FACTORS AFFECTING POPULATIONS OF CEREAL APHIDS AND THEIR BEETLE PREDATORS

by

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ABSTRACT

The role of natural enemies, in particular ground beetles (Coleoptera:Carabidae) in the population dynamics of cereal aphids was investigated and factors that could influence predation were also studied. The theme of integrated control was continued with studies of the effects of aphids on yield losses of wheat.

The voracity of carabids for aphids was studied in laboratory experiments and predation by carabids was investigated in insectary and glasshouse experiments. In the field, exclusion techniques comprising insecticide treated areas and insect-proof cages, and introduced aphids, were used to manipulate populations of natural enemies and the resulting effects on aphid populations were studied. In addition, experiments in an insectary were undertaken to examine factors affecting the movement of adult coccinellids and to study the effect of natural enemies on late season aphid populations.

Movement and dispersal of aphids was studied to assess the potential importance of aphid predation at ground level. Factors affecting the dislodgement of aphids by weather were studied and voluntary movement of aphids was investigated in laboratory experiments. Dispersal of aphids through a wheat crop was also investigated and a descriptive model of aphid population spread was developed.

Fungicides are often applied at the flowering stage of cereal growth, a time when aphid increase rate is at a maximum and when predation by polyphagous predators is most important. Thus, the effect of fungicides

on aphid reproduction rate and on the consumption of aphids by ground beetles was investigated in laboratory experiments.

Plots of wheat from the field experiment were harvested to examine the effect of aphid populations on yield loss. In addition, the effect of interactions between aphids and plant growth on the relationship between aphid numbers and yield was investigated in experiments with plots of wheat in an insectary.

CHAPTER 1

INTRODUCTION

1.1 Introduction

In recent years cereal aphids have rapidly become regarded as a major pest. This may be due, in part, to a greater awareness of the damaging potential of these insects, though there is also evidence that aphids have become more abundant and widespread since the 1950's (Heathcote, 1970). The increase in cereal acreage has no doubt contributed to the problem of attack by aphids as these insects are highly adapted to exploit the transient cereal ecosystem and are therefore likely to increase in abundance as more land is used for cereals. Moreover, cereal yields have remained fairly constant in recent years, despite improved farming techniques, better yielding varieties and better use of nitrogen (Fiddian, 1973), all of which makes the pest problem more economically important.

The aphid problem is not restricted to Great Britain. Serious increases in aphid abundance have been reported in Europe from Finland to Spain, in the Americas from Canada and U.S.A. to Venezuela, Brazil, Argentina and Chile. South Africa, Australia and New Zealand have also been affected - thus cereal aphids are a cosmopolitan pest (Baranyovits, 1973). The problem is such that in Brazil between 1971 and 1972 crop damage by the cereal aphid Metopolophium dirhodum was estimated at £10 million despite £2 million of insecticidal treatment (Eastop, 1973 in Baranyovits, 1973).

Seven species of aphid attack cereals in Great Britain, spending the winter on a primary host and migrating to the cereal crop in the spring

(George, 1974). Three are of major importance; English Grain Aphid - Sitobion (Macrosiphum) avenae (F), Rose Grain Aphid - Metopolophium (Acyrthosiphon) dirhodum (Walk.) and Bird Cherry-Oat Aphid - Rhopalosiphum padi (L). The other four species which are of less consequence are; Metopolophium festucae (Theo.), Rhopalosiphum insertum (Walk.), R. maidis (Fitch.) and Sitobion fragariae (Walk.).

1.2 Natural Regulation of Aphid Numbers

Populations of many aphid species are regulated by intraspecific factors, which include emigration of alatae, reduction in fecundity and increase in mortality with crowding. Emigration is the most common mode of population regulation in many species, for example, Aphis fabae (Scop.) (Way and Banks, 1967), Myzus persicae (Sulz.) (van Emden, Eastop, Hughes and Way, 1969), Brevicoryne brassicae (L.) (Way, 1968). In cereals, emigration has been observed to cause the population collapse of R. padi (Adams and Drew, 1964, Rautapää, 1976) and many researchers consider that the population development of S. avenae in the field is regulated in the first place by intraspecific factors, mainly emigration (Rabbinge, Ankersmit and Pak, 1979, Vereijken, 1979). Vereijken (1979) found that S. avenae had a sharp reaction to crowding, producing alatiform nymphs at very low population densities and he concluded that the development of winged forms depending on colony size, followed by emigration, could later reduce the population by half. Moreover, Watt (1979) found that the growth stage of cereals exerted an effect on aphids, decreasing their fecundity and increasing mortality with ripening, but no interaction between plant growth stage and alate production was observed.

Natural enemies attacking cereal aphids occur in three groups; parasites, pathogens and predators.

Dean (1974 d) found high rates of parasitism in the field, when different parasite species attacked S. avenae and M. dirhodum but aphid densities were comparatively low making percentage parasitism high even with small numbers of parasites. Jones (1972) found that hyperparasites slowed the build up of primary parasites and lowered overwintering numbers, and she considered that hyperparasitism could be a major factor producing the apparent four yearly cycle of aphid outbreaks. Some other instances of heavy parasite attack have been recorded by Phillips (1916) and Jansen (1959) although Latteur (1971 and 1973) and Rautapää (1976) considered parasitism to be unimportant.

The major fungal pathogen of cereal aphids (Entomophthora spp) is dependent on high microclimatic humidity for the sporulation of the fungal fruiting bodies, and hence the spread of the disease is most rapid in wet weather (Dean and Wilding, 1971 and 1973). Dean and Wilding concluded that fungal attack on cereal aphids could often be more important in reducing aphid numbers than predators or parasites and this has been corroborated by Latteur (1971), Carrillo, Mellado and Pino (1974) and Dedryver, Vible and Anglade (1977).

Van Emden (1966) noted that predators rarely achieved striking control of aphid populations, the major limitation being poor synchronization between the start of aphid population growth and the ingress of predators. Indeed, Dean (1974 d) concluded that parasites were more likely to synchronize with, and help to control, immigrant aphids, than were predators. In addition, at low temperatures, predator voracity is reduced to a greater extent than aphid multiplication rate and thus aphids are able to escape control (Dunn, 1952, Frazer and Gilbert, 1976). Predators are usually fairly numerous and can easily spread throughout the small

fields of Britain, but the most voracious predators (in cereals, the Syrphidae (Dean 1974 d, 1975, Jones, 1972)) reach the crops too late for synchronization with the start of aphid population growth. This, together with periods of low temperatures, common in British summers, tends to decrease the effectiveness of predators relative to aphid multiplication rate.

The numerical response of predators to cereal aphid populations is produced by immigration and reproduction. Kieckhefer and Miller (1967) found that there was no evidence of reproductive activity of predators within the cereal crop (possibly due to low numbers of aphids) and that there was no correlation between number of adult predators and subsequent number of larvae. They concluded that, in the fields observed, increases in predator numbers did not result from reproduction within the crop but from movement into cereals from nearby crops (for example coccinellids moved in from nearby alfalfa). However, with predators such as syrphids, and to a lesser extent, coccinellids, where the larvae constitute the aphid eating stage, reproduction of adults in the crop is obviously important. However, aphid densities required to attract such predators and stimulate egg laying are not known.

Predatory control of aphids has been implicated in many studies (Forbes, 1962, Potts and Vickerman, 1974, Rautapää, 1976). Correlations between measures of predator and aphid abundance have been used to assess the effect of predators on aphid populations (Rautapää, 1972 a, 1975, 1976, Potts and Vickerman, 1974). However, studies have tended to ignore such factors as, the considerable sampling errors involved in most methods of estimating predator densities (Frazer and Gilbert, 1976), the effect of temperature on the predator-prey relationship (Dunn, 1952, Frazer and

Gilbert, 1976), and the diurnal cycle of predator abundance (Vickerman and Sunderland, 1975). More realistic models of the role of predation in the population dynamics of aphids have been the simulation models of Frazer and Gilbert, (1976) and Rabbinge, Ankersmit and Pak, (1979). The model of Rabbinge et al (1979) gave a reasonably accurate simulation of the aphid population development and collapse in three years although several assumptions were made and only predation by Syrphus corollae (Fab.) was included in the model since relevant data for only this predator species was available. They reasoned that the inclusion of the effects of Entomophthora and parasites and predators acting later in the population decrease would result in an improved simulation of aphid population dynamics but would not influence the major conclusions. These were that, in cereals, the aphid population collapse is triggered by the emigration of alatae and amplified by biotic mortality factors.

The influence of polyphagous predators on aphid populations has been accorded little relevance in the past. However, recent investigations (Potts and Vickerman, 1974, 1975, Sunderland, 1975, Vickerman and Sunderland, 1975, Edwards and George, 1976, Edwards, Sunderland and George, 1979), have stimulated new interest in the role of general feeders in the population dynamics of cereal aphids. Sunderland (1975) found that eleven species of ground beetle (Coleoptera:Carabidae) had fed on cereal aphids and discovered that aphids formed a primary component of the diet of Agonum dorsale (Pont.) and Forficula auricularia (L.). He concluded that such polyphagous predators could be of value as natural control agents because of their propensity to stay in the crop during periods of low pest density, thus being present when aphids move into the crop and start to increase. Vickerman and Sunderland (1975) also found that predator activity

occurred on a daily cycle, aphid specific and polyphagous predators being active on the plants and feeding on aphids at night whereas by day little activity occurred. Field plot experiments by Edwards and George (1977) demonstrated the influence of carabid abundance on aphid numbers and Dunning, Baker and Windley (1975) concluded that ground beetles were important in the population dynamics of Myzus persicae on sugar beet. Moreover, recent experiments manipulating polyphagous predator densities in confined areas of a winter wheat crop (Edwards, Sunderland and George, 1979) have shown large effects on resulting aphid populations.

1.3 Forecasting Aphid Numbers

Unlike Aphis fabae (Scop.) whose bionomics is favourable to forecasting, the life-cycle of cereal aphids is not conducive to predictive estimation (Way and Cammell, 1973). Many gaps are present in the knowledge of cereal aphid biology, for instance, apart from one study (Dean, 1974 a) there is no published research on the overwintering of cereal aphids.

'Rothamsted' suction trap catches provide useful indications of the timing and scale of migrations of Aphis fabae and Phorodon humuli (Schrank.) (Way and Cammell, 1973), but attempts to relate numbers of cereal aphids caught in suction traps with weather conditions and subsequent densities in the crop have, for the most part, been unsuccessful, both in Britain (Dean, 1973 a, 1974 a) and in the U.S.A. (Kieckhefer and Lytle, 1976). However, trap catches can predict the time when alatae should begin to arrive in the crop (George, 1974, Sparrow, 1974), although there are discrepancies according to species (Dean, 1974 b). Dean (1973 a) concluded that suction trap catches of cereal aphids were of dubious value in predicting aphid abundance in the field, although recent investigations by Dewar (personal communication) may modify this.

Outbreaks of cereal aphids have generally been ascribed to mild winters (Jansen, 1959, George, 1974, Robert and Rouzé-Jouan, 1975 and Breniaux, Lescau and Moreau, 1976), although Vickerman (1977b) concluded that aphid outbreaks were the result of colder than average weather in the spring. He found significant associations between peak aphid numbers and deviations from long term mean March and April temperatures and also between log peak aphid numbers (per m^2) and log number of 'air frost days' in April. The mechanism postulated to account for these relationships was that high spring temperatures encouraged the early development of large populations of grass aphids and other aphids, in turn giving rise to large numbers of parasites and predators which were able to migrate into cereals early in the season to control the aphids quickly. In cold springs the converse occurred. Whilst spring temperature undoubtedly has the effect on the ecological relationship between predators and other aphid species that Vickerman claims, nevertheless the predictive relationship makes the unproven assumption that predators and parasites constitute the sole controlling element on cereal aphid populations in the summer and ignores other equally important factors, such as the number of alate immigrants to the crop and temperatures throughout the summer. Thus the statistical relationships obtained between aphid numbers in the summer and weather parameters in the spring could be artifacts resulting from chance associations or from the combinations of transformations used e.g. log peak aphid numbers vs log (n + 1) 'air frost days'.

The present cereal aphid forecasting system in Britain is based on information from the Rothamsted Aphid Bulletin and the Agricultural Development and Advisory Service's (ADAS) spray warnings. Advance warning of aphid immigration is given from the suction trap catches since aphids

are mostly caught in the traps before being found in the field an average of 22 days later (George, 1974). ADAS monitor fields in each cereal growing area to assess the level of pests and they give warning of cereal aphid outbreaks to local farmers. If aphid numbers are high, farmers are advised to sample their crops for aphids and to spray if numbers are greater than an average of 5/ear and increasing at flowering or over 10/ear at the end of flowering. Thus farmers are obliged to sample their crops twice to make sure that aphid numbers are increasing.

1.4 Effect of Aphids on Cereal Yield

Table 1.1 gives a summary of some field investigations of the influence of aphid numbers on yield.

Some general points can be noted. Judging by the number of publications, Sitobion avenae seems to be the most important aphid species and winter wheat the most important crop. The economic thresholds of aphid attack set by George (1975) and Wetzel, Freier and Abdalla (1975) of 5-6 aphids/ear at the beginning of flowering incorporate a predictive element of aphid population growth before pesticide application. Levels of 25-50 aphids/tiller given by other authors are the populations at which control measures should be taken immediately and take no account of the delay between crop sampling and pesticide application which invariably occurs in farming practice.

Kolbe (1973) concluded that, in Europe overall cereal yields are primarily determined by plant density and number of grains per ear. This is because, although higher yields can theoretically be best obtained from those varieties with the largest grain size, the critical time for grain formulation is so short (about 40 days) and generally occurs in unsettled

TABLE 1.1 EFFECT OF APHIDS ON YIELD

Country	Crop	Aphid Species	Economic Threshold Level	Peak Numbers	Plant Growth Stage	Grain Weight or Number Reduction	% Loss	% Gain From Control	Author
Great Britain	Winter Wheat	S. avenae	5/ear		Beg. Flowering	Weight			George 1975
	Wheat	S. avenae		111/stem	Post Anthesis	Weight	14		Wratten 1975
	Wheat	M. dirhodum		68/stem	Post Anthesis	Weight	7		Wratten 1975
	Spring Wheat	M. dirhodum		6-50/stem	Ear Emergence	Weight & No.			Lowe 1974
West Germany	Wheat & Oats	S. avenae M. dirhodum	25-50/tiller	25-50/tiller	During Flowering	Weight & No.	25	20	Kolbe 1969
light Soil	Wheat	S. avenae		67	Flowering	Weight 7%		14	Kolbe 1970
heavy Soil	Wheat	S. avenae	> 20/tiller	35	Flowering	No. 23%		10	Kolbe 1970
U.S.A.	Barley	R. padi	25-30/tiller						Stern 1967
Canada	Wheat	S. avenae		74		Weight			Harper 1973
Chile	Wheat	M. dirhodum			During Flowering	Number			Carillo et al 1974
					After Flowering	Weight			
Ukraine	Spring Wheat	S. avenae	6.6/ear		Milky Ripe				Kamancheko 1976
	Winter Wheat	S. avenae	25-30/plant	180-240/ear		Weight	18.4		Dyadechko and Ruban 1975
			10% infest.[n]	80-110/ear		Weight	7		
U.S.S.R.	Winter Wheat	S. avenae	25% infest.[n]	- 225/ear		Weight	8-9		Shurovenkov 1975
East Germany	Winter Wheat	S. avenae R. padi	3-5/ear		Flowering Milky Ripe	Weight			Wetzel, Freier and Abdalla 1975
	Winter Wheat	S. avenae	30/ear 400 A.I.			No. 8% Weight 21%	20 (40/ear)		Freier & Wetzel 1976
Finland	Barley	R. padi	25/tiller	121/tiller	Flowering	Weight	29.6 B		Rautapää and Uoti 1976
	Oats	R. padi		157/tiller			23.7 O		
	Wheat	R. padi		27/tiller			7.2 W		
Bulgaria	Wheat	S. avenae	40/ear		Flowering	Weight	19.1		Grigorov 1976

weather conditions, that the varieties with high thousand grain weight show considerable variation in resultant yield from year to year. The yield factor that is affected by aphids is strongly influenced by the growth stage of the plant (Kolbe, 1973, Carrillo et al, 1974). Thus the number of grains per ear is affected from the end of tillering until the end of flowering (F.E. 5-10 (Feekes and Large, 1954)) and thousand grain weight during the ripening period (F.E. 11).

The relationship between variation in yield and aphid index (product of aphid numbers and time) was initially assumed to be linear (Rautapää 1966, 1968 a, 1968 b) but more recent studies have shown that the logarithm of yield (as thousand grain weight or number of grains per ear) is better correlated with aphid index (Rautapää, 1972, Freier and Wetzel, 1976).

Recent research indicates that honeydew can have a far greater damaging effect on the plant than has been hitherto suspected. Vereijken (1979) suggested that black mould growing on honeydew could account for half of the yield loss of wheat, nutrient drain from aphid comprising the other half. However, this hypothesis has yet to be corroborated from other sources.

1.5 Modern Farming Practice - Effect on Pest Problems

The farmer's main aim is to maximise crop production and profit and he has traditionally approached this by striving to produce a pure culture or monoculture of the crop. Central to this trend has been the increasing use of agrochemicals, i.e. herbicides, fungicides and insecticides on the farm (Potts and Vickerman, 1975). The general decline of dicotyledonous weeds to their present low levels is associated with the high use of

herbicides - 95% of the fields at North Farm, Sussex were treated with herbicides in 1976 (Potts, 1976). Moreover, since the advent of systemic fungicides (particularly ethirimol and tridemorph) farmers have been able to ignore genetic resistance to fungal attack when choosing varieties (Potts and Vickerman, 1975), although fungal strains resistant to fungicides are now developing (Priestley and Wolfe, 1977). In addition, the spraying of foliar aphicides is becoming commonplace (14% of North Farm fields sprayed in 1976) because of the increasing importance of cereal aphids (Baranyovits, 1973) and the greater feasibility of aerial application of aphicides (Potts, 1971).

The use of agrochemicals has immediate and long term effects on the cereal ecosystem. Many chemicals have both an indirect destabilising effect on the ecosystem in addition to direct toxic action. Vickerman (1974) found that the elimination of the weed Poa trivialis in barley by applications of the herbicide Mecoprop resulted in a reduction of total number of arthropod taxa but an increase in the number of aphids, possibly as a result of reduced predation. Similarly, Pollard (1968) found that elimination of the bottom flora of a hedge using herbicide (Paraquat/Diquat) reduced the numbers of most carabids, but an indirect effect was implicated as there was an increase in numbers of open field species (Bembidion obtusum (Serv.) and Tachus quadristriatus (Schrank)). Direct toxic effects of some herbicides on aphid predators have been observed both in the field, where 2-4D amine reduced coccinellid populations (Adams and Drew, 1965) and in the laboratory, where 2-4D amine was highly toxic to coccinellid larvae (Adams, 1960).

Agrochemicals can have unsuspected effects on predators. For instance, Pirimicarb, while having no effect on adult coccinellids had an extremely toxic

action on the equally important syrphid larvae (Laska, 1974).

Long term studies on the South Downs study area in Sussex have implicated the increasing use of herbicides as a major factor in the decline of Grey Partridge populations (Potts, 1970). The use of herbicides and the decline in undersowing have resulted in low arthropod numbers in spring when the Grey Partridge chicks require arthropod food (Southwood and Cross, 1969). This results in heavy chick mortality and has led to the unprecedented decline of the species. Fungicides, too, have been held responsible for the decreasing abundance of the mycetophagous and aphidophagous staphylinid Tachyporus (Potts, 1971). Long term effects of pesticides on the cereal ecosystem have been studied experimentally (Vickerman and Sunderland, 1977). They found that the aphicide, Dimethoate, had a severe effect on the cereal ecosystem for two weeks after application, and long term influences were evident up to two months after treatment. They came to the conclusion that the use of insecticides on cereal crops could exacerbate pest problems because of the pesticides' long lasting and widespread effects on arthropod predators.

To conclude, the trend towards cereal monoculture results in a simplification of ecosystem organization which in turn leads to a reduction in diversity. This seems to be the direction in which cereal farming is moving. The importance of ecosystem diversity in pest control is controversial. Many authors (Murdoch, 1975, van Emden and Williams, 1974) have come to the conclusion that diversity by itself does not enhance pest control presumably because any changes in diversity are produced by economically neutral insects. However, Potts and Vickerman (1974) have shown that, in the cereal ecosystem at least, fields of high faunal diversity

have greater proportions of predators leading to reduced pest numbers. Thus the general conclusion that natural control systems associated with diversity are important in pest control seems to be valid.

Whether the cereal ecosystem is becoming more unstable as a result of modern farming methods is not known. It is to answer this question that the Game Conservancy have, for a number of years, been monitoring populations of arthropods in cereals using the Dietrick suction sampler in the hope of obtaining associations between changes in pest and natural enemy numbers and relating these to farming practice.

It is generally accepted that cereal aphids have become an increasing problem in the last decade. This seems to be due to an increase in abundance both of the pest itself and of entomologists studying the problem. Changes in modern farming practice involving the increasing use of agrochemicals and fertilizers have undoubtedly contributed to the upsurge in abundance of cereal aphids and should be taken account of if a successful programme for integrated control in cereals is to be established.

1.6 Objectives of the Study

The major aim of the present study was to investigate the ecological relationships of cereal aphids and in particular to establish the role of polyphagous predators, especially ground beetles (Coleoptera:Carabidae) in the population dynamics of cereal aphids.

The voracity of carabids was investigated in laboratory experiments and aphid predation by carabids was studied in insectary and glasshouse experiments. Finally exclusion techniques were used to examine the effects of polyphagous predators on cereal aphids in the field.

The role of natural enemies in cereal aphid population dynamics was studied both in an insectary where experiments were carried out with aphid parasites and coccinellids, and in the field where insect-proof cages were used to exclude aphid specific predators from areas of the crop.

Movement and dispersal of aphids in the field was important since it would be useful to know how much predation could occur at ground level. With this in mind, factors affecting the dislodgement of aphids by weather, and the voluntary movement of aphids were investigated in laboratory experiments. Dispersal of aphids was also studied in the field and a descriptive model of aphid population spread was developed.

The use of agrochemicals in cereals is widespread and fungicides are often applied at the flowering stage of plant growth, the critical time for aphid population growth, its effect on yield and predation by polyphagous predators. Thus the effect of fungicides in aphid reproductive rate and on consumption of aphids by ground beetles was investigated in laboratory experiments.

Finally, the economic importance of cereal aphids results from the loss of yield that they produce. The consequences of predator exclusion on yield losses of wheat due to aphids were assessed from the field experiment of 1977 and interactions between aphids and plant growth factors and their effect on yield losses were examined in the insectary experiments.

CHAPTER 2

GROUND BEETLES AND CEREAL APHID PREDATION

2.1 Introduction

Overall studies of the cereal ecosystem have emphasized the importance of the influence of predators on aphid abundance (Potts and Vickerman, 1974, Rautapää, 1976), and the role of polyphagous predators as predators of cereal aphids has received much attention in field studies (Sunderland 1975, Vickerman and Sunderland, 1975).

The objectives of the present work were:-

(a) to determine the potential predation pressure by ground beetles on cereal aphids by measuring aphid consumption in laboratory experiments,

(b) to assess aphid predation by ground beetles alone in insectary and glasshouse experiments,

(c) to discover the effect of polyphagous predators on cereal aphid populations in the field by manipulating the predator populations.

2.2 Laboratory Studies on the Aphid Consumption of Ground Beetles

(i) Introduction

There has been interest in the food requirements of ground beetles for some time (Burgess and Collins, 1911). Field investigations involving the dissection of adults and identification of gut contents have revealed that ground beetles consume a wide variety of plant and animal material (Davies, 1953, Luff, 1974a, Sunderland, 1975, Anderson, 1976) and this has also been shown in laboratory studies of food preferences (Kalbacik-Wasylik, 1971, Best and Beegle, 1977a). Consumption of specific prey items by ground beetles such as house fly eggs (van Dinther and Mesik, 1965, van Dinther, 1966), cabbage root fly eggs (Mitchell, 1963), black cutworm (Best and

Beegle, 1977b), noctuid larvae (Price and Shepard, 1978), Collembola (Ersting, 1977) and Myzus persicae (Tamaki and Olsen, 1977) have been investigated in the laboratory. However, there have been no studies on the consumption of cereal aphids by ground beetles and the effect of sex and body weight on food consumption has been ignored.

Two species of ground beetle were used in the present experiments; Agonum dorsale, because of its known importance as a cereal aphid predator (Sunderland, 1975, Jones, 1979), and Pterostichus melanarius (Ill.), a predaceous species common in cereals and also known to eat aphids (Sunderland, 1975). Five experiments on the aphid consumption of these beetles were carried out. In the first, the aphid consumption by larvae and callow adult A. dorsale was determined. In the second experiment the aphid consumption of A. dorsale adults was compared with that of two smaller carabids abundant in cereals, Notiophilus biguttatus (Fab.) and Bembidion lampros (Herbst.) and the consumption of three cereal aphid species by A. dorsale was compared. Particular interest centered on the comparison of aphid consumption by gravid and non-gravid females and by males, as Sunderland (1975) found that in the field a greater proportion of females contained aphid remains than males. Beetles were frequently seen climbing plants in the cultures and the eggs laid on leaves were also evidence of plant climbing ability. However, the extent to which aphids were eaten on plants was unknown and so an experiment was devised to investigate this. In the final experiments the food requirements of P. melanarius were estimated by assessing the amount of frozen aphids (cereal aphids and pea aphids [Acyrthosiphon pisum]) eaten per day. This enabled comparisons to be made between experiments and allowed greater replication as large stocks of live aphids were not required. Differences in consumption of male, gravid and non-gravid female beetles were investigated.

(ii) Feeding Techniques

1. A. dorsale - larvae

Larvae of A. dorsale were successfully fed using the following technique. A circular wad of cotton wool soaked in water was placed in the bottom of a 9 cm diameter petri dish, excess water was squeezed out and two circles of filter paper were placed on top. A well fitting lid was placed on the dish in order to provide a high humidity. Dempster and Coaker (1974) found evidence for carabid predation on the eggs of the small white cabbage butterfly (Pieris rapae) and as there were stocks of eggs available these were used to feed the first instar larvae, later instars being fed with cereal aphids.

2. A. dorsale - adults

Callow adults emerging from pupae were kept in 14 cm diameter petri dishes with 1 cm moist peat and sand to produce a suitable habitat and allow access to all the aphids introduced. Mature A. dorsale and the other beetle species were fed in the same way.

3. Consumption of aphids on plants

To ensure beetle activity the following experimental conditions were required; high atmospheric humidity within the apparatus, strong plants to bear the weight of the beetles, and well established aphids to reduce the risk of movement between observations.

The apparatus consisted of bulb-growing containers $6\frac{1}{2}$ cm diameter and 8 cm high with a clear perspex domed cover 25 cm tall. In three batches of ten pots, barley seeds (cv Mazurka) were sown in 5 cm of John Innes/peat mixture per pot, the batches being sown at five day intervals. When the seedlings had grown to about 3 cm the pots were

transferred to a cold room at 5°C for ten days to cold harden. The barley plants were then infested in a glasshouse with two apterous Metopolophium dirhodum per plant and left for ten days to allow the growth of plants and aphid populations. Finally, the leaves were trimmed to allow the covers to be placed over, and the adult aphids were removed.

4. P. melanarius - consumption of frozen aphids

Individual beetles were housed in plastic drinking cups 7½ cm high with 5 cm moist peat/sand mixture and a tight fitting top with holes for ventilation. The containers were placed on a galvanised tray in a fully randomised design in a constant temperature room at 16°C with a 16-hour daylength. The beetles were starved for two days before the start of the experiment and then fed with frozen aphids presented in small bottle tops, 1½ cm diameter, on the soil surface. The aphids were weighed on a balance accurate to 0.5 mg, and then placed in the beetle container. The amount left uneaten was weighed the next day.

To account for moisture loss from the frozen aphids a control container was set up identical with the experimental containers but without a beetle. In the control, most of the moisture loss occurred during the day, for example, from an overall weight loss of 20.9%, 14.2% occurred by day and 6.7% by night. In the beetle treatments, however, most of the weight loss occurred by night, for example, from an average daily weight loss of, say, 62.6%, 19.6% reduction occurred by day and 43% by night. Thus most of the moisture loss occurred by day and most of the aphid consumption by night. Hence the initial weight of aphids given to the beetle was corrected for moisture loss (using the percentage loss of weight of the control) and the following day's weight of aphids remaining subtracted from this value to give the amount actually eaten by the beetle.

(iii) Experiment 1

Food Consumption by A. dorsale Larvae and Callow Adults

Materials and Methods

Twenty newly hatched larvae were placed in rearing containers described above in a constant temperature room at 20°C. First instar larvae were fed daily with P. rapae eggs on pieces of cabbage leaf and second and third instars were fed with I-III instar cereal aphids (M. dirhodum and S. avenae) on pieces of barley leaf. A large excess of eggs and aphids was introduced so that there was always prey left over the following day.

Just prior to pupation half of the larvae were transferred to pots (9 cm diameter by 9 cm deep) containing 3 cm moist peat and sand. Callow adults that emerged were fed on eggs of P. rapae and nymphs of pea aphid (Acyrthosiphon pisum) and S. avenae successively.

Results

No P. rapae eggs were eaten on the first day after hatching or for two days prior to moulting. Since each instar lasted for approximately seven days, food was only consumed by first instar larvae on four days. Overall, the larvae consumed about 37 P. rapae eggs during the first instar, 120 cereal nymphs in the second instar, and 140 aphids in the third larval instar. There were no significant differences between the consumption of the two cereal aphid species by second instar larvae (F ratio - 0.09), nor any difference in consumption between second and third larval instars (F ratio - 1.40) (table 2.1).

The emerging adults were completely white, with a soft cuticle which rapidly hardened and gained colour, the process being complete after

four days. Callow adults were initially fed on eggs of P. rapae but when given aphids, they took two days to adjust to the new food source.

(iv) Experiment 2

Food Consumption by Adult A. dorsale and Other Small Beetle Species

Materials and Methods

Males (3 specimens), non-gravid and gravid females (3 and 5 specimens respectively) of A. dorsale were taken from a laboratory culture and their aphid consumption was compared with that of A. dorsale collected from the field in early June (7 specimens) and field-collected Notiophilus biguttatus (7 specimens) and Bembidion lampros (10 specimens). Male A. dorsale were initially distinguished by their smaller size and more pointed abdomen, while females were substantially larger, with a rounded abdomen and gravid females were larger still having an abdomen somewhat distended beyond the elytra.

Individual beetles were weighed on a balance accurate to 5 mg and the experimental containers were arranged in a randomised design in a constant temperature room at 20°C.

The cereal aphid species R. padi, M. dirhodum and S. avenae were fed to the beetles on pieces of barley leaf for 5, 3 and 3 days in succession respectively, ensuring that nymphs only were used and that aphid numbers well in excess of consumption were provided. Other aphids were fed to the beetles on single days only; Myzus persicae on chinese cabbage leaf, eggs of Pieris rapae on pieces of cabbage leaf, and pea aphids (Acyrthosiphon pisum) on broad bean leaves, two days being given for the beetles to adjust to the size of the latter aphids.

TABLE 2.1 FOOD CONSUMPTION RATES OF CARABID BEETLES

Differences significant to $p < 0.05$ shown by arrows

Beetle Species	Cereal Aphid Nymphs (No. Eaten/Day)			Other Food (No./Day)			Average Weight of Beetle mg
	R. padi	M. dirhodum	S. avenae	Myzus persicae nymphs	Pieris rapae eggs	Acyrthosiphon pisum nymphs	
Agonum dorsale							
1 – larvae 1st instar					9.2 ± 0.4		
2nd instar		17.2 ± 1.6	16.5 ± 1.8				
3rd instar			19.4 ± 1.8				
2 – callow adult			24.9 ± 2.3		34.1 ± 2.9	10.3 ± 4.0	
3 – adult male	7.7 ± 4.5	12.5 ± 1.0	8.8 ± 5.2	70.0 ± 15.0	70.0 ± 15.0		12.5 ± 0.5
4 – gravid female	28.1 ± 2.4	37.7 ± 6.5	31.6 ± 4.8	104.0 ± 12.5	96.7 ± 8.8	24.2 ± 10.7	22.8 ± 1.1
5 – non-gravid female	4.0 ± 2.5	13.9 ± 1.5	12.2 ± 2.9	57.0 ± 10.9	91.4 ± 12.4	10.4 ± 4.3	17.0 ± 1.2
6 – field-collected beetles		20.1 ± 1.5	17.5 ± 3.8	101.7 ± 13.0	100.0 ± 21.6	9.0 ± 4.4	
F RATIO for differences between 3, 4, 5 and 6	30.1 $p < 0.001$	45.7 $p < 0.001$	3.9 $p < 0.05$				
Notiophilus biguttatus	2.8 ± 0.7	5.1 ± 1.2					6.6 ± 0.3
Bembidion lampros	3.1 ± 0.3	2.0 ± 0.5					1.8 ± 0.2

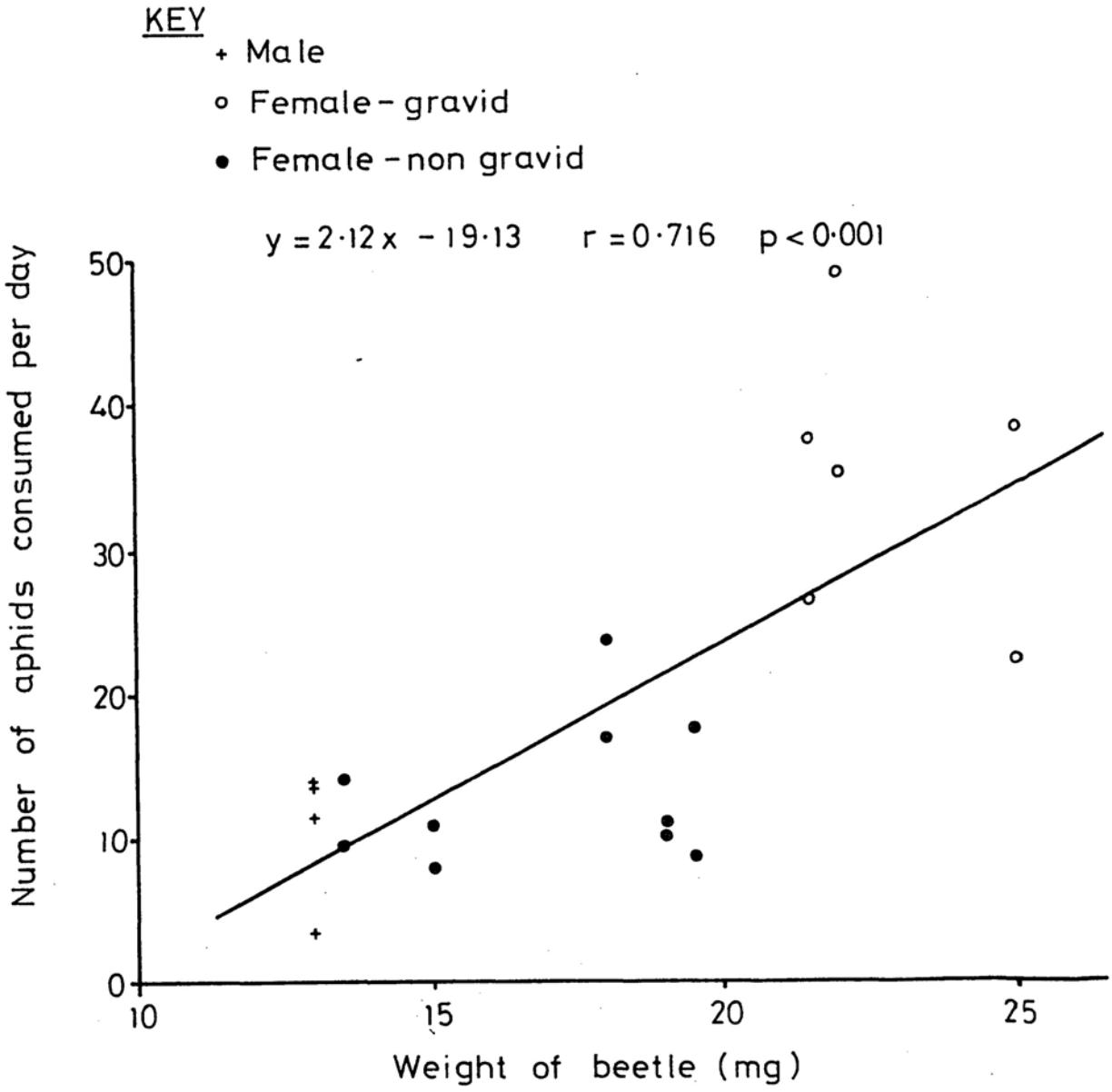
Results

Gravid female A. dorsale consumed significantly more of all the cereal aphid species than the other beetle classes (table 2.1). Moreover, field-collected beetles consumed more M. dirhodum than males or non-gravid females, and aphid consumption by N. biguttatus and B. lampros was in all cases lower than that of A. dorsale (table 2.1). Finally, non-gravid female A. dorsale ate significantly less R. padi than the other aphid species (table 2.1). The aphid consumption of A. dorsale collected from the field represented an average cereal aphid consumption that could be expected from a beetle population in the field but as these were not weighed or sexed further analysis could not be carried out.

There was a linear relationship between aphid consumption and beetle weight (figure 2.1) and gravid females may, therefore, have eaten more than others because of their greater body weight. Using beetle weight as a covariate in the analysis of variance was not successful as the weights of gravid females did not overlap with the weights of the other females and were grouped separately (figure 2.1).

A. dorsale displayed a wide-ranging taste for other aphid species. It ate large numbers of M. persicae despite the hairs on the chinese cabbage leaves, but fewer pea aphids were eaten (table 2.1). Indeed, numbers of M. persicae and P. rapae eggs eaten per day were roughly the same (table 2.1) and thus these smaller prey items probably possessed equivalent food value for an Agonum adult as the larger pea aphid and cereal aphid nymphs. Moreover, as with callow adults in experiment 1, the beetles took two days to adjust to the larger size of pea aphid before eating them.

Figure 2.1 Experiment 2 Relationship Between Consumption of Cereal Aphids and Weight of *A. dorsale*



(v) Experiment 3

Consumption of Aphids on Plants by A. dorsale Adults

Materials and Methods

The pots of barley with aphids arranged randomly on a bench in a constant temperature room at 18°C, and one adult Agonum dorsale was placed in each pot, the aim being to transfer the beetles the next day to the next batch of pots with aphids, and reintroduce aphids on the plants used previously.

In the first trial (trial A), aphids were provided on pieces of leaf on the soil surface as well as on the plant to check that the beetles were active.

However, no aphids were eaten on the plants although the first leaf was no more than 3 cm from the soil surface. The beetles were left in the same containers for a further three days and checked daily but there was still no change in aphid numbers.

The experiment was then modified (trial B), and aphids were provided on leaves of barley on the surface of the soil and on leaves resting against the stem of the barley plant.

Results

Although the beetles were active and ate aphids on the soil surface they did not eat aphids on the plants (table 2.2). The beetles may have climbed the plants and not eaten any aphids but this is unlikely since aphids would have been disturbed and would have fallen off and there was no evidence of this occurring. However, aphids on the leaf resting against the barley stem were eaten and it may be possible that the beetles were unable to climb vertically but were able to negotiate an incline.

Table 2.2 Experiment 3 Aphid Consumption by A. dorsale on Small Barley Plants

		Number of Aphids Eaten/Day		
		Soil Surface	Angled Leaf	Leaves of Plant
TRT A Aphids provided on soil and plant	1	2.5		0
	2	8.0		0
	3	7.5		0
	4	25.5		0
	Mean	10.9 ± 5.0		
TRT B Aphids provided on soil, angled leaf and plant	5	19.0	6.0	0
	6	13.0	4.5	0
	7	8.0	8.0	0
	8	9.0	9.5	0
	9	24.0	5.5	0
	Mean	14.6 ± 3.0	6.7 ± 0.9	

In the cultures the barley plants were seldom upright and were mostly leaning over allowing the beetles ready access to the leaves. Moreover, plant climbing is more likely to be practised by gravid females which were present in the cultures but not in the experiment.

(vi) Experiment 4

Consumption of Frozen Cereal Aphids by P. melanarius

Materials and Methods

The aphid consumption of male and female beetles from laboratory cultures was compared with the consumption by male and female beetles caught in a cereal field, (21st September) and male and female beetles kept together in pairs. Three replicates per treatment were used, a total of 18 beetles, and the beetles were fed on frozen S. avenae for five days using the technique described above. Male and female beetles were

distinguished by external morphology in a similar way to A. dorsale and were weighed at the end of the experiment. The beetle containers were arranged in a randomised design in a constant temperature room at 16°C.

Results

Mean consumption of aphids for the period of the experiment was linearly related to the weight of the beetle (figure 2.2). Analysis of variance showed that there was no significant difference between mean aphid consumption by male and female beetles and that aphid consumption of laboratory cultured and field collected beetles did not differ significantly (table 2.3a). However, when beetle weight was taken into account as a covariate in the analysis it was found that males consumed significantly more than females and field collected beetles more than laboratory cultured ones (table 2.3b). This analysis is slightly suspect, however, as it assumes a linear increase in aphid consumption with beetle weight which was not shown by male beetles alone (figure 2.2), possibly due to the small range of weights, although female beetles alone demonstrated the relationship (figure 2.2).

The aphid consumption of male and female beetles kept together in pairs in the containers was substantially lower than the values expected from the aphid consumptions of individual beetles (figure 2.2). Actual aphid consumption was 36% less than the expected consumption derived from the regression equation (table 2.3c).

(vii) Experiment 5

Consumption of Frozen Pea Aphids by P. melanarius

Materials and Methods

The experiment was carried out in a similar manner to experiment 4, using 7 males, 7 gravid females and 10 non-gravid female P. melanarius all

Figure 2.2 Experiment 4 Relationship Between Weight of Frozen Cereal Aphids Eaten Per Day and Weight of P. melanarius

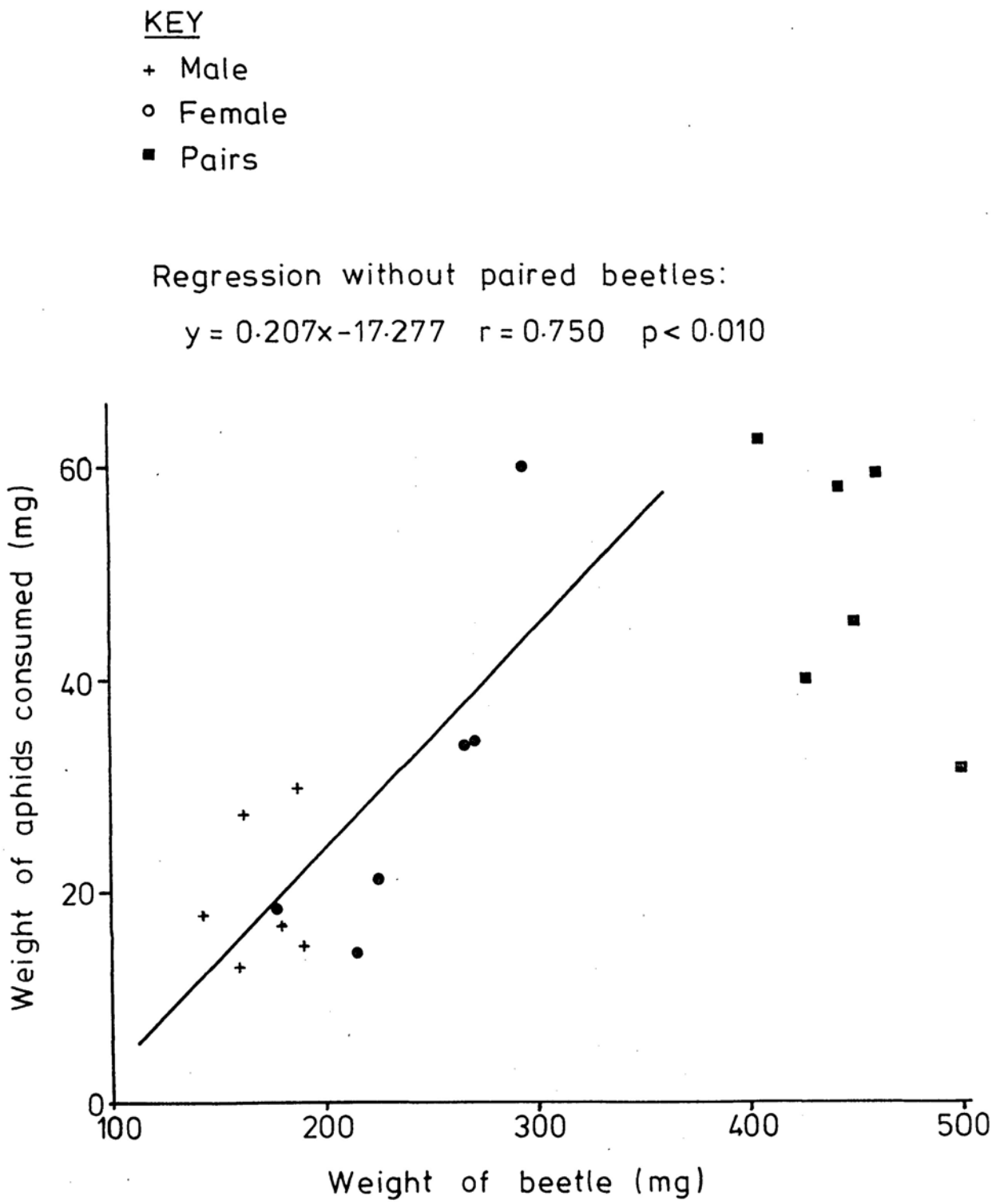


Table 2.3 Experiment 4 Cereal Aphid Consumption by P. melanarius

(a) Mean Aphid Consumption – weight of aphids eaten per day (mg/day)

Grand Mean: 25.3

Sex	Male	Female	Variance Ratio ($F_{1,8}$)	
	20.2	30.4	1.703	n.s.
Environment	**Lab.**	**Field**		
	22.5	28.1	0.525	n.s.
Environment	**Lab.**	**Field**		
Sex				
Male	15.1	25.4	0.349	n.s
Female	29.9	30.9		

(b) Mean Aphid Consumption – adjusted for covariate weight of beetle
i.e. aphids eaten per day per mg of beetle

Sex	Male	Female	Variance Ratio ($F_{1,7}$)	
	32.7	17.9	6.363	$p<0.05$
Environment	**Lab.**	**Field**		
	19.2	31.5	10.146	$p<0.05$
Environment	**Lab.**	**Field**		
Sex				
Male	25.4	40.1	0.425	n.s.
Female	13.0	22.8		

(c) Comparison of Expected Aphid Consumption by Paired Beetles with Actual Consumption

Weight aphids eaten/day	Expected	Actual	
	70.70	40.05	
	75.56	45.62	
	77.32	59.20	Paired T test
	83.42	62.30	$t = 4.93$ df = 5
	85.62	31.60	$p<0.01$
	73.70	58.05	
Mean	77.72	49.47	36.4% decrease

of which had been collected from a cereal field at the end of September. The beetle containers were arranged in a randomised design in a constant temperature room at 16°C and the daily consumption of frozen pea aphids was determined for 5 days for the individual beetles. Six pairs of male and female beetles per container were then set up and aphid consumption for the 12 individual beetles and 6 pairs was determined daily for a subsequent six days. The beetles were weighed at the beginning and end of the experiment and were dissected at the end of the experiment to discover the number of eggs in the oviducts of the gravid females.

Expected values for aphid consumption of paired beetles were derived from the percentage voracity of the individual beetles in part II of the experiment (table 2.4d).

Results

As in experiments 3 and 4, aphid consumption was proportional to the body weight of the beetles (figure 2.3). Analysis of variance showed that gravid and spent females consumed significantly more aphids than male beetles (table 2.4a). However, females were generally heavier than males and so would be expected to eat more. The factor of beetle weight was incorporated into the analysis as a covariate and aphid consumptions were weighted for the beetle weights. It was now evident that spent female beetles consumed proportionally more than gravid females or males and that there was no difference between males and gravid females (table 2.4a). The use of beetle weight as a covariate was justified by the increase in statistical precision it afforded, as shown by the covariate efficiency of 1.205 i.e. 20.5% increase in precision, and a decrease in the coefficient of variation from 28.5% to 22.4%. Separate regressions were fitted to the aphid consumptions by spent females and their weights,

Table 2.4 Experiment 5 Consumption of Pea Aphids by P. melanarius

(a) Mean Aphid Consumption - Part I (5 days)

Sex	Number Replicates	Mean Weight of Aphids Eaten Per Day mg/day			
		Unadjusted for Beetle Weight	Diffs. $p<0.05$	Weight of Beetle Taken into Account (Covariate)	Diffs. $p<0.05$
Male	7	43.6	↕	58.0	↕
Female (gravid)	7	67.1		58.5	
Female (non-gravid)	10	80.9	↕	76.8	↕
Variance Ratio		$F_{2,21} = 8.12$	$p<0.01$	$F_{2,20} = 4.34$	$p<0.05$

Key: Diffs. = Differences

(b) Mean Aphid Consumption - Part II (6 days)

Sex	Number Replicates	Mean Weight of Aphids Eaten Per Day mg/day			
		Unadjusted for Beetle Weight	Diffs. $p\leq0.05$	Weight of Beetle Taken into Account (Covariate)	Diffs. $p<0.05$
Male	4	38.2	↕	36.8	↕
Female (gravid)	4	52.8		53.6	
Female (non-gravid)	4	60.8	↕	61.5	↕
Variance Ratio		$F_{2,9} = 5.66$	$p<0.05$	$F_{2,8} = 4.64$	$p<0.05$

↕* (nearly significant to 5%)

Key: ↕ * nearly significant to 5%

Table 2.4 Experiment 5 Consumption of Pea Aphids by P. melanarius

(continued)

(c) Analysis of Difference in Aphid Consumption Part I - Part II

Change in Aphid Consumption Part I - Part II	DDF	Number Replicates	Mean Beetle Weight mg
Positive (Increase in Consumption)	>0	4	184
Negative (Decrease in Consumption)	<0	8	259

$F_{1,10} = 11.05 \quad p < 0.01$

(d) Comparison of Expected and Actual Aphid Consumption of Paired Beetles

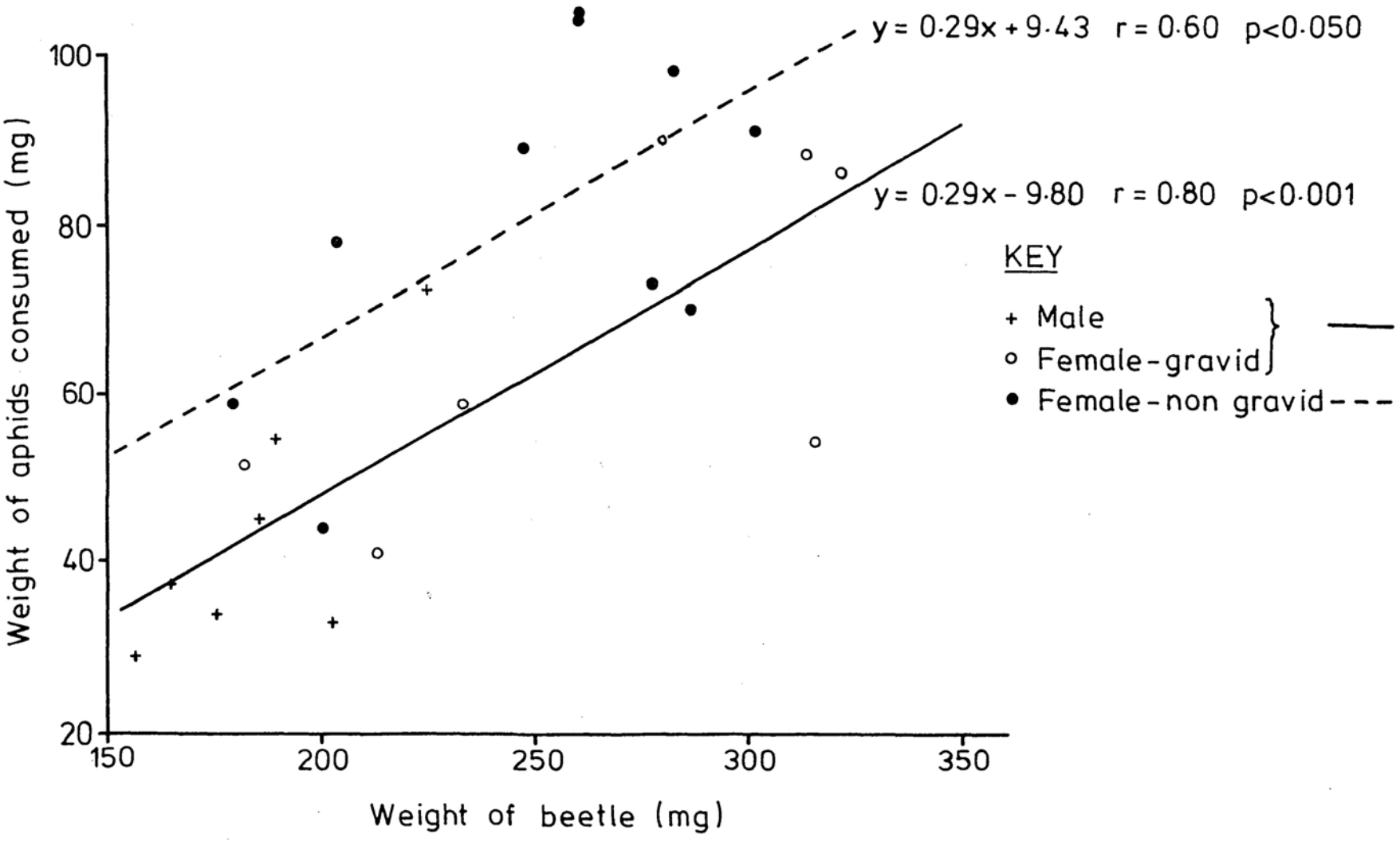
Aphid consumption per day as percentage of body weight (part II):-

Male	21.9%
Female - gravid	21.9%
Female - non-gravid	25.6%

	Weight of Beetle Part II mg	Actual Aphids Consumed/Day mg	Expected Weight Aphids Consumed/Day mg
	455.0	116.8	108.9
	425.5	95.7	93.2
	405.5	68.8	103.7
	365.5	83.0	89.6
	382.0	81.2	92.5
	458.5	81.5	110.4
Means	415.3	87.8	99.7

Paired T test $t = 1.71 \quad df = 5 \quad p < 0.2$ n.s.

Figure 2.3 Experiment 5 Relationship Between Mean Daily Consumption of Pea Aphids in Part I and Initial Weight of *P. melanarius*



and the consumptions by males and gravid females and their weights (figure 2.3) which gave slopes of the same value but different intercepts. The intercepts indicated that spent females consumed about 20 mg of aphids/day more than gravid females or males, a conclusion supported by the differences in mean consumptions adjusted for beetle weight given in table 2.4a.

Analysis of aphid consumptions in the second half of the experiment showed similar differences between males and females (table 2.4b) but in contrast to the first analysis the use of beetle weight as a covariate did not improve the precision achieved since the covariate efficiency was 0.75, i.e. the precision decreased and the coefficient of variation increased from 19.1 to 19.9%.

Mean aphid consumption by males decreased slightly from the first to second half of the experiment but there was a substantial decrease in the aphid consumption by females as seen from the comparison at tables 2.4a and b. The difference in aphid consumption was expressed as a percentage of the consumption in the first half and, when plotted against beetle weight gave two groups of points (figure 2.4), one group showing an increase in consumption from part I to part II and the other a decrease. Regression analysis on all data was not used since the data values did not show a continuous relationship but were clumped together in two discrete groups. The data were analysed using analysis of variance of beetle weights for treatments of increase in aphid consumption from part I to part II, represented by DDF >0 (i.e. positive) and a decrease in aphid consumption, represented by DDF <0 (i.e. negative), DDF being a factor derived from the percentage difference in aphid consumptions. The analysis (table 2.4c) showed that heavy beetles (average weight 259 mg)

Figure 2.4 Experiment 5 Percentage Difference in Aphid Consumption from Part I to Part II Related to Beetle Weight

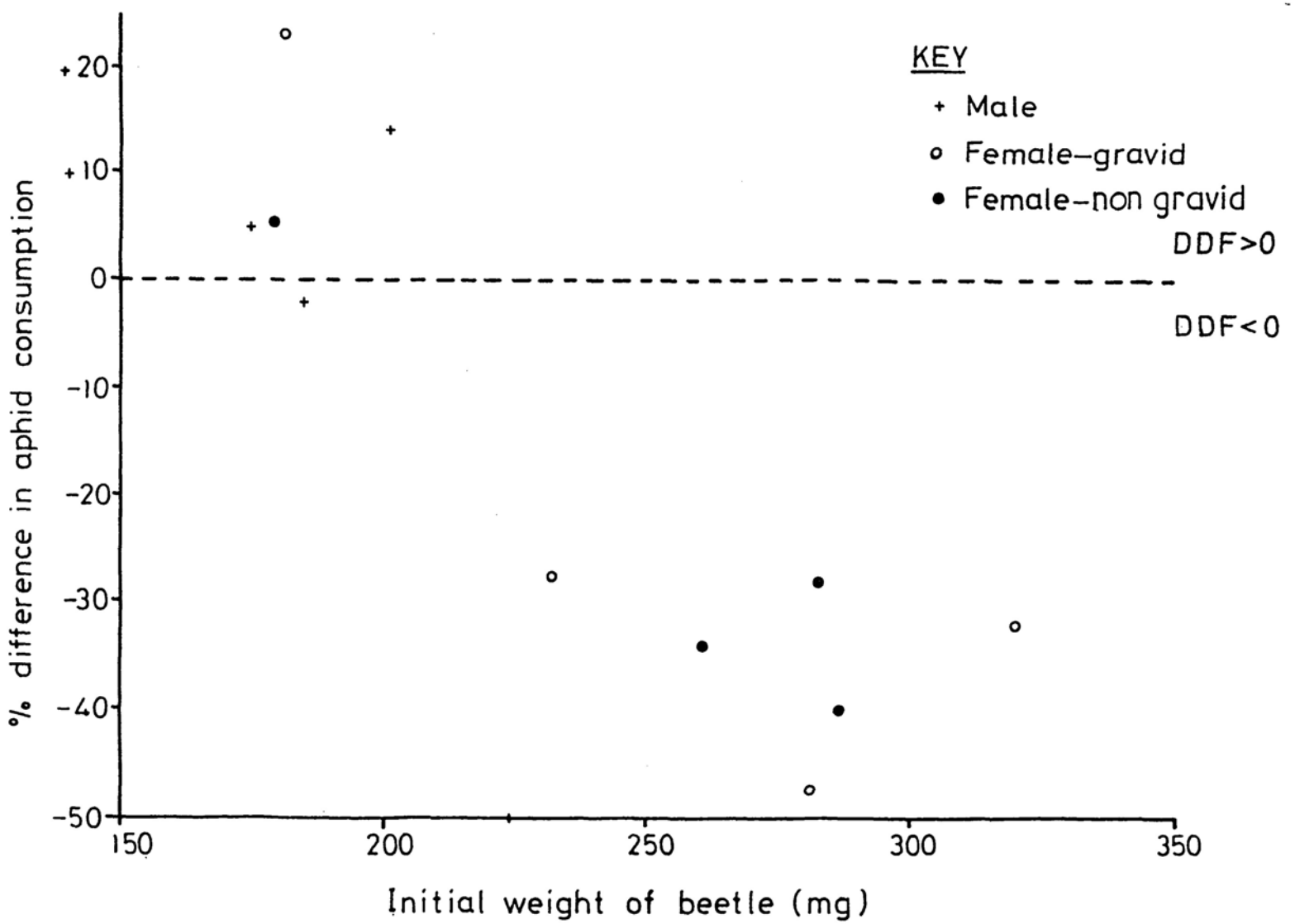
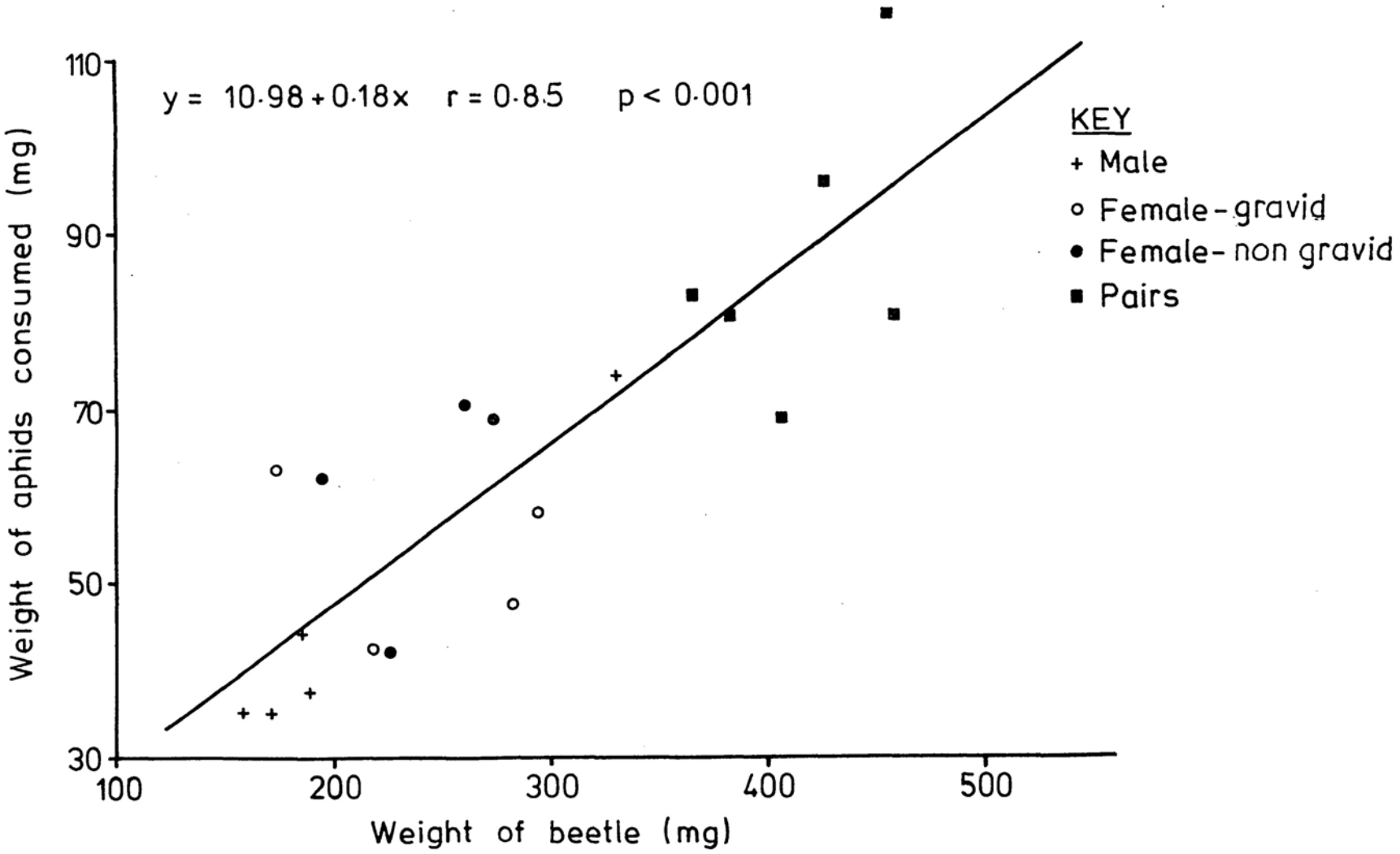


Figure 2.5 Experiment 5 Relationship Between Mean Daily Aphid Consumption in Part II and Beetle Weight



underwent a reduction in mean aphid consumption in part II of the experiment while light beetles (mean weight 184 mg) increased their consumption. This effect seemed independent of the sex and reproductive state of the beetles as seen in figure 2.5 although sex was not incorporated into the analysis because it would produce an unbalanced design. Moreover, there was no significant correlation between percentage difference and beetle weight within each group ($r = 0.26$ and 0.25 for increased and decreased aphid consumption groups respectively).

The aphid consumption by the beetle pairs in the second half of the experiment (part II) was of the same order in relation to their weight as the aphid consumption by the individual beetles (figure 2.5). Indeed there was no significant difference between the expected daily aphid consumption and the amount actually eaten per day (table 2.4d).

No eggs were laid, and gravid females contained 3.1 ± 0.8 eggs per female on dissection.

(viii) Discussion

The linear relationship between food consumption and beetle body weight held true for the two carabid species used, which were of disparate sizes, Agonum dorsale and Pterostichus melanarius, and it may be advisable to take account of this in other experiments involving the food consumption of beetles.

Gravid female A. dorsale ate more aphids than males or non-gravid females but they were heavier and did not eat proportionally more aphids than the others. Non-gravid females were probably spent, having laid their eggs before the experiment was carried out in June. Thus it

seems that oviposition in A. dorsale does not require a boosted intake of food. The aphid consumption of larvae was relatively high for their small size, presumably because this was the growth phase of the species. Callow adult A. dorsale had similar aphid consumptions to mature adults.

Aphid consumption by P. melanarius in experiment 5 was of a different order to that of A. dorsale. Here, female Pterostichus without eggs consumed proportionally more than gravid females or males. This was explicable in terms of the life cycle of P. melanarius, which is similar to the better known life cycle of P. madidus (Fab.) (Briggs, 1965, Luff, 1973). P. melanarius adults used in the present experiments were collected in late September at the end of the autumn activity period (iv) (Luff, 1973). At this stage, about half the female beetles in the field would be gravid and half spent, having laid eggs previously. Hence, the non-gravid females used in experiment 5 were likely to have been spent females that had already laid their eggs. Luff (1973) stated that some females survive the winter and lay further eggs in mid-June of the next year. Thus, once female beetles have laid all their eggs, food consumption would presumably increase to provide fat deposits for overwintering and egg production the next year. The small number of eggs in the ovaries of gravid females (approximately 3/female) were unlikely to have reduced food consumption by blocking the gut and thus at this stage in their life cycle gravid females have a genuinely lower food requirement than spent female P. melanarius.

Notiophilus biguttatus and Bembidion lampros consumed low numbers of aphids (about 3/day) but they could be important predators if they occur in large numbers as in brassicas in spring (Coaker, 1965).

A. dorsale males and females without eggs ate less R. padi than they did of other aphid species even though it was a smaller size, and it seemed to be a less palatable aphid species. Consumption of prey by A. dorsale was, to some extent, related to prey size and hence biomass. Thus comparative estimates of food consumption of beetles might best be made in terms of both weight and numbers of prey items eaten. With P. melanarius aphid consumption was measured as weight of aphids eaten, which, when expressed as a percentage of body weight, gave comparable estimates of consumption rates (table 2.4d). The frozen cereal aphids used in experiment 4 seemed to be less palatable to P. melanarius than the pea aphids, since the beetles ate less than half the quantity cereal aphids on average than pea aphids and the differences in consumption of cereal aphids between the sexes were not large enough to be significant. Moreover, the greater consumption of pea aphids conforms with the known ecology of P. melanarius in cereals where larger food items are more commonly present in the gut (Sunderland, 1975).

