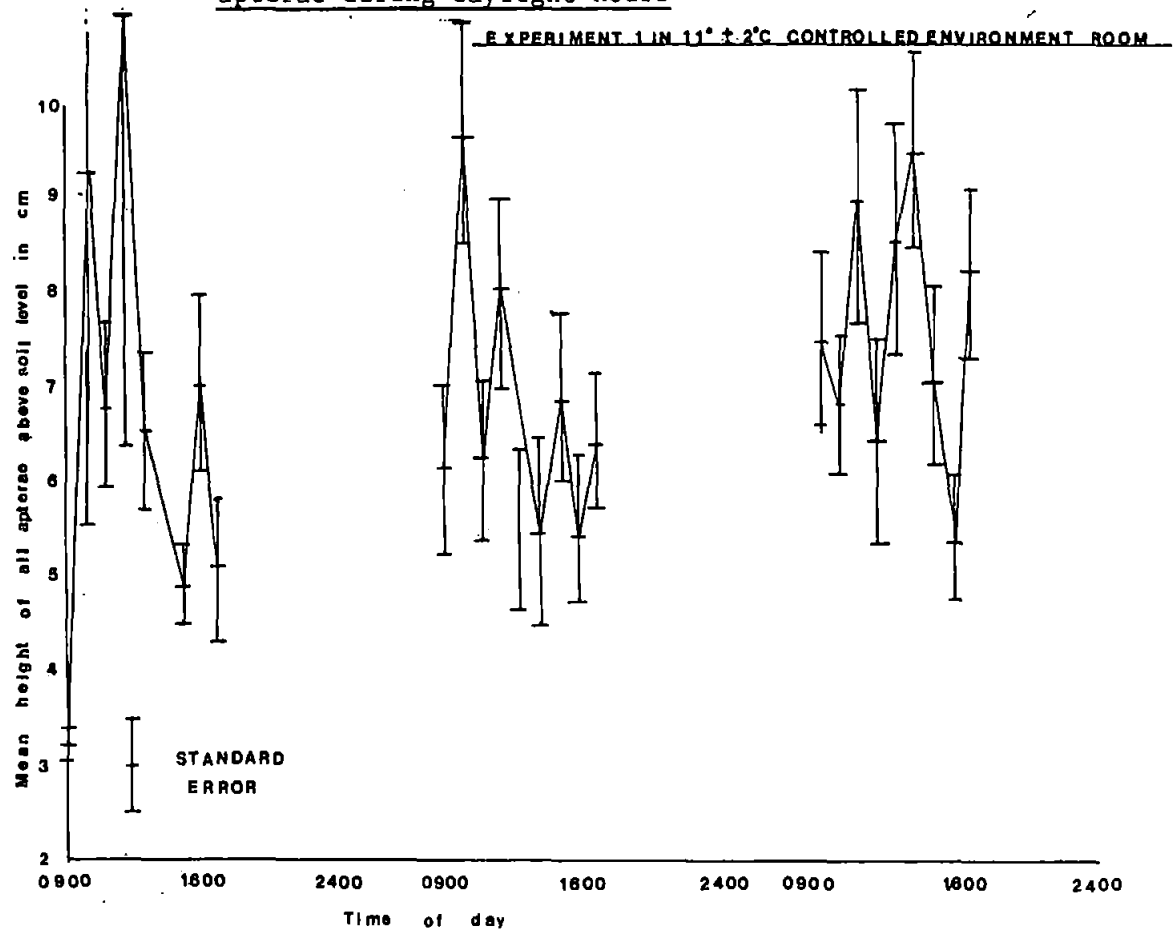
In a similar manner to the results in the field experiments, no overall pattern of vertical movement of apterae emerges. The interpretation of the distributions obtained in Fig. 4.21 was also hampered by the lack of records on some occasions in some experiments.

However, there was a greater spread in the range of heights of apterae (Fig. 4.21). At $11^{o} \pm 2^{o}C$, the general trend of movement on days 1 and 2 of experiment 1 is downwards, but not on day 3 and in the other two experiments. Overnight, there appears to be movement both upwards (Day 2-3 expt. 3) and downwards (Day 1-2 expts. 1 and 2).

At $6^{o} \pm 2^{o}C$, in all three experiments, there appears to be a general movement upwards throughout the day, and in most cases, apterae appear to remain fairly stationary overnight, as in the field (Fig. 4.21 a & b).

As in the field experiments, the mean heights of apterae above soil level were then calculated for each hour of sampling and plotted against time. There was no significant correlation or regression between time of day and height of apterae ($r^2 = 0.485$), but the shape of the relationship obtained was similar (Fig. 4.21).

Figure 4.21 To show the mean height above ground level of R.padi apterae during daylight hours



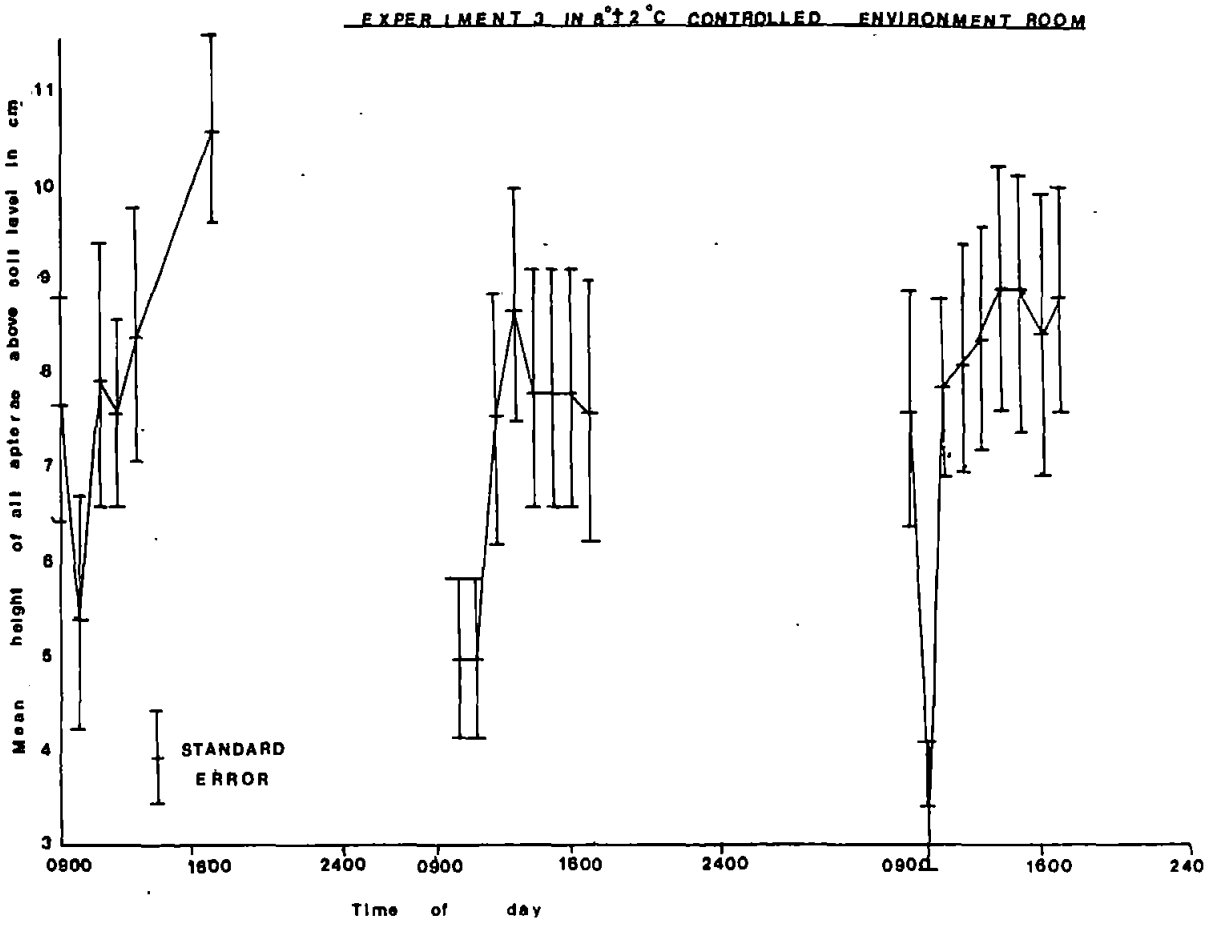
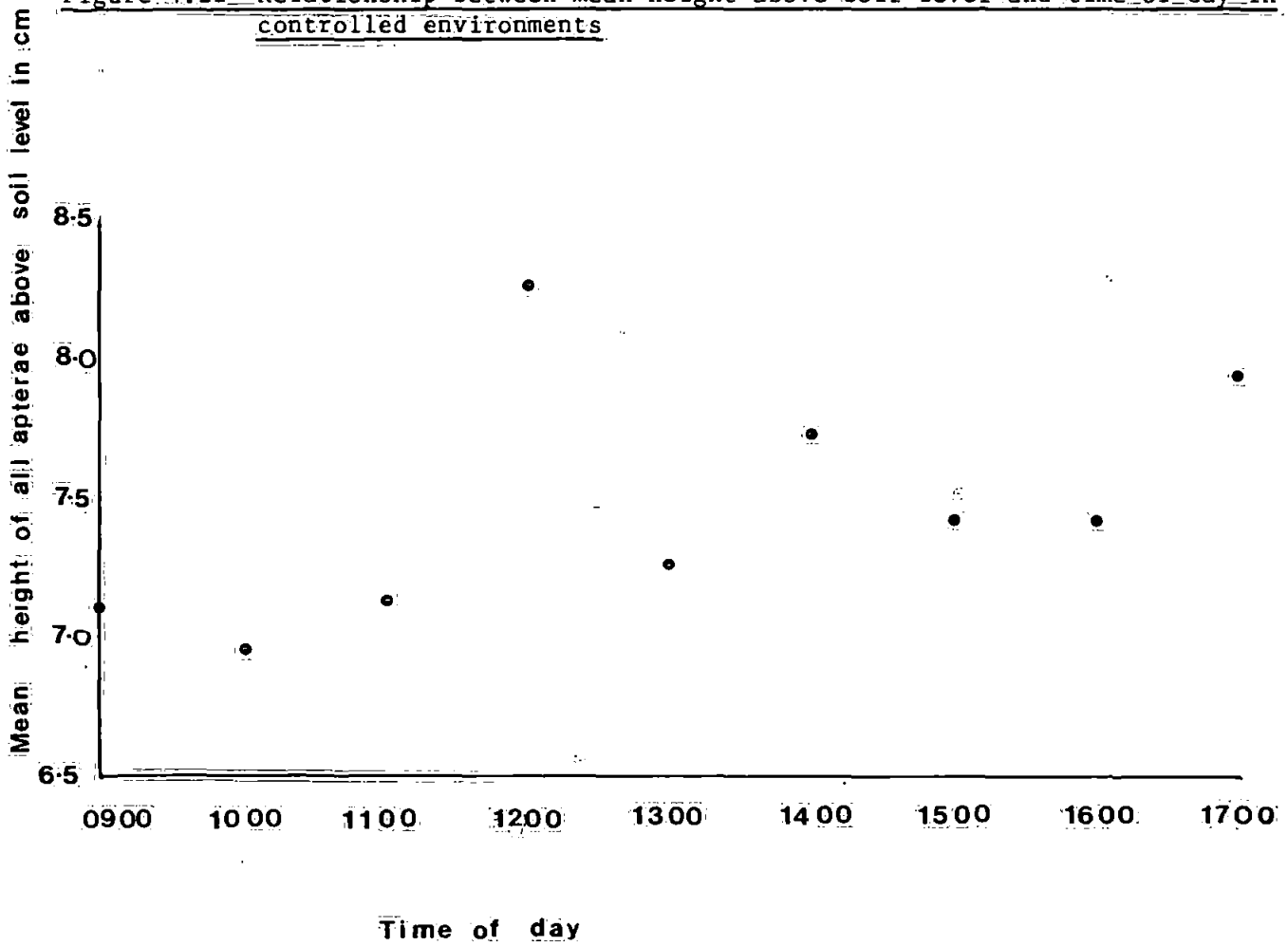


Figure 4.22 Relationship between mean height above soil level and time of day in controlled environments



4.7.5 Discussion

The results obtained in the field suggest that in two experiments the height above soil level of apterae on crop plants is significantly related to temperature in the crop canopy. In all field experiments, a significant overall trend of upward movement by the apterae throughout hours of daylight was seen.

In the controlled environment experiments, although the data obtained showed a slight similar trend, this was not significant. This suggests that this observed phenomena is induced by some environmental stimulus which was not present in the controlled environment room and is not an innate tendancy of apterous R. padi.

However, several factors may contribute to these results. Whilst it could be argued that too few experiments were used, as suggestions are based on a limited selection of all experiments conducted over 1984-1985 in Section 4.4, it was felt that restricting data to similar times of year would remove as much of the experimental variation as possible.

The hourly records of temperature revealed that apterae remained stationary, as in 2R7 when overnight temperature dropped to -1.5^{o}C. The apterae were still capable of movement the following day.

Although conditions in the controlled environment rooms were made as "fieldlike" as possible, these experiments were conducted in May - June 1985, and the innate seasonality of the R. padi culture is unknown. This may exert an influence on all the results of the controlled environment investigations.

The apterae could be moving in response to changing

nutrient distributions in the "vehicle" wheat plants. Indeed, Jepson (1983) suggested that movement of apterous M. persicae can be related to changes in the rate and content of translocate flow during leaf development.

Beween January and March, when the field experiments were conducted, winter wheat is photosynthesizing most in the higher leaves. The sugars produced will tend to stay in the higher leaves as translocation is very slow in the phloem vessels at this time of year. The lower leaves are partially shaded from the weak winter sun, and so photosynthesize less (Milthorpe and Moorby 1974). It could be speculated that the upward movement observed in apterous R. padi on winter wheat could be partly a response to increases in the sugar content of the higher, younger, leaves. However, if this was the case, the apterae would tend to remain on these leaves all the time which,clearly, they do not. Smith (1981), and Watson (1983) confirmed the results of Section 4.3, i.e. that apterae were found inside the youngest leaves, sheltered from rain and wind, and so there is very little inducement to the apterae to walk into the soil at low temperatures, as suggested by Bassett (pers. comm.).

