THE ROLE OF PARASITES IN THE CONTROL OF MYZUS PERSICAE (SULZER) POPULATIONS IN SOUTH-EAST SCOTLAND

by

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For my parents

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SUMMARY

Investigations were carried out into the importance of natural enemies, particularly parasites, in the regulation of seasonal changes in Myzus persicae (Sulzer) populations on brussels sprouts in the east Lothian area approximately 24 km east of Edinburgh.

Myzus persicae were found to colonise the sprout plants as early as the end of May, in 1973, and the beginning of June, in 1974. The populations studied in 1974 increased to greater levels of density than were found in 1973 and reached their peak in the middle of August compared to the middle of July the year before.

It was shown that migration of the aphids, from the populations studied from the end of May, occurred from the sixth week of colonisation. In those populations studied later in the season migration occurred from the fourth week of colonisation.

In all populations a distinct time lag was found between the arrival of aphids in the crop and the detection of parasitism in the aphid population. The overall effect of the parasite species complex upon the Myzus persicae population, as estimated by the percentage parasitism, was greater in 1973 than in 1974 although no more than 15 per cent mortality was recorded in any of the populations studied that year.

The effects of parasitism were related to changes in the aphid population density and this relationship appeared only to exist if the sites containing the population had a degree of shelter.

Myzus persicae was found to be parasitised by at least eight species in two genera of primary parasites and by at least five species in five genera of hyperparasites. The Aphidius rosae group of primary parasites was new to the records of parasites of Myzus persicae in Britain.

Diaeretiella rapae M^{c}Intosh was the dominant species of the primary parasites although the percentage occurrence of this species was much reduced in 1974. This reduction was compensated by an increase predominately in the Aphidius urticae group and Praon volucre Haliday. Alloxysta ? ancylocera Cameron and Asaphes vulgaris Walker were the dominant hyperparasite species in 1973 with the former the most common in 1974. The levels of hyperparasitism were higher in 1973 than in 1974 and its presence would tend to limit the effectiveness of the primary parasites in controlling the aphid populations.

Laboratory investigations showed that Myzus persicae was more adapted to lower temperature regimes than its most common primary parasite Diaeretiella rapae. This adaptation is thought to enable the aphid to survive the winter anholocyclically and to commence development much earlier in the spring than would its main parasite. The higher threshold of development and slower developmental rate of the parasite would therefore limit the effectiveness of this parasite species in controlling Myzus persicae populations.

Diaeretiella rapae was also found to prefer Brevicoryne brassicae (L) as a host in the field and it is argued that this would also limit the effectiveness of the parasite complex in controlling Myzus persicae populations.

Myzus persicae could also be destroyed by predators and by fungal disease. The presence of predators, specifically the Syrphidae, were much less common in 1974 than in 1973 and were detected in the populations a lot later in the season. Fungal disease was to be found in all the populations although no more than 10 per cent of the total population was destroyed in this way. The presence of these two mortality factors, especially around the mid-season peak, must, along with parasitism, reduce the aphid population. However, it is thought that this reduction is too late in the season to be of economic significance especially where the control of virus diseases transmitted by Myzus persicae is concerned.

INTRODUCTION

AND

LITERATURE REVIEW

Aphids are among the most important crop pests in the world. Myzus persicae (Sulzer) is considered to be the most notable species as it causes direct damage to plants and is also able to transmit over 100 virus diseases on about thirty different botanical families, including major crops such as tobacco, sugar beet, brassicas and potatoes (van Emden, Eastop, Hughes and Way, 1969).

In Scotland, as in most countries, Myzus persicae is economically important as a vector of potato viruses, particularly leaf roll and to a lesser degree veinal necrosis and severe mosaic virus (Scottish Agricultural Colleges Technical Note No.3, 1975). Any increase in the spread of these viruses is important to the seed potato industry, particularly in Scotland where about sixty per cent of the total acreage of certified seed potatoes in Great Britain is produced. A considerable tonnage of this seed is exported each year to England, Wales and abroad (Hay, 1969). The value of the seed potato crop lies in the absence of aphids, or at least a low rate of spread of the aphid-borne virus disease (Whitehead, 1925; Todd, 1961).

Aphids have not been a serious problem in Scotland for many years, due to crop protection measures and weather restraints, and growers have been able to reduce the more important virus diseases to a very low level. During the three years 1972 to 1975, however, aphid migrations from winter hosts have been earlier than usual and populations on potatoes have been unusually high, especially in 1974, with a corresponding increase in the incidence of aphid-borne virus diseases (Scottish Agricultural Colleges Technical Note No.3, 1975).

Aphid populations have a number of biological attributes which enable them to achieve a high level of importance as pests and which makes effective control difficult. When conditions are suitable they have a high level of parthenogenetic, viviparous reproduction, with a short development period and the occurrence of overlapping generations of winged migratory forms (alatae) and wingless colonising forms (apterae) (Ôtake, 1966).

Myzus persicae alternates between a primary and a secondary host during the full year with the production of complex polymorphic forms (Hille Ris Lambers, 1966). The species may survive the winter in one of two ways depending on the climate prevailing in the region. The production of eggs as the overwintering stage occurs under cold winter conditions - a holocyclic life cycle, but during mild winters Myzus persicae may overwinter viviparously on crops, weeds, in glasshouses, on stored mangolds and sugar beet (Davies, 1934; Jacob, 1941; Broadbent, Cornford, Hull and Tinsley, 1949; Shaw, 1955; Fisken, 1959a; Agyen-Sampong, 1972) - an anholocyclic life cycle.

The possession of an anholocyclic life cycle confers a selective advantage on the aphid population as eggs produced in a holocyclic life cycle will give rise to later populations in the spring. These populations are more likely to be affected by natural enemies than anholocyclic populations (van Emden et al., 1969). This is because the anholocyclic form of Myzus persicae often colonises very young plants, and on these the natural enemies can only exert efficient control several weeks after the appearance of alate virginoparae (Bonnemaison, 1966). This advantage of anholocycly is likely to be

enhanced by agricultural and horticultural practices which provide a continual supply of suitable host plants, for example brassicas (van Emden et al.,1969).

The use of chemical methods for control has resulted in the appearance of resistant populations (Shiga, 1967). When insecticides have been used to prevent the spread of viruses by controlling their aphid vectors they have been either unsuccessful or only partially successful (van Emden et al., 1969). Watson and Plumb (1972) believed that insecticides often failed to control viruses because they were introduced early during the growing season when aphids were few and that later the introduced virus spread within the crop as the aphid population developed. They also found that virus spread could be prevented by systemic insecticides but subsequent introduction of viruses from outside sources could not be prevented.