In experiment 5 the relationship between beetle weight and difference in aphid consumption between part I and part II showed that beetles heavier than c. 210 mg reduced their consumption after 5 days while those lighter than c. 210 mg increased their aphid consumption. Although a linear regression could not be used in the circumstances, further points in the 200–250 mg beetle weight range would probably have enabled a negative linear relationship to be established rather than the jump from increase to decrease in aphid consumption shown in figure 2.4. Thus it seems that large beetles become satiated more quickly than do small beetles, and since females are, on the whole, larger than males, this tends to blur differences in food consumption between the sexes, which was

indeed observed in part II. This differential satiation of beetles was also responsible for the reduction in the slope of the relationship between aphid consumption and beetle weight for part I and part II (0.29 and 0.18 respectively, figures 2.3 and 2.5). Moreover, interference between beetles was also reduced; after a period of feeding (5 days) in part I of experiment 5 there was no reduction in aphid consumption by pairs of beetles in part II, but consumption of cereal aphids from scratch in experiment 4 was reduced by 36% when beetles were paired (table 2.3c).

In the field, satiation of the appetite of ground beetles probably has a large effect on factors affecting food consumption; its change with beetle weight, differences between sexes and reproductive status, and the effect of interference between beetles. It seems that if P. melanarius has had sufficient to eat, the beetle population will display a fairly homogenous response to additional food, but when hungry, sex and reproductive status exert a large effect on food consumption.

The fact that A. dorsale did not climb the plants in experiment 3 may have been a consequence of deficiencies in the apparatus rather than any biological factor affecting the beetles, as they frequently climbed plants in the cultures and also ate aphids from the angled leaves in the experiment. Although the barley plants used were certainly strong enough to support the weight of the beetles, a stem of greater circumference such as mature wheat would have enabled them to get a grip on the surface more easily and thus climb vertically. Indeed A. dorsale has been shown to climb substantially sized sugar beet plants in the field (Dunning et al, 1975). However, it would be very difficult to produce a replicated

experiment using large plants with covers to ensure high humidity and prevent the escape of beetles, and thus experiments on plant climbing may be restricted to field investigations.

In the field, Sunderland (1975) suggested that the efficiency of ground beetle species as potential agents of natural control of aphids could be influenced by the sex ratio and time of breeding in relation to the timing of critical periods in the cycle of pest abundance. From these criteria the life cycle of Agonum dorsale is well synchronised with cereal aphid phenology to take maximum advantage of the aphids. In the spring, adult A. dorsale move from their overwintering aggregations in hedgerows and grass verges into the cereal crop. Gravid females then lay eggs at the end of May and beginning of June at about the time of the main cereal aphid immigration and the larvae develop while the aphids are establishing and starting to increase rapidly. Thus the life history stages of the beetles with the highest consumption rates (gravid females and II and III instar larvae) tend to be present during the normal period of aphid immigration.

Basedow (1973) estimated the population density of A. dorsale in North Germany at 6 000–11 000 individuals per hectare. Using an average cereal aphid consumption of 20 aphids per beetle per day and an average crop density of $1\frac{3}{4}$ million wheat tillers per acre, A. dorsale has the potential to consume 20–35 cereal aphids per 100 tillers per week. Although many factors have been ignored to produce this figure such as searching efficiency of the beetle, effect of temperature on aphid consumption, and numbers of beetles active, it does illustrate that ground beetles are capable of influencing cereal aphid populations in the early stages of their increase. Indeed, when large numbers of A. dorsale

were active, for example in 1975, they seemed to have had a large effect on aphid populations (Jones, 1979).

2.3 Ground Beetles and Aphid Predation in Insectary and Glasshouse Experiments

(i) Introduction

A large insectary (about 18 ft by 18 ft) with plastic netting sides and a glass roof (the 'tygan' house) and a glasshouse were used in 1976 and 1977 to house experiments investigating the role of ground beetle predators on aphid populations in plots of winter wheat.

The object of the 1976 experiment in the tygan house was to investigate the effect of ground beetle numbers on aphid populations using Agonum dorsale as the experimental predator. In 1977, two beetle species were used in a similar experiment, Demetrias atricapillus (L.) and Pterostichus madidus (Fab.), the former known to climb plants and the latter an epigeic species (Sunderland, 1975). The glasshouse experiment in 1977 used different techniques to make the habitat within the plots more favourable for beetle predation on aphids. Two carabid species were used, Pterostichus madidus and Nebria brevicollis (Fab.), and an alternative food source (frozen pea aphids or boiled mince) was supplied to assess the possible effect of a diversionary food source on aphid predation.

(ii) Materials and Methods

The soil in the insectary was prepared by steaming and digging, and 12 plots, 1.22 m by 0.91 m, were marked out in the autumn of the year previous to the experiment. For the 1976 experiment, wheat (cv Bouquet) was sown in five rows of 16 seeds per row in December 1975 (rows 0.76 m long and 0.13 m apart) and for the 1977 experiment the seeds (cv Flinor)

were first germinated in Jiffypots prior to planting out at the same rate as the previous year. Barriers were erected and dug in enclosing each plot. In the 1976 experiment these consisted of corrugated plastic lawn edging 15 cm high and in the 1977 experiment they were of polythene sheeting 46 cm high. Bricks, stones and lengths of rolled up newspaper were used to provide ground cover for the beetles and the plots were watered regularly.

For the glasshouse experiment 12 plots 1.5 m x 1.8 m were marked out on 1st October 1977 and wheat seedlings that had been prevernalised in a cold room at 5°C for 8 weeks were planted in six rows. Polythene barriers, 46 cm high, were dug into the soil around each plot and straw was laid down along the edges of the plot to provide ground cover. The plots were watered frequently, wetting the straw thoroughly, and overhead mercury lamps were used to extend daylength to 12 hours.

In the 1976 insectary experiment plant germination and subsequent growth was poor in some plots possibly due to uneven soil fertility. Sitobion avenae was introduced in early May, and more were added in late May after slow population increase. Agonum dorsale was introduced on May 20th in a randomized experimental design. Plant growth was considerably better in the 1977 experiment and the second and fourth rows of plants were removed. Powdery mildew affected many plants in spring 1977 and the fungicide Ethyrimol was sprayed in March and May to check the disease. A sheet of polythene was nailed along the west side of the insectary to protect the plots from the strong prevailing wind. Sitobion avenae were introduced into each plot on small pieces of leaf on May 12th and the beetles. Demetrias atricapillus and Pterostichus madidus

were introduced at low, medium and high levels on May 14th (figures 2.7 and 2.8). In the glasshouse experiment smaller plants were used and Rhopalosiphum padi was introduced at low densities. Aphids were introduced on October 12th and again two days later and Pterostichus madidus and Nebria brevicollis were introduced on October 20th (figure 2.9). Alternative food (frozen pea aphids or boiled mince) was provided in five petri dishes in 6 plots with a dish at the side giving an estimate of moisture loss (figure 2.13).

Aphids were sampled in each plot a day before the introduction of the beetles and thereafter twice a week. In the 1976 insectary experiment and the 1977 glasshouse experiment all the plants in each plot were sampled, adult alatae and apterae and nymphs being recorded per plant. Because of the prolific plant growth, the plots were subsampled in the 1977 insectary experiment, 15 tillers per row being sampled in the first week, 10/row in the next week and 5-10/row thereafter, and aphid numbers were recorded separately for each row of plants (two outer rows and a middle row).

In the 1977 glasshouse experiment reductions of aphid numbers provided evidence of beetle predation and numbers eaten were calculated as follows:-

As the carabid species used are known to be nocturnal (Vickerman and Sunderland, 1975) predation was assumed to have occurred solely in the dark.

Numbers of aphids eaten could be calculated by subtracting the actual number sampled from the potential number produced assuming unimpeded aphid increase. However, predation occurred while aphids were reproducing and estimates of aphid kill would need to take this into account.

This was achieved by dividing the 12 hour night into two 6 hour periods over which aphid reproduction proceeded followed by predation. Thus in plots where predation had occurred, aphids increased unimpeded (at the same rate as the control) during two 6 hour periods of daylight and at night were reduced by predation after each 6 hour period of increase.

(iii) Results

In the 1976 insectary experiment there was no unequivocal evidence of predation as A. dorsale did not reduce aphid numbers in any of the treatments (figure 2.6). Moreover, there was no significant relationship between the initial rate of increase (between 20/5-24/5) of aphids in plots and beetle densities ($r = 0.2950$ $p > 0.1$) neither was there any significant correlation between aphid increase per tiller for the first week of population growth (20/5-27/5) or the second week of increase (27/5-7/6) and beetle numbers ($r = -0.2913$ $p > 0.1$, and $r = 0.5058$ $p > 0.05$, respectively) (table 2.5). In addition, combinations of beetle numbers and measures of plant density had no significant associations in multiple regressions with rates of aphid increase (table 2.5).

Table 2.5 1976 Insectary Experiment

Multiple Regressions of Beetle and Plant Factors and Aphid Increase Rate

Variables:

	X1	Number of beetles per plot
	X2	Number of tillers per plant
	X3	Height of plant cm
	X4	Number of plants per plot
	Y1	Rate of increase of aphids per plot 20th-24th May
	Y2	Rate of increase of aphids per plot 24th-27th May
	Y3	Rate of increase of aphids per tiller 20th-27th May
	Y4	Rate of increase of aphids per tiller 27th/5-7th June

Figure 2.6 1976 Insectary Experiment Effect of Density of A. dorsale on the Growth of Aphid Populations

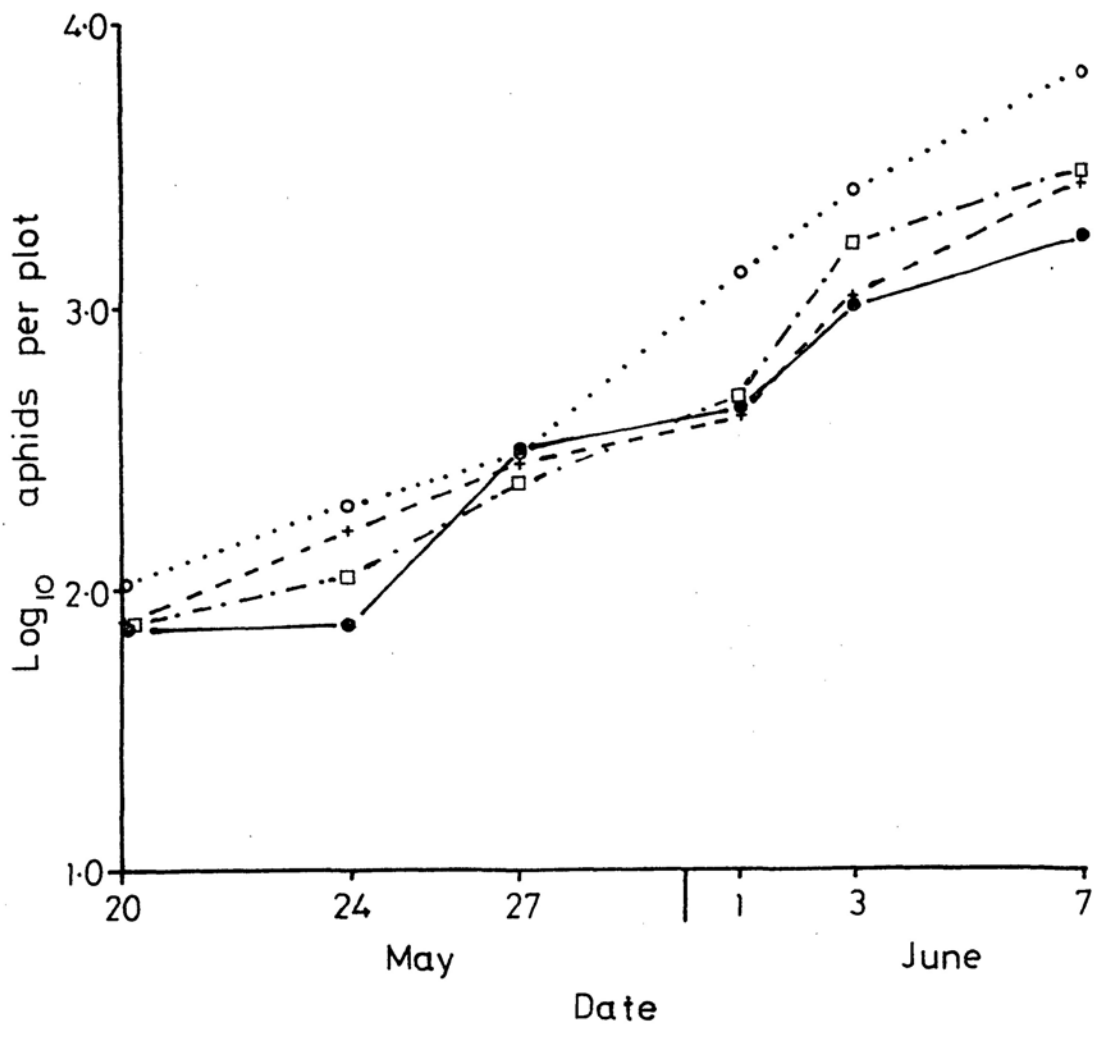


Table 2.5 1976 Insectary Experiment (cont.)

% variance accounted for

Y	X1	X1 + X2	X1 + X3	X1 + X4	DF = 10
Y1	-0.8	-7.3	1.7	-1.5	
Y2	13.3	5.3	3.8	4.1	no significant associations
Y3	-0.7	-1.8	-3.8	-10.2	
Y4	18.1	18.5	13.1	11.7	

It was hoped that the greater ground cover in the 1977 insectary experiment, the larger beetle numbers present and the foliage climbing habits of D. atricapillus would produce a substantial impact on aphid numbers. However, D. atricapillus soon escaped from the plots and no trace of this species was to be found within a few days of introduction. P. madidus was detected beneath the ground cover but none of the beetle treatments had any significant impact on aphid numbers (figures 2.7 and 2.8). Moreover, beetle numbers had no effect on aphid increase rates, either in the first week after introduction or overall (table 2.6). However, a few P. madidus unearthed on June 16th contained aphid remains upon dissection (table 2.7) showing that some aphids had been eaten.

In the glasshouse experiment of 1977 there was a decrease of aphid numbers in two treatments shortly after the beetles were introduced (figure 2.9). The decrease of aphid numbers between successive dates, while aphids in the control were increasing, provided evidence of aphid predation and the consumption of alternative food also indicated that beetle activity and predation was occurring (figure 2.13). Further evidence for predation was provided by the relationship between percentage decrease of aphid numbers and total weight of beetles per plot (figure 2.10).

Figure 2.7 1977 Insectary Experiment Effect of Density of *D. atricapillus* on Aphid Population Increase

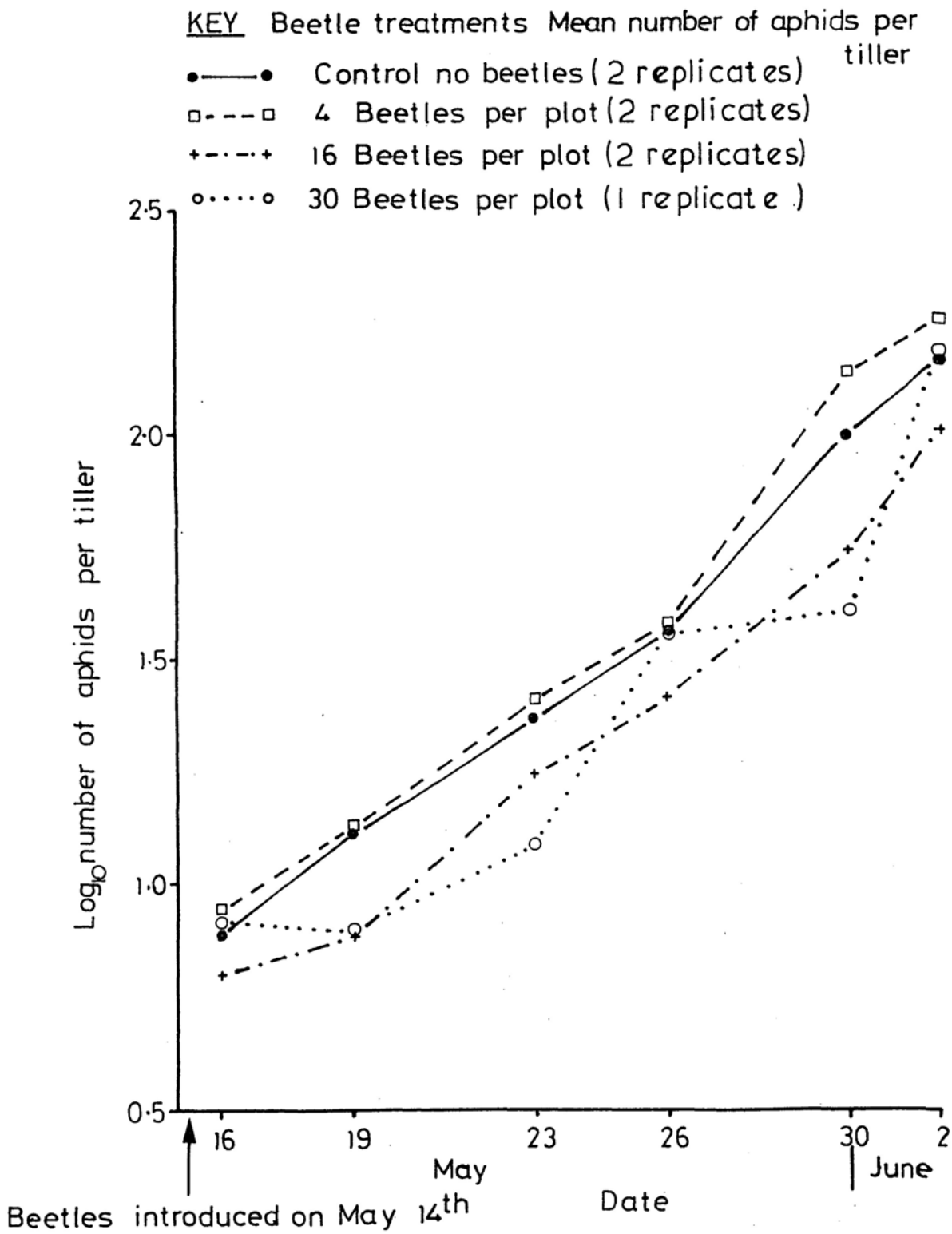


Figure 2.8 1977 Insectary Experiment Effect of Density of P. madidus on Aphid Population Increase

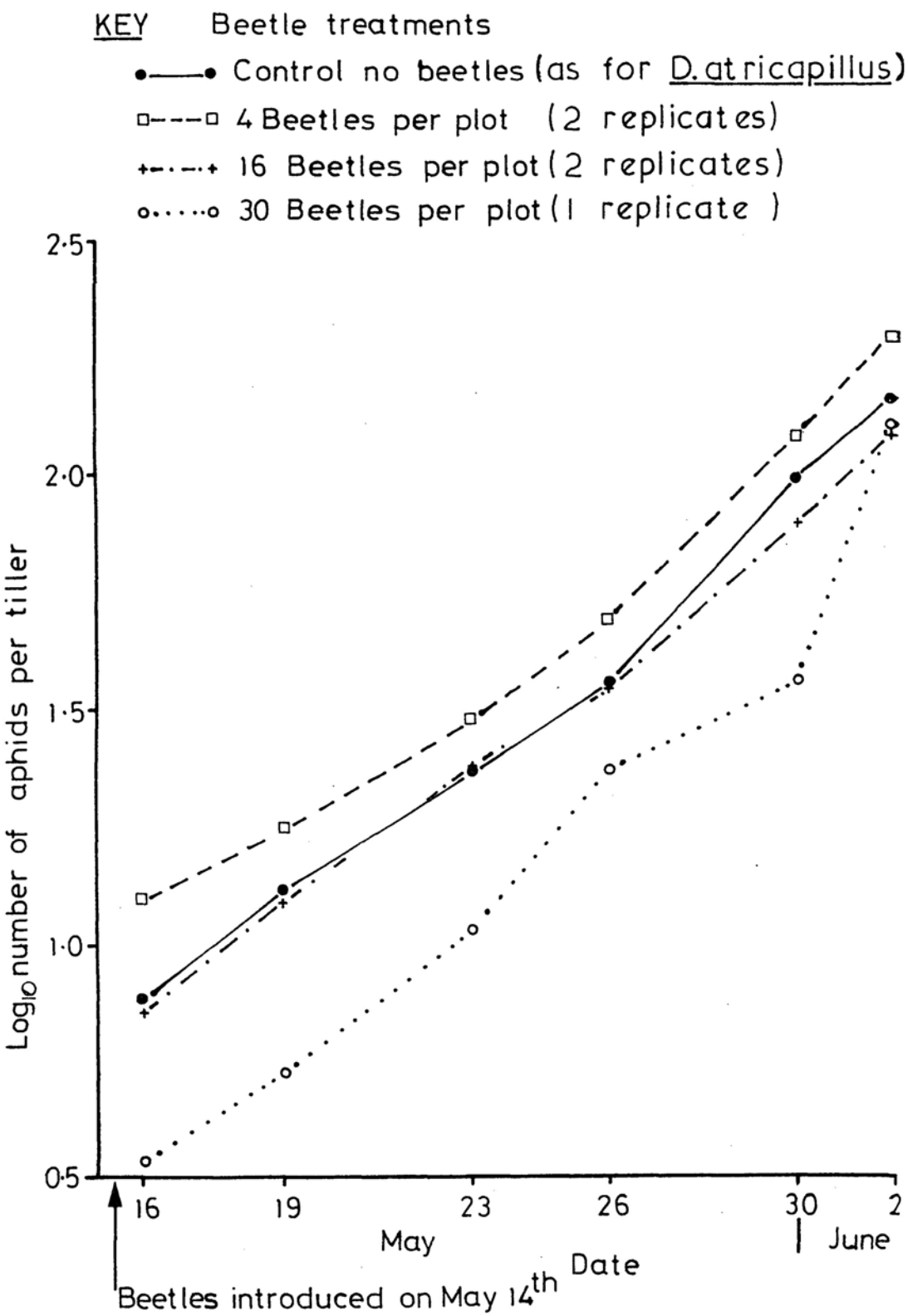


Table 2.6 1977 Insectary Experiment

Linear Regressions of Aphid Increase Rates Against Beetle Numbers

	Regression Coefficients			Degrees	Level of
	Slope	Intercept	Correlation	Freedom	Signific.
1. Aphid increase rate 16-25/6 (y)					
P. madidus (x_1)	0.020	2.625	0.265	5	>0.1 n.s.
D. atricapillus (x_2)	-0.040	3.168	-0.472	5	>0.1 n.s.
All (x_3)	-0.010	2.889	-0.125	10	>0.1 n.s.
2. Aphid increase rate 16/5-2/6 (y)					
P. madidus (x_1)	0.016	3.266	0.480	5	>0.1 n.s.
D. atricapillus (x_2)	-0.010	3.513	-0.290	5	>0.1 n.s.
All (x_3)	0.002	3.403	0.062	10	>0.1 n.s.

Key: Signific. = Significance

Table 2.7 Recovery of P. madidus (June 16th) and Numbers with Aphid Remains in Gut

Beetle Treatment		Plot No.	Number of Beetles Recovered (16th/6)	No. Containing Aphids
Pterostichus madidus	4	8	3 (2♂,1♀)	1 (♂)
P. madidus	16	12	4 (4♀)	3 (3♀)
P. madidus	30	5	7 (5♀,2♂)	2 (2♂)

Aphid consumption between 19th and 21st October was calculated and averaged 5.9 ± 1.1 aphids/night for N. brevicollis while P. madidus ate 8.1 ± 1.9 aphids/night (difference not significant by T test, t = 0.52).

Figure 2.9 1977 Glasshouse Experiment Effect of Ground Beetle Numbers on Aphid Populations

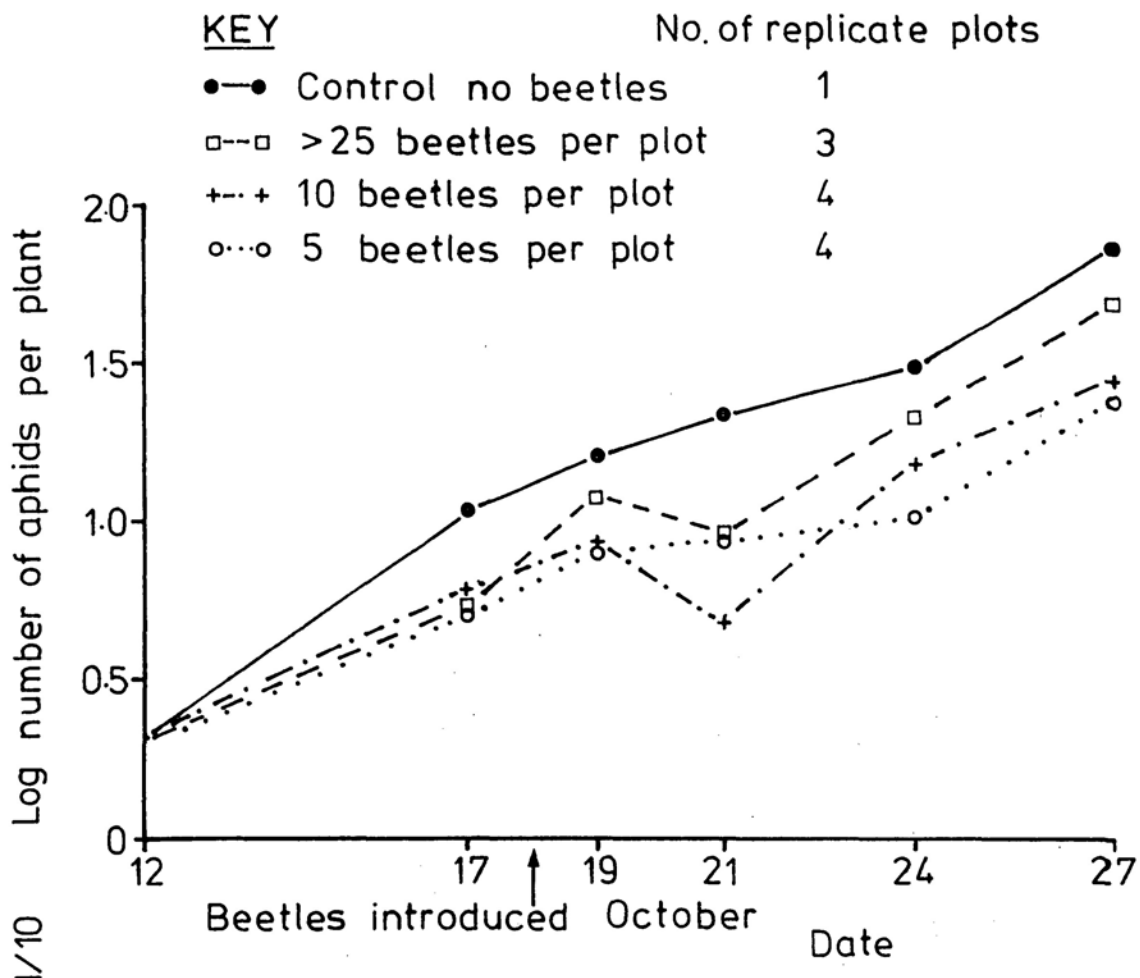
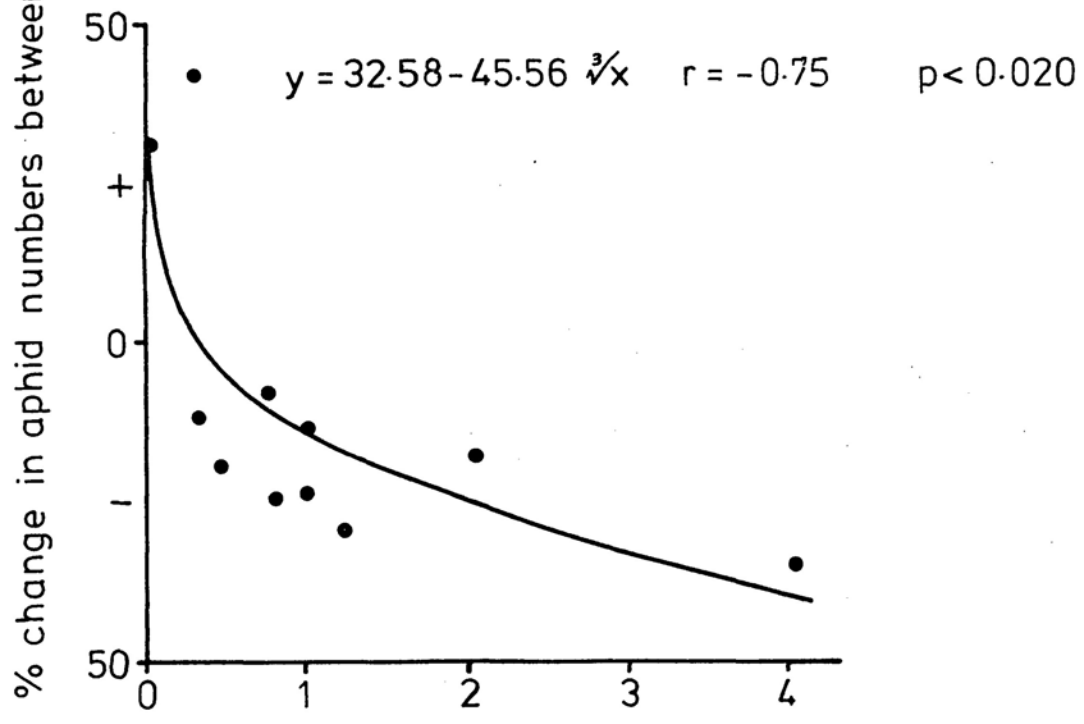


Figure 2.10 Relationship Between Percentage Change of Aphid Numbers Between 19-21/10 and Total Beetle Weight Per Plot



Weight of beetles was used as an indicator of voracity as laboratory experiments had shown that consumption of aphids was proportional to beetle weight. Overall aphid consumption increased with total weight of beetles but the relationship was curved (figure 2.11). Thus total voracity underwent a relative decrease with beetle density and this was reflected in the decrease of aphid consumption per individual with increasing beetle numbers (figure 2.12B). A similar situation occurred with the consumption of alternative food. Total consumption of alternative food did not increase with beetle numbers and consequently the consumption per beetle rapidly decreased with increasing beetle density (figure 2.12A). This suggests that interference between beetles for both aphids and the alternative food source was increasing with beetle density. Moreover, the consumption of alternative food decreased more rapidly with beetle density than did aphid consumption indicating that competition between beetles was more marked where the food resource was present in a comparatively small area. This is substantiated to some extent by observations of the behaviour of feeding beetles in laboratory cultures. The beetles were fed with boiled mince in petri dishes and would often fight over a piece of meat.

Consumption of the alternative food decreased rapidly after the first day (figure 2.13) but increased slightly in some treatments after a further week.

(iv) Discussion

The insectary experiments of 1976 and 1977 were carried out on a smaller scale than the experiments of Edwards and George (1976) and Edwards Sunderland and George (1980) and the ground beetles had no apparent effect on aphid populations, for the following reasons:-

Figure 2.11 Relationship Between Total Aphid Consumption Per Plot and Total Weight of Beetles Per Plot

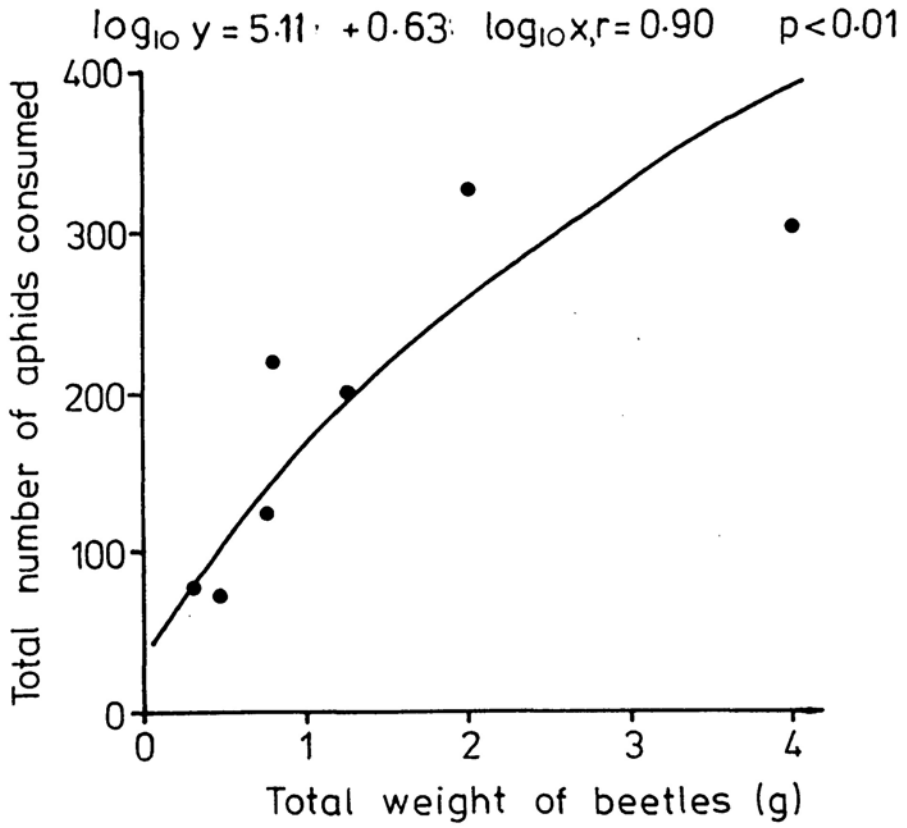


Figure 2.12 Relationship Between Food Consumption Per Beetle Per Night and Number of Beetles Per Plot

A. Mg Alternative Food Eaten Per Beetle Per Night (y)

B. No. Aphids Eaten Per Beetle Per Night (y)

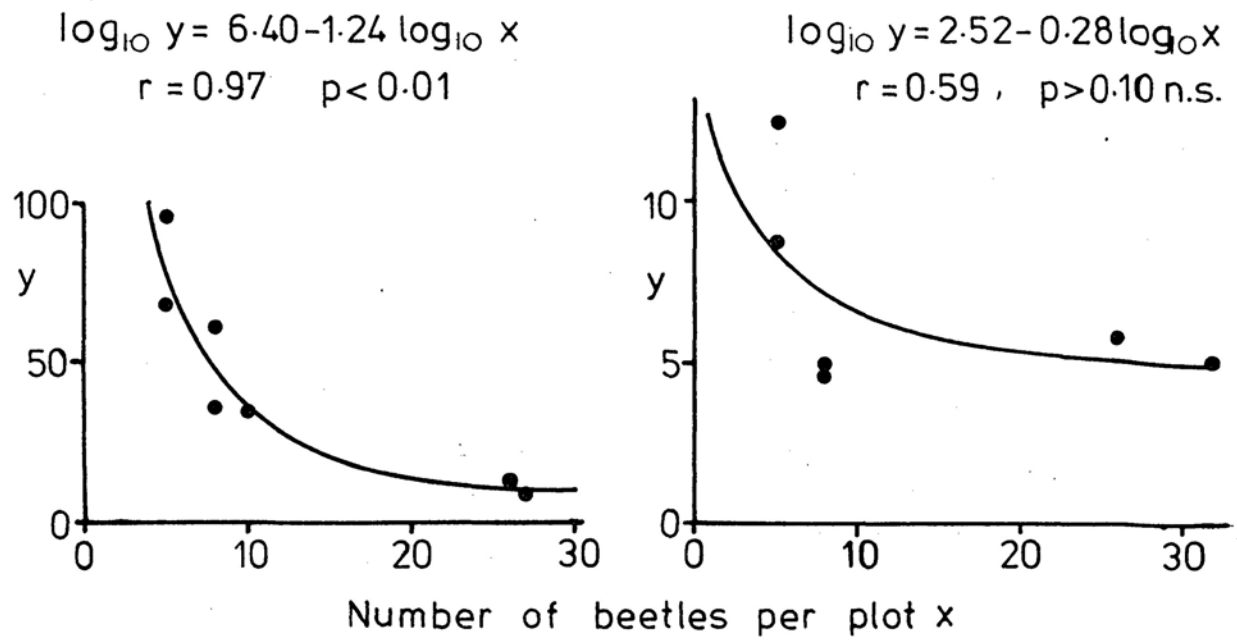
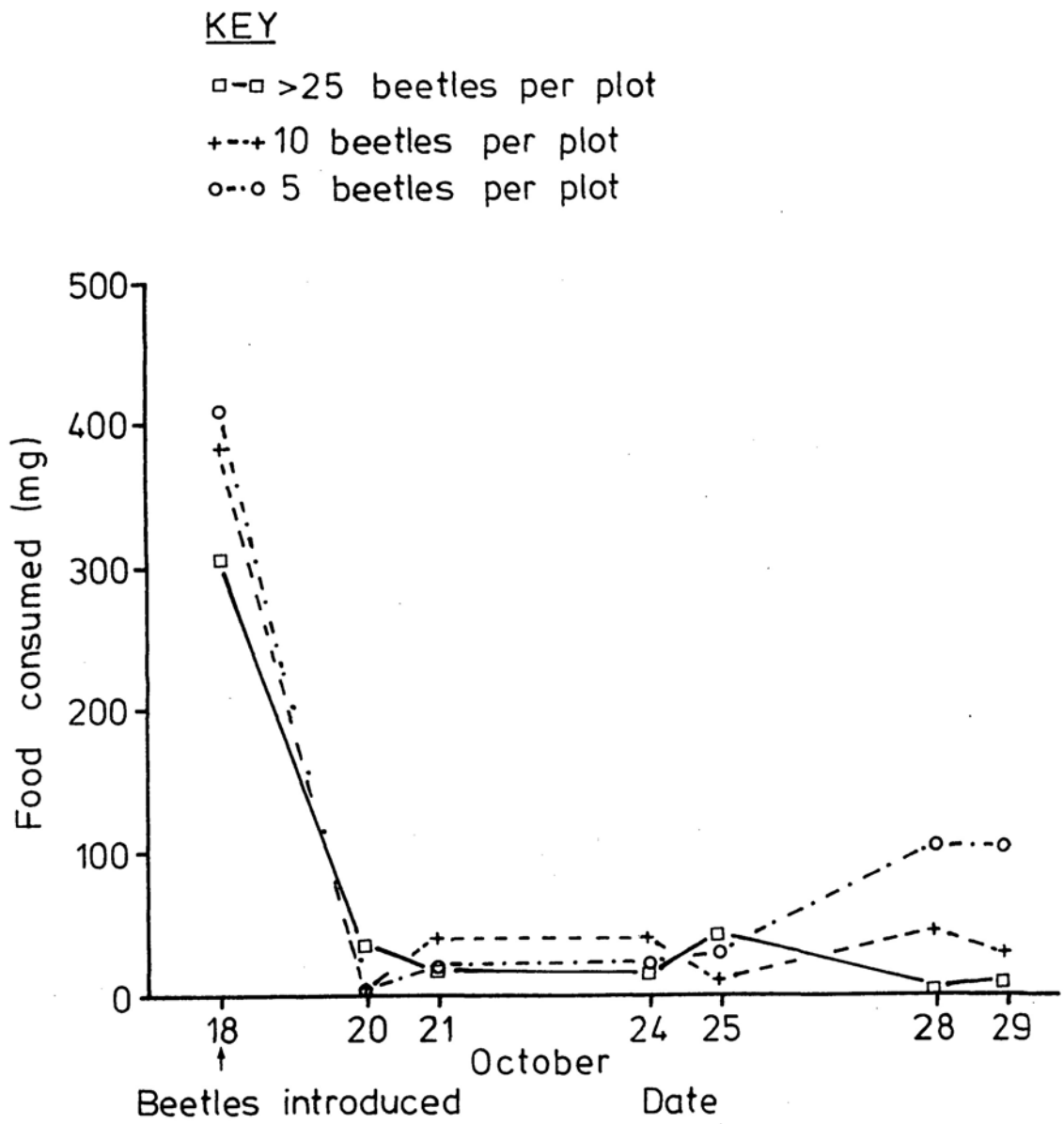


Figure 2.13 Mean Consumption of Alternative Food Per Night for Beetle Treatments



(1) Habitat segregation. The cereal plants were at an advanced growth stage (Feekes' scale 9) with the aphids present on the upper leaves. However, the beetles were restricted to the ground zone and as they were unable to climb the vertical stems, predation could only take place when aphids occurred on or near to the ground. The plots were protected from the direct effects of wind and rain and thus there was little movement of aphids into the ground zone and little opportunity for predation.

(2) Lack of beetle activity. The surface of the soil was dry and weed free and although ground cover was provided and the plots were watered regularly, it seemed likely that the beetles had to a great extent been rendered inactive or suffered mortality as a result of the dry conditions. However, aphid remains found in the guts of P. madidus in the 1977 experiment indicated that a certain amount of beetle activity and predation had occurred in the ground zone but this factor was unimportant in the overall aphid population dynamics.

The insectary experiments demonstrated that habitat diversity was probably important in providing suitable conditions for ground beetle activity. Rivard (1966) and Thiele (1964) emphasized the importance of microclimate humidity on the activity of carabids and Speight and Lawton (1976) suggested that weed cover in a crop encouraged carabid activity because of the resulting higher ground humidity.

In the 1977 glasshouse experiment the ground cover provided by the straw appeared to be a major factor in encouraging carabid predation, albeit for a short period. The wheat plants were fairly small but robust allowing

beetles to eat aphids from the plants. Predation occurred at low aphid population levels and between 20–60% of the aphid population was consumed in two days. The subsequent increase of aphids (when further decrease might have been expected) was either due to an increase in aphid reproductive rate or to the cessation of predation. Aphid increase in the control plot remained constant (figure 2.9) and the course of the subsequent aphid increase was probably a general decrease in beetle activity as shown by the reduction in alternative food consumption.

The number of R. padi eaten by Nebria brevicollis and Pterostichus madidus was of the same order as the aphid consumption of Agonum dorsale in the laboratory. A. dorsale males and spent females consumed about five R. padi per day and the larger N. brevicollis and P. madidus, both populations doubtless comprising mainly spent individuals, consumed six and eight aphids per night respectively. Similarly, consumption of the alternative food (frozen pea aphids) in the glasshouse experiment was of the same order as that found in the laboratory (experiment 5). P. madidus consumed 21.5% of its body weight and N. brevicollis slightly more, 35.7%, which compared with an average consumption for males and spent female P. melanarius of about 28% of body weight. Thus estimates of aphid consumption in the laboratory related well to consumption in the experimental plots.

The insectary and glasshouse experiments showed that factors influencing the activity of ground beetle populations were of great importance in determining the extent of aphid predation. The aggregation of beetles in areas of a cereal crop with greater ground cover (Speight and Lawton, 1976) could result in a reduction in prey consumption by individual beetles

through interference (1977 glasshouse experiment and experiment 4, section 1), although this may depend on the degree of hunger of the beetles (experiment 5, section 1). To conclude, factors affecting the activity and population density of ground beetles may be more important than the voracity of beetles for aphids in determining the amount of predation on cereal aphids that occurs in the field, a conclusion also reached by Frank (1971).

2.4 Effect of Polyphagous Predators on Cereal Aphid Populations in the Field

(i) Introduction

Results from a field experiment in a crop of winter wheat in 1975 suggested that polyphagous predators, especially the carabid species Agonum dorsale, had had a significant effect on the increasing aphid population.

Polyphagous predators commonly present in cereal fields include the Carabidae, Staphylinidae, Aranae, Dermaptera and larval Coleoptera. The importance of these in the population dynamics of cereal aphids during the summer was investigated using exclusion methods to manipulate predator populations in parts of the crop. Large cages were used to contain a constant population of ground beetles and to exclude immigrant predators such as coccinellids and syrphids, and areas of the crop were treated with granular insecticides to reduce populations of ground dwelling polyphagous predators.

The field experiments were carried out in two years, in 1976 using cages and in 1977 using replicated plots on an insecticide treated area and in the untreated crop.

(ii) Materials and Methods

The field experiments were carried out in both years in a 19 acre field of winter wheat (cv Score).

1976 Experiment

Three cages were used, one on an insecticide treated area of crop, one with extra ground beetles introduced and one unmodified with the normal field density of carabids.

An area of the field (c 70 x 55 m) was treated with Birlane (chlorfenvinphos) on 30/10/1975 and Sevin on 19/1/1975 to kill ground beetles and thus reduce their density. A cage was subsequently erected on May 26th on this area, giving the reduced predators treatment, C1. For the boosted predator treatment, a cage (C2) was erected on May 26th on the untreated crop and 735 polyphagous ground predators (265 carabids, 391 staphylinids and 79 others) were introduced on May 27th and 28th giving an increased density of 158 predators per m^2. The third cage, C3, was erected on the untreated part of the field with no further modifications and constituted the normal predator density treatment.

The cages (dimensions 3.05 m x 1.83 m x 1.83 m) were constructed of galvanised steel tube and were covered by terylene netting (mesh size 1 x 0.25 mm), the edges of which were buried to a depth of about 10 cm to prevent movement of beetles out of the plots. Movement of predators from the predator depleted and boosted treatments (cages C1 and C2) was further restricted by a corrugated plastic barrier, 23 cm high, dug in around the cages and covered with an insecticidal laquer (diazinon). A transect was formed by the removal of two rows of plants from the centre of the cage along which the aphids were sampled.

Figure 2.14 Plot Layout for Field Experiment 1976

Summary of treatments:-

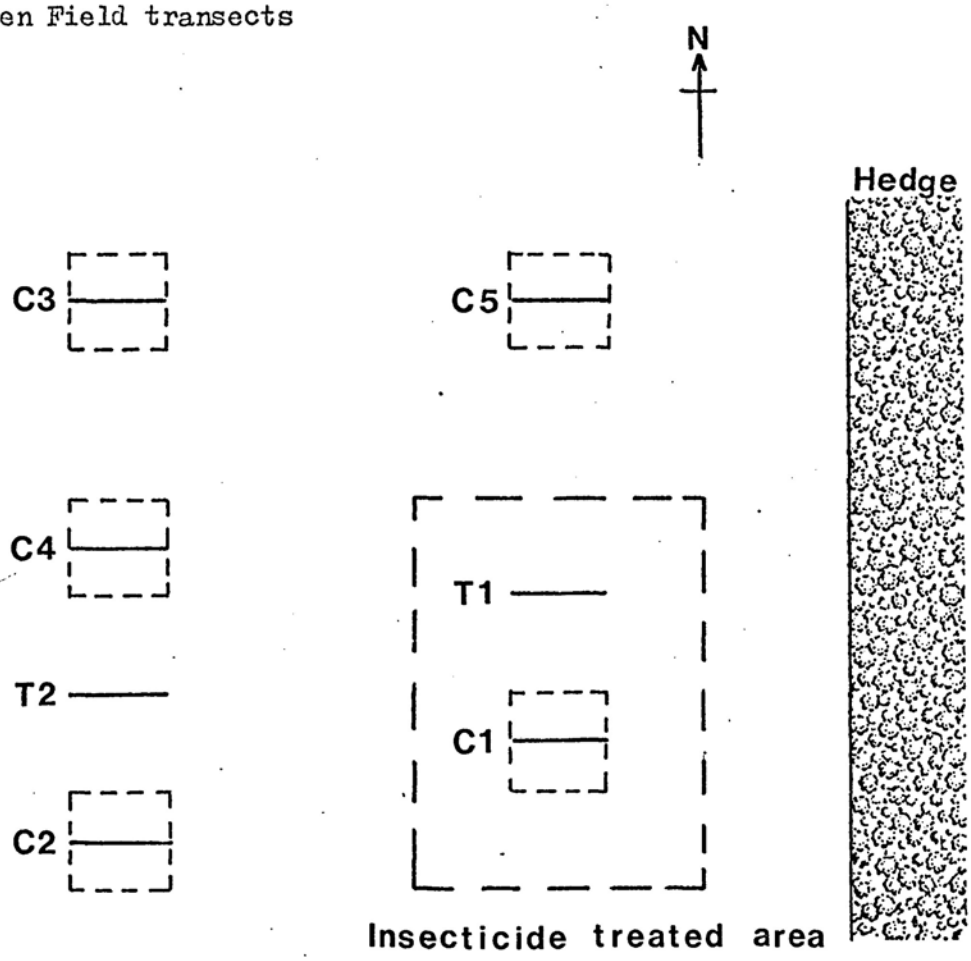
C1 - Ground predator populations depleted

C2 - Ground predator populations boosted

C3 - Ground predator populations at normal level

C4, C5 } Aphid specific predators partially excluded (Chapter 3)

T1, T2 } Open Field transects



Two uncaged transects (T1 and T2) were established in a similar manner, one on the insecticide treated area (T1) adjacent to cage C1 and the other in the open field (T2) near to cage C2 (figure 2.14).

The efficacy of the insecticidal treatment was measured by catches of ground predators in 10 pitfall traps.

Sampling methods for aphids are detailed in Chapter 3.

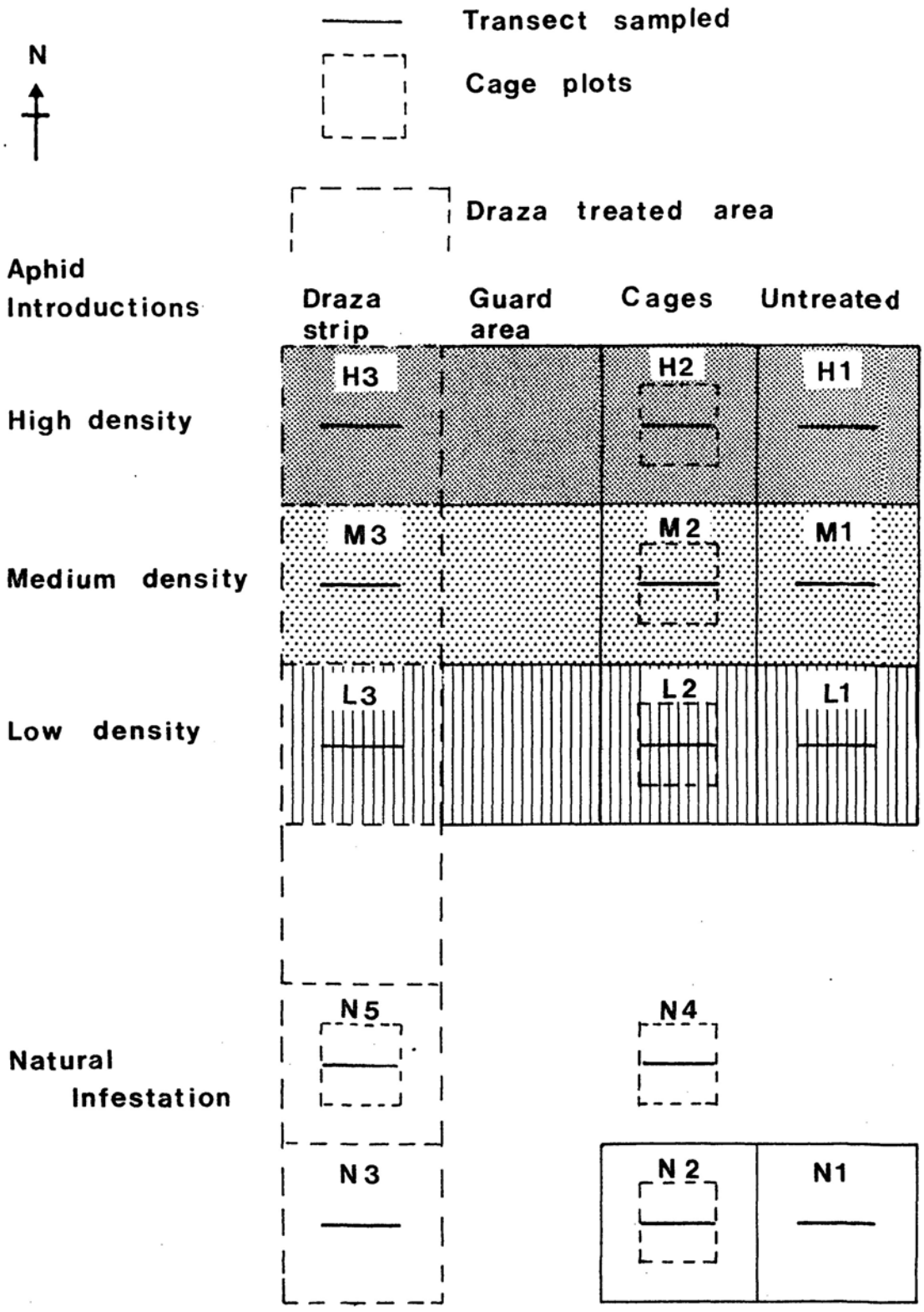
1977 Experiment

A central part of the field was divided into four strips, each 33.5 m x 5.5 m (figure 2.15). One strip was treated with Draza (methiccarb) on April 12th and 26th and June 16th and Birlane (chlorfenvinphos) on May 9th to reduce numbers of ground predators, the adjacent strip was a guard region, cages were erected on the next strip and the final strip was the open field control. Four to five plots, 6.7 m x 5.5 m were marked out on each strip and two rows of plants were removed from the centre of each plot to give access for sampling, as before. Aphids (S. avenae) were introduced on May 2nd and again two weeks later on pieces of leaf into each strip at three levels - low (120/plot), medium (360/plot) and high (1200/plot), the remainder of the plots being infected solely from natural immigration. The arrangement of the plots is given in figure 2.15.

Populations of polyphagous predators were sampled by Game Conservancy staff using pitfall traps, D-Vac samples (5 'sucks'/sample), and ground search of 0.1 m^2 quadrats to give average densities for Open Field and Draza treatments.

Aphids were sampled in a similar way to the 1976 experiment (see Chapter 3).

Figure 2.15 Plot Layout for Field Experiment 1977



(iii) Results

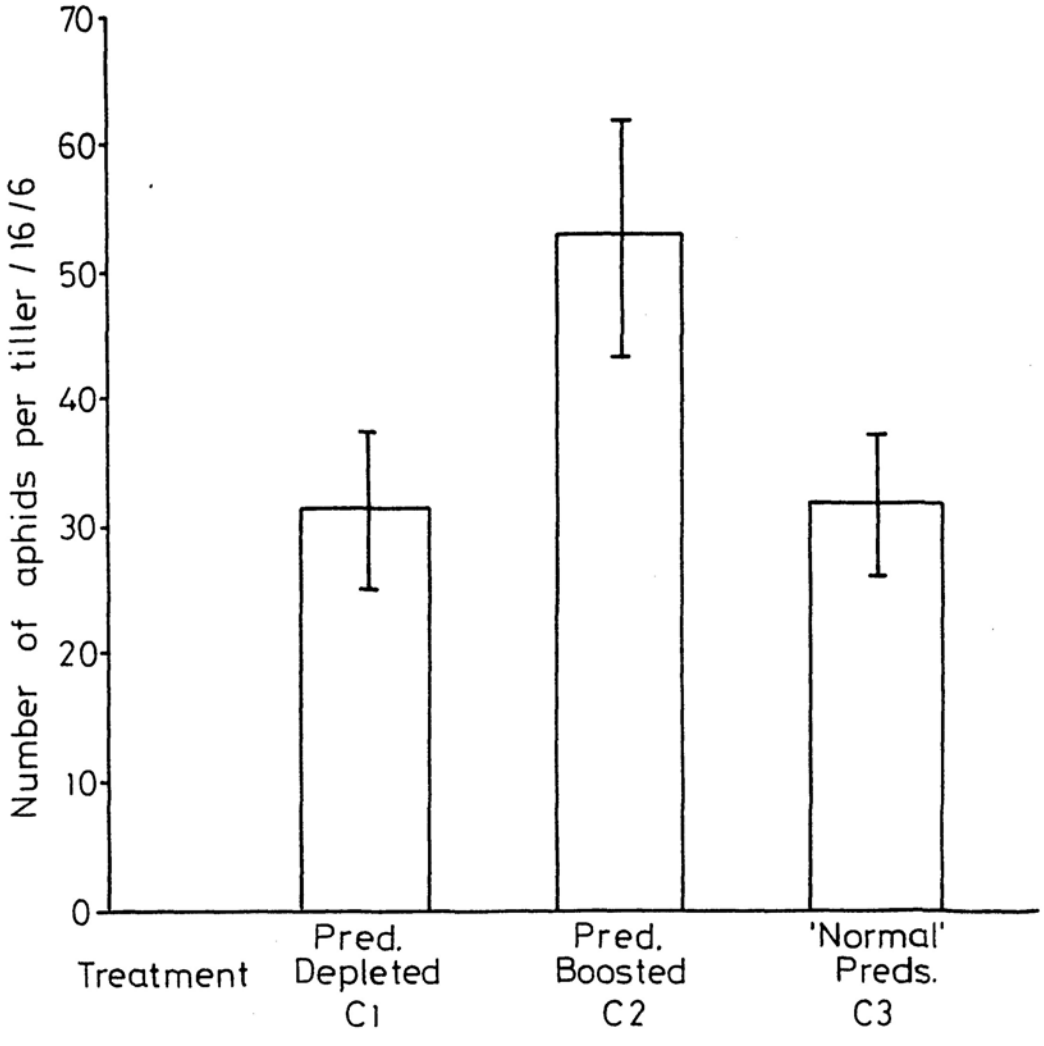
1976 Experiment

Numbers of ground beetles were greatly reduced by the insecticide treatment. Sixty beetles were caught in the pitfall traps between April 21st and May 5th in the treated area whereas over twice as many (147) were caught in the untreated field. Moreover, between May 5th and the time of caging 57 carabids and 22 staphylinids were removed. Predator numbers were increased in the boosted predator treatment (C2) by 158/m^2, assessed by pitfall catches.

The cage treatments showed differences in aphid increase rates between the start of the aphid population increase on May 24th and peak numbers in the open field on June 16th that would be expected from the nature of the treatments. Thus, the predator excluded cage, C1, had the highest rate of aphid increase (7.4 times/week) and the other two cages lower at 6.4 times/week. However, in the open field transects (T1 and T2), aphids increased more slowly in the insecticide treated area (T1 - 7.4 times/week) than in the transect on the untreated field (T2 - 7.6 times/week). Hence the differences in increase rates between the cages could have been due to natural variation as, in the absence of replication, there was no measurement of within treatment variability. Indeed, on June 16th, at peak aphid levels in the field, aphid numbers in the predator boosted cage (C2) were substantially higher than in the other cages (figure 2.16) and thus the increased density of ground beetles had little overall impact.

After the aphid peak in the open field on June 16th, aphids in the cages continued to increase until June 25th. Although there were differences in increase rates between the cage plots (C1 - 3.6 times/week,

Figure 2.16 1976 Field Experiment Aphid Levels in Predator Manipulated Plots on June 16th, with 95% Confidence Interval Limits



C2 and C3 - 2.5 times/week) it seems unreasonable to attribute these differences to predation since the activity of the ground beetles had declined with the hot weather and aphid numbers were too high for a significant effect to be expected.

To conclude, polyphagous ground predators had little effect on aphids in 1976 in the field investigated, which may have been due to the deleterious effect of the hot, dry weather on predator activity within the crop.

1977 Experiment

Fourteen species of ground beetles were trapped in the field representing 16% of the polyphagous predator taxa present (table 2.8). All the carabid species were predatory and able to feed on aphids. Pterostichus melanarius was the largest beetle species occurring, medium sized beetles included; Agonum dorsale, three species of Amara, Demetrias atricapillus, Harpalus aeneus (Fab.), Loricera pilicornis (Fab.) and Nebria brevicollis, and the small beetles were, Asaphidion flavipes (L.), two species of Bembidion and Trechus quadristriatus (Schr.); Tachyporus hypnorum (Fab.), T. chrysomelinus and T. nitidulus constituted the known aphidophagous staphylinidae present.

The insecticide treatment effectively reduced both the number of taxa (by 75%) and the population (by 63%) of polyphagous predators from the normal levels in the open field. In the open field, coleoptera larvae were most numerous constituting 53% of the total population (table 2.8), but these, together with the carabids, were greatly affected by the insecticide treatment being reduced by 74% and 67% respectively

Table 2.8 Composition of the Population of Polyphagous Predators in 1977

Taxon	Number of Taxa		Density (Total 27/4-6/7)			
			OPEN FIELD		DRAZA	
	No.	% of Total	No./m^2	% of Total	No./m^2	% of Total
Carabidae	14	15.7	150	13.7	51	12.6
Staphylinidae	17	19.1	88	8.1	53	13.0
Coleoptera larvae	15	16.9	577	52.8	148	36.6
Aranae	42	47.2	267	24.5	151	37.5
Dermaptera	1	1.1	10	1.0	1	0.2
Total	89		1092		404	

and were relatively less abundant in the Draza treated strip. Staphylinid adults and spiders, however, were less affected by the insecticide, being reduced by 40% and 43% respectively, and they increased in relative abundance in the Draza strip (table 2.8).

Aphids increased at a greater rate between June 20th and July 4th in the Draza plots than in the Open Field (table 2.10a) which gave rise to greater peak aphid populations in all plots; significantly greater in all but the H plot (figure 2.17). The differences in aphid numbers were probably accounted for by differences in predation pressure from polyphagous predators especially Tachyporus larvae in the Open Field and Draza plots (table 2.9). The difference in aphid levels between the treatments increased as a consequence of the higher rate of aphid increase in the Draza plots until, by July 4th, aphid numbers in this treatment were 50% higher than in the Open Field, (figure 2.17). However, during this period the numbers of polyphagous predators did not increase (figure 2.18, table 2.9)

Figure 2.17 1977 Field Experiment Comparison of Aphid Populations (with 95% Confidence Interval Limits) Between Treatments on July 4th

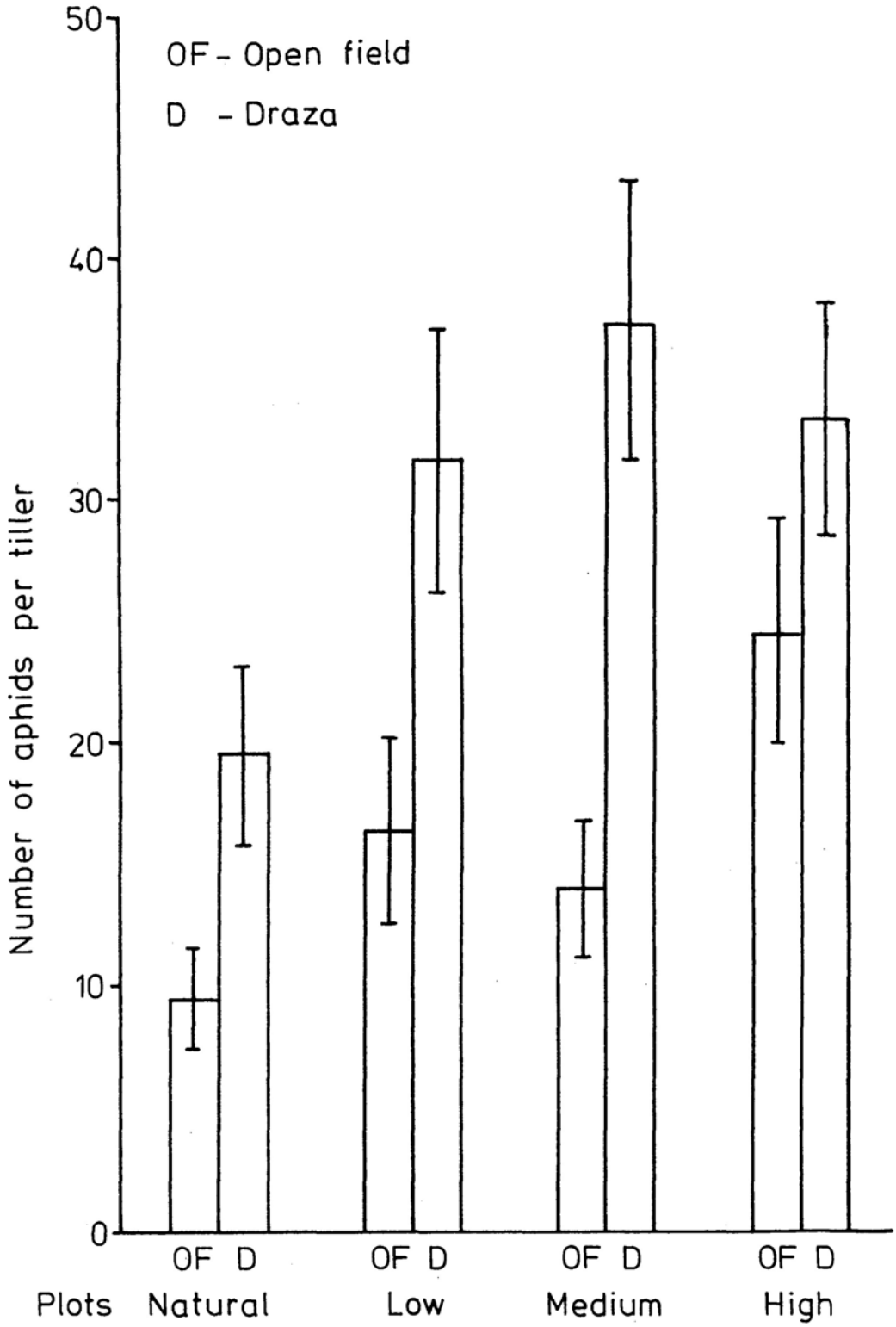


Figure 2.18 1977 Field Experiment Effect of Insecticide Treatment on Polyphagous Predators and Resulting Aphid Populations

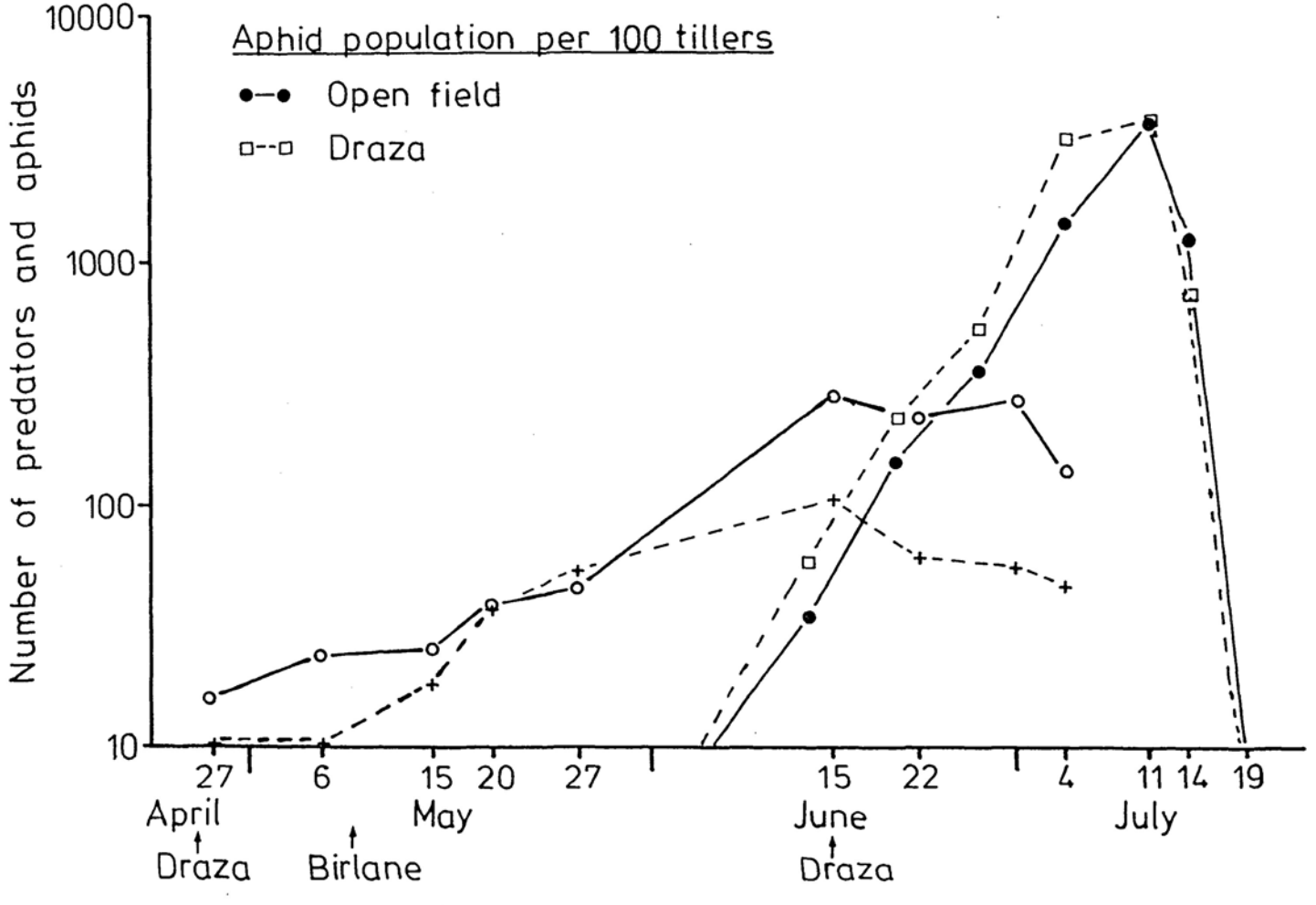


Table 2.9 Effect of Draza Treatment on Density of Tachyporus Larvae

Date	Density Tachyporus Larvae (nos./0.5m^2)		% of Total Polyphagous Predators	
	OPEN FIELD	DRAZA	OPEN FIELD	DRAZA
27th May	8	4	17.2	7.1
15th June	97	22	33.6	21.4
22nd June	73	17	31.3	27.4
30th June	90	15	32.7	26.3
6th July	26	16	18.3	34.8

although an increase in predation pressure would have been required to produce the observed differences in aphid numbers. The increase in predation was probably supplied by an increase in the voracity of Tachyporus larvae as they matured. Predator populations then dropped by July 6th when the larvae were pupating (figure 2.18, table 2.9).