The absence of the upward trend of apterae movement in the controlled environment rooms can be explained by the lack of environmental stress being experienced by the cereal plants. There is unlikely to be an environmental temperature or light gradient within the crop canopy. Therefore, photosynthesis is not concentrated in the higher, younger leaves, but is more uniform. Consequently, apterae distribution is also more uniform.

Apterae are capable of surviving in the soil on decomposing plant material (which is releasing useable plant sugars)

(Kendall and Bassett pers. comm.). The soil washing technique (Section 4.5) produced some evidence that apterae were in or on the soil, especially after an overnight temperature of -9°C (in the deep freeze). However, these aphids may have been in the soil because they had fallen dead from the plants due to chill injury. The results of this Section suggest that apterae do not exhibit a tendency to move into the soil as was first envisaged. Rather, they follow the sugar gradient within the host plant, and remain sheltered and stationary in adverse climatic conditions. Their increase in numbers on sunny winter days at the tops of leaves could well be due to their emerging from the "leaf curls" of the youngest leaves. This does not represent a dichotomy of results, since a vertical limit or position on plants could exist, above which apterae remain in position on the leaves at night, and below which, they move into the soil.

4.7.5 Conclusions

1. In the field, apterous R. padi were seen to exhibit a tendency to move up the crop plants during the day, which was statistically significant.
2. The mean height of apterae above soil level is significant, and positively related to temperature.
3. As the upward movement tendency was not observed in the controlled environment room experiments, it is thought that this process is due to an environmental stimulus.
4. The environmental stimulus mentioned in 3 above is probably a combination of abiotic factors such as temperature acting on the apterae, plus biotic factors such as photosynthesis in the host

plants (also related to abiotic factors themselves).

4.7.6 Suggestions for further work.

1. Extension of the experiment to include measurements of plant sugar content at regular time intervals during the hours of daylight in the field and in controlled environments.

2. Observation of apterae through 24 hour periods, using infra-red light, to discover the amount and importance of nocturnal movement.

CHAPTER FIVE

GENERAL DISCUSSION AND CONCLUSIONS

Before the Second World War, the enthusiasm with which agrochemicals were received reflects the inadequacies of the traditional non-chemical methods of pest control (Wigglesworth 1975). This led to the self-perpetuating dependence of agriculture on pesticides, and they became regarded, and in fact were, almost the only solution to crop pest protection problems (Pimental 1982).

Within ten years, however, 2 major drawbacks to purely chemical control of insect pests emerged :-

1. The selection of resistant pest strains.

2. The destruction of natural enemies, which enabled unrestricted resurgence problems after spraying, and also to the development of new pests e.g. red spider mite, Panonychus ulmi (Koch.) in fruit orchards. The situation was exacerbated by the new crop cultivars of the "Green Revolution" which were selected for high yields, but are often highly susceptible to pests and diseases.

By 1976, the era of Integrated Pest Management or Integrated Control had begun, as the biological and ecological "roots" of pest control were re-remembered (Dahlsten 1983).

Integrated control is an ecological approach to pest management and involves integration of chemical, biological and cultural techniques (Chapter one, part one). The use of economic thresholds is emphasized, the least disruptive effective procedure should be chosen, and the grower needs a holistic perspective of the ecosystem (Dahlsten 1983).

Barley Yellow Dwarf virus is carried to cereal crops by viruliferous R. padi and S. avenae alate aphids from September to

November. An effective system for forecasting the extent of the disease in crops is desirable, as the incidence of BYDV is irregular, and depends upon the strain of prevalent virus. (For example, no effects on yield were seen at Anthony 1982-1985, even though in a "high risk" area, with high numbers of aphids). Also, spraying in the last week of October-first week of November has been shown to be cost-effective when crop infestation reaches 5% or more in winter wheat. (Kendall and Smith 1983).

Forecasting must therefore aim to identify when this threshold is likely to be exceeded. The understanding and quantification of dispersal of apterae in winter crops is a major component of this. Although R. padi and S. avenae apterae were found throughout the winter at Anthony over the three winters sampled, the results of this project show that it is in the autumn and early winter up to the end of December/ early January that most dispersal (and therefore spread of BYDV) is likely to occur. After this time aphid numbers drop. Those that do survive are likely to move less as mean daily temperatures rarley exceed 7-9^{o}C. In addition, the effects of any virus they spread are likely to be negligible on such an advanced crop (Kendall et al. 1982).

Four different investigations in this project simulated or calculated dispersal rates of R. padi. It is appreciated that there are dangers in extrapolating from these small scale experiments and simulations to the real field situation. Nevertheless, taking the results at face value, a series of predictions can usefully be made about apterous R padi behaviour in the field. Simulations from the changes in spatial distribution, and the speeds of movement

calculated from direct observation of apterae walking on the soil surface in controlled environment rooms suggest that apterous R. padi are capable of walking large distances. Simulation produced estimates of mean daily distances dispersed or displaced as 0.83m per day, and observations show speeds of 0.76m per hour at $11^{o}\pm^{o}C$ and 0.54m per hour at $6^{o}\pm 2\ ^{o}C$. Obviously it would be unreasonable to assume that apterae would spend 24 hours a day walking. Field observations suggest that most movement occurs around the late morning/mid-day. A mean daily temperature of between 7 - $9^{o}C$ as an activity threshold appears to exist for movement. However, above threshold, apterae moved in some experiments, and not in others. This unknown stimulus could be wind, as its effects were not investigated. The several factors controlling movement of apterae are complex and interacting. As well as abiotic factors such as wind and temperature, biotic factors such as host plant nutrition, and intrinsic factors within the aphids themselves, their physiological, social and behavioural history are likely to be important.

Current ADAS recommendations are regionally based (Chapter one part 2), with respect to cereal aphid and BYDV control. This work suggests that mean daily temperatures are likely to be an important factor in determining the regional vulnerability of crops. Therefore forecasting the likely amount of BYDV damage is dependent upon the accuracy of forecasting weather which will occur from the time of sowing until December. Forecasting a mild autumn is difficult!

Nevertheless, the mean temperatures in areas can be calculated from metereological records. The number of days with mean daily temperatures in excess of $7^{o}C$ may be a useful measure of risk.

The location and aspect of crops should also be considered. For example, crops on south western estuaries and coastlines have been found to be particularly vulnerable. They are not only in an area of mild climate, but also tend to be exposed to the prevailing west and south west winds. If wind does increase dispersal then this should also be taken into consideration.

The severity of the problem in cereals is dependent upon the virus strain prevalent in a particular year. If the weather is likely to be cold after spraying then a treatment may not be necessary since dispersal and reproduction may be low, and applying an autumn insecticide would not be beneficial. However, if the temperature then became very mild in December, BYDV damage could occur due to an increase in secondary spread if the virus strain was severe.

Studying the dispersal of R.padi apterae by the methods used in this project has accumulated information on the nature of field behaviour. A risk assessment used in conjunction with the Infectivity Index could be one means by which insecticide use is rationalised. It is hoped that this, together with the identification of the activity threshold, will help in increasing understanding of the cereal aphid/BYDV interaction in autumn cereals and will be able to be used in increasing the rationalisation of insecticide application. That this approach is essential is illustrated by the observed significant effects on the non target fauna or cereal fields in this project, which has implications in the environment as a whole.

An increased level of integrated control of cereal aphids and BYDV in the UK will be achieved by good cultural practices such

as prevention of infection of new crops from improper disposal of previous crop residues, and the use of disease resistant crop varieties together with rational pesticide use.

Whatever the recommendations, the actual use of insecticides depends upon how "environmentally aware" a grower may be with regard to unnecessary pesticide applications, and the importance of the cereal crop to the farm income.

Given the extreme "r strategist" position of aphids in the r-K continuum of species suggested by Southwood (1977), it is unlikely that biological control of cereal aphids in the autumn could ever be achieved, and that plant breeding for resistance to BYDV may be the best avenue to pursue. Nevertheless, the importance of natural enemies should not be forgotten. This, coupled with the relatively low cost of chemical control means that the realistic goal of applied agricultural researchers must be the improvement of forecasting or risk assessment.

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APPENDICES

APPENDICES

APPENDIX 1

List of Chemical Sprays used at Anthony Estate Farm - Scientific Name and Function

Commercial Name	Scientific Name	Function
Avenge	Diphenzoquot methylsulphate	Selective post-emergent herbicide for wild oats in cereals
Bayleton	Triadmethon	Systemic fungicide to control mildew, brown and yellow rusts
Bavistim	Carbendazim	Systemic leaf and soil fungicide, controls root diseases and eyespot
Calyxin	Triademethon	Systemic fungicide to control powdery mildews and brown and yellow rusts
Captofol	Captofol	Systemic fungicide to control Septoria
CMPP	Mecoprop	Selective post-emergence herbicide for annual dicot. weeds
Corbel	Fenpropimorph	Systemic fungicide controls powdery mildews
Cycocel	Chlormequatchlorine	Growth regulator, shortens and strengthens stems, reduces lodging and increases yield
Cypermethrin	Cypermethrin	Contact and stomach acting insecticide
Oxytrilcm	Toxynil	Contact post-emergent herbicide to control annual dicot. weeds in cereals
Stomp	Pendemethalin	Selective, pre-emergent herbicide to control annual dicot. weeds in cereals
Sumicidin	Fenvalerate	Contact, highly-active field-persistent aphicide

APPENDIX 2A

Analysis of Variance Tables of the Mean Total Catch per Trap Line per Month

(a) 1982-83 b = 2 ∴ log transformation

Source of Variation	DF	SS	MS	VR and Significance
Month	9	1.4773	0.1641	2.859 **
Trap Line	9	5.8426	0.6492	11.31 **
Error	81	4.6488	0.0574	
Total	99	11.9686		

(b) 1983-84 b = 1.82 ∴ transformation = x** 0.016

Source of Variation	DF	SS	MS	VR and Significance
Month	10	0.08478	0.00848	3.926
Trap Line	9	0.01966	0.00216	0.219
Error	90	0.88697	0.00986	
Total	109	0.99142		

** = significant at 0.01% level

APPENDIX 2B

An Example of a Genstat Programme used to perform the Analyses of Variance on the Eight Groups of Polypredators

```
Genstat V         Release 4.04
Copyright 1982 Lawes Agricultural Trust (Rothamsted Experimental Station)

 1      'REFERENCE' ANOVA
 2      'UNIT' $ 60
 3      'FACTOR' TIME $ 10
 4      'FACTOR' BLOCK $ 3
 5      'FACTOR' DECIS $ 2
 6      'INPUT' 2
 7      'READ' TIME, TOTAL, DECIS, BLOCK
 8      'INPUT' 1
 9      'TREATMENTS' DECIS*TIME
10      'BLOCKS' BLOCK
11      'ANOVA' TOTAL
12      'RUN'
```

This programme is for the data set 1984I2, which had 10 occasions.

APPENDIX 2C

Key to Nomenclature of Data Sets produced by dividing the whole year's data into meaningful blocks used in the tables

Name	Year	Time Period and Description	
D1A82	1982-83	Nov 20 - Dec 21	Pre-fence erection
D1B82		Dec 23 - Jan 18	Fences up, pre-treatment
D2 82		Jan 20 - Apr 21	Post 1st insecticide application
D3 82		Apr 28 - Jun 29	Post 2nd insecticide application
D4 82		Jun 30 - Aug 5	Post 3rd insecticide application
D83	1983-84	Oct 3 - Apr 26	Post 1st insecticide application
D84		Apr 30 - Jul 2	Post 1st insecticide application similar time period to D382
D84I2		Jul 5 - Aug 20	Post 2nd insecticide application

APPENDIX 2D

Key to Columns presented in Raw Data Sets

Raw Data - sum of predators caught in each plot on each sampling occasion

Key to column contents:

C1	Occasion Number	
C2	Total predator catch	
C3	Larvae catch	
C4	Staphylinidae	
C5	Aranea	
C6	Nebria brevicolis	Catch per plot - sum of 10 pitfall traps
C7	Trechus quadristriatus	
C8	Large adult carabidae	
C9	Medium adult carabidae	
C10	Small adult carabidae	
C11	Deltamethrin treatment; 2 = treated, 1 = control	
C12	Block number	
C13	Days since start	

D1A82

1	7	4	0	0	1	2	1	0	0	1	2	1	2
1	9	5	0	0	1	3	1	0	3	2	1	1	2
1	18	3	1	3	5	6	5	0	7	1	2	2	2
1	12	0	0	1	1	10	1	0	10	2	1	2	2
2	9	1	1	0	3	4	3	0	4	1	2	1	4
2	11	0	0	0	6	2	6	0	5	2	1	1	4
2	23	3	0	0	17	2	17	0	3	1	2	2	4
2	6	1	1	0	4	0	4	0	0	2	1	2	4
3	11	3	0	0	3	3	3	0	5	1	2	1	7
3	15	1	1	0	8	5	8	0	5	2	1	1	7
3	19	3	0	0	10	3	10	1	5	1	2	2	7
3	11	3	1	0	3	1	3	1	3	2	1	2	7
4	2	1	0	1	0	0	0	0	0	1	2	1	11
4	7	6	0	0	1	0	1	0	0	2	1	1	11
4	5	4	0	0	1	0	1	0	0	1	2	2	11
4	7	7	0	0	0	0	0	0	0	2	1	2	11
5	4	2	0	0	2	0	2	0	0	1	2	1	16
5	11	1	0	0	5	5	5	0	5	2	1	1	16
5	10	3	1	0	5	1	5	0	1	1	2	2	18
5	4	0	0	0	0	3	0	1	3	2	1	2	18
6	5	1	0	0	4	0	4	0	0	1	2	1	21
6	5	2	0	0	3	0	3	0	0	2	1	1	21
6	5	0	0	1	1	1	1	2	1	1	2	2	21
6	7	2	0	0	3	2	3	0	2	2	1	2	21
7	3	0	1	0	2	0	2	0	0	1	2	1	27
7	1	0	1	0	0	0	0	0	0	2	1	1	27
7	4	1	0	0	3	0	3	0	0	1	2	2	27
7	3	1	0	0	1	1	1	0	1	2	1	2	27
8	4	0	0	0	2	2	2	0	2	1	2	1	29
8	0	0	0	0	0	0	0	0	0	2	1	1	29
8	0	0	0	0	0	0	0	0	0	1	2	2	29
8	5	2	0	0	1	2	1	0	2	2	1	2	29
9	1	0	0	0	1	0	1	0	0	1	2	1	34
9	5	0	0	0	5	0	5	0	0	2	1	1	34
9	0	0	0	0	0	0	0	0	0	1	2	2	34
9	9	0	0	0	0	0	0	0	0	2	1	2	34