Such findings emphasise the importance of control by natural enemies in the non-crop or alternative crop habitat (Shiga, 1967; van Emden et al., 1969). As a solution to insect pest problems in Britain the application of biological control has not been considered promising because of unpredictable weather (Taylor, 1955). More recent studies on the effect of uncultivated land on the distribution of Brevicoryne brassicae (L) on an adjacent crop indicated the significance of such habitats in providing a reservoir of natural enemies, provided alternative host plants of the pest were present (van Emden, 1965). The effect of the parasites on the aphid in the adjacent crop however, appeared to bear no significant relation to edgegrowth factors since the parasitised adult aphids were evenly distributed through the crop.

The control of virus vectors by introducing natural enemies is attractive for economic and environmental reasons but it has not so far been very successful in achieving significant control (Watson and Plumb, 1972). Biological control workers have, in general, been reluctant to undertake projects where the transmission of virus diseases are involved, even when control might be possible. Stubbs (1966) reported on the control of the carrot aphid, Cavariella aegopodii (Scopoli), in Australia and Tasmania, by a parasite, Aphidius salicis Haliday, which had been introduced from California. This was the first case in which the population of a vector was so strongly depressed by the action of a natural enemy that the incidence of the disease caused by the carrot motley dwarf virus was significantly reduced. Unfortunately the reduction in the aphid population through the action of the parasite plus the normal fall in the aphid populations to an undetectable level in the summer resulted in the disappearance of the parasite (Stubbs pers.comm., 1975). Other reasons for the parasites' very early disappearance were suggested by Stubbs included the presence of a native hyperparasite or the failure of the parasite to adapt to the climatic conditions in Australia.

The quantitative effects of natural enemies as well as other factors which help to regulate numbers of aphids are only partly understood and for only a few species, for example Aphis fabae Scopoli (Way, 1967; Way and Banks, 1964, 1967, 1968) and Brevicoryne brassicae (Hafez, 1961; Hughes, 1963; van Emden, 1965) when they are pests, but little data is available for Myzus persicae (van Emden et al., 1969).

The significance of natural enemies in the control of aphids is little understood in either the fundamental or the applied sense especially in annual crops. This is not so for perennial crops where integration of chemical and biological control has been achieved for a number of aphid species. Most notable of these successes are the control of the spotted alfalfa aphid, Therioaphis maculata (Buckton) reported by Stern, Smith, van den Bosch and Hagen (1959) and control of the walnut aphid, Chromaphis juglandicola (Kaltenbach) reported by Frazer and van den Bosch (1973). These results were achieved by the introduction of exotic natural enemies which became adapted to their new habitat and this may explain the lack of obvious success in many biological control programmes. Many natural enemies are not regarded as important biotic mortality agents in their native habitats and they cannot therefore be expected to perform effectively in new areas (Smith, 1962). However, Smith states that if the pests, either native or cosmopolitan in occurrence, already have associated with them all their major parasites and predators, then those natural enemies must be either partially or completely ineffective in providing adequate suppression and it is such partially effective natural enemies that are the ones which fit into the integrated control concept. This was effectively demonstrated by Nawrocka (1972) who supplemented the effectiveness of the natural enemies Diaeretiella rapae M^{c}Intosh and the larvae of syrphids, coccinellids, chrysopids and cecidomyids with insecticide. The chemical was applied within ten days of the first appearance of Brevicoryne brassicae on white cabbage in Poland. This resulted in a check in the aphid population growth allowing the natural enemies to become established in the later stages of plant growth. The aphid population was kept below economic levels.

The determination of the economic level may itself create problems in assessing the effectiveness of natural enemies. The levels which are set may often preclude economic control by parasites and predators even although these enemies are highly effective population regulators (van den Bosch, 1971).

In nature the parasites and other natural enemies act as agents of the community mechanism to limit the aphid population number but if the resultant fluctuations cause significant damage to crops man will tend to believe that the natural mechanisms are ineffective, although such fluctuations are normal in nature (Starý, 1970). It would appear therefore that the term effectiveness is difficult to define since a degree of control which will allow aphid numbers to exceed the threshold value in some crops may be "effective" in a crop with a very short growing season by at least reducing the population peak maximum (Hodek, Hagen and van Emden, 1972).

The role of parasites in the natural limitation of aphids is of basic significance (Starý, 1970) and Myzus persicae is subject to parasitism by a number of the Aphidiidae, the ichneumonid family which contains most of the important parasites of aphids (Dunn, 1949; Mackauer, 1968; Mackauer and Starý, 1967; Starý, 1970; Agyen-Sampong, 1972). Evaluation of these natural enemies has only been carried out intensively in potatoes and cruciferous crops and these cases have been complicated, partly because Myzus persicae is often scarce and ephemeral on crops and therefore difficult to study (van Emden et al., 1969). Further complications in analysing the effects of parasites arise when the aphid population is intermixed with other aphid species on any one plant

or group of plants (Pimentel, 1961; Shiga, 1967; Hagen and van den Bosch, 1968; Starý, 1970). The use of selective insecticides which kill the natural enemies but not the aphid will provide almost the only quantitative evidence of the controlling action of natural enemies (Hille Ris Lambers, Reestman and Schepers, 1953; Shorey, 1961).

Reports of effective control of Myzus persicae appear to be restricted to glasshouse environments. Wyatt (1970) obtained complete elimination of Myzus persicae on chrysanthemums in glasshouses when there was an unintentional introduction of Aphidius matricariae Haliday. He considered that this level of control was not economical on susceptible varieties since the reduction of the aphid population was not possible until the aphids became self limiting. Harbaugh and Mattson (1973) achieved effective control of Myzus persicae when they released eight lacewing, Chrysopa carnea, larvae per greenhouse snapdragon, Antirrhinum majus, four at a time over a period of eight weeks.

Control in greenhouses must be attributed to the almost closed environment and the artificially maintained continuity of parasite and prey as well as to favourable environmental conditions. McLeod (1937) and Hussey (1965) reported that control of Myzus persicae by Aphidius matricariae was only effective at daily temperatures of 18.3°C or more. This is because the temperature optimum of aphid and parasite can differ (Hughes, 1963; Starý, 1970; Agyen-Sampong, 1972). This was also true for the lacewing larvae which took a week longer at 21°C to control aphids effectively than in a 24°C greenhouse (Harbaugh and Mattson, (1973).