The 36% difference in aphid increase rates between the two treatments produced a significant increase in mean aphid index of 27% (table 2.10a). Differences in yield between the treatments were further reduced; the mean reduction in weight of grain per ear was 3% and that of thousand grain weight was 2% (table 2.10a). However, when the regression equations (table 2.10b) were used to assess the difference between means, percentage differences rose to 7% and 4% for weight of grain per ear and thousand grain weight respectively. Thus the insecticide treatment produced an increase in aphid increase rate of 36%, which in turn increased aphid index by 27% and reduced yield by 7%.

Table 2.10a Comparison of Biotic Factors in Open Field and Draza Plots

Treatment	Rate Aphid Inc. 2/6-4/7 Times/Week		Aphid Index		Wt. of Grain/Ear gm		Thousand Grain Wt. gm	
	OPEN FIELD	DRAZA	OPEN FIELD	DRAZA	OPEN FIELD	DRAZA	OPEN FIELD	DRAZA
1. High initial aphid infestation	3.60	4.44	501	573	1.65	1.77	56.1	55.3
2. Medium initial aphid infestation	3.17	5.60	364	504	1.74	1.77	57.1	58.9
3. Low initial aphid infestation	3.21	3.99	397	483	1.79	1.75	58.8	56.6
4. Natural initial aphid infestation	2.89	3.50	289	411	2.21	1.87	63.4	59.8
Means	3.22	4.38	387	492	1.85	1.79	58.8	57.7
% Change From OPEN FIELD	+36.0		+27.1		-3.2		-1.9	
Paired t Test	t = 2.75		t = 6.68		t = 0.58			
3 Deg. Freedom	$p < 0.1$		$p < 0.01$		$p \sim 0.6-0.7$			

Key: Inc. = Increase Wt. = Weight

Table 2.10b Regression Equations Between Aphid Index and Yield

(a) y = Weight of Grain/Ear

y = 2.39 - 0.0013 Aphid Index . r = -0.702 p = 0.052

(b) y = Thousand Grain Weight

y = 68.1 - 0.0223 Aphid Index r = -0.790 $p < 0.02$

To conclude, predation by polyphagous predators, in particular, by the larvae of the staphylinid Tachyporus, did not merely affect the initial establishment of aphids but appeared to have a dynamic effect on the increase of aphid populations in the field in 1977. Moreover, the differences in resulting aphid index were sufficient to produce a substantial difference in mean yield per treatment. Ground beetles were not abundant and had little influence on the course of events but spiders were an important component of the fauna and probably made an important contribution to the overall level of predation by polyphagous predators.

(iv) Discussion

Potts and Vickerman (1974) developed the concept that polyphagous predators could have an important role in cereal aphid population dynamics from their work on floral and faunal diversities within cereal fields. They found that as aphid numbers decreased through June faunal diversity increased giving a significant correlation with change in aphid density. They suspected that the dynamic relationship between faunal diversity and aphid numbers was due to the predatory component of the diversity indices. This was borne out when they found a significant correlation between the proportion of predatory arthropods in the samples and the diversity indices of the fields. However, the classic aphid specific predators such as coccinellids, syrphids and chrysopids were not numerous enough to be important and thus it was concluded that polyphagous predators were the important agents of changes in aphid abundance. Similar effects were demonstrated by Vickerman (1974). Plots sprayed with herbicide to reduce floral diversity suffered a significant reduction in numbers of a third of the arthropod taxa present, the largest reduction being in the numbers of staphylinids (Tachyporus spp). However, aphid

numbers increased and this was attributed to reduced predation brought about by the herbicide treatment.

The 1977 field experiment also showed the effects of predator exclusion, when cereal aphids, at higher levels than those found by Potts and Vickerman (1974) and Vickerman (1974), increased at a faster rate when released from the retarding influence of Tachyporus predation. Predation by Tachyporus spp adults and larvae on aphids in the field was documented by Vickerman and Sunderland (1975) when they found that 30% of adult and 14% of larval Tachyporus had fed on aphids. However, this probably underestimated predation because of the insensitivity of the precipitin test used. Moreover, they found that polyphagous predators were both more numerous in the crop by night - 3-20 times as many Tachyporus larvae were found by night than by day depending on the sampling method (D-Vac or Sweep Net) -, and more had eaten aphids by night, - 17% of predators sampled during the day contained aphids, whereas 67% contained aphids in the night samples. Thus, as crop sampling in 1977 was by day it is likely that the numbers of polyphagous predators were underestimated.

The large effect that polyphagous predators exerted on aphid increase rate in 1977 becomes more understandable when considered in terms of Rabbinge, Ankersmit and Pak's (1979) hypothesis of aphid population growth in cereals. They maintained that aphids undergo two generations in the field; alate immigrants constitute the first generation and their offspring which develop into apterous mothers produce the second generation of nymphs which mostly become alate adults. The apterae provide the major reproductive capacity of the population and therefore predation of the first generation of nymphs, in this case by polyphagous

predators, which are destined to become reproductive apterae is relatively more effective than predation, at a later time, of aphids that are going to emigrate anyway.

In 1976, ground predators had no demonstrable effect on aphid populations. Environmental conditions were obviously unsuitable for beetle activity because, as in the insectary, the crop was free from weeds and the microclimate was hot and dry.

In 1977, staphylinids, in particular Tachyporus larvae, together with spiders were important predators of cereal aphids, carabids forming a minor component of the polyphagous predator fauna. However, in certain years, e.g. in 1975, ground beetles can become the major predatory component of the polyphagous predator fauna and can have a substantial influence on populations of cereal aphids (Jones, 1979). Agonum dorsale is particularly important in this respect because of its dietary requirement for cereal aphids (Sunderland, 1975), its voracity and its plant climbing ability in certain circumstances.

CHAPTER 3

THE ROLE OF NATURAL ENEMIES IN CEREAL APHID POPULATION DYNAMICS

3.1 Introduction

Many publications of field studies of cereal aphids have mentioned the supposed importance of natural enemies in the control of aphid populations (e.g. Latteur, 1971, Carrillo, Mellado and Pino, 1974, Konteu, 1975, Grigorov, 1976, Dedryver, Vible and Anglade, 1977) but few attempts have been made to quantify the effect of predators. Jones (1972) and Dean (1974d) drew conclusions concerning the relative importance of parasites and predators in the control of aphids in the field but did not quantify the effect of the natural enemies. Rautapää (1972a, 1975, 1976) demonstrated quantitative relationships between measures of predator and aphid abundance (indices) from experiments in small cages (1972 and 1975) and from field work over a number of years (1976). The occurrence of linear relationships between predator and aphid indices was taken to prove that the relationships were a result of cause and effect. However, in the cage experiments, some unexpected correlations were produced, others that may have been expected were not produced and there was considerable variation between the two experiments. These effects may have been a consequence of ignoring the development of coccinellid larvae when calculating indices of abundance. Moreover, more complex models of predator-aphid interactions in the field (Frazer and Gilbert, 1976, Rabbinge, Ankersmit and Pak, 1979) have now superceded this approach.

Estimates of the accuracy of assessment of predator densities have generally been lacking in field studies, although Frazer and Gilbert (1976)

have demonstrated the errors that can be incurred by ignoring the problem of sampling accuracy. Numbers of predators sampled in the field can be influenced by their behaviour (e.g. circadian behaviour (Vickerman and Sunderland, 1975) and effect of temperature (Frazer and Gilbert, 1976)), by the efficiency of the sampling method used (e.g. visual counts of predators (Dean, 1974d), D-Vac (Potts and Vickerman, 1974), sweep net (Vickerman and Sunderland, 1975)) in addition to the absolute density present. Moreover, it can be argued that the number of predators in a sample is often more dependent on ancillary factors, such as those mentioned above, than on the absolute density of predators in the field. This produces further difficulties in trying to quantify the effect of predators on aphid populations.

The present field experiments undertaken in 1976 and 1977 sought to manipulate predator densities by using exclusion methods and different aphid densities in the crop in order to assess the resulting effect on aphid populations, and thereby establish more clearly the importance of natural enemies.

The effect of aphid density on movement of adult coccinellids between plots of wheat in an insectary was also investigated by manipulating aphid populations with insecticide sprays, introducing marked coccinellids and noting the resulting movement.

Finally, the effect of natural enemies (parasites and coccinellid larvae) and other factors on late season aphid populations was studied in the insectary in 1976 and 1977.

3.2 Field Experiments

Materials and Methods

In the 1976 field experiment, aphid specific predators were excluded from areas of the crop using large terylene covered cages erected at two different times; firstly, after the initial immigration of alatae and secondly, later in the season after the immigration of coccinellid adults. In the 1977 experiment cages were also used to exclude large natural enemies and aphids were introduced into the crop at three densities, in addition to the natural infestation, to investigate possible density dependent interactions with natural enemies.

A similar aphid sampling method was used in 1976 and 1977. The four corners of each transect were sampled separately by different individuals to avoid sampling bias. Sequential tillers along the sides of the transect were examined for the presence of aphids at approximately weekly intervals, the number of tillers examined being reduced as aphid numbers increased. Aphids were counted in three categories, alatae, apterae and nymphs, and in 1977 were recorded for the separate parts of the plant on which they occurred (ear, flag leaf, lower leaves). Aphid species were recorded separately at one corner of each transect on most sampling occasions and in 1977 numbers of aphid colonies per tiller were also recorded.

Numbers of mummified and diseased aphids were noted, and on some occasions samples of wheat ears were returned to the laboratory and the numbers of parasites emerging from mummies were counted three days later. Aphids from field and caged plots in the 1977 experiment were brought back to the laboratory (R. Hall, unpublished), placed on barley plants

under perspex covers and the number diseased was determined three days later. Predators were sampled by Game Conservancy staff (Dr. K. D. Sunderland) in 1976 and 1977 using the D-Vac suction sampler, ground search and pitfall trapping techniques. Alatiform IV instar cereal aphids were also recorded from the D-Vac samples and expressed as a percentage of total number of aphids sampled.

In both years, aphids were sampled by a team of four including the author and the latter identified the aphid species and counted diseased and parasitised aphids in the field and was responsible for co-ordinating the weekly sampling programme and subsequent production of results.

To summarise: in 1976 the treatments consisted of two open field transects (T1 and T2), three 'early' cages (C1, C2 and C3) and two 'late' cages, erected on June 11th, (C4 and C5) (figure 2.14). In 1977 the treatments comprised the insecticide treated Draza strip (the 'Draza' treatment; plots N3, L3, M3 and H3), the caged plots (the 'Cages'; plots N2, L2, M2, H2 and N5) and the untreated plots (the 'Open Field' treatment; plots N1, L1, M1 and H1), with aphids introduced at high (H), medium (M) and low (L) levels, together with a natural (N) infestation (figure 2.15).

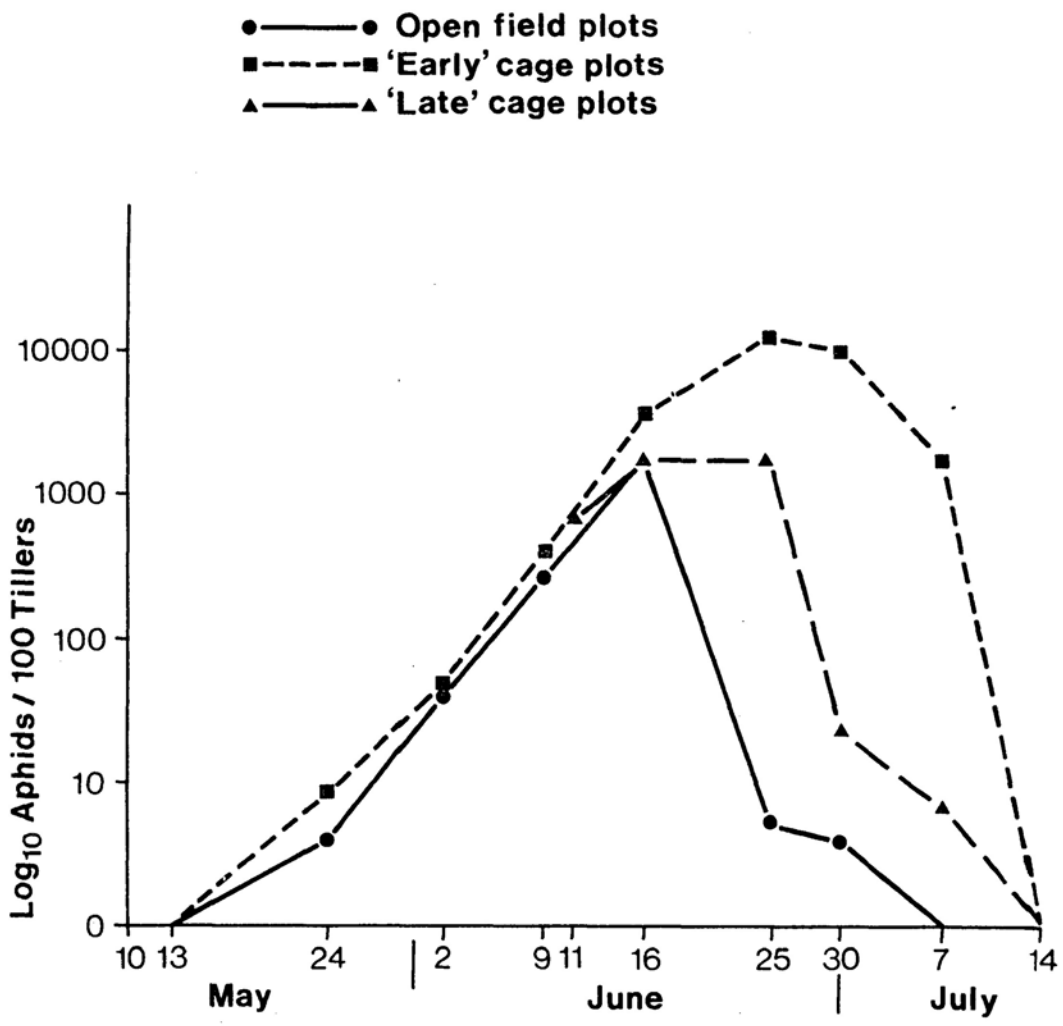
The extent of parasitism by Hymenoptera was assessed as the number of mummified aphids as a proportion of the aphid population at the previous sampling date, to allow for the delay of parasite development.

Results

(a) General pattern of aphid population growth and decline

In the 1976 field experiment, within each of the three major treatments, detailed above, the aphid populations followed similar courses (figure 3.1).

Figure 3.1 1976 Field Experiment Seasonal Course of Aphid Populations



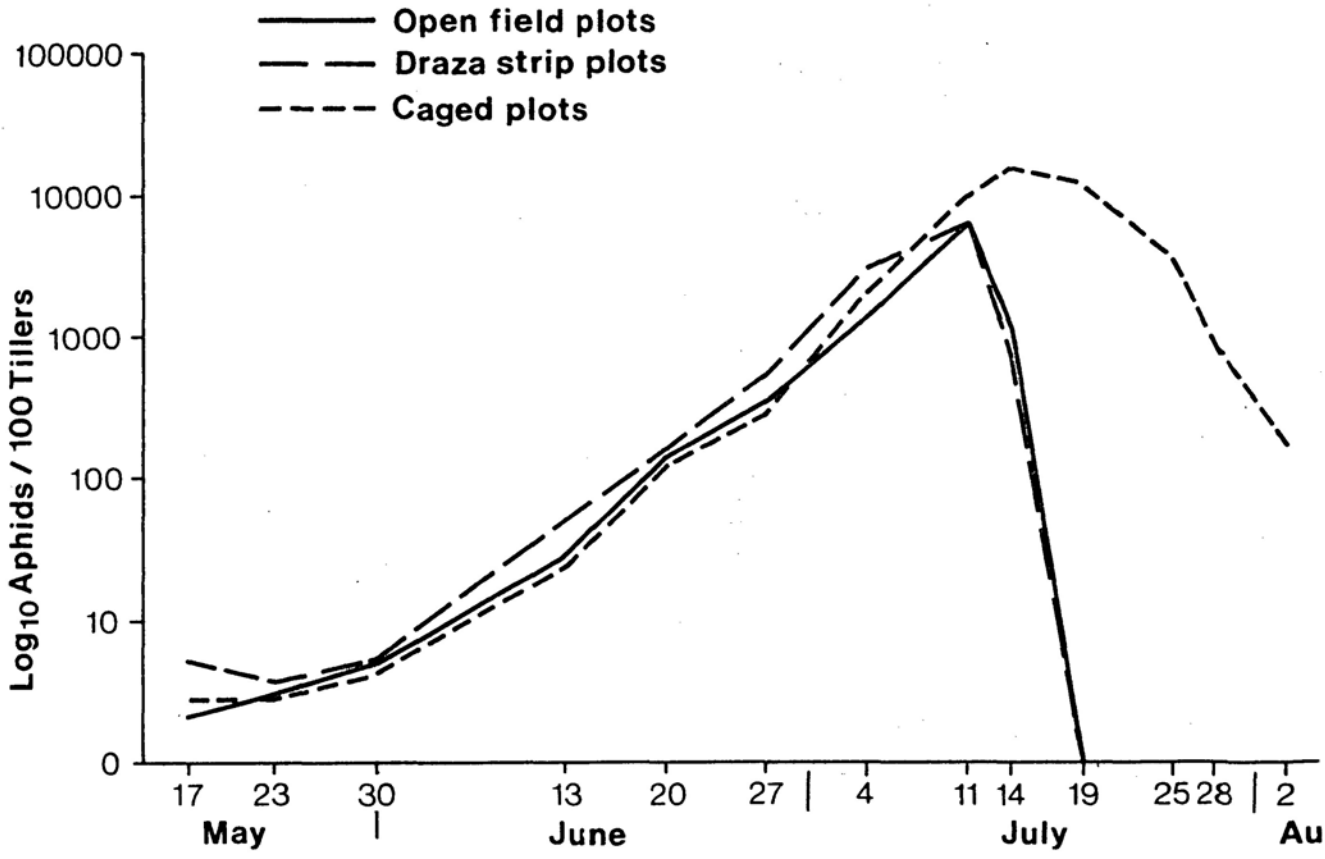
In the open field, the aphids multiplied at an exponential rate (7.5 times per week) from the time of initial establishment between May 13th and 15th to the highest recorded level on June 16th. Numbers then fell rapidly, so that, by June 25th very few aphids were left. In the early cages the aphid populations again increased exponentially (6.5 times per week) until June 16th and continued to increase, albeit at a reduced rate, until June 25th, when the numbers started to fall slowly to zero on July 14th. In the late cages, erected on June 11th, aphid populations were similar on June 16th and 25th, after which they fell rapidly.

The pattern of aphid population increase and decline in the 1977 field experiment was similar to that of 1976 (figure 3.2). After an initial period of establishment of the artificially introduced aphids, aphids increased in the uncaged plots at an approximately constant rate of 3-3.5 times per week between the end of May and peak levels on July 11th. Aphid increase rates in the Draza plots were higher than in the Open Field plots due to the exclusion of polyphagous predators (Chapter 2, section 24) and in some Draza plots (L3 and M3) aphids reached peak numbers on July 4th. Aphid populations in the uncaged plots decreased rapidly after the peak but aphids in the cages continued to increase for a short period at a reduced rate and then they decreased slowly.

Temperatures were higher in the summer of 1976 than in 1977; mean maximum and minimum temperature for June 1976 was 22.0°C and 11.2°C, whereas that for June 1977 was 16.2°C and 9.5°C.

Peak aphid numbers in the uncaged crop seemed to be higher in 1977 than in 1976. However, comparisons of the confidence intervals of mean peak numbers for the two years and of individual population variances

Figure 3.2 1977 Field Experiment Seasonal Course of Aphid Populations



with the pooled variance (table 3.1) showed that this was not necessarily so. Indeed, it seemed that the difference between T1 and T2 within the field in 1976 was greater than the difference between 1976 and 1977.

Table 3.1 Comparison of Aphid Statistics at Peak Populations 1976 & 1977

	June 16th 1976		July 11th 1977	Combined 1976 & 1977
	T1	T2	N1	
Number observations	76	80	82	238
Mean	19.4	27.6	30.7	26.0
Variance	326.8	484.7	379.2	416.6
95% Confidence interval	± 4.1	± 4.9	± 4.3	± 2.6
Range	15.3–23.5	22.7–32.5	26.4–35.0	23.4–28.6

Key: T1, T2 and N1 are the plot numbers

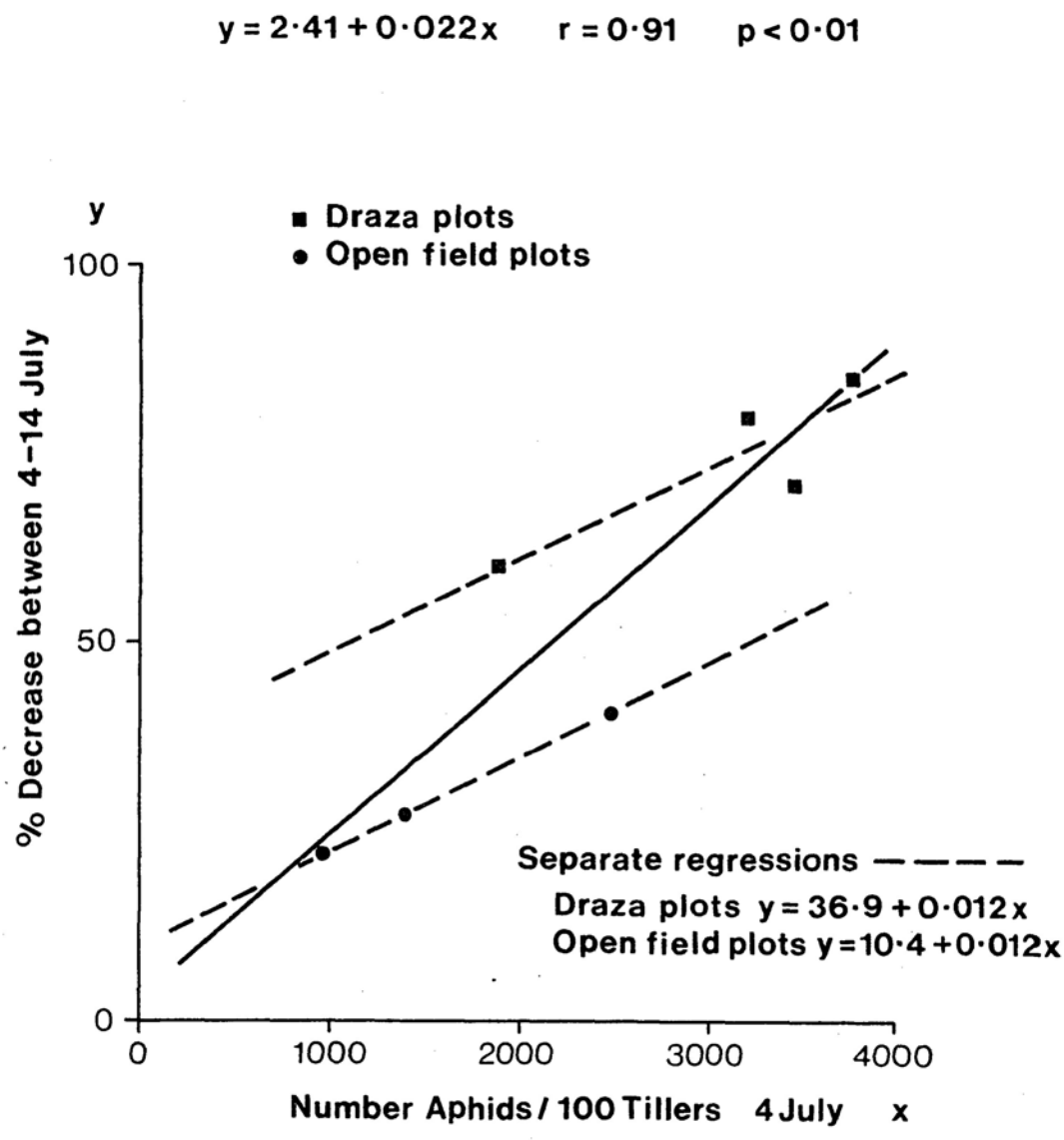
In 1977, aphid populations in the Draza plots were higher than in the Open Field plots by July 4th, but they did not reach higher peak numbers on July 11th and fell more rapidly to July 14th (figure 3.2). The aphid decrease between July 4th and 14th was of a density dependent nature since the percentage decrease in aphid numbers was proportional to the density of aphids on July 4th (figure 3.3). This applied to both the Draza and Open Field treatments (neglecting L1 where aphid numbers increased) but the single regression line of figure 3.3 could be regarded as two separate relationships for the two treatments, in which case parallel slopes but different intercepts are produced (dotted lines in figure 3.3).

(b) Mortality factors affecting cereal aphid populations

(i) Polyphagous predators

The effect of these is described in Chapter 2.

Figure 3.3 1977 Relationship Between Percentage Decrease of Aphids Between July 4th and 14th and Number of Aphids on July 4th



(ii) Aphid specific predators

In 1976, aphid specific predators present in the crop were coccinellids (Coccinella septempunctata (L), C. 11-punctata (L) and Propylea 14-punctata (L)) and syrphids (mainly Syrphus corollae). Predator numbers in the crop increased rapidly from June 10th as a result of large scale immigration and reached a peak on June 24th (figure 3.4). At this time, coccinellid larvae were the most numerous predators ($96/m^2$) although syrphid larvae were also abundant ($59/m^2$). The late cages were erected after the immigration of coccinellid adults had started (June 11th) and evidently trapped some adults, for substantial numbers of coccinellid larvae were subsequently seen.

In contrast, coccinellids were never very abundant in the 1977 field experiment. In mid-May a few were seen in the artificially infested plots, but eggs were not found until July 4th in some Draza plots. Syrphids (mainly Syrphus balteatus (Deg.) and S. corollae) were more abundant. The first larvae were found on July 4th and they were attracted to the higher aphid densities in the Draza plots (figure 3.5). Numbers increased rapidly until July 15th, but then decreased as the larvae pupated (figure 3.5).

(iii) Parasites

In 1977 the most common parasite species was Aphidius uzbeckistanicus, but in 1976 the parasite species were not identified. In both years percentage parasitism was unrelated to aphid populations in caged and uncaged plots. Percentage parasitism was low in both years, reaching 5% in 1976 and 4% in 1977 at peak aphid populations in the uncaged plots.

Figure 3.4 1976 Relative Abundance of Aphid Specific Predators and Cereal Aphids in the Open Field Plots

(Predator Densities Courtesy of K. D. Sunderland)

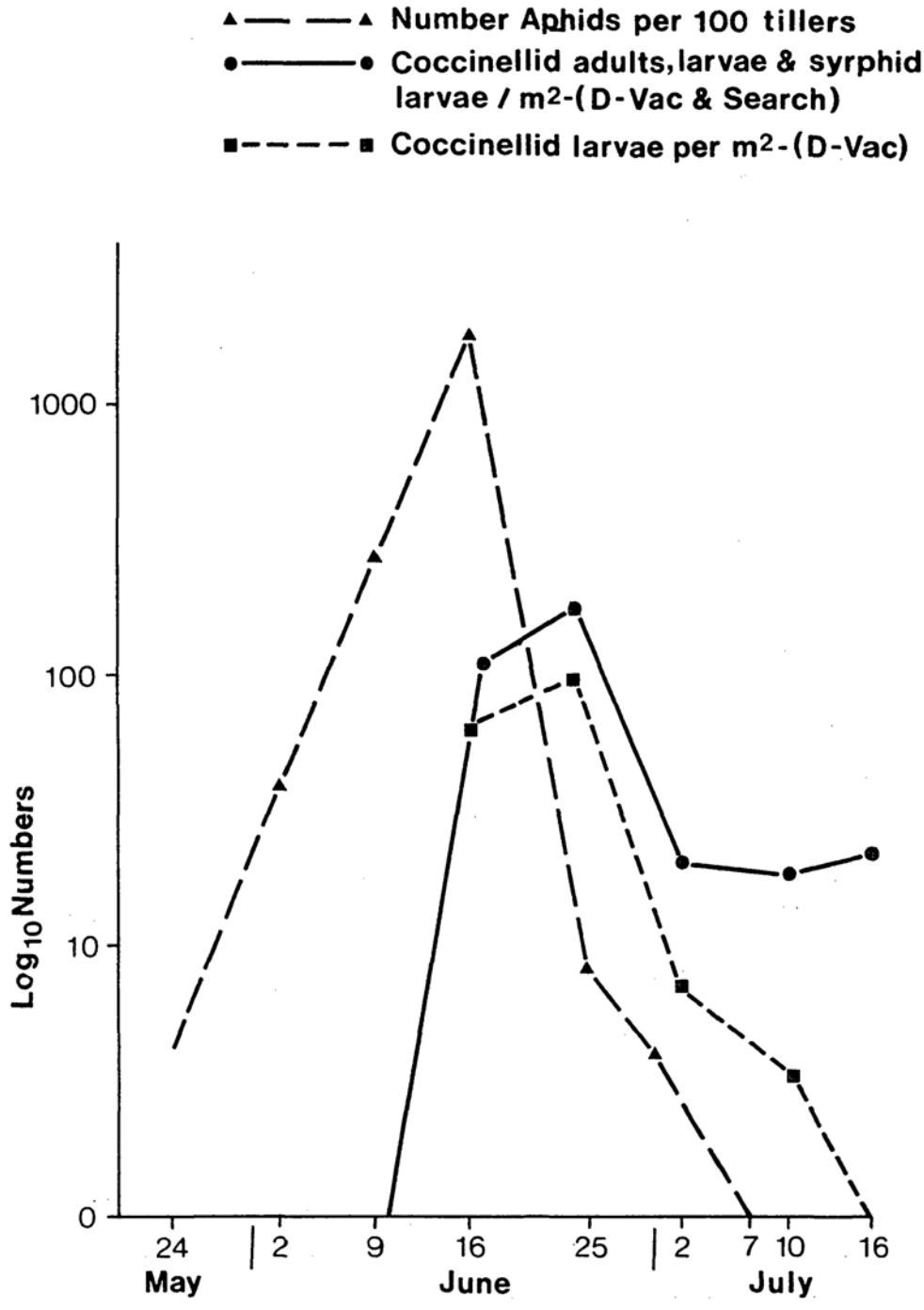
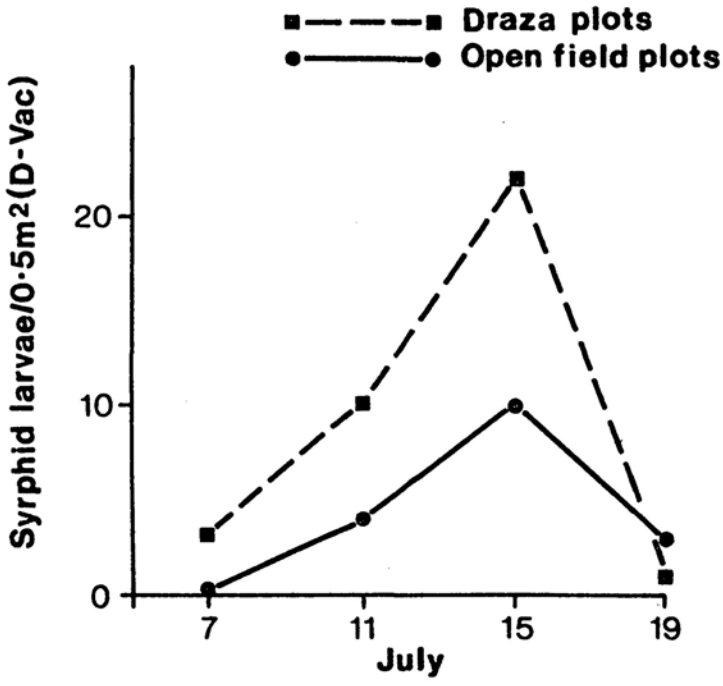


Figure 3.5 1977 - Density of Syrphid Larvae in D-Vac Samples

(Courtesy of K. D. Sunderland)



(iv) Disease

In 1976, the dry microclimatic conditions prevented the establishment and spread of fungal disease of aphids. However, in 1977, an epizootic of Entomophthora spp developed rapidly in the uncaged plots from July 7th and at the aphid peak on July 11th accounted for 30–40% mortality in the Open Field plots (figure 3.6). Percentage of diseased aphids sampled in the field increased in proportion to the aphid population density, at peak numbers on July 11th, in the Draza plots but not in the Open Field plots (figure 3.7). However, diseased aphids sampled in the field totalled, at most, only 2% of the aphid population.

Figure 3.6 1977 Aphid Mortality from Entomophthora (Laboratory Assay)

(Courtesy of R. A. Hall)

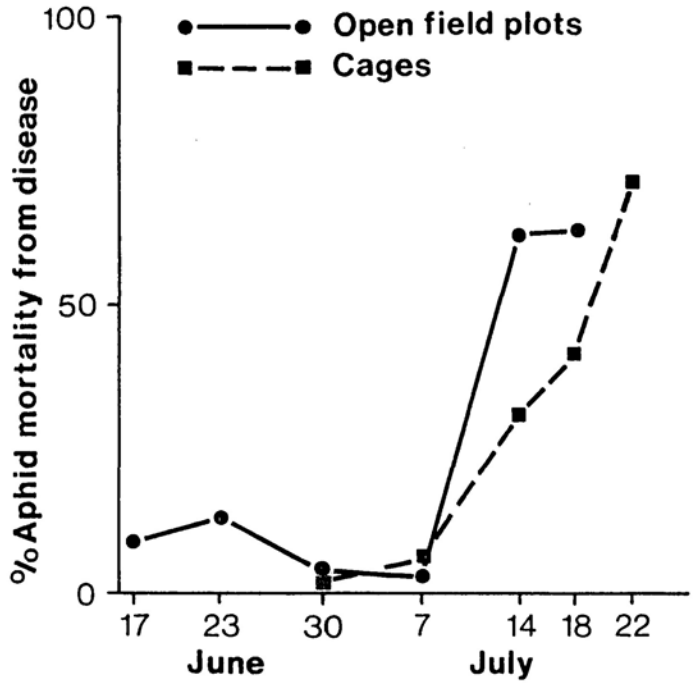
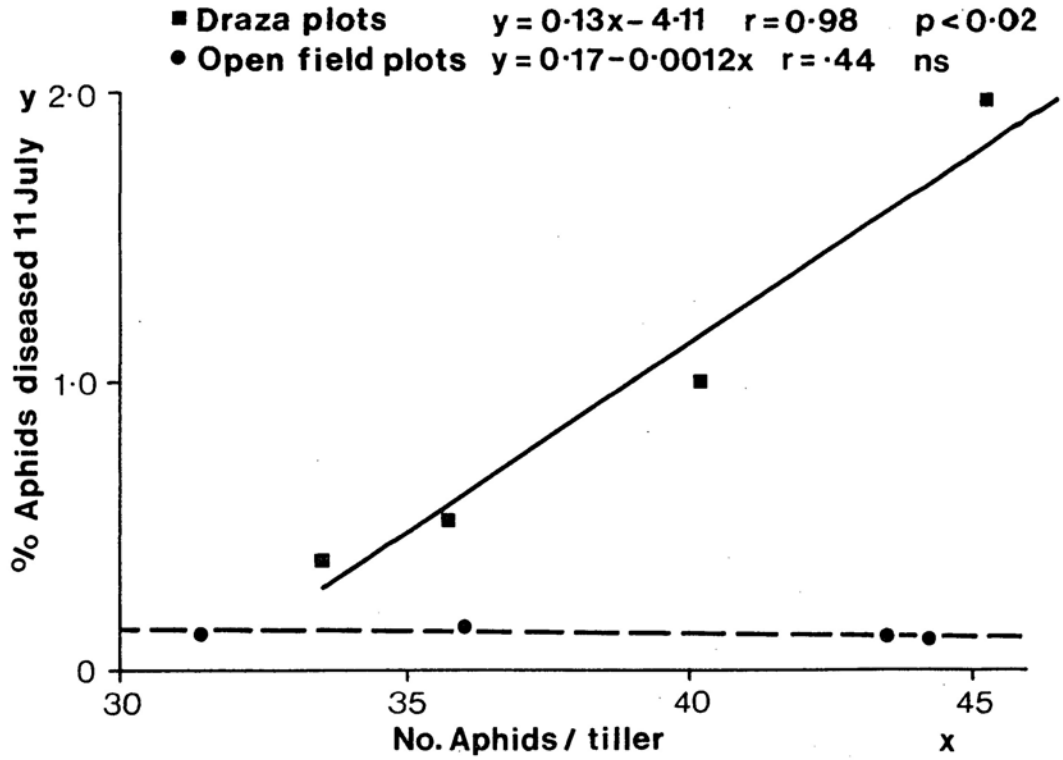


Figure 3.7 1977 Relationship Between Percentage Diseased Aphids in Uncaged Plots and Aphid Numbers (Both on July 11th)



(v) Emigration of alatae

Alatiform instars were not sampled in 1976 and therefore the effect of emigration could not be accurately assessed.

In 1977 the percentage of alatiform nymphs (mainly IV) of the total aphid population from the D-Vac samples increased with the rising aphid population reaching nearly 30% at peak aphid numbers (figure 3.8). Most of the adult alatae produced took off from the plants, since in both 1976 and 1977 the percentage of alates sampled on the plants decreased with increasing aphid population, reaching 2.2% at peak numbers in 1976 and 1.5% in 1977, even though the proportion of potential alates had increased.

A simple model (I. J. Wyatt, unpublished) was used to predict aphid numbers with emigration increasing at a greater rate than aphid population. The model consists of the following equation:-

$$N_{T+1} = N_T \cdot q - K_o \cdot p$$

where:-

N_T = Aphid numbers on day T

q = Rate of increase of aphids in absence of predators (times/day)

K_o = Number of alatae flying per day

p = Increase rate of alatiform nymphs (times/day).

The parameter values were obtained from the regressions of $\log_{10}$ numbers of aphids and alatiform nymphs with time between June 20th and July 11th (figure 3.9). June 20th was regarded as day zero, the initial number of aphids, No, was the intercept on the log. aphids vs time

Figure 3.9 1977 Theoretical Effect of Continuous Alate Emigration on Aphid Populations

A Regressions

(1) Aphid population (Open Field and Draza treatments) vs time (days)

■– – – – – – – – $\log_{10} y = 0.065x + 2.29$ r = 0.97 p 0.001

(2) Alatiform nymphs vs time (days)

▲— — — — — $\log_{10} y = 0.107x + 0.76$ r = 0.97 p 0.001

B Model

Parameters

No = 190 aphids/100 tillers ($=N_T$ at day 0)

q = 1.18 times/day

K_o = 1.93 alates/day

p = 1.28 times/day

Equation

$$N_{T+1} = N_T \cdot q - K_o \cdot p$$

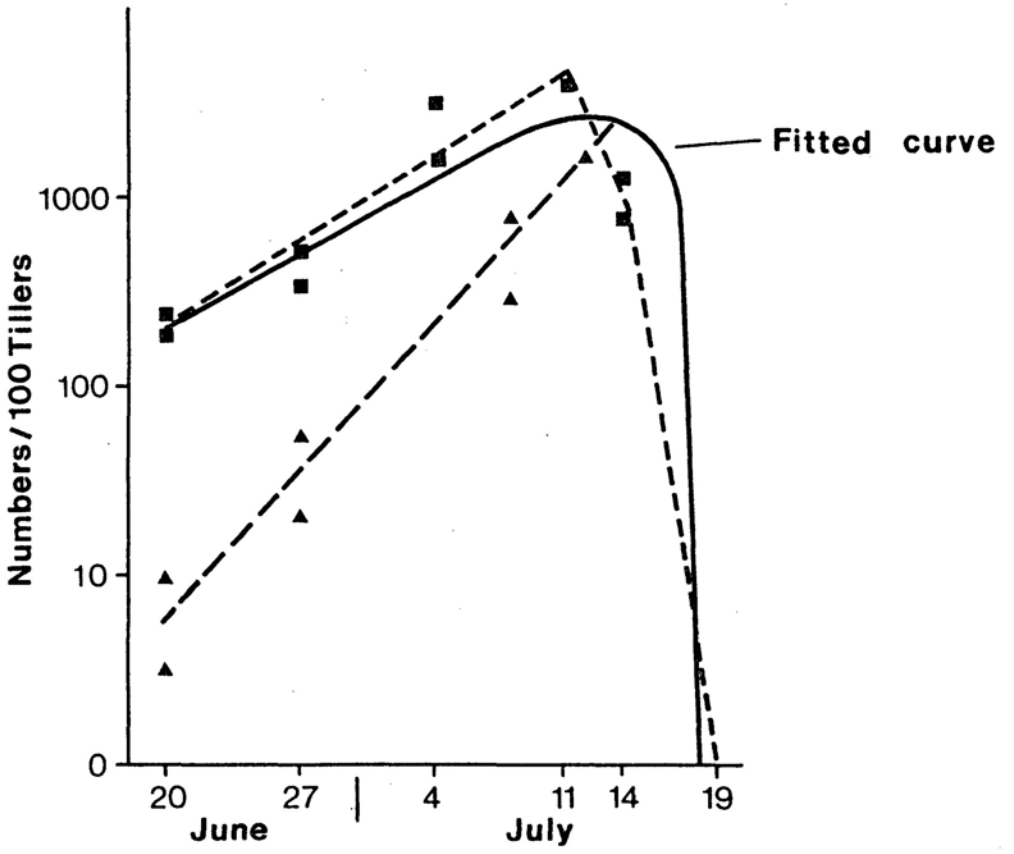
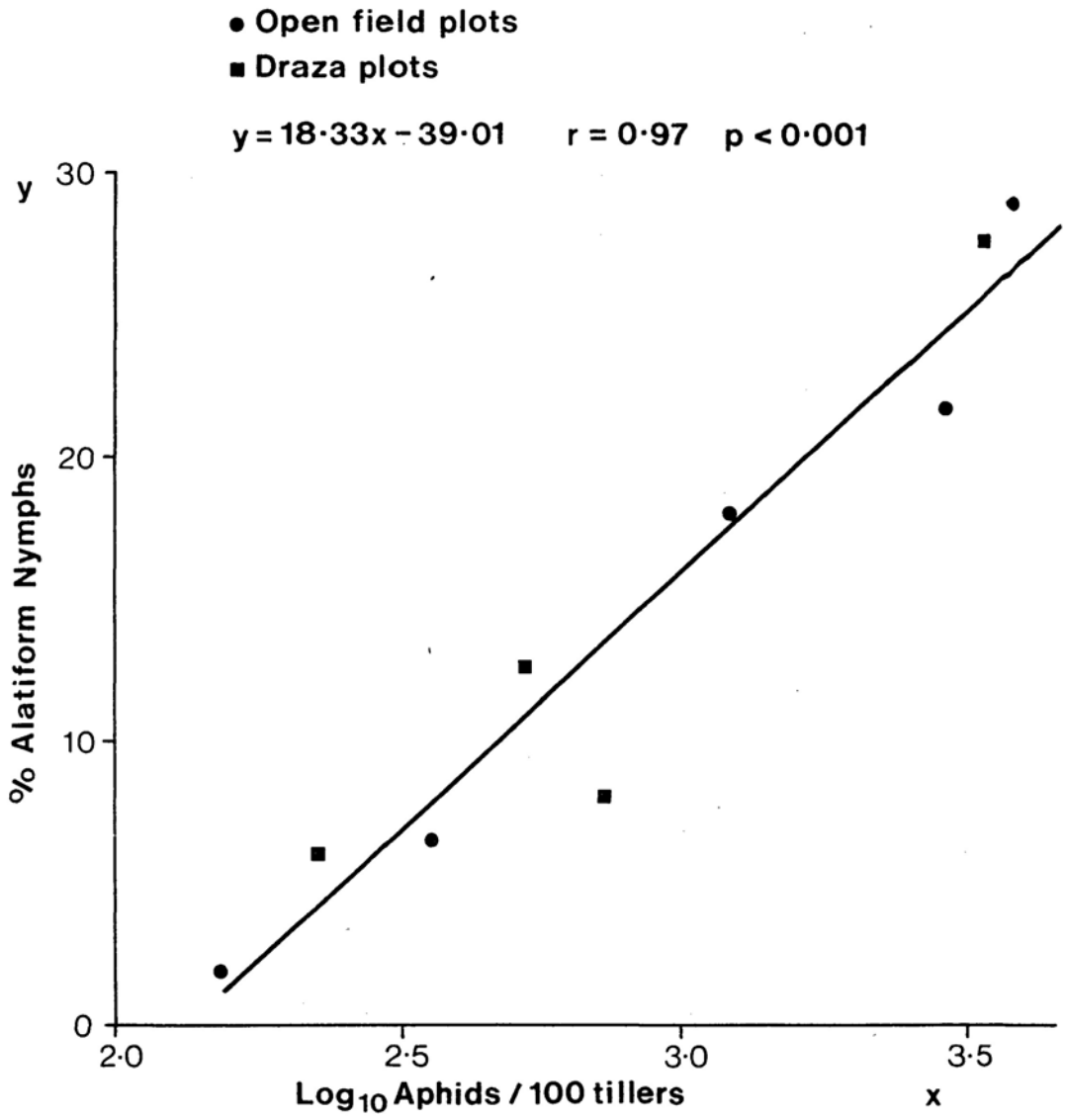


Figure 3.8 1977 Relationshp Between Alatiform Nymphs as a Percentage of the Total Population and Aphid Numbers Between June 21st and July 15th

(Alatiform Nymphs Sampled by D-Vac - K. D. Sunderland)



regression and the rate of increase, q, was the slope. Similarly, the number of alatae taking off per day, K_o, was the intercept of the alatiform instars vs days regression and was adjusted for a developmental time for nymphs to flight mature adults of approximately three days, and the rate of increase, p, was the slope of the aforementioned regression.

Insertion of these parameter values into the model (figure 3.9) produced a curve which, like the aphids in the uncaged plots, increased to a peak and then decreased rapidly, but with slight differences in peak numbers reached and the timing of the peak.

(vi) Growth stage of crop

In 1976, aphids reached a peak when the crop growth stage was between flowering and watery-ripe (table 3.2(a)). Crop development was slower in 1977, due to the lower temperatures, and aphids reached peak numbers at the milky ripe stage, slightly more advanced than in 1976 (table 3.2(b)). In neither year was there any noticeable difference in crop growth stage between the caged and uncaged plots.

(c) Aphid population dynamics in the cages

In, 1976, aphid populations increased at a similar rate in the early cages as in the open field (6.5 and 7.5 times/week respectively) and aphids in the early cages continued to increase for nine days after the peak of aphid numbers in the open field. However, aphid increase rates were lower for this period (June 16th-25th) than for the previous three weeks of population growth and the difference in increase rates was related to the populations on June 16th (table 3.3(a)).

In 1977, the cage covers tended to have a detrimental effect on the initial stages of population increase by preventing the colonization of

Table 3.2

a Development of the Wheat Crop in 1976

Date	Growth Stage	Feekes Scale*
9th June	Ears emerging	10.1-10.2
16th June	Flowering	10.5.2
25th June	Watery ripe-Milky ripe	10.5.4-11.1
30th June	Milky ripe	11.1
7th July	Milky ripe	11.1
14th July	Dough ripe	11.2

b Growth Stages of Wheat in All Plots in 1977

Date	Growth Stage	Feekes Scale*
16th June		Mostly 10.4
20th June	All ears out of sheath	10.5-10.5.1
27th June	Flowering complete	10.5.2
4th July	Flowering over-Watery ripe	10.5.4
11th July	Milky ripe	11.1
14th July	Milky ripe	11.1

Key:- *(Large, 1954)

Table 3.3 Effect of Aphid Population Density on Rates of Increase in the Cages

a 1976

Variable	Cages		
	C1	C2	C3
No. aphids/tiller 16th June	28.9	53.2	31.7
% reduction in rate of increase (24/5-16/6 and 16/6-25/6	31.7	50.4	46.1

b 1977

Dates	Rates of Increase Per Day			
	H2	M2	L2	N2
27th June-11th July	0.181	0.306	0.316	0.159
11th July-14th July	0.179	0.068	0.241	0.002
Paired T test t = 2.312 df = 3 p<0.2				
No. aphids/tiller 11th July	280.1	163.4	51.5	48.9
% reduction in rate of increase 11th-14th July	1.09	77.7	23.6	99.0

plants by immigrant alatae. This was most evident in plot L2, which over the period between May 30th and June 27th had an aphid increase rate of 2.01 times/week, whereas the associated uncaged plots, L1 and L3 had increase rates of 3.99 and 4.05 times/week respectively.

Rates of aphid increase in the cages with introduced aphids (i.e. H2, M2 and L2) during the mid phase of aphid population growth between June 27th and July 12th were smaller in proportion to the initial numbers on June 27th (figure 3.10). In addition, the aphid increase rates decreased as aphids reached peak numbers, but the differences were not significant (table 3.3(b)) and furthermore were unrelated to the aphid densities prior to the time of peak numbers on July 11th (table 3.3(b)).

Numbers of alates sampled on plants in 1976 were initially lower in the cages than in the open field (figure 3.11). In the late cages, alate numbers continued to increase between June 16th-25th, although the aphid populations remained level (figure 3.1). Similarly, in the early cages numbers of alatae increased between June 25th and 30th, although the aphid populations decreased over this period. Percentage alates sampled on plants at peak aphid numbers was low (3% in early cages and 4% in the late cages) and in the early cages was only marginally related to aphid numbers (C1 - 3.2% alatae, 162 aphids/tiller, C2 - 3.6% alatae, 174 aphids/tiller, C3 - 2.4% alatae, 114 aphids/tiller).

In contrast to the 1976 experiment, alatae were more abundant in the cages than the uncaged plots in 1977 (figure 3.12). Large numbers of alates were not trapped in the cage covers until July 4th (table 3.4), after which time the numbers trapped increased rapidly. The percentage alatae on the plants of aphid population remained fairly constant at

Figure 3.10 Relationship Between Rate of Aphid Increase Per Day (June 27th–July 12th) in the Cages and Initial Number of Aphids on June 27th

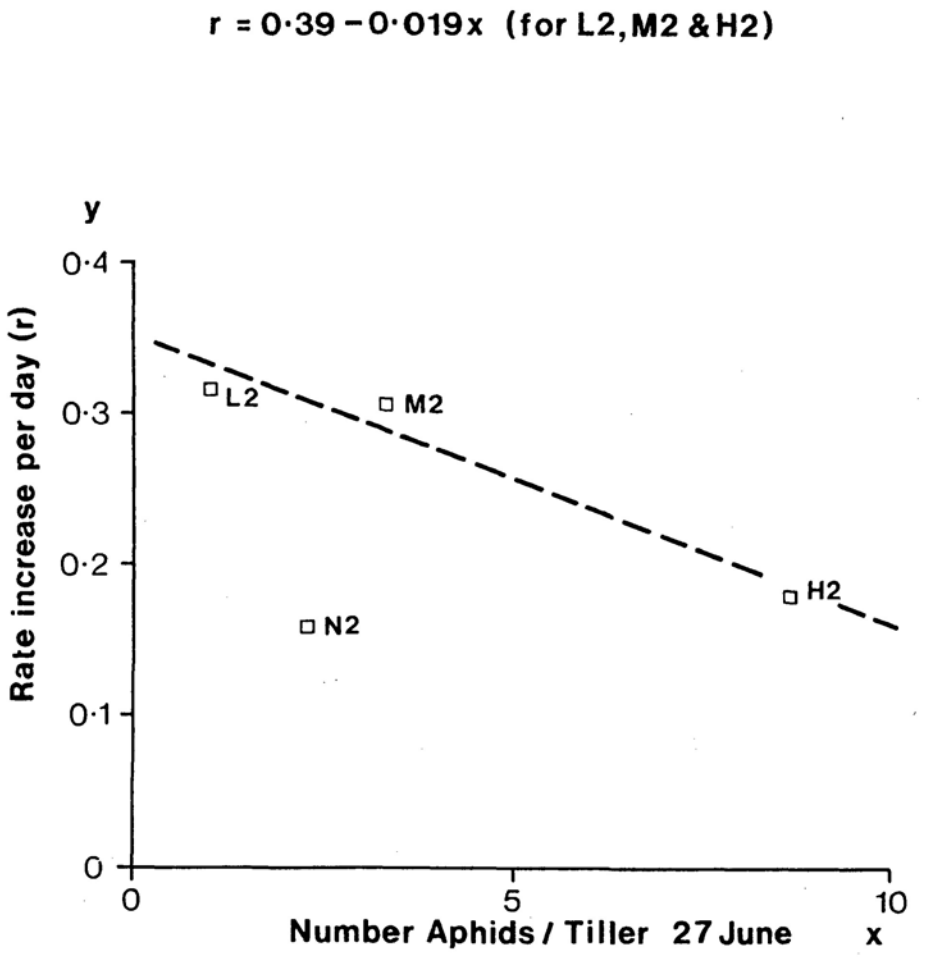


Figure 3.11 1976 Number of Alatae Sampled on Plants in Caged and Uncaged Plots

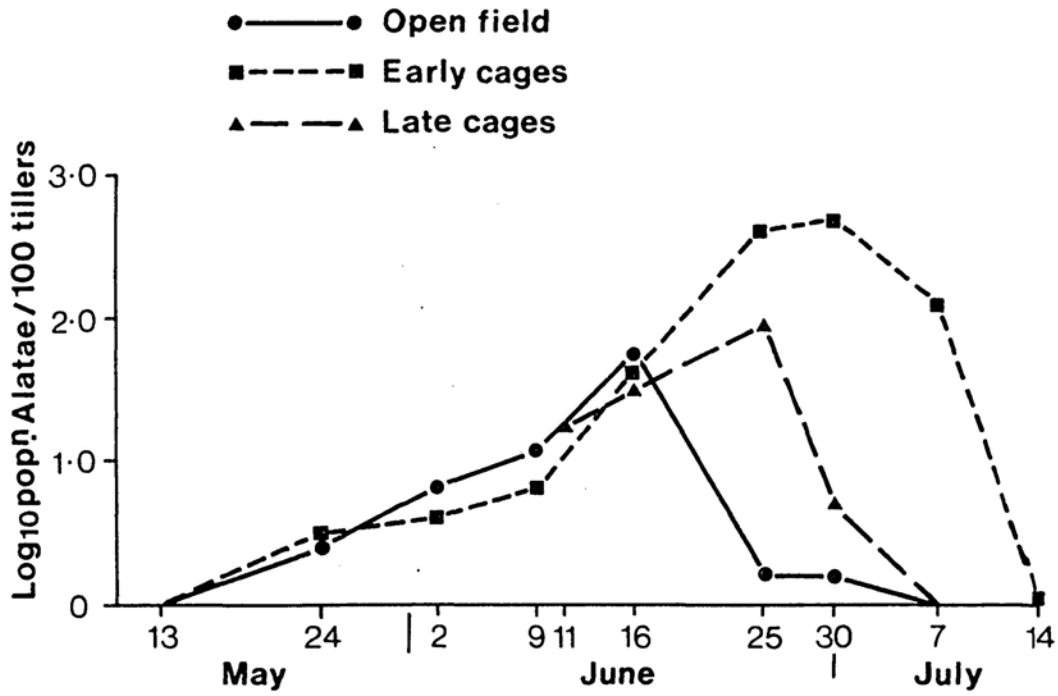


Figure 3.12 1977 Aphid Populations and Numbers of Alatae on Ears and Flag Leaves in Cage H2

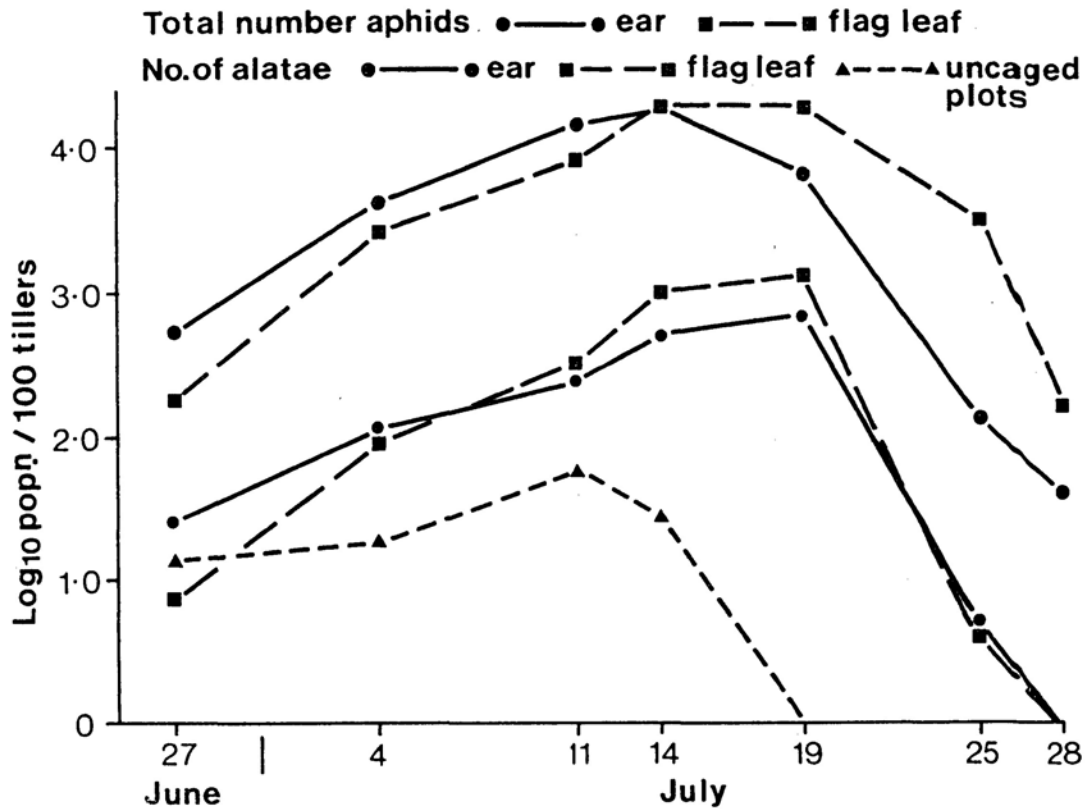


Table 3.4 1977 - Alatae Trapped in Cage Covers

Date	Cages			
	H2	M2	L2	N2
13th June	63	12	0	0
20th June	14	2	3	4
27th June	340	50	4	0
4th July	4-5 000	—	—	250

3-4% until peak aphid numbers were reached, after which the percentage rose to 7%, because alate numbers increased between July 14th-19th while the total aphid population declined (figure 3.12).

In 1977, peak aphid populations reached in the artificially infested cages were in similar proportions to the initial levels of introduction (ratio for levels of introduction for L2, M2 and H2 - 1:3:10, ratio of peak numbers reached - 1:2:4.5). Thus aphids increased from their initial densities to reach synchronous peak numbers independent of the 'carrying capacity' of the wheat plants.

In 1976, aphid populations in the early cages did not decrease at a rate proportional to peak numbers probably because the peak populations were not sufficiently different to show different rates of decrease. Parasites gained entry to the early cages and mummies were first found on June 9th. Numbers of mummies increased exponentially at a constant rate in each cage (average - 6.1 times/week) until June 30th. However, this increase rate was slightly less than that of the aphids in cages (6.8 times/week between May 24th and June 16th) and thus percentage parasitism remained fairly constant at 3-4%. Numbers of parasites were unrelated to

aphid numbers present and rate of increase of mummies increased with the rate of aphid increase but was unrelated to initial numbers of aphids or parasite/aphid ratio. As before, it seems that differences in aphid and parasite numbers between cages were not sufficiently large to show any meaningful associations.

In 1977, however, the aphid population decline in the cages was proportional to peak numbers reached (figure 3.13); a density dependent response. Although aphid populations on the flag leaves were rising between July 14th and 19th, while aphids on the ear were decreasing (figure 3.12), the relationship between rates of aphid decrease and peak numbers was the same for both categories (figure 3.14). This suggested that a common factor, natural enemies, played a large part in accelerating the aphid decrease.