D1B82

1	1	0	0	0	0	1	0	0	1	1	2	1	1
1	3	1	0	0	2	0	2	0	0	2	1	1	1
1	0	0	0	0	0	0	0	0	0	1	2	2	1
1	2	1	0	0	1	0	1	0	0	2	1	2	1
2	9	7	0	0	1	1	1	0	1	1	2	1	4
2	4	0	1	0	2	0	2	0	0	2	1	1	4
2	8	7	0	0	0	1	0	0	1	1	2	2	4
2	11	9	0	1	0	1	0	0	1	2	1	2	4
3	14	13	0	0	1	0	1	0	0	1	2	1	13
3	15	13	1	0	1	0	1	0	0	2	1	1	13
3	11	9	1	0	1	0	1	0	0	1	2	2	13
3	14	13	1	0	0	0	0	0	0	2	1	2	13
4	13	13	0	0	0	0	0	0	0	1	2	1	16
4	10	8	0	0	2	0	2	0	0	2	1	1	16
4	8	7	1	0	0	0	0	0	0	1	2	2	16
4	14	13	0	0	1	0	1	0	0	2	1	2	16
5	21	21	0	0	0	0	0	0	0	1	2	1	23
5	9	9	0	0	0	0	0	0	0	2	1	1	23
5	10	10	0	0	0	0	0	0	0	1	2	2	23
5	4	4	0	0	0	0	0	0	0	2	1	2	23

D2 82

1	2	2	0	0	0	0	0	0	2	1	2
1	9	9	0	0	0	0	0	0	1	1	2
1	2	2	0	0	0	0	0	0	2	2	2
1	4	4	0	0	0	0	0	0	1	2	2
2	5	5	0	0	0	0	0	0	2	1	6
2	9	9	0	0	0	0	0	0	1	1	6
2	7	6	1	0	0	0	0	0	2	2	6
2	2	2	0	0	0	0	0	0	1	2	6
3	7	6	0	0	1	0	0	1	2	1	9
3	11	9	1	1	0	0	0	0	1	1	9
3	7	6	0	0	0	0	0	0	2	2	9
3	8	6	2	0	0	0	0	0	1	2	9
4	3	3	0	0	0	0	0	0	2	1	13
4	9	9	0	0	0	0	0	0	1	1	13
4	5	3	2	0	0	0	0	0	2	2	13
4	5	5	0	0	0	0	0	0	1	2	13
5	4	4	0	0	0	0	0	0	2	1	16
5	4	4	0	0	0	0	0	0	1	1	16
5	5	4	1	0	0	0	0	0	2	2	16
5	5	5	0	0	0	0	0	0	1	2	16
6	3	3	0	0	0	0	0	0	2	1	23
6	5	5	0	0	0	0	0	0	1	1	23
6	5	5	1	0	0	0	0	0	2	2	23
6	6	6	0	0	0	0	0	0	1	2	23
7	1	1	0	0	0	0	0	0	2	1	27
7	1	1	0	0	0	0	0	0	1	1	27
7	0	0	0	0	0	0	0	0	2	2	27
7	2	2	0	0	0	0	0	0	1	2	27
8	1	0	1	0	0	0	0	0	2	1	30
8	1	1	0	0	0	0	0	0	1	1	30
8	0	0	0	0	0	0	0	0	2	2	30
8	0	0	0	0	0	0	0	0	1	2	30
9	9	8	0	1	0	0	0	0	2	1	37
9	2	2	0	0	0	0	0	0	1	1	37
9	2	2	0	0	0	0	0	0	2	2	37
9	6	5	0	1	0	0	0	0	1	2	37
10	16	14	0	1	1	0	0	1	2	1	41
10	5	5	0	0	0	0	0	0	1	1	41
10	6	5	0	1	0	0	0	0	2	2	41
10	11	8	3	0	0	0	0	0	1	2	41
11	5	1	0	0	1	0	0	1	2	1	46
11	5	5	0	0	0	0	0	0	1	1	46
11	3	3	0	0	0	0	0	0	2	2	46
11	4	4	0	0	0	0	0	0	1	2	46
12	3	0	1	1	0	0	0	0	2	1	50
12	2	1	0	1	0	0	0	0	1	1	50
12	2	1	1	0	0	0	0	0	2	2	50
12	3	3	0	0	0	0	0	0	1	2	50
13	2	0	0	1	0	0	0	0	2	1	57
13	4	1	0	3	0	0	0	0	1	1	57
13	6	6	0	0	0	0	0	0	2	2	57
13	8	7	1	0	0	0	0	0	1	2	57
14	11	8	0	0	0	0	0	0	2	1	60
14	5	2	1	2	0	0	0	0	1	1	60
14	3	0	1	1	0	0	1	1	2	2	60
14	5	3	1	1	0	0	0	0	1	2	60
15	7	5	0	2	0	0	0	0	2	1	64
15	5	4	1	0	0	0	0	0	1	1	64
15	8	4	0	4	0	0	0	0	2	2	64
15	8	3	0	5	0	0	0	0	1	2	64
16	4	2	0	2	0	0	0	0	2	1	68
16	4	3	0	0	1	0	0	1	1	1	68
16	1	0	0	0	0	1	0	1	2	2	68
16	4	3	0	1	0	0	0	0	1	2	68
17	3	1	1	1	0	0	0	0	2	1	71
17	1	1	0	0	0	0	0	0	1	1	71
17	2	0	0	2	0	0	0	0	2	2	71
17	4	3	0	1	0	0	0	0	1	2	71
18	2	1	0	1	0	0	0	0	2	1	74
18	3	1	1	1	0	0	0	0	1	1	74
18	2	1	0	1	0	0	0	0	2	2	74
18	2	0	0	2	0	0	0	0	1	2	74
19	6	3	0	1	0	2	0	2	2	1	82
19	5	3	0	2	0	0	0	0	1	1	82
19	2	0	0	1	0	0	1	1	2	2	82
19	4	0	0	4	0	0	0	0	1	2	82
20	4	2	0	1	0	0	1	1	2	1	85
20	2	1	0	1	0	0	0	0	1	1	85
20	2	0	0	2	0	0	0	0	2	2	85
20	5	1	0	4	0	0	0	0	1	2	85
21	8	2	1	3	2	0	0	2	2	1	88
21	5	0	0	5	0	0	0	0	1	1	88
21	1	0	0	1	0	0	0	0	2	2	88
21	7	1	0	6	0	0	0	0	1	2	88
22	6	0	1	3	2	0	0	2	2	1	92
22	5	0	0	2	3	0	0	3	1	1	92
22	4	0	1	3	0	0	0	0	2	2	92
22	6	1	0	4	1	0	0	1	1	2	92
23	5	0	0	3	0	2	0	2	2	1	96
23	3	0	0	0	1	2	0	3	1	1	96
23	5	0	1	2	2	0	0	2	2	2	96
23	5	1	0	4	0	0	0	0	1	2	96

D3 82

1	8	1	1	1	0	0	4	0	1	5	2	1	4
1	6	0	2	1	0	0	2	0	0	2	1	1	4
1	0	0	0	0	0	0	0	0	0	0	2	2	4
1	11	0	3	2	0	0	5	0	1	6	1	2	4
2	3	0	0	1	0	0	2	0	0	2	2	1	9
2	8	0	0	1	0	0	7	0	0	7	1	1	9
2	6	0	2	0	0	0	4	0	0	4	2	2	9
2	4	0	0	0	0	0	3	0	0	3	1	2	9
3	6	0	0	0	0	1	3	3	0	6	2	1	13
3	3	0	0	0	0	1	1	2	0	3	1	1	13
3	2	0	0	0	0	0	2	0	0	2	2	2	13
3	5	0	0	0	0	1	1	4	0	5	1	2	13
4	0	0	0	0	0	0	0	0	0	0	2	1	16
4	3	0	0	1	0	1	1	1	0	2	1	1	16
4	4	0	0	1	0	1	0	3	0	3	2	2	16
4	1	0	0	0	0	0	1	0	0	1	1	2	16
5	6	1	0	1	0	0	3	0	1	4	2	1	21
5	7	0	0	0	0	0	2	2	1	5	1	1	21
5	2	0	1	1	0	0	0	0	0	0	2	2	21
5	1	0	0	1	0	0	0	0	0	0	1	2	21
6	3	0	0	0	0	0	1	1	1	3	2	1	24
6	4	0	0	0	0	2	1	2	1	4	1	1	24
6	1	0	1	0	0	0	0	0	0	0	2	2	24
6	3	0	0	0	0	1	1	1	1	3	1	2	24
7	16	0	1	4	0	1	5	5	1	11	2	1	29
7	15	0	1	2	0	5	5	8	0	13	1	1	29
7	8	0	2	1	0	1	0	4	0	4	2	2	29
7	9	0	1	2	0	2	1	5	0	6	1	2	29
8	4	0	0	1	0	0	3	0	0	3	2	1	35
8	11	0	3	0	0	5	3	5	0	8	1	1	35
8	4	0	0	0	0	0	4	0	0	4	2	2	35
8	9	0	0	0	0	2	6	2	0	8	1	2	35
9	35	0	2	0	0	11	17	16	0	33	2	1	44
9	38	0	1	0	0	15	15	22	0	37	1	1	44
9	26	0	3	1	0	6	14	8	0	22	2	2	44
9	22	0	3	2	1	5	11	6	0	17	1	2	44
10	41	0	0	2	0	17	20	20	0	40	2	1	49
10	29	0	0	3	0	11	12	12	0	24	1	1	49
10	38	0	4	0	0	13	18	13	2	33	2	2	49
10	7	0	0	0	0	4	3	5	0	8	1	2	49
11	16	0	0	1	4	8	5	9	0	14	2	1	51
11	14	0	1	0	8	5	8	5	0	13	1	1	51
11	7	0	1	0	2	2	2	3	1	6	2	2	51
11	3	0	0	0	0	2	1	2	0	3	1	2	51
12	17	0	0	2	9	0	9	5	1	15	2	1	55
12	25	0	0	3	16	0	17	4	0	21	1	1	55
12	16	0	1	3	6	1	6	6	0	12	2	2	55
12	11	0	0	0	1	0	2	9	0	11	1	2	55

D4 82

1	16	0	0	2	2	4	0	6	0	14	2	1	6
1	24	6	3	1	11	7	11	7	1	20	1	2	6
1	15	0	1	0	6	1	12	1	0	13	2	3	6
1	13	0	0	0	2	4	7	6	0	13	1	4	6
2	4	0	0	0	2	2	2	2	0	4	2	1	10
2	6	0	0	1	0	3	0	4	1	5	1	2	10
2	7	0	0	0	2	4	4	4	0	8	2	3	10
2	10	0	1	0	2	4	5	4	0	9	1	4	10
3	10	0	0	0	4	4	5	5	0	10	2	1	15
3	7	0	1	1	1	0	3	4	0	4	1	2	15
3	0	0	0	0	0	0	0	0	0	0	2	3	15
3	5	0	0	0	0	4	0	5	0	5	1	4	15
4	12	0	0	0	4	3	7	3	0	12	2	1	16
4	10	0	2	0	1	2	5	3	0	8	1	3	16
4	8	0	0	0	0	2	6	2	0	8	2	3	16
4	4	0	0	0	1	0	3	1	0	4	1	4	16
5	5	0	0	0	0	2	7	2	0	5	2	1	20
5	0	0	0	0	0	0	0	0	0	0	1	2	20
5	3	0	0	0	1	0	3	0	0	3	2	3	20
5	4	0	0	0	1	2	2	2	0	4	1	4	20
6	13	0	0	0	1	11	2	11	0	13	2	1	24
6	6	0	0	0	2	1	6	2	0	6	1	2	24
6	4	0	0	0	2	0	4	0	0	4	2	3	24
6	3	0	0	0	2	0	3	0	0	3	1	4	24
7	3	0	0	0	0	3	0	3	0	3	2	1	27
7	3	0	0	0	2	0	3	0	0	3	1	2	27
7	1	0	0	0	0	1	0	1	0	1	2	3	27
7	0	0	0	0	0	0	0	0	0	0	1	4	27
8	10	0	0	1	1	4	5	4	0	9	2	1	31
8	4	0	0	0	3	0	4	0	0	4	1	2	31
8	2	0	0	0	1	0	2	0	0	2	1	3	31
8	0	0	0	0	0	0	0	0	0	0	1	4	31
9	25	2	0	0	8	4	19	6	0	25	2	1	39
9	2	0	0	0	0	0	2	0	0	2	1	2	39
9	1	0	0	0	0	0	0	1	0	1	2	3	39
9	4	0	0	0	2	0	4	0	0	4	1	4	39
10	19	0	0	0	5	6	11	8	0	19	2	1	42
10	2	0	0	0	0	1	1	1	0	2	1	2	42
10	2	0	0	0	1	1	1	1	0	2	2	3	42
10	2	0	0	0	0	0	2	0	0	2	1	4	42