On field crops the effectiveness of parasites seems to be disappointingly low (Dunn, 1949; Ôtake, 1966; Agyen-Sampong, 1972). Barbagallo, Inserra and Foster (1972), working with Myzus persicae on potatoes in Sicily, found parasites and fungus disease to be of little importance in population control although the infestation of aphids lasted only two months.

The problem with field studies to determine the effects of natural enemies arises from what is meant by the term effectiveness. Many people classify a species of parasite to be effective or ineffective by the degree of parasitisation obtained from the ratio of mummified to non-mummified aphids observed in the colonies. However, a parasite can be effective when it attacks a relatively lower number of individuals in a period of low density (Starý, 1970).

Environmental conditions will largely determine the effectiveness of parasites and other natural enemies. Bodenheimer and Schiffer (1953) regard it as a fact that parasite populations are normally reduced in numbers, either permanently or periodically, by various external factors, to a greater degree than are the populations of the hosts. They claim this to be the only explanation for the non-existence of accumulative parasitisation in successive generations. Bodenheimer and Schiffer also regard parasites as being ecologically more 'sensitive' to favourable or unfavourable climatic conditions. The adult stage of the aphidiid parasites is the only stage which is influenced directly by various conditions of temperature and relative humidity with the developing parasite only being affected indirectly through the hosts' response to changing environmental conditions (Starý, 1970). Temperature would

appear to be the main limiting factor as parasites require slightly higher levels for optimum breeding efficiency than do their aphid hosts (Hafez, 1961; Hughes, 1963; Starý, 1970; Agyen-Sampong, 1972), although one could theoretically select for a parasite species that was adapted to lower temperature conditions (Mackauer, 1968).

When associated with an agricultural ecosystem of annual plants, aphids have an initial advantage over their natural enemies. Their lower threshold of development and parthenogenetic type of reproduction allows them to become established in the new environment before the arrival and build up in natural enemies. Jacob (1944) found that parasite attack began about one month after the aphid infestation had become established. Hille Ris Lambers (1955) reported that if aphid populations on potatoes had such a favourable start then large numbers were produced, culminating in a sharp decline in numbers in mid-season but if they were limited by natural enemies, earlier in the season, the population curve rose more slowly and descended more gradually, with small increases in numbers later in the season.

The presence of hyperparasitism is often considered a limiting factor in the effectiveness of the primary parasites (Dunn, 1949; Hafez, 1961; Ôtake, 1966; Agyen-Sampong, 1972). Hyperparasites act by producing a 'damping' of typical parasite/host oscillations but the considerable levels of hyperparasitism found in the field may be exaggerated by prior dispersal of unparasitised primary parasites caused, perhaps, by interference at increasing density levels (Way, 1966). Way found the evidence pointed towards dispersal of some individuals when mutual interference occurred between parasites when the density of their

population rose above a critical level. The density at which a particular species disperses or begins to disperse will affect its efficiency in biological control. Smith (1966), however, found hyperparasites to be unimportant when observing population changes of Acyrthosiphon spartii (Koch) on broom.

The effects of hyperparasitism tend to become more evident later in the season with the resultant peak of emergence for the primary parasites always preceding that of the hyperparasites (Sedlag, 1959). This distinct time difference could be utilised in an integrated control programme to protect the primary parasite population and allow a greater proportion to overwinter, providing that sufficient aphid hosts were present. This was successfully used by De Bach (1949) when he retarded the secondary parasite, Lygocerus, by using a differential insecticide, without harm to the primary mealy bug parasite Anarhopus.

Starý (1972) suggested that an integrated control approach around a certain crop is important but believed that the neighbouring ecosystems should be taken into consideration. He proposed the concept of multilateral control of aphids and stressed the avoidance of studying an ecosystem without regard to neighbouring ecosystems in which sources of the key pests might occur.

In Scotland, except for Davies' short survey of forty-three centres in Scotland in 1936 (Davies, 1939), it is only recently that attention has been paid to the bionomics of potato virus vectors, particularly Myzus persicae. The studies have been few and in general have been related to the species' overwintering abilities and the significance of this on the infestation of potato crops in the following year. Shaw (1955)

studied the overwintering of Myzus persicae in north-east Scotland and found it was uncommon for this species to overwinter successfully on brassicas. On the other hand, Fisken (1959a,b) postulated that overwintering and spring multiplication sites of Myzus persicae on brassicas was important for the infestation of local crops and may also have been of wider significance regarding virus spread in the east of Scotland. In an earlier report Fisken (1955) observed that potato crops in close proximity to market gardens became infested with high populations of the aphids, but crops ten miles distant were relatively free from the aphid even in mid-August. Todd (1961) found that this relationship was not a necessary consequence, for on some crops growing within a few miles of Musselburgh, the brassica centre of east Scotland, and especially further to the south and west, the spread of virus disease on potatoes did not exceed that at some other sites many miles distant.

Howell (1974), reporting on field studies carried out in south eastern Scotland from 1962 to 1969, found that the spread of virus disease did not correlate well with distance from the market garden area of Musselburgh and he suggested that spread of the disease in south Scotland is mainly from sources within the crop. He claimed that brassicas and glasshouses are more widely distributed than suggested by Fisken and may be found from Edinburgh to Dunbar. These sites could be regarded as potential aphid overwintering sites with the brassica locations varying to some extent with crop rotation.

In none of these cases was the influence of natural enemies investigated although Todd (1961) suggested that the overwintering factor which Fisken suggested might well be important but it was obviously very susceptible to other, not clearly defined, influences.

Todd (1961) and Howell (1973) suggested that climate plays an important role in the build up and dispersal of aphid populations. Howell (1973) found that the temperature in the month of April was critical for aphid population development in any one year and Todd (1961) supported Fisken's (1959a, 1959b) suggestion that aphids are dispersed by prevailing winds but he believed that there could be other correlated factors such as relatively lower humidities eastward from the Musselburgh area.

Agyen-Sampong (1972) made the first major investigation into the seasonal changes of aphids, particularly Myzus persicae on brussels sprouts, and the importance of the natural enemies from autumn 1968 to spring 1971 in the Edinburgh area. He found that Myzus persicae overwintered anholocyclically on weeds, particularly on dock plants, but rarely on brassica crops. This is supported by work carried out in England by Heathcote, Dunning and Wolfe (1965) who found that a small percentage of arable weeds could be a possible source of viruliferous aphids in the spring, but since these weeds are extremely numerous they could still provide a formidable source of infective aphids.