Natural enemies small enough to gain entry to the cages were hymenopterous parasites (mainly Aphidius uzbeckistanicus) and the fungal pathogen Entomophthora spp. Ears of wheat which were brought back to the laboratory showed that field sampling generally underestimated the number of mummified aphids present and during most of July parasites emerged from about a third of the mummies (table 3.5). Percentage parasitism was low at the aphid peak and it increased only in the later stages of the population decline. Disease was a major mortality factor in the cages, as in the plots outside. However, the rate of mortality increase due to Entomophthora was much slower in the cages than outside (figure 3.7). Nevertheless, at the peak of aphid populations in the cages, disease accounted for at least 30% aphid mortality, accelerating the population decline as the epizootic spread. There seems no reason to suppose that Entomophthora did not spread in response to aphid density,

Figure 3.13 1977 The Decline and Fall of Aphid Populations in the Cages

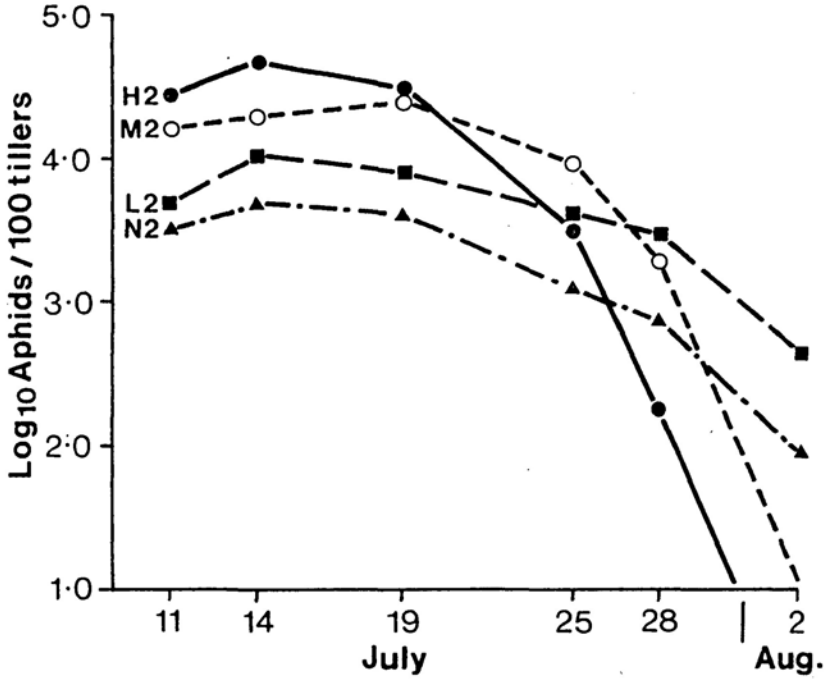


Figure 3.14 1977 Relationship Between Rates of Aphid Decrease from Peak Numbers on Ears and Flag Leaves in the Cages to the Peak Aphid Populations

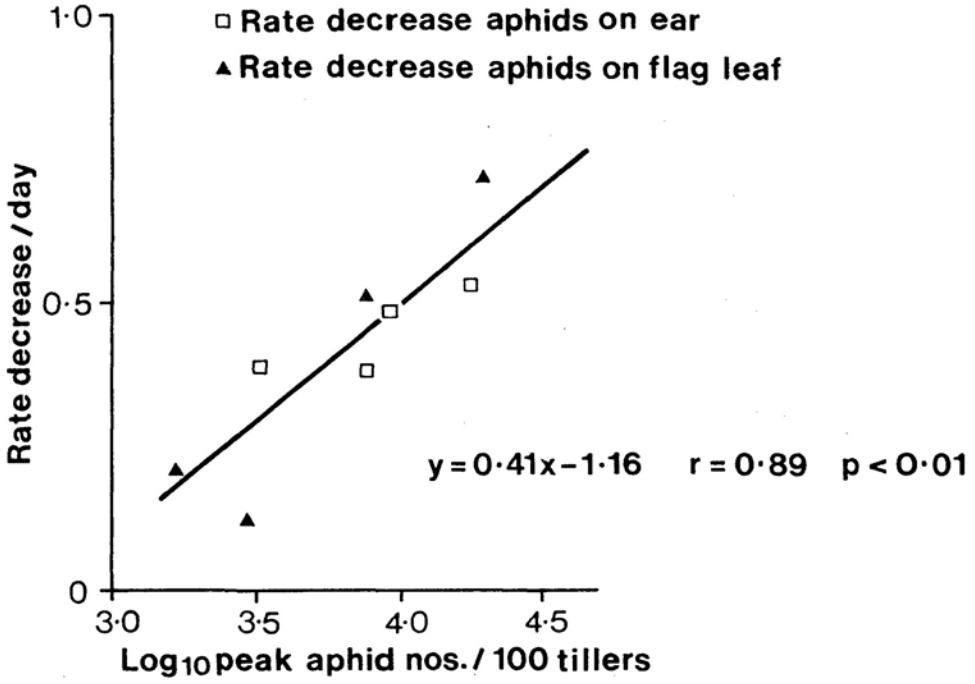


Table 3.5 1977 - Number Parasites/100 Tillers in Cage H2

Date	No. Mums Sampled on Crop	No. Mums in Lab. Sample	No. Parasites Emerged	% Emergence	% Parasitism
27/6					24.9
4/7	77.5	290	215	74.1	1.2
11/7	312.5	270	97	36	0.6
14/7	570	600	180	30	—
19/7	560	—	—	—	2.3
25/7	—	2460	720	29.3	16.6
28/7	1620	2573	537	20.9	32.6
2/8		2270	60	2.6	—

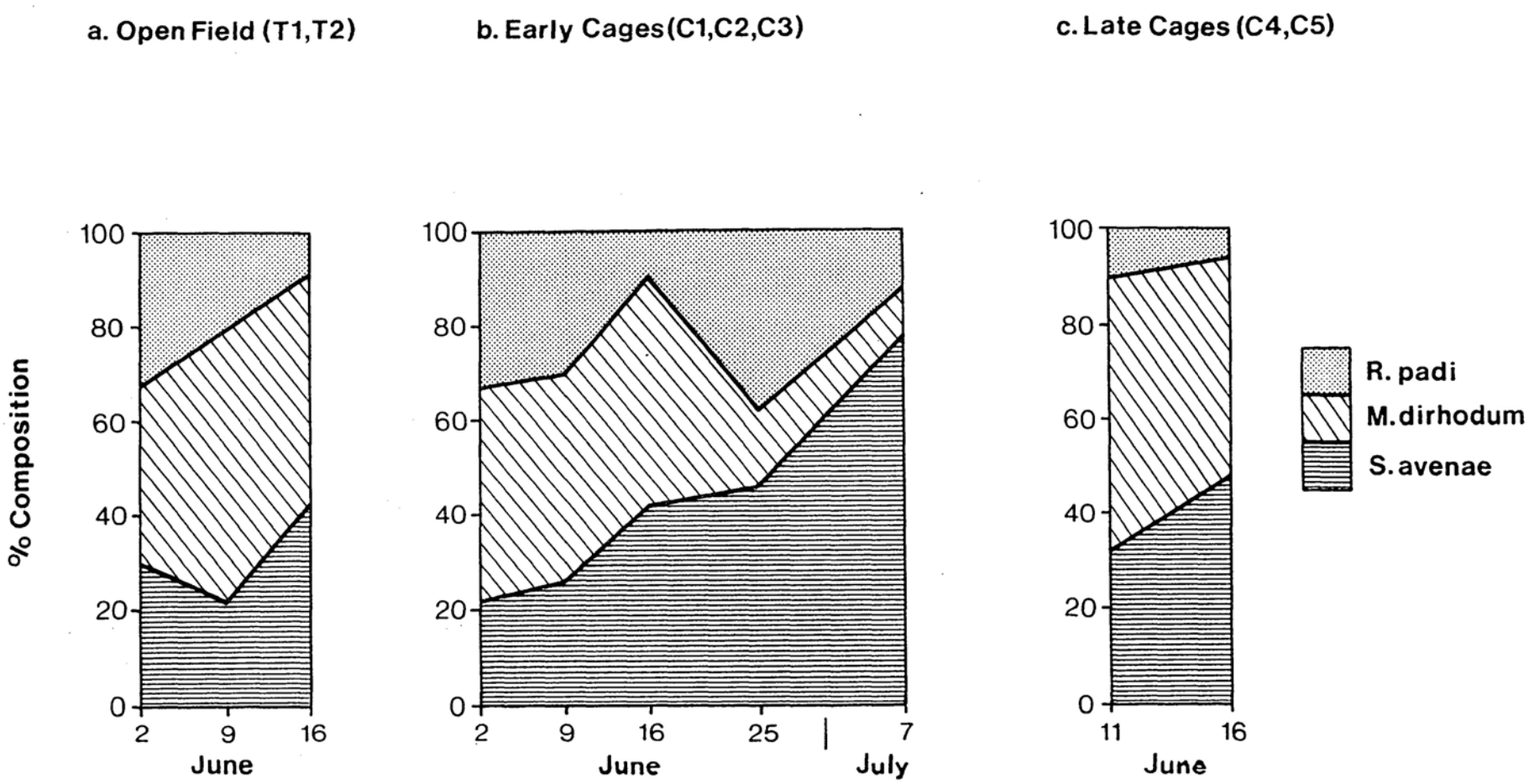
which would then account for the marked density dependent decrease of the aphid populations between the cages (figures 3.13 and 3.14). Indeed, in cage H2 on July 19th, the decreasing aphid populations on the ears had a higher incidence of observed diseased aphids (14.7%) than did the flag leaf population (8.8%) which had remained at the same level (figure 3.12).

(d) Aphid species composition

All three of the major cereal aphid species (S. avenae, M. dirhodum and R. padi) were present in varying proportions in both years.

In 1976, S. avenae and M. dirhodum were the dominant species and in the open field and late cages they occured in roughly equal proportions at peak numbers (figure 3.15(a) and 3.15(c)); 80% of S. avenae residing in the ears and all the M. dirhodum on the flag leaves. In the early cages, S. avenae increased in overall importance as its rate of increase

Figure 3.15 1976 Species Composition of Cereal Aphids



on the ears was greater than that of M. dirhodum on the flag leaves (14.0 times/week and 8.1 times/week respectively). Errors in the identification of nymphs were the cause of the high proportion of R. padi recorded on June 25th in the early cages (figure 3.15(b)). Ignoring this sample, R. padi was generally of minor importance but it persisted to the end of the season, moving up the stems to the bases of the ears as the plants ripened.

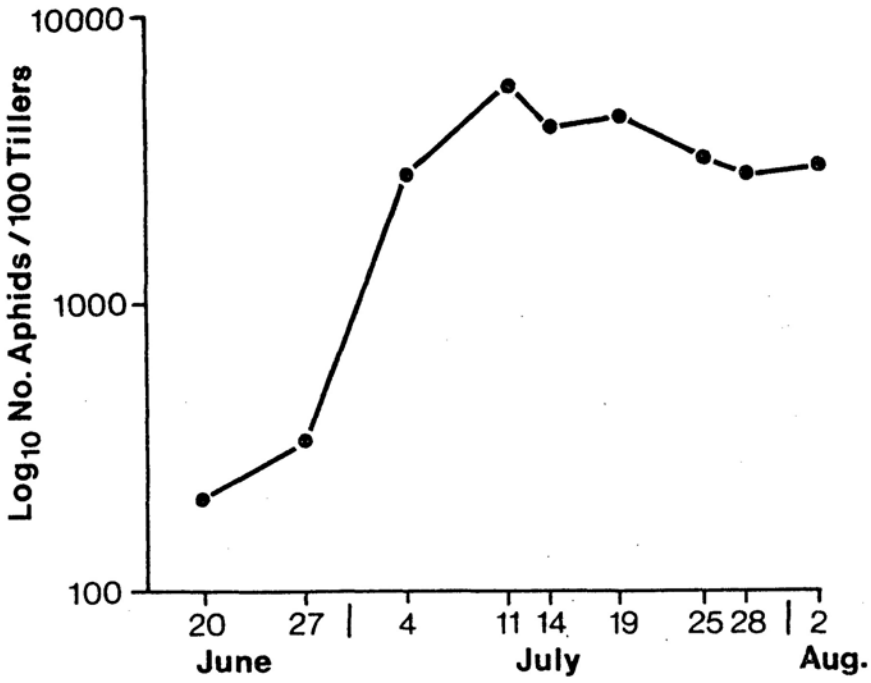
S. avenae was the dominant aphid species in the uncaged plots in 1977, M. dirhodum only occurring in low numbers, and, as in 1976, S. avenae occurred mainly on the ears, M. dirhodum being restricted to the flag leaves. In the cages, M. dirhodum on the flag leaf was more important, constituting 20–30% of the increasing aphid population (table 3.6) and

Table 3.6 Percentage Metopolophium dirhodum of Total Population 1977

Date	Mean % M. dirhodum		
	Cages	Open Field	Draza
13th June	8.0	3.6	10.0
20th June	24.5	5.2	0.3
27th June	30.3	7.4	14.6
4th July	24.6	3.5	5.1
11th July	21.9	3.1	13.8
14th July	32.3	26.6	29.3
19th July	54.5	—	—
25th July	68.6	—	—
28th July	95	—	—
2nd August	100	—	—

the species increased in relative abundance as the overall aphid population declined because aphid numbers decreased less rapidly on the flag leaf than on the ear (figure 3.12). R. padi was not generally abundant in the crop, although it became the dominant aphid species in one cage, N5 (figure 3.16). This species occurred on the leaf sheaths of the flag and lower leaves and the population increased to a high density where it w a s unaffected by the factors producing the population changes in the other cages.

Figure 3.16 Populations of R. padi in Cage N5



Discussion

In the 1976 field experiment, the absence of an aphid sample between June 16th and 25th was unfortunate because aphids probably increased in the cages and open field to reach peak numbers between these dates.

Indeed, a field sample of aphids on June 18th revealed that higher numbers were present than on June 16th (K. D. Sunderland, personal communication). Thus, the population maxima were probably reached later in the open field and earlier in the cages than indicated by the results obtained.

Comparisons of peak aphid numbers sampled between 1976 and 1977 showed that when the variability of the populations was taken into account there was no significant difference in aphid densities between the years. Thus, comparisons of mean numbers of aphids can lead to misleading conclusions if the variability of the populations is not accounted for.

Mean temperatures in 1976 were substantially higher than in 1977 and were evidently responsible for the greater rate of aphid increase in 1976 which conforms with the relationship between aphid increase rate and temperature found by Jones (1979).

Densities of aphid specific predators were probably underestimated because of the sampling inefficiency of the D-Vac suction sampler and because samples were taken by day.

High numbers of aphid specific predators were present in the crop in both years and there was evidently great aphid mortality from predation. However, the lateness of the predator immigration relative to the aphid immigration and the short period of time between the predator immigration and the aphid population peak (about seven days in both 1976 and 1977) suggests that predators did not regulate aphid populations that were increasing but exerted their effect on populations that had already become self-regulating. In the late cages in 1976 partial exclusion of coccinellids resulted in a delayed decrease of aphid populations.

The low percentages of mummies found in the field in both years indicated that parasites were relatively ineffective natural enemies. In the cage plots parasitism was more obvious in 1976, when disease was not present, than in 1977. In the former year, numbers of mummies sampled continued to increase while the aphid population decreased but the rate of increase of parasites was less than that of aphids, which suggests that parasites were merely following aphid populations and not regulating them. Field sampling generally underestimated the numbers of mummies present, particularly at high levels. Furthermore, parasite emergence from the samples taken back to the laboratory showed that about two-thirds of the mummies present in the field had either hatched already or were not viable.

Field samples of diseased aphids tended to underestimate the true mortality from this source, since only by the laboratory tests could the number of potential disease victims be established. In addition, at high levels of disease in the field, numbers of diseased aphids were underestimated in a similar way to the field sampling of mummies. The spread of Entomophthora was evidently sensitive to aphid density and was probably the major factor accounting for the density dependent aphid mortality in the Draza treatment and in the cages. Although information is lacking with regard to laboratory tests of disease in aphids from the Draza plots, the increase in percentage diseased aphids in field samples with aphid density suggests that Entomophthora was indeed responsible for much of the aphid mortality in that treatment. In the cages, the slower spread of Entomophthora may have been due to the exclusion of infected immigrants, and the different environmental conditions within the cages (for example, reduced wind speed (Woodford, 1973)) may have

also influenced spore dispersal. Moreover, even on the ears and flag leaves of plants in the same cage, diseased aphids were distributed as a consequence of previous aphid density which would explain the same relationship of aphid decrease with density for aphid populations on both the ear and flag leaf.

The increase in proportion of alatiform instars with aphid population in 1977 showed that some emigration of alatae was evidently a powerful factor regulating the population increase, and this was probably also true in 1976. Although making many assumptions, the model showed that the emigration of alatae on its own, and without any additional mortality, could regulate the population increase of aphids and produce a rapid decline, a conclusion also reached by other workers (for example, Vereijken (1979)).

In 1976, the aphid population decline was out of phase with the stage of plant growth known to result in reduced aphid fecundity and increased mortality (late milky ripe; Watt, 1979). In 1977, these factors may have had a greater effect on aphids as the population peak occurred at the milky ripe stage in both caged and uncaged plots.

In both years S. avenae was the dominant aphid species presumably because of the high number of immigrants and because of its high rate of increase on the ears of wheat, as also found by Watt (1979). M. dirhodum decreased less rapidly on the flag leaves in the cages in 1977 because of its lower initial numbers but it seemed more susceptible to parasitism, as also reported by Dean (1974d) and Dransfield (1975). The isolated occurrence of R. padi on a small area of crop in cage N5 in 1977 is difficult to explain and more difficult still is the persistence of the

population at a high level when aphids in the other cages had decreased and disappeared altogether. Indeed, this aphid species seems to differ greatly from S. avenae and M. dirhodum, since, although above 15°C it has an r_m 4-16 times as large as the other two aphid species (Dean, 1974c) and is generally common in suction trap catches at 40 feet (Dean 1974b), it is far less common on cereals than S. avenae or M. dirhodum (Dean, 1974c).

The range of aphid populations produced in the cages in 1977 suggested that crowding could perhaps affect the aphid increase rate. In the mid-phase of aphid increase in 1977 rates of increase were inversely proportional to initial numbers of aphids, but the slowing of the population growth from July 11th-14th before the peak in the cages was not affected by aphid numbers. However, in 1976 the aphid increase rate was reduced in proportion to initial populations but this was probably an artifact resulting from the lack of a sample between June 16th and 25th indicating the peak numbers. Thus, a crowding effect on aphid fecundity immediately before the peak was absent.

The persistence of aphid populations in the cages may have been a result of alatae returning to the plants and reproducing. If this were the case it would invalidate many of the conclusions to be drawn from the cage treatment in the experiment. However, several factors suggest that alatae could not have produced the increased aphid numbers in the cages.

At all stages of the aphid population increase, numbers of adult apterae exceeded numbers of alatae on the plant and thus, for alatae to have an effect on population growth their fecundity would need to be many times greater than that of apterae. However, the reverse is usually the

case, fecundity of apterae being greater than that of alatae. Percentage alatae of the populations in the cages remained fairly constant until the population peak, suggesting that newly mature alatae were flying from the plant in increasing numbers as in the open field; numbers trapped in the cage covers tend to confirm this. However, at the first stage of the aphid population decline from the peak, numbers of alatae on the plants increased noticeably and the coincidence of these events suggests that the extra production of alatae and the overall population decline were causally linked.

The larger proportion of alates sampled on plants in the cages in 1977 compared to the uncaged plots could be explained in terms of light intensity thresholds for aphid take-off (Johnson, 1969, p.258). The cage covers can reduce the light intensity by half (Woodford, 1973) and evidently the light intensity in the dull summer of 1977 could have been reduced within the cages to below the threshold of take off. In the brighter 1976 season when alate numbers within the cages were less than in the field, the light intensity was evidently sufficiently high within the cages to be above the threshold for take-off.

To summarize, alates could only have produced the increased numbers in the cages either by flight-mature adults reproducing before take-off or by alates flying down and settling on plants which were already crowded to reproduce at a greater rate than apterae. Evidence presented above and consideration of aphid biology makes either of these possibilities strongly unlikely.

Numbers of alates trapped in the cage covers did increase to high levels in late July of 1977. Most of these died, many from infection by

Entomophthora but some alates which had crawled down the side of the cage did indeed settle on plants adjacent to the cage side. However, plants on which this had occurred were immediately apparent and were not part of the sample rows.

The second major objection to the use of cages as control predator exclusion plots is that the cage covers may have delayed the maturation of the wheat plants by the reduction of light intensity, allowing apterae to continue reproducing after aphid fecundity in the field had been affected by the ripening of the plants (Watt, 1979). However, in both 1976 and 1977, there was no noticeable difference in crop growth stage between plants in the cage and field plots. Indeed, light intensity has little effect on crop development (Ford, Pearman and Thorne, 1976), temperature being the most important factor. Thus, although the cage covers can reduce the light intensity by 50% (Woodford, 1973) this is of no consequence with regard to crop maturation. Moreover, temperatures were unaffected by caging in 1977 (R. Hall, personal communication) and therefore the cages had little effect on the ripening of the wheat.

Thus, it seems that the cages did indeed act as control predator excluded plots for the field experiments with little distortion of the aphid population dynamics through the retention of alatae in the covers. Hence, it should be possible to formulate a model of events which would account for the aphid population dynamics in both the caged and uncaged plots in both years.

A logistic model has often been used in the past to describe the population increase of fast reproducing organisms in simple ecosystems. Taking the cage plots of the 1977 experiment, if the logistic form of

population growth was followed, aphids which had been introduced at different levels would reach similar peak numbers, determined by the carrying capacity of the plants, at successively later dates. However, the noticeable aspect of the population maxima reached in the cages was their synchrony, which suggested that a time factor rather than a density factor was responsible for determining the point at which the aphid populations started to decrease. Moreover, aphid density did not seem to affect the slowing of population growth just before peak numbers as might be expected from a logistic growth form. Indeed, there was only a three day delay between population maxima in the cages and uncaged plots in 1977 (and no difference in the timing of the peaks in a similar experiment in 1979 - R. Chambers, personal communication). Furthermore, an aphid sample between June 16th and 25th in the 1976 experiment, would probably have shown that, as in 1977, the population peaks in the cages and open field were reasonably close together.

Thus, the timing of the population maximum and of the aphid decrease was determined by factors acting, to a great extent, independently of aphid density. Two causes immediately spring to mind. Firstly, in the latter stages of wheat ripening, aphid populations undergo a decrease in fecundity and an increase in natural mortality (Watt, 1979). As shown above, the cages had little effect on the plant growth stage, hence these factors would act in a similar way in the cage and open field. However, as also discussed above, the population maxima occurred at a growth stage before these negative effects of plant ripening could have had a significant impact on the aphid populations. Secondly, emigration of alatae could be the intraspecific factor responsible. The simple model of I. J. Wyatt (unpublished) showed that emigration alone could

produce the population decline in the uncaged plots but it would not explain the synchronous population peaks in the cages in 1977. However, the more complex model of Rabbinge, Ankersmit and Pak (1979) can provide a feasible explanation for the aphid population dynamics in both years, in caged and uncaged plots. In order to understand its application to the present field results, an outline of the model will be described and the principles applied to the results of the 1976 and 1977 field experiments.

The model starts with the immigration of alatae which give rise to apterous offspring which in turn become the reproductive element of the aphid population. Rabbinge et. al. postulate that most of the offspring produced from these initial apterae develop into alatiform nymphs and thence into adult alatae, which immediately fly away from the plant. Factors acting on this process determine the timing of the population peak. Thus cereal aphids have two generations of population growth in the field, the first being immigrant alatae and resulting apterous offspring, and the second being the adult apterae and offspring which all develop into alatae. The flattening and initial decline of the aphid populations was well accounted for by syrphid larval predation in two of three years of comparisons examined (1975 and 1976). However, the final part of the population collapse was not well simulated because the model did not incorporate an extra effect of natural enemies such as parasites, fungal disease and increased natural mortality. Moreover, in 1977 an epizootic of Entomophthora produced a decline in the aphid population in the field well before the simulated population, as the model did not include the action of this fungal pathogen. Thus Rabbinge et. al. propose that the population collapse is triggered by emigration

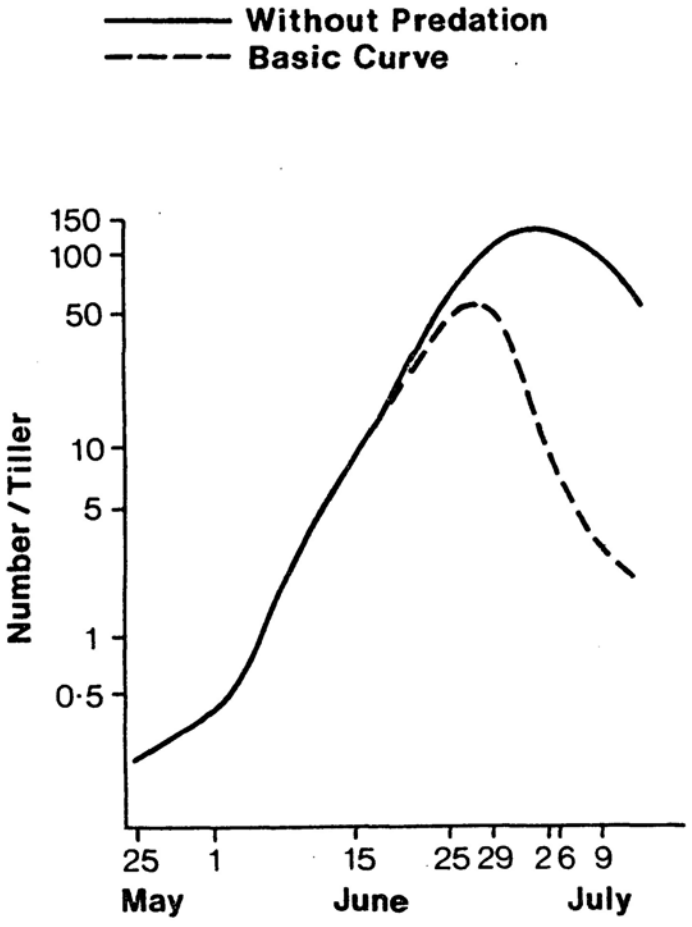
of alatae and amplified by biotic mortality factors. The effect of predation is difficult to evaluate from field observations alone, but in the model calculations this becomes clearer. During the initial phase of population growth, the influence of aphid specific predators was negligible, but the phase of flattening and collapse was delayed considerably by their absence (figure 3.17). The contribution of predation is clear from table 3.7 where the simulated number of aphids killed by predators is given.

It is now immediately apparent that the aphid population curve produced in the cages corresponds with the population curve without predation generated by the model. Thus, the absence of natural enemy mortality alone can account for both the increased populations in the cages and the approximate synchrony of the population peaks between caged and uncaged plots, which confirms previous deductions about the side-effects of caging. Moreover, the model can also account for the synchronous population maxima in the cages, because the developmental rate of the second generation of nymphs is the same for all the treatments and therefore the aphid populations become self-regulating at the same point and at a similar ratio to their initial levels of introduction. The difference in the pattern of decrease between Draza and Open Field treatments in 1977 was probably a result of the greater increase rate of aphids in the Draza plots giving crowded conditions more quickly, and producing alatiform instars more quickly, and therefore populations became self-regulating sooner. The reaction of syrphids and Entomophthora to the increased densities then produced a faster decrease of aphids. A similar explanation can be given for the population dynamics in the 1976 experiment. The average temperatures were higher than in 1977, and

TABLE 3.7 DISAPPEARANCE OF APHIDS IN NUMBERS PER TILLER IN 1976 CAUSED BY PREDATION, ABIOTIC MORTALITY AND EMIGRATION BASED ON MODEL CALCULATIONS - RABBINGE ET. AL. (1979)

Date	Time (Days)	Growth Stage of Plant	Mortality		Emigrants (Winged Females)	Actual No. of Aphids (total)
			Predation and Parasitism	Abiotic		
24th May	5	10	0	0.001	0	0.3
29th May	10	10.1	0	0.004	0	0.4
	15	10.2	0	0.03	0	1.5
	20	10.3	0	0.05	0	5.6
	25	10.5.1	0.2	0.3	0.02	13.6
	30	10.5.2	4.0	1.0	0.27	40.6
	35	10.5.3.	25.0	5.9	5.4	68.4
	40	11.1	99.8	12.2	20.0	22.3
9th July	45	11.1	119.6	13.3	24.1	5.0
	50	11.2	121.3	13.4	26.0	4.1

Figure 3.17 Effect of Predation on the Total Number of Aphids in 1976 According to the Simulation Model of Rabbinge et. al. (1979)



populations increased to similar peak levels because although aphid fecundity was greater, the developmental rate of the second generation was quicker and self-regulation occurred sooner.

Conclusions

Results from the field experiments suggested that emigration of alatae was responsible for determining the point at which aphid numbers started to decrease in both the field and cage plots. Moreover, it was

apparent that the cages merely excluded some natural enemies (e.g. syrphids and coccinellids) and retarded the spread of others (e.g. Entomophthora) so that the differences in peak numbers of aphids were solely a result of the prevention of mortality from natural enemies. However, the mechanism accounting for the effect of the cages was obscure until the simulation model of Rabbinge, Ankersmit and Pak (1979) was considered. Using the principles involved in the model the effect of the cages in the experiment was clearly accounted for, hence the conclusion of Rabbinge et. al. (loc. sit.), that the aphid population collapse was triggered by emigration and amplified by natural enemies, was found to be valid for the field experiments at North Farm in 1976 and 1977.

3.3 Insectary Experiments

(i) Movement of Coccinellid Adults

(a) Introduction

In the field experiments, different aphid densities occurred in adjacent plots and it was possible that coccinellids could have moved from one plot to another and hence confused the effects of the treatments. Thus an experiment was carried out in the insectary to investigate the extent of coccinellid movement and the response to aphid density.

(b) Materials and methods

Adult Coccinella septempunctata were collected from a nearby field of spring barley on a sunny day in late June. They were divided into six batches and a marking of enamel paint was applied to the elytra of each beetle to facilitate subsequent identification.

On June 28th aphid densities were manipulated by spraying the aphids in four plots with Pirimicarb (a systemic insecticide harmless to coccinellids); three plots were sprayed with a non-persistent insecticide (Nicotine) to reduce aphid numbers and the remainder were left untreated (table 3.8). The strong prevailing wind quickly removed all traces of the insecticides and the coccinellid adults were introduced the next day into the previously sprayed plots (table 3.8, figure 3.18).

Each plot was sampled at intervals for aphids and coccinellid eggs, larvae and adults but considerable difficulty was encountered in sampling all the beetle stages.

Figure 3.18 Layout of Coccinellid Movement Experiment

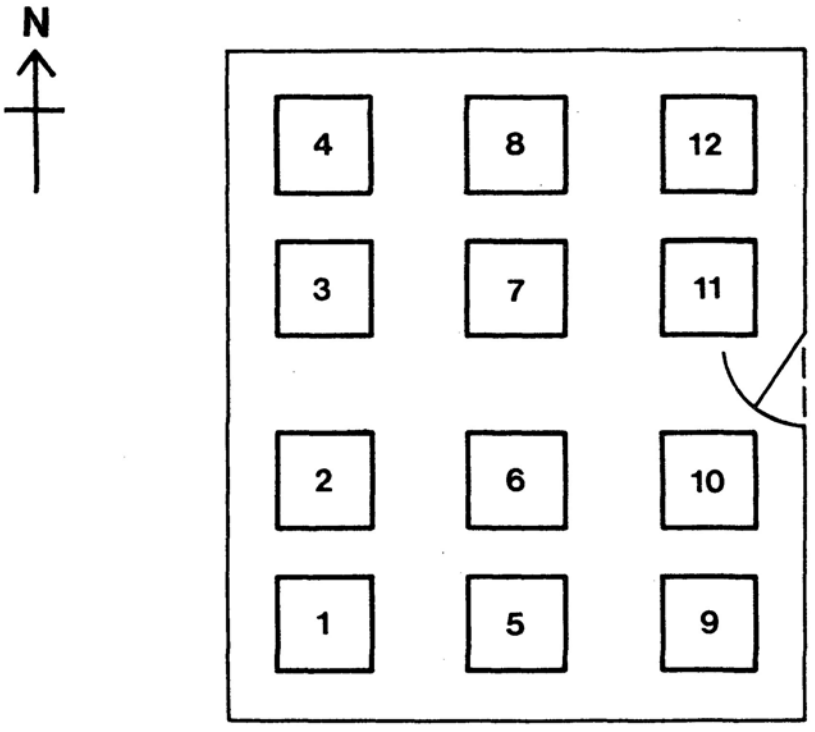


Table 3.8 Treatments Used and Resulting Coccinellid Movement

Plot	Insecticide Spray	No. Coccs. Introduced	Colour Marking	No. Aphids Per Tiller (1/7)	No. Coccs./Plot 1/7		
					Remain.	Immig.	Total
1	Pirimicarb	50	Orange	0		2	2
2	—	—	—	23		5	5
3	—	—	—	240		6	6
4	Nicotine	50	Grey	228	13	4	17
5	Nicotine	75	Green	250	28	4	32
6	Pirimicarb	50	Gold	0	16	4	20
7	—	—	—	75		0	0
8	—	—	—	286		0	0
9	Nicotine	60	Yellow	197	21	2	23
10	—	—	—	150		5	5
11	Pirimicarb	50	Blue	0	12	1	13
12	—	—	—	192		5	5

Key: Coccs. - Coccinellids; Remain. - Remaining; Immig. - Immigrant

Possible directions of movement were limited by the position of the plot of introduction of the beetles (figure 3.18), for example, beetles introduced into Plot 1 could only move north and east. Distances moved (in terms of plot units) by the beetles were calculated by the following method which was reasonably free of bias.

The component of movement was calculated on a similar basis to the triangle of velocities, each direction of movement having two components at right angles. The distance of each component (in plot units) from the

source plot was multiplied by the number of beetles undertaking the given move. The components were calculated for all inter-plot movements and summed to give the total component of movement in each compass direction (table 3.9). This was divided by the total number of beetles recovered that could have moved to plots in each compass direction (includes beetles that did not move) to give the net distance moved in each compass direction. For example, beetles from Plots 1, 5, 6, 9 and 11 but not 4 (figure 3.18) could have been found in northerly plots, hence the northerly component of beetles that moved from these plots was divided by the number of beetles that moved plus the number of sedentary beetles recovered. Thus the mean distance moved per beetle accounted for the potential number moving as well as the actual number of beetles that moved.

Table 3.9 Direction of Movement of Coccinellids

Direction of Movement	Component of Movement	Total Recovery of Beetles that Could Have Moved	Mean Distance Moved/Beetle
Northerly	41	115	0.36
Southerly	8	57	0.14
Easterly	15	83	0.18
Westerly	15	99	0.15

(c) Results

Of the 335 coccinellid adults introduced into the plots on June 29th, only 40% were found by the next sampling date, July 1st. Moreover, by July 6th only 6% of the original numbers were found and thus the factors

influencing the movement of coccinellids were examined for the first sampling date only.

By July 1st, only 30% of the coccinellids sampled had moved to new plots, 70% remaining in their original plot. A greater percentage (of numbers introduced) of coccinellids was recovered from plots with high aphid densities but the correlation between percentage recovery of coccinellids and aphid density was not significant ($r = 0.59$, $n = 5$ $p > 0.1$).

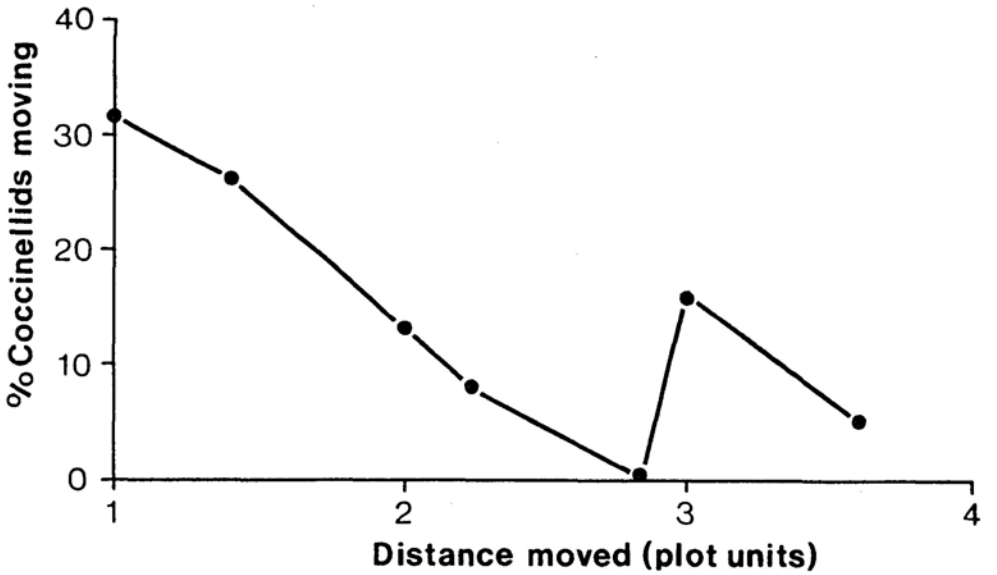
Of the beetles that moved, most moved to adjacent plots, 1 and 1.4 plot units distant (figure 3.19(a)) and numbers moving decreased with distance, apart from the long distance migrators which moved the maximum distance of 3 and 3.6 plot units. This is consistent with walking being the main mode of locomotion; coccinellids found three or more plot units from their source probably flew, and these represent 30% of the total numbers moved.

The short distances moved per beetle reflect the fact that the majority of beetles recovered had not moved from their plot of introduction (table 3.9). Beetles seemed to move the greatest distance in a northerly direction possibly because the prevailing wind was from the south west (table 3.9).

There was a negative relationship between movement to a plot and beetles already there (figure 3.19(b)). However, although aphid densities had no effect on the number of adults recovered from a plot (figure 3.19(c)), numbers of coccinellid larvae sampled on July 13th before much movement of larvae had taken place were positively correlated with cumulative numbers of aphids (as aphid index) (figure 3.20).

Figure 3.19 Factors Affecting Movement of Coccinellids

(a) Distance – Percentage of Total Number of Coccinellids Moving



(b) Crowding – Number of Other Coccinellids Moving to a Plot

$y = 2{\cdot}44 - 0{\cdot}26x \quad r = 0{\cdot}424 \quad p < 0{\cdot}05$

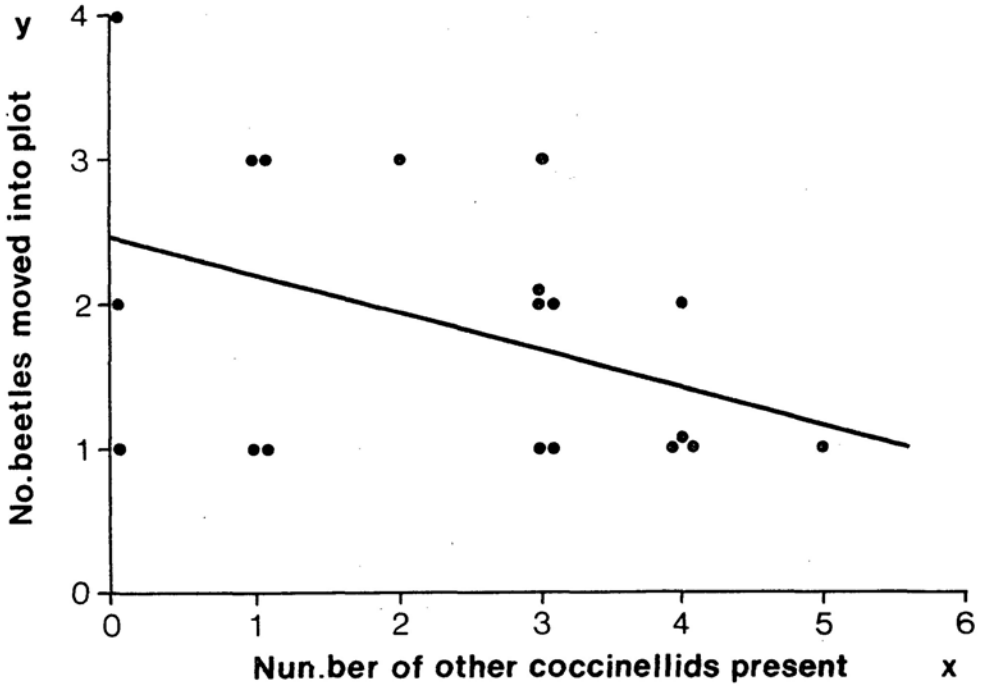
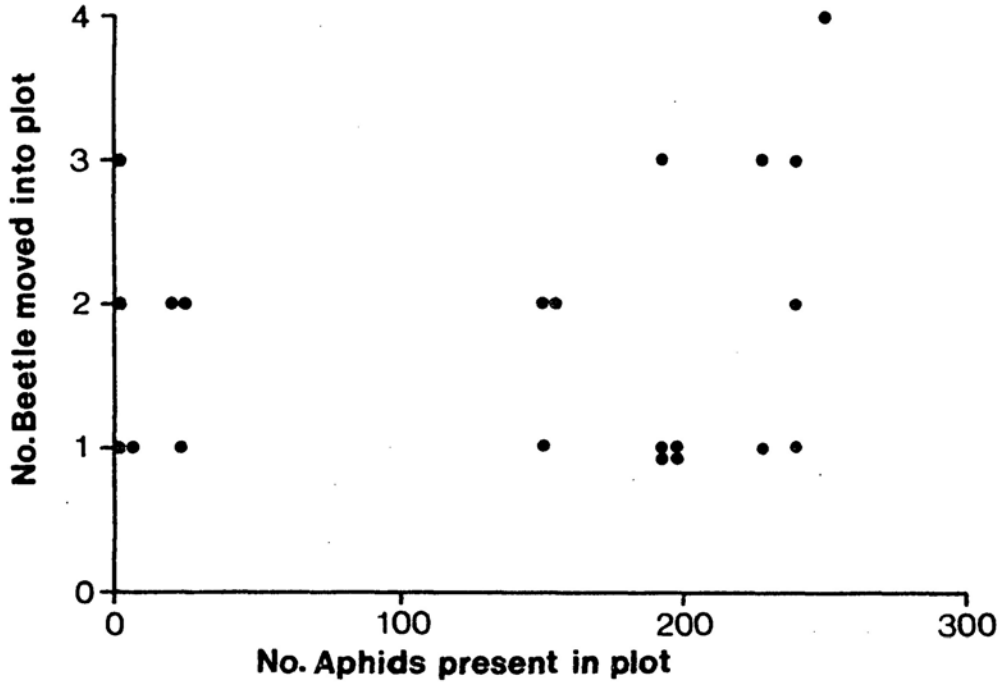


Figure 3.19 Factors Affecting Movement of Coccinellids

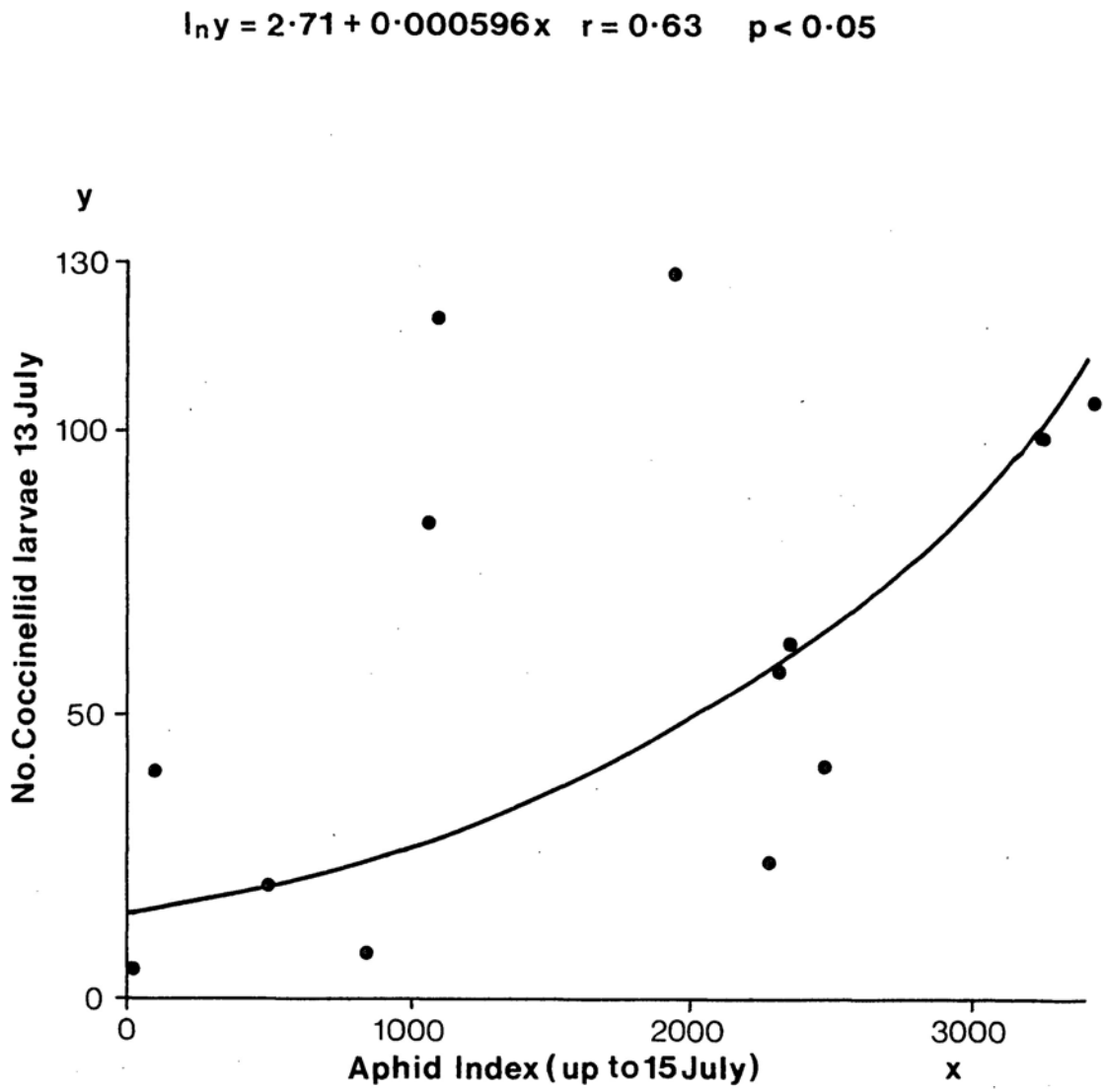
(c) Aphid Density in Destination Plot



(d) Discussion

The overall impression from the experiment was that there was a lack of coccinellid movement. The results showed that a small proportion of beetles moved a small distance (affected by prevailing wind) to plots at random irrespective of aphid numbers and that no clumping of adults in response to pheromonal factors occurred, rather the converse - movement tended to even out beetle density. The relatively high numbers found in distant plots were probably beetles that had flown along the sides of the insectary and failing to escape landed in the nearest plot. Moreover, coccinellid behaviour observed in this experiment can be considered to be fairly representative of their behaviour in the field

Figure 3.20 Aggregation of Coccinellid Larvae with Aphid Index



since it coincides to a large extent to field behaviour observed by Frazer and Gilbert (1976).

Even though beetles moved little and few eggs were found, the relationship between larval numbers and aphid index (figure 3.20) suggested that eggs had indeed been laid in response to aphid density. This relationship could equally have been produced by increased survival of larvae in plots with more aphids. The true mechanism is probably a combination of both these factors.

Although coccinellid adults are brightly coloured their retiring behaviour makes observations of their numbers very difficult. Frazer and Gilbert (1976) noted that whereas coccinellids in the laboratory actively searched their environment for prey they were much less active in the field (crop - alfalfa) and the authors concluded that all laboratory behavioural studies were suspect until verified in the field. Moreover, Vickerman and Sunderland (1975) found that many predators in cereals were active mainly at night and that aphid predation mostly occurred in darkness. However, apart from this work little attention has been paid to the nocturnal behaviour of predators.

To conclude, aphids have an indirect effect on the dispersal of coccinellids within a crop. Adult beetles move infrequently and for short distances but number of eggs laid and larval survival depends on aphid densities in the vicinity of ovipositing females.

In addition, sampling by visual counts underestimates numbers of both adults and larvae. Numbers of coccinellids estimated by observation depends both on their population density and their activity on the particular sampling occasion. Hence visual counts give a relative estimate of

population activity in a similar way to pitfall trapping of ground beetles. Thus calculations of predator pressure based on visual counts of coccinellids can be misleading, for example, Rautapää's (1972, 1975) studies of the effect of C. septempunctata on R. padi.

(ii) Effect of Natural Enemies on Late Season Aphid Populations

(a) Introduction

Parasites gained entry to the insectary in 1976 and the effect of these and an abiotic factor (temperature) on the late season aphid populations was studied. In the 1977 experiment, coccinellid larvae produced from the coccinellid movement experiment were sampled to ascertain their distribution with aphid density and their effect on aphid populations.

(b) Materials and methods

In 1976, following the experiment on aphid predation by ground beetles, most plots were sprayed at intervals with insecticide to investigate the effect of aphids on yield (Chapter 6). In those plots which were not sprayed, i.e. Plots 1, 4 and 7, numbers of Sitobion avenae (adult apterae, alatae and nymphs) and mummified aphids on ten tillers were counted at intervals from late June to late July.

In 1977, aphids were sampled in all the plots and the coccinellid larvae were sampled to determine their effect on aphid numbers. However, the larvae were difficult to count on the plants, since it was hard to find those that were not on the leaves and difficult to avoid counting twice those that were visible. After the aphids disappeared by July 18th, coccinellid larvae were removed by hand and aspirator and numbers were more accurately assessed by these means.

(c) Results

During late June and early July in 1976 there was continuous sunny weather and high temperatures. Aphid populations present in the insectary underwent a sudden decline in early July (figure 3.21) during a spell of high temperatures. When the temperature decreased later in July, aphid numbers increased again. Populations decreased gradually from July 19th onwards (figures 3.21 and 3.22) and numbers of alatae and mummies increased at the beginning of the decline (figure 3.22).

In the 1977 experiment, aphids decreased from higher densities but rates of decrease were not related to peak numbers (figure 3.23). Moreover, the patterns of aphid decrease were not consistent within each spray treatment previously applied. Larger numbers of alatae were observed flying from plants, compared to 1976, which was undoubtedly due to the overall higher numbers of aphids present. Alatae tended to climb to the top of the ears to take off and take-off also occurred from the flag and lower leaves.

Visual counts of coccinellid larvae on plants were less accurate than collection by hand and aspirator. A count on July 16th totalled 650 larvae, but two days later a total of 2570 larvae were collected by hand and aspirator. Mean temperatures in the insectary were fairly high (18–28°C), and the most voracious III and IV instar larvae were produced rapidly and these accelerated the decline of the aphid populations. A few callow and unmarked second generation coccinellid adults were found from July 13th onwards and eggs laid by these gave rise to a rapid increase in larval numbers, a further 540 being collected on July 20th and 300 on July 26th. The larvae moved extensively so that by July 18th

Figure 3.21 1976 Experiment Effect of Temperature on Aphid Populations

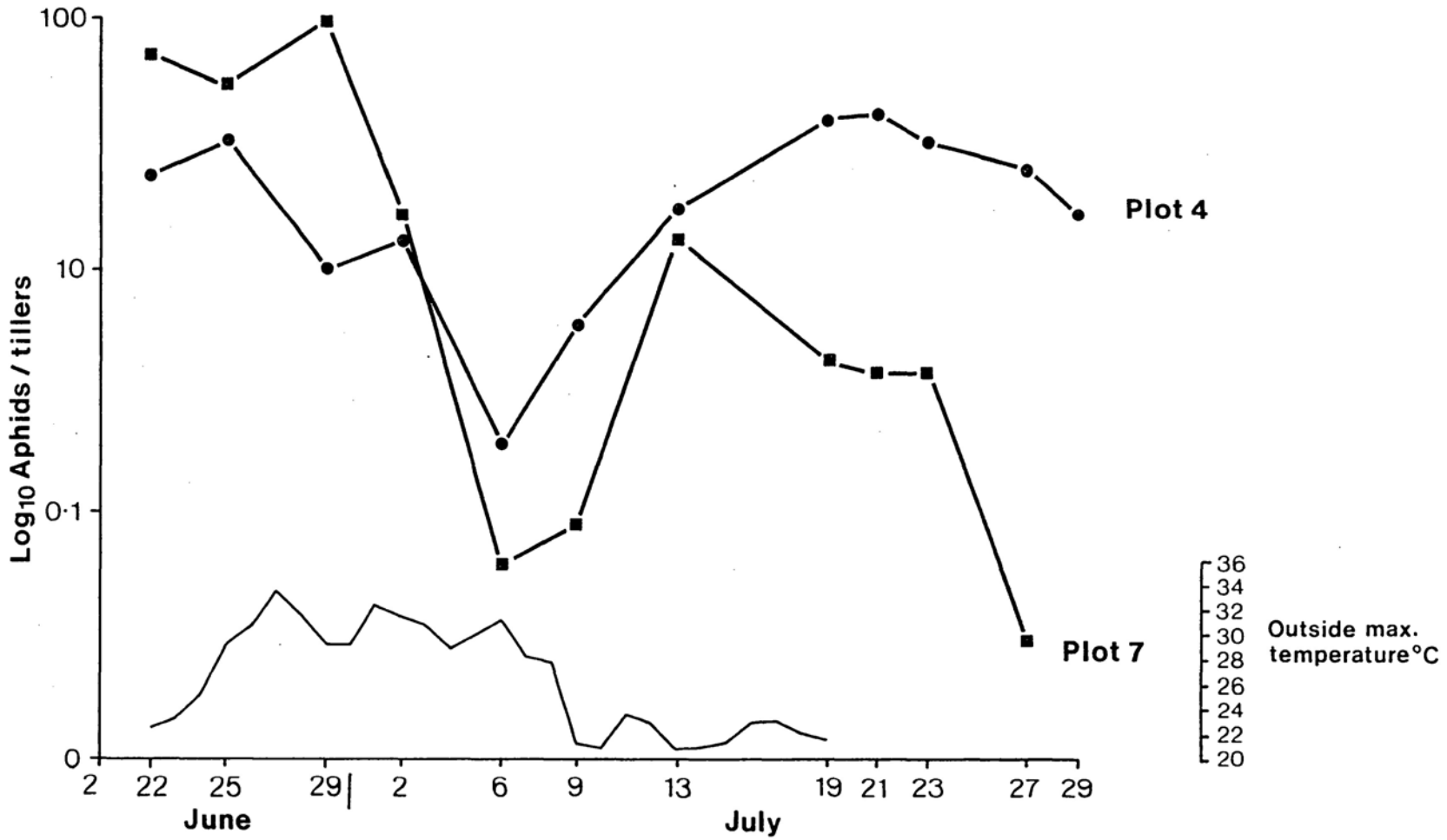


Figure 3.22 1976 Experiment Numbers of Apterous Aphids, Alatae and Mummies During Wheat Ripening (Plot 1)

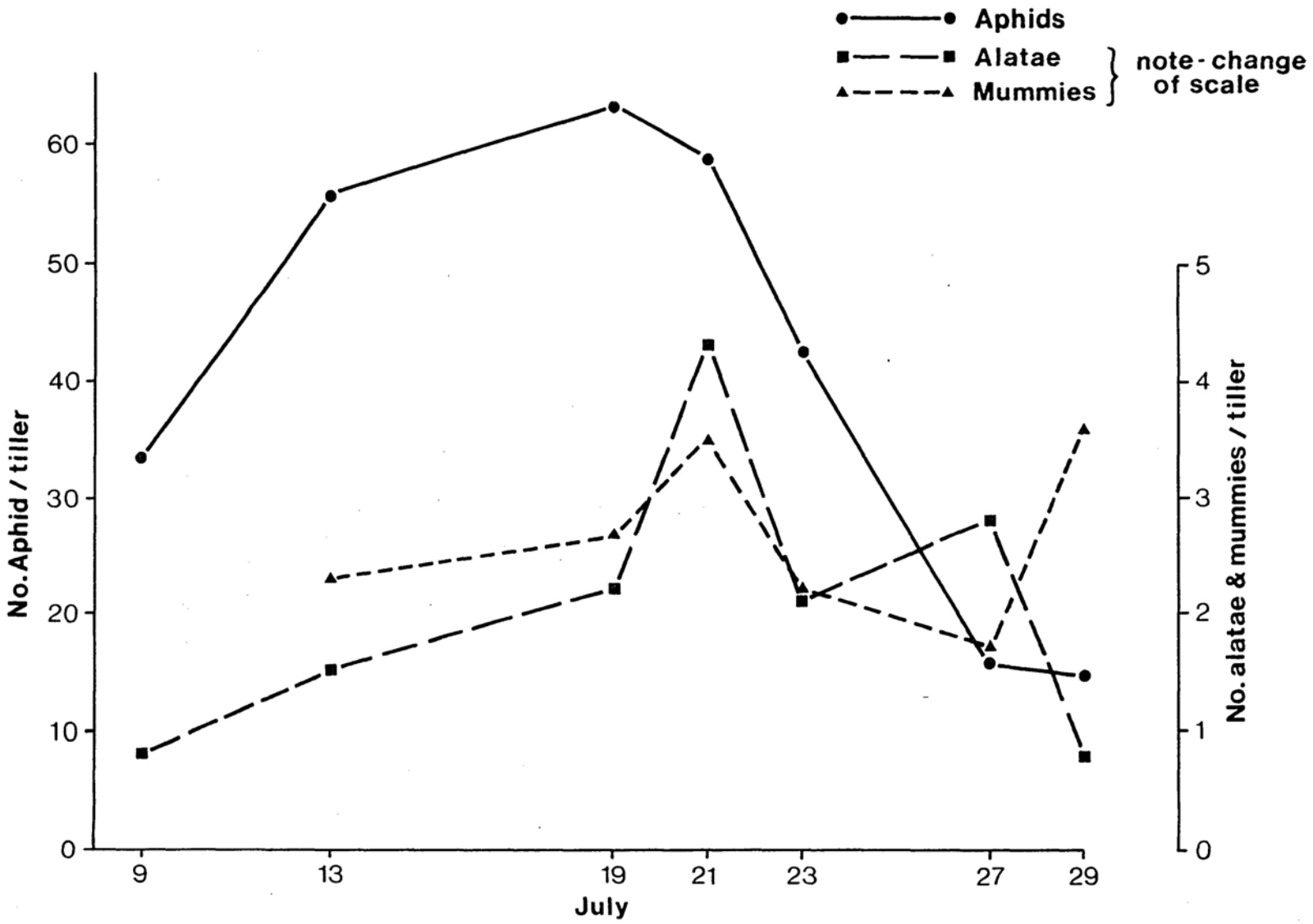
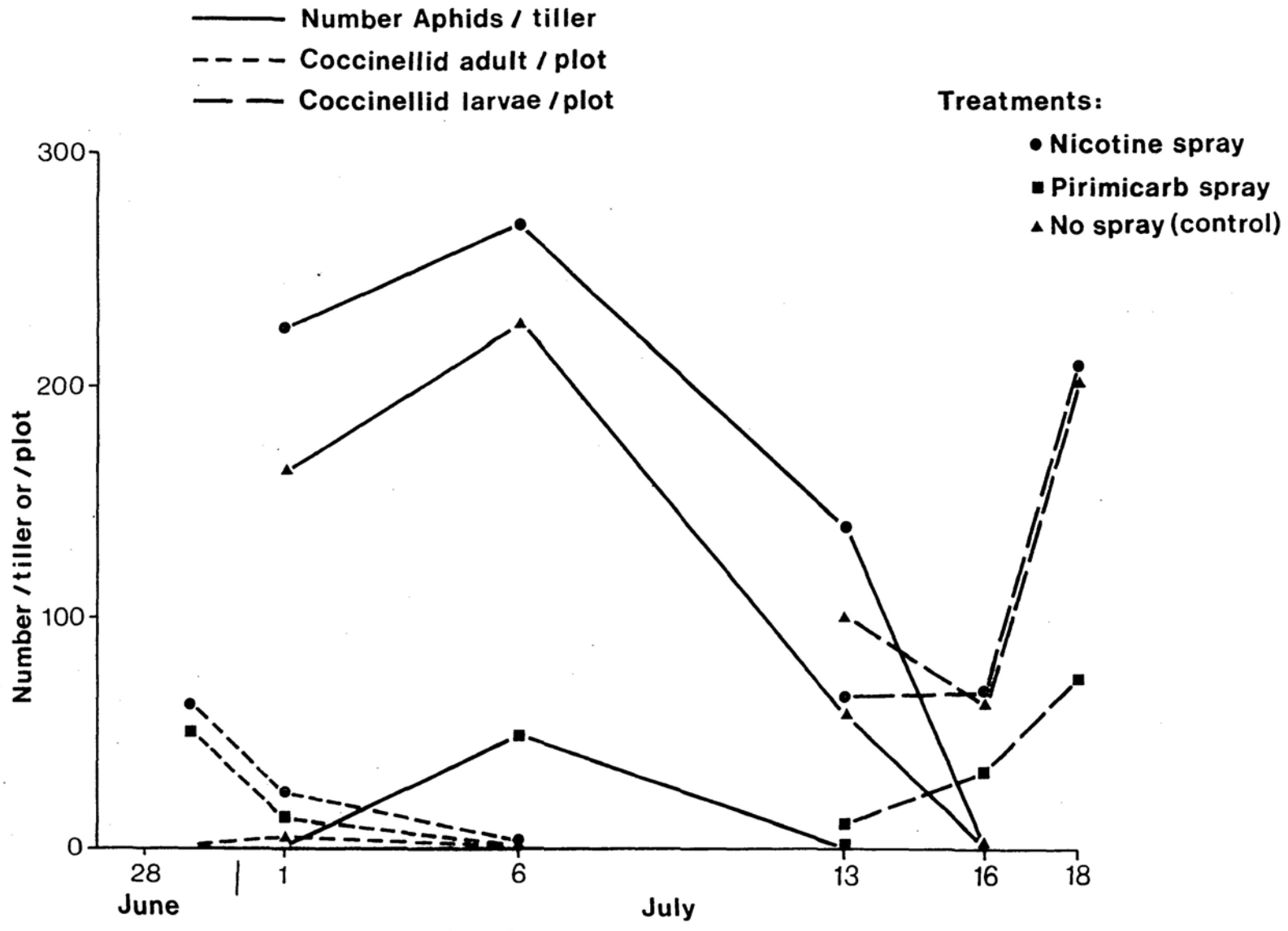


Figure 3.23 1977 Experiment Mean Numbers of Aphids, Coccinellid Adults and Larvae During Wheat Ripening



a third of the total number present occurred outside the plots. Finally, although the larvae occurred in every plot, the decline of aphids was not related to the numbers of larvae present.

(d) Discussion

In 1976, the decrease of aphid numbers in early July was almost certainly a result of mortality from continuous thermal stress. In the laboratory, Dean (1974c) found that, at 30°C, adult apterous S. avenae suffered 50% mortality in eight days, the immature stages suffering 100% mortality. The July decrease of aphid numbers is compatable with these results, the aphid decrease starting about five days after the advent of 30°C maximum temperature.

In the field experiments, aphids in the cages reached similar peak numbers and persisted for similar lengths of time to aphids in the insectary (table 3.10). This suggests that a similar regulatory process affected aphid populations in the insectary, i.e. emigration regulated the population increase and natural enemy mortality exerted its effect on top of the self-regulatory process. The more abrupt decline of aphid

Table 3.10 Comparison of Persistence of Aphids in the Insectary and Field Experiments

Experiment	Peak No. Aphids/Tiller	Time Present (Days)	Time Taken For Decrease (Days)
Insectary 1976	290	70	8–10
Insectary 1977	200–450	62–67	5–7
Field Experiment Cages 1976	160	62	20
Field Experiment Cages 1977	100–480	58–63	14–19

populations in the insectary experiments was probably a consequence of the previous treatments. For example, in 1976 aphid numbers were increasing after the period of high temperatures and before the final decrease (figures 3.21 and 3.22) and in 1977 the insecticide treatment for the coccinellid movement experiment had a similar effect (figure 3.23). Thus, the population decreases in the field cages and insectary experiments were not closely comparable and this may explain the lack of a density dependent population decline in the insectary.

As in the field experiments, the low numbers of mummies suggested that parasites had had little effect on aphid numbers in the 1976 experiment. Moreover, the increase in numbers of alatae on plants heralding the population decline was also similar to events in the field cages. Thus, in the 1976 experiment, emigration of alatae was probably the factor most responsible for the decrease of aphid numbers.

In 1977, the distribution of coccinellid larvae on July 13th, before much larval movement took place, was probably a consequence of egg laying by adult females in response to aphid density, (figure 3.20, section (i)). Larvae, undoubtedly affected the aphid population decrease (compare the rates of decrease in figures 3.22 and 3.23) but because of the inaccuracies of the sampling, the extensive movement of larvae between plots, and the simultaneous effect of emigration, no relationships were found between numbers of larvae and rates of aphid decrease.

CHAPTER 4

MOVEMENT AND DISPERSAL OF CEREAL APHIDS

4.1 Introduction

Movement of cereal aphids occurs in two ways; it can either be voluntary walking or flying, or it can be produced by external factors such as weather and therefore be involuntary. Ferrar (1969) asserted that involuntary movement of Myzus persicae was less important than voluntary movement.

A few researchers have noted the importance of rain in the reduction of aphid populations (Wadley, 1931, Dunn and Wright, 1955), and Dhalival and Singh (1975) found that heavy rain (one centimetre in 24 hours) would considerably reduce the population of nymphs and adults of Macrosiphum miscanthii on the leaves of wheat.

From studies of aphid colonization and distribution in spring cereals, Dean (1973a and 1973b) found that mainly older nymphs and apterae moved between tillers and that Sitobion avenae was more 'restless' than Metopolophium dirhodum. He concluded that S. avenae had behaviour patterns that ensured its rapid dispersal over the whole field at low population densities. Ito (1952a, 1952b and 1960), however, postulated a different mechanism for aphid dispersal. He found that, in the laboratory, an aphid species on a barley plant tended to choose a 'preferred niche' and multiply there until it reached a 'saturation density' after which it would move to cover the whole plant. This behaviour was modified when other aphid species were present on the plant, and aphids then moved from their preferred niches at lower saturation densities and also emigrated

lower populations. Wyatt (1969) found that a similar sequence of events was responsible for the dispersal of Myzus persicae on chrysanthemums and he found that differences in the palatability of varieties, together with preferences for leaves of a certain age played a large part in determining the distribution of the aphids as the population increased.

Aphid colonies on potted wheat plants were used in two experiments to investigate both the extent to which wind and rain could dislodge aphids and the interactions of these factors with aphid colony size, and aphid dislodgement in the field produced by a rainstorm was also studied. The dispersal of aphids through a field of winter wheat in an aphid 'outbreak' year, namely 1977, and movement between plant and ground was described using information from the development and spread of aphid colonies through the field and the trapping of aphid by sticky traps.

Lowe (1971) emphasized the role of behavioural patterns in the dispersal of three aphid species over beans. He concluded that differences in behaviour of walking individuals could have produced the different patterns of spatial distribution on the bean plants. Walking behaviour of cereal aphids was also investigated in the present chapter, but from the aspect of searching for plants. The searching behaviour of three cereal aphid species for wheat plants was studied in an experimental arena, in light and dark conditions, in order to determine the efficiency with which aphids could find a plant and therefore the potential risk of predation in the field while walking from one plant to another.

Finally, using information on the proportion of tillers infested by aphids and the number of aphid colonies with aphid population, a model was derived to describe the increase in the number of plants infested by aphids as the population increased.

4.2 Dislodgement and Dispersal of Cereal Aphids

(i) Experiment 1

Effect of Weather and Colony Size on Aphid Dislodgement

Introduction

The effect of weather on the number of aphids dislodged from aphid populations on wheat plants was examined by exposing aphid colonies on leaves to ambient weather conditions of wind, rain and low temperature and noting the changes in aphid numbers on successive days.

Materials and Methods

Colonies of S. avenae on the leaves of large, single-tillered wheat plants were used, the plants being tied to a stake to prevent them being blown over. To enable individual colonies to be readily located at successive samples, lines were drawn with a black felt-tip pen 5 cm apart across each leaf on both upper and lower leaf surfaces marking out zones of approximately equal area. Each zone was numbered, and discrete colonies of adult apterae and nymphs were recorded in each zone.

Two treatments (A and B) were used to examine the effect of weather on aphid dislodgement; treatment A to study dislodgement from small newly established colonies, and treatment B to study dislodgement from larger, well established aphid colonies. A third treatment (C) was used to study colony development in undisturbed conditions in a glasshouse. For treatment A, four plants were placed in a glasshouse in proximity to heavily infested plants (on March 28th) and left overnight to become infested. The distribution of aphids on the plants was recorded on March 31st and the plants were placed outside in an exposed position in a grass border of a playing field and aphid colonies were recorded on

successive days until April 5th. Four plants were also used in treatment B; five apterous adult aphids were introduced onto each plant, and populations were allowed to increase for five days in a small glasshouse before being placed outside (on April 4th) in the same exposed position as treatment A. Treatment C was the same as treatment B but the plants were retained in the glasshouse.

In treatments A and B, losses of aphids between samples were primarily due to dislodgement by wind and rain, since no predators were observed which could have eaten aphids and voluntary movement of aphids was inhibited in adverse environmental conditions, as found from laboratory observations. Moreover, it was quickly apparent that losses of aphids were independent of the scale of the wind or rain and thus the use of linear regression techniques was not feasible. Therefore, the data were analysed as follows:-

(1) Overall trends in numbers of aphids, colonies and aphids per colony per plant are shown from the plots of these variables on successive days (figures 4.1, 4.3 and 4.5).

(2) The distribution of aphid colonies on successive days was compared and the number of aphids dislodged from colonies and the number of aphids gained in colonies through coalescing of colonies or reproduction, was recorded. Numbers of colonies losing aphids were also quantified, together with those colonies unaffected from one day to the next, new colonies produced from fragmentation of larger colonies and those colonies increasing in size through coalescing of existing colonies or reproduction. The data were expressed as percentages of the total numbers between samples (e.g. table 4.2(a) and (b)).

In order to investigate the influence of crowding, the changes in numbers of aphids and colonies were recorded for six colony size categories, namely 1, 2–5, 6–10, 11–15, 16–20 and >20 aphids per colony. For clarity, only variation in aphid dislodgement and colonies losing aphids with increasing colony size is presented in the text (figures 4.2 and 4.4); the effect of colony size on the other processes is shown in an appendix.