D83

1	6	0	0	1	5	0	5	5	0	1	2	1	4
1	4	0	0	0	4	0	4	4	0	2	1	1	4
1	1	0	0	0	0	0	1	1	0	1	2	2	4
1	5	0	0	0	4	0	4	4	1	2	1	2	4
1	7	0	0	0	6	0	7	7	0	1	2	3	4
1	13	0	0	1	7	1	10	10	2	2	1	3	4
2	1	1	0	0	0	0	0	0	0	1	2	1	7
2	0	0	0	0	0	0	0	0	0	2	1	1	7
2	4	1	1	2	0	0	0	0	0	1	2	2	7
2	0	0	0	0	0	0	0	0	0	2	1	2	7
2	1	0	0	1	0	0	0	0	0	1	2	3	7
2	10	1	0	4	3	1	3	3	0	2	1	3	7
3	1	0	0	0	1	0	1	1	0	1	2	1	11
3	0	0	0	0	0	0	0	0	0	2	1	1	11
3	0	0	0	0	0	0	0	0	0	1	2	2	11
3	0	0	0	0	0	0	0	0	0	2	1	2	11
3	1	0	0	1	0	0	0	0	0	1	2	3	11
3	4	0	0	1	3	0	3	3	0	2	1	3	11
4	2	0	0	0	2	0	2	2	0	1	2	1	15
4	1	0	0	0	1	0	1	1	0	2	1	1	15
4	0	0	0	0	0	0	0	0	0	1	2	2	15
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7	2	0	0	1	0	2	0	0	2	2	30
7	6	0	0	0	3	1	0	4	2	3	30
7	20	0	0	0	14	5	0	19	1	3	30
8	1	0	0	1	0	1	0	1	1	1	34
8	2	0	0	1	0	2	0	2	2	1	34
8	6	0	0	1	2	3	1	6	1	2	34
8	4	0	0	0	0	4	0	4	2	2	34
8	14	0	0	0	1	13	0	14	2	3	34
8	25	0	1	0	19	5	0	24	1	3	34
9	4	0	1	0	3	0	0	3	1	1	41
9	4	0	0	2	3	1	0	4	2	1	41
9	10	0	0	0	8	0	0	8	1	2	41
9	4	0	0	0	3	0	0	3	2	2	41
9	0	0	0	0	0	0	0	0	2	3	41
9	21	0	0	1	21	0	0	21	1	3	41
10	7	0	0	0	3	4	0	7	1	1	48
10	3	0	0	0	3	0	0	3	2	1	48
10	5	0	0	1	2	2	0	4	1	2	48
10	3	0	0	1	0	2	0	2	2	2	48
10	1	0	0	0	1	0	0	1	2	3	48
10	17	0	0	2	14	1	0	15	1	3	48

APPENDIX 2E

Analysis of Variance Table for Yield of Crop at Rumleigh

1982	Source	Df	SS	MS	VR	Significance
	Block	1	5.22	5.22	2.806	Not sig.
	Treatment	-1	2.15	2.15	1.156	Not sig.
	Error	1	1.86	1.86		
	Total	3	9.23			
1983	Block	2	2.48	1.24	0.617	Not sig.
	Treatment	1	7.93	7.93	3.945	Not sig.
	Error	2	4.02	2.01		
	Total	5	14.43			

APPENDIX 2F(a)

Summer Population Counts 1983 Sitobion avenae

Date	Block	Plot	Row	Flag leaf			Ear			Total on Tillers			Grand Total		
				Alate	Adult	Nymph	Alate	Adult	Nymph	Alate	Adult	Nymph	Alate	Adult	Nymph
9 Jun	1	C	1	2	0	23	3	0	18	5	0	41	9	0	58
	2	C	2	2	0	10	2	0	7	4	0	17			
	1	T	3	3	0	22	4	0	10	7	0	32	11	0	60
	2	T	4	1	0	21	3	0	7	4	0	28			
14 Jun	1	C	1	0	0	7	0	0	3	0	0	10	1	0	19
	2	C	2	0	0	2	1	0	7	1	0	9			
	1	T	3	1	2	26	4	5	15	3	7	41	7	7	115
	2	T	4	0	0	9	4	0	65	4	0	74			
20 Jun	1	C	1	0	0	0	20	37	89	20	37	89	49	42	179
	2	C	2	0	0	2	29	5	88	29	5	90			
	1	T	3	0	1	0	61	22	123	61	23	123	62	60	133
	2	T	4	0	2	1	1	35	9	1	37	10			
30 Jun	1	C	1	0	0	0	14	62	155	14	62	155	20	94	242
	2	C	2	0	0	0	6	32	87	6	32	87			
	1	T	3	0	0	0	0	0	0	0	0	0	0	0	1
	1	T	4	0	0	1	0	0	0	0	0	1			

APPENDIX 2F(b)

Summer Population Counts 1984 S. avenae

Key

C1	Alates
C2	Adults
C3	Nymphs
C4	Block (1, 2 or 3)
C5	Treatment (1 = Control, 2 = Treated)

C1	C2	C3	C4	C5
0	0	0	1	1
0	2	20	1	1
0	0	0	1	1
0	0	0	1	1
0	23	2	1	1
0	0	4	1	1
0	0	0	1	1
0	0	0	1	1
0	0	0	1	1
0	0	0	1	1
0	0	0	1	1
0	1	19	1	1
0	0	0	1	1
0	0	0	1	1
0	0	0	1	1
0	0	0	1	1
0	0	0	1	1
0	1	7	1	1
0	0	0	1	1
0	3	1	1	1
0	0	0	1	1
0	0	5	1	1
0	0	1	1	1
0	0	0	1	1
0	0	2	1	1
0	0	12	1	1
0	1	5	1	1
0	1	2	1	1
0	0	1	1	1
0	0	0	1	1
0	0	0	1	1
0	0	1	1	1
0	0	0	1	1
0	0	0	1	1
0	2	0	1	1
0	1	1	1	1
0	0	4	1	1
0	0	0	1	1
0	3	23	1	1
0	0	0	1	1
0	0	0	1	1
0	13	26	1	1
0	0	0	1	1
0	0	0	1	1
0	1	4	1	1
0	0	0	1	1
0	24	31	1	1
0	1	0	1	1
0	3	3	1	1
0	0	0	1	1
0	0	0	1	2
0	0	0	1	2
0	1	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	1	13	1	2
0	0	0	1	2
0	0	0	1	2
0	0	7	1	2

C1	C2	C3	C4	C5
0	1	4	1	2
0	0	2	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	1	1	1	2
0	1	2	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	2	2	1	2
0	1	6	1	2
0	0	0	1	2
0	1	15	1	2
1	0	0	1	2
0	0	0	1	2
0	0	1	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	0	0	1	2
0	1	0	1	2
0	0	0	1	2
0	0	4	1	2
0	0	0	1	2
0	0	16	1	2
0	4	10	1	2
0	1	10	1	2
0	2	0	1	2
1	1	0	2	1
0	1	0	2	1
0	0	0	2	1
0	0	0	2	1
0	1	0	2	1
0	0	0	2	1
0	0	2	2	1
0	2	1	2	1
0	0	0	2	1
0	1	0	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	1	0	2	1
1	0	0	2	1
0	0	0	2	1
0	0	0	2	1

C1	C2	C3	C4	C5
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	3	16	2	1
0	0	0	2	1
0	1	1	2	1
0	0	0	2	1
0	0	0	2	1
0	7	14	2	1
0	1	0	2	1
0	2	6	2	1
0	0	0	2	1
0	0	0	2	1
1	3	5	2	1
0	0	0	2	1
0	0	0	2	1
0	0	3	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
1	2	6	2	1
0	0	0	2	1
0	0	3	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	1
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	5	93	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	3	2	2
0	0	0	2	2
0	0	3	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	5	2	2
0	0	0	2	2
0	0	2	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	8	15	2	2

C1	C2	C3	C4	C5
0	0	0	2	2
0	30	50	2	2
0	1	1	2	2
1	6	14	2	2
0	0	0	2	2
0	0	0	2	2
0	2	4	2	2
0	0	0	2	2
0	0	0	2	2
0	15	31	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
1	0	0	2	2
0	0	3	2	2
0	0	1	2	2
0	0	0	2	2
0	0	0	2	2
0	0	0	2	2
0	2	19	2	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	4	0	3	2
0	0	8	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	1	3	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	0	5	3	2
0	0	2	3	2
0	0	1	3	2
0	0	0	3	2
3	1	17	3	2
0	1	32	3	2
0	7	43	3	2
0	0	0	3	2
0	0	30	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	1	14	3	2
0	0	4	3	2
0	0	3	3	2
0	0	1	3	2
0	0	0	3	2
0	0	1	3	2
0	0	2	3	2
0	0	0	3	2
1	1	7	3	2
0	0	0	3	2
0	1	2	3	2
0	0	0	3	2
0	0	0	3	2

C1	C2	C3	C4	C5
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	2
0	0	1	3	2
0	0	0	3	2
0	0	0	3	2
0	0	0	3	1
0	0	0	3	1
0	0	0	3	1
0	1	0	3	1
0	0	2	3	1
0	0	0	3	1
0	0	90	3	1
0	0	0	3	1
0	0	0	3	1
0	0	2	3	1
0	0	1	3	1
1	0	0	3	1
0	0	0	3	1
0	0	0	3	1
0	0	0	3	1
0	0	0	3	1
0	0	0	3	1
0	0	5	3	1
0	0	0	3	1
0	0	0	3	1
1	1	9	3	1
0	0	2	3	1
0	0	1	3	1
0	1	0	3	1
0	0	5	3	1
0	0	5	3	1
0	0	0	3	1
0	0	0	3	1
0	0	0	3	1
0	0	1	3	1
0	0	0	3	1
0	0	0	3	1
0	0	0	3	1
0	0	0	3	1
0	0	4	3	1
0	0	0	3	1
0	2	48	3	1
0	0	0	3	1
1	0	2	3	1
0	0	0	3	1
0	0	0	3	1
0	0	0	3	1
0	2	0	3	1
0	1	4	3	1
0	1	0	3	1
0	1	13	3	1
0	1	0	3	1
0	0	0	3	1
0	0	0	3	1
[illegible]	[illegible]	0	3	1

APPENDIX 3A1

Maryfield Aphid Counts, Yield, Height and BYDV Code for each 1m Section

Row	Section	Jan - March Aphids			N	Crop Characteristics		
		S.avenae	R.padi	Total		BYDV Code	Yield in gms	Height in m
1	1	0	2	2		14	13.87	602
	2	0	3	3		27	15.84	815
	3	0	2	2		21	15.39	756
	4	1	3	4		29	19.17	859
	5	2	13	15		26	11.90	626
	6	1	4	5	8	22	16.57	721
	7	1	6	7		23	19.80	888
	8	0	2	2		19	14.69	739
	9	1	1	1		26	20.46	816
	10	0	10	10		26	16.95	741
2	1	0	4	4		14	13.87	602
	2	0	4	4		27	15.84	815
	3	0	5	5		21	15.39	756
	4	0	3	3		29	19.17	859
	5	1	16	17		26	11.90	626
	6	0	5	5	7	22	16.57	721
	7	1	1	2		23	19.80	888
	8	0	0	0		19	14.69	739
	9	3	8	11		26	20.46	816
	10	3	10	13		26	16.95	741
3	1	0	0	0			12.04	698
	2	0	4	4			15.70	774
	3	0	3	3			26.99	882
	4	0	1	1			8.41	590
	5	0	3	3			21.88	947
	6	2	1	3	7	Data Lost	17.38	800
	7	1	2	3			20.63	747
	8	0	0	0			13.05	823
	9	1	1	2			16.55	862
	10	0	0	0			20.72	866
4	1	0	1	1			17.57	849
	2	0	1	1			14.65	752
	3	0	3	3			14.12	804
	4	0	5	5			19.64	817
	5	7	2	9			15.10	819
	6	0	1	1	7	Data Lost	21.38	778
	7	1	0	1			18.99	783
	8	1	5	6			10.59	698
	9	1	1	2			19.53	754
	10	0	8	8			20.67	864

N = No. of Sampling Occasions

APPENDIX 3A1 cont.

Row	Section	Jan - March Aphids			N	Crop Characteristics		
		S.avenae	R.padi	Total		BYDV Code	Yield in gms	Height in m
5	1	0	5	5		23	23.20	912
	2	0	0	0		21	21.61	888
	3	2	1	3		24	18.06	856
	4	0	0	0		22	19.61	901
	5	3	1	4	5	23	21.85	910
	6	0	0	0		34	24.08	881
	7	0	0	0		30	17.50	759
	8	1	1	2		16	18.16	705
	9	1	2	3		22	14.06	783
	10	0	0	0		23	16.16	861
6	1	0	0	0		25	20.27	836
	2	0	0	0		29	15.18	804
	3	0	0	0		20	18.60	949
	4	1	0	1		21	18.35	871
	5	1	0	1		19	17.48	838
	6	0	0	0	5	16	14.02	639
	7	0	0	0		23	21.59	946
	8	0	0	0		25	23.86	930
	9	0	0	0		18	21.28	803
	10	1	1	2		18	23.50	839
7	1	0	0	0		10	7.40	317
	2	0	0	0		21	15.86	652
	3	0	0	0		25	12.07	736
	4	0	2	2		29	13.70	677
	5	0	0	0		32	12.37	832
	6	3	0	3	6	33	9.33	793
	7	0	0	0		35	11.18	824
	8	0	0	0		37	14.71	821
	9	2	2	4		33	16.14	797
	10	0	9	9		28	19.38	797
8	1	0	0	0		10	7.40	317
	2	0	0	0		21	15.86	652
	3	0	0	0		25	12.07	736
	4	0	0	0		30	13.70	677
	5	0	2	2		32	12.37	832
	6	0	1	1	4	33	9.33	793
	7	0	3	3		35	11.18	824
	8	0	1	1		37	14.71	821
	9	0	1	1		33	16.14	797
	10	0	1	1		28	19.38	797

APPENDIX 3A1 cont.