Agyen-Sampong (1972) found a number of factors which he considered limited the effectiveness of parasites. These were the fast developmental rate and lower threshold of the aphid host as compared to that of its parasite. Hyperparasitism further reduced their effectiveness with 39.4 per cent and 46.9 per cent hyperparasitism occurring in 1969 and 1970 respectively.

He suggested that another possible limiting factor was the harvesting of the brassicas during the autumn. This destroyed some of the

overwintering aphid mummies and suddenly reduced the host populations which could be parasitised.

Way, Murdie and Galley (1969) found mummies of Brevicoryne brassicae overwintering on the leaf litter below brassica plants and that a large proportion of these were destroyed by active predators (Carabidae and Staphylinidae). They considered that about two to three per cent of Diaeretiella rapae mummies were destroyed or removed by harvesting but that soil cultivation in winter drastically reduced the numbers of emerging adult primary parasites, hyperparasites and syrphids.

Very little is known of the possible value of different methods of control in south east Scotland other than by the use of insecticides against pests attacking brassicas. Further studies into the quantitative effects of natural enemies upon Myzus persicae populations are required before a true evaluation of their effectiveness can be made.

OBJECT OF INVESTIGATION

1. FIELD

Reports of recent increases in the incidence of aphid-borne virus diseases in potatoes clearly emphasise the need for a greater understanding of the bionomics of economically important aphid species such as Myzus persicae (Sulzer). As reported in the literature there are only a few published studies of detailed analysis of Myzus persicae populations and, apart from surveys by Davies (1939); Shaw (1955); Fisken (1959a, 1959b); Todd (1961) and Howell (1973,1974), the only detailed information with particular reference to south east Scotland is that provided by Agyen-Sampong (1972).

It was the object of this study to expand upon the information reported by Agyen-Sampong and to assess the effect that parasites may have on seasonal fluctuations in Myzus persicae populations. Much of the study is a survey of the aphid and parasite species complex which is found in association with commercial brussels sprout (Brassica oleracea var gemmifera) crops throughout the growing season.

In order to observe and analyse the seasonal population changes an integral part of the investigation is the design of a regular crop sampling method based on the systems used by Church and Strickland (1954) and Hughes (1963). In addition, the phenology of the annual cycle of aphids, parasites and predators is clarified by the use of water trapping methods based on those described by Moericke (1951) and Fisken (1959a,1959b).

The influence of temperature, sunshine and rainfall on the populations of aphids and parasites is analysed particularly in regard to their

direct effects early in the season. The data required for analyses is obtained from a continuous monitoring of seasonal changes in the abiotic factors by means of suitable recording equipment or from information supplied by the Meteorological Office when methods of field recording of such data were not readily available.

It is to be expected that a short term study will not provide answers to all questions relating to Myzus persicae population changes in the area but by limiting the investigation to the field certain aspects of the aphids' ecology can be clarified for this local situation. It is also hoped to stimulate further research and suggestions for future study are outlined.

2. LABORATORY

Laboratory studies in controlled conditions provide few complete answers to specific field questions. Field conditions are a complex series of interrelationships and interactions and accurate simulation is difficult, if not impossible to achieve. However, certain laboratory studies are a useful guide to the trends occurring in relation to particular field problems.

Temperature, for example, is considered to be one of the most important factors influencing insect populations, particularly since the rate of insect development is dependent upon the temperature regimes to which insects are exposed (Campbell, Frazer, Gilbert, Gutierrez and Mackauer, 1974). Nevertheless it must be borne in mind that as a key factor in the environment, temperature interacts with other factors such as humidity, light and food (Howe, 1967; Starý, 1970).

Every insect species has its threshold of development which is the point on the temperature scale below which no development takes place (Siddiqui, Barlow and Randolph, 1973). Insects also require to be exposed to a particular temperature level over a period of time in order to complete its development and this is considered to be a thermal constant (Andrewartha and Birch, 1954).

Campbell et al., (1974) consider the thermal constant to be of greatest significance as it largely determines the number of generations an insect species will have in one season. It being normally assumed that the thermal constant will remain unchanged even if the temperature does not remain constant, as under field conditions, where there are diurnal oscillations (Hughes, 1963).

There have been a number of studies, based on the above ideas, on the association between Brevicoryne brassicae and its primary parasite Diaeretiella rapae (Hafez, 1961; Hughes, 1963). The development of Myzus persicae by itself has been reported by Weed (1927); Lal (1950); Sylvester (1954); MacGillivray and Anderson (1958); Barlow (1962) and Agyen-Sampong (1972). There are few published reports on the interaction between Myzus persicae and its parasites although Agyen-Sampong produced some data on the aphid and its primary parasite Praon volucre Haliday, among others.

Results from field studies, from this investigation, showed that Diaeretiella rapae was the most common primary parasite of Myzus persicae. A series of investigations into the development of these species was therefore begun.

It was the purpose of the laboratory studies to provide information that can be related to the situation in the field. Derivation of the theoretical threshold of development and the thermal constant for the two species studied, along with additional information on longevity, fecundity and rate of development, will provide for a clearer understanding of the effectiveness of Diaeretiella rapae in controlling local populations of Myzus persicae.

MATERIALS AND METHODS

1. FIELD

General description of habitats under investigation

The sites chosen to study the bionomics of aphid species and their natural enemies, with particular reference to Myzus persicae and its primary parasite Diaeretiella rapae, infesting brassica crops were situated on an east Lothian farm approximately 24 km (15 miles) east of Edinburgh (Figure 1).

The main host plant chosen for the investigation was Brussels sprout (Brassica oleracea var gemmifera) which allowed observations to be made throughout most of the year, under varying seasonal and ecological conditions. This crop, along with other brassicas comprised the bulk of the farm's crop production and no insecticides were applied to the plants during the period of investigation.

Weed plants were controlled by steerage hoeing in the early part of the season when the crop plants were still well spaced. No treatment to the plants occurred later in the season either within the sites or in the remainder of the fields containing the sites.

Crop areas of different crop planting dates were chosen as investigational areas and within each crop one or two sites were selected to give different types of ecological habitats, for example open and sheltered aspects, and were chosen to avoid crop margin effects.