Results

The effect of wind and rain on aphid losses varied according to the treatment. In treatment A, where 79% of the colonies and 45% of the aphids were in the lowest two colony size categories (i.e. 1 and 2–5 aphids/colony), most of the population loss occurred in the first day of exposure to the weather (figure 4.1). Heavy rain and strong winds were prevalent on March 31st (table 4.1) when the plants were first exposed, but the wind subsided the next day and the rain became a drizzle which ceased by April 3rd. The inclement weather on the first day dislodged 63% of the aphids (table 4.2(a) (i)) and affected 80% of the colonies (table 4.2(b) (i)). Moreover, an equal proportion of aphids was lost from all colony sizes except the largest (>20) (figure 4.2(a) (i)), and likewise an equal proportion of colonies were affected in the same way (figure 4.2(b) (i)), the large colonies fragmenting to form new ones. As the weather mollified in the following days the aphids became acclimatized to the conditions. This was reflected in a decrease in the percentage of aphids dislodged and colonies losing aphids and a corresponding increase in aphids and colonies remaining unchanged (table 4.2(a) (i) and table 4.2(b) (i) & (ii)). Aphids being lost mainly from the more numerous smaller colonies (figure 4.2(a) (ii) & (iii) and

Figure 4.1 Experiment 1 Treatment A - Overall Changes in Numbers of Aphids and Colonies

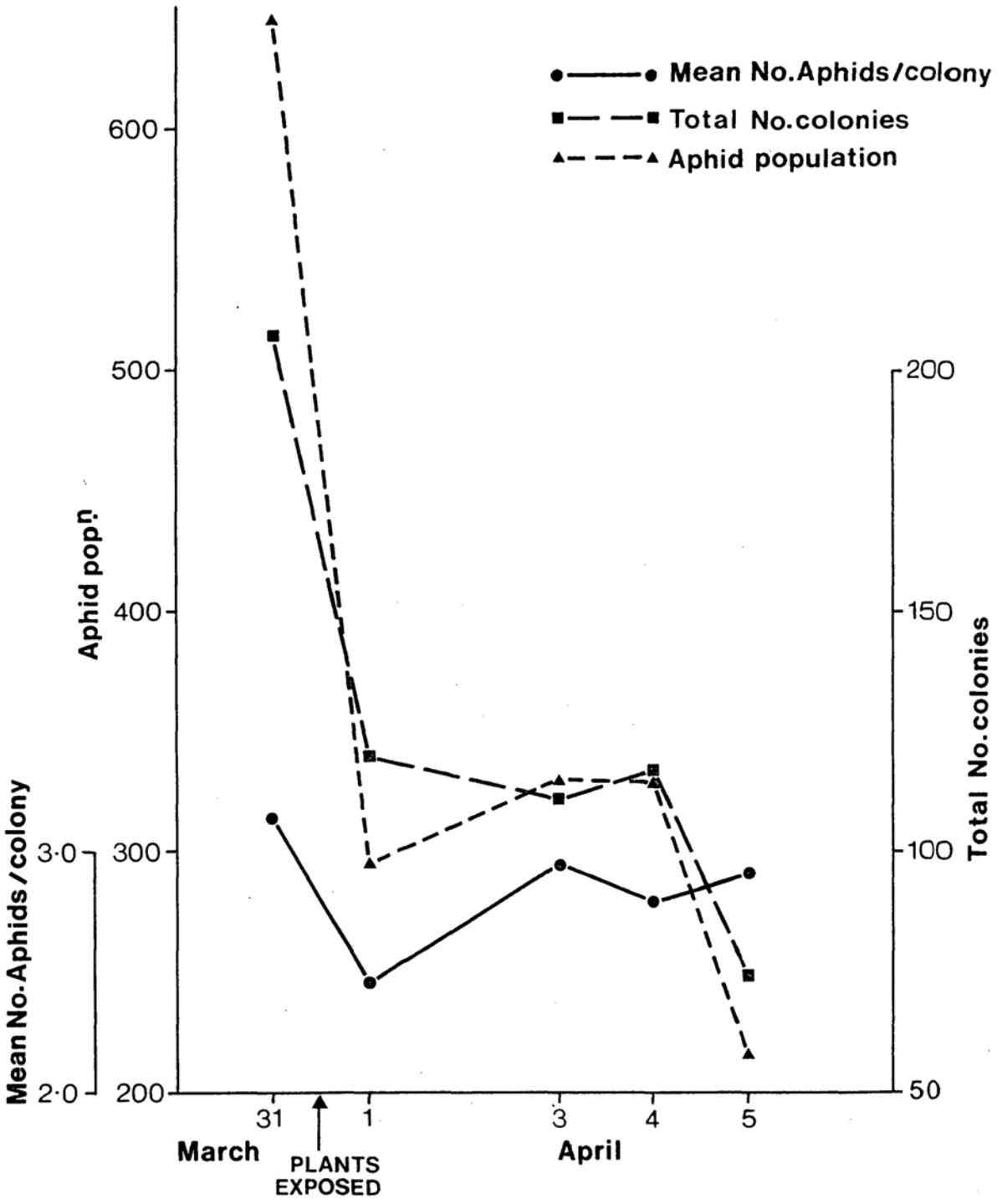


Table 4.1 Weather Conditions Over the Period of Experiment 1

Date	Glasshouse Temperature		Rain Fallen	Outside Temperature		Average Wind Speed (ms^{-1}) & Direction		Treatment
	Max.	Min.	mm	Max.	Min.			
31st March	—	—	12.1	9.4	1.3	5.4	S.W.	A
1st April	17.2	14.4	5.8	10.7	4.7	3.0	S.W.	A
2nd April	—	—	0.3	10.5	6.5	2.5	N.	A
3rd April	27.8	11.1	0	10.7	3.5	2.2	N.	A
4th April	24.4	14.4	0	8.8	0.7	1.4	N.	B
5th April	27.8	16.7	0	10.8	1.8	1.3	N.E.	B
6th April	26.1	15.6	1.1	10.7	4.6	1.8	S.W.	B
7th April	23.3	17.8						
12th April	28.9	12.8						
13th April	27.8	15.0						
14th April	27.8	16.1						
15th April	22.8	12.8						

Temperatures recorded in ^{o}C

figure 4.2(b) (ii) & (iii)). New colonies were formed between April 1st–3rd from the fragmentation of large colonies and colonies gained aphids over this period from the coalescing of small colonies and a certain amount of reproduction (table 4.2(b) (iii) and (iv)), the latter occurring especially in the 2–5 colony size category which contained a large proportion of apterae. Finally, a greater percentage of alatae was dislodged than apterae or nymphs (table 4.2(a)) and this consistently occurred in all colony sizes.

Table 4.2 Experiment 1 Treatment A

a Changes in Average Numbers of Aphids

		DATE		
		31/3-1/4	1-3/4	3-4/4
(i) % Aphids Dislodged*	Alatae	89 (16)	100 (1)	0
	Apterae	71 (146)	29 (15)	9 (4)
	Nymphs	60 (478)	17 (58)	5 (17)
	TOTAL	63 (640)	19 (74)	5 (21)
(ii) % Increase in Aphid Numbers*	Apterae	0	8 (4)	2 (1)
	Nymphs	1 (11)	26 (86)	6 (21)
	TOTAL	1 (11)	23 (90)	6 (22)
(iii) Total Number of Aphids	Alatae	18	1	0
	Apterae	205	52	43
	Nymphs	795	337	343
	TOTAL	1018	390	386

* Actual numbers in brackets

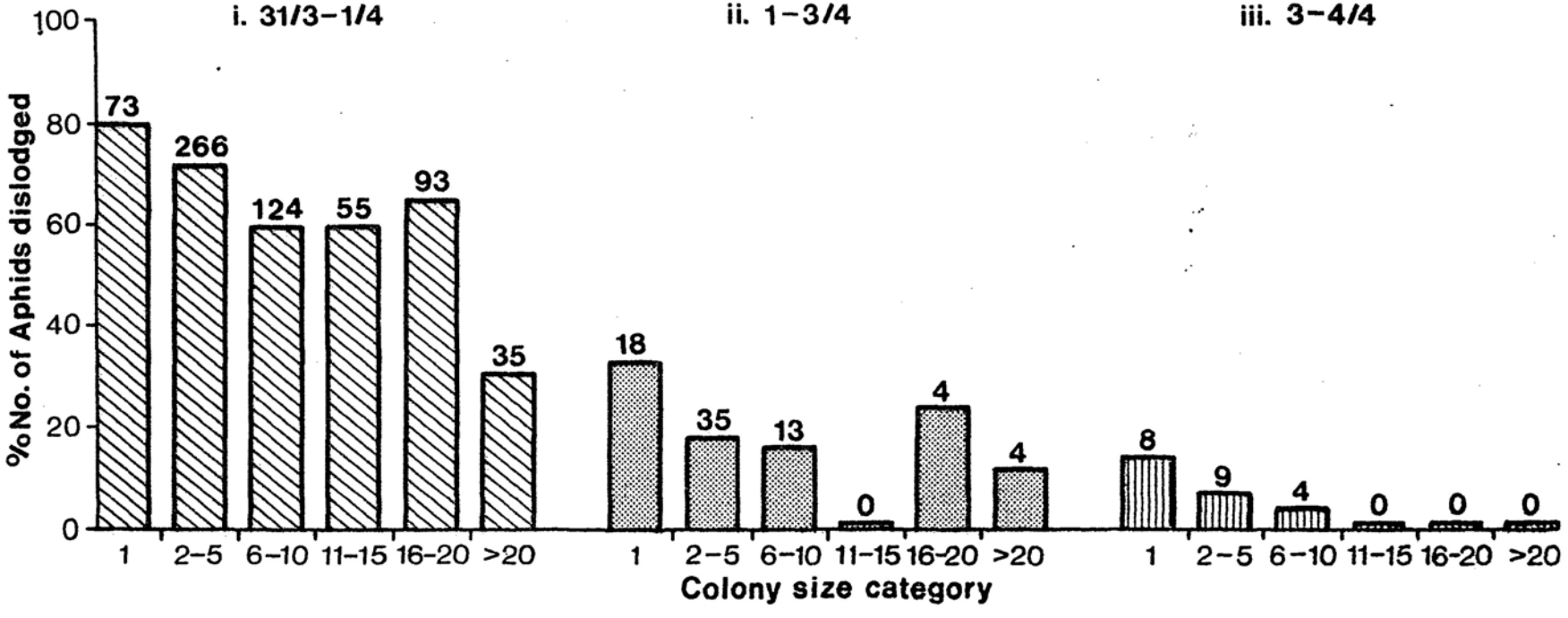
b Changes in Number of Colonies

	DATE		
	31/3-1/4	1-3/4	3-4/4
(i) % Colonies Losing Aphids*	80 (210)	33 (46)	14 (18)
(ii) % Colonies Unaffected *	13 (34)	33 (46)	66 (82)
(iii) % New Colonies *	5 (13)	11 (16)	6 (8)
(iv) % Colonies Gaining Aphids*	3 (7)	23 (32)	14 (17)
Total Number of Colonies	264	140	125

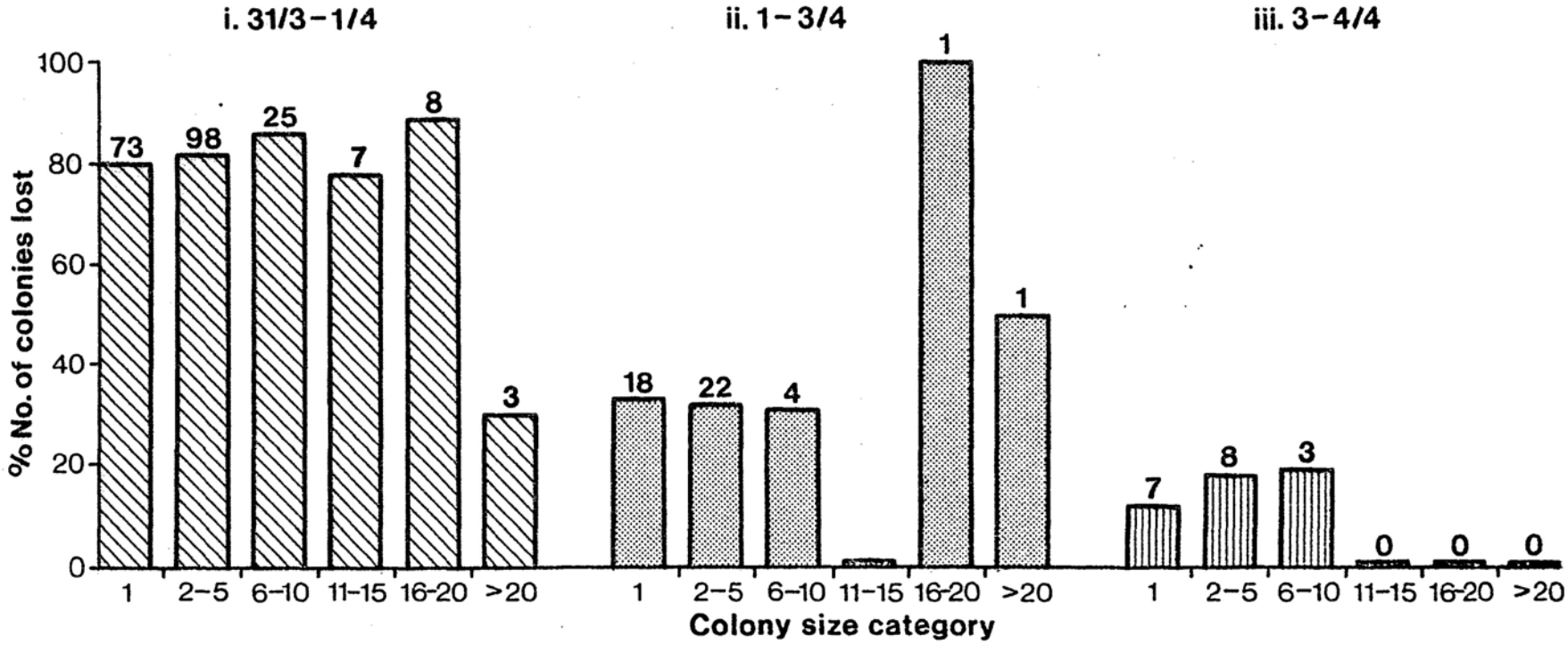
* Actual numbers in brackets

Figure 4.2 Experiment 1 Treatment A - Losses in Numbers of Aphids and Colonies for Aphid Colony Sizes

(a) % aphids dislodged from colonies (actual numbers)



(b) % colonies lo sing aphids (actual numbers)



In treatment B, where 66% of the aphids and 24% of the colonies were in the >20 colony size category, a different pattern of aphid dislodgement was evident. In contrast to treatment A, the aphid population decreased more gradually with exposure to weather, and the mean colony size decreased rapidly from April 5th onwards, due to colony fragmentation (figure 4.3). Temperatures and wind speeds were roughly constant over the period that the plants were exposed (April 4th, 5th and 6th) and the only rain that occurred was showers on the final day (April 6th) (table 4.1). Losses of aphids in the first day exposed were small, only 8% of aphids being dislodged but 37% of the colonies were affected (table 4.3(a) (i) and table 4.3(b) (i)). Moreover, a greater proportion of colonies was affected in the three higher colony size categories (i.e. 11-15, 16-20 and >20 aphids/colony) (figure 4.4(b) (i)) than in the smaller colonies. The next day, (April 5th), overall aphid losses increased to 29% (table 4.3(a) (i)), the largest colonies (>20) losing aphids and fragmenting to form new colonies (figure 4.4(a) (ii)), some aphids conglomerating with existing colonies, to increase their size (table 4.3(b) (iii)). The shower of rain on the final day (April 6th) increased aphid dislodgement, affecting 38% of the population and 53% of the colonies but losses were unrelated to the size of the colony (figure 4.4(a) (iii), 4.4(b) (iii)). As in treatment A, relatively more apterae were dislodged than nymphs.

In treatment C, the mean rate of aphid population growth was fairly constant at 5.6 fold per week. Initially, there was a rapid increase in colony size with little increase in total number of colonies (figure 4.5) and by April 7th the colony size reached a stable level (approximately 22 aphids/colony) which continued for five days, aphids moving away to form

Figure 4.3 Experiment 1 Treatment B - Overall Changes of Aphid Numbers and Colonies

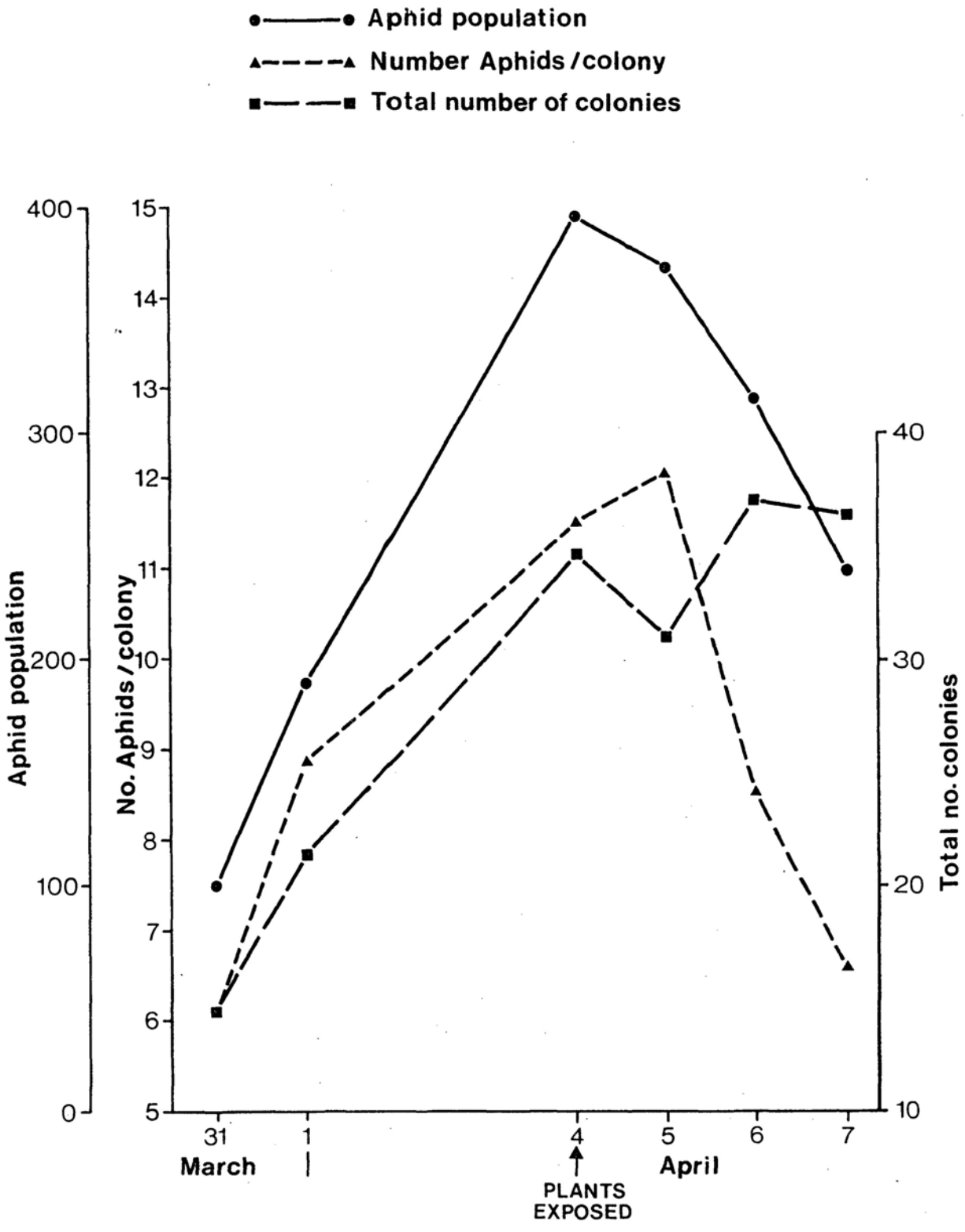


Table 4.3 Experiment 1 Treatment B

a Changes in Average Numbers of Aphids

		DATE		
		4–5 April	5–6 April	6–7 April
(i) % Aphids Dislodged*	Apterae	9 (6)	41 (24)	45 (15)
	Nymphs	7 (84)	28 (311)	38 (279)
	TOTAL	8 (90)	29 (335)	38 (294)
(ii) % Increase in Aphid Numbers*	Apterae	0	3 (2)	0
	Nymphs	6 (72)	5 (55)	0.7 (5)
	TOTAL	6 (72)	5 (57)	0.6 (5)
(iii) Total Number of Aphids	Apterae	64	58	33
	Nymphs	1125	1108	742
	TOTAL	1189	1166	775

* Actual numbers in brackets

b Changes in Numbers of Colonies

	DATE		
	4–5 April	5–6 April	6–7 April
(i) % Colonies Losing Aphids*	37 (29)	25 (25)	53 (39)
(ii) % Colonies Unaffected*	43 (34)	21 (21)	24 (18)
(iii) % New Colonies*	5 (4)	30 (30)	19 (14)
(iv) % Colonies Gaining Aphids*	12 (15)	24 (24)	4 (3)
Total Number of Colonies	79	100	74

* Actual numbers in brackets

Figure 4.4 Experiment 1 Treatment B - Losses in Numbers of Aphids and Colonies for Aphid Colony Sizes

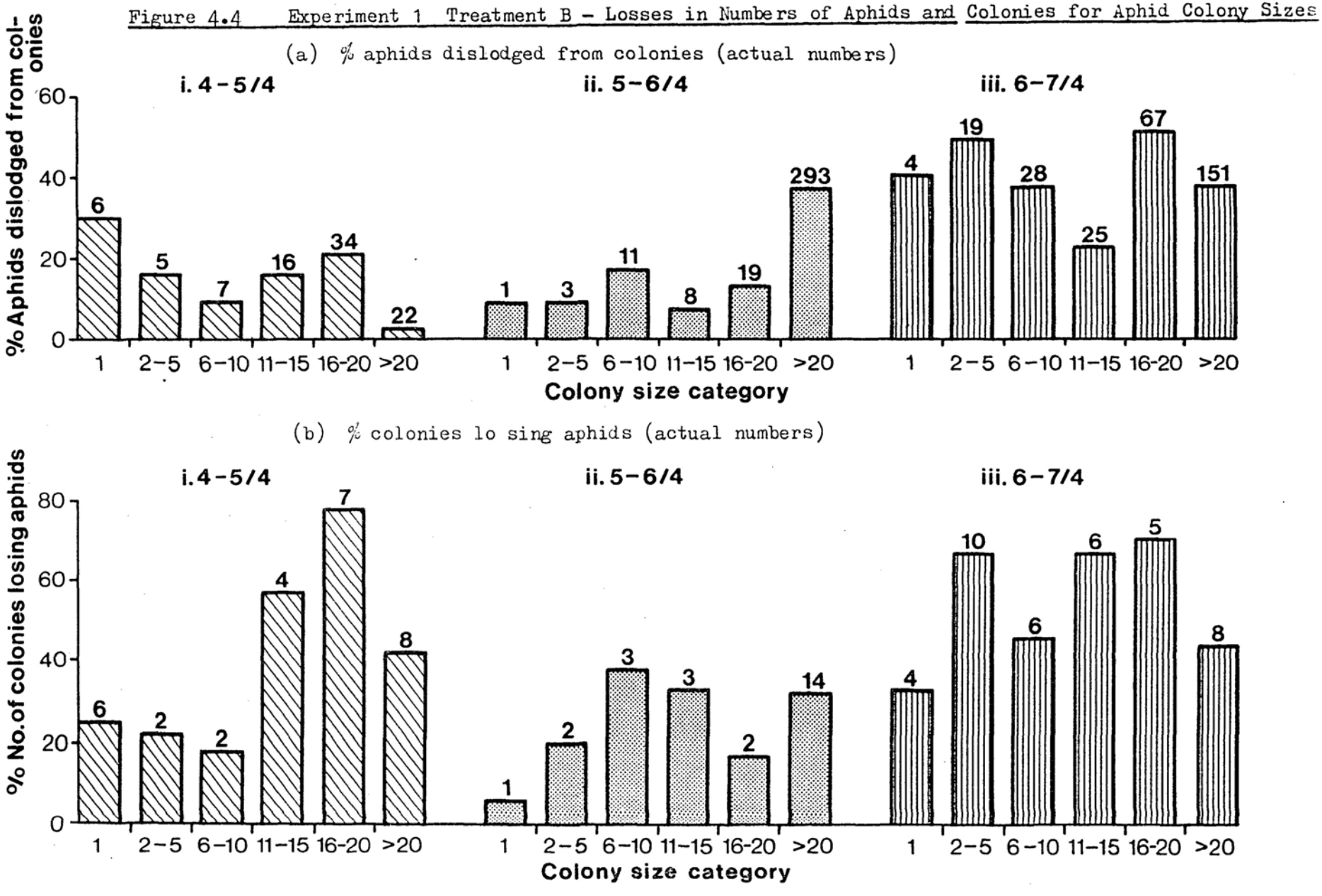
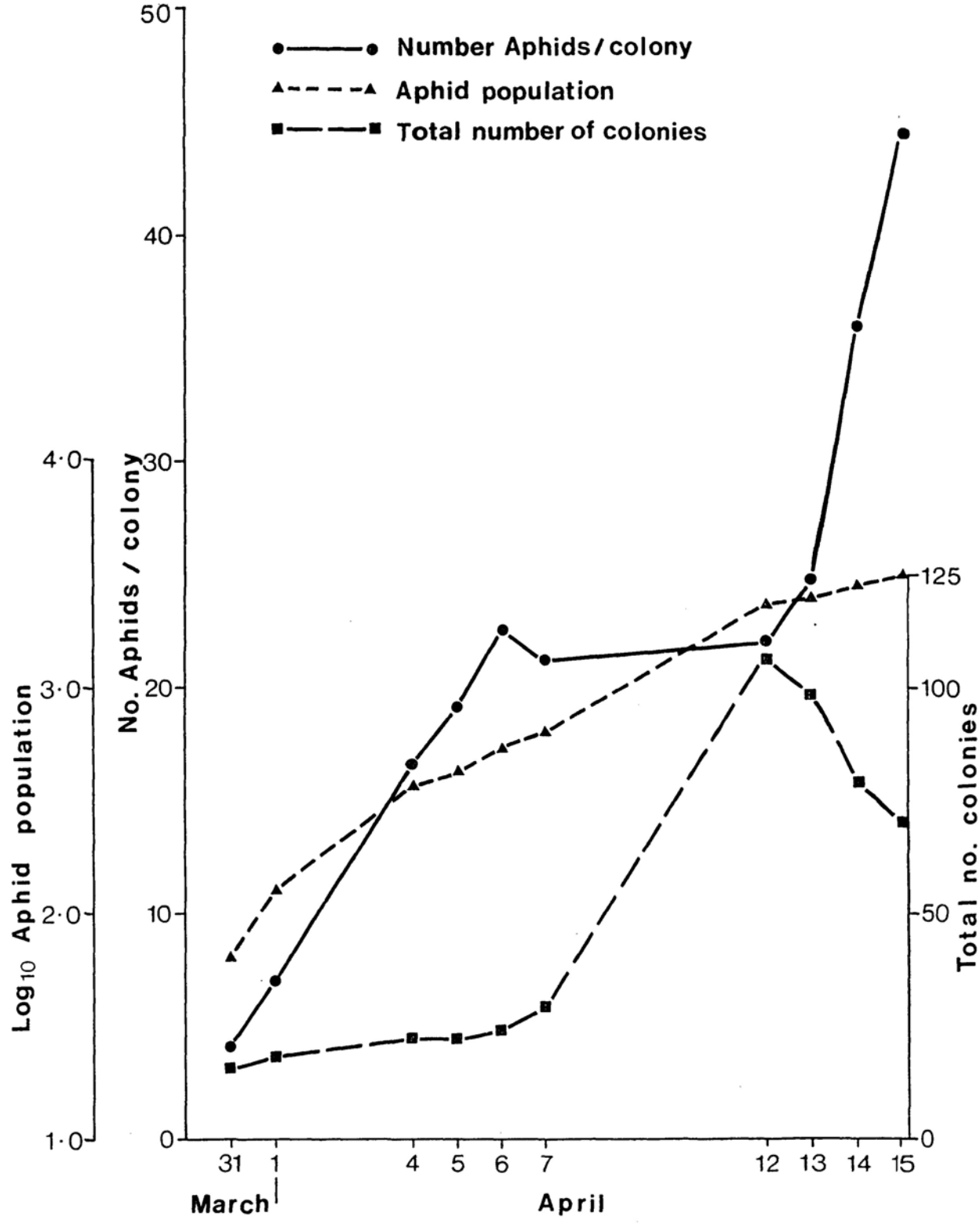


Figure 4.5 Experiment 1 Treatment C - Aphid Colony Development on Wheat in the Glasshouse



new colonies. Subsequent reproduction resulted in the coalescing of colonies and the disruption of colony structure as the leaves became increasingly crowded.

Discussion

The results from treatment A showed that newly established aphid colonies were particularly prone to dislodgement by wind and rain but that they quickly acclimatized to the adverse conditions. This implies that wet and windy weather in early summer will hinder the establishment of aphid colonies from immigrant alatae but once established these will remain unmoved.

In treatment B, the larger colonies tended to fragment in the wind, and aphid dislodgement was also greater than in the smaller, less crowded colonies. Rain dislodged aphids to a greater extent than wind but, in contrast to the effect of wind, numbers dislodged were not related to colony size.

In both treatments adults were dislodged to a greater extent than nymphs presumably because of their larger size.

Reproduction by apterae evidently occurred while the plants were exposed to the weather, as illustrated by a few colonies that substantially increased in size. Losses of aphids were not corrected for numbers that may have been produced and dislodged before being sampled and thus dislodgement was likely to have been somewhat underestimated. However, aphid reproductive rate was probably low in the low temperatures and adverse conditions prevailing and thus the error incurred in ignoring the effect of reproduction was small, and would not be likely to affect the overall conclusions drawn.

Aphid population growth and colony development in treatment C (figure 4.5) showed the point at which voluntary movement of aphids occurred in response to crowding. Adult apterae produce discrete colonies of mother aphid and offspring which remain intact until the first generation of nymphs produced has matured. At this point, the new adults move from the colony to find a new feeding site, or if alatae, to fly away, and are obviously prone to dislodgement; hence aphid dispersal is likely to be greatest at this phase. The point at which voluntary movement can be expected to have an important influence in population dispersal in the field depends on the developmental time of the nymphs (about $7\frac{1}{2}$ days in treatment C) and by the same token, the population level at which voluntary movement mostly takes place depends on the number of progeny produced in this time i.e. maximum colony size (22 aphids/colony in treatment C). The connection between this and Wyatt and White's (1977) determination of aphid r_m values is immediately apparent, since by their calculation the intrinsic rate of natural increase (r_m) equals a constant (0.74) multiplied by the log. of the number of progeny produced in the aphid's developmental time, d (Md) divided by the developmental time (d). Indeed, for treatment C, calculation of the expected rate of increase from the peak colony size (i.e. Md = 22) and time taken to reach it (i.e. d - $7\frac{1}{2}$ days) gives a daily rate of increase (r = 0.305) approximately equal to the actual rate of increase observed (r = 0.307). Thus it can be concluded that, although environmental conditions are different in the field compared with treatment C, voluntary movement of aphids in the field may be linked with their intrinsic rate of natural increase (r_m).

(ii) Experiment 2

Effect of Simulated Rain on Aphid Colonies

Introduction

The effect of rainfall a l o n e on the dislodgement of aphids from colonies was investigated by applying a water spray to aphids on mature wheat plants and noting the aphid numbers dislodged.

Materials and Methods

A watering-can rose attached to the end of a hosepipe, which was secured about 1.3 m above the ground, produced a water spray giving the effect of rainfall. Well established colonies of S. avenae on the ears, flag leaves and lower leaves of mature wheat plants 80 cm high were placed underneath the rose and aphid numbers dislodged were noted after application of the simulated rain for successive short intervals of time.

Three treatments were used. Heavy rain was simulated by directing the water spray downwards over the plants. The momentum of the water droplets striking the aphids and the plant was considerable since droplets were ejected from the rose under pressure and velocity was also gained from their descent under gravity. Light rainfall was simulated by pointing the spray upwards and allowing the water droplets to fall gently under gravity (distance from plant to maximum spray height was about 180 cm). Under natural conditions most rain strikes the plant at an angle and this was achieved in the present experiment by directing a spray of water, produced by a spray nozzle attachment, horizontally and placing a plant with aphids in its path (about 2 m away) such that the rain struck the plant at an angle of approximately 45°.

The rainfall was measured by a collecting vessel, 12.7 cm in diameter, under the spray near the plant, but the amount of water collected was purely a comparative measure of the rainfall striking the plant (table 4.4(a)).

Results

Simulated heavy rain was applied for one minute and then a further five minutes. Initially, it affected a greater proportion of colonies in the ear than in the flag or lower leaves (table 4.4(b)), but there was little difference in the proportions of aphids dislodged. However, after a further five minutes of rain, aphid losses were greatest from the lower leaves (table 4.4(b)). Moreover, percentages of aphids dislodged and colonies affected in the exposed ear and flag leaf were independent of colony size (figure 4.6(a) and (b), (i) and (ii)), but aphid dislodgement from the more sheltered lower leaves tended to increase with colony size (figure 4.6 (a) and (b), (iii)).

Light rain applied over 10 and 20 minutes affected few colonies and dislodged a negligible proportion of aphids even when applied over 20 minutes (table 4.4(d)).

Finally, moderate rain at an angle had a greater overall effect on numbers of colonies and aphids on the evidently more exposed flag leaf than on the ear (table 4.4(c)). Indeed, in this treatment the pattern of aphid losses was the reverse of the heavy rain treatment. Aphid dislodgement on the flag leaf was independent of colony size (figure 4.7(a) and (b), (ii)) and was generally higher than on the ear, where aphid losses increased with colony size (figure 4.7(a) and (b), (i)).

Table 4.4 Experiment 2 Effect of Simulated Rain on Aphid Colonies

a Relative Amounts of Rain Applied

Rainfall	Amount mm	Duration min	Rate mm/min
1. Heavy	320	1	320
2. Moderate	260	1	260
3. Light	340	20	17

b Effect of Heavy Rain

Part of Plant	% Colonies Affected By Rain After		% Aphids Dislodged After			
			1 min		5 mins more	
	1 min	5 mins more	Apterae	Nymphs	Apterae	Nymphs
Ear	89 (8)	0	50 (2)	48 (37)	0	0
Flag Leaf	73 (22)	10 (3)	50 (2)	36 (60)	50 (1)	12 (13)
Lower Leaf	59 (55)	34 (32)	33 (2)	48 (241)	0	27 (72)

c Effect of Moderate Rain from the Side (1 minute only)

Part of Plant	% Colonies Affected By Rain	% Aphids Dislodged	
		Apterae	Nymphs
Ear	50 (14)	64 (14)	39 (111)
Flag Leaf	82 (9)	82 (26)	72 (283)

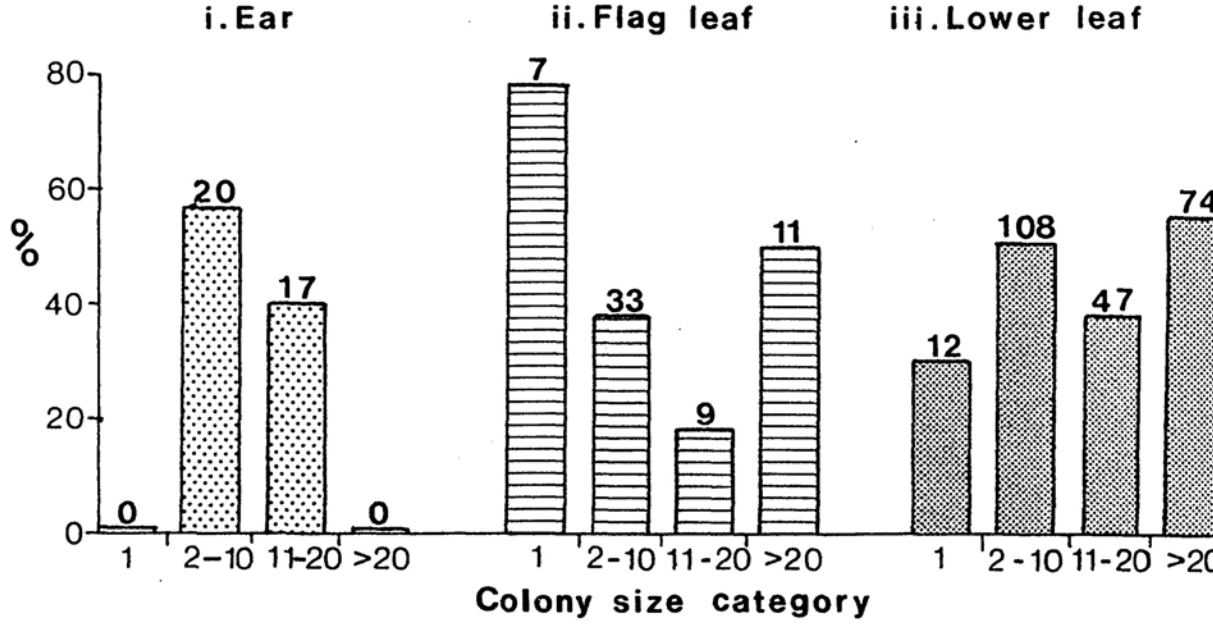
d Effect of Light Rain

Part of Plant	% Colonies Affected by Rain		% Aphids Dislodged			
			10 mins		20 mins	
	10 mins	20 mins	Apterae	Nymphs	Apterae	Nymphs
Ear	8 (4)	4 (2)	0	2 (5)	0	0
Flag Leaf	14 (1)	0	0	2 (1)	0	0

Actual numbers in parentheses

Figure 4.6 Experiment 2 1. Effect of Heavy Rain on Aphid Colonies Taking into Account Part of Plant and Colony Size

(a) % aphids dislodged from colonies (actual numbers)



(b) % colonies lo sing aphids (actual numbers)

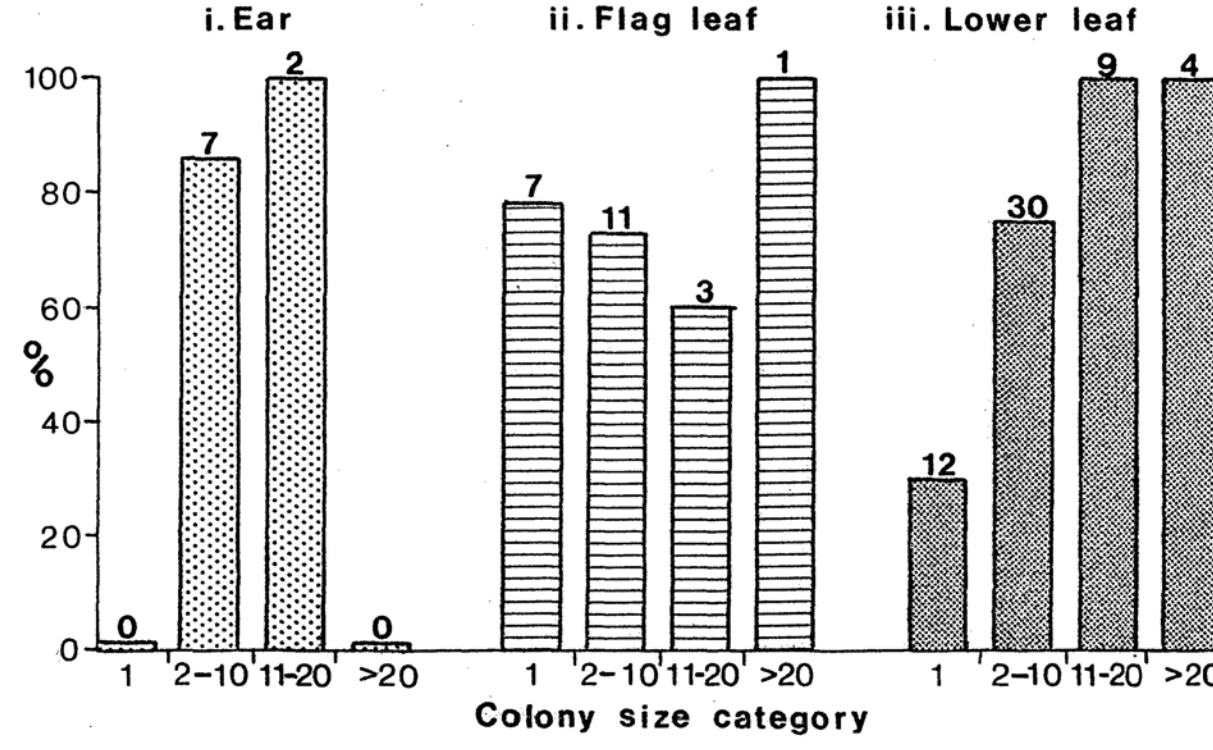
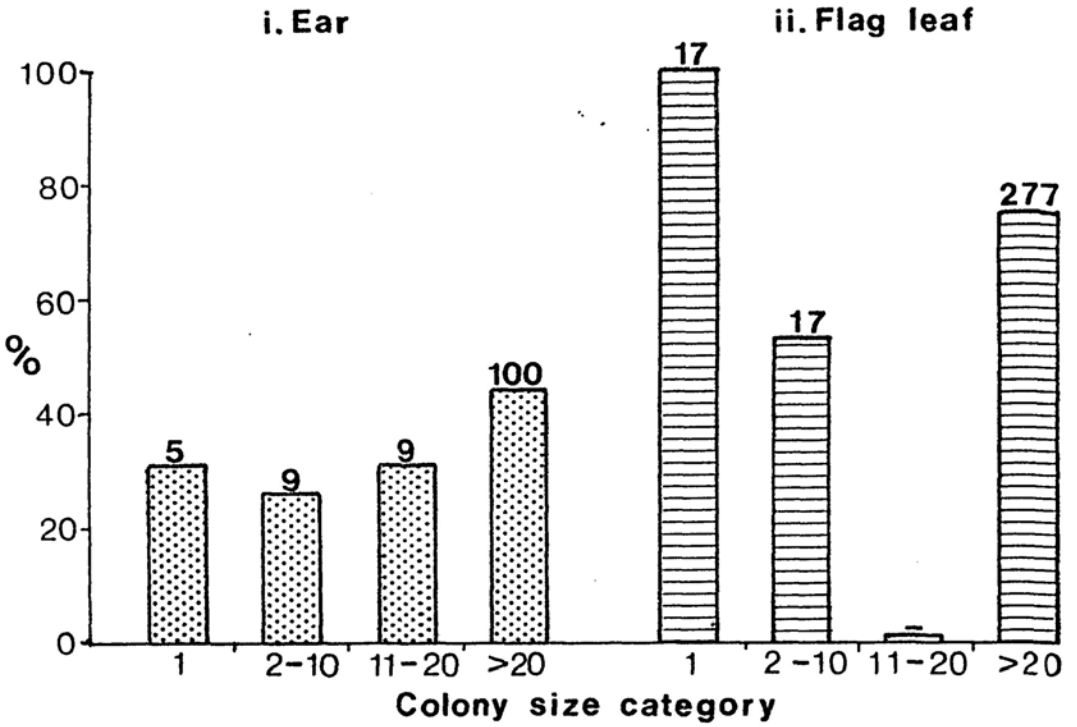
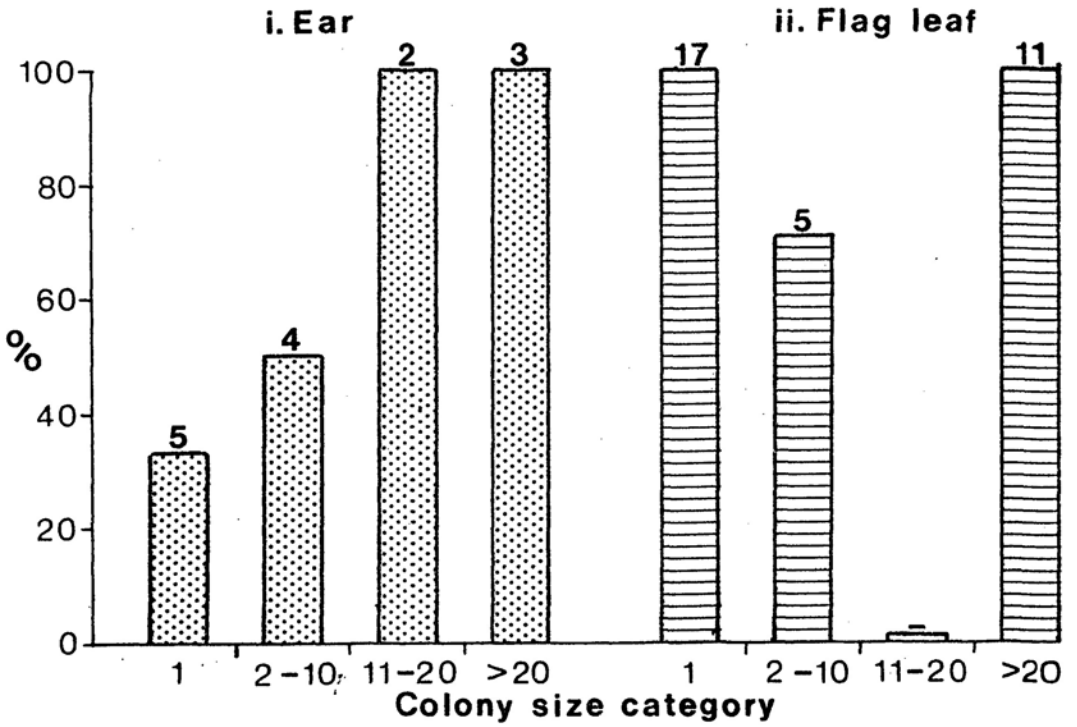


Figure 4.7 Experiment 2 2. Effect of Moderate Rain on Aphid Colonies Taking into Account Part of Plant and Colony Size

(a) % aphids dislodged from colonies (actual numbers)



(b) % colonies loosing aphids (actual numbers)



Discussion

Shelter had a marked effect on the pattern of aphid losses resulting from the simulated heavy and moderate rainfall. The degree of shelter offered by the various parts of the plant depended on the angle at which the rain was incident on the plant. With rain directly overhead only the lower leaves of the plant had any degree of shelter, as might be expected, but rain at an angle produced a sheltered area in the shadow side of the ear. On areas of the plant exposed to the direct effect of the rain aphids were dislodged independently of colony size, which was also seen with the exposed leaves of experiment 1, whereas in the sheltered areas, proportionally more aphids were dislodged from the larger colonies. Moreover, heavy rain had little further effect on aphid dislodgement after its initial impact.

(iii) Experiment 3

Aphid Dislodgement in the Field

Introduction

Two aspects of the spread of aphids through the field were investigated in the field experiment in 1977. The effect of rain on aphid populations and average colony size in the field plots early in the season was examined from aphid samples before and after a rainstorm. Secondly, sticky traps were erected in caged and uncaged plots to assess numbers of aphids falling to the ground at the population peak and during the decline of aphids in the field.

(a) Effect of a Rainstorm on Aphid Populations Early in the Season

Materials and Methods

A severe thunderstorm on June 13th, 1977 prevented aphid sampling for half of the day, sampling being continued on June 15th. Thus most

plots were partly sampled on June 13th and partly on the 15th. The effect of the rainstorm on aphid dislodgement was investigated from the comparison of average colony size on June 13th and 15th, before and after the rain and from the comparison of expected aphid population on June 15th with numbers sampled. The expected population was calculated by multiplying aphid numbers per plot on June 13th by the mean increase rate per day over the period May 30th–June 20th for each plot.

Results

A large amount of rainfall fell in a short time on June 13th and the wind was also strong (table 4.5). However, a reduction in colony size which could have been expected to result from this severe weather

Table 4.5 Experiment 3 Weather Conditions Over the Period of the Test

Date	Rainfall mm/day	Average Wind Speed Over 24 hrs ms^{-1}	Temperature °C	
			Maximum	Minimum
12th June	14.3	4.5	15.9	7.2
13th June	16.8	5.1	21.2	11.8
14th June	0	3.3	18.2	13.9
15th June	0	3.3	13.5	11.7

did not occur (table 4.6). Moreover, although the overall mean number of aphids was reduced by 21% (expected compared to observed) the difference between expected and actual numbers of aphids was no greater than that due to chance (table 4.6). Evidently, the variation within the samples for each date was greater than the difference between expected and observed numbers i.e. the differences were merely a result of natural variation.

Table 4.6 Experiment 3

Effect of Rainfall on Aphid Colony Size and Population Level in the Crop

Plot	No. Aphids Per Colony		No. Aphids Per 100 Tillers	No. Aphids Per 100 Tillers 15/6		Rate Increase Per Day
	13/6	15/6	13/6	Actual	Expected	30/5-20/6
H1	3.62	4.23	29.0	48.0	39.3	1.164
M1	6.41	2.92	109.0	20.5	153.5	1.187
N1	2.60	6.16	6.5	37.0	9.3	1.197
H2	5.96	5.42	107.0	65.0	159.5	1.221
M2	8.28	4.33	38.7	39.0	71.7	1.361
N2	2.44	4.66	11.0	14.0	15.1	1.170
H3	3.59	4.27	66.5	79.0	94.0	1.189
M3	3.84	4.50	96.0	72.0	69.0	1.199
L3	5.50	5.71	58.7	183.0	93.5	1.262
N3	3.93	2.33	21.0	21.0	28.8	1.170
Means	4.62	4.87	54.3	57.8	73.4	1.170
% Difference	+5.5			-21.2		
Paired t Test	0.223			0.793		
DF	9			9		
Significance	$p>0.8$ n.s.			$p<0.5$ n.s.		

Discussion

The comparisons show that heavy rainfall and strong winds did not significantly influence either the aphid colony size or population density

early in the season. This was probably due to two factors. The small number of aphids present were probably in sheltered positions in the ear, and the rain and low temperature the previous day (table 4.5) would have acclimatized the aphids to some extent.

(b) Catches of Aphids in Sticky Traps

Materials and Methods

Aphids and other cereal arthropods were caught on sticky traps placed in several of the experimental plots in the 1977 field experiment. The sticky traps, four in number, consisted of a wooden frame, 1.06 m x 24 cm, with a sheet of polythene attached, upon which was spread a solution of sticky polybutene. Wooden legs were attached to two of the traps to raise them 30 cm from the ground. The traps occupied about three-quarters of the width of the transect and were adjacent to approximately 85 tillers. The traps were placed leeward with respect to the prevailing wind and the raised traps were about one-third of the height of the crop.

Results

Where traps at ground level and raised on legs were placed in the open field in the same transect or in similar treatments more aphids were caught on the raised (H) than the ground level (L) traps (e.g. July 11th-12th, H3 (H) - 401, H1 (L) - 360, July 12th-15th, N4 (H) - 548, N4 (L) - 227). However, in the cage (H2) roughly equal numbers of aphids were caught in the raised and ground level traps (table 4.7(a)). Catches of parasites and diptera did not show consistent differences between raised and ground level traps.

In the open field, the bulk of aphids caught were nymphs, together with a few apterae, but in the cage, substantial numbers of alatae were caught (table 4.7(b)), having been trapped in the cage covers.

Table 4.7 Experiment 3

a Catches of Insects in Sticky Traps

Dates	Plot	Total No. Aphids	Parasites	Miscellaneous Diptera
11th–12th July	H2 L	420	20	8
	H1 L	360	1	85
	H3 H	401	14	132
	N7 H	304	2	28
	N6 L	184	9	145
12th–15th July	N6 L	268	13	100
	N4 H	548	4	6
	N4 L	277	5	249
	H2 H	1312	31	4
15th–19th July	N7 H	90	9	145
	N4 L	140	3	35
	H2 L	1289	40	6
	H2 H	1182	105	4

Key:- L – Trap at Ground Level
H – Trap Raised 0.3 m from Ground

b % Composition of Aphid Population Caught

Dates	Average of Uncaged Plots			Average of Cage		
	Alatae	Apterae	Nymphs	Alatae	Apterae	Nymphs
11th–12th July	5.4	10.9	84.7	54.3	7.4	38.3
12th–15th July	8.3	13.5	78.2	34.0	9.4	56.6
15th–19th July	16.5	10.4	73.0	44.3	1.1	54.6

c % Aphids Dislodged From Plants

Dates	Uncaged Plots				Cage			
	Total	Al.	Ap.	Nym.	Total	Al.	Ap.	Nym.
11th–12th July	10	47.8	18.2	8.9	1.5	33.0	3.0	0.7
12th–15th July	24	—	—	—	5.5	27.4	2.2	2.7
15th–19th July	100	—	—	—	3.0	26.0	4.4	2.0

Key:- Al. – Alatae; Ap. – Apterae; Nym. – Immature Nymphs

However, numbers trapped as a percentage of those on the plants (table 4.7(c)) showed that, in both open field and cage plots proportionally more alatae were dislodged than apterae or nymphs. In addition, in the open field, percentage dislodged increased as the aphid population decreased i.e. numbers of aphids dislodged decreased less rapidly than numbers on the plants, but in the cage the percentage dislodged did not increase greatly because the aphid population on the plants was not decreasing rapidly.

Discussion

The differences in catches of aphids in the open field on raised and ground level traps were probably due to the angle of descent of the dislodged aphids. When dislodged from the ears and flag leaves of the plants by the weather, aphids are likely to have a strong lateral component to their descent to the ground and thus raised traps will intercept a greater number of falling aphids before they reach ground level traps. In the cage, where the wind velocity was reduced and aphids were also present on the lower leaves of plants, aphids fell vertically and were caught in equal numbers by raised and ground level traps.

Percentage aphids dislodged from plants (table 4.7(c)) showed that the larger adult aphids were more prone to dislodgement than the smaller nymphs, presumably because of their greater size. This was in agreement with the results of experiment 1, treatments A and B, where again proportionally more adult aphids were dislodged than nymphs. However, in the field, behavioural factors may also have been of importance since the alatae were potential migrants about to take off and apterae may have been moving voluntarily which was not the case in experiment 1.

As the aphid population in the open field decreased proportionally more aphids were dislodged, indeed, aphids were observed restlessly moving over the ears while the decreasing populations were being sampled. This may have been due to two factors. Firstly, the aphids are liable to get more restless as the plant matures and becomes less favourable, and secondly, predators will tend to disturb and dislodge many aphids. Inside the cage, the proportion dislodged was less because aphids were protected from the wind and predators.

(iv) Discussion

Experiment 1 showed that once aphids have acclimatized to the effects of weather, numbers dislodged are independent of the severity of wind and rain. Thus it seems to be the shock effect of a change in conditions from calm to windy, dry to rain, which produces the mechanical dislodgement of aphids. Where the shock is mild as with wind, numbers of aphids blown off increase with the crowding effect of colony size, but with the severe shock of rain (usually accompanied by low temperature) all aphids in exposed positions were vulnerable to dislodgement.

The direct action of wind and rain is modified by the effect of shelter. Thus, even in the extreme simulated rainfall of experiment 2, aphids were sheltered to some extent from the effect of the rain. Shelter in the crop is greater than with individual plants and probably accounted for the lack of effect of the rainstorm early in the season.

Obviously, continued severe weather will produce increased dislodgement of aphids, as in experiment 1, treatment B, but periods of rain will have a proportionally greater effect at high aphid numbers than low numbers. Thus, widespread dislodgement of aphids in the field

has only been observed at high aphid populations (Wadley, 1931, Dunn and Wright, 1955, A. Dewar, personal communication).

In 1977, population dispersal through the field was mainly a result of immigration and voluntary movement since dislodgement of aphids by the weather was small. The spread of aphid colonies through the field can be seen from the relationship between percentage infestation and number of colonies per 100 tillers (section 4, figure 4.8). Immigration of alatae produced the initial colonisation of the crop and thus early in the season percentage tiller infestation was directly proportional to the number of colonies present i.e. one colony/tiller. As the aphid population increased, the number of aphid colonies increased faster than the number of tillers infested and thus new colonies tended to occur on tillers that already had aphids. Hence, at the population peak in 1977 there was an average of 2.7 colonies per tiller. Moreover, in both 1976 and 1977 field experiments, complete coverage of the field by aphids, i.e. 100% tiller infestation only occurred at the time of peak aphid numbers. The distribution of aphid colonies and its increase with aphid population increase lends support to the hypothesis that voluntary movement of aphids was mainly responsible for aphid dispersal in the field experiments. Indeed, in the hot summer of 1976, when rate of aphid increase was high, aphid dispersal was correspondingly fast, and in 1977, with a lower rate of increase, aphid dispersal was slower. This provides corroborative evidence for the association between voluntary movement of aphids and their increase rate which was postulated from experiment 1, treatment C.

Movement of aphids was greatly increased around the time of the population peak because of the production of the new generation of aphids

from the existing colonies. This in itself tends to increase aphid movement, as described from treatment C, experiment 1, the more so, because the adults produced are mostly alates which move to the tops of plants to fly away. Moreover, the deterioration of plant suitability to aphids with ripening (Watt, 1979) would also tend to promote aphid movement. Aphid specific predators are also common in the field at this time and their searching behaviour tends to dislodge aphids (Dixon, 1958) and increase their movement between plants (Tamaki, Halthill and Hathaway, 1970, Roitberg and Myers, 1978, Roitberg, Myers and Frazer, 1979). This is confirmed by the observations of the restlessly moving aphids as populations declined in 1977 and by the increase in the percentage aphids caught in sticky traps.

Conclusions

Population dispersal of aphids within a field is risky and therefore the aphids tend to minimize the time spent moving as far as possible. Conditions favourable for aphid population increase produce an aphid 'outbreak' (Jones, 1979), and when this occurred in the 1976 and 1977 field experiments, the aphid population in the field was remarkably stationary, only occupying all the plants at peak populations. Aphids are initially well sheltered from the adverse effects of inclement weather and little movement occurs. However, disruptive influences increase as aphid populations increase (crowding results in proportionally greater dislodgement from weather and in more voluntary movement) and after the aphid population peak and lead to an unstable, restless population. At this stage, natural enemies and weather dislodge increasing numbers of aphids which undoubtedly causes great mortality. Aphids moving at this time are trying to escape adverse conditions and would not necessarily

display the same plant searching behaviour as the aphids which disperse to new plants, outlined in the next section.

In some instances, notably in 'non-outbreak' years, aphids disperse widely through the crop at relatively low population densities. However, the reason for this could hardly be, as Dean (1973b) suggested, that 'a static and gregarious aphid would rapidly destroy the infested tiller', since aphids reached very high numbers in the cages and field plots of the 1976 and 1977 field experiments and the plants, although reduced in yield, were not destroyed. Moreover, other aphid species in favourable conditions will indeed multiply to numbers sufficient to destroy the host plant, for example, Aphis fabae on field beans (Way and Banks, 1967). The increased mobility or 'restlessness' of S. avenae and M. dirhodum observed by Dean (1973b), compared to the present account, may be because the spring cereal crops used were intrinsically less palatable than winter wheat, in the same way that Myzus persicae is more restless on less palatable chrysanthemum varieties (Wyatt, 1969), and may also be because the environmental conditions were less favourable for rapid population growth.

Thus, behavioural characteristics displayed by cereal aphids were generally more important in determining the extent of aphid movement within a crop, than the direct effect of physical dislodgement by wind or rain. These behavioural characteristics included:-

(1) Selection of a sheltered niche on the plant. For S. avenae this was under the arch of a bending leaf, or at the base of the florets in the wheat ears.

(2) Increase in voluntary movement with crowding.

(3) Avoidance of predators.

(4) Acclimatization to occasional adverse conditions.

(5) 'Restlessness' in adverse conditions.

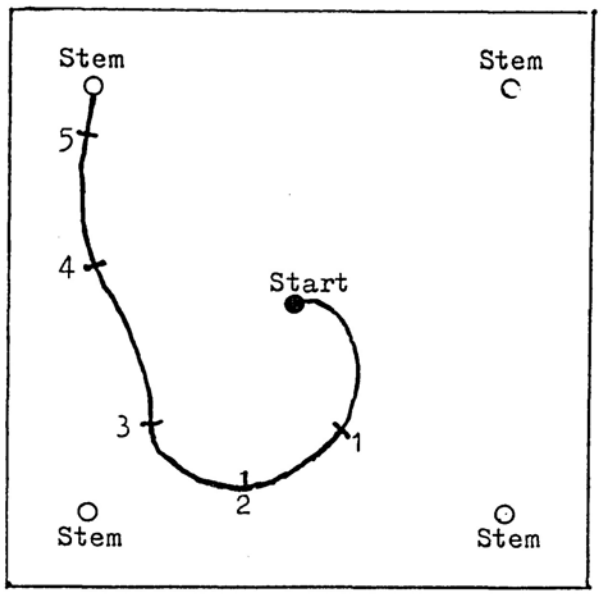
4.3 Walking Behaviour of Cereal Aphids

Materials and Methods

Walking aphids were observed searching for a plant on an arena of smooth card with a wheat stem at each corner. The card was 35 cm square and the four wheat stems protruded through holes 5 cm in from the edge thus allowing aphids approaching from any angle the opportunity to climb up a stem. The light was provided by a fluorescent light 45 cm directly overhead to avoid any directional bias and the experiment was carried out in a constant temperature room (18–20°C).

The test aphid was released from the centre of the board $17\frac{1}{2}$ cm equidistant from each stem, and its path was traced by a pencil mark on the card until it reached a stem. The location of the aphid every 30 seconds was also marked on the card and the total time spent moving was recorded by a stopwatch. The walking behaviour of the aphid was then quantified from the path traced on the board. The distance that the aphid walked between successive marks was recorded and the relative direction in which the aphid was moving was given by a compass bearing with eight subdivisions, the observer facing North. A 'turn' was defined as a difference in compass direction of movement between successive marks and 'turns' were measured in units of 45°, corresponding to differences in compass direction of movement, and whether executed clockwise or anticlockwise from the previous direction of movement.

Example of path of aphid:-



This would be recorded as:-

30 Second Marker	Distance	Compass Direction	Turn
1	11.5 cm	S.	45° C
2	8.0 cm	S.W.	90° C
3	9.0 cm	N.W.	
4	13.0 cm	N.W.	45° C
5	10.0 cm	N.	
10 secs	2.0 cm	N.	

Variables Calculated

1. Distance - 53 cm.
2. Time walking - 2.67 cm.
3. Av. speed - 19.9 cm/min.
4. Number of turns - 3.
5. Distance between turns - 13.25 cm.
6. Response to plant - 2 cm.
7. Total angle clockwise - 180°.
8. Number of turns clockwise - 3.

Key:- C - Clockwise

The first four variables are self explanatory. The distance between turns was the total distance travelled divided by the number of turns plus one. The distance for response to a plant was the distance from which the aphid seemed to detect a stem and move

straight to it. Although this measure was somewhat subjective, most aphids showed a definite response to a stem before climbing it and the variable gave a measure of the strength of visual response to the plant. Angle turned was summed for clockwise and anticlockwise directions and number of turns were also calculated for each direction.

Aphids occasionally reached the edge of the card and some tended to walk along the edge - 'tramlining' - these were gently encouraged to leave the edge and if this was not successful the trial was abandoned. Most aphids did not encounter the edge of the card.

Each trial was repeated with several different aphids per treatment and means and standard errors were calculated for each class of variable.

Insects tend to be less sensitive to light of longer wavelengths (Chapman, 1969) and so, to investigate aphid walking behaviour in darkness, red light was used. Red acetate sheet was attached over a lamp to give a pool of red light 45 cm in diameter, and the light intensity was reduced by a rheostat. Thus it was possible to trace the aphid's path as before in conditions dark to the aphid.

The three common cereal aphid species were used. Small apterae of Sitobion avenae from a laboratory culture and large apterae which had been reared on wheat plants were tested and the walking behaviour of large apterae in red light was also studied. Movement of Metopolophium dirhodum apterae and alatae was studied in white light and red light. Finally, the movement of alatae and apterae of Rhopalosiphum padi in white light was studied. Most of the alatae took off and the behaviour of individuals that made short flights across the test arena was compared with those that did not land back in the arena.

Results

As with most behavioural experiments the experimental variability was rather high, ranging from 7% standard error of the mean for the variable of distance between turns of M. dirhodum in red light (table 4.9, line 5) to an average of 25-30% for most variables for S. avenae. Walking behaviour of aphids in dim red light was generally less variable than in white light, for example, for distance travelled by M. dirhodum apterae in white light the standard error was $\pm$ 15% of the mean, in red light it was $\pm$ 10%. However, although the direction of turning was fairly consistent within each trial, the summed angle of turn clockwise and anticlockwise was particularly variable within treatments.

A total angle turned of 360° in one direction indicated that the aphid had moved in a complete circle. As the aphid tended to move outwards from the centre while turning this resulted in a spiral path.

Bearing in mind the proviso of high within-treatment variability, general conclusions can be drawn about the tendency of aphid species to display a characteristic walking behaviour.

(a) Sitobion avenae

The larger aphids walked at a similar speed to the smaller aphids but they tended to walk further and made more turns before reaching a stem (table 4.8, lines 1&4). Aphids in all the treatments tended to have an anticlockwise bias in the turns made and this was most pronounced with the small apterae. Although large apterae seemed to respond to a stem from a greater distance than the small apterae they still spent more time finding a stem.

TABLE 4.8 WALKING BEHAVIOUR OF SITOBION AVENAE

Variables	White Light		Red Light
	Small Apterae(5)	Large Apterae(5)	Large Apterae(5)
1. Distance travelled cm	60.70 ± 15.22	119.6 ± 30.49	205.1 ± 54.23
2. Time walking min	3.82 ± 1.17	6.92 ± 1.62	8.42 ± 1.54
3. Average speed cm/min	16.97 ± 1.35	18.00 ± 2.44	23.42 ± 3.69
4. Number of turns	4.40 ± 1.25	9.6 ± 2.25	11.0 ± 2.43
5. Distance between turns cm	11.28 ± 1.58	11.7 ± 1.62	16.56 ± 1.87
6. Distance for response to plant cm	2.00 ± 0.27(3)	6.0 ± 1.1 (3)	2.70 ± 0.66
Total angle turned:			
7. Clockwise - degrees	54.0 ± 33.1 (1)	270 ± 51 (1)	378 ± 149
8. Clockwise - number of turns	0.8 ± 0.37(2)	3.60 ± 0.51(2)	4.8 ± 1.66
9. Anticlockwise - degrees	288 ± 147	468 ± 164	504 ± 162
10. Anticlockwise - number of turns	3.2 - 1.59	6.0 - 2.17	6.2 - 2.2

Variables with same number in brackets significantly different $p<0.05$ from comparison of confidence interval limits

The number of turns (y) made by individual apterae in all the treatments was linearly related to the distance walked (x):

$y = 0.046 + 2.451 \quad r = 0.872 \quad DF = 13 \quad p \leq 0.001$

The walking behaviour of the large apterae in the dark did not differ greatly from their walking behaviour in the light. Aphids tended to walk further before finding a plant but did not take much extra time as they walked faster. More turns were executed but aphids tended to walk further between turns in the dark, perhaps because of their greater walking speed. The anticlockwise bias to the turning movements was also reduced.

(b) Metopolophium dirhodum

When aphids of this species were placed in the centre of the arena they sometimes remained still for several minutes. This was a 'thanatosis' or death feigning reaction. If aphids did not start to walk after five minutes they were replaced.