Row	Section	Jan - March Aphids			N	Crop Characteristics		
		S.avenae	R.padi	Total		BYDV Code	Yield in gms	Height in m
9	1	1	1	2		28	19.76	664
	2	1	0	1		32	14.87	784
	3	6	0	6		24	21.76	894
	4	0	0	0		18	21.63	783
	5	0	0	0	9	18	15.95	796
	6	1	0	1		21	18.07	789
	7	5	0	5		25	27.66	905
	8	2	0	2		30	16.30	890
	9	1	0	1		18	15.51	798
	10	0	0	0		21	19.44	867
10	1	0	0	0		21	18.64	752
	2	0	0	0		22	24.66	903
	3	0	1	1		22	22.33	762
	4	0	0	0		30	12.64	843
	5	0	1	1	4	26	16.24	788
	6	0	0	0		18	14.11	718
	7	0	0	0		30	11.97	607
	8	0	1	1		22	19.64	720
	9	0	0	0		23	17.03	629
	10	0	0	0		18	22.33	841

APPENDIX 3A2

Abbotscourt Aphid Counts, BYDV Code for each 1m Section

Row	Section	Oct - Dec Aphids			N	Jan - Mar Aphids			N	BYDV Code	Yield	Height
		S.avenae	R.padi	Total		S.avenae	R.padi	Total				
1	1	0	3	3		4	4	8		34	17.17	664
	2	1	2	3		2	6	8		37	13.30	573
	3	2	3	5		2	6	8		44	12.46	615
	4	0	10	10		2	4	6		33	12.15	601
	5	0	3	3		0	7	7		40	14.08	695
	6	0	1	1	13	0	5	5	10	38	15.60	694
	7	0	5	5		1	14	15		31	12.05	548
	8	0	3	3		2	8	10		38	13.88	673
	9	0	5	5		1	5	6		30	14.65	605
	10	1	7	8		1	2	3		31	18.98	742
2	1	0	16	16		3	4	7		30	11.73	729
	2	0	15	15		1	8	9		30	11.70	646
	3	1	26	27		1	12	13		26	19.30	812
	4	0	16	16		1	14	15		36	14.98	834
	5	0	10	10		2	10	12		25	16.60	805
	6	0	5	5	8	0	7	7	13	25	16.35	785
	7	0	4	4		3	11	14		34	17.93	803
	8	0	11	11		0	7	7		25	16.12	792
	9	1	7	8		1	8	9		30	15.45	780
	10	0	13	13		1	5	6		33	12.72	736
3	1	3	76	79		0	22	22		35	15.42	836
	2	0	124	124		3	15	18		29	14.06	828
	3	9	69	78		3	18	21		36	13.66	827
	4	0	41	41		2	24	27		27	12.88	786
	5	0	40	40		0	17	17		28	14.33	785
	6	0	54	54	14	0	13	13	10	26	16.71	815
	7	0	19	19		0	7	7		25	14.34	795
	8	0	32	32		3	19	22		26	11.97	693
	9	0	55	55		3	9	12		26	18.30	791
	10	0	34	34		2	3	5		27	14.49	810
4	1	0	28	28		0	29	29		28	14.81	741
	2	0	15	15		0	17	17		32	14.91	725
	3	2	12	14		0	9	9		23	13.49	660
	4	1	19	20		1	15	16		25	19.09	736
	5	0	29	29		0	10	10		24	11.06	636
	6	0	21	21	12	0	6	6	7	28	15.83	689
	7	0	19	19		0	3	3		33	11.02	666
	8	1	21	22		3	11	14		30	14.51	676
	9	0	4	4		1	9	10		27	16.44	703
	10	0	7	7		0	5	5		27	20.07	736

N = No. of Sampling Occasions

APPENDIX 3A2 cont.

Row	Section	Oct - Dec Aphids			N	Jan - Mar Aphids			N	BYDV Code	Yield	Height
		S.avenae	R.padi	Total		S.avenae	R.padi	Total				
5	1	0	4	4		0	0	0		28	15.41	758
	2	0	1	1		0	1	1		21	14.93	797
	3	0	9	9		0	1	1		16	14.46	776
	4	0	2	2		0	6	6		27	17.62	756
	5	0	3	3		0	1	1		27	18.43	761
	6	0	2	2	11	0	0	0	4	31	16.49	762
	7	0	0	0		0	1	1		27	13.69	697
	8	0	0	0		0	1	1		31	15.18	643
	9	0	0	0		0	0	0		25	17.56	680
	10	0	0	0		1	1	2		24	14.60	764
6	1	0	3	3		0	16	16		32	12.43	757
	2	0	6	6		0	7	7		20	16.35	797
	3	0	26	26		0	5	5		28	15.68	776
	4	0	2	2		0	10	10		29	16.99	756
	5	0	6	6		0	3	3		23	16.02	761
	6	0	3	3	10	0	2	2	1	24	17.90	762
	7	0	0	0		0	3	3		27	13.36	697
	8	0	1	1		0	8	8		30	13.88	643
	9	0	8	8		0	6	6		28	15.80	680
	10	0	1	1		2	2	4		27	16.83	764
7	1	0	7	7						16	10.70	531
	2	0	3	3						23	13.27	718
	3	0	13	13						16	13.73	672
	4	0	9	9						21	9.29	609
	5	0	6	6						24	17.31	834
	6	0	4	4	9	Not Sampled				23	16.05	623
	7	0	3	3						30	14.35	788
	8	0	5	5						23	13.26	794
	9	0	11	11						34	14.72	773
	10	0	15	15						31	12.81	825
8	1	0	4	4						24	12.05	859
	2	0	3	3						21	18.17	875
	3	0	5	5						20	10.62	760
	4	0	0	0						24	15.49	844
	5	0	9	9						23	13.24	802
	6	0	4	4	10	Not Sampled				21	13.82	786
	7	0	3	3						28	13.23	717
	8	0	2	2						28	14.53	774
	9	0	13	13						24	15.42	757
	10	0	0	0						29	15.43	779

APPENDIX 3A2 cont.

Row	Section	Oct - Dec Aphids			N	Jan - Mar Aphids			N	BYDV Code	Yield	Height
		S.avenae	R.padi	Total		S.avenae	R.padi	Total				
9	1	0	7	7						26	17.18	890
	2	0	1	1						24	13.02	847
	3	0	1	1						23	11.25	945
	4	0	3	3						23	13.50	957
	5	0	5	5	10	Not Sampled				36	8.78	799
	6	0	2	2						30	7.43	785
	7	0	1	1						29	11.41	838
	8	0	6	6						31	14.63	823
	9	0	14	14						27	17.77	844
	10	0	2	2						24		833
10	1	0	2	2						19	9.98	576
	2	0	0	0						23	15.02	760
	3	0	0	0						25	10.00	679
	4	0	0	0						23	11.96	681
	5	0	0	0	6	Not Sampled				18	9.16	535
	6	0	0	0						22	8.54	558
	7	0	0	0						26	12.36	656
	8	0	0	0						26	15.68	764
	9	0	1	1						26	14.00	739
	10	0	3	3						32	16.30	824

APPENDIX 3A3

Longwet Aphid Counts and Crop Characteristics for each 1m Section

Row	Section	Oct - Dec Aphids			N	Jan - Mar Aphids			N	Crop Characteristics	
		S.avenae	R.padi	Total		S.avenae	R.padi	Total		Yield in gms	Height in m
1	1	0	78	78		0	20	20		17.98	686
	2	1	55	56		0	15	15		17.57	811
	3	1	65	66		1	16	17		16.97	595
	4	1	44	45		0	10	10		14.58	744
	5	0	30	30	15	0	13	13	7	8.58	528
	6	1	41	42		0	24	24		13.27	726
	7	1	42	43		0	12	12		23.95	822
	8	7	54	61		2	14	16		15.37	803
	9	3	41	44		2	8	10		17.37	824
	10	2	78	80		1	19	20		21.16	817
2	1	1	44	45		0	11	11		11.03	548
	2	0	39	39		0	11	11		17.25	690
	3	0	48	48		2	15	17		14.34	776
	4	1	69	70		2	9	11		19.78	797
	5	1	38	39	15	0	8	8	5	14.09	701
	6	6	32	38		2	9	11		18.59	797
	7	0	43	43		1	8	9		18.80	796
	8	3	36	39		0	10	10		17.16	786
	9	4	35	39		0	7	7		18.76	807
	10	0	27	27		0	7	7		15.14	706
3	1	0	36	36		0	1	1		18.35	862
	2	1	25	26		0	10	10		17.84	810
	3	3	20	23		0	1	1		15.55	740
	4	2	14	16		0	1	1		15.77	727
	5	0	24	24	13	0	6	6	4	16.79	822
	6	14	8	22		0	4	4		16.67	840
	7	4	29	33		1	5	6		19.82	860
	8	1	11	12		0	8	8		16.28	853
	9	0	17	17		0	9	9		19.21	774
	10	0	13	13		0	9	9		16.97	866

N = No. of Sampling Occasions

APPENDIX 3B

Reagents

1. Purified γ - globulin diluted in coating buffer.
2. Enzyme labelled γ - globulin diluted in PBS-tween containing 2% PVP and 0.2% ovalbumin.
3. Enzyme substrate; p-nitrophenyl phosphate (Sigma Chemicals); 0.6 mg/ml in substrate buffer.
4. Test and control. Samples extracted or diluted in PBS-tween containing 2% PVP polyvinylpyrolidine (PVP) and 0.2% ovalbumin.

Buffers

1. PBS (Phosphate Buffered Saline) plus 0.05% tween 20

	KH_2PO_4	(0.2g)
	$Na_2HPO_4\ 12H_2O$	(2.9g)
	NaCC	(8g) in 1 litre
	KCC	(0.2g)
Optional	NaN_3 (preservative)	(0.2g)

pH 7.4

2. Coating Buffer

	Na_2CO_3	(1.59g)
	$NaHCO_3$	(2.93g)
Optional	NaN_3 (preservative)	(0.2 g)

pH 9.6 freshly made every two weeks

3. Substrate Buffer

Diethanolamine	(97 mls)
H_2O	(800 mls)

+ HCC to give pH 9.8 stored in dark bottle.

Washing carried out with a dilute (10%) solution of PBS-tween without the PVP and ovalbumin.

The reactions were stopped with 3M NaOH solution.

Appendix 4A

```
C       PROGRAM TO SIMULATE APHID MOVEMENT
C       ==================================
        REAL STEP,DIST
        INTEGER G05DYF,X
        INTEGER IONE,ITWO,ITHREE,IFOUR,IFIVE,ISIX,ISEVEN,IEIGHT,ININE,ITEN
        INTEGER NDAY,NAPHID,LEFT,RIGHT
        CHARACTER*32 NAME
        OPEN (5,FILE='SIM')
        LEFT=0
        RIGHT=0
        IONE=0
        ITWO=0
        ITHREE=0
        IFOUR=0
        IFIVE=0
        ISIX=0
        ISEVEN=0
        IEIGHT=0
        ININE=0
        ITEN=0
        PONE=0.0
        PTWO=0.0
        PTHREE=0.0
        PFOUR=0.0
        PFIVE=0.0
        PSIX=0.0
        PSEVEN=0.0
        PEIGHT=0.0
        PNINE=0.0
        PTEN=0.0
        SUM=0.0
        PRINT*,'ENTER NAME OF RESULTS FILE'
        READ (*,'(A)')NAME
        OPEN (6,FILE=NAME)
        PRINT *,'ENTER STEP LENGTH OF APHID IN METRES(EG 0.10)'
        PRINT *,'REMEMBER DATA SET NEEDS TOTAL NO OF APHIDS AT TOP'
        READ *,STEP
        PRINT *,'ENTER NUMBER OF DAYS FOR RUN TO LAST'
        READ *,NDAY
        READ (5,100)NAPHID
100     FORMAT (I3)
        WRITE (6,90)NDAY,NAPHID,STEP
90      FORMAT('DAYS OF RUN',1X,I2/'NO APHIDS',1X,I2/'STEP/DAY',1X,F5.3)
        CALL G05CCF
              DO 500 I=1,NAPHID
              READ (5,120)DIST
120           FORMAT (F5.3)
                    DO 200 J=1,NDAY
                    X=G05DYF(1,10)
                    IF(X.LE.5.0)THEN
                    DIST=DIST-STEP
                    LEFT=LEFT+1
                    ELSE
                    DIST=DIST+STEP
                    RIGHT=RIGHT+1
C                   DIST+STEP =MOVE TO RIGHT
C                   DIST-STEP=MOVE TO LEFT
                    ENDIF
200                 CONTINUE
        IF((DIST.GE.0.0).AND.(DIST.LT.1.0))THEN
        IONE=IONE+1
        ELSEIF((DIST.GE.1.0).AND.(DIST.LT.2.0))THEN
        ITWO=ITWO+1
        ELSEIF ((DIST.GE.2.0).AND.(DIST.LT.3.0))THEN
        ITHREE=ITHREE+1
        ELSEIF ((DIST.GE.3.0).AND.(DIST.LT.4.0))THEN
```

```
      IFOUR=IFOUR+1
      ELSEIF ((DIST.GE.4.0).AND.(DIST.LT.5.0))THEN
      IFIVE=IFIVE+1
      ELSEIF ((DIST.GE.5.0).AND.(DIST.LT.6.0))THEN
      ISIX=ISIX+1
      ELSEIF ((DIST.GE.6.0).AND.(DIST.LT.7.0))THEN
      ISEVEN=ISEVEN+1
      ELSEIF ((DIST.GE.7.0).AND.(DIST.LT.8.0))THEN
      IEIGHT=IEIGHT+1
      ELSEIF ((DIST.GE.8.0).AND.(DIST.LT.9.0))THEN
      ININE=ININE+1
      ELSEIF ((DIST.GE.9.0).AND.(DIST.LT.10.0))THEN
      ITEN=ITEN+1
      ENDIF
500         CONTINUE
      SUM=IONE+ITWO+ITHREE+IFOUR+IFIVE+ISIX+ISEVEN+IEIGHT
     *+ININE+ITEN
      PONE=IONE/SUM
      PTWO=ITWO/SUM
      PTHREE=ITHREE/SUM
      PFOUR=IFOUR/SUM
      PFIVE=IFIVE/SUM
      PSIX=ISIX/SUM
      PSEVEN=ISEVEN/SUM
      PEIGHT=IEIGHT/SUM
      PNINE=ININE/SUM
      PTEN=ITEN/SUM
      WRITE(6,360)PONE,PTWO,PTHREE,PFOUR,PFIVE,PSIX,PSEVEN,PEIGHT,
     *PNINE,PTEN
      WRITE(6,370)SUM
370   FORMAT('SUM OF ALL APHIDS DATA FILE SIM',F8.3)
360   FORMAT('ONE',F8.3/'TWO',F8.3/'THREE',F8.3/'FOUR',F8.3/'FIVE',F8.3
     */'SIX',F8.3/'SEVEN',F8.3/'EIGHT',F8.3/'NINE',F8.3/'TEN',F8.3)
      WRITE(6,300)LEFT,RIGHT
300   FORMAT('NO OF LEFT MOVES',I4/'NO OF RIGHT MOVES',I4)
      WRITE(6,350)IONE,ITWO,ITHREE,IFOUR,IFIVE,ISIX,ISEVEN,IEIGHT,
     *ININE,ITEN
350   FORMAT('ONE',I3/'TWO',I3/'THREE',I3/'FOUR',I3/'FIVE',I3/'SIX',I3/
     *'SEVEN',I3/'EIGHT',I3/'NINE',I3/'TEN',I3)
      STOP
      END
```