From crop A, 1973 two sites were selected and given the codes $A_1$73 and $A_2$73. Site $A_1$73 was situated in the apex of a triangular shaped field and was sheltered on three sides by trees and a disused railway

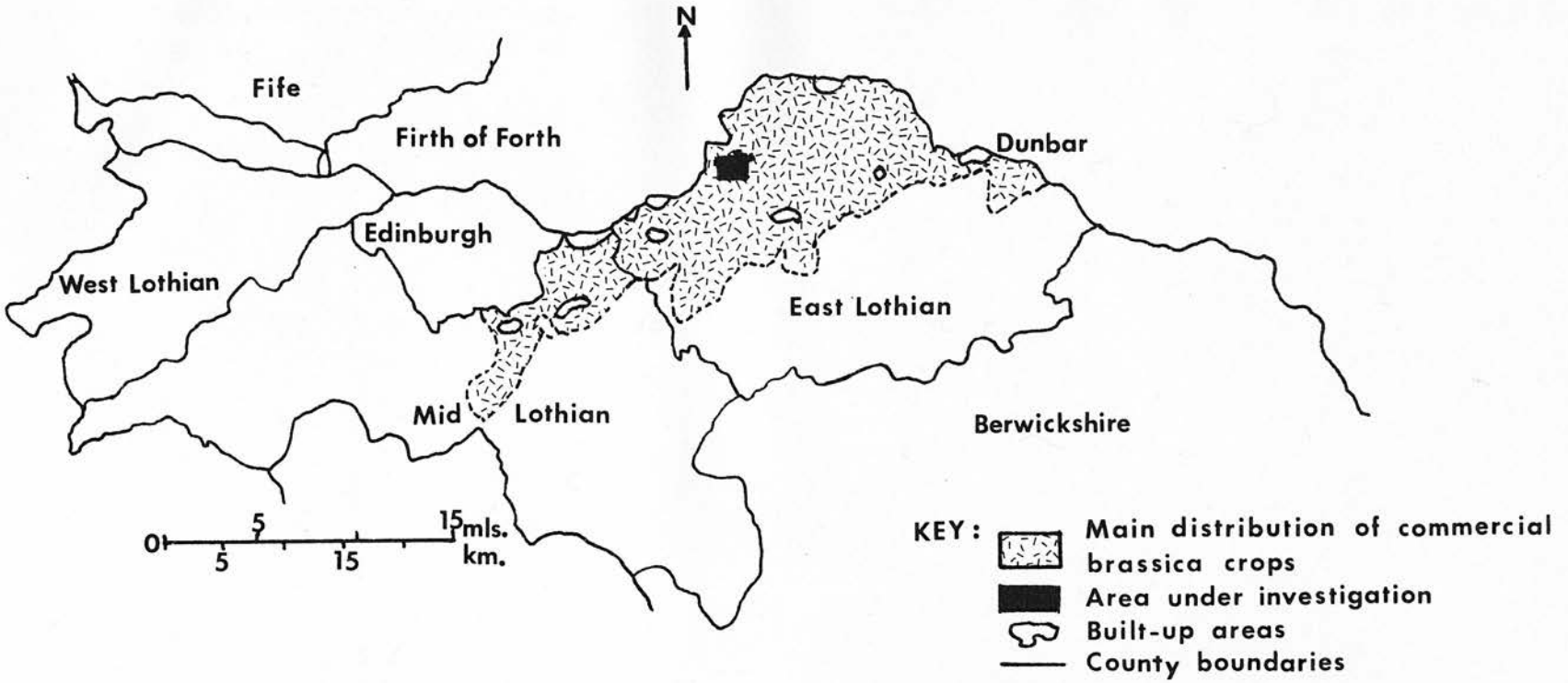


Figure 1. Relative position of area under investigation together with an indication of the main distribution of commercial brassica crops (Modified from Howell, 1974).

embankment. The southern face was open to the remainder of the crop. Site $A_2$73 was placed towards the base of the field and was exposed on all four sides.

The total field contained 22 acres of light, sandy soil. Three varieties of sprout were planted. These were Peer Gynt, Top Score and Lancelot of which Top Score was the prominent variety within the sampling areas. The crop was planted in the last week of May and harvested in September. The neighbouring fields were of grass and cereal.

In crop B, 1973 only one site was used and this was coded $B_1$73. The site was situated towards one corner of a 31 acre field and was partially sheltered on two sides by a wall and conifer plantation. The soil was similar in texture to that in field A73 and the varieties of sprout were the same. This crop was planted in early June and harvested in late November. The adjacent fields contained grass, cereals and sprouts.

The field adjacent to crop B contained crop C which had been used as an initial sampling area during the winter of 1972/1973 (coded C72). A similar sample adopted elsewehere in 1973 was used on the crop now coded C73. This field of 30 acres contained predominately F_1 Hybrid Thor variety of sprouts. The crop of 1973 was planted in the middle of June and harvested in February 1974. In 1972/1973 the crops were of a similar age at harvesting. The surrounding crops were of potato, grass, cereals and sprouts. The sites were exposed on all four sides.

In 1974 the number of sites studied was reduced to two and these were ecologically different from previous years. Site $A_3$74 was separated from the previous year's site by the disused railway embankment and was situated in a field of 45 acres. Only half of this acreage was planted with sprouts (variety Percival), the remainder contained barley. The site was exposed although with some partial shelter from a wood to the north of the area.

Site $B_2$74 was contained in a 26 acre field with less than half of this acreage planted in potatoes. The remainder had been planted with the sprout variety Thor and was separated from the potato crop by a grass track.

Site $A_3$74 was first to be planted, at the beginning of June. The crop was harvested a month later than occurred in 1973. Site $B_2$74 was planted three weeks later and harvested in January, 1975.

All sampling sites were 1000m^2 and were considered to be of sufficient size to minimise any upset to the ecosystem by sampling. The plants at each site were transplanted at intervals of 0.45m with 0.60m between rows. The study area did not exceed 95m above sea level.

Crop sampling

The leaves of the Brussels sprout plants were classified into three categories: upper, young leaves; middle, mature leaves; lower, senescing leaves. Church and Strickland (1954) suggested that since each plant carried about thirty mature and ten immature leaves, to sample about ten per cent of the plant material only required the

removal of three leaves at random from each plant. They believed that the bulking of these samples would result in the loss of some information but it was not practicable to keep individual three-leaf samples separate for analyses in view of the increased handling time.