Alatae and apterae had similar plant finding behavioural characteristics when walking in light (table 4.9). Thus, distance walked to the plant, average speed, number of turns and distance between turns were approximately the same and both turned in a clockwise direction more often than anticlockwise. The aphids were fairly efficient at finding a stem as seen from the short distance walked and small number of turns made and this was probably due to their good visual perception of the upright stems. The importance of vision was underlined by the aphid's behaviour in the dark. Both alatae and apterae walked significantly further, turned more often, responded to the stem from a shorter distance before climbing it. Moreover, walking speed was slightly slower and rate of turning (as

TABLE 4.9 WALKING BEHAVIOUR OF METOPOLOPHIUM DIRHODUM

Variables \ Treatments (no. replicates)	White Light		Red Light	
	Apterae (10)	Alatae (10)	Apterae (5)	Alatae (5)
1. Distance travelled cm	47.65 ± 7.31(1)	43.75 ± 5.69(2)	127.6 ± 12.75(1)	121.10 ± 24.81(2)
2. Time walking min	3.14 ± 0.50	2.33 ± 0.30	8.89 ± 1.09	8.28 ± 1.27
3. Average speed cm/min	16.11 ± 1.52	19.58 ± 1.14	14.66 ± 1.14	14.27 ± 1.43
4. Number of turns	2.60 ± 0.45(3)	2.70 ± 0.47(4)	9.00 ± 0.84(3)	11.80 ± 1.77(4)
5. Distance between turns cm	14.00 ± 1.96	13.03 ± 1.93	12.80 ± 0.94	9.40 ± 1.44
6. Distance for response to plant cm	5.45 ± 1.22(7)	4.70 ± 0.78(8)	2.10 ± 0.24(7)	1.80 ± 0.12(8)
Total angle turned:				
7. Clockwise - degrees	144 ± 40.7	130.5 ± 41.1	306 ± 26	198 ± 27 (5)
8. Clockwise - number of turns	1.8 ± 0.44	1.6 ± 0.4	4.4 ± 0.6	3.4 ± 0.5 (6)
9. Anticlockwise - degrees	54 ± 17.5	90.0 ± 21.2	360 ± 55	612 ± 123.7 (3)
10. Anticlockwise - number of turns	0.8 ± 0.2	1.1 ± 0.28	4.6 ± 0.4	8.4 ± 1.4 (6)

Variables with same number in brackets significantly different $p<0.05$ from comparison of confidence interval limits

indicated by the lower distance between turns) was greater in the dark. Directional preference for turning also changed in the dark; apterae covered nearly a circle in both clockwise and anticlockwise directions, but alatae consistently turned in an anticlockwise direction.

As above, the number of turns made (y) increased linearly with distance walked (x):

$y = 0.080x - 0.542 \quad r = 0.883 \quad DF = 28 \quad p < 0.001$

(c) Rhopalosiphum padi

Unlike M. dirhodum, all the alatae that were tested took off at some stage; those that made short flights merely flew for a few seconds before alighting back on the arena, but more commonly, the alatae took off after a short distance and flew towards the light. Alatae making short flights across the arena had similar pre-flight walking characteristics to apterae, but those alatae that flew away tended to turn more frequently, as inferred from the shorter distance between turns (table 4.10). Both categories of alatae tended to turn clockwise more often than anticlockwise but with apterae the converse was true (table 4.10).

As with the other aphid species, there was a linear relationship between number of turns made (y) and distance walked (x):

$y = 0.086x + 0.837 \quad r = 0.831 \quad DF = 19 \quad p < 0.001$

Discussion

Certain apsects of cereal aphid walking behaviour seemed to be fairly constant between species and therefore may be an intrinsic component of aphid behaviour. In particular, the tendency to turn was relatively consistent between the species, distance between turns being fairly constant

TABLE 4.10 WALKING BEHAVIOUR OF RHOPALOSIPHUM PADI

Variables	Apterae(10)	Alatae	
		Short Flights(4)	Flight Off Arena(7)
1. Distance travelled cm	74.85 ± 16.27(1)	61.38 ± 12.27(2)	22.79 ± 2.59(1)(2)
2. Time walking min	11.03 ± 2.32	10.29 ± 1.86	5.58 ± 0.91
3. Average speed cm/min	7.32 ± 0.82(3)	5.89 ± 0.57	4.53 ± 0.66
4. Number of turns	6.40 ± 1.77	7.00 ± 2.48	3.43 ± 0.43
5. Distance between turns cm	11.33 ± 1.33(4)	12.01 ± 4.85	5.22 ± 0.51(4)
6. Distance for response to plant cm	3.25 ± 0.75	2.25 ± 0.25	
Total angle turned:			
7. Clockwise - degrees	166.5 ± 91.9	292.5 ± 142.9	122.1 ± 21.3
8. Clockwise - number of turns	2.8 ± 1.41	4.75 ± 2.06	2.29 ± 0.36
9. Anticlockwise - degrees	238.5 ± 60	213.7 ± 131.7	70.71 ± 35.2
10. Anticlockwise - number of turns	3.7 ± 0.93	2.25 ± 1.65	1.14 ± 0.59

Variables with same number in brackets significantly different $p<0.05$ from comparison of confidence interval limits

(11.7, 14 and 11.3 cm/turn for S. avenae, M. dirhodum and R. padi apterae respectively), and increase in number of turns with distance walked was also similar (slopes for relationship between number of turns and distance walked were, 0.046, 0.080 and 0.086 for S. avenae, M. dirhodum and R. padi respectively). Moreover, the average angle turned (i.e. total angle turned divided by number of turns) irrespective of direction was also fairly constant (mean for S. avenae, M. dirhodum and R. padi apterae respectively was 78°, 74° and 66°).

Thus the turning behaviour seemed to be fairly constant to all the cereal aphid species but the degree to which it was expressed depended upon the length of time that the aphid took to find a stem. This was dependent on a combination of speed of walking and the strength of the visual perception of upright stems, which seemed to be unique to each species. Hence, when the visual component of plant finding behaviour was negated in dim red light (equivalent to darkness), M. dirhodum produced a radical change in its behaviour pattern, whereas S. avenae did not greatly change its walking behavioural characteristics. An olfactory response to the wheat stem could also have been involved but this possibility was not investigated.

Directional preference for turning (measured by cumulative angle turned clockwise or anticlockwise) was probably not part of an intrinsic behavioural pattern of aphids. Thus, apart from M. dirhodum alatae in dark and light conditions, there were no significant differences in total angle turned or number of turns anticlockwise or clockwise between any of the treatments. However, it was noticeable that individual aphids often turned consistently in one direction and would walk in a spiral path from the starting point until responding to a stem. Hence, a 'turn'

in one direction may be more likely to be followed by a 'turn' in the same direction than in the opposite direction. It can be argued that this would tend to increase the chances of finding a stem.

Aphid behaviour in darkness was of importance, not only for its illustration of the aphid's dependence on vision for locating plants, but also, because a decrease in the efficiency of finding a plant would increase the aphid's risk of being eaten. Indeed, there was a marked increase in the time spent searching for a plant and in the distance walked - by 3-4 times with M. dirhodum - so that the risk of predation on the ground would be proportionally greater at night. Reinforcing this is the fact that, in cereals, most ground beetles in particular (Luff, 1978) and aphid predators in general (Vickerman and Sunderland, 1975) are mainly active at night and thus predation of aphids on the ground is only likely to occur at night. However, tillers in the field are much closer together than in the experimental arena, rows being separated by about 18 cm with little space within a row, so that, even in darkness, aphids that have been dislodged could quickly locate plant stems to climb (within minutes), making predation of moving aphids on the ground an unlikely event, even at night. Hence most aphid predation is probably of stationary aphids on plants, and ground beetles would have to climb up wheat plants to find and eat cereal aphids. However, aphids that have been dislodged from plants rarely climb past the bottom two leaves (personal observation) and even large beetles such as P. melanarius have been observed scrambling over plants in laboratory cultures and thus in the tangled understory of a typical wheat crop, predation of aphids by ground beetles lower down the plant could be extensive. Thus, aphids that have been dislodged from plants are at a greater risk of predation from ground predators, albeit as an indirect consequence of their dislodgement.

4.4 Relationship Between Tiller Infestation and Aphid Populations

Introduction

Conventional models describing the increase in tiller infestation with aphid population fit an S-shaped curve (logistic) between percentage tillers infested (x) and log. number of aphids per tiller (y) using the regression method of least squares (Vereijken, 1979, figure 4.12; the plot of probit y against x is very similar to the above relationship). However, although logistic relationships for the 1976, and 1977 field data gave high coefficients of correlation, they produced a poor fit to the data at high infestation levels (figures 4.11 and 4.12). Thus an alternative phenomenological approach was adopted to derive a descriptive model, the model parameters being fitted by the method of maximum likelihood.

The linking process between aphid numbers and tiller infestation is their relationships with number of aphid colonies. Thus, equations describing the increase in tiller infestation with colony numbers and the increase in colony numbers with aphid population were combined to give a model of the increase in tiller infestation with aphid population.

Materials and Methods

In the field experiment of 1977, aphid colonies were recorded individually and the number of colonies per sample, together with the number of tillers infested was extracted from the raw data for each sampling date. Information on aphid colonies was unavailable from the 1976 field experiment but number of tillers infested was obtained from the field data.

Results

The best relationship obtained between percentage tillers infested (P) and number of colonies per 100 tillers (Z) was between $^1/P$ and $^1/Z$ (figure 4.8). For this relationship to be valid the intercept should not be significantly different from 0.01 and thus 95% confidence interval limits were calculated for the intercept and slope which showed that this indeed was the case.

From the regression of $^1/P$ against $^1/Z$:

$$^1/P = {}^1/a(^1/Z) + {}^b/a$$

$$^1/a = 0.980 \pm 0.025$$

$$^b/a = 0.00224 \pm 0.0240$$

$$r = 0.996 \quad p < 0.001$$

rearranging:

$$P = \frac{a.Z}{1 + bZ} \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(1)$$

Similarly, log. number of colonies per 100 tillers (Z) was related to log. aphid numbers per 100 tillers (N). Hence:

$$\text{In } Z = q + s \cdot \text{In } (N) \qquad \text{where } q = -0.646$$

$$s = 0.753$$

$$r = 0.981 \quad p < 0.001$$

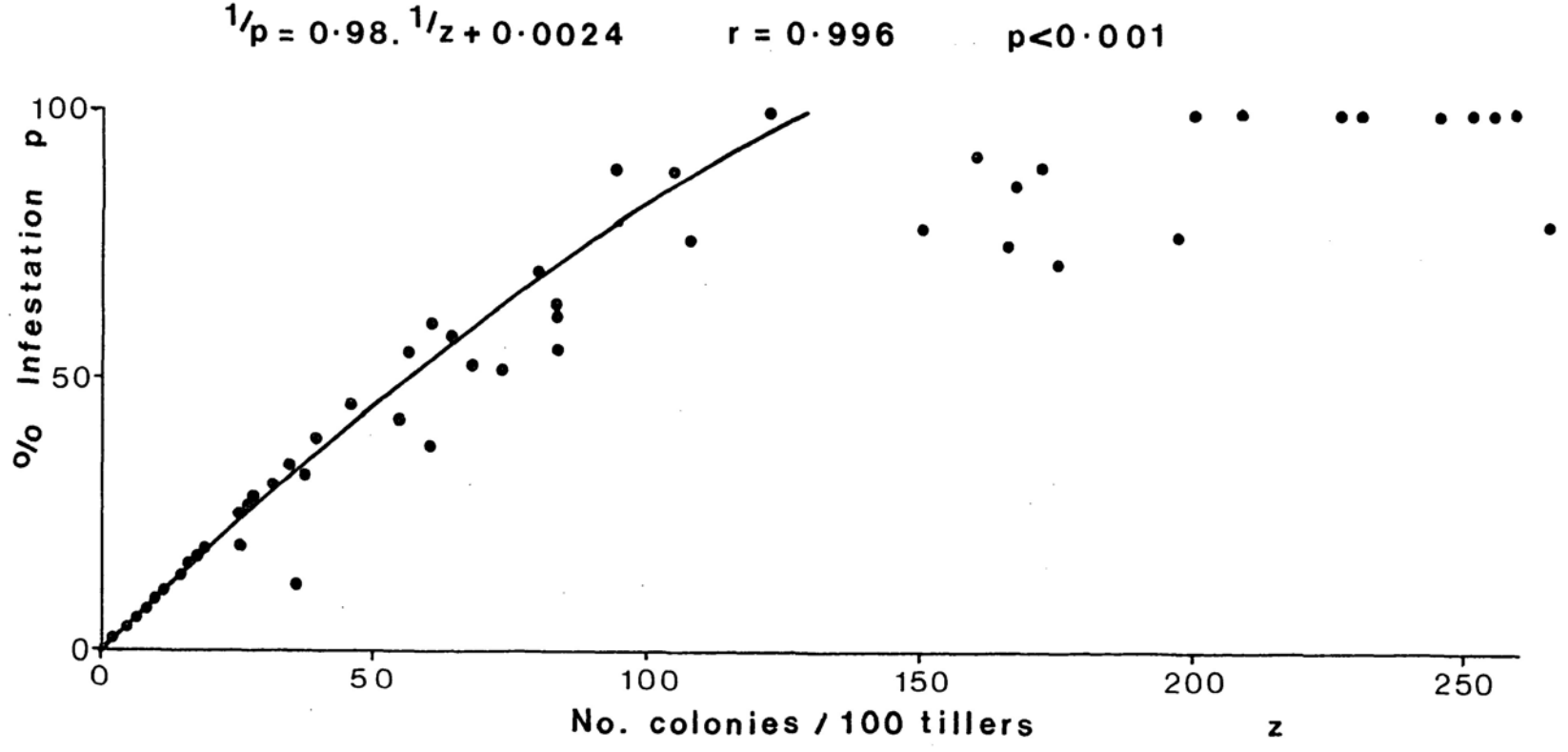
and rearranging:

$$Z = e^q.N^s \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(2)$$

Substituting (2) in (1) we have:

$$P = \frac{a.e^qN^s}{1 + be^qN^s} \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(3)$$

Figure 4.8 Relationship Between Proportion of Tillers Infested and Number of Colonies per 100 Tillers - Data from 1977 Field Experiment (L)



Values for the parameters ae^q, $be^q + s$ were obtained using a maximum likelihood program with log. residuals.

These parameters were determined for models for the 1977 and 1976 field data (table 4.11(a), (i)) but at high aphid populations the predicted infestation exceeded 100% (figure 4.9), which was not feasible, and so a term was incorporated in the program restricting values of P to less than or equal to 100%. Thus:-

$$P = \frac{ae^qN^s}{1 + be^qN^s} \qquad \text{when} \qquad N < \left[\frac{100}{e^q(a+b)}\right]^{1/s}$$

$$\text{and} \quad P = 100 \qquad \text{when} \qquad N \rightleftharpoons \left[\frac{100}{e^q(a+b)}\right]^{1/s}$$

This constituted model A (table 4.11(a)).

For the 1977 model in particular, values of s were close to unity and an alternative model was fitted with two parameters only. Thus:-

$$\text{when} \quad s = 1 \qquad P = \frac{ae^qN}{1 + be^qN} \qquad \ldots\ldots\ldots\ldots\ldots\ldots(4)$$

This model (model B) was fitted to the 1976 and 1977 data with and without restriction of $P \leqq 100\%$ (table 4.11(b), (i) and (ii)). Although the model produced a good fit to the 1977 data (figure 4.9) it gave a poor description of the 1976 data (figure 4.10) as the 100% infestation level was not reached.

This could have been a consequence of the log. weighting of the residuals and so a square root transformation of the residuals was used with the same model. This was model C (table 4.11(c)) which gave a

Table 4.11 Model Parameters Derived by Maximum Likelihood

1 Log. Weighted Residuals

(a) Model A

$$P = \frac{ae^q N^s}{1 + be^q N^s}$$

P – Percentage tillers infested

N – Number of aphids/100 tillers

ae^q, be^q, s – Constant ± 95% confidence interval limits

		1977	1976
(i) No restriction on P	ae^q	0.252 ± 0.087	0.896 ± 0.279
	be^q	0.00865 ± 0.00125	0.00784 ± 0.00227
	s	0.957 ± 0.080	0.789 ± 0.099
	resid. ss	0.0380	0.0483
	D.F.	54	21
(ii) P restricted to peak value 100	ae^q	0.299 ± 0.110	0.963 ± 0.347
	be^q	0.00550 ± 0.00359	0.00536 ± 0.00733
	s	0.898 ± 0.098	0.747 ± 0.146
	resid. ss	0.0374	0.0462
	D.F.	54	21

Key: resid: – residual

(b) Model B

When s = 1 $P = \frac{ae^{q}N}{1 + be^{q}N}$ Rectangular hyperbola

		1977	1976
(i) No restriction on P	ae^{q}	0.212 ± 0.020	0.521 ± 0.114
	be^{q}	0.00188 ± 0.00032	0.00545 ± 0.00187
	resid. ss	0.0381	0.0798
	D.F.	55	22
(ii) $P \leqq 100$	ae^{q}	0.208 ± 0.020	0.524 ± 0.112
	be^{q}	0.00187 ± 0.00034	0.00548 ± 0.00188
	resid. ss	0.0380	0.0789
	D.F.	55	22

2 Square Root Weighted Residuals

(c) Model C

$P = \frac{ae^{q}N}{1 + be^{q}N}$

		1977	1976
(i) No restriction on P	ae^{q}	0.213 ± 0.021	0.365 ± 0.073
	be^{q}	0.00187 ± 0.00026	0.00334 ± 0.00087
	resid. ss	0.222	0.242
	D.F.	55	22
(ii) $P \leqq 100$	ae^{q}	0.207 ± 0.021	0.367 ± 0.076
	be^{q}	0.00183 ± 0.00028	0.00337 ± 0.00093
	resid. ss	0.217	0.242
	D.F.	55	22

Key: resid: - residual

Figure 4.9 Comparison of Models A, B and C for Their Prediction of the Spread of Aphids at High Levels of Tiller Infestation – Data from 1977 Field Experiment

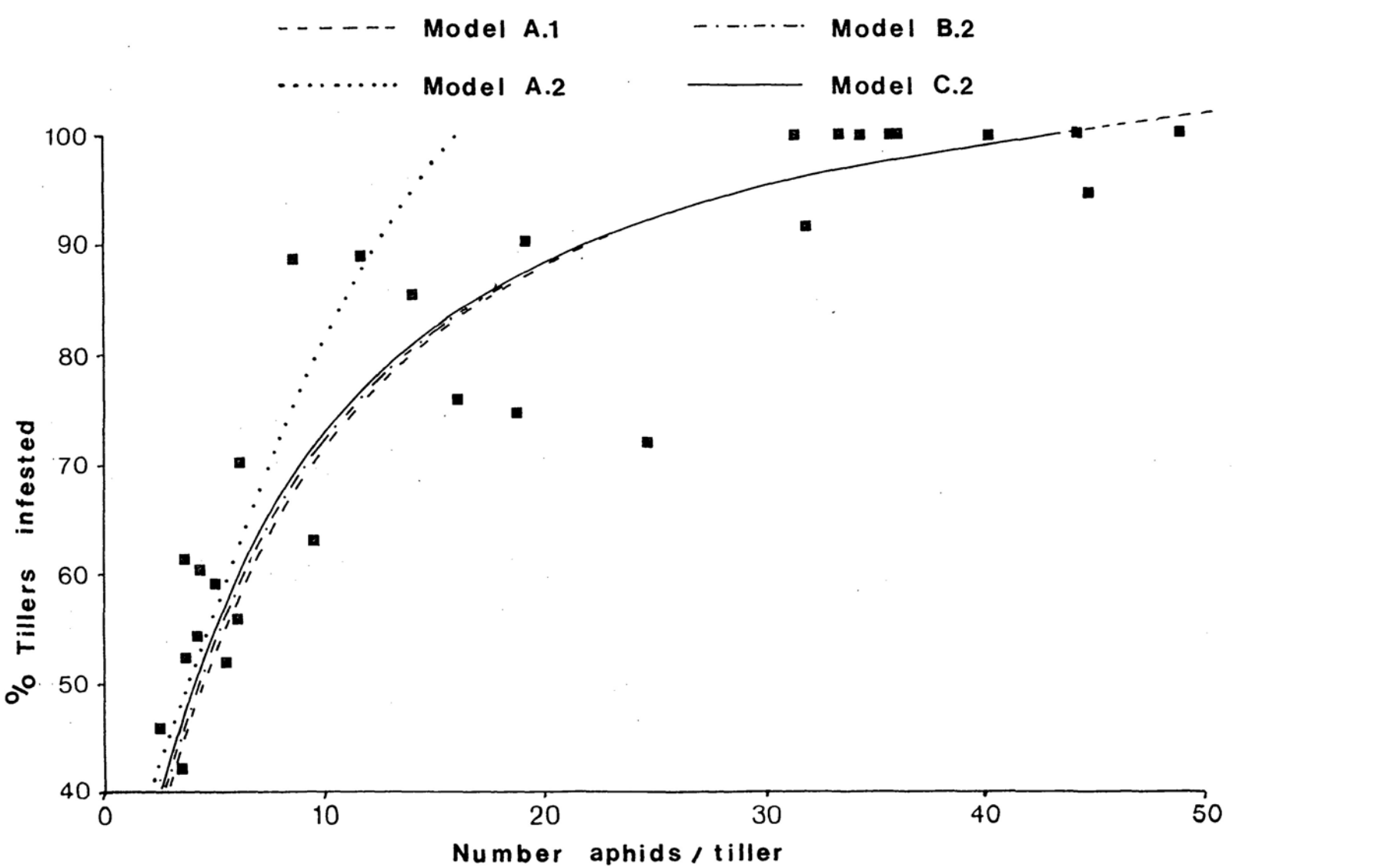
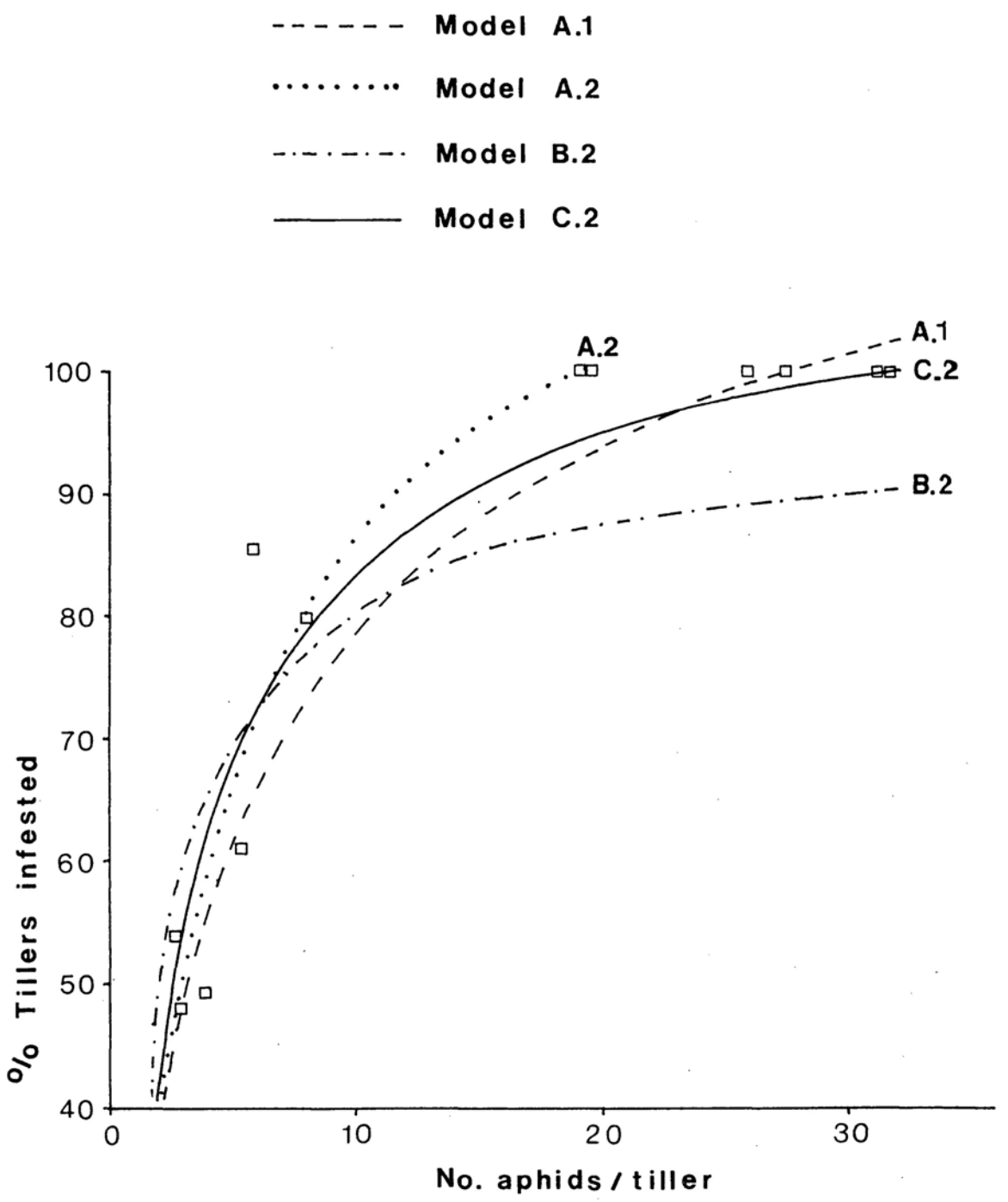


Figure 4.10 Comparison of Models A, B and C for Their Fit to the Spread of Aphid Infestation - Data from the 1976 Field Experiment



reasonably accurate description of the 1976 data and differed little from the other models with the 1977 data (figures 4.9 and 4.10). The curve produced by this equation is a rectangular hyperbola and thus at $N = 0$, $dP/dN = ae^q$, i.e. the constant ae^q is equivalent to the initial maximum rate of infestation.

Discussion

The most suitable model to describe the relationship between percentage tillers infested and aphid population was selected using the criteria of a good visual fit to the data and simplicity, i.e. the fewer the parameters the better.

For the 1977 field data, models A(i), B and C produced very similar curves (figure 4.9), because the constants were similar (table 4.11(a), (b) and (c)). In the three parameter model (model A), restriction of P to values equal to or less than 100% displaced the curve leftwards so that full infestation (100%) was reached at a much lower population level than when P was allowed to increase beyond 100% (model A(i)). However, restriction of P had no great effect on models B and C (table 4.11(b) and (c)). Moreover, since the residual sum of squares was similar for models A and B and curve C fitted equally as well, there was little to choose between the models and the choice of best model rested on the 1976 data.

Fewer data were available from the 1976 field experiment and therefore comparison of the fit of the model curves was more difficult. As before, restriction of $P \leq 100$ in model A (A(ii)) displaced the curve leftwards relative to the unrestricted curve A(i) (figure 4.10). The two parameter model (model B), gave a poor fit because values of 100%

infestation were not reached at all (figure 4.10) and residual sums of squares were appreciably greater (table 4.11(b)), but when square root weighted residuals were used (model C) an adequate fit to the data was produced (figures 4.10 and 4.12). Thus model C was adopted to describe both 1976 and 1977 field data.

The accuracy with which the model described the data was reduced by two main factors; firstly, the lack of data for high infestation levels (80-99%) especially for the 1976 experiment and secondly the large variation in the few data values at high infestation levels obtained (figure 4.10). Data from field experiments in other years may cast some light on the source of this variation. Even so, model C produced a far superior fit to both the 1976 and 1977 field data than did the logistic model (figures 4.11 and 4.12), possibly due to the symmetrical nature of the logistic model. In figures 4.11 and 4.12 the shape of the rectangular hyperbola is distorted because of the log. transformation of the x axis.

Comparisons of predicted populations from given levels of infestation for model C and a logistic model with 1976 and 1977 field experiment data with the logistic model of Vereijken (1979) give an insight into the consequences of the different descriptions of aphid population spread in the field (table 4.12). The logistic model for the 1977 data predicts similar aphid populations for given levels of tiller infestation as the logistic relationship of Verijken (1979). However, model C, which provided the best description for the field data of 1976 and 1977, produces greatly different aphid densities for given tiller infestations (by a factor of 2 for the 1977 data) (table 4.12(a)). Thus, with 90% of

Figure 4.11 Spread of Aphid Infestation with Population Increase - 1977 Field Experiment

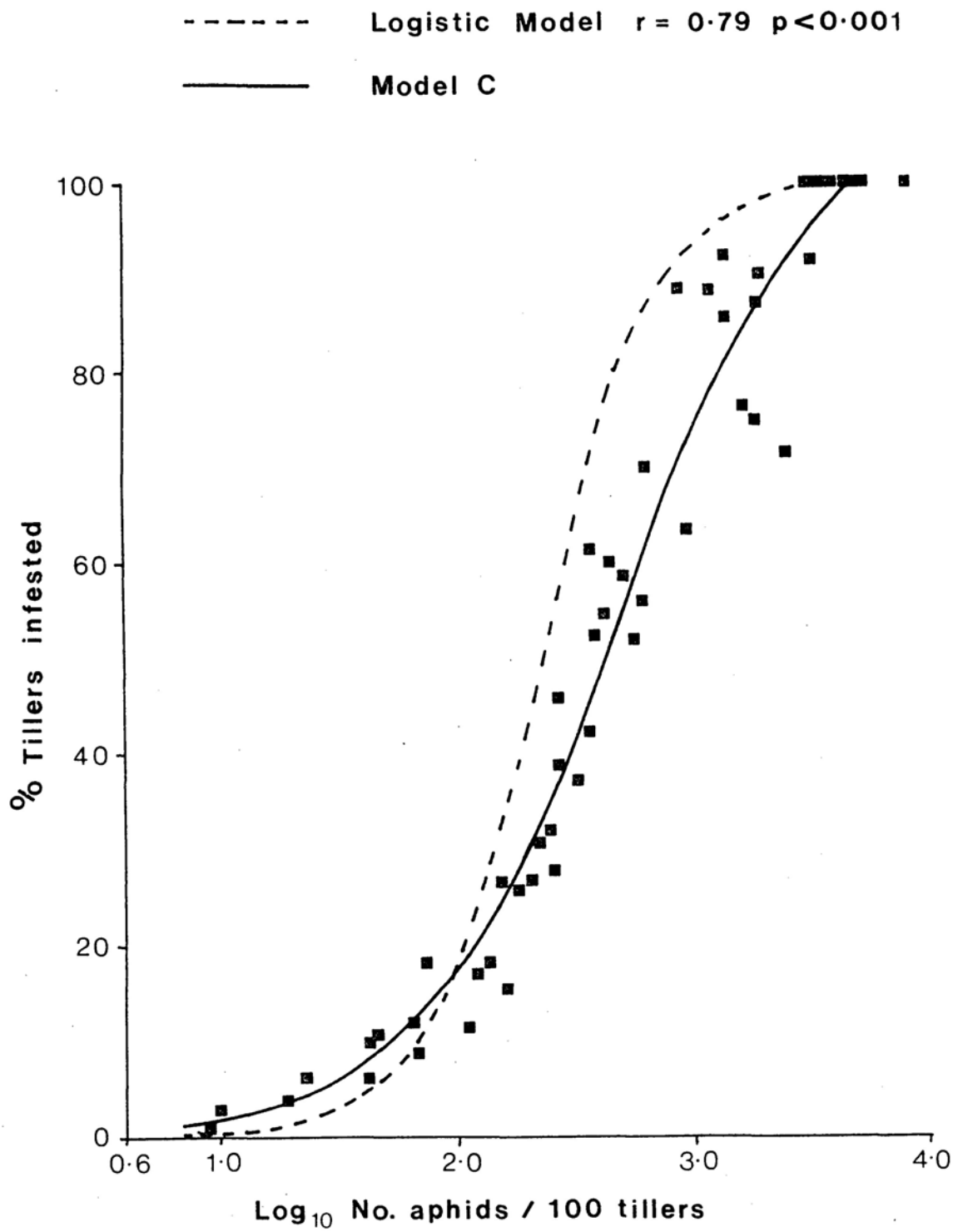


Figure 4.12 Spread of Aphid Infestation with Population Increase - 1976 Field Experiment

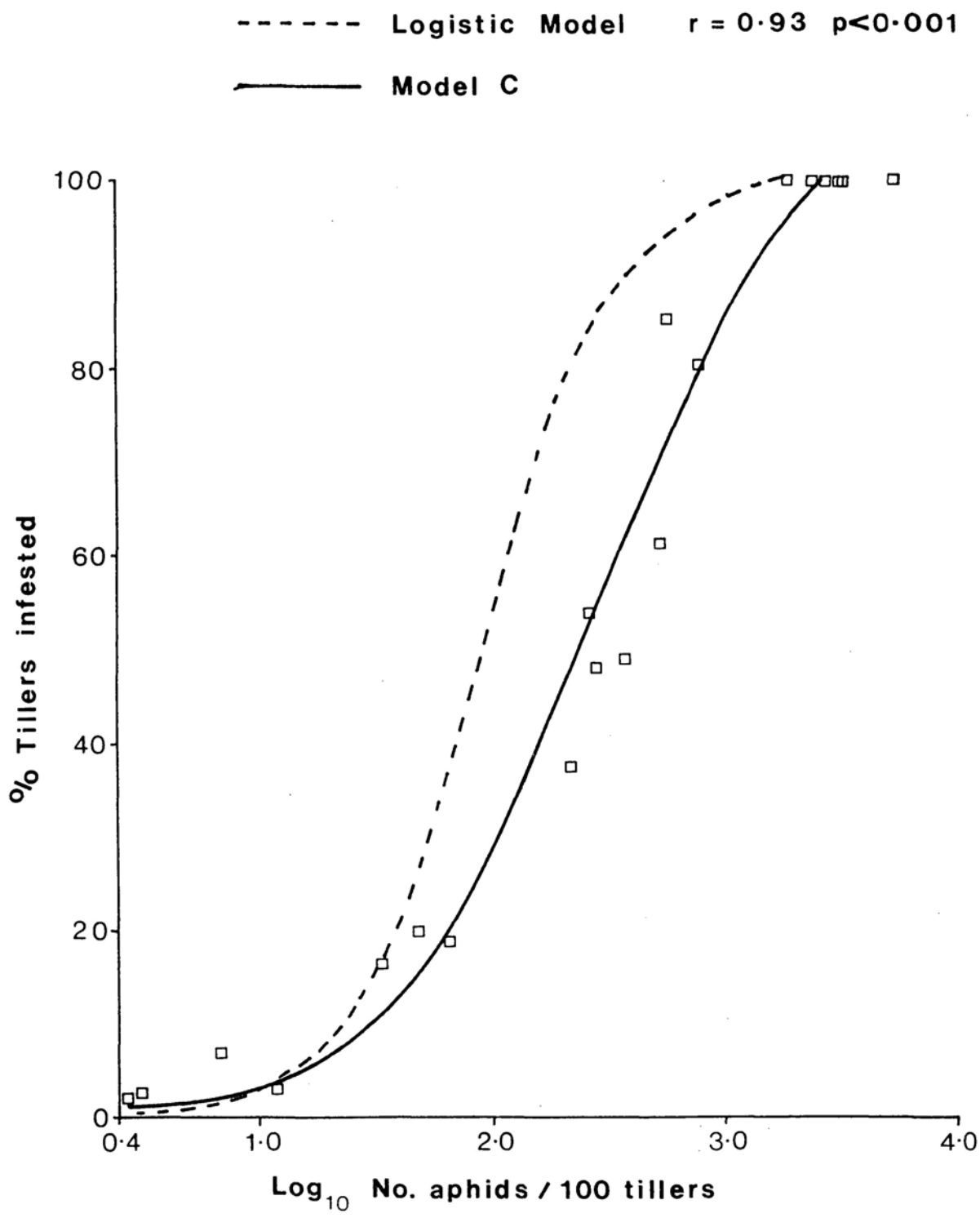


Table 4.12(a)

Aphid Population Per Tiller for Given Levels of Tiller Infestation

Comparison of predicted populations from Vereijken (1979), Model C 1977 and 1976 and logistic model for 1977 and 1976 North Farm experiments.

% Tillers Infested	Predicted Aphid Population Per Tiller				
	Vereijken (1979)	Model C		Logistic Model	
	n = 49	1977 n = 57	1976 n = 24	1977 n = 57	1976 n = 24
50	1.8	4.4	2.5	2.2	0.9
60	2.6	6.25	3.7	2.8	1.2
70	3.7	9.0	5.4	3.6	1.6
80	5.7	13.5	8.2	4.8	2.2
85	7.5	16.8	10.5	5.9	2.8
90	10.4	21.8	14.1	7.6	3.7
95	16.9	29.5	20.1	11.2	6.0

Key: n = number of samples used

Table 4.12(b)

Estimated tiller infestation for various economic threshold levels.

Number of Aphids Per Tiller	% Tillers Infested	
	1977	1976
5	54	68
10	73	84
15	83	91

tillers infested the logistic model of Vereijken (1979) predicted a population of 10.4 aphids per tiller whereas model C predicts 21.8 aphids per tiller for 1977 and 14.1 aphids per tiller for 1976. However, it is difficult to assess whether model C would fit the data of Vereijken better than the logistic as percentage infestations are plotted as probit transformations (figure 4.12, Vereijken, 1979). Moreover, he combined data from field experiments from 1973 to 1977 but the confidence interval limits of the parameters of model C (table 4.11(c)) show that the parameter values are probably significantly different for the 1976 and 1977 field experiments at North Farm. Thus Vereijken's plot may contain a further source of error.

In Holland, Vereijken (1979) recommended economic thresholds for aphid control to be set at 80% infestation at flowering, equivalent to 5 aphids per ear, and 90% after flowering, equivalent to 10 aphids per ear. The model presented here suggests that aphid populations may be badly underestimated and that true numbers present at these levels of tiller infestation are more in the region of 14 and 22 aphids per tiller respectively! Thus, levels of infestation for economic control may have to be revised downwards to 55% and 70% for flowering and post flowering infestations respectively (table 4.12(b)).

Finally, although immigration of alatae was greater in 1977 than in 1976 (K. D. Sunderland, personal communication) the initial maximum rate of infestation (ae^q) was slower in 1977 ($ae^q = 0.21$) than in 1976 ($ae^q = 0.37$), probably because the higher temperature in 1976 encouraged a faster population dispersal.

CHAPTER 5

EFFECTS OF AGRICULTURAL CHEMICALS, IN PARTICULAR FUNGICIDES, ON APHIDS AND APHID PREDATION BY GROUND BEETLES

5.1 Introduction

Fungal diseases of cereals are a major cause of yield loss and have necessitated much work in combating disease through plant breeding for resistant varieties and fungicide development programmes. In the absence of fungicides, mildew attack would cost £50 million per year in terms of yield loss of spring barley alone (Cock, 1976). Even with extensive breeding for resistant varieties diseases are still a problem because the fungal pathogens also develop damaging new races. Indeed, the high rates of fertilizer necessary for reaching maximum yield potential create a better environment for fungal disease. Thus the demand for effective fungicides has always been present, but until the late 1960's the fungicides available were only of a protective nature and relied on the complete covering of the foliage for their effect. The systemic fungicides now available combine therapeutic and prophylactic action thus making the timing and frequency of applications less crucial. Modern fungicides are not wholly successful against all fungal diseases however, there being generally poor control of the deep seated pathogens such as leaf rusts and Botrytis. Conversely, diseases such as powdery mildew which affect the surface layer of cells in a leaf are well controlled by a number of different fungicides.

All is not straight-forward with regard to fungicide use however. The economic benefits are not clear since there has been little success in

correlating disease control with yield increases. Indeed, it is only for the control of mildew in spring barley that routine fungicide use is economically worthwhile (Ministry of Agriculture, Fisheries and Food, ADAS Booklet No.*). Moreover, tridemorph used against mildew is phytotoxic on certain wheat varieties. Selection for resistance to fungicides has occurred in certain races of fungal pathogens, the carbendazim generators (benzimidazoles and thiophanates) having given rise to the greatest number of cases (Pearson, 1978). Ethyrimol insensitive strains have also been recorded and seed treatment of winter barley with ethyrimol is not now recommended.

Interest in the effects of fungicides on arthropods stemmed from the discovery by Parr and Binns (1970) of the acaricidal action of benomyl. Further work by Cranham (1971) and Tomlin (1977) demonstrated the toxicity of certain fungicides to mites and collembola. Sagenmuller (1977) and Vickerman (1977a) investigated the systemic effect of certain fungicides on the reproductive rate and mortality of S. avenae and M. dirhodum in laboratory experiments and in the field, Bailiss, Partiss, Hodgson and Stone (1978) showed that benomyl had a persistent effect on populations of Aphis fabae and Acyrthosiphon pisum on field beans.

Chemicals used in agriculture can often have unsuspected side effects on pest and natural enemy species (Potts and Vickerman, 1975). Vickerman (1974) found that herbicide sprays substantially reduced the arthropod fauna of cereals and Pollard (1968) found that the elimination of the bottom flora of a hedgerow by herbicide substantially reduced the numbers of carabids present. Direct toxic action of herbicides on coccinellids has been demonstrated in the laboratory (Adams, 1962) and in the field (Adams and Drew, 1965). The ecological side effects of fungicide use are

* Agricultural Science Service. The use of fungicides on cereals. 1977.

not so clear however. Nanne and Radcliffe (1971) found that treatment of potatoes with non-systemic fungicides protected Myzus persicae from infection with insect pathogenic fungi, and resulted in increased aphid populations. Conversely, Wilding, Brobyn and Best (1978) found that, while many systemic fungicides inhibited the germination of Entomophthora in vitro, fungicide application in the field had no effect on the proportion of Aphis fabae infected.

In the present work a range of fungicides approved for use against diseases of wheat (ADAS Booklet No.) were tested for contact effects on the reproduction of M. dirhodum using the method of Wyatt and White (1977) to estimate the intrinsic rate of natural increase, r_m. This had clear advantages for this type of investigation since it allowed the accurate calculation of aphid r_m with much less trouble than the Birch method (Birch, 1948), incorporating into that figure the essential components of aphid reproduction, namely, fecundity, reproductive rate and natural mortality, over the period of time that these were most important.

Fungicides have been found to influence the feeding of tetranychid mites (Jackson and Ford, 1973) and thus the effect of contamination of aphids on predator feeding could have repercussions on the mortality of aphids from natural enemies. This aspect was also investigated in the present work. Preliminary tests showed that dinoseb-amine (a herbicide) and tridemorph (a fungicide) had a strong contact insecticidal effect and these chemicals were selected for laboratory experiments on the consumption of contaminated aphids by ground beetles.

See footnote p187.

5.2 Effect of Fungicides on Aphid Reproductive Rate

(i) Experiments 1 and 2

Contact Effect of Fungicides on Aphid Reproduction

Materials and Methods

The plant material used was barley which had been hardened off for three weeks in a cold glasshouse, there being 10-12 plants per pot. Adult apterous M. dirhodum were placed on some barley plants and allowed to deposit young overnight. The following day the adults were removed and the progeny were left to develop in a constant temperature room at 22°C.

Six fungicides were used in each experiment made up to the concentration recommended for field application. Pots of barley were sprayed with a hand sprayer (two pots per chemical) until a thorough and even coverage of the leaves was obtained. The plants were left to dry overnight and the aphids at 4th instar stage (20/treatment) were then sprayed with a hand sprayer held 15 inches above the container they were in. The largest leaf of the appropriate barley plant was then folded and placed in a 50 mm glass tube, a treated aphid was carefully placed on the leaf and the tube was stoppered with cotton wool. The reproduction of these sprayed aphids on sprayed plants was now monitored. The apparatus was returned to the same constant temperature room and checked daily to determine the first day of reproduction (usually within one or two days of spraying). The length of time from birth to the onset of reproduction was called the development time (d) (Wyatt and White, 1977). Aphids were examined daily and the progeny were removed at intervals for a period equal to the reproductive period of d days. The total progeny produced in that time (Md) was then determined. Finally, the r_m value of individual aphids was calculated as $0.74 \log_e Md/d$ (Wyatt and White, 1977).

Some aphids died immediately on contact with a fungicide and others died before their effective reproductive life was over. However, the r_m value per aphid took mortality during the experiment into account as it was calculated from the total number of offspring produced by the individual aphid whether the aphid lived for more than d days or a shorter length of time.

In experiment 1, tridemorph was applied to the plants and aphids and the aphids alone.

Results

The results of experiments 1 and 2 are summarised in table 5.1.

In treatments where there was immediate mortality with no production of offspring (i.e. r_m value of zero) the mean r_m value given in table 5.1 is lower than that calculated from mean number of progeny and mean developmental time.

Tridemorph (Calixin) and mixtures with tridemorph produced substantial aphid mortality and thiophanate-methyl (Cercobin) also had a great effect on aphid r_m. Carbendazim in combination with mancozeb (Kombat) produced a significant reduction in aphid reproduction, but on its own or with maneb (Lucel) had no effect.

(ii) Experiment 3

Effect of Leaf Deposits of Fungicide on Aphid Reproduction

Materials and Methods

The same method as in experiments 1 and 2 was adopted except that the spray was applied only to the plants and not the aphids. Two aphid species were used, M. dirhodum and the red form of S. avenae, the experiment taking place in a constant temperature room at 22°C.

TABLE 5.1 EFFECT OF FUNGICIDES ON THE REPRODUCTIVE RATE OF METOPOLOPHIUM DIRHODUM

Chemical	% Active Ingredient Applied	No. Replics.	Mean No. Progeny Produced (Md)	Mean Developmental Time (Days)	Mean r_m Value	LSD $p<0.05$	Increase Rate (Times/Wk)	% Mortality of Adults During Experiment
EXPERIMENT 1								
1 Control (water)		17	35.9	8.2	0.321	↕	9.5	5.9
2 Benodanil	0.5	16	32.3	8.0	0.313	↕	9.0	25.0
3 Carbendazim/Maneb	0.15/0.96	14	38.4	8.1	0.334	↕	10.4	0
4 Tridemorph – on plant & aphids	0.345	21	13.0	8.0	0.152	↕	2.9	61.9
5 Tridemorph – on plant alone	0.345	12	13.7	8.25	0.196	↕	3.9	75.0
6 Ethyrimol	0.274	19	33.8	8.1	0.320	↕	9.4	10.5
7 Oxycarboxin	0.375	15	30.3	8.3	0.300	↕	8.2	20.0
Variance Ratio $F_{6,103} = 9.401$ $p<0.001$								
EXPERIMENT 2								
1 Control (water)		11	34.7	7.7	0.336	↕	10.5	27.3
2 Carbendazim	0.12	19	25.4	7.2	0.308	↕	8.7	36.8
3 Thiophanate-methyl	0.35	18	1.0	7.7	0.033	↕	1.3	100.0
4 Triadimefon	0.05	17	31.2	7.4	0.336	↕	10.5	29.4
5 Carbendazim/Mancozeb	0.17/0.9	12	16.4	7.6	0.193	↕	3.9	58.3
6 Tridemorph + Carbendazim	0.21 + 0.05	18	0	7.4	—	↕	—	100–immediate
7 Tridemorph + Polyram	0.21 + 0.08	18	0	7.5	—	↕	—	100–immediate
$F_{4,76} = 29.68$ $p<0.001$								

KEY: Replics. = Replicates

Results

The mean r_m value of M. dirhodum was significantly higher in the carbendazim treatment than in the control, but carbendazim/mancozeb (Kombat) had no effect (table 5.2). There was a significant reduction of r_m with thiophanate-methyl.

The red form of S. avenae did not adapt well to the experimental technique used as evident from the high mortality during the experiment. Reproduction by this species within each treatment varied widely so that no significant differences could be detected between the mean r_m values.

(iii) Experiment 4

Effects of More Fungicides on Aphid Reproduction Using a Modified Technique

Materials and Methods

The same method was used as in experiments 1 and 2 initially, but having sprayed aphids and plants, a different procedure was followed. The twenty treated aphids were placed on the treated barley plants and a conical perspex cover 25 cm high with ventilation holes was placed over the plants and sealed at the bottom. Aphids and progeny were removed after four days and the adults were transferred to freshly sprayed plants. The experiment was terminated after $7\frac{1}{2}$ days (equal to the average developmental time of the aphids). The average number of offspring per aphid was calculated by dividing the total progeny by the initial number of aphids (twenty).

Triforine applied directly to the aphids caused immediate mortality, so the aphid increase rate was determined for the chemical applied to the foliage alone. The aphicidal effect of this chemical at two concentrations on five aphid species was also investigated.

TABLE 5.2 EXPERIMENT 3 EFFECT OF LEAF DEPOSITS OF FUNGICIDE ON APHID REPRODUCTION

Chemical	% Active Ingredient Applied	No. Replicates	Mean No. Progeny Produced (Md)	Mean Developmental Time (Days)	Mean r_m Value	LSD $p<0.05$	Increase Rate (Times/Wk)	% Mortality of Adults During Experiment
A <u>Metopolophium dirhodum</u>								
1 Control (water)		4	24.5	7.0	0.337	↕ ↕	10.5	0
2 Carbendazim	0.12	4	41.5	7.0	0.395		15.9	0
3 Thiophanate-methyl	0.35	4	15.25	7.0	0.286		7.4	0
4 Carbendazim/Mancozeb	0.17/0.9	4	27.0	7.0	0.346		11.3	0
5 Oxycarboxin	0.375	4	26.25	7.0	0.346		11.3	0
$F_{4,15} = 6.11$ $p<0.01$								
B <u>Sitobion avenae</u>								
1 Control (water)		2	13.0	8.0	0.238		5.3	100
2 Carbendazim	0.12	5	5.8	8.0	0.120		2.3	100
3 Thiophanate-methyl	0.35	5	2.4	8.0	0.066	none	1.6	100
4 Carbendazim/Mancozeb	0.17/0.9	5	8.2	8.0	0.165		3.2	100
5 Oxycarboxin	0.375	5	7.0	8.0	0.145		2.8	100
$F_{4,17} = 1.22$ n.s.								

Table 5.3 Experiment 4

a Further Effects of Fungicides on Aphid Reproduction

Chemical	% Active Ingredient	Overall Daily r_m	Increase Rate (Times/Week)
1 Control (water)		0.347	11.35
2 Captafol	0.7	0.345	11.19
3 Chlormequat	0.7	0.368	13.15
4 Chlorquinox	0.025	0.339	10.72
5 Triadimefon	0.05	0.344	11.11
6 Zineb	0.64	0.325	9.23
7 Triforine (applied to leaf only)	0.092	0.350	11.59

b Effect of Direct Application of Triforine on Various Aphid Species

Aphid Species	Number Aphids	% Mortality + Triforine		Control (Water)
		0.092 % a.i.	0.046 % a.i.	
Metopolophium dirhodum	20	100	100	0
Sitobion avenae	20	100	100	0
Rhopalosiphum padi	20	100	100	0
Myzus persicae	30	100	100	0
Aphis gossypii	20	100	100	0

Results

None of the fungicides tested had a marked effect on the average r_m value of M. dirhodum (table 5.3). Triforine was lethal when sprayed directly on the aphids and killed all five aphid species within 10-15 minutes of application (table 5.3b) but had no effect when applied to the foliage alone.

(iv) Discussion

A summary of the results obtained is given in table 5.4.

The experimental technique used showed the contact effect of the fungicides on aphid r_m. Spraying of aphids and plants gave coverage of the aphids together with contact from contaminated leaves, and spraying plants alone produced aphid contact with the contaminated leaf. No systemic effects were likely to have occurred since the aphids were only present on the plants for a short period of time. This may explain the differences between some of the results obtained and published records. For example, Vickerman (1977a) and Sagenmuller (1977) found that carbendazim reduced aphid reproduction by a systemic action but in the present experiments only when formulated with mancozeb ('Kombat') did it have a contact effect on aphid r_m. Moreover, benomyl and thiophanate are converted to carbendazim within the plant and it is this that is responsible for the systemic effect on aphid reproduction (Clemons and Sisler, 1969). Indeed, thiophanate-methyl had a pronounced contact effect on aphid r_m in addition to its known systemic effect (Sagenmuller, 1977). Certain disparaties in results are not easily explained however. Aphid reproduction was greatly affected by contact with tridemorph both alone and in mixtures with carbendazim and polyram, but Sagenmuller (1977) found that the

TABLE 5.4 CONTACT EFFECT OF FUNGICIDES COMMONLY USED ON WINTER WHEAT ON CEREAL APHID REPRODUCTIVE RATE

	Chemical Name	Manufacturer's Name	Manufacturer	Plant Diseases Controlled	ADAS Approved	Sig. Decrease of Aphid r_m *
1	Benodanil	Calirus	BASF	Yellow rust, Brown rust	A	-
2	Carbendazim	Bavistin	BASF	Eyespot, Septoria	A	-
3	Carbendazim/Maneb	Delsene M	PBI	Septoria, Eyespot, Mildew	A	-
4	Carbendazim/Mancozeb	Kombat	Hoechst	Septoria, Eyespot, Mildew	A	*
5	Chlormequat	Cycocel	BASF	Growth Retardant	A	-
6	Ethyrimol	Milgo	ICI	(In barley) Mildew, Septoria	A	-
7	Oxycarboxin	Plantvax	ICI	Brown rust, Yellow rust	A	-
8	Thiophanate-methyl	Cercobin	Murphy	Septoria, Eyespot, Mildew	A	*
9	Triadimefon	Bayleton	Bayer	Mildew, Yellow rust, Brown rust	A	-
10	Tridemorph	Calixin	BASF	Mildew, Yellow rust	A	*
11	Tridemorph/Carbendazim	Calixin + Bavistin	BASF	Mildew, Yellow rust		*
12	Tridemorph/Polyram	Calixin + Polyram	BASF	Mildew, Yellow rust	A	*
13	Triforine	Saprol	Shell	Powdery mildew (in barley)	A	*
14	Zineb	Polyram	BASF	Yellow rust	A	-
	Others					
15	Captafol	Sanspar	ICI			-
16	Chlorquinox	Lucel	Fisons			-

systemic uptake of tridemorph stimulated the production of nymphs. Other results did agree with published data, triadimefon and chlormequat having no effect on reproduction, as reported by Vickerman (1977a) and Rautapää (1972b). A newly tested fungicide, triforine, had a high toxicity to aphids from direct application but a plant spray alone had no effect on aphid reproduction.

Fungicides previously untested and found to have no contact effect on aphid r_m were:- benodanil, carbendazim/maneb, ethyrimol, oxycarboxin, zineb, captafol and chlorquinox.

5.3 Effect of Food Contamination by Agrochemicals on the Feeding of Ground Beetles

(i) Experiment 1

Herbicide, Dinoseb-amine

Materials and Methods

The effect of chemical contamination of food on the aphid consumption of Pterostichus melanarius was studied using a modification of the feeding technique already described (Chapter 2 - section 1). Frozen pea aphids were spread evenly over filter paper in petri dishes and the herbicide was applied using a Potter tower. Two millilitres of the solution were sprayed on each dish and the aphids were allowed to dry and then put into a container to be stored in a freezer. Three concentrations of herbicide were used, made up by successive dilutions from the commercial solution; these were 1 part to 25, herbicide:water, 1:100 and 1:400, the control being water.

Beetles were taken from laboratory cultures and weighed at the beginning and at the end of the experiment. Six replicates were used for each of the four treatments, consisting of three male and three female beetles, apart from the control (five females and one male). The beetles were kept in containers similar to those already described (Chapter 2 - section 1) and they were fed daily with the appropriate frozen aphids for nine days. The containers were arranged in a fully randomised design on a shelf in a constant temperature room at 17.5°C and 16 hour daylength.

Results

A cursory survey of the results revealed that the herbicide treatment seemed to affect aphid consumption only in the first three days of the experiment. Therefore, the mean consumption per day per beetle for the initial three days was analysed, together with the mean consumption for the remainder of the experimental period and the overall mean consumption (table 5.5a).

The influence of the herbicide on aphid consumption was marked but transient (table 5.5a). Neglecting the control, aphid consumption during the first three days halved with fourfold increases in herbicide concentration. However, the differences in aphid consumption between the sexes, although large, were not significant, neither was there a significant interaction between herbicide level and sex of beetle (table 5.5b). Incorporating beetle weight into the analysis as a covariate did not improve the precision of the analysis and therefore was not considered further. Aphid consumption increased after three days in the two most concentrated herbicide treatments (1:25 and 1:100) but decreased in the remaining two treatments (table 5.5a, column 5) and this equalised

Table 5.5 Effect of Dinoseb-amine on Aphid Consumption by P. melanarius

a For Different Time Periods

1. Herbicide Treatment Level	Mean Aphid Consumption Per Day mg/day				5. Difference in Aphid Consumption	
	2. Day 1-3		3. Day 4-10		4. Day 1-10		Day 4-10 - Day 1-3	
	Means	LSD*	Means	LSD*	Means	LSD*	Means	LSD p<0.01
1 1:25	11.83		27.58		22.33		+ 15.74	
2 1:100	20.07		41.97	None	35.52	None	+ 19.34	
3 1:400	46.23		26.54		33.10		- 11.84	
4 Control	39.00		30.19		34.98		- 11.18	
Variance Ratio	$F_{3,20} = 4.90$		$F_{3,18} = 1.19$		$F_{3,18} = 1.08$		$F_{3,17} = 10.60$	
* p<0.05	p<0.05		n.s.		n.s.		p<0.001	

b Two Factor Analysis of Aphid Consumption for Day 1-3

FACTOR	VARIATES			VARIANCE RATIO
Sex	Male		Female	
	20.5		31.6	$F_{1,12} = 1.505$ n.s.
Herbicide Level	1	2	3	
	11.8	20.1	46.2	$F_{2,12} = 5.26$ p<0.05
Herbicide Level	1	2	3	
Sex				
Male	3.9	16.9	40.6	$F_{2,12} = 0.092$ n.s.
Female	19.7	23.2	51.9	

the differences in aphid consumption and resulted in the absence of significant differences over the whole of the experiment (table 5.5a, columns 3 and 4).

Mean aphid consumption increased with beetle weight (figure 5.1) as found previously (Chapter 2, section 1). Moreover, the weight of beetles changed during the course of the experiment and the magnitude of the change was related to the total quantity of aphids consumed (figure 5.2). The slope represented the efficiency of conversion of aphid biomass into beetle biomass and the intersection of the regression line on the x axis ($x = o$) represented the amount of food required to maintain body weight. Two regression lines were considered, line A included all the points but line B excluded two obvious outliers and gave a substantially better correlation and better visual fit to the data (figure 5.2). For line A the slope was 0.063 ($\cong$ 6.3% conversion efficiency) and x intercept was 205.5 mg ($\cong$ 22.8 mg/day) and for line B the slope was 0.09 ($\cong$ 9% c.e.) and the x intercept was 229 mg ($\cong$ 25.4 mg/day).

The changes in mean aphid consumption after three days, when the herbicide ceased to have an effect, may have been a consequence of heavier and therefore more voracious beetles being assigned to the herbicide treatments 1 and 2. To take account of this, the change in aphid consumption was plotted against beetle weight (figure 5.3). Two groups of points were evident, beetles that had initially been affected by the herbicide (treatments 1 and 2) but subsequently increased their aphid consumption and beetles that had been initially unaffected (treatments 3 and 4) and decreased their consumption of aphids. A parallel regression analysis on these two groups of points showed that the intercepts were

Figure 5.1 Experiment 1 Relationship Between Mean Daily Aphid Consumption for All Treatments and Initial Beetle Weight

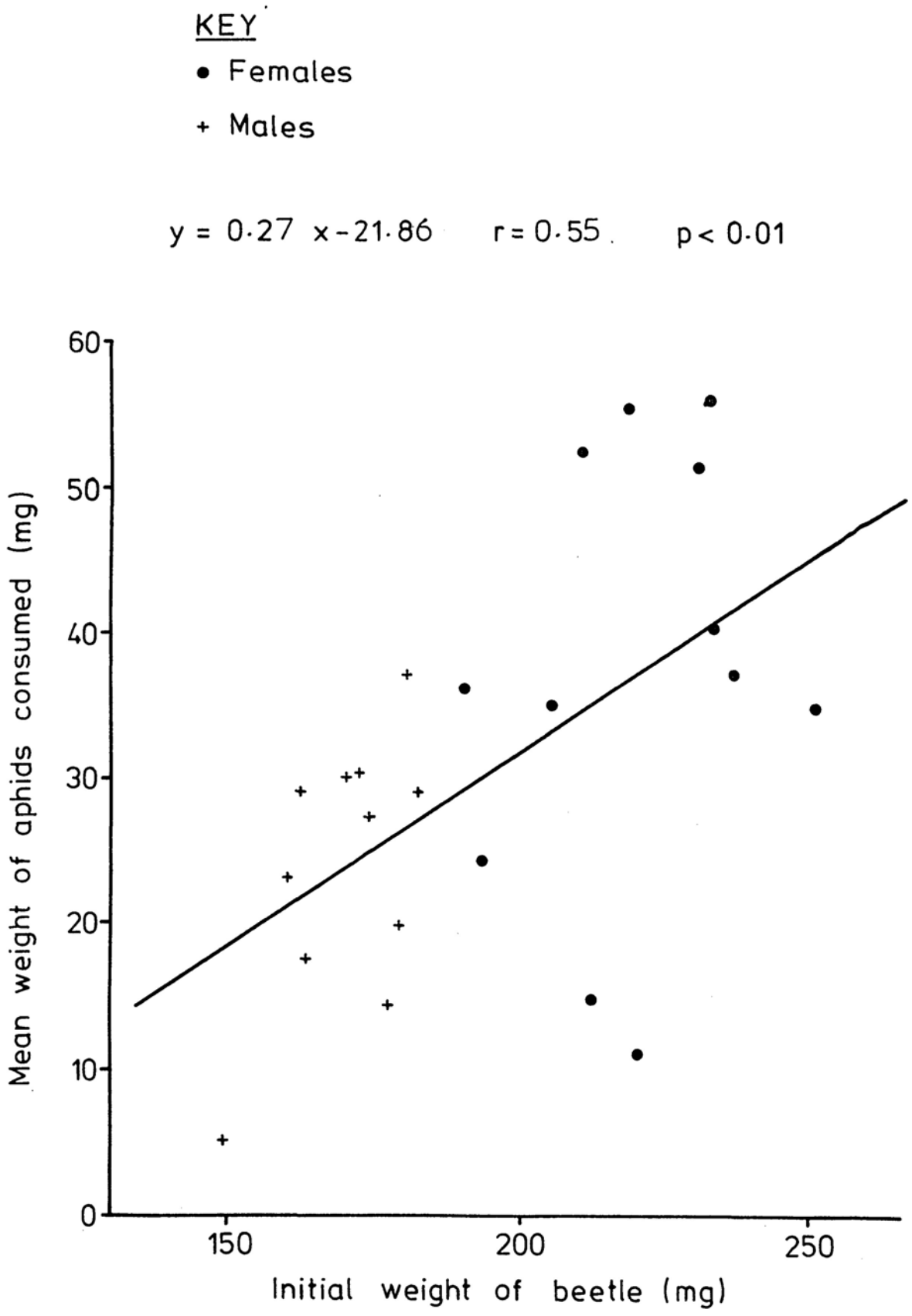


Figure 5.2 Experiment 1 Net Change in Beetle Weight from Start to End of Experiment Produced by Differences in Aphid Consumption

KEY

• Females

+ Males

Regression

A. $y = 0.063x - 12.95$ $r = 0.66$ $p < 0.001$

B. $(y = 0.090x - 20.62$ $r = 0.84$ $p < 0.001$ - ignoring 2 outliers)

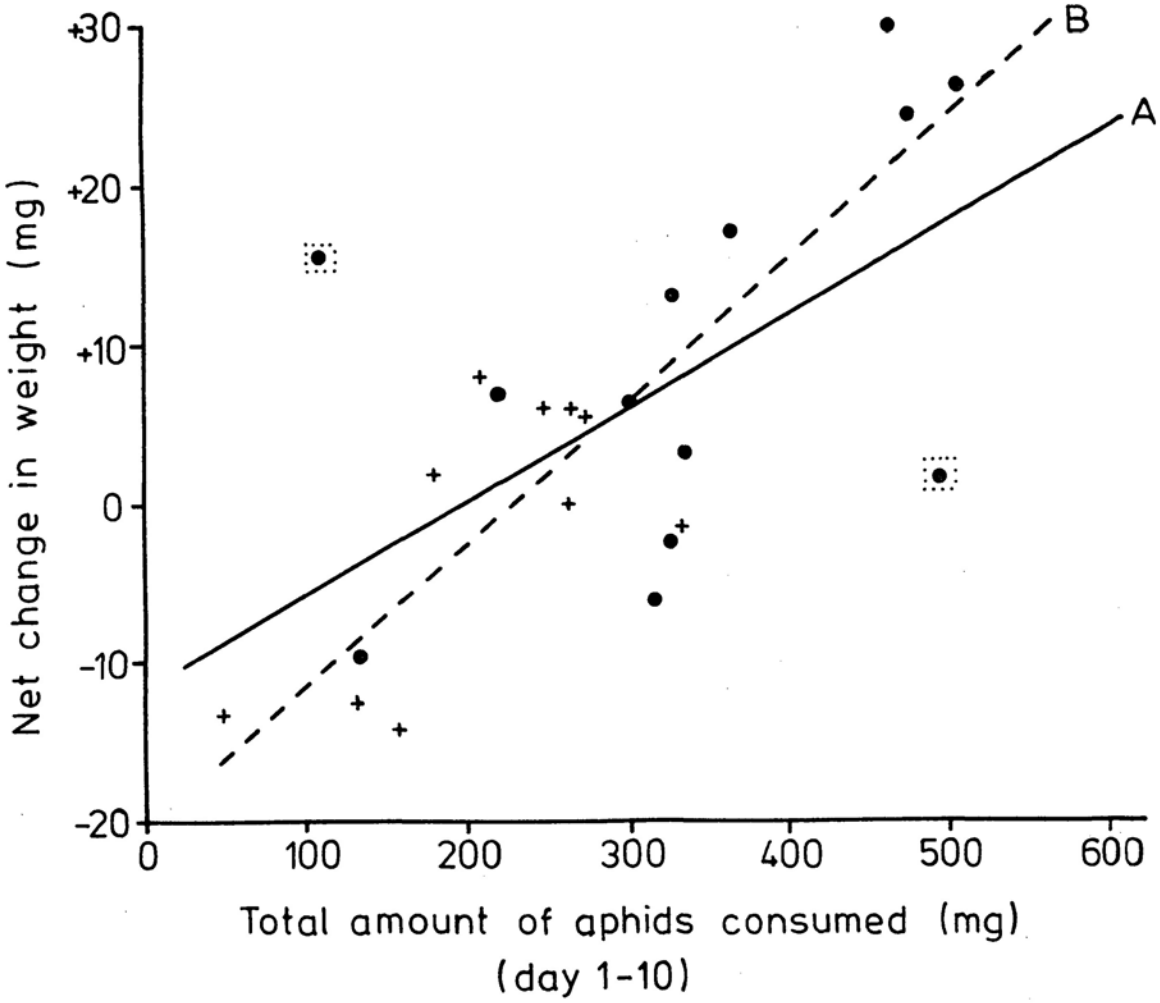
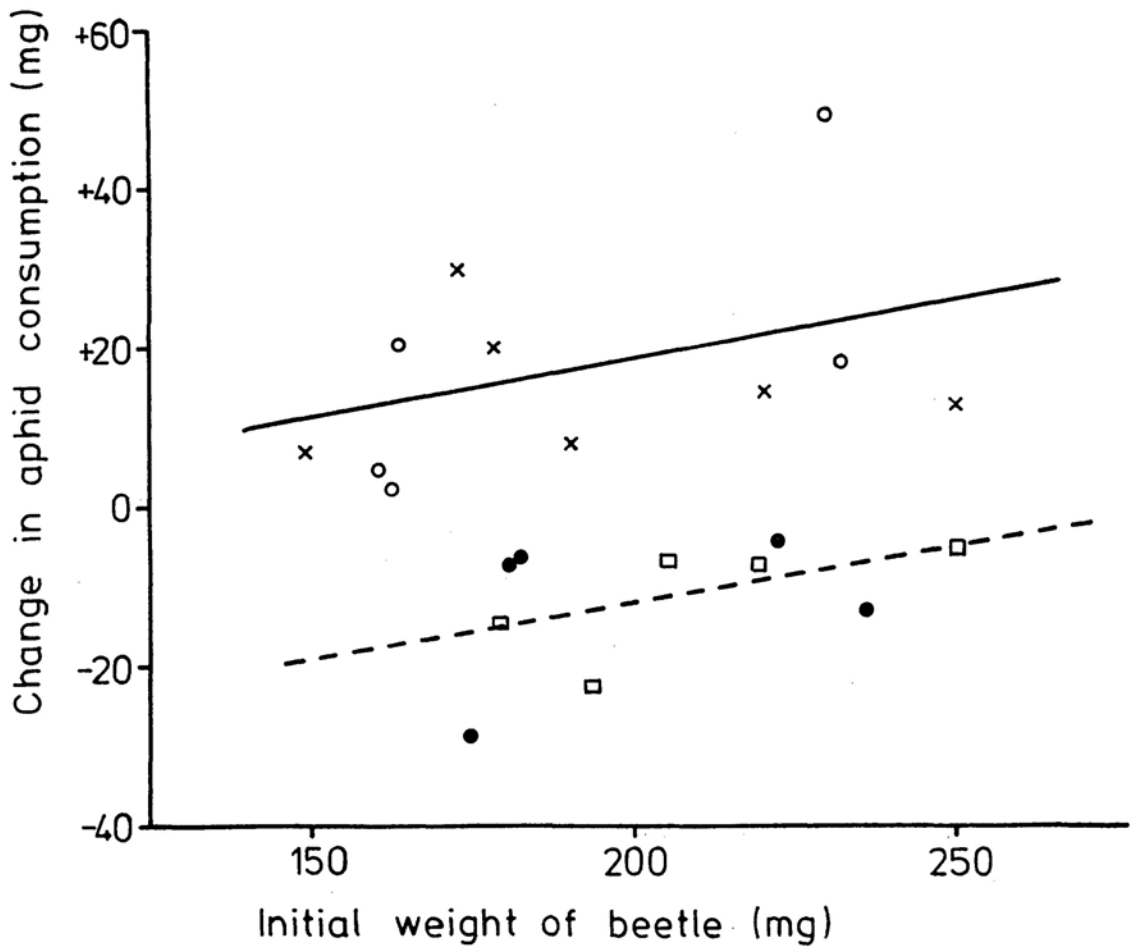


Figure 5.3 Experiment 1 Effect of Beetle Weight and Herbicide Treatment on Change of Mean Aphid Consumption After Three Days (Day 4–10 – Day 1–3)

KEY

Symbol	Herbicide level	Fitted parallel regression
×	1	—— s = 0·147 i = −10·66
o	2	
•	3	- - - s = 0·147 i = −41·40
□	Control	



significantly different from each other ($T_{18} = -6.55$, $p<0.001$) which is equivalent to significantly different means, but the slopes were not significantly different, either from each other, or zero i.e. there was no significant relationship between change in consumption and weight of beetle.