Example of model output

```
DAYS OF RUN 13
NO APHIDS 39
STEP/DAY 0.900
ONE    0.065
TWO    0.032
THREE    0.065
FOUR    0.323
FIVE    0.065
SIX    0.097
SEVEN    0.032
EIGHT    0.065
NINE    0.161
TEN    0.097
SUM OF ALL APHIDS DATA FILE SIM     31.000
NO OF LEFT MOVES 246
NO OF RIGHT MOVES 261
ONE  2
TWO  1
THREE  2
FOUR 10
FIVE  2
SIX  3
SEVEN  1
EIGHT  2
NINE  5
TEN  3
```

APPENDIX 4B

Relationships between Environmental Variables and Dispersal Rate Produced by Simulation of Aphid Movement at Abbotscourt and Longwet, 1983 - 84 and 1984 - 85

Environmental Variable	Correlation Coefficient
Mean daily temperature	- 0.283
Mean daily grass minimum temperature	- 0.481
Mean daily rainfall	- 0.369
Mean daily wind speed	- 0.119
Lowest grass minimum temperature	- 0.325
Maximum daily rainfall	- 0.189
Mean a.m. relative humidity	- 0.235
Mean p.m. relative humidity	- 0.356
Mean daily relative humidity	- 0.315

(n = 15)

APPENDIX 4C(1)

Experiments at Skardon Place Jan - March 1984

EXPT	Time in Hours since Release	Total Number Found	Number of Apterae Found						
			(Release point)	Distance classes from release					
			1	2	3	4	5	6	7
1S1	0(start)	60	60						
	19	12	12						
	20	23	23						
	21	18	16	2					
	22	10	9	1					
	24	14	11	3			1		
	26	8	7	1					
	44	2	2						
	45	3	3						
	46	2	2						
	47	1	1						
	48	0	0						
1S2	0(start)	30	30						
	1	21	21						
	3	10	9	1					
	5	11	11						
	6	10	10						
	24	7	7						
	25	10	8	2					
	26	4	4						
	48	6	6						
	49	2	2						
	50	0	0						
1S3	0(start)	57	57						
	20	52	52						
	21	29	29						
	23	26	26						
	24	21	20	1					
	26	15	14	1					
	43	8	8						
	44	7	4	3					
	45	11	4	7					
	46	5	2	3					
	47	5	2	3					
	48	6	2	4					
	49	7	3	4					
	67	5	3	2					
	68	5	3	2					
	69	5	2	3					
	70	6	1	3	2				
	71	5	3	1	1				

EXPT	Time in Hours since Release	Total Number Found	Number of Apterae Found (Release point) 1	Distance classes from release 2	3	4	5	6	7
1S4	0(start)	45	45						
	18	40	40						
	19	28	25	3					
	20	17	16	1					
	21	18	15	2		1			
	22	11	8	2		1			
	23	13	9	3		1			
	24	11	9	1		1			
	25	4	4						
	26	3	3						
	42	11	10	1					
	43	8	7	1					
	44	8	7	1					
	45	5	4	1					
	46	9	8	1					
	48	10	8	1	1				
	49	8	5	1	2				
	50	6	4	1	1				
	66	7	5	2					
	67	6	4	2					
	68	7	5	1	1				
	69	6	5		1				
	70	4	3		1				
	71	4	3		1				
	72	4	3		1				
	90	4	3		1				
	91	4	4						
	92	4	4						
	93	3	3						
1S5	0(start)	55	55						
	16	48	31	7	5	5			
	17	61	27	7	10	4	13		
	18	37	14	2	2	11	5	3	
	19	50	12	5	13	6	11	3	
	20	31	12	6	4	3	6		
	21	46	19	5	8	3	7	4	
	22	40	17	4	13	1	1	4	
	23	27	16	2	2	3	3	1	
	24	26	8	2	4	3	6	3	
	40	24	6	0	7	3	2	5	1
	41		5	0	1	7	1	4	1
	42		6	1	2	6	6	1	2
	43		6	3	4	3	3	1	7

EXPT	Time in Hours since Release	Total Number Found	Number of Apterae Found (Release point) 1	Distance classes from release 2	3	4	5	6	7
~~S5~~	44	22	4	2	1	6	5	0	4
cont.	45	22	4	2	0	8	3	0	5
	46	15	2	0	1	6	1	0	5
	47	14	2	0	1	7	2	0	4
	48	18	2	0	2	8	4	0	2
	64	17	2	2	2	5	4	1	1
	65	17	2	1	0	8	4	1	1
	55	13	2	1	0	7	2	0	1
	67	14	2	1	0	9	0	1	1
	68	17	2	1	1	8	0	4	1
	69	15	2	1	0	9	0	1	2
	70	15	1	1	1	7	2	3	0
	71	10	1	0	0	6	1	0	2
	72	11	1	0	1	6	1	0	2

APPENDIX 4C(2)

Experiments at Skardon Place November - December 1984

EXPT	Time in Hours since Start	Total Number Found	Number of Apterae Found (Release point)	Distance classes from release					
			1	2	3	4	5	6	7
2S 1	0(start)	58	58						
	19	42	42						
	20	43	42	1					
	21	40	39	1					
	22	31	29	1	1				
	23	22	21	2					
	24	26	24	2					
	25	25	26	2					
	42	36	33	3					
	43	35	32	2	0	1			
	44	27	22	4	1				
	46	34	25	5			2	1	1
	47	27	22	2	1	1	1		
	48	28	23	2	1	1	1		
	66	6	6						
	67	12	9	2	1				
	68	20	14	2					4
	69	22	15	1	1				5
	70	12	5	1				1	5
	71	14	8	1			1	1	3
	72	12	8	1				1	2
2S 2	0(start)	44	44	1	2				
	19	26	23	2	1				
	20	17	14	2	1				
	21	19	15	1	2		1		
	23	20	16		2	1	1		
	24	16	15					1	
	25	14	10		2	1	1		
	42	20	19					1	
	43	20	17		2		1		
	44	15	13		1	1			
	45	17	6		1	2	4	4	
	46	15	11				1	2	1
	47	14	6			1	4		3
	48	13	4				1	2	6
	49	11	3			1	1	3	3
	66	7	4		1			1	1
	67	10	4		1		1	3	1
	68	9	3	1				1	4
	69	10	4	1			2	2	1
	71	5	2	1			1		1
	72	10	2			1	3	4	
	73	5	2			1		2	
	96	5	1					1	3

EXPT	Time in Hours since Start	Total Number Found	Number of Apterae Found (Release point)	Distance classes from release					
			1	2	3	4	5	6	7
2S3	0(start)	37	37						
	18	32	31			1			
	19	24	22		1			1	
	20	28	22		3	1	1	1	
	21	21	17			2	1	1	
	22	34	21	1	1	4	1	3	3
	23	31	17	1		5	2	3	2
	24	26	15	1	1	1	2	4	2
	25	22	15		1	1		4	1
	42	22	11		2	2	1	4	2
	43	18	5		1	1	6	4	1
	44	19	7			2	4	1	5
	45	19	7			3	3	1	5
	46	21	6		1	4	3	1	6
	47	12	3		1	2	1		5
	48	12	5		1				4
	49	11	6		1	1	1		2
	66	18	6		1		2	5	4
	67	13	3		1		2	3	4
	68	13	5		1		1	2	4
	69	6	1		1		1		3
	70	10	3		1		2	1	3
	71	11	3		1		2		5
	72	7	2				1		4
	73	5	3						2
	90	13	1	1	1		1	2	7
	96	16	7		1		2	1	5
2S3N (no disturb-ance)	0	20	20						
	96	28		4			6	10	8
2S4	0(start)	34	34						
	18	25	25						
	19	22	21				1		
	20	20	20						
	21	14	13				1		
	22	14	14						
	23	13	13						
	25	16	16						
	42	13	13						
	43	11							
	44	12	12						
	45	8	8						
	46	8	8						

EXPT	Time in Hours since Start	Total Number Found	Number of Apterae Found						
			(Release point)	Distance classes from release					
			1	2	3	4	5	6	7
2S4	47	11	11						
cont:	48	13	11	1	1				
	66	8	6	2					
	67	7	7						
	68	7	6				1		
	69	8	8						
	70	8	8						
	71	7	6				1		
	72	6	5				1		
	73	5	5						
	95	4	3	1					
2S4N (no disturb-ance)	0	40							
	95	1	1						

APPENDIX 4C(3)

Experiments at Rumleigh January - March 1985

EXPT	Time in Hours Since Start	Total Number Found	Number of Aphids Found						
			(Release point)	Distance classes from release					
			1	2	3	4	5	6	7
2R1	0	24	24						
	17	7	6	1					
	18	9	9						
	19	11	11						
	20	9	9						
	21	3	3						
	22	4	3	1					
	23	3	3						
	24	3	2	1					
	42	4	3	1					
	43	4	3	1					
	44	3	3						
	45	4	4						
	46	3	2	1					
	47	3	2	1					
	48	3	2	1					
2R2	0	47	47						
	17	33	32	1					
	18	39	36	2	1				
	19	40	34	4	2				
	20	29	27	1	1				
	21	31	29	1	1				
	22	32	26	5		1			
	23	25	21	3	1				
	24	24	20	3	1				
	41	21	18	2	1				
	42	18	16	2					
	43	19	13	3	1	2			
	44	15	12	3					
	45	10	7	3					
	46	10	7	3					
	47	13	10	3					
	48	14	9	4				1	
	65	5	4	1					
	66	4	3	1					
	67	4	3	1					
	68	5	5						
	69	4	4						
	70	5	5						
	71	6	6						
	72	3	3						

EXPT	Time in Hours Since Start	Total Number Found	Number of Aphids Found (Release point)	Distance classes from release					
			1	2	3	4	5	6	7
2R3	0(start)	65	65						
	17	36	36						
	18	29	29						
	19	33	33						
	20	26	26						
	21	32	32						
	22	30	30						
	23	31	30	1					
	41	11	11						
	42	25	25						
	43	29	29						
	44	27	27						
	45	29	29						
	46	25	25						
	47	23	23						
	48	25	25						
	65	28	28						
	66	28	28						
	67	27	27						
	68	31	31						
	69	25	25						
	70	25	25						
	71	24	24						
	72	25	25						
2R4	0(start)	37	37						
	17	27	27						
	18	26	25	1					
	19	28	27	1					
	20	23	22	1					
	21	22	21	1					
	22	24	23	1					
	23	27	23	4					
	24	22	18	4					
	41	11	9	2					
	42	13	11	1	1				
	43	19	17	1	1				
	44	21	19	1	1				
	45	34	30	3	1				
	46	24	20	2	2				
	47	33	29	2	2				
	48	29	26	1	2				
	65	22	21	1					
	66	17	16	1					
	67	17	15	1	1				
	68	18	17	1					
	69	19	18	1					

EXPT	Time in Hours Since Start	Total Number Found	Number of Aphids Found						
			(Release point)	Distance classes from release					
			1	2	3	4	5	6	7
2R4	70	20	18	2					
cont.	71	20	18	2					
	72	16	14	2					
2R5	0(start)	42	42						
	17	32	27	5					
	18	31	29	1	1				
	19	29	28		1				
	20	28	25	1	2				
	21	20	18	2					
	22	23	23						
	23	27	24	2	1				
	24	23	20	2			1		
	40	10	9	1					
	41	11	10	1					
	42	9	7	1		1			
	43	7	5	2					
	44	9	9						
	65	4	4						
	66	3	3						
	67	4	2	1			1		
	68	2	2						
	69	3	3						
	70	2	1	1					
	71	3	2	1					
	72	3	3						
	89	3	3						
	90	1	0		1				
	91	0	0						
	92	1	0		1				
	93	0	0						
2R6	0(start)	187	180	7(on soil)					
	1	152	142	10					
	2	139	131	8					
	3	138	128	10					
	4	96	81	14	1				
	5	113	102	10	1				
	6	116	100	12	2	2			
	24	108	94	9	5				
	25	121	107	7	6	1			
	26	104	91	4	7	1		1	
	27	100	91	4	4		1		
	28	95	86	7	1		1		

EXPT	Time in Hours Since Start	Total Number Found	Number of Aphids Found (Release point) 1	Distance classes from release 2	3	4	5	6	7
2R6	29	93	83	3	3	2	2		
cont.	30	93	85	2	3	1	1	1	
	31	108	96	6	3	1	2		
	48	93	87	6					
	49	85	74	8	3				
	50	98	83	13	2				
	51	85	72	8	4			1	
	52	88	75	8	3				
	53	79	67	9		2		1	
	54	79	66	7	5			1	
	55	69	62	6				1	
	72	65	58	7					
	73	73	51	10			11	1	
	74	68	64	3	1				
	75	52	43	6	3				
	100	54	54						
2R7	0(start)	90	90						
	1	67	67						
	2	52	51	1					
	3	54	46	8					
	4	55	50	1	3	1			
	5	38	36	1		1			
	6	50	45	4		1			
	7	48	44	3					
	24	31	26	4		1			
	25	32	27	5					
	26	34	27	5		2			
	27	39	32	5	1		1		
	28	40	35	3		1	1		
	29	40	28	10	2				
	30	38	31	5	2				
	31	31	22	9					
	32	27	22	5					
	48	27	18	6	1	2			
	49	33	22	10		1			
	50	26	17	9					
	51	26	19	7					
	52	22	14	8					
	53	11	8	2	1				