Hughes (1963) modified this method by taking twin three-leaf samples from individual kale plants. He used one subsample to estimate aphid populations by washing and counting the aphids by means of an electronic aphid counter devised by Lowe and Drumgoole (1958). The second sample was used in the estimation of parasitism of the aphid population by storing the 'live' aphids for three days at 15^{o}C in plastic boxes after removing any mummified aphids. This was done in order to assess any further mummification after one instar period.

The method adopted in the present study involved a single three-leaf sample from each plant. The leaves were systematically searched, for the presence of aphids, back in the laboratory. Those aphids present were classified according to species, developmental stage and whether or not they were dead. If dead, then the cause of death was recorded as either the action of parasites (mummified aphids) or the action of fungal disease (granular aphids). The presence or absence of eggs, larvae or pupae of aphidophagous predators were also recorded. All 'live' aphids were stored in plastic boxes at room temperature. Any subsequent mummification was recorded on the third and sixth day after sampling.

Sampling was carried out on a weekly basis and in such a manner that sites were sampled in the same order of rotation to allow for diurnal

movement of organisms. The method for selection of plants to be sampled was the same for all sites. These plants varied from week to week according to the selection of random numbers obtained from Fisher and Yates (1963).

The corners of each site were marked by bamboo canes which were initially numbered from one to four in clockwise rotation. The sequence was then randomised to reduce any bias in the sampling procedure. Commencing from pole one the plants were counted consecutively until the first random number was reached. This plant was then sampled by removing three leaves at random. This procedure was repeated until the desired number of plants was reached, and sampled to give three separate bulked samples of upper, middle and lower leaves.

During the winter period of 1972/1973, at site C72, no leaves were removed but instead in situ counts were carried out in the field on the leaves that would normally have been removed. This process was found to be tedious and accuracy in identification and counting could not be guaranteed. Consequently the method described above was adopted for the remainder of the study.

At the start of each sampling season the plants were not of sufficient size to enable separation into the three stratas of plant growth. Until this was possible only one single sample of infested leaves was removed from each site. This enabled a greater surface area of plant material to be searched resulting in earlier detection of aphids in the site. The change to the three-leaf sample varied from site to site depending on the variety of sprout and on the suitability of environmental conditions for rapid growth of the plants.

In 1973/1974 thirty plants were sampled in the above manner at each site, apart from site $B_1$73 where plants were extremely slow to develop and only two leaves per plant were removed - one from the upper half of the plant and the other from the lower half.

In 1974/1975 at sites $A_3$74 and $B_2$74 a total of fifty plants were sampled since samples could be processed more efficiently in the laboratory.

Analyses of field samples

The analyses of the field samples was designed to evaluate the effect of parasites on changes in the aphid populations.

The degree of parasitisation that occurs within an aphid population can influence the description of a parasite as effective or ineffective in controlling that population. This level of parasitism can be determined by several methods.

Dissection of living aphids without regard to the developmental stage or instar of the aphid, as recommended by Starý (1970), will result in a more detailed picture of parasitism than the dissection of advanced aphid instars only (Sluss, 1967). The disadvantages of dissection lie in the difficulties of identification of different parasite species from eggs, larvae or pupae, together with the time taken in dissecting large numbers of aphids.

Hughes (1963) obtained mortality rates from the ratio of parasitised aphids to the number of fourth and adult instars which would have shown the symptoms of parasitism one instar period later.

Agyen-Sampong (1972) evaluated parasitism by two methods. Firstly by rearing weekly collections of advanced apterous nymphs from sprout plants in incubators or in the laboratory under conditions of about 20°C and 75 per cent relative humidity for a period of fourteen days. Daily checks were made and the ratio of mummified aphids to total aphids sampled was taken as the rate of parasitism. Secondly he made direct counts of mummified aphids in the field with parasitism calculated on the basis of the proportion of mummies to the sum of apterous adults, advanced nymphs and mummies found on the plants. This second method tended to give lower values and was considered to be less reliable than the first method although the values obtained could not be taken as an absolute rate of parasitism for the whole aphid population.

During this study, since the percentage of various aphid instars in a colony can change for various reasons (Starý, 1970), the complete samples of aphids were stored in plastic boxes in the laboratory for a period of six days, without regard for the instar distribution, after the removal of mummified or diseased aphids and predators. The temperature in the boxes ranged from 18-23°C with 60-80 per cent relative humidity. Every third day the samples were checked and any mummified aphids were removed. The ratio of the total mummified aphids to complete sample of aphids (living plus dead) could then be taken as the rate of parasitism occurring in the sampled population on the day of sampling.

This treatment of weekly samples enabled the proportion of the aphid population that was viable on the day of sampling to be distinguished

from that which might or might not reproduce after the occurrence of parasitism. Prior to storing the 'live' aphid sample, information on the bionomics of the aphid population was obtained. All aphids found were identified and counted according to species and instar distribution.

Whether collected on the day of sample or later, parasitised aphids were counted and classified according to host species, instar of aphid at which mummification occurred and the colour and form of the mummy. If the mummy was that of a Praon species, it was recognised by its tent-like structure, attached to the leaf with the dead aphid above. The more common Aphidius/Diaretus type of cocoon was the typical aphid shape as the parasite completes all stages of development inside the aphid's skin. An empty aphid case was distinguished by the presence of an emergence hole with or without a small flap hinged to the aphid's body.

Each week's collection of mummified aphids was placed in a 75mm x 25mm glass rearing tube at a density of one per square of plant tissue per tube (Figure 2). The tubes were then stoppered with cotton wool bungs. All tubes were coded according to site, week of sample, day mummification observed, the plant strata from which the sample was taken and the mummies catalogue number for record purposes.