(ii) Experiment 2

Fungicide, Tridemorph

Materials and Methods

The same feeding technique as in the previous experiment was used. The concentrations of tridemorph tested were more dilute than before (1:100, 1:316 and 1:1000), the commercial application rate being one part to 400 parts of water. A different method of applying the chemical was adopted in order to obtain a more uniform contamination of the aphids. Aphids were sandwiched between two sheets of filter paper in a Büchner funnel in a vacuum filtration apparatus and 20 ml of the required solution was poured in, allowed to stand for one minute and then sucked through. This was repeated for a second batch of frozen aphids and thereafter for the other concentrations and the water control.

Two males and four females were used per treatment, and were weighed at the start and finish of the experiment and food consumption was assessed daily for 6 days. The containers were placed in the same constant temperature room as before at 17.5°C and 16 hour daylength.

Results

In contrast to the reaction of the beetles to food contamination by Dinoseb-amine, there were no significant differences between the aphid consumptions in the different treatments for the initial three days

Table 5.6 Effect of Tridemorph on Aphid Consumption by P. melanarius

Fungicide Level	Mean Aphid Consumption Per Day mg/day						Difference in Aphid Consumption	
	Day 1-3		Day 4-6		Day 1-6		Day 4-6 - Day 1-3	
	Means	Sig. Diffs.*	Means	Sig. Diffs.*	Means	Sig. Diffs.*	Means	Sig. Diffs.*
1 1:100	54.6	None	60.8	None	57.7	None	+ 6.2	
2 1:316	60.0		59.9		60.0		- 0.1	
3 1:1000	51.4		66.5		59.0		+ 15.2	
4 Control	49.2		71.9		60.6		+ 22.7	
Var. Ratio	0.27		0.44				2.39	
$F_{3,20}$	n.s.		n.s.				n.s.	

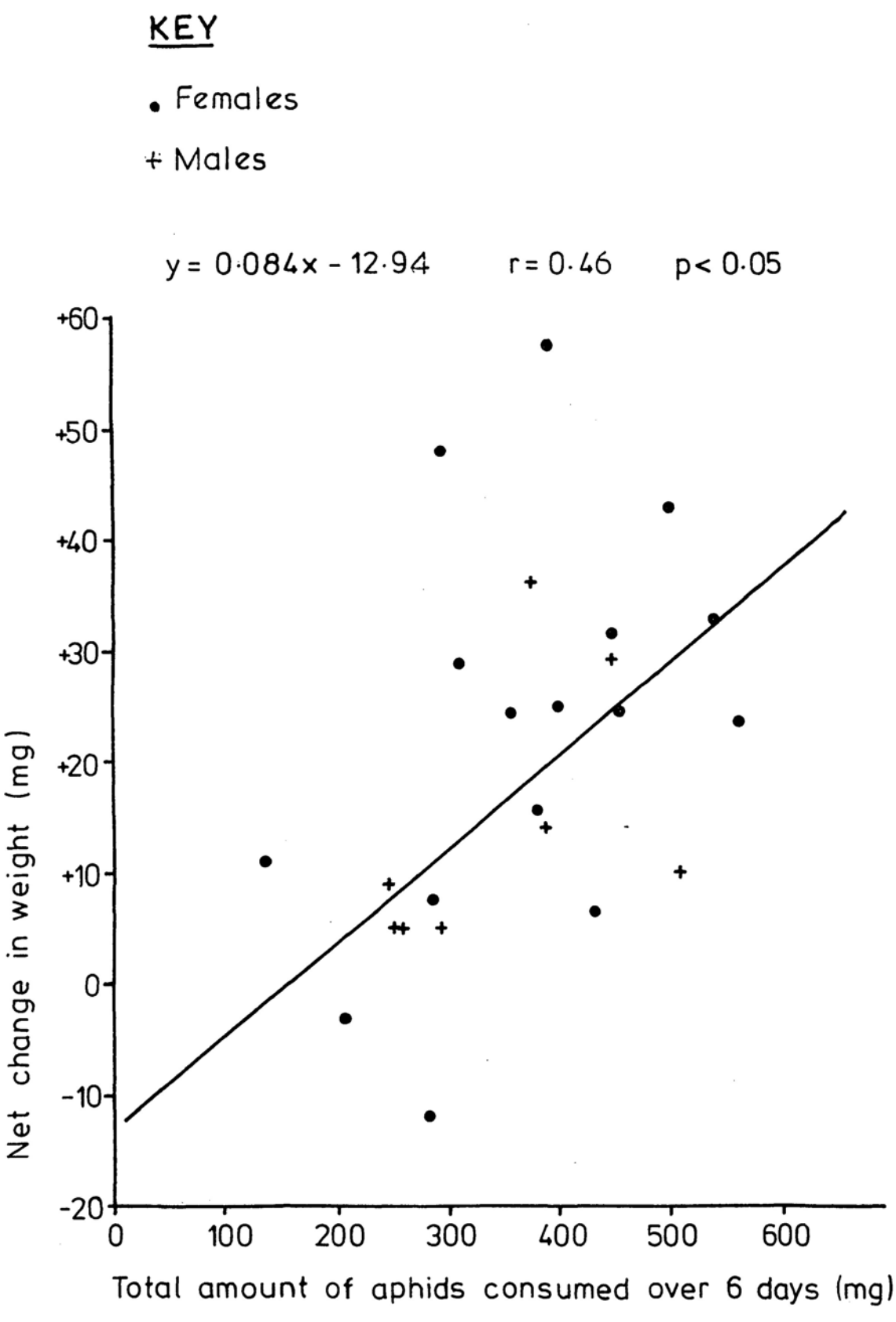
*at $p<0.05$

(table 5.6) and although the differences became larger for the second period of three days they were still not significant (table 5.6).

Again, in contrast to experiment 1, there was no association between mean aphid consumption over the period of the experiment and beetle weight ($r = 0.156$, $p>0.1$) possibly because the mean aphid consumptions were obtained for a smaller number of days. However, the change in beetle weight from the start to the end of the experiment was correlated with the total amount of aphids consumed (figure 5.4), giving a slope of 0.084 (8.4% conversion efficiency) and an x intercept of 153.5 mg aphids consumed in 6 days (25.6 mg/day), for maintenance of body weight.

Aphid consumption tended to increase during the experiment (table 5.6, column 5) but there was no consistent pattern to the increases possibly due to the large amount of variability within the experiment and the lack of initial treatment effects.

Figure 5.4 Experiment 2 Relationship Between Change of Beetle Weight and Total Quantity of Aphids Consumed



(iii) Discussion

In experiment 1, five female beetles laid eggs (mean number per female = 7.8 ± 1.1) and most of the females appeared to be gravid, thus in accordance with the previous experiment on aphid consumption by beetles (Chapter 2, section 1, experiment 5, figure 2.3) the regression line fitted both males and females together (figure 5.1).

The consumption of aphids by beetles in experiment 1 was only affected by the high concentration of herbicide for a limited period of three days. As the beetles became more hungry consumption of heavily contaminated aphids increased by 118% while control consumption decreased by 33% so that average aphid consumption over ten days differed little. Once the beetles in treatments 1 and 2 had overcome their aversion to the contaminated aphids, the extra amount of food eaten per day was given by the difference between the intercepts in figure 5.3 and amounted to 30.7 mg/day. This represented an average increase in voracity (i.e. weight of aphids eaten as a percentage of body weight) of 16%. Moreover, in the second experiment, tridemorph had no effect on aphid consumption, even for an initial period. This would tend to reduce the ecological impact of chemical use in the field since the effect of local concentrations of chemical on prey or the build up of high levels through a food chain could be overridden by hungry predators. However, it does imply that chemicals can easily be concentrated within the bodies of predatory beetles with resulting effects on their main predators, the birds.

Relationships between the aphid consumption and beetle weight variables in the three experiments on the consumption of pea aphids by P. melanarius (experiments 1 and 2, experiment 5, Chapter 2, section 1)

did not always show a consistent pattern. The relationship between changes in aphid consumption during the experiments and beetle weight were different for each experiment carried out; aphid consumption was not related to beetle weight in experiment 2 and there was no relationship between change in beetle weight and total aphid consumption in experiment 5, Chapter 2. These differences may be due to the different origin of the beetles, those in experiment 5, Chapter 2, having been recently caught in the field, while beetles in experiments 1 and 2 had been kept in laboratory cultures for some months. In the case of changes in aphid consumption differences may also have been due to the means being based on consumptions over different time periods. However, for experiments 1 and 2 the values for conversion efficiencies for aphid into beetle biomass (9% and 8.4%) and food consumption for body weight maintenance (25.4 and 25.6 mg/day) were remarkably similar, indicating that these were perhaps intrinsic factors of P. melanarius biology.

CHAPTER 6

APHIDS AND YIELD LOSSES OF WHEAT

6.1 Introduction

There have been many studies of the effect of feeding damage by aphids on the yield of cereals, encompassing the major aphid species (S. avenae, M. dirhodum and R. padi) and the major cereals (wheat, barley and oats) and some results are summarized in table 1.1.

The consequence of the prevention of aphid mortality from natural enemies in the 1977 field experiment was the production of considerable aphid burdens on the wheat plants. Hence it seemed relevant to study the effect of aphids on yield loss for this experiment.

The effect of nitrogenous fertilizers on aphid population growth and on interactions with yield has been investigated in the field (Carrillo and Mellado, 1975 and Carrillo and Mundaca, 1976) and the effect on aphid reproduction in the laboratory (Vereijken, 1979). However, the influence of plant growth on the effect of aphids on yield has been afforded little attention. Thus investigations were carried out on the effect of plant height and number of tillers per plant on the interaction between aphids and yield using plots of wheat in an insectary in a year of poor plant growth (1976 experiment) and vigorous growth (1977 experiment).

The importance of timing of aphid infestation in relation to the growth stage of wheat on the yield components affected is acknowledged (Kolbe and Linke, 1974, Carrillo, Mellado and Pino, 1974, Wratten, 1975)

but the relative influence of aphid infestations before and after flowering, the critical stage of growth for grain determination, is unknown. Multiple regressions were used to analyse the relative importance of aphid infestations at flowering and after flowering on the components of yield in the 1977 insectary experiment. Moreover, Watson and French (1971) found that the yield of wheat plants was influenced by the spacing of the rows and thus, in the 1977 experiment, the effect of row spacing from the three rows of plants in each plot on the interaction between aphids and yield was investigated.

6.2 Field Experiment 1977 - Consequences of Predator Exclusion on Yield Losses of Wheat Due to Aphids

Materials and Methods

The wheat in all the plots in the 1977 North Farm field experiment (Chapter 2) was harvested. Eight groups of fifty ears were taken, four from the four sampled corners of the transect, and four groups from rows behind the transect to allow for edge effects.

Yield parameters for each group of ears were determined separately. Groups were subsampled in the following way to avoid bias. Ears of each group of fifty were spread out, ranked by length and from one end every fifth ear was taken and examined individually for number of sterile and fertile spikelets, number of grains and total weight of grains. Thus ten ears were analysed per group in this way and the average yield per plot was based on a representative sample of eighty ears.

Aphid indices (sum of aphid numbers at each sampling date multiplied by the time on the plant) were calculated for each plot and regression

analysis was used to analyse associations with the yield variables. Since there were no control plots with zero aphids yield losses were calculated from the appropriate regression equation.

Indices were calculated for aphid numbers up to flowering (June 27th) - 'flowering' aphid index and from then until the extinction of the populations - 'post-flowering' aphid index.

Results

It was concluded in Chapter 3 that the exclusion of aphid specific predators by the cages played a primary part in allowing aphids to increase to higher levels than in the open field. The resulting effect on yield is shown in table 6.1. The higher aphid levels in the cages

Table 6.1 Effect of Predator Exclusion by Caging on Yield of Wheat

Initial Aphid Infestation Level	Wt. Grain/Ear gm		'000 Grain Wt. gm		No. Grains/Ear	
	Caged Plots	Av. Uncaged Plots	Caged Plots	Av. Uncaged Plots	Caged Plots	Av. Uncaged Plots
High	0.586	1.710	28.55	55.71	20.51	30.70
Medium	0.822	1.754	34.03	57.98	24.15	30.26
Low	1.429	1.771	50.28	57.71	28.43	30.69
Natural	1.715	2.039	53.32	61.59	32.16	33.05
Mean	1.138	1.819	41.55	58.25	26.31	31.18
% Dec. from Uncaged Plots	37.4%		28.7%		16.2%	
Paired t test	t = 3.328		t = 3.240		t = 2.325	
3 D.F.	$p \leq 0.05$		$p \leq 0.05$		$p < 0.1$	

Key:- Wt. - weight; '000 - thousand; Av. - average; Dec. - decrease

caused decreases of 37%, 28% and 16% in weight of grain/ear, thousand grain weight and number of grains per ear respectively.

Regression analysis showed that the best associations between yield and aphid index were obtained with a log. transformation of yield against aphid index (table 6.2 (ii), figure 6.1). Correlations with peak aphid numbers were generally inferior, although not greatly so and a log. transformation of aphid index reduced the fit considerably (table 6.2 (ii)). The combination of 'flowering' and 'post-flowering' aphid indices (X3 + X4) did not give appreciably better correlations with the yield variables as they were already highly correlated with total aphid index (table 6.2 (ii)). The multiple regression using X3 + X4 is not statistically valid as these two aphid indices are not independent, there being a significant correlation between them ($r = 0.5136$, $p < 0.05$). Thus equations are given of the regressions of log. yield variables against total aphid index (table 6.2 (ii)). Comparison of slopes shows that thousand grain weight decreased more rapidly with aphid index than did number of grains per ear (by 1:7 times), hence aphids had a greater effect on grain weight than grain numbers. These differences are more clearly shown by the percentage yield losses for the three yield variables (table 6.3).

6.3 Insectary Experiments - Interactions Between Aphids and Plant Growth Factors on Yield Loss of Wheat

Materials and Methods

In the 1976 insectary experiment, plots still infested with aphids from the ground beetle experiment (Chapter 2) were sprayed at intervals with a systemic insecticide (Pirimicarb) to produce different periods of

Figure 6.1 1977 Field Experiment Relationship Between Weight of Grain Per Ear and Aphid Index

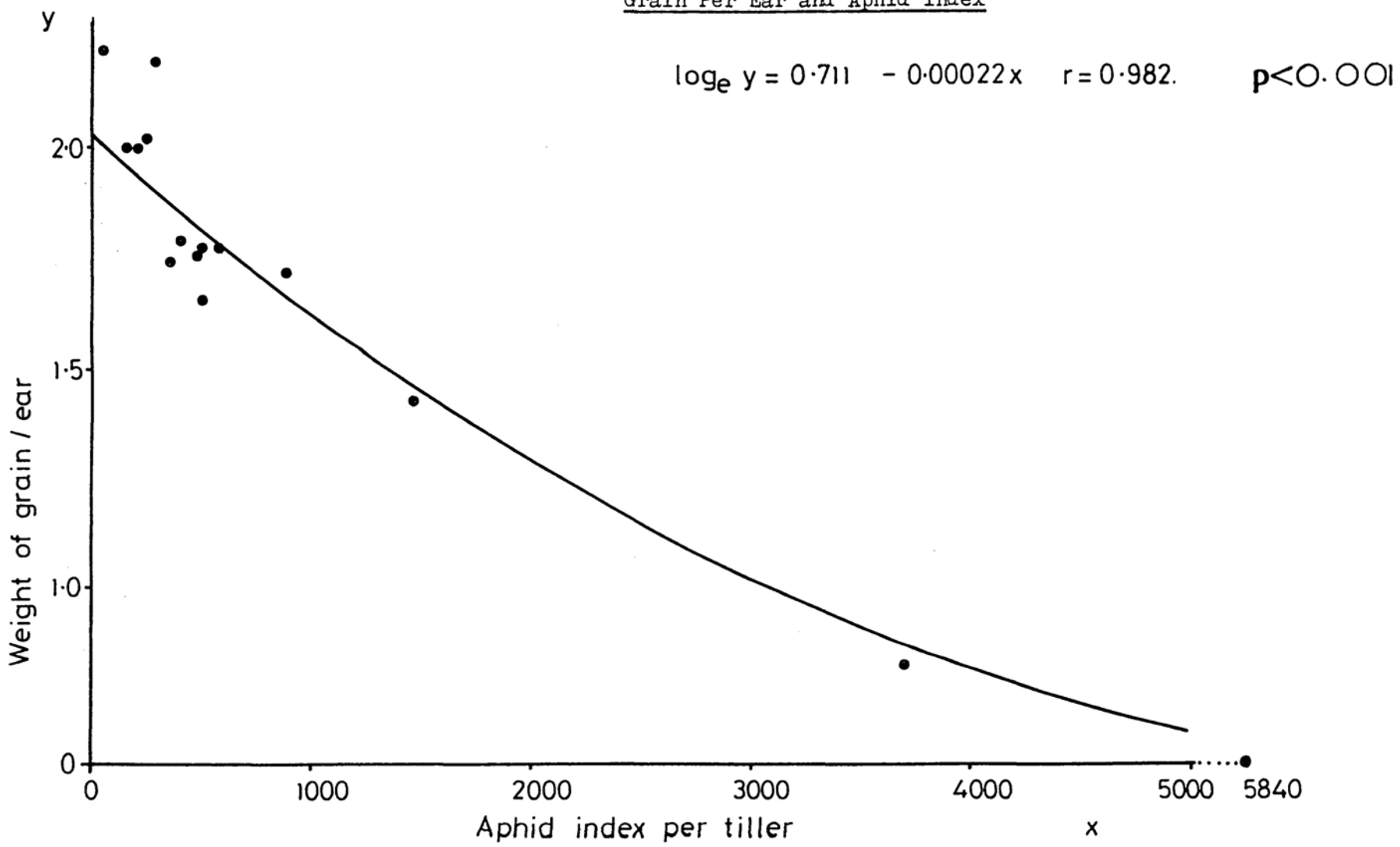


Table 6.2 Regression Analysis of Factors Affecting Yield

1977 Field Experiment

(i) Variables

X1	Total aphid index
X2	Peak numbers of aphids per tiller
X3	'Flowering' aphid index
X4	'Post-flowering' aphid index
Y1	Weight of grain per ear gm
Y2	Thousand grain weight gm
Y3	Number of grains per ear

(ii) Regressions

% Variance Accounted For DF = 15

	X1	logX1	X2	logX2	X3	X4	X3 + X4
Y1	87.4		83.5				
Y2	93.6		89.1				
Y3	85.0		83.9				
$\log_e$Y1	96.2	71.0	93.9	62.8	25.1	96.1	96.1
$\log_e$Y2	97.1	70.2	93.7	61.0	22.2	97.1	96.9
$\log_e$Y3	89.7	68.4	89.3	62.4	28.6	89.5	90.0

(iii) Equations

	% V.a.f.	
$\log_e Y1 = 0.711 - 0.000224\ X1$	96.2	$p<0.001$
$\log_e Y2 = 4.129 - 0.000142\ X1$	97.1	$p<0.001$
$\log_e Y3 = 3.491 - 0.0000819\ X1$	89.7	$p<0.001$

Figure 6.2 1976 Insectary Experiment Relationship Between Weight of Grain Per Ear and Number of Tillers Per Plant

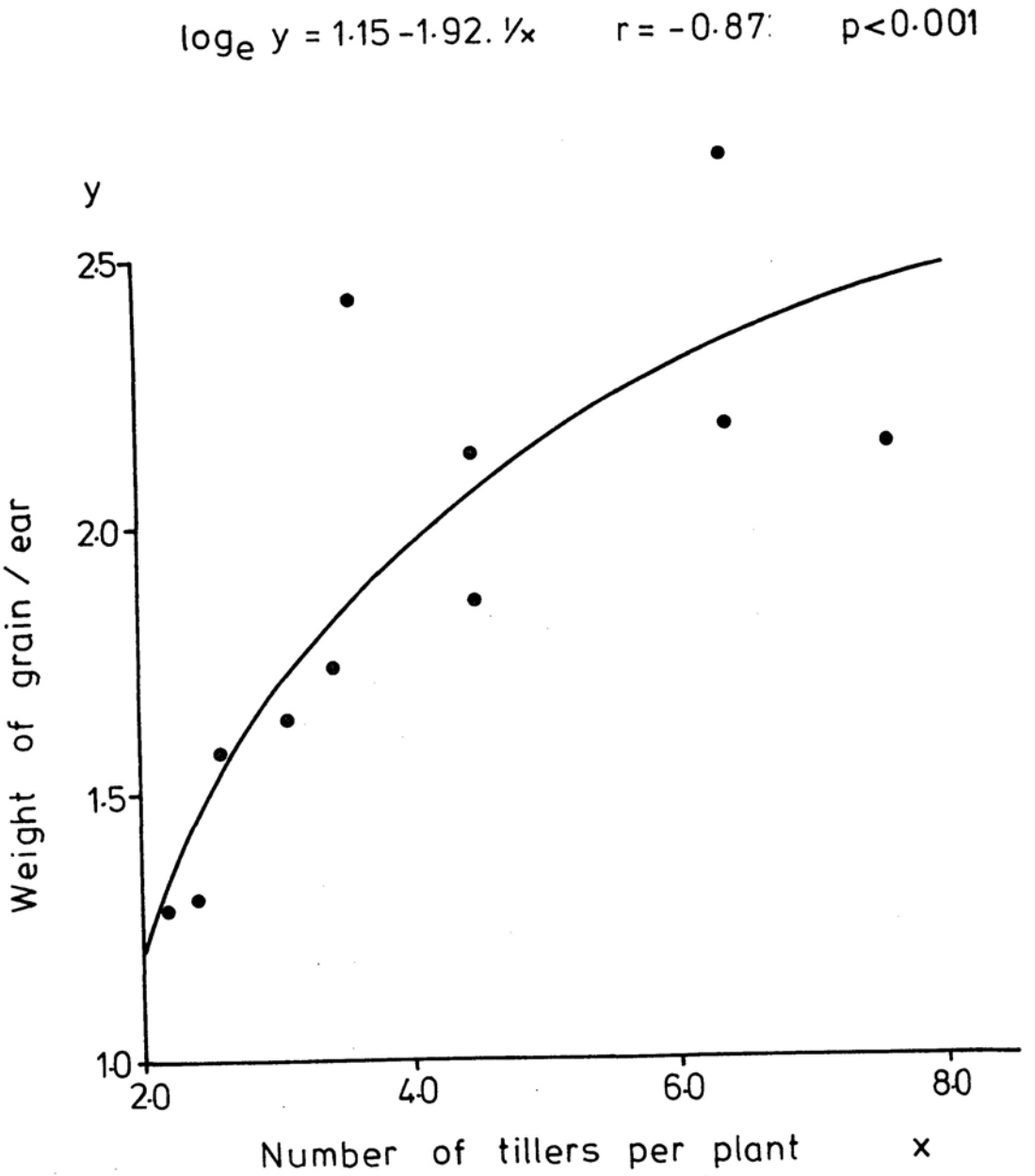


Table 6.3 Reduction in Yield by Aphid Pressure

1977 Field Experiment

(a) Aphid Index

Yield Parameter	% Yield Loss for Aphid Index		
	100	500	1 000
Weight Grain Per Ear	2.22	10.60	20.07
Thousand Grain Weight	1.41	6.86	13.25
No. Grains Per Ear	0.82	4.01	7.87

(b) Peak Aphid Numbers

Yield Parameter	% Yield Loss for Peak Nos./Tiller		
	5	25	50
Weight Grain Per Ear	1.4	6.8	13.2
Thousand Grain Weight	0.9	4.4	8.5
No. Grains Per Ear	0.5	2.6	5.1

aphid infestation and therefore different aphid indices. In 1977, different aphid indices resulted from the insecticide treatments and predation by coccinellid larvae in the coccinellid movement experiment.

In both years the plots were harvested when ripe at the beginning of August. In 1976, the height of tillers (to the top of the ear) was measured and the number of tillers per plant was counted for ten plants in the plot selected at random. These and a further fifteen ears were harvested from the plot. From these ears, the yield parameters weight of grain per ear, thousand grain weight and number of grains per ear were determined. In addition, the nitrogen content of the grain was analysed and expressed as percentage nitrogen. A different procedure was followed in 1977. All the stems from a row in the plot were cut at the base and collected together in a bundle, and the number of tillers per plant was recorded from the stubble. The harvested tillers were then spread out on a bench, the lengths of twenty representative tillers were measured and all the ears were removed. This was repeated for all the rows of every plot. The number of fertile and sterile spikelets of the ears of each row was counted and the grain was completely extracted. The total grain from the row was weighed and a sample of 250 grains was taken to determine the yield variables as in the 1976 experiment.

Aphid indices in the 1976 experiment were calculated for aphid numbers up to the flowering of the plants on June 12th (10.5.2 - Feeke's scale) - 'Flowering' aphid index, and for aphids from then until the insecticide spray - 'Post-flowering' aphid index, total aphid index being the sum of the two separate aphid indices. In the 1977 experiment, aphids were sampled separately from each row so that independent aphid indices could be calculated for the two outer rows of the plots (01 and 02) and the

middle row (M). Three categories of aphid index were again calculated. As before, 'flowering' aphid index covered the period of aphid infestation until flowering (June 2nd) and 'post-flowering' aphid index covered the remaining period until the extinction of the aphid populations (by July 18th), total aphid index again being the sum of the two.

Since all the plots contained aphids from previous experiments there were no control plots with zero aphids and yield losses were calculated from the appropriate regression equations.

Results

(a) 1976 Experiment

Linear regressions between all the variables (table 6.4(b) (ii)) revealed that the aphid indices were generally poorly correlated with the yield variables but that the measures of plant vigour (height of plant and number of tillers/plant) were well correlated with yield. A reciprocal transformation of number of tillers per plant (X5) gave improved correlations with the logarithm of the yield variables (figure 6.2, table 6.4(b) (ii)) but correlations between yield and aphid indices were not improved.

Although the yield variables were poorly correlated with total aphid index (X1) on its own, when combined with the reciprocal of number of tillers per plant ($^1/X5$) in a multiple regression the two factors accounted for 91% and 88% of the variance of log. weight of grain per ear and number of grains per ear (table 6.4(c)). For log. thousand grain weight, total aphid index combined with untransformed number of tillers per plant provided the best fit (66.5% V.a.f.). Incorporating height of plant (X4) with aphid index in multiple regressions against

Table 6.4 1976 Experiment

Relationships Between Aphid and Plant Variables and Yield

(a) Parameters

X1	Total aphid index
X2	'Flowering' aphid index
X3	'Post-flowering' aphid index
X4	Height of plant m
X5	Number of tillers per plant
Y1	Weight of grain per ear gm
Y2	Thousand grain weight gm
Y3	Number of grains per ear
Y4	Percentage nitrogen

(b) Correlation Matrices

(i) Untransformed data

X1	-0.284	-0.197	-0.290	0.098
X2	-0.501	-0.373	-0.525	0.396
X3	-0.205	-0.137	-0.206	0.031
X4	0.821	0.728	0.791	-0.275
X5	0.750	0.708	0.696	-0.209
	Y1	Y2	Y3	Y4

DF = 9

Significance Level for Correlation Coefficient

p	r
0.05	0.602
0.02	0.685
0.01	0.735
0.001	0.847

Table 6.4 (b) continued

(ii) Transformed data

X1	-0.261	-0.187	-0.276	0.100
X2	-0.502	-0.381	-0.515	0.376
X3	-0.181	-0.126	-0.194	0.037
X4	0.838	0.740	0.797	-0.260
$^1/X5$	-0.873	-0.734	-0.853	0.200
	$\log_e Y1$	$\log_e Y2$	$\log_e Y3$	$\log_e Y4$

(c) Regressions

Multiple Regression - Percentage Variance Accounted For

	X1	X2+X3	X1+$^1/X5$(X5)	X1+X4	X2+X3+$^1/X5$(X5)	X2+X3+X4
$\log_e Y1$	-3.5	8.8	91.4	66.0	90.3	74.7
$\log_e Y2$	-7.2	-5.8	54.5 (66.5)	44.5	48.1 (63.1)	55.5
$\log_e Y3$	-2.7	11.0	88.4	58.5	86.9	60.6
$\log_e Y4$	-10.0	-7.3	-17.7	116.0	-22.2	-22.2

Equations	% V.a.f.	
$\log Y1 = 1.377 - 0.000118\ X1 - 2.073\ ^1/X5$	91.4	$p \leq 0.001$
$\log Y2 = 3.510 - 0.0000588\ X1 + 0.0489\ X5$	66.5	$p < 0.01$
$\log Y3 = 4.404 - 0.0000808\ X1 - 1.356\ ^1/X5$	88.4	$p < 0.001$

Table 6.4 continued

(d) Percentage Yield Losses

(i)

% Loss From Yield Variable	Aphid Index			
	100	500	1000	Average (1567)
Y1	1.2	5.7	11.1	16.9
Y2	0.6	2.9	5.7	8.8
Y3	0.8	4.0	7.8	11.9

(ii)

% Loss From Yield Variable	Number of Tillers/Plant		
	Maximum (7.6)	Average (4.25)	Minimum (2.2)
Y1	0	19.3	48.8
Y2	0	15.1	23.2
Y3	0	13.1	35.5

For Average Number of Tillers Per Plant (4.25) and Aphid Index (1567):

(iii)

Yield Parameter	Overall % Decrease	% Due To Aphid Index	% Due To No. Tillers/Plant
Y1	48.9	27.5	72.5
Y2	37.5	30.7	69.3
Y3	40.0	28.4	71.6

yield gave inferior correlations as did the combination of 'flowering' and post-flowering' aphid indices (X2 and X3) with plant factors (table 6.4(c)). Percentage nitrogen gave poor associations with all the combinations (table 6.4(c)). and was not considered further.

Changes in aphid index and number of tillers per plant affected grain number (Y3) more than grain weight (Y2) (table 6.4(d) (i) and (ii)) and overall yield (weight grain/ear) was affected most as would be expected since it combined both Y1 and Y2. Because a reciprocal transformation of number of tillers per plant was used in the multiple regressions with weight of grain per ear (Y1) and number of grains per ear (Y3) (table 6.4(c), percentage losses for these yield variables increased more rapidly with decreasing tillers per plant than did percentage loss for thousand grain weight (Y2) which employed the untransformed plant variable in the regression (table 6.4(d) (i) and (ii)). Taking average levels for number of tillers and aphid index, number of tillers per plant was responsible for about 70% of the decrease and aphid index about 30%.

To conclude, in this experiment plant growth was poor probably because of poor soil fertility and consequently yield was affected more by the factors influencing plant growth, as measured by number of tillers per plant, than by aphid numbers.

(b) 1977 Experiment

Because of the better plant growth in this experiment total aphid index was significantly correlated with all the yield variables, accounting for 51.2%, 68.4% and 30.8% of the variance of weight of grain per ear (Y1), thousand grain weight (Y2) and number of grains per ear (Y3).

However, the yield-aphid index relationship was obviously curved (figure 6.3) and a logarithmic transformation (to base e) of the yield variables gave improved associations with aphid index (55.9%, 74.4% and 32.0% of the variance of log Y1, Y2 and Y3 respectively) (figure 6.4, table 6.5(b) and (c)).

Following the conclusions drawn from the 1976 experiment, the plant variables were analysed individually to assess their suitability for inclusion in multiple regression analyses against yield. Variation in height of plants was very small and there were no differences in height between outer and middle rows (mean heights for row 0, M and 02 were 1.033 m, 1.039 m and 1.033 m respectively) hence this factor was not used further. There were significantly fewer tillers per plant in the middle row (mean 3.55) than the two outer rows (means 5.03 and 4.83) ($F_{2,22} = 9.55$, $p<0.01$). However, the incorporation of number of tillers per plant (X4) with total and 'flowering' aphid indices (X1 and X2) in multiple regressions against yield did not give substantial improvements of fit (table 6.5(c)).

The variables which provided the best fit with yield were 'flowering' and 'post-flowering' aphid indices in a multiple regression (table 6.5(c)). Substantially better associations were obtained with this combination than with total aphid index alone and this was particularly noticeable with the yield variables involving grain number (Y3 - number of grains per ear and Y1 - weight of grain per ear).

A measure of the relative importance of the timing of aphid infestations was given by the ratio of the slopes of 'flowering' aphid index over 'post-flowering' aphid index in the multiple regressions. The ratios are

Figure 6.3 Effect of Aphid Pressure (Aphid Index) on the Yield of Wheat (As Wt. Grain/Ear)

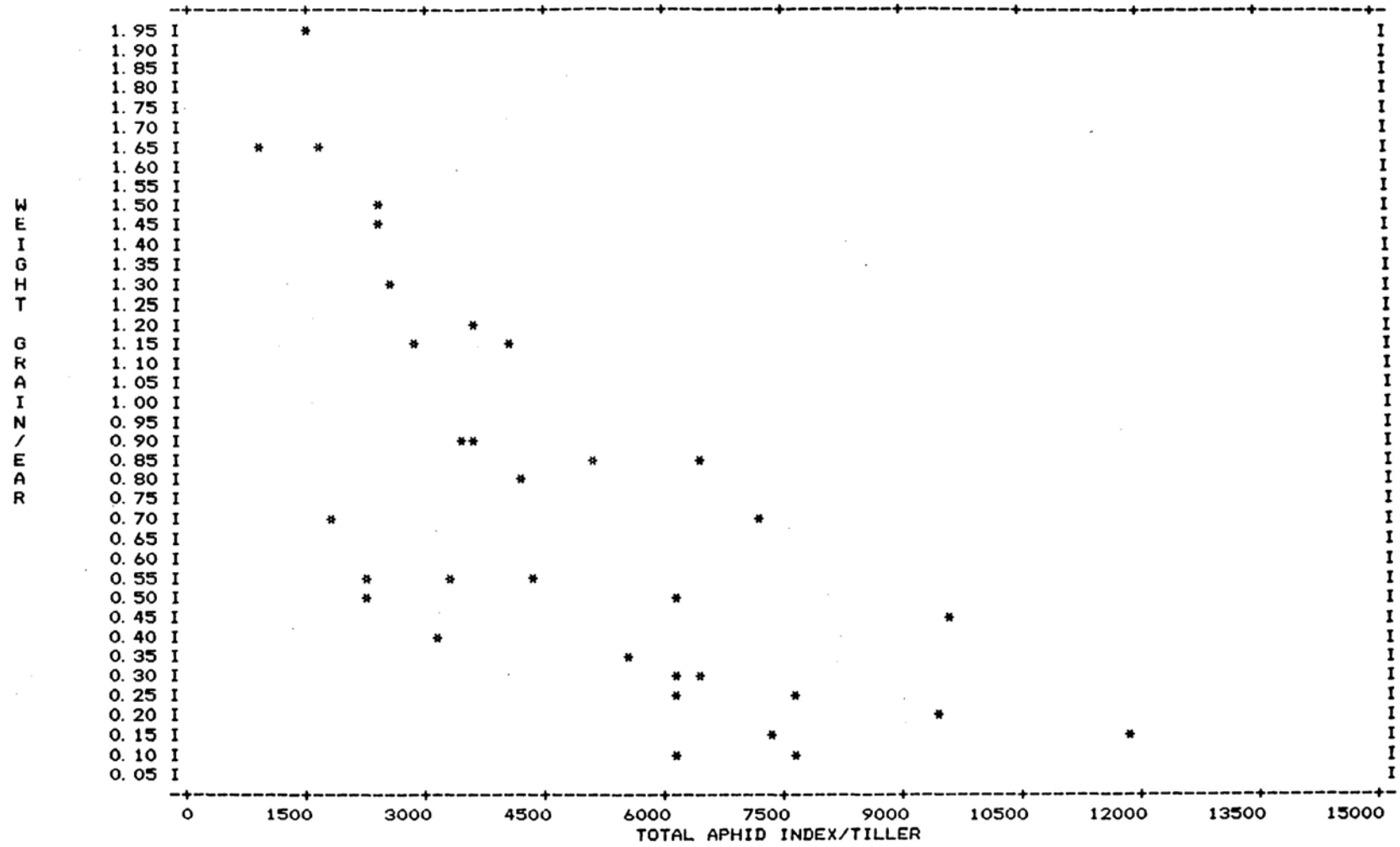


Figure 6.4 Relationship Between Log. Yield (Wt. Grain/Ear) and Aphid Index

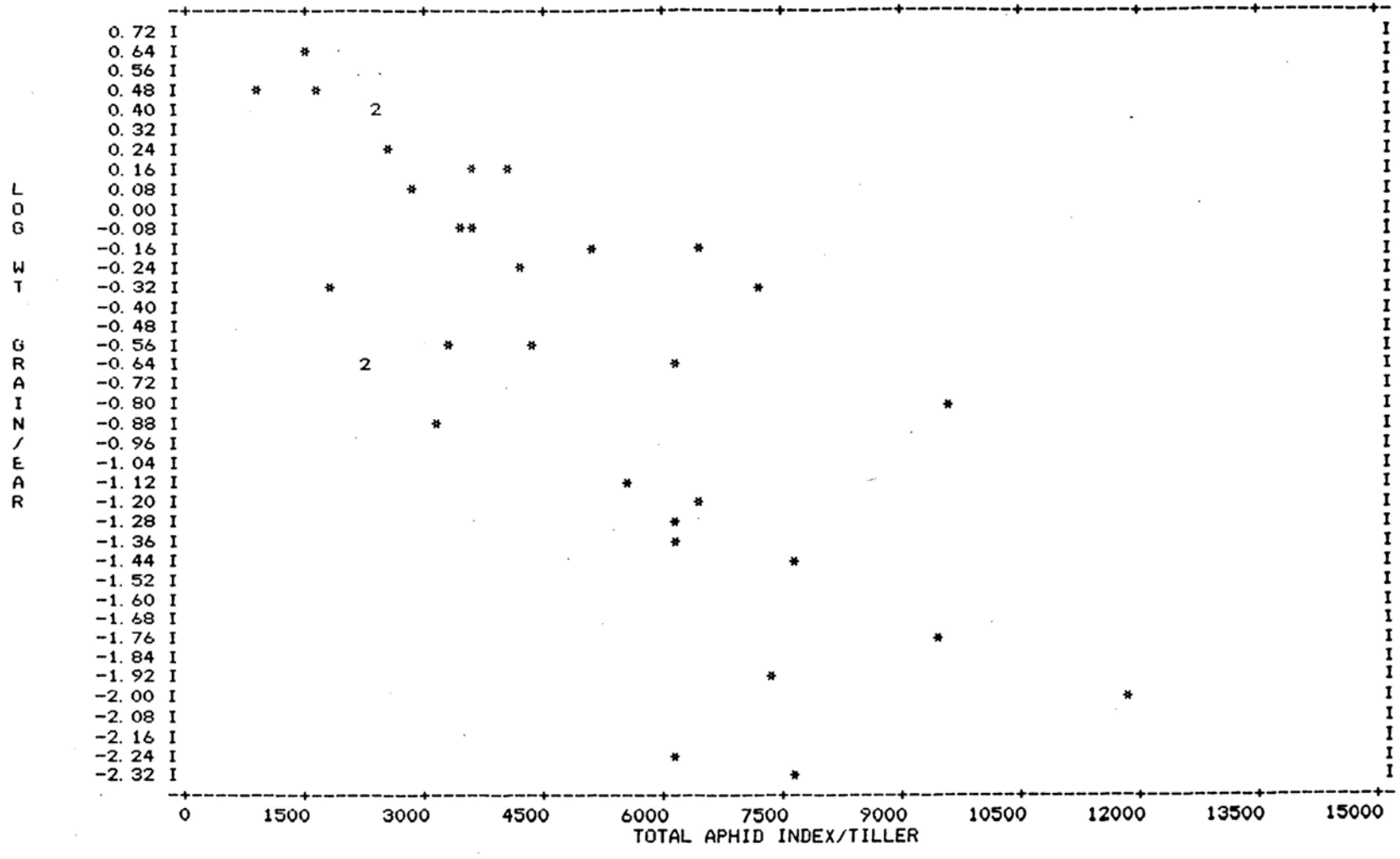


Table 6.5 1977 Experiment

Analysis of Factors Affecting the Yield of Wheat

(a) Variables

X1	Total aphid index
X2	'Flowering' aphid index
X3	'Post-flowering' aphid index
X4	Number of tillers per plant
Y1	Weight of grain per ear gm
Y2	Thousand grain weight gm
Y3	Number of grains per ear

(b) Correlation Matrix

X1	-0.757	-0.867	-0.584
X2	-0.483	-0.343	-0.561
X3	-0.705	-0.832	-0.522
X4	0.158	0.107	0.178
	$\log_e$Y1	$\log_e$Y2	$\log_e$Y3

DF = 31

Significance Level for Correlation Coefficient

p	r
0.05	0.349
0.02	0.409
0.01	0.449
0.001	0.554

Table 6.5 continued

(c) Regressions

Multiple Regression - Percentage Variance Accounted For

Yield Variable	X1	X2	X2 + X3	X1 + X4	X2 + X4
$\log_e$Y1	55.9	20.9	72.2	57.2	23.1
$\log_e$Y2	74.4	8.9	80.5	74.8	8.1
$\log_e$Y3	32.0	29.3	56.8	33.2	33.1

Total Aphid Index Alone	% V.a.f.	
$\log_e Y1 = 0.559 - 0.000240\ X1$	55.9	$p<0.001$
$\log_e Y2 = 3.453 - 0.000137\ X1$	74.4	$p<0.001$
$\log_e Y3 = 3.933 - 0.000104\ X1$	32.0	$p<0.001$

'Flowering' and 'Post-flowering' Aphid Indices	% V.a.f.	
$\log_e Y1 = 1.338 - 0.00150\ X2 - 0.000226\ X3$	72.2	$p<0.001$
$\log_e Y2 = 3.791 - 0.000537\ X2 - 0.000133\ X3$	80.5	$p<0.001$
$\log_e Y3 = 4.468 - 0.000972\ X2 - 0.0000946\ X3$	56.8	$p<0.001$

Table 6.5 continued

(d) Percentage Yield Losses

(i) Regressions with Total Aphid Index

Yield Factor	% Yield Loss for A.I. 100	500	1000	Average A.I. 4645
Y1	2.4	11.3	21.3	67.1
Y2	1.4	6.6	12.8	47.1
Y3	1.0	5.1	9.9	38.2

(ii) Regressions with 'Flowering' and 'Post-Flowering' Aphid Indices

Yield Factor	% Yield Loss 'Flowering' A.I. 100	500	1000	Average A.I. 657
Y1	13.9	52.8	77.7	62.7
Y2	5.2	34.3	41.6	29.7
Y3	9.3	38.5	62.2	45.6

Yield Factor	% Yield Loss 'Post-Flowering' A.I. 100	500	1000	Average A.I. 3989
Y1	2.2	10.7	20.3	59.5
Y2	1.3	6.4	12.4	41.2
Y3	0.9	4.6	9.0	31.4

Table 6.5(d) continued

For Average 'Flowering' (657) A.I. and 'Post-Flowering' A.I. (3989)

(iii)

Yield Factor	% Decrease Overall	% Due to 'Flowering' A.I.	% Due to 'Post-Flowering' A.I.
Y1	84.9	52.2	47.8
Y2	58.6	40.0	60.0
Y3	63.8	62.8	37.2

Key: (to all parts of table 6.5) A.I. - Aphid Index

largest, i.e. 'flowering' aphid index has its greatest influence, with the yield variables involving grain number (Y3 - ratio 10, Y1 - ratio 6.6, Y2 - ratio 4).

The relative effect of aphid infestations on grain number and grain weight depends, in this instance, on the aphid variables used in the regression analysis. If total aphid index is used, the slopes of the regressions and the percentage yield losses show that aphids have a bigger effect on grain weight than on grain number (table 6.5(c) and 6.5(d) (i)). However, if the combination of 'flowering' and 'post-flowering' aphid indices are used, the relative effects of aphids on grain weight and numbers will depend on the proportions of the component aphid indices. Taking the average aphid index occuring in the present experiment, when 'post-flowering' aphid index was six times as great as 'flowering' aphid index, the percentage decrease of number of grains per ear was slightly greater than that of thousand grain weight (64% and 59% respectively) (table 6.5(d) (iii)).

The effects of the different slopes of the regressions are best illustrated by considering percentage yield reductions (table 6.5(d)). Percentage yield losses due to 'flowering' aphid index were of a greater scale than those resulting from 'post-flowering' aphid index (table 6.5(d) (ii)), which were similar to percentage losses with total aphid index (table 6.5(d) (i)). Taking average experimental values again, to give the proportions of the aphid indices, 'flowering' aphid index contributed 63% of the decrease of number of grains per ear, 'post-flowering' aphid index producing the remaining 37%, whereas for thousand grain weight, 'flowering' aphid index contributed 40% of the decrease and 'post-flowering' aphid index 60% (table 6.5(d) (iii)). For overall yield, weight of grain per ear (Y1), these effects even out, 'flowering' aphid index contributing 52% to the decrease and 'post-flowering' aphid index 48%. Finally, the combination of the two aphid indices indicates a much greater percentage yield reduction for all the yield variables than does total aphid index alone (table 6.5(d) (iii) compared to table 6.5(d) (i), percentage reduction in Y1 - 67% and 85% for total aphid index and 'flowering' and 'post-flowering' aphid indices respectively). Comparison of percentage losses due to 'flowering' and 'post-flowering' aphid indices alone, at fixed aphid indices (table 6.5(d) (ii) - 500 A.I. in the present example) shows that the damage per aphid on weight of grain per ear was approximately five times as great for aphids at flowering than after flowering. Similarly, reduction in thousand grain weight and number of grains per ear per aphid was 5.4 times and 8.4 times as great, respectively, at flowering than after flowering.

Thus, significantly different consequences result when variation in yield is accounted for by 'flowering' and 'post-flowering' aphid indices

instead of the total aphid index. These are; aphids before flowering became proportionally more important than those after flowering, aphids affect grain numbers more than grain weight, and percentage losses are greater.

Effect of plant competition between rows on the aphid index - yield relationship

A parallel regression technique was used to analyse differences in the yield-aphid index relationship between outer and middle rows of the plots. Separate regressions of log. weight of grain per ear (Y1) against 'flowering' (X2) 'post-flowering' (X3) aphid indices for outer (O) and middle (M) rows gave the following equations.

$$\log Y1(O) = 1.450 - 0.00163\ X2(O) - 0.000201\ X3(O)$$
$$\log Y1(M) = 1.610 - 0.00165\ X2(M) - 0.000310\ X3(M)$$

A common slope was then fitted and the significance of the reduction in fit tested (parallel slopes):

$$\log Y1(O) = 1.555 - 0.00160\ X2(O) - 0.00023\ X3(O)$$
$$\log Y1(M) = 1.146 - 0.00160\ X2(M) - 0.00023\ X3(M)$$

Variance Ratio $F_{2,27} = 1.63$ n.s.

Thus the individual slopes were not significantly different from the common slope and therefore not from each other.

A common intercept and slope was then fitted and tested for a reduction in fit compared with the individual intercepts:

$$\log Y1 = 1.338 - 0.00150\ X2 - 0.000226\ X3$$

Variance Ratio $F_{1,29} = 7.44$ $p<0.05$

Thus the intercepts for outer and middle rows were significantly different.

Thus the nature of the relationship between yield and the aphid indices was different for outside and middle rows of plants, the slopes being parallel and the intercept lower in the middle than outside rows.

For the other yield variables, thousand grain weight and number of grains per ear, a similar pattern of differences emerged. The variance ratio for difference between the slopes of outer and middle rows with log. thousand grain weight was nearly significant ($F_{2,27}$ = 2.30; $F_{2,27}$ at $p<5\%$ = 3.35) and the difference between intercepts was significant at $p<0.05$ ($F_{1,29}$ = 4.67). With number of grains per ear there was no difference between slopes ($F_{2,27}$ = 1.07) but significantly different intercepts ($F_{1,29}$ = 6.00, $p<0.05$) with outer and middle rows.

6.4 Discussion

Effect of Aphids on Yield in the Field and Insectary Experiments

The yield-aphid index relationships from the North Farm field experiment for 1977 were of a similar nature to those reported elsewhere in the literature. Peak numbers of Sitobion avenae at similar levels to those produced by the experimental treatments have been found by Wratten (1975) (111/stem), Kolbe (1969) (50/tiller), Harper (1973) (74/tiller) and Dyadechko and Ruban (1975) (180-240/ear), control yield (as intercept of regression of log. weight grain per ear against aphid index) was of a similar level to that found by Wratten (1975) (1.6 gm/ear) and Kolbe (1969) (average grain weight 45-55 mg). However, percentage yield loss for 1000 aphid index was slightly higher than that found by Rautapää (1966) (10%) but similar to that found by Carrillo et. al. (1974) (20%).

However, in the insectary experiments the control yield (as defined above) was higher than in the field experiment, which was mainly due to greatly increased grain numbers, the individual grain weight being less (table 6.6). This was probably due to the change in growth pattern of the wheat in the insectary produced by higher temperatures and better growing conditions early in spring.

Table 6.6 Control Yields (As Intercept on the Best Fit Log. Yield-Aphid Index Regression) in the Field and Insectary Experiments

Experiment	Control Yields			Number of Spikelets Per Ear
	Weight Grain Per Ear g	Thousand Grain Weight g	No. Grains Per Ear	
North Farm 1977	2.04	62.2	32.8	19.1
Insectary 1976	2.73	33.4	81.8	20.8
Insectary 1977	3.81	44.3	87.4	23.4

The variability of plant growth in the 1976 insectary experiment was probably a result of variations in soil fertility as the insectary had not been used for several years previously. Moreover, despite Wratten's (1975) assertion to the contrary, aphids seem to have had some influence on grain numbers after flowering, possibly through seed abortion and this has also been found by Rautapää (1966) and Hinz and Daebler (1976). In the 1976 experiment percentage nitrogen in the grain varied little and was not correlated with any of the aphid or plant factors, a situation similar to that reported by Wratten (1978) and presumably a consequence of similar causes. The high correlations achieved by the regression equations between yield and aphid index over a large range of aphid

densities suggest that the extrapolation of the regression line to yield at zero aphid index (i.e. the intercept) is valid. In addition, there seems no reason to suppose, as does Vereijken (1979), that yield losses are of a different scale at high aphid densities.

For the 1977 insectary experiment, using the criteria of goodness of fit, the combinations of 'flowering' and 'post-flowering' aphid indices undoubtedly provided a better explanation of the variation in yield than did total aphid index alone. Indeed, in so far as correlation can be taken to imply cause and effect and an increase in fit a better explanation of that cause, then the 'flowering' and 'post-flowering' aphid index model is to be preferred as a description of the mechanism which caused the yield losses in the experiment. However, there was no equivalent effect with results from the field experiment and absolute measures of yield losses which could determine the correct model could not be obtained, since there were no control plots with zero aphids, all the plots having had aphid treatments. An experiment with separate treatments of pre- and post-flowering aphid infestations may be illuminating, although Rautapää (1966) found no significant yield differences using these treatments.

The effect of spacing of wheat plants on the yield per tiller was investigated by Watson and French (1971) and they concluded that the increase in yield of plants in widely spaced rows was due to increased uptake of nitrogen. A similar effect was seen in the 1977 insectary experiment where control yields (i.e. intercepts of the yield-aphid index regressions) were significantly higher in the outer rows of the plots compared to the middle row of plants. The lack of significant differences between the slopes of the yield-aphid index regressions indicated that

aphids did not interact with plant competitive effects, such as reduced nitrogen uptake, reduction in photosynthesis by shading, competition for water, etc.

Economic Thresholds

The increased numbers of aphids in the predator exclusion (caged) plots caused an average yield reduction (as weight of grain per ear) of 37% compared to the uncaged plots. Thus factors which reduce the effectiveness of natural enemies could have consequent large effects on the resulting yield.

Economic thresholds of yield loss from aphids have been given at 5 aphids/ear (George, 1975), 15/ear (Latteur, 1976), 25-50/tiller (Kolbe, 1969) (see table 1.1 for more examples). Percentage yield reduction in the 1977 field experiment for 5, 25 and 50 aphids per tiller is given in table 6.3(b). Significant yield reduction probably only occurred at 25 aphids/tiller. In the 1977 field experiment, peak aphid numbers in the control plot (N1) were 30.7 $\pm$ 2.15 per tiller which produced an average yield reduction (as weight of grain per ear) of 8.3% with a range of 7.8-8.9% due to the variation in aphid numbers. The natural variation in yield production is unlikely to exceed this degree of yield loss, hence this level of aphids probably produced a statistically significant decrease in yield relative to an uninfested crop and therefore would have been worth spraying with insecticide. In Great Britain spraying is recommended at the flowering stage if aphid numbers are greater than 5/ear and increasing (George, 1975). In the 1977 field experiment, aphid numbers were 3.6/tiller at flowering in plot N1 and these increased to damaging numbers two weeks later. Thus, although peak numbers of 5/tiller would produce

negligible yield loss as seen from table 6.3(b), increase from this level after the flowering stage gave rise to significant damage in the 1977 field experiment. The prevention of economic loss in these circumstances depends upon accurate assessment of aphid densities at the flowering growth stage and subsequent aphid increase to damaging levels. Farmers are generally unable to spend time counting aphids in individual fields and in Holland the association between probit percentage infested ears and $\log_{10}$ aphid numbers (equivalent to logistic curves in figures 4.11 and 4.12) has been used to provide an alternative means of estimating aphid numbers (Vereijken, 1979). However this method of estimating aphid numbers from tiller infestation may have to be revised in the light of the conclusions drawn in Chapter 4, section 3). Farmers sample fifty ears in the crop to determine the percentage of ears infested which gives a measure of the number of aphids present. Accurate prognosis of aphid population growth is essential for the provision of reliable advice to farmers in order to avoid control measures being taken when damage has already been wreaked or when aphids are about to decrease naturally. This was observed in the South Downs in 1976 when a farmer was spraying fields by helicopter when our sampling indicated that aphid populations had already collapsed.

Yield losses do not always have a direct relationship with aphid numbers, however, since plant growth can have a substantial effect on potential yield production as illustrated by results from the 1976 insectary experiment. In the field there are often areas of the crop that have poor growth, both at the edges where cultivation may be less intense and in patches where soil fertility is low. Aphids are often more noticeable on these areas but may only be responsible for 30% of the

reduction in yield compared to the healthy crop, about 70% of the difference being due to poor plant growth. Thus a farmer may be tempted to spray the perimeter of a field to control aphids, as recommended by Wetzel (1972) when the major cause of yield loss is poor plant growth which he can do nothing to correct retrospectively.

Associations between yield and aphid indices from the 1977 insectary experiment demonstrated the importance of aphid infestations during flowering especially with regard to the effect on grain numbers. Thus control of a given number of aphids will produce a greater saving of yield if undertaken during flowering than during milky-ripe growth stage. This factor is reflected in the latest attempt at establishing a workable economic threshold for aphids in wheat. Vereijken (1979) suggested that a threshold of 5 aphids/ear would be satisfactory at flowering, but after flowering the threshold should be raised to 10 aphids/ear. This agrees with present advice given to farmers in Great Britain (George, 1975). However, such a threshold is likely to be exceeded in many years over the country and may bring farmers to the conclusion that it would be economically worthwhile to make a routine spray of insecticide at flowering. This would inevitably give rise to the well known ecological hazards associated with regular input of noxious chemicals into an ecosystem, namely elimination of predators followed by pest resurgence, selection of resistant strains of pest and phytotoxicity. Indeed, pest problems in other agricultural crops could be exacerbated by the widespread and regular use of insecticides for aphid control (Vickerman and Sunderland, 1977).

To conclude, the present economic threshold in Great Britain and Holland is adopted to minimize the risk of development of damaging aphid

infestations in the crop, however, it can be argued that until aphid population development and subsequent damage can be accurately predicted, no meaningful economic threshold can be drawn.

Variability of Yield Production

In field trials the natural variability of yield per tiller is often so high that aphids have to reach high levels before significant yield losses occur (Vereijken, 1979). Indeed, the high economic thresholds given by several workers, Kolbe (1969), Stern (1967), Frier and Wetzel (1976), may be a consequence of this large variability. Thus measures of within plot variability of aphids and yield per tiller would be useful to determine whether aphids could have an effect on the variation of yield by interacting with plant nutritional status. A reduction in yield variation would be achieved by selective attack on healthy tillers and an increase by proportionally greater yield reduction on the low quality plants. For moderate infestations this may be as important as the overall reduction in yield since the production of grains smaller than the size retained by the combine harvester gives greater wastage at harvesting.

The determination of an economic threshold depends upon a consistent relationship between yield loss and pest numbers so that the economic benefits of pest control can be established. However, in cereals the yield loss at the economic threshold has a great deal of variability associated with it. For example, Vereijken (1979) calculated that for a threshold of 15 aphids/car the yield loss was 180 $\pm$ 230 kg/ha or 128% variation around the mean. This has three causes:-

(1) Errors in the regression analysis of yield against aphid numbers due to the number of observations.

(2) Errors in observation of aphid numbers and determination of yield.

(3) Damage per aphid is not constant. This is affected by the timing of aphid numbers relative to plant growth stage, factors affecting plant growth altering the maximum attainable yield and effect of aphid honeydew and saprophytic mould on photosynthesis.

Arguably, the variation in damage per aphid is the most important factor causing variation in yield reduction. The insectary experiments suggest that the first two factors affecting damage per aphid i.e. timing of aphid infestation and effect of plant growth, have a quantifiable impact on the relationship between aphids and yield and therefore can reduce the unexplained variation. Moreover, Vereijken (1979) purports to show that honeydew contributes 50% of the total damage caused by aphids, the remaining 50% being damage resulting from extraction of sap. However, it remains to be seen whether honeydew can account for yield loss to a similar degree of accuracy as aphids have in the present experiment.

CHAPTER 7

GENERAL DISCUSSION

7.1 Population Dynamics of Aphids and the Importance of Predation

The description of the development of aphid populations presented here is based on factors affecting aphids in winter wheat in 1976 and 1977, which were both 'outbreak' years and therefore the explanations may not necessarily apply to events in other years.

In the field of winter wheat studied at North Farm, immigration of alatae was greater in 1977 than in 1976. This was reflected by the effect of the cages in 1977 which delayed the initial increase of aphids relative to the field plots. Moreover, the different aphid densities in the artificially infested plots were supplemented by the large numbers of alate immigrants. However, the population establishment, as measured by the initial maximum rate of infestation, was quicker in 1976 than in 1977, presumably because of the higher ambient temperature. At this stage, with an expanding population, aphid dislodgement by weather depends on the sharpness of the change in weather conditions, the level of crowding (i.e. the number of large aphid colonies) and the degree of shelter offered by the plant. Even a heavy thunderstorm dislodged negligible numbers of aphids when they had been acclimatized to inclement weather, and were not affected by crowding in large colonies and were well sheltered. Moreover, the aphid's searching behaviour for plants ensures that they would spend a minimum amount of time on the ground before ascending a plant, thereby incurring little risk of predation on the ground.

The capacity of ground beetles for predation of cereal aphids is large; adult Agonum dorsale can eat up to thirty-eight aphids per day, and larvae twenty per day. Indeed, the consumption of aphids depends upon the size of the beetle but in A. dorsale is independent of the reproductive status of the beetle. This suggests that egg laying does not have a disproportional effect on aphid consumption. In the larger Pterostichus melanarius, however, reproductive status of the beetles has an effect on aphid consumption since spent females consumed proportionally more for their size than did gravid females or males.

The activity of ground beetles and therefore their potential for aphid predation is greatly dependent on environmental conditions such as microclimate humidity. In the 1976 field experiment, and 1976 and 1977 insectary experiments, the dry conditions were evidently not suitable for beetle activity and aphid predation was low. However, with favourable environmental conditions, as in the 1977 glasshouse experiment, even large carabid species can search small plants to find and eat aphids. In the 1977 field experiment, however, predation by other polyphagous predator groups was more important, the exclusion of the staphylinid, Tachyporus spp, giving rise to higher rates of aphid increase.

Systemic fungicides are normally applied at the flowering stage of plant growth and hence have the potential to affect aphid populations greatly. Many fungicides had no effect on aphid mortality, some affected reproductive rate, and others killed aphids outright. By slowing the rate of aphid increase in the field, fungicides could increase the chances of predatory control, since aphid consumption by ground beetles was unaffected by fungicide contamination, which would also probably be the case with aphid specific predators.

Aphid populations are naturally self-regulating and cereal aphids are no exception. When the effect of predators was reduced by the cages, aphids showed the dynamics of populations regulated mainly by emigration, with natural enemies hastening the decline of the populations to produce a density dependent response. In the uncaged plots aphid specific predators (coccinellids and syrphids) and disease (Entomophthora) affected aphid populations that were already self-regulating and by doing so reduced the maximum numbers reached and accelerated the decline but did not greatly influence the timing of the population peak. Thus the population collapse was triggered by emigration and amplified by biotic mortality factors. Moreover, the action of wind was enhanced by natural enemies, aphid crowding and the ripening of plants and produced extensive aphid dislodgement as populations were decreasing.

Finally, the yield was affected in proportion to the number of aphids present and the time spent on the plant. Natural enemies were very important in this regard since the net effect of their exclusion was a significant decrease in yield. Plant factors modified the effect of aphids on yield. Aphids were proportionally more damaging at an early growth stage (flowering), particularly affecting grain number, and were more damaging on less vigorous plants (measured by number of tillers per plant). Yield losses were consistent with an economic threshold of five aphids per ear, provided that aphid numbers would otherwise increase. A rectangular hyperbola model gave a good description of the relationship between percentage plants infested and aphid population, and, were this to be used in place of counts of aphid numbers to determine economic thresholds in the field, then percentage of tillers infested by aphids for the economic threshold would be about 55%.

7.2 Possibilities for Increasing the Effectiveness of Natural Enemies

(1) Attraction of aphid specific predators into the field early in the season. This has been tried by artificially introducing aphids into the field (1977 North Farm field experiment) or by using artificial attractants (R. Chambers, unpublished) but has not been successful perhaps because predators are not active in sufficient numbers at the right time.

(2) Introduction of predators from laboratory reared stocks to synchronize with aphid immigration. The use of parasites in this way has not been successful (R. Chambers, pers. comm.) and the method is not feasible over the large area of cereals grown.

(3) Manipulation of polyphagous predator populations. As more is discovered about the population dynamics of the important ploy phagous predators such as A. dorsale and Tachyporus spp possibilities may arise of feasible cultural measures to increase or stabilize populations of these predators so that large populations become more frequent and more effective.

(4) Fungal pathogens are the natural enemy group most appropriate for direct use in the field. Verticillium lecanii has been used successfully to control aphids on chrysanthemums in commercial glasshouse trials (Hall, 1979), and it may be possible to use the fungal pathogen of cereal aphids, Entomophthora spp in a similar way in cereals. However, major obstacles are present because Entomophthora spores are airborne and therefore cannot be applied as a spray and development of an aphid-controlling epizootic in the field is very dependent on high humidity and a high aphid density.

(5) Measures reducing the intrinsic rate of natural increase (r_m) of cereal aphids are, in my opinion, the most promising area for increasing the effectiveness of natural enemies in the field. Reduction in r_m could be produced by cereal varieties resistant to aphid increase (Lowe, 1978) or perhaps by the judicious use of systemic fungicides affecting aphid reproduction. This would delay the production of large aphid populations relative to plant growth stage so that peak numbers would tend to occur on more mature plants and would therefore be more affected by decreasing natural fecundity and increasing natural mortality (Watt, 1979). Moreover, a reduction in r_m, while increasing the importance of aphid mortality from natural enemies would also decrease the importance of synchronization between aphid and predator immigration and thus would greatly increase the potential for natural enemy control of aphid populations. Finally, the peak aphid numbers occurring later in the plant growth stage would exert proportionally less effect on yield.