EXPT	Time in Hours Since Start	Total Number Found	Number of Aphids Found (Release point)	Distance classes from release					
			1	2	3	4	5	6	7
2R8	0(start)	27	27						
	1	22	20	2					
	2	19	19						
	3	11	10	1					
	4	9	4	5					
	5	8	5	3					
	6	9	4	5					
	7	6	5	1					
	24	5	3		1	1			
	25	1	1						
	26	1	1						
	27	2	0	2					
	28	4	2	2					
	29	3	2	1					
	30	4	2	2					
	31	3	1	2					
	48	2	2						
	49	1	0	1					
	50	1	0	1					
	51	1	0	1					
	52	3	1	2					
	53	1	0	1					
	54	2	1	1					
	72	1	0	1					
2S9	0(start)	383	383						
	1	215	214	1					
	2	204	193	5	6				
	3	178	170	3	4	1			
	4	176	174	2					
	5	134	128	4	1	1			
	6	132	125	5	1	1			
	7	133	123	8		2			
	24	134	118	13		5	1		
	25	126	112	11		2	1		
	26	104	80	10	1	3	1		
	27	84	70	10	3	1			
	28	84	76	6	2				
	29	96	78	15		3			
	30	88	70	14	2	2			
	31	79	63	9	2	5			
	48	87	71	7	1	8			
	49	73	60	7	1	5			
	50	83	69	8	1	5			
	51	85	73	8	1	3			
	52	83	72	9		2			
	53	94	84	8		2			
	54	81	63	12	5				1
	55	97	87	5		2	1	1	1
	80	41	32	5	1	3			

APPENDIX 4D

Controlled Environment Room

EXPT	Time in Hours Since Start	Total Number Found	Number of Aphids Found						
			(Release point)	Distance classes from release					
			1	2	3	4	5	6	7
1 at 11° ± 2°C	0(start)	95	95						
	1	72							
	2	79	77	1	1				
	3	69	67	1		1			
	5	65	60	1	2	2			
	6	75	68	4	2	1			
	7	65	56	5	3	1			
	10	63	50	7	4	2			
	24	61	50	1	4	6			
	30	65	51	9		5			
	48	66	39	17	6	3			
	52	53	30	13	3	2	1		
	72	56	27	14	7	7	1		
	79	36	16	14	2	3			
	96	37	20	11	3	4			
	100	45	18	13	9	5			
2 at 11° ± 2°C	0(start)	129	129						
	6	90	85	3	1	1			
	24	72	52	15	3	2			
	30	68	44	12	2	7	1		
	48	72	51	3	6	9	3		
3 at 11° ± 2°C	0(start)	56	56						
	5	39	36	1	2				
	8	46	43	1	1	1			
	24	42	41		1				
	28	40	33	2		5			
1 at 6° ± 2°C	0(start)	126	126						
	1	111	111						
	2	125	125						
	4	106	92	14					
	6	79	70	8	1				
	7	77	71	5	1				
	8	76	69	5	2				
	24	69	57	10	1	1			
	25	64	47	13	1	3			
	26	64	50	9	4	1			
	27	62	48	9	4	1			
	29	70	58	10	1	1			
	30	76	58	14	2	2			
	31	73	56	12	4	1			
	48	65	51	10	4				
	49	65	38	21	6				
	50	64	36	21	7				

EXPT	Time in Hours Since Start	Total Number Found	Number of Aphids Found (Release point) 1	Distance classes from release 2	3	4	5	6	7
1 at 6° ± 2°C cont.	51	59	37	19		3			
	52	55	35	17		3			
	53	46	28	14	3	1			
	54	46	25	16	3	2			
	55	72	35	23	8	6			
2 at 6° ± 2°C	0(start)	52							
	8	36	32	13	1				
	24	34	32	2					
	29	35	31	4					
	32	33	31	2					
	48	33	30	2	1				
	56	36	29	4	3				
3 at 6° ± 2°C	0(start)	44	44						
	4	34	33			1			
	5	33	31		1	1			
	7	32	30		1	1			
	24	36	34			2			
	25	35	32		2	1			
	26	35	32		2	1			
	27	39	36		1	2			
	28	33	31		1	1			
	30	32	31			1			
	48	32	30		1	1			
	49	35	31		3	1			
	50	34	31		2	1			
	51	34	29	1	2	2			
	52	34	29	1	2	2			
	53	36	29		2	5			
	54	34	28	1		5			
	55	32	26			5			
	56	40	31	2	1	6			
	72	32	22	2	1	7			
4 at 6° ± 2°C (increasing to 9°C)	0(start)	49	49						
	8	51	50	1					
	24	47	46	1					
	30	48	47	1					
	32	44	40	4					
	48	43	37	3	2	1			
	72	46	31	7	1	7			
5 at 6° ± 2°C	0(start)	34	34						
	24	29	25	3	1				
	30	31	26	3	2				
	48	20	15	3	1	1			
	56	25	19	3	2	1			
	72	34	26	5	2	1			

APPENDIX 4E

Summary of Investigations into the Effects of Temperature on Dispersal Rates of R.padi

EXPT	Temp. Regime Day °C	Night °C If -4°C reduces to -9°C	APHIDS Number Released Alates	Adults	1st Instar Nymphs	2nd-4th Instar Nymphs	4th Instar Alati-form Nymphs	Total	Number Recaptured (all recaptures on release plant unless specified) Alates	Adults	1st Instar Nymphs	2nd-4th Instar Nymphs	4th Instar Alati-form Nymphs	Total	Notes	Mean Distance Dispersed In cm
1	5	-4	1	1	14	20	5	37		1	13	16	2	35		
												2			At release point in soil	0.2
												1			At plant 7cm in soil	
2	5	-4		4	5	18	1	28		3	2	13	2	28		
												1			On plant 10cm dist	
										1	2				On plant 5.5cm dist	1.2
												3			At release point in soil	
												1			At plant 7cm in soil	
3	5		1	2	2	26	6	37		2	2	26	5	37		
										1		1			On plant 10cm dist	0.5
4	5	-4	1	3	2	8	0	14	1	3	0	5	0	10		
												1			At release point in soil	0.0
5	5	-4	1	2	6	4	2	15		2	5	3		11		
												1			On plant 14cm dist	1.3
1	11±2	-4	2	4	2	9	3	20	2	3	5	8	3	20	3 1st instars deposited during expt.	
												1			On plant 13.5cm dist	
										1					On plant 5.5cm dist	
2	11±2	-4	1	5	5	7	1	19	0	3	7	5		21		
									1	1		1			On plant 10cm dist	
										1		1			On plant 5.5cm dist	1.2
												(11)			Nymphs deposited on plant 10cm dist	
3	11±2	-4	1	6	6	6	0	13	1	4	6	4	0	13		
										2		2			At release plant in soil	0.0
4	11±2	-4	1	3	3	13		20	1	2	3	7	3	20	3 4th instars developed into adults	
										1		2			On plant 14.5cm dist	1.95
												1			On plant 10cm dist	
5	11±2	-4		3	3	14		20		2	4	6		16		
										1		1			On plant 13.5cm dist	2.66
												2			In soil 14.5cm dist	
1	5	5	1	8	20	28		57	1	8	18	28		57	Developed from 1st instars	
												2				
2	5	5		1	5	13	1	20		1	5	13		19	1 shed cuticle found, so 1 nymph could have developed into an alate	Not calcul-ated
3	5	5	1	4	14	22	1	39	1	4	2	21	21	28	Staphylinid beetle found in soil	
4	5	5		1	3	13	1	18		1	3	23	1	28	Increases due to deposition of 1st instar nymphs	
												6				
5	5	5		4	10	30	3	37		4	10	30	3	37		
											3				Deposited during experiment	

APPENDIX 47 (1) ADULTS

The Time in Seconds spent by R.padi individuals observed Walking in the Soil Engaged in Various Activities in Controlled Environment Rooms

Aphid observed	Temp.	Plant Related Activities			Direction of Walking								Burrowing into Soil	Turning on Soil	Orientate on Soil	Gap Related Activities	Stone Related Activities
		Encounter	Walking on Stem or Leaves	Stopped	NW	N	NE	E	SE	S	SW	W					
1	5°									19	17			31	488	23	22
2							18	23	41	153	98	20		14	57	103	73
3					18		36	6		17				48	461	14	
4	6/7°				7		4	12	28	19	48	121		39	190	78	53
5					16	43	9						9	27	254	173	69
6					18	61	100	49						63	31	41	237
7					59	41	0	15		120	59	43		7	80	91	85
8					4	95	53	60	25	46	23	37		68	53	75	61
9								73	71	160	35	12			26	43	180
10					13	38	60	13		92	61	98		8	14	100	103
11					7	89		14		17	38	35		136	87	107	57
12						11	29	123	86	98				33	149	63	8
13					39	61	57	64	9	19				8	126	83	34
14						26	116							105	211	94	48
15						20	171	81	17	15	9			10	53	127	95
16					6	31		14	79	52	11	20	45	18	223	44	42
17					30	157	73	60	13	88	10				23	85	61
18		14	44		125	22					9	93	16	67	69	66	75
19					28	78	35	51	41	19	32	79		61	105	26	45
20					61	58		8	13	55	56	75		30	137	72	35
21										8				104	488		
22				30		19	30	10		12	14	13		116	233	14	109
23	9°				122	32						44			137	89	176
24							62	41	8	36		2		11	16	61	32
25		9	132	53			10	103	44	4	16				100	124	5
26					24	116	56	30						8	42	169	152
27	10°				21	83	8	26		28	43			99	152	117	23
28		17			217	31				24	27	110		25	46	73	123
29			327				34	20		19	11	16		3	153		17
30		144	54	185		69	15	36				19			6	4	65
31					142	43	30	113	21	8	9	89		71	17	24	136
32						94	26	9	28	157		6		11	14	29	226
33					35	37	7			79	18	63		103	64	84	111
34		6	40		44	71		65				115		76	40	80	183
35						33		36	17	118	32	11		27	59	103	164
36		9	182	98	18	61	46	94		11	16			11	135	9	139
37	11°		35		45	66						48			5	72	58
38					63		49	36	29	14	64	45		30	49	100	121
39		3	30		53	33	49					31		15	17	193	174
40							20	37	79	71	28	4		4	45	132	180
41		8	28		17	80		20		24		34		79	17	41	277
42		17			217	31				24	27	110		25	46	73	123
Total Time		227	879	366	1451	1730	1203	1342 649	1626		811	1393	70	1611	4820	3099	3990

APPENDIX 4F (2) NYMPHS

Aphid observed	Temp.	Plant Related Activities			Direction of Walking								Burrowing into Soil	Turning on Soil	Orientate on Soil	Cap Related Activities	Stone Related Activities
		Encounter	Walking on Stem or Leaves	Stopped	NW	N	NE	E	SE	S	SW	W					
1	5°				59	53	10			19	44	52			63	134	164
2						27	10	33	17	35		19	262	16	100	81	
3						117	110	84		30		2		31	66	121	39
4					12	48	111	101	19	34					35	118	22
5						15	41	74	56	131	31	63		40	29	82	38
6	6/7°					64		11		15		24		44	363	0	38
7		8	11		12			20	17	68	18	29		74	44	105	194
8					10	29		37	38	14	11	35		93	20	83	230
9					13		21			56	84	39	18	100	55	63	151
10					33	48	47	14		36	16	60		110	70	59	107
11					30	157	73	60	13	88	10				23	85	61
12	9°				36	112	22			53		92		53	108	86	38
13					14	70	6	8		83	134	92		22	47	102	28
14	10°				8	107	77		22	3		21		26	28	161	147
15						28	113								406	53	
16		11	59	62	12	43	14		50	84				38	52	70	105
17					49	107	21	19		96				49	88	80	91
18															600		
19		4	154	30	11		40	38	19	78	16	14		15	13	109	59
20		101	39					38	33	170	46	14		33	34	20	82
21			139	102		110			7	72	60	11		25	24	16	34
22					89	99	3	19	93	6	8	13		70	18		99
23					72	10		24				115		307	64	50	
24										45	229	211		51	84		
25						480				80					14		26
26						100				199		78			129		94
27						49		99		358				30	18		46
28						41				314		193			36	16	9
29	11°				16	79	69	17	68	7	25			48	157		69
30					13	60	18	17			10	59			40	33	68
31										16	50	34			7	96	92
32						49	50	35	74	4				4	83	41	260
33		7	140		4				15	42	39	64			84	81	125
34			41			11		9		85	98	18			82	65	191
35						50								24	391	46	89
36					27	5	6		12	12	22	47		20	108	157	144
37					5					47	88	14			213	135	98
38					35	6	41	24	27			15			184	117	157
39		11	110	60	37	5					85	4		4	32	131	121
40	5°				24	93	17	15	27	4		67		62	70	87	134
41	6/7°					13	41	35	37	8				98	78	121	169
Total Time		142	693	254	571	2285	955	831	634	2392	1124	1499	780	1487	4162	2804	3435

APPENDIX 4G

Summary of Observations of Apterous R Padi at Different Temperatures

1. At 6 ± 2°C

Life Stage and Number		Mean Angle of Turn	Total Distance Moved in mm	Mean Step Length	No. of Turns in each Class (in °) to right and left								
					0-20	21-40	41-60	61-80	81-100	101-120	121-140	141-160	161-180
Adult	1	22.3	112	3.7	15	6	0	2	-	-	0	0	0
Adult	2	37.4	120	4.3	12	3	6	3	1	0	1	0	0
Adult	3	*											
Adult	4	33.2	72.5	2.9	12	2	8	0	0	1	0	0	0
Nymph	5	55.9	79.5	3.2	5	3	1	5	0	2	2	0	0
Adult	6	50.2	74.5	2.8	8	5	0	6	0	2	0	0	2
Adult	7	39.7	101.5	4.1	9	4	3	1	0	2	2	0	0
Adult	8	23.5	6	1.5	1	2	0	0	0	0	0	0	0
Adult	9	*											
Adult	10	*											
Adult	11	48.3	15.5	1.7	3	2	2	0	0	1	1	0	0
Adult	12	28.6	95.5	3.3	10	6	7	1	0	0	0	0	0
Adult	13	74.7	6.5	2.2	0	0	1	0	0	0	0	0	0
Adult	14	46.1	123.0	4.2	9	4	8	2	0	0	1	1	0
Adult	15	40.0	132.0	4.6	12	2	5	3	2	3	0	0	0
Nymph	16	26.9	83.5	2.8	14	6	4	2	0	0	0	0	0
Adult	17	67.9	11.5	1.4	2	0	0	3	0	0	1	0	1
Nymph	18	49.3	37.0	3.4	4	0	2	1	2	0	1	0	0
Nymph	19	*											
Nymph	20	48.6	92.5	3.4	7	6	5	1	0	1	2	1	0
Nymph	21	42.1	73.5	2.6	8	2	8	4	0	0	2	0	0
Nymph	22	*											
Adult	23	37.8	68.0	2.8	8	2	5	3	0	1	1	0	0
Adult	24	39.4	47.5	2.5	4	7	5	0	0	0	0	1	0
Nymph	25	44.7	8.0	1.3	0	3	2	0	0	0	0	0	0
			1360										
$\bar{x}$		42.8	68	2.94	7.5	3.3	3.6	2	0.25	0.65	0.7	0.2	0.2
s.e.		3.00	± 9.40	± 0.22	± 1.01	±0.49	±0.64	0.39	0.14	0.21	0.18	0.08	0.11

* = Impossible to analyse, as either no movement in the 10-minute observation time, or track too confused to follow.