During both years all parasitised aphids were reared under laboratory conditions of 18-23^{o}C with the tubes inspected daily for signs of emergence. All adult parasites that emerged were identified, sexed and counted according to their date of emergence, species and the

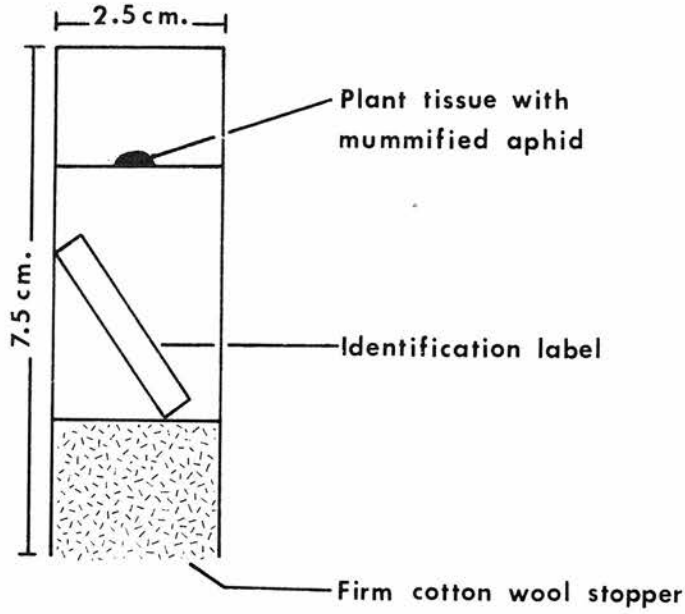


Figure 2. Diagrammatic representation of parasite emergence tube used in the course of this study.

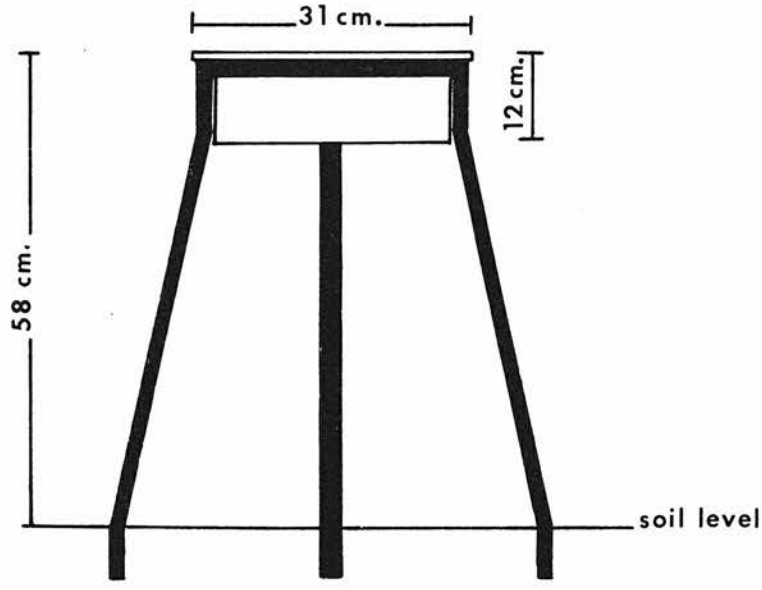


Figure 3. Schematic illustration of water trap in use from 1973 to 1975 in order to assess aerial populations of aphids, parasites and predators.

developmental stage of the aphid. The rearing of mummified aphids to produce emergent adult parasites also enabled distribution, numbers and degree of parasitism by secondary parasites to be recorded.

The degree of fungal attack on aphids was determined from the ratio of diseased aphids to total aphids sampled. Predators were recorded according to the presence of eggs, larvae or pupae and some successful attempts were made to rear the various stages through to adults for identification.

Aerial sampling

To assess aerial populations of aphids, parasites and predators a series of water traps was set up at specified sites during 1973/1974 and 1974/1975. The form of trap used was based on that described by Moericke (1951) and Fisken (1959a,1959b) and on that proposed by Costa and Lewis (1967) and Taylor and Palmer (1972).

The water trap consisted of a plastic bowl 31cm in diameter and 12cm in depth. The trap was painted, both inside and out, with British Standard Prime Yellow (B.S. 0-001), usually called Canary Yellow. The pigments contained within this paint are thought to have a broad spectrum of attraction to flying insects.

The trap was filled to a depth of 2-5cms with a water, detergent, formalin mixture (Lewis, 1959). The function of the detergent was to cause trapped insects to sink to the bottom by removing the surface tension of the water. The formalin reduces bacterial and fungal attack on the trapped insects and the amount of formalin in the mixture had to be increased markedly in the summer when the risk of deterioration of trapped specimens was greatest.

The trap was suspended from a metal tripod with the rim of the trap at a height of 58cm above soil level. This height corresponded to that achieved by the sprout plants during the growing season (Figure 3). During 1973 the traps were situated at sites A_1 and A_2. In 1974 a trap was situated at each of the sites studied that year.

The possible positions of the traps were restricted as placing them in the actual crop would tend to interfere with normal farm practices, particularly in the early part of the season. Consequently all traps were placed towards the headlands but as much in the open as possible. At site $B_2$74 the trap was placed on the edge of the track which ran between the potato and Brussels sprout crops.

All traps were visited once a week and the mixture containing the trapped specimens was bottled and returned to the laboratory for analyses. The traps were refilled to the required depth with fresh solution.

All aphids trapped by the above method were counted with a separate subtotal for the Myzus persicae alates that were found. Those parasites that were known to attack the aphids that infested the sampled crop were isolated from the mixture and counted according to sex and species. All adult predators were counted and identified at least to genus level.

Meteorological data

The main environmental factors measured in the course of this investigation were maximum and minimum temperatures, rainfall and

sunshine. The information on the latter two, plus additional data on temperature, were provided by the Agricultural Section of the Meteorological Office in Edinburgh. Their data came from the recording station at Haddington, approximately 5km south of the study area.

In the field, temperatures were measured continuously on thermographs situated at sites $A_1$73, C73, $A_2$74 and $B_2$74. The recording charts were analysed to provide daily or weekly maximum and minimum temperature readings and were replaced at weekly intervals.

The recorders were placed in a protective box which was slatted on two sides to allow free access to air currents. The box was painted white to reflect the sun's rays and prevent a temperature build up inside the box and also to provide only those recordings that could be equated to those of the free air. The height of the machine in the box corresponded approximately to the middle region of the plants and were situated as close to the crop as possible.

The data obtained could be used to correlate changes in the aphid or parasite populations with changes in environmental conditions and to determine what role these abiotic factors had in bringing about those changes.

2. LABORATORY

Effect of temperature on the development of Myzus persicae and its primary parasite Diaeretiella rapae

In all the experiments the developing aphids were reared under artificial daylight at controlled temperatures of 5^{o}, 10^{o}, 15^{o}, 20^{o}C. These conditions were maintained in a Gallenkamp cooled incubator with a fitted Compenstat controller together with upper and lower limit safety thermostats allowing temperature control to within a single degree.

Illumination was provided by two Philips 8-watt fluorescent lights, each producing an intensity of lighting equivalent to 350 lumens, which should be sufficient for aphid rearing. Agyen-Sampong (1972) successfully reared Myzus persicae on leaf discs at half this level of illumination. Both lights were connected to a Londex Rotaset electronic time switch which controlled the 12-hour photoperiod simulated at all temperatures.

A stock culture, initiated from Myzus persicae collected from the sampling area, was maintained in a temperature range of 15^{o} to 25^{o}C on Asparagus/Kale or Chinese cabbage plants. Both these plant types were found to be suitable as hosts as they had a non-waxy surface which increased the plants susceptibility to attack by Myzus persicae (Way and Murdie, 1965; Sparrow pers.comm.).

The plants were reared in plastic pots on John Innes Potting Compost No.2 and illuminated by means of Philips 160 watt mercury blended lamps providing a 16-hour photoperiod during the winter months.

All cultures were reared in an insect proof cage consisting of a wood frame covered with muslin and containing a removable glass panel for viewing and easy access. The top panel was also of glass in order to provide the plants with maximum available light.

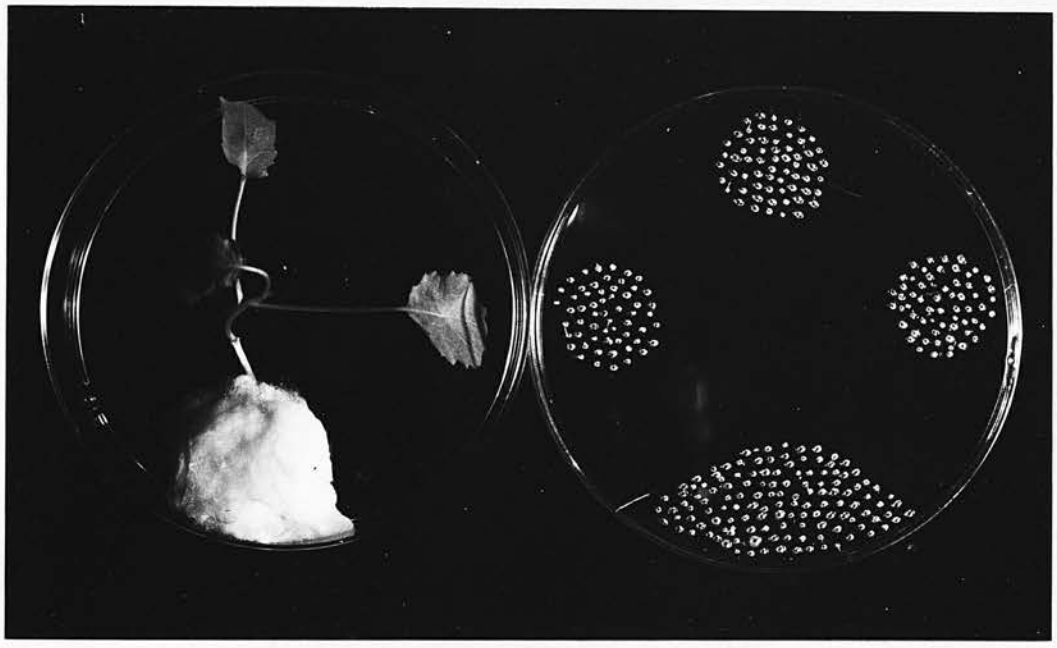
At the start of any series of development experiments advanced stage apterous nymphs were transferred from the stock cultures to the experimental growth chambers, described below. These nymphs were allowed to complete their development to adult apterae under the defined experimental conditions.

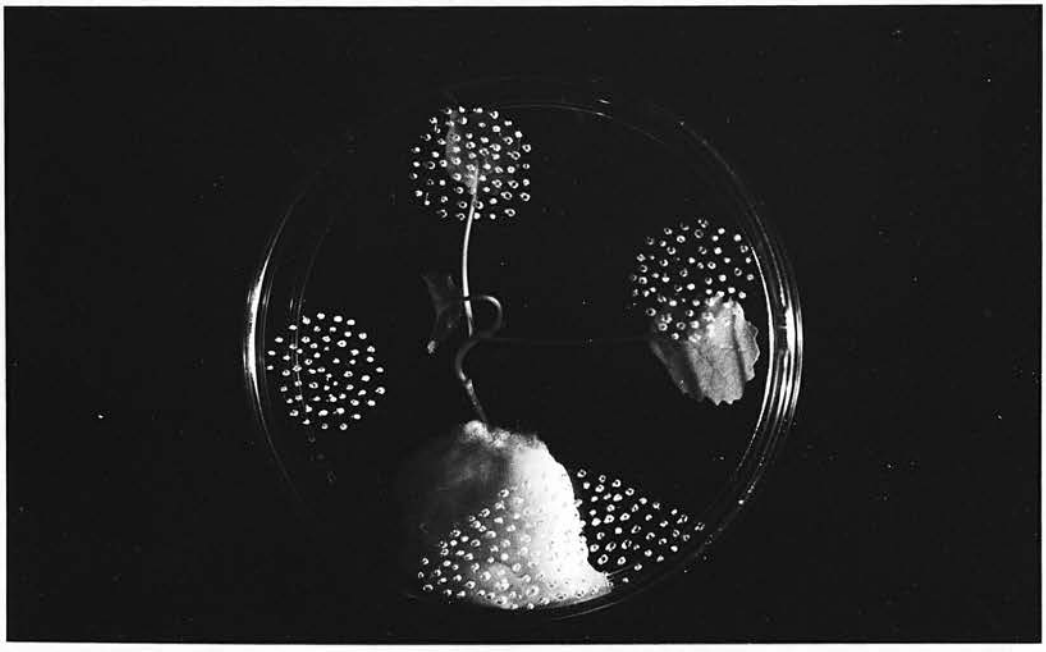
As the mature aphids produced progeny these young first stage nymphs were transferred individually to other chambers. All transference was achieved by the use of a fine camel hair brush moistened with water. Daily observations of the cultures were made and the following developmental records were made:-

1. Stage of aphid development (recorded as nymphs 1, 2, 3; nymphs 4 apterous and 4 alate; apterous and alate adults).
2. Time period to reproductive phase.
3. Total and daily frequency of nymphs produced.
4. Longevity of individual aphids.

The individual aphids were reared on single Asparagus/