7.3 Integrated Control of Cereal Aphids

Present aphid control schemes are based solely on economic thresholds of yield loss and ignore the consequences of chemical use on the cereal ecosystem as a whole. In addition to the problems of aphid resistance to chemicals, of population resurgence of aphids and phytotoxicity, new pests may be created by the regular and indiscriminate use of agricultural chemicals in the same way that fruit tree red spider mite became a major pest problem in orchards (Collyer, 1953a, 1953b, Collyer and Kirby, 1955 and 1959) and whitefly has become a major pest on cotton in the Sudan (N. W. Hussey, personal communication).

Thus the control of aphids should be considered in the context of effects on the cereal ecosystem as a whole and researchers need to be able to predict expected levels of aphid infestations and potential damage so that control measures can be planned and executed at the optimum time. Fundamental research to achieve this objective is in three parts:-

(1) Prediction of the timing and scale of aphid immigration. The major sources of summer migrants are not known but investigations on this topic and the survival of cereal aphids over winter and in the spring are proceeding. Moreover, although efforts to use aphid catches in suction traps to predict immigration into the crop have been unsuccessful, new theories are being tested which may improve the situation (A. Dewar, pers. comm.).

(2) Prediction of aphid population development in the summer. This requires a knowledge of the population dynamics of aphids and their predators, pathogens and parasites. The simulation model developed by Rabbinge, Ankersmit and Pak (1979) produced a reasonable description of aphid population development in the field in the years 1975-1977 but they found that because of the paucity of information concerning the action of natural enemies aphid mortality from this source was poorly represented in the model.

(3) Prediction of damage to plants caused by aphids. Despite much research yield losses in the field remain largely unpredictable partly because aphid numbers cannot be accurately predicted and partly because the factors influencing the variation in yield loss per aphid are not fully understood.

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APPENDIX 1

SAMPLING PRECISION OF PLANT COUNTS OF APHIDS AND THE D-VAC SAMPLER

The sampling of aphids from a cereal crop is generally carried out either by visual inspection of plants and counting the aphids present or using a suction sampler to remove aphids from an area of crop for subsequent counting.

The sampling precision of both these techniques was investigated.

A.1 Plant Counts of Aphids

Introduction

Most aphid sampling has been carried out by the inspection of fixed numbers of cereal tillers or parts of plants, for example, ears (e.g. Wratten (1975), Rautapää (1976) among others). However, the units in which aphid populations have been expressed are often a source of confusion. Aphid populations have been expressed as numbers per tiller, per 100 tillers, per ear, per plant and even per 0.3 m row of plants, all of which makes comparisons difficult. In addition, the figures for aphid population size quoted are often mean values and comparisons are made without regard to population variability.

Sampling plans have been developed for pests in other crops, such as cabbage root fly in brassicas (Finch et. al., 1978) which enable population data from Britain and Canada to be compared. However, there have been no attempts to produce a sampling plan for aphids in cereals.

Using results from three contrasting years of aphid abundance (1976, 1977 and 1978) at North Farm, a sampling plan was devised which was suitable for the sampling of small experimental plots in cereal fields and which would enable sampling to be carried out at a constant level of precision.

Materials and Methods

The level of tolerance or sampling precision required from an aphid sample is the mean number of aphids expressed as a percentage of the 95% confidence interval limits for that sample, i.e. CI x 100/mean.

The sampling plan was a plot of the number of tillers to be sampled for a given level of tolerance against the mean number of aphids per tiller. The number of tillers to be sampled was calculated using the following equation:-

$$n \geq \frac{4.s^2}{a^2.(\bar{x})^2} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(1)$$

where n is the number of tillers to be sampled, a, the tolerance level selected and $\bar{x}$ and s^2, the mean and variance of the sample used. This is equivalent to equation (14) in Karandinos (1976).

For a precision level of 20%, a = 0.2 and the number of tillers to achieve that precision level with a population mean of $\bar{x}$ is:-

$$n = \frac{100.s^2}{(\bar{x})^2} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(2)$$

Following Finch, Skinner and Freeman (1978) a 20% tolerance level was selected and using sample means and variances from the 1976, 1977 and 1978 field experiments a plot of number of tillers to be sampled against

population mean was produced. The transformation used to describe the curve was obtained using the power law relationship between log. variance and log. mean (Taylor, 1961):-

$$\text{i.e. } \log_e s^2 = a + b.\log_e \bar{x}$$
$$\text{or } s^2 = e^a.\bar{x}^b \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(3)$$

Substituting in equation 2:-

$$n = \frac{100.e^a.\bar{x}^b}{\bar{x}^2} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(4)$$

Taking logs:-

$$\log_e n = (2 + a) - (2 - b).\log_e \bar{x} \quad \ldots\ldots\ldots\ldots\ldots(5)$$

Thus a logarithm transformation of both axes was required and the resulting equation should also be related to the power law regression equation.

Results

The level of tolerance or precision achieved from the number of tillers sampled varied greatly throughout the season (table A.1). In particular, samples at peak aphid numbers were more accurate than those before and after the peak. Sample sizes for constant tolerance levels (10% and 20%) were calculated and compared with the number of tillers actually sampled (table A.1). A level of 10% is the precision level usually adopted (Southwood, 1966), but this level of tolerance would result in very large numbers of tillers having to be sampled. For example, in plot N1 from June 27th to July 14th, 1500, 950, 160 and 420 tillers would have been sampled for a 10% precision level. Finch et. al. (1978) adopted a 20% tolerance level which would give the more realistic

sample sizes of 380, 240, 40 and 105 tillers to be sampled (table A.1).

Table A.1 Aphid Statistics for Plot N1, 1977 Experiment

Date	No. Tillers Sampled	Mean No. Aphids Per Tiller	± 95% Confidence Interval Limits	Tolerance Achieved %	No. of Tillers to be Sampled for: 10% Tol.	20% Tol.
13/6	400	0.125	± 0.12	94.50	37 196	9 299
20/6	250	0.65	± 0.28	43.23	4 862	1 215
27/6	150	3.59	± 1.13	31.46	1 515	379
4/7	200	9.49	± 2.02	21.29	944	236
12/7	82	30.72	± 4.30	14.00	161	40
14/7	40	7.45	± 2.44	32.73	419	105

Regression analysis for the relationship between log. variance and log. mean of the 1976, 1977 and 1978 aphid samples gave the following equation:-

$$\log_e s^2 = 0.8159 + 1.3491 \log_e \bar{x} \quad r = 0.986 \quad p < 0.0001$$

which, from equation 5, gave the following theoretical relationship between number of tillers to be sampled (n) and aphid population mean ($\bar{x}$):-

$$\log_e n = (2 + 0.82) - (2 - 1.35).\log_e \bar{x}$$
$$= 2.82 - 0.65 \log_e \bar{x}$$

The actual relationship from figure A.1 was:-

$$\log_e n = 2.875 - 0.68 \log_e \bar{x} \quad r = -0.870 \quad p < 0.0001$$

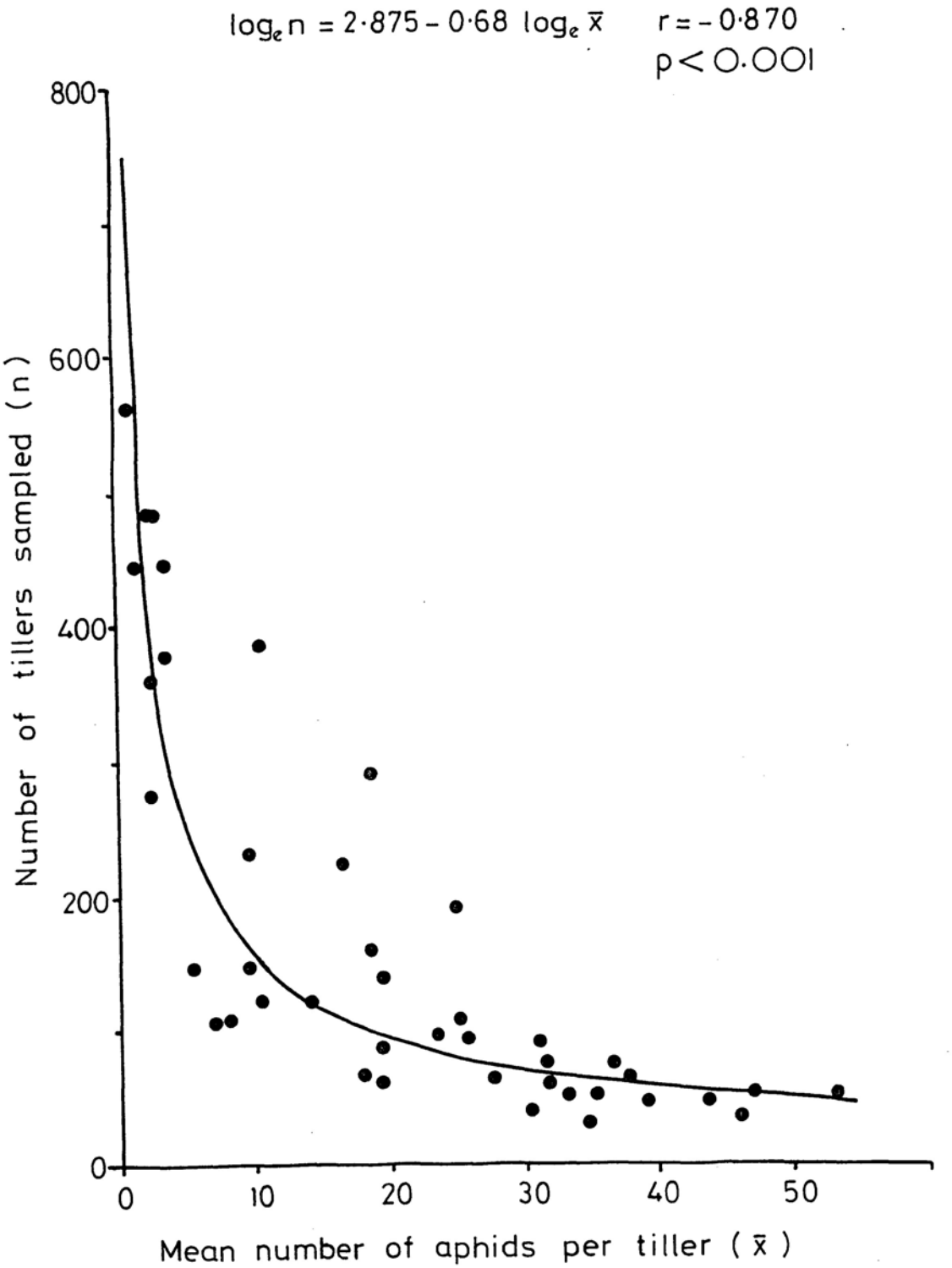
and thus there was a reasonably accurate agreement between the theoretical expectation and the actual plot.

In the field, a small preliminary sample would be used to estimate the mean number of aphids per tiller and an estimate of the sample size to achieve 20% tolerance could be obtained either from figure A.1 or table A.2.

Table A.2 Overall Sampling Plan for Tiller Counts of Aphids in Small Plots

Mean No. Aphids/Tiller	No. Tillers to be Sampled for 20% Tolerance
1	750
2	467
3	354
4	292
5	251
8	182
10	157
12	138
15	119
20	98
25	78
30	74
35	67
40	61
45	56
50	52

Figure A.1 Sampling Pattern for Tiller Sampling of Aphids on Wheat at 20% Tolerance



Discussion

A number of advantages would accrue from the adoption of a constant precision level in an aphid sampling programme. The population growth pattern would be more accurately followed, particularly at the crucial periods immediately before and after the peak. Comparisons of aphid populations between plots would be made easier since, with the adoption of a 20% tolerance level, for example, aphid population means would have to differ by more than 20% to be significant at the 5% level.

A characteristic of the logarithmic relationship between sample size and population mean is that the sample size increases very rapidly at low aphid numbers (figure A.1). Indeed, at aphid densities lower than one per tiller the time taken for sampling will usually prevent the sample size for 20% tolerance from being reached. For example, in plot N1 on June 20th 1977, the sample size for 20% precision was 1215 tillers, but only 250 tillers could be sampled in the time available. Similarly, Rabbinge et. al. (1979) found that 600 tillers was the maximum that they could sample in one day irrespective of the precision level used. Thus, accurate comparisons of aphid populations cannot be made at aphid densities below one per tiller unless large samples are taken, a conclusion supported by Barideau, Dagnelie and Latteur (1975).

A.2 Sampling Precision of the D-Vac Suction Sampler

Introduction

The D-Vac suction sampler, deriving from Dietrick's design (Dietrick, 1961), has proved to be an invaluable tool for sampling arthropod populations in cereals (Potts and Vickerman, 1974, Vickerman and Sunderland, 1975) particularly with regard to the long term monitoring of

arthropod populations in cereals (Potts, 1976, Vickerman, 1977). However, although the D-Vac has been evaluated for sampling weevils in alfalfa (Stevens and Steinhauer, 1973) and irrigated pasture (Pruess and Whitmore, 1976) and has been extensively used for population studies in cereals, there has been little work on the sampling precision in cereals using the machine. Thus the number of D-Vac samples required for various arthropod populations has been a matter of guesswork and the present investigation was undertaken to put the sampling procedure for the D-Vac on a more sound basis. To achieve this a large number of samples were taken (eighty) to obtain a relationship between the log. mean and log. variance of ten groups of eight samples. This would then form the basis for a sampling plan giving the number of samples necessary for various levels of arthropod abundance.

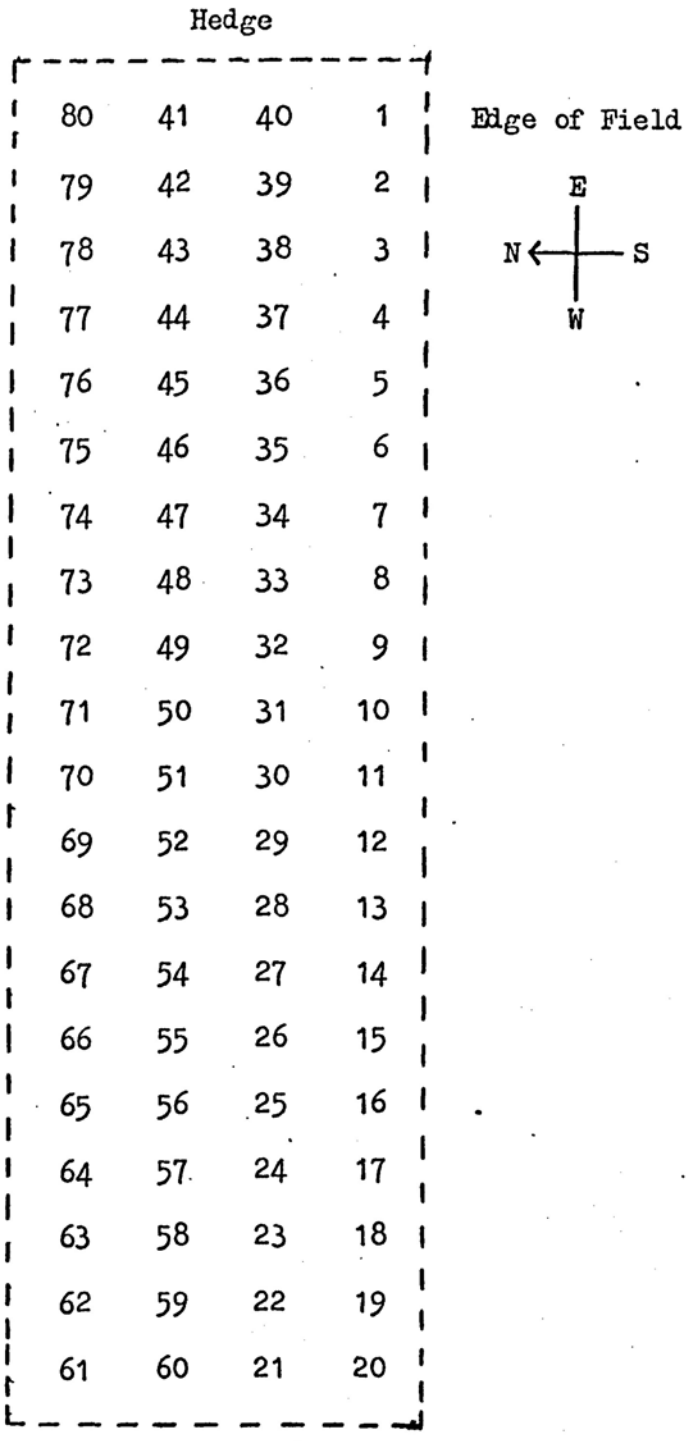
Materials and Methods

A standard Dietrick suction sampler (Dietrick, 1961) was used to take a series of arthropod samples in a field of winter wheat on July 14th, 1977. Each sample consisted of a 'suck' lasting one minute from an area of 0.1 m^2, and a total of eighty samples was taken from a grid layout (figure A.2). The samples were stored at $-20^{\circ}C$ and subsequently sorted into twelve arthropod groups per sample (table A.3).

In order to devise a sampling plan comparable with that already established for visual counts of aphids (above) a linear relationship between log. variance and log. mean of the samples was required (Finch et. al., 1978).

As each suction sample was discrete it was not possible to obtain the variance of arthropod numbers within the sample. Samples were

Figure A.2 Grid Layout of D-Vac Samples Taken



Distance between samples 3 m

Distance between rows 5 m

TABLE A.3 ARTHROPOD GROUPS SAMPLED BY D-VAC

Arthropod Category	Numbers/Sample			Variance	No. Samples With Zero Arthropods	s.e. / Mean x 100%	No. Samples For 20% Precision
	Mean	Minimum	Maximum				
1. Aphids	273.3	102	869	14 386	0	4.9	39
2. Diptera	45.6	15	119	447	0	5.2	42
3. Collembola(A) - Gmuridae	28.7	1	141	737	0	10.6	85
4. Collembola(B) - Sminthuridae	4.3	0	18	17.3	10	10.9	87
5. Thrips	27.1	5	72	188	0	5.7	46
6. Hymenoptera	6.4	0	21	16.7	1	7.2	58
7. Hemiptera	1.8	0	10	4.2	28	12.8	102
8. Larvae	14.4	1	38	49.2	0	5.4	43
9. Spiders	2.0	0	9	3.8	17	10.6	85
10. Mites	1.4	0	11	5.6	40	18.8	150
11. Coleoptera	2.4	0	8	3.4	11	8.6	69
12. Others	0.1	0	3	0.2	—	—	—

therefore grouped into units of eight on the computer, and the mean and variance of each group was calculated together with the regression of log. mean against log. variance for the ten groups. To avoid any bias, the samples were mixed randomly, producing a different set of eight per group and log. mean regressed against log. variance as before. This was repeated five times for each arthropod category giving five correlations between log. mean and log. variance (table A.4). The standard error as a percentage of the mean was also calculated (table A.3). In addition, frequency distributions of arthropod numbers were plotted (figures A.4, A.5, A.7, A.9 and A.10) and contour maps of arthropod spatial distributions were plotted (figures A.3, A.6 and A.8). The contour levels run from 0 to 9, but to improve clarity only the even contours are shown.

Results and Discussion

No significant associations were found between log. mean and log. variance for any of the five combinations of samples in any of the arthropod categories (table A.4). For some categories this was to be expected since there were many samples with zero values for the less common arthropods (table A.3), for example, half the total number of samples taken had no mites. For the remainder, the absence of the expected association between log. mean and log. variance may have been because there was a limited range of arthropod densities due to all the samples having been taken on the same date.

However, certain conclusions can be drawn about the relative accuracy of the D-Vac for sampling each arthropod category. A measure of the variability of a population is provided by the standard error and if this is small relative to the population mean, fewer samples will be required

Table A.4 Associations Between Log_{10} Means and Log_{10} Variance

(10 Groups of 8 Samples)

Category	% Variance Accounted For Log_{10} Mean vs Log_{10} Variance				
	1	2	3	4	5
1. Aphids	-11.8	8.9	-10.0	-0.8	1.5
2. Diptera	-11.6	17.2	1.3	-4.4	-10.4
3. Collembola(A) - Gnuridae	-12.2	-8.1	-8.4	-12.3	-8.9
4. Collembola(B) - Sminthuridae	16.7	12.9	10.6	2.8	38.5
5. Thrips	-12.4	-12.1	-12.0	-12.4	-4.8
6. Hymenoptera	-11.6	7.9	-10.4	-12.4	-1.7
7. Hemiptera	-11.0	-12.1	-9.4	-10.5	18.1
8. Larvae	11.4	-12.4	10.4	-12.2	2.2
9. Spiders	-4.5	28.0	-9.2	-12.5	5.2
10. Mites	-6.4	-7.6	-9.0	-11.1	39.1
11. Coleoptera	-6.3	-2.5	27.0	-12.5	-7.1

to give an accurate estimate of the population mean and variance. When population variability was represented by the standard error as a percentage of the mean, the arthropod categories could be arranged in four groups.

The first group consisted of aphids, Diptera, thrips and larvae (mainly staphylinid larvae) and had a standard error of 5-6% of the mean. These were the most abundant arthropods and were consequently the ones most accurately assessed by the D-Vac sampling, 42-46 samples being needed for 20% precision (table A.3). The frequency distributions of this group

were similar in shape and those for aphids and Diptera are shown in figures A.3 and A.4. Contour maps of aphids and Diptera (figures A.5 a and b) show patchy spatial distributions with four to five areas of high density. Moreover, the hedge has no influence on the spatial distribution of insects in this group. Aphids, which were numerically the dominant component of the cereal fauna, were decreasing when the samples were taken and the spatial distribution at peak numbers may have been more even since all the tillers were infested at that point.

Group two consisted of Hymenoptera and Coleoptera and had a standard error of 7-9% of the mean. The spread of frequencies was wider than in the first group (figure A.6) and thus a greater number of samples was required for 20% precision (fifty-eight and sixty-nine respectively). There were generally low numbers of these insects with a few patches of high abundance (figure A.7). As for group one the hedge had no influence on distribution and the individuals of this group were probably more mobile than those of group one.

The third group, with standard errors of 10.12% of the mean, consisted of the Collembola (Gnuridae and Sminthuridae), Hemiptera and spiders. These were naturally associated into two sub-groups; Hemiptera and Gnuridae, and spiders and Sminthuridae. The spatial distribution of the first sub-group was greatly influenced by the hedge (figure A.8 a). A gradient of abundance from low numbers in the interior of the crop to high numbers at the hedge occurred within six metres of the edge of the field. This suggested that the infestation of Hemiptera and Gnuridae was a result of movement of these insects into the crop from the grassy verge and hedge. The spatial distribution of the second sub-group, Sminthuridae and spiders, was unaffected by the hedge (figure A.8 b).

Figure A.3 Frequency Distribution of Aphids

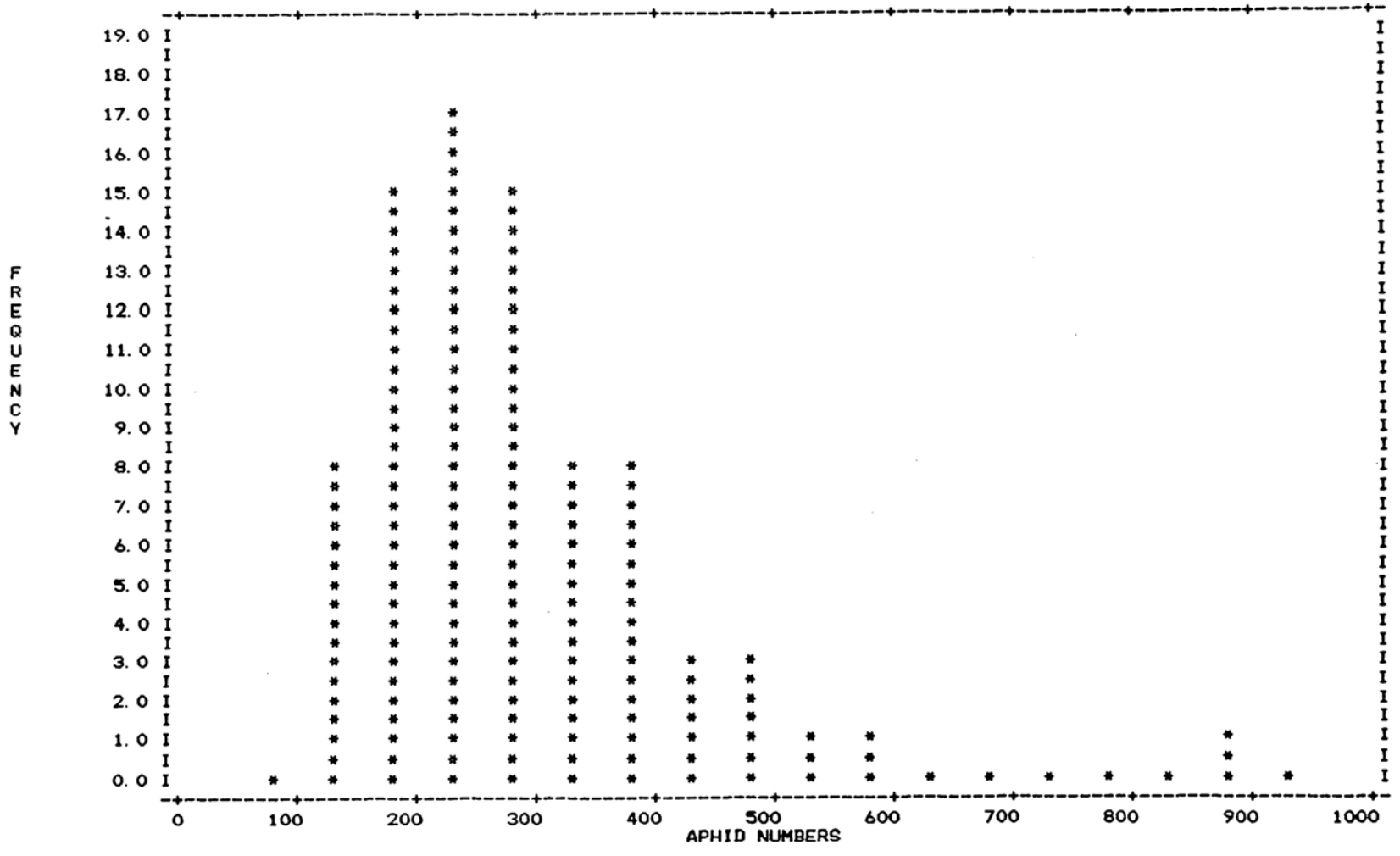


Figure A.4 Frequency Distribution of Diptera

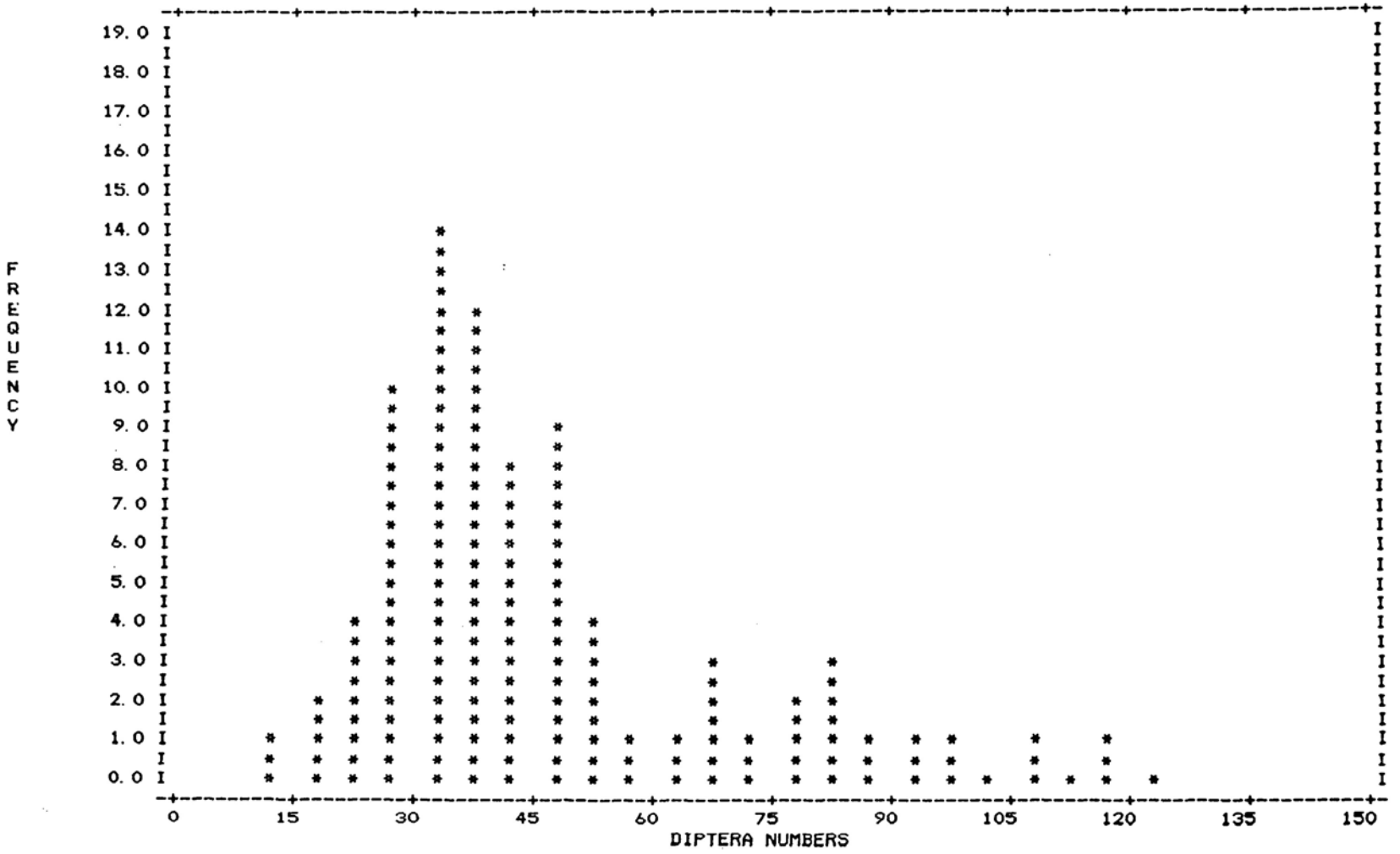


Figure A.5 Contour Maps (Spatial Distribution)

(a) Aphids (C.I. - 50)



(b) Diptera (C.I. - 10)



Interior of Field

Edge of Field

C.I. - Contour Interval

Figure A.6 Frequency Distribution of Hymenoptera

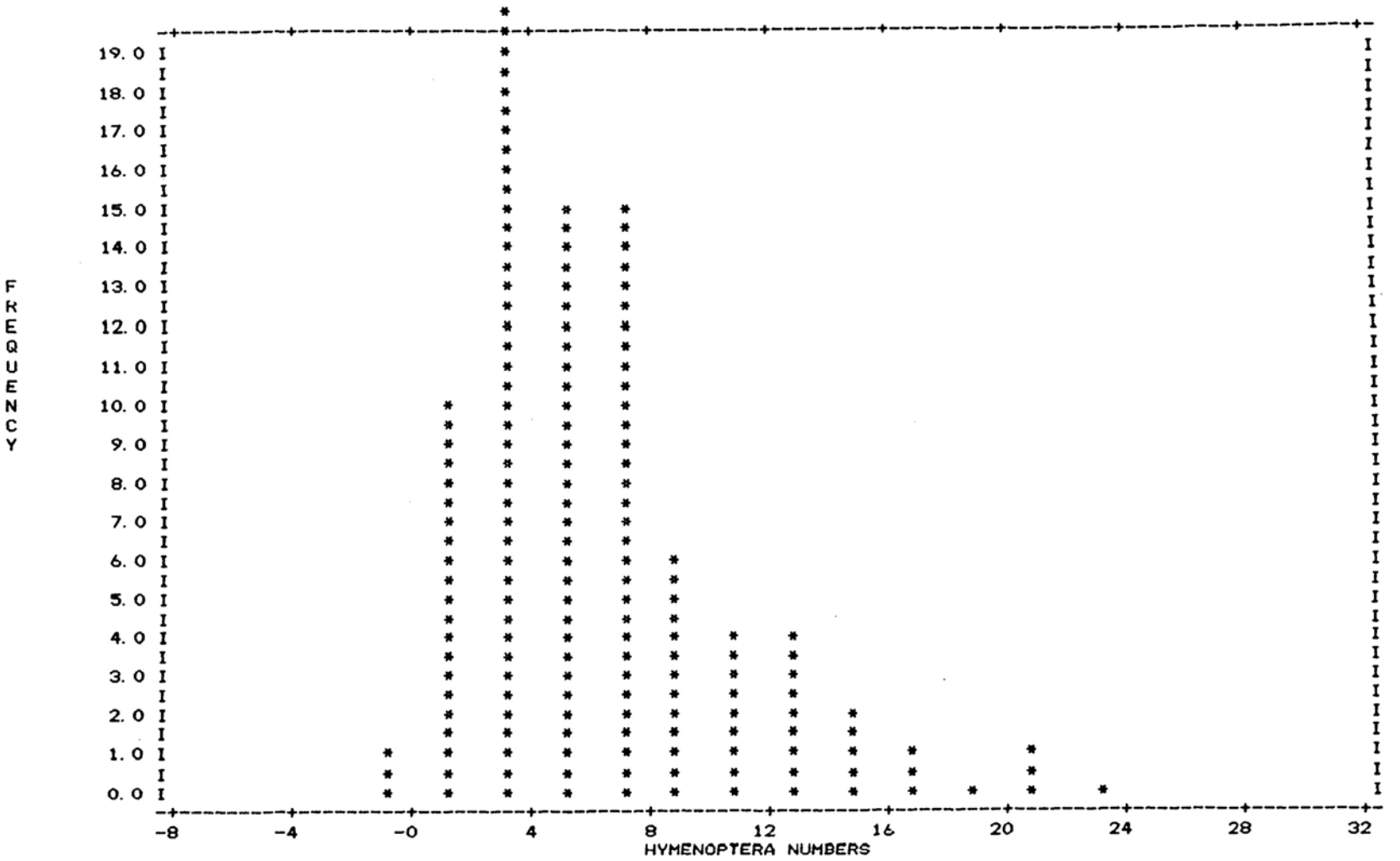
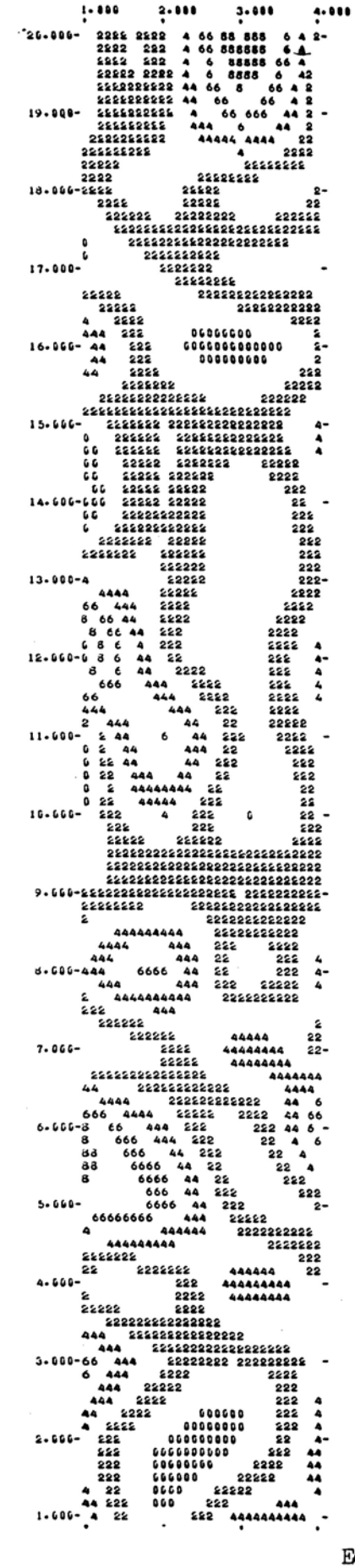


Figure A.7 Contour Map (Spatial Distribution) of Hymenoptera

(Contour Interval – 1)



Interior of Field

Edge of Field

Figure A.8 Contour Maps (Spatial Distributions)

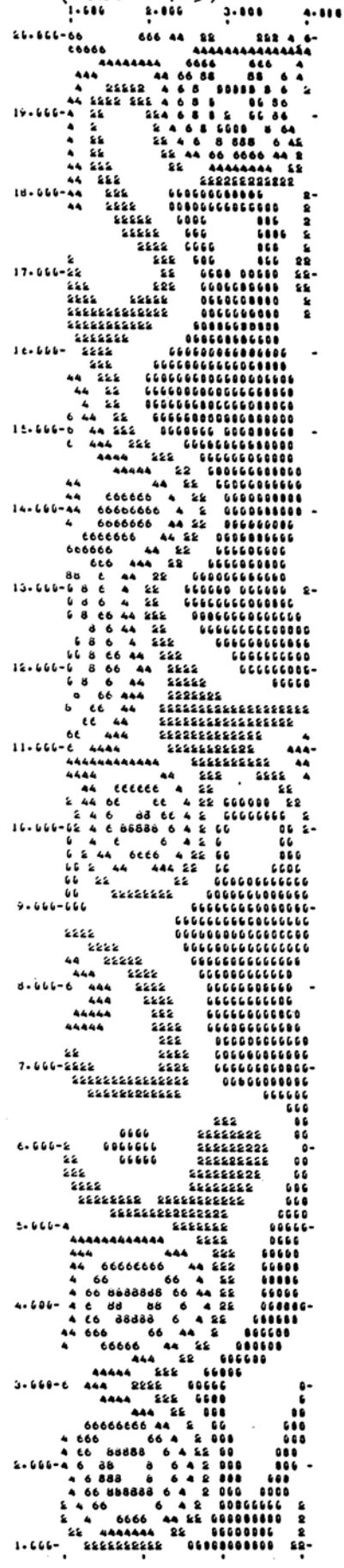
(a) Hemiptera (C.I. -3)



Interior of Field

Edge of Field

(b) Collembola - Sminthuridae (C.I. - 7.5)



C.I. - Contour Interval

Figure A.9 Frequency Distribution of Hemiptera

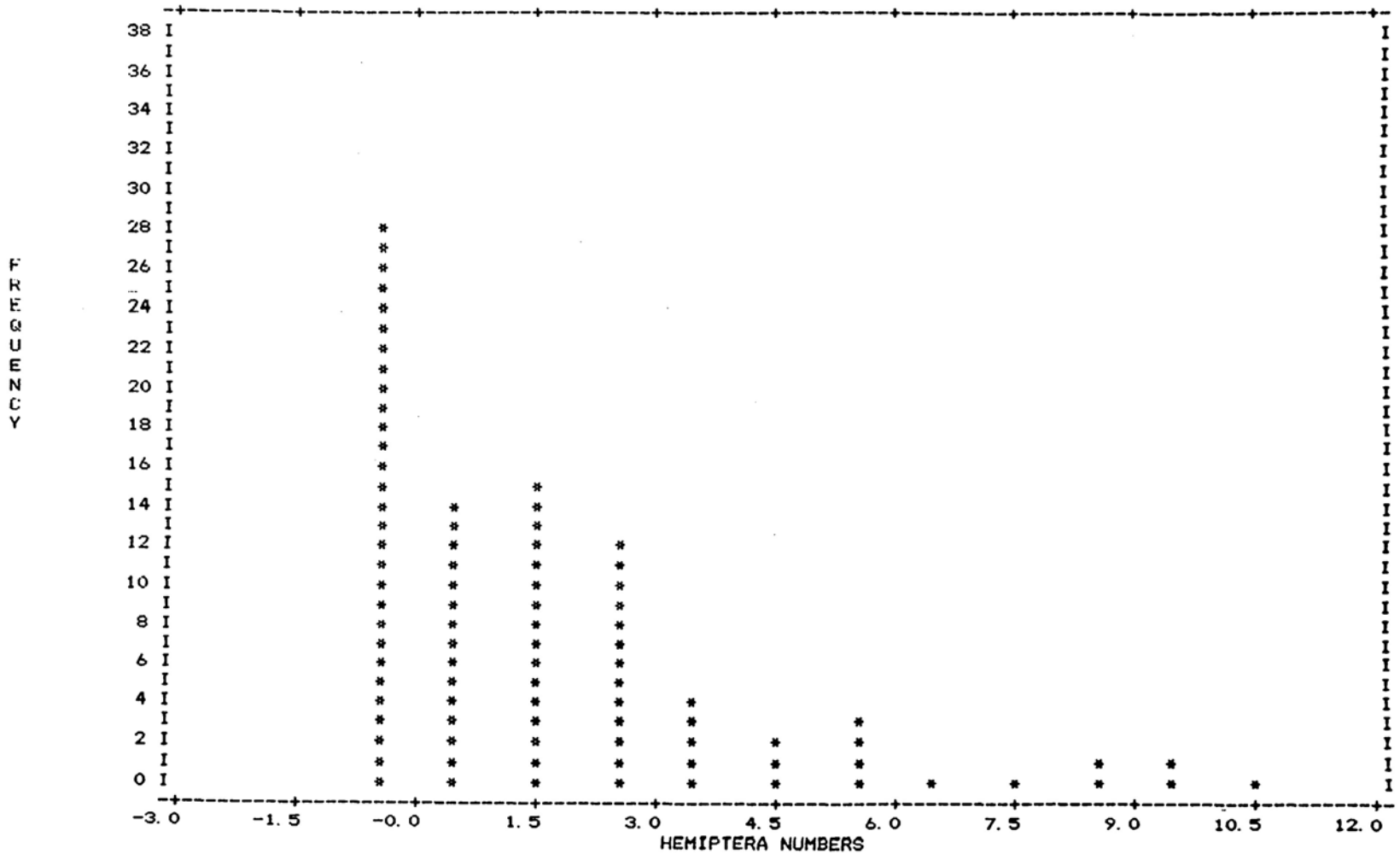
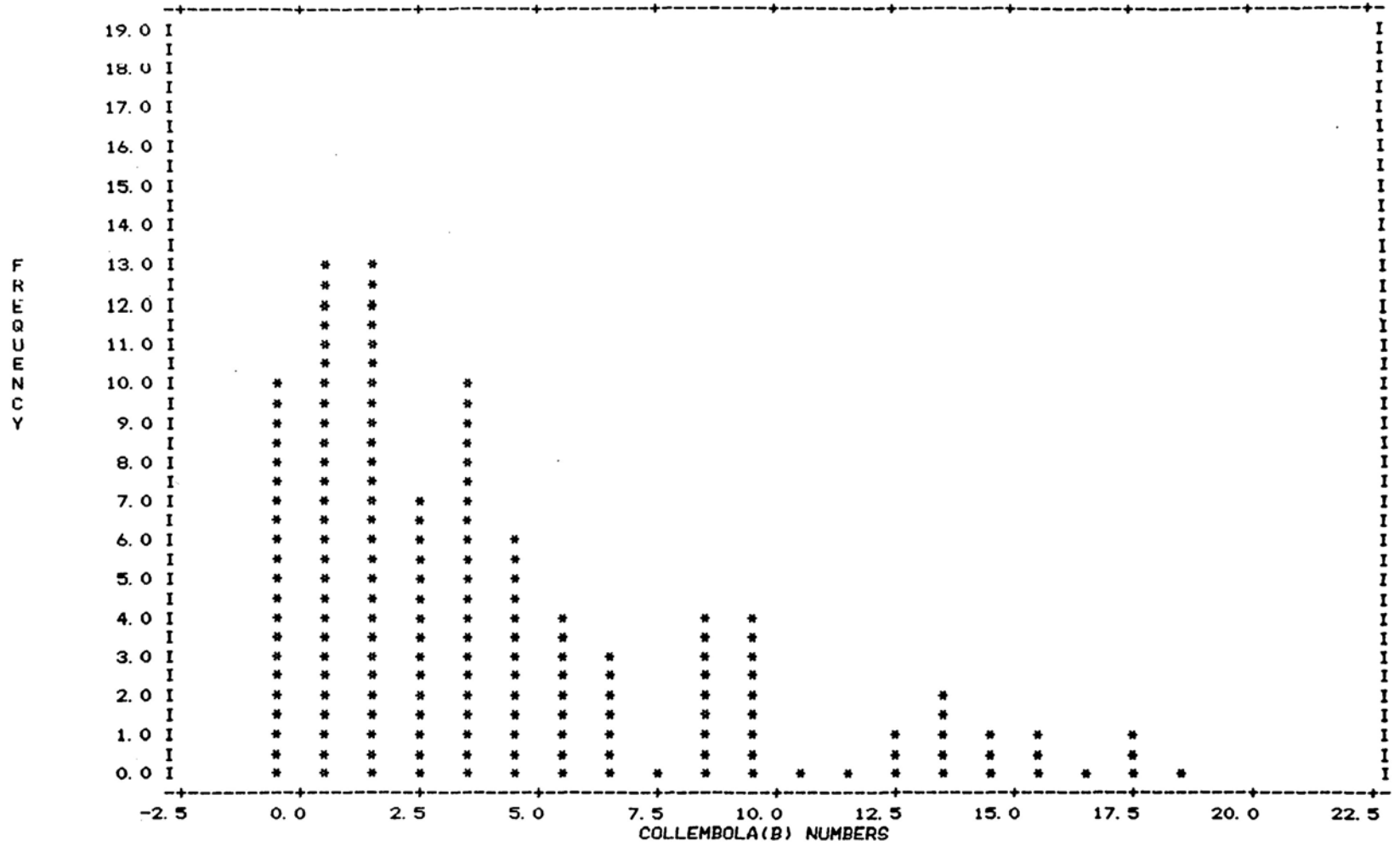


Figure A.10 Frequency Distribution of Collembola(B) - Sminthuridae



Instead, there were four to five patches of moderate numbers against a background of very low numbers, which could have been produced as a result of environmental influences, reaction to prey density (spiders), or a purely intra-specific aggregative response. The frequency distributions (figures A.9 and A.10) reflect the nature of the spatial distributions of both groups. Problems are likely to be encountered if arthropods from this third group are to be sampled. Because of the patchy nature of the spatial distributions, a small number of random samples in a field could produce very low numbers of Collembola, Hemiptera and spiders. However, if sampling takes place at the edge of a field or by chance in an area of high numbers, their density will be overestimated. Thus, for 20% precision, at the mean densities sampled, large numbers of samples need to be taken (eighty to a hundred, table A.3).

The last group, the mites, have the highest percentage standard error of the mean (19%) and only occurred next to the hedge. These were probably not cereal dwellers but had dispersed from the edge of the field.

Conclusions

An accurate sampling plan for the D-Vac could not be derived as there was no relationship between the log. mean and log. variance of the groups used. A greater spread of arthropod numbers was needed to provide a greater range of values for mean and variance. This could for instance, have been achieved by taking twenty samples at weekly intervals during June and July instead of eighty samples on one date.

However, at the population densities sampled an estimate can be made of the number of samples required to give a sampling precision of 20% by the method employed in part A. Thus, for aphid, Diptera, thrip and larvae densities of 270, 45, 30 and 15 per 0.5 m^2 respectively about forty samples

or 'sucks' would give a reasonable level of sampling precision (20%) (table A.3). For Hymenoptera and Coleoptera at 6 and 2 per 0.5 m^2 respectively sixty to seventy samples would be needed and for Collembola (Gnuridae and Sminthuridae), Hemiptera and spiders at 28, 4, 2 and 2 per 0.5 m^2 respectively ninety to a hundred samples would be needed.

There is an important distinction to be made between the frequency distribution of an insect population, which is the frequency with which different densities of insects occur in the field, and its spatial distribution, which is the physical arrangement of insect densities. For example, Hemiptera and Sminthuridae had similar frequency distributions but radically different spatial distributions resulting from different causes.

Shelter provided by hedgerows can have a direct physical effect on the deposition of flying insects in a field (Lewis, 1969, 1970) but this effect can be modified in floristically diverse hedgerows by insects emanating from the hedgerow itself (Bowden and Dean, 1977). The lack of hedge effects on most of the arthropod groups was not perhaps surprising because the samples were all taken on one day with no regard to wind direction. However, the hedgerow, which was as floristically diverse as that described by Bowden and Dean (1977) had an obvious influence on the distributions of Hemiptera (mainly plant bugs) and Gnuridae. Thus, both these phytophagous species were probably migrants from plants in the hedge, the wheat being a secondary host.

The sampling method used does not estimate the efficiency of the D-Vac in catching arthropods. However, a rough estimate of sampling efficiency of aphids can be obtained because the field experiment was

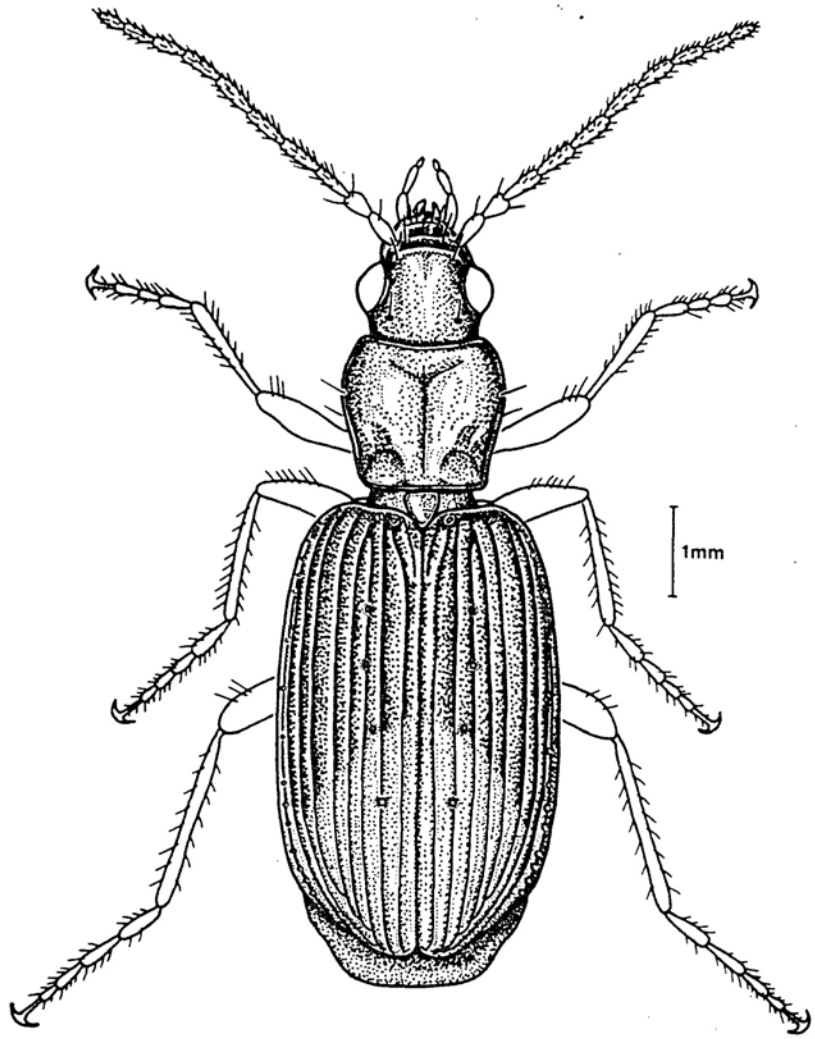
being sampled on the same day (Chapter 3). The average aphid density in the control plot, N1, was seven per tiller, and taking an average of 200 tillers per 0.5 m^2 it can be seen that the D-Vac recovered only c.20% of the aphids present. This agrees with other investigations which have shown that at high populations, 30% of aphids on the plant have been removed (A. Dewar - personal communication).

APPENDIX 2

A drawing of the

Major Aphidophagous Species of

Ground Beetle - *Agonum dorsale*



Agonum dorsale (Pont.) ♀

APPENDIX 3

DETAILS OF FIELD AND INSECTARY EXPERIMENT RESULTS NOT INCLUDED IN THE MAIN TEXT

Table A.5 Aphid Population Data for the 1976 Field Experiment

TREATMENT / PLOT / DATE	Mean Number of Aphids Sampled Per 100 Tillers						
	OPEN FIELD		EARLY CAGES			LATE CAGES	
	T1	T2	C1	C2	C3	C4	C5
May 13	0	0	0	0	0		
24	2.75	3.25	3.75	12.00	7.00		
June 2	33.00	47.75	36.25	67.25	65.00		
9	262.7	238.7	251.3	530.8	376.9		
11	——	——	——	——	——	790.6	574.4
16	1 939	2 756	3 140	5 324	3 171	2 589	1 922
25	18.7	8.75	16 260	17 420	10 120	2 356	1 795
30	1.25	2.50	11 920	12 360	6 593	2.5	41.25
July 7	0	0	2 898	1 846	1 064	0	6.25
14			0	0	0		0

NOTES:

1. Plot layout is shown in figure 2.14.
2. Average number of aphids per treatment is shown in figure 3.1.

Table A.6 1976 Field Experiment

Number of Mummified Aphids Sampled Per 100 Tillers

Date	Open Field		'Early' Cages			'Late' Cages	
	T1	T2	C1	C2	C3	C4	C5
June 9	0	0.5	0.5	3	2.5	—	—
16	58	49	5	10	26	66	36
25	113	134	113	183	51	204	107.5
30	—	—	500	435	693	126	175
July 7	—	—	188	374	301	58	24

KEY: — not recorded

0 none present

NOTE:

Only unhatched mummies were counted as far as possible.

TABLE A.7 APHID POPULATION DATA FOR THE 1977 FIELD EXPERIMENT

PLOT / DATE	Mean Number of Aphids Sampled Per 100 Tillers												
	H1	H2	H3	M1	M2	M3	L1	L2	L3	N1	N2	N3	N5
May 9	1.41	0.24	4.39	2.00	6.99	0.62	0.52	0.76	1.96		0	0	0
17	2.93	7.63	2.8	1.36	0	14.07	0	0	0	0	0	0	0
23	4.38	2.79	6.48	3.65	4.54	1,14	0	0	1.98	0	0	0.33	2.37
30	9.25	6.25	6.25	5.50	0.25	3.75	1.25	7.5	2.25	2.75	3.25	4.25	—
June 13	43.25	74.75	72.75	64.75	39.5	42	18.25	9.5	89	12.5	9.0	21	—
20	257	447	232	197	135	176	152	69	268	154	119	226	214
27	422	865	626	384	331	369	265	102	607	358	231	501	324
July 4	2 479	7 920	3 452	1 411	1 917	3 759	1 174	564	3 201	961	1 603	1 870	2 816
11	4 418	28 014	4 521	3 591	16 342	3 576	4 360	5 151	3 352	3 140	4 837	4 020	5 860
14	1 463	47 860	1 009	1 025	20 050	544	1 704	10 625	628	745	4 910	760	4 015
19	0	31 436	0	0	25 644	0	0	7 280	0	0	3 915	0	4 458
25		3 238			9 372			4 234			1 284		3 202
28		184			2 099			3 028			754		2 842
August 2		0			10			731			88		2 947

NOTES: (With reference to table A.7)

1. Plot layout is shown in figure 2.15.
2. Average number of aphids per treatment is shown in figure 3.2.
3. Decrease of aphid populations in the cages is shown in figure 3.13.

Table A.8 1977 Field Experiment

Numbers of Mummified and Diseased Aphids Per 100 Tillers

(a) Mummified Aphids Sampled Per 100 Tillers

Date	H1	H2	H3	M1	M2	M3	L1	L2	L3	N1	N2	N3
June 13	1	1	1	0	0	0	0	0	2	0	0	1
20	0	0	0	1	0	0	0	0	0	0	0	0
27	0	0	0	0	0	1	0	0	0	1	0	1
July 4	8	78	13	6	0	10	0.5	0	17	0	6	0.5
11	24	313	53	28	0	33	34.8	0	54	17	5	20
14	127	570	160	17	5	25	92	80	96	16	0	20
20	—	560	—	—	30	—	—	5	—	—	82	—
25	—	—	—	—	—	—	—	—	—	—	220	—
28	—	1620	—	—	—	—	—	—	—	—	25	—

(b) Entomophthora Infected Aphids Sampled Per 100 Tillers

Date	H1	H2	H3	M1	M2	M3	L1	L2	L3	N1	N2	N3
June 13	—	—	—	—	—	—	—	—	—	—	—	—
20	0	0	0	1	0	0	0	0	2	0	0	2
27	0	0	0	2	0	0	0	0	1	0	0	0
July 4	6	35	3	0	2	0	0	0	0	2	0	0
11	0	75	90	5	5	19	5	0	13	5	16	40
14	—	—	—	15	0	20	—	—	—	8	10	4
20	—	2740	—	—	450	—	—	150	—	—	141	—
25	—	1895	—	—	—	—	—	—	—	—	5	—
28	—	200	—	—	—	—	—	—	—	—	—	—

KEY: — not recorded

0 none present

NOTE:

Only unhatched mummies were counted as far as possible.

TABLE A.9 APHID INDICES AND YIELD VARIABLES FOR THE 1977 FIELD EXPERIMENT

Plot	Total Aphid Index	'Flowering' A.I.	'Post-Flowering' A.I.	Peak Aphid Nos. Per Tiller	Weight Grain Per Ear gm	1000 Grain Weight gm	No. Grains Per Ear
H1	502	38	464	44.2	1.65[illegible]	56.08	29.44
H2	5 844	70	5 774	478.6	0.586	28.55	20.51
H3	573	47	526	45.2	1.786	55.33	31.96
M1	364	35	329	35.9	1.740	57.09	30.48
M2	3 704	26	3 678	256.4	0.822	34.03	24.15
M3	504	30	474	35.8	1.768	58.86	30.03
L1	397	21	376	43.6	1.793	58.80	30.49
L2	1 466	10	1 456	106.3	1.429	50.28	28.43
L3	483	55	428	33.8	1.748	56.62	30.88
N1	289	24	265	31.4	2.207	63.37	34.83
N2	883	18	865	49.1	1.715	53.32	32.16
N3	411	36	375	40.2	1.870	59.81	31.26
AD1	195	18	177	20.3	2.000	61.34	32.60
AD2	106	19	87	6.8	1.902	59.71	31.85
AD3	163	15	148	15.2	2.008	61.12	32.85
AD4	29	4	25	1.4	2.232	64.61	34.54
N6	252	20	232	20.5	2.041	61.34	33.28

NOTES: KEY: A.I. - Aphid Index

1. Results from plots AD1, 2, 3 and 4 are from a separate aphid immigration experiment not presented here.
2. The above data was used for the regressions shown in table 6.2.

TABLE A.10 APHID AND YIELD FOR THE 1976 INSECTARY EXPERIMENT

	VARIABLES	PLOTS 1	2	3	4	5	6	7	8	9	10	11	12	
1	No. A. dorsale/plot	1	2	8	0	2	0	4	1	6	2	7	4	*
2	Total A.I./tiller	1 250	1 636	769	2 400	1 052	1 530	1 839	—	2 872	2 784	179	930	–
3	'Flowering' A.I.	367	553	254	602	251	170	212	—	212	285	179	310	–
4	'Post-flowering' A.I.	883	1 083	515	1 798	801	1 360	1 634	—	2 660	2 499	0	620	–
	Rate inc. aphids/plot													
5	20/5 to 24/5	1.242	1.267	1.250	0.970	1.225	1.080	1.075	1.148	1.142	1.136	1.154	1.108	*
6	24/5 to 27/5	1.179	1.237	1.326	1.541	1.339	1.572	1.249	1.094	1.029	1.195	1.075	1.320	*
	Rate inc. aphids/tiller													
7	20/5 to 27/5	3.950	6.108	3.083	2.999	4.250	4.973	2.518	2.293	1.880	2.818	4.051	2.378	*
8	27/5 50 7/6	6.122	2.977	8.365	3.939	4.359	2.007	12.793	3.872	7.459	6.008	4.539	5.206	*
9	Av. height plant m	0.914	0.739	1.028	0.616	0.925	0.816	0.961	0.790	1.034	1.021	1.013	0.838	*–
10	Av. no. tillers/plant	2.625	3.1	6.4	2.4	4.5	2.2	4.5	2.5	6.4	7.6	3.6	3.44	*–
11	No. tillers/plot	100	30	200	30	100	50	90	45	170	85	140	60	*
12	Wt. grain/ear gm	1.576	1.637	2.689	1.307	2.137	1.290	1.862	—	2.198	2.148	2.434	1.738	–
13	1000 grain wt. gm	34.87	38.15	44.23	32.68	36.17	34.12	36.72	—	38.90	41.72	42.85	34.47	–
14	No. grains/ear	45.20	42.91	60.80	40.00	59.08	37.81	50.71	—	56.50	51.49	56.80	50.42	–
15	Percentage Nitrogen	32.29	39.40	30.91	30.11	29.86	32.59	30.15	—	33.39	30.59	31.16	30.81	–

KEY: A.I. – Aphid Index; inc. – increase; Av. – average; Wt. – weight.

NOTES: See page 295

NOTES: (With reference to Table A.10)

1. Mean aphid numbers per plot for the four treatments of control (plots 4 and 6), 1-2 beetles/plot (plots 1, 2, 5, 8 and 10), 4 beetles/plot (plots 7 and 12) and 6-8 beetles/plot (plots 3, 9 and 11) are shown in figure 2.6.

2. Variables 5 and 6 - the rate of increase is times/day.

3. Variables 7 and 8 - the rate of increase is times/week.

4. Variables used in table 2.5 indicated by *.

5. Variables used in table 6.4 indicated by -.

6. Error in yield determination of plot 8 not included in analysis in table 6.4.

Table A.11 1976 Insectary Experiment

Effect of Aphids on Yield of Wheat - Insecticide Treatments

Plot Number	Date Spraying Pirimicarb	Mean Nos. Aphids/Tiller
11	June 8	87.4
8	11	73.3
3	15	170.1
12	18	130
5	22	75.3
2	25	23.9
10	29	294.1
9	July 2	26.5

Plots 1, 6, 4 and 7 were unsprayed.

Table A.12 1977 Insectary Experiment

Experimental Treatments and Rates of Aphid Increase

Beetle Species	No. of Beetles/Plot	Plot No.	Aphid Inc. Times/Wk. 16/5-23/5	16/5-2/6
Control	0	7	3.85	3.43
	0	10	1.98	3.28
Pterostichus madidus	4	2	1.56	3.73
	4	8	2.87	3.11
	16	9	2.81	3.13
	16	12	3.64	3.19
	30	5	3.04	4.10
Demetrias atricapillus	4	4	3.96	3.93
	4	11	2.21	3.47
	16	1	3.19	3.76
	16	3	2.68	2.77
	30	6	1.53	3.24

KEY: Inc. - increase; Wk. - week.

NOTES:

1. Layout of the plots as in figure 3.18.
2. Regressions of aphid increase rate against beetle numbers are shown in table 2.6.
3. Mean aphid numbers per treatment are shown in figures 2.7 and 2.8.
4. Treatments used in the coccinellid movement experiment (part of the 1977 insectary experiment) are given in table 3.8.
5. Mean numbers of aphids, coccinellid larvae and adults for the treatments are shown in figure 3.23.

Table A.13 1977 Insectary Experiment - Aphid Indices & Yield Variables

Row Plot	Total A.I.	'Flow.' A.I.	'Post-Fl.' A.I.	No. Till. /Plant	Wt. Grain /Ear gm	1000 Grain Wt. gm	No. Grains /Ear
01							
1	1 576	463	1 113	2.00	1.645	33.3	49.40
2	2 883	924	1 959	5.33	1.127	24.6	45.80
3	5 143	495	4 648	5.80	0.846	15.6	54.27
5	7 575	582	6 993	3.13	0.235	10.0	23.50
6	3 640	468	3 172	4.66	1.176	23.8	49.44
7	4 344	818	3 526	6.86	0.571	22.9	24.92
8	5 482	980	4 502	6.00	0.335	13.4	25.02
9	7 380	637	6 743	3.26	0.144	10.4	13.84
10	2 456	546	1 910	5.47	1.484	31.4	47.14
11	1 864	783	1 081	6.50	0.717	22.1	32.44
12	9 658	677	8 979	6.64	0.452	13.6	33.21
M							
1	849	501	348	2.78	1.645	38.1	47.28
2	3 500	640	2 860	4.07	0.891	22.5	39.59
3	6 190	320	5 870	3.85	0.510	14.8	34.48
5	6 150	252	5 898	3.71	0.263	12.7	20.68
6	3 567	404	3 163	3.79	0.918	21.2	43.28
7	3 210	858	2 352	3.53	0.414	17.8	23.26
8	6 140	1 120	5 020	3.66	0.104	10.7	9.69
9	6 524	461	6 063	3.00	0.311	12.4	25.08
10	2 543	676	1 867	3.86	1.289	29.3	43.98
11	2 238	923	1 315	3.40	0.532	18.5	28.72
12	9 389	519	8 870	4.20	0.179	9.0	19.92
02							
1	1 533	346	1 187	4.35	1.942	34.6	56.12
2	4 006	612	3 394	5.30	1.132	20.4	55.49
3	6 205	560	5 645	5.43	0.280	14.8	19.01
5	7 131	296	6 835	5.13	0.724	17.1	43.36
6	4 209	563	3 646	5.73	0.786	20.2	38.92
7	3 244	951	2 293	4.66	0.552	18.0	30.66
8	7 603	1 544	6 059	3.66	0.101	7.9	12.87
9	6 419	428	5 991	4.20	0.850	19.2	44.25
10	2 341	486	1 885	5.26	1.464	28.5	51.35
11	2 293	915	1 378	5.73	0.521	22.0	23.66
12	11 906	924	10 982	4.20	0.131	9.0	14.56

Key: A.I. - Aphid Index; 'Flow.' - flowering; 'Post-Fl.' - post-flowering
Till. - tillers; Wt. - weight

Notes:

1. Data used in multiple regressions shown in table 6.5.

2. Error in yield determination of plot 4 - these results not used.

TABLE A.14 1977 GLASSHOUSE EXPERIMENT - BEETLE TREATMENTS AND APHID PREDATION

TREATMENT	Control	High Beetle Density			Medium Beetle Density				Low Beetle Density			
BEETLE SPECIES		N. brevicollis		P. madidus	N. brevicollis		P. madidus		N. brevicollis		P. madidus	
PLOTS	6	1	2	5	7	12	8	9	3	4	10	11
VARIABLES												
1 No. beetles/plot	0	32	27	26	10	8	10	8	5	5	5	5
2 Total wt. beetles/plot gm	-	2.05	1.63	4.06	0.60	0.46	1.77	1.24	0.30	0.32	0.81	0.78
3 Av. wt. beetles mg	-	64.1	60.4	156.2	60	57.5	177	155	60	64	162	156
4 No. aphids eaten/night 19-21/10	-	164	—	152	-	37	—	40*	0	40	44*	63
5 No. aphids/beetle/night	-	5.125	—	5.85	-	4.625	—	5.0	0	8.0	8.8	12.6
6 Consumption of alternative food (18/10) gm	-	-	0.224	0.341	-	0.289	—	0.486	0.341	-	—	0.480
7 No. plants/plot	40	64	54	52	40	32	40	30	34	34	34	36

* Dates 19-24/10 for variable 4

NOTES:

1. Mean aphid numbers per treatment are shown in figure 2.9.
2. The beetle species used were Nebria brevicollis and Pterostichus madidus.
3. Missing values for aphid predation (variables 4 and 5) were due to the absence of an aphid sample in these plots on 21st October.