APPENDIX 4G

Summary of Observations of Apterous R Padi at Different Temperatures

2. At 11 ± 2°C

Life Stage and Number		Mean Angle of Turn	Total Distance Moved in mm	Mean Step Length	0-20	21-40	41-60	61-80	81-100	101-120	121-140	141-160	161-180
Nymph	1	24.7	130	5.2	8	13	2	1	0	0	0	0	0
Adult	2	35.9	16	2.7	6	3	2	1	0	1	0	0	0
Adult	3	39	118	7.9	2	4	2	4	1	0	0	0	0
Nymph	4	40.7	121.5	4.7	10	5	2	3	1	0	2	0	0
Nymph	5	42.7	117	3.9	11	3	8	3	0	1	0	2	0
Nymph	6	33.2	134	3.7	12	4	5	3	1	1	0	0	1
Nymph	7	33.8	122	4.1	10	6	11	0	0	1	0	0	0
Adult	8	19.6	110	7.9	6	3	2	2	0	0	0	0	0
Adult	9	69	112	3.8	4	7	7	3	1	3	0	3	1
Nymph	10	44.8	101	5.3	5	3	6	2	0	0	0	1	0
Nymph	11	36.8	95.5	4.6	10	3	2	3	0	1	1	0	0
Nymph	12	40.4	103.5	4.3	10	4	4	1	0	2	1	1	0
Nymph	13	31.2	91.	4.8	5	7	3	3	0	0	0	0	0
Nymph	14	38.6	87	3.1	10	8	3	1	2	2	1	0	0
Adult	15	3.0	82.5	3.4	7	6	7	0	0	3	0	0	0
Nymph	16	8.5	13.5	1.4	5	4	0	0	0	0	0	0	0
Adult	17	9.2	183.5	7.1	9	9	4	0	1	0	0	0	
Adult	18	54.8	188.5	6.1	7	4	5	5	2	1	2		
Nymph	19	10	10.5	1.5	5	1	0	0	0	0	0	0	0
Adult	20	55.1	27	1.6	5	2	2	0	2	1	2	0	0
Nymph	21	51.5	13.5	1.4	3	0	2	0	2	1	0	0	0
Adult	22	20.5	84.5	5.0	9	4	3	0	0	0	0	0	0
Adult	23	*											
Adult	24	42.7	117.5	3.9	11	3	8	3	0	1	0	2	0
Adult	25	33.7	122	4.1	10	6	11	0	0	1	0	0	0
$\bar{x}$		33.9	95.9	4.2	7.5	4.7	4.2	1.6	0.5	0.8	0.4	0.4	0.1
s.e.		± 3.24	± 10.0	± 0.37	0.58	0.57	0.63	0.32	0.16	0.19	0.15	0.16	0.06

* = Impossible to analyse, no movement in 10-minute period.

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Field Assessment of the Effects of Deltamethrin on Polyphagous Predators in Winter Wheat[a]

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In the south-west of England, cereal aphids can spread barley yellow dwarf virus and reproduce during winter. Ground-living polyphagous predators may be important in controlling these active cereal aphids. This 2-year study investigated the effect of deltamethrin on predator numbers, using pitfall traps. A randomised block design was used in an area of winter wheat (cv. Aquilla) in which deltamethrin-treated and control plots were surrounded by polyethylene barriers. Pitfall catches of polyphagous predators were reduced by about 30% in the treated plots compared with the control plots.

1. Introduction

Research over the past decade has shown the potential value of polyphagous predators, especially the Carabidae, Staphylinidae, Areneida and Dermaptera in contributing to the natural control of the populations of arable crop pests, such as cereal aphids.[1–3] In particular, they have been shown to have potential in limiting, during the spring, the population increase of *Sitobion avenae* (Fabr.) and *Metopolophium dirhodum* (Wlk.) in the UK[4–6] and of *Rhopalosiphum padi* (L.) in Sweden (Chiverton, P., private communication). In the UK, the trend towards earlier sowing of winter cereals at the expense of spring varieties, and the autumn migrations of viruliferous cereal aphids into the young crops, have necessitated control by correctly-timed insecticide sprays, commonly containing synthetic pyrethroids. Some aphids, particularly *R. padi*, can over-winter and reproduce in the mild winters of south-west England; the apterous progeny spread barley yellow dwarf virus (BYDV) within the crop.[7]

Ground living polyphagous predators may be important in controlling these populations of winter cereal aphids and the associated spread of BYDV. However, the application of insecticides before or during this period may have an adverse effect on natural control. This is an investigation of the effect of deltamethrin, an insecticide recommended for use in autumn, on the numbers of potential predators caught in pitfall traps in winter wheat. It is recognised that the use of pitfall traps is limited, as the catches reflect the activity as well as the numbers of predators.[8] Furthermore, there is evidence that some insecticides may increase the activity and the numbers captured in pitfall traps.[6,9]

2. Experimental methods

2.1. Treatments and plot design

A randomised block design was used in an area of winter wheat (cv. Aquilla). Each subplot was surrounded by polyethylene barriers (0.4 m high) dug into the soil to a depth of 0.15 m.[10] Half of the subplots were sprayed with deltamethrin ('Decis', Roussel-Uclaf Ltd, France) using a knapsack sprayer at a rate of 7.5 g a.i. ha^{-1}. Each subplot contained a 2-m length of grass/weeds,

[a]Based on a poster presented at the symposium *Pyrethroid insecticides in the environment* on 12–13 April 1984, organised by the Pesticides Group, Society of Chemical Industry.

to provide an uncultivated area for the polyphagous predators.[11] In 1982–1983 there were four equal subplots of 105 m^2, and the spray was applied on 18 January 1983. In 1983–1984 there were six equal subplots of 115 m^2, and the spray was applied on 29 September 1983.

2.2. Sampling

All adult Carabidae were identified to species, and other potential predators were identified to taxonomic group (see Results section). In both years, ten dry glass pitfall traps, 80 mm in diameter, were set in each subplot, at a distance of 3 m apart. The numbers of each taxonomic group were recorded every 5–7 days in January–March, and every 3–4 days at other times when there was higher predator activity. Recording continued from November–April 1982–1983, and September–April 1983–1984.

2.3. Mark and recapture experiment

All adult *Nebria brevicolis* (Fabricus) caught in the pitfall traps from 3 November to 15 December 1983, were marked on the elytra with enamel paint using colour codes to identify the subplot in which they were caught and then released.

3. Results

Thirteen species of adult carabids were found (Table 1). All other predators were classed as carabid and staphylinid larvae, spiders and adult staphylinids. The faunal composition of the pitfall catches varied throughout the growing season; for example, carabid and staphylinid larvae were the most abundant during November–January, while *Pterostichus cupreus* (L.) and *Amara aeneus* (Degeer) began to appear in April. Some species dominated the capture data (Table 1), and the conclusions drawn apply to larvae and the dominant adult Carabidae (*Nebria brevicolis* and *Trechus quadristriatus*). A chi-squared test showed that the polyphagous predators were distributed at random within the subplots; hence a square-root transformation of the data was used in statistical analyses.

Figures 1 and 2 show the numbers caught in treated and control subplots in each of the two years. There was no significant difference in the mean numbers of the commonest polyphagous predators caught in the different subplots before treatment in both years, indicating that there was little environmental heterogeneity.

Table 1. The numbers and percentages of polyphagous predators captured

		1982–1983		1983–1984	
	Predator group and species (where appropriate)	Number captured	Percentage of total	Number captured	Percentage of total
Adult carabids	*Agonum dorsale* (Pont)	17	1.8	3	0.2
	Amara aeneus (Degeer)	0	0	2	0.1
	Amara ovata (F.)	0	0	1	0.1
	Asaphidion flavipes (L.)	3	0.3	0	0
	Bembidion lampros (Herbst)	0	0	2	0.1
	Harpallus aenus (F.)	6	0.6	1	0.1
	Loricera pillicornis (F.)	20	2.2	1	0.1
	Nebria brevicolis (F.)	116	12.6	362	24.4
	Notiophillus biguttatus (F.)	13	1.4	28	1.9
	Pterostichus cuprues (L.)	0	0	7	0.4
	Pterostichus maididus (F.)	1	0.1	8	0.5
	Pterostichus melanarius (Ill.)	0	0	1	0.1
	Trechus quadristriatus (Schrk.)	88	9.6	75	5.1
	Sub-total	*264*	*28.6*	*491*	*33.1*
Adult staphylinids		46	5.0	30	2.0
Carabid and staphylinid larvae		502	54.5	943	63.7
Spiders		110	11.9	17	1.2
	Total	*922*		*1481*	

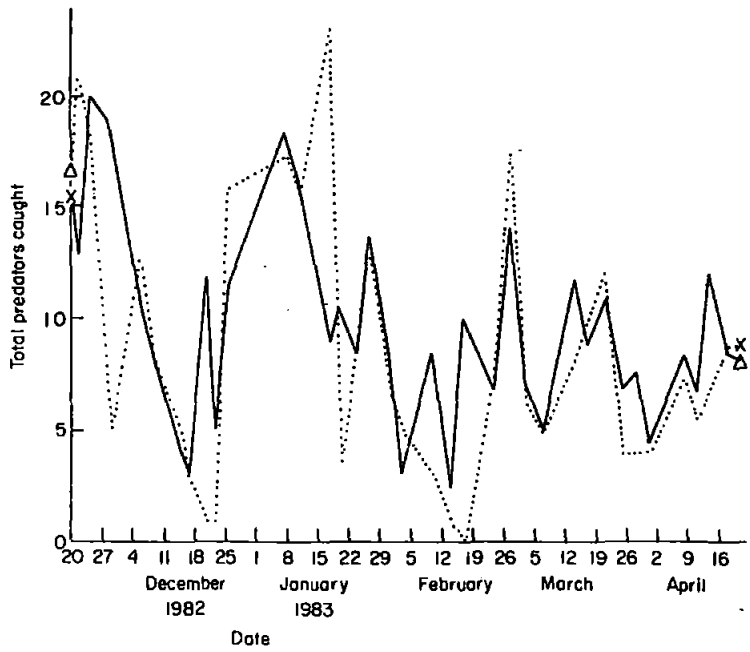

Figure 1. Total numbers (square-root transformation) of polyphagous predators caught on each trapping occasion in 1982–1983: (——) control plots; (. . . .) deltamethrin-treated plots. Standard error ±0.53.

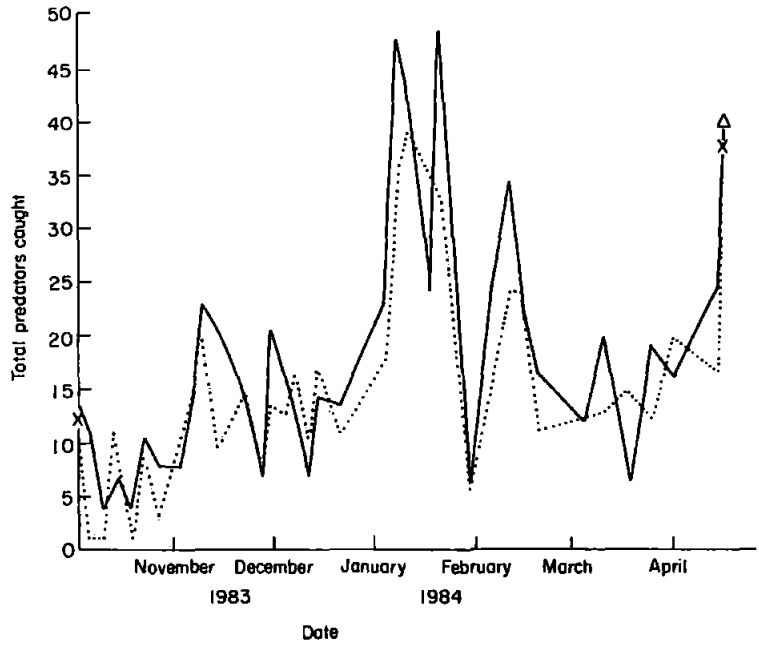

Figure 2. Total numbers (square-root transformation) of polyphagous predators caught on each trapping occasion in 1983–1984: (——) control plots; (. . . .) deltamethrin-treated plots. Standard error ±0.675.

The numbers of larvae caught over both years followed the same pattern. The first larvae appeared in the control plots in early November, and the numbers increased steadily up to a maximum in mid-January (total of 97 larvae). After this time, the percentage of larvae remained over 80% until April. There was an overall reduction of about 30% in the number of predators caught in the deltamethrin-treated plots compared with the control plots ($P<0.05$ 1982–1983; $P<0.01$ in 1983–1984).

A total of 294 beetles were marked, and 130 of them (44.2%) were recaptured. Of these, 22 (7.5%) were recaptured in a different subplot to that where first captured.

4. Discussion and conclusions

All the species of Carabidae that were caught have been shown to prey on aphids,[1] and it is recognised that carabid and staphylinid larvae, spiders and adult staphylinids eat aphids. The carabid caught in the largest numbers was *N. brevicolis* and this species was given a cereal aphid predator ranking of 0.041 by Sunderland and Vickerman.[3] The large numbers of larvae caught in the winter months indicate that predation may continue throughout the year. The reduction of numbers caught in treated plots probably reflects reductions in the abundance of polyphagous predators. Insecticides have been shown to increase the activity and capture rate of predators,[6,9] but not to decrease them. As the barriers were not completely efficient in preventing intermingling between subplots, as shown by the mark and recapture experiment, the reduction in numbers caused by deltamethrin may have been underestimated.

Deltamethrin, and other insecticides applied in autumn may have two effects on polyphagous predators. Firstly, spraying in autumn may reduce the size of the populations of carabid and staphylinid beetles in the spring by killing the larvae in autumn and winter. Secondly, natural control of aphids by polyphagous predators in winter may be reduced.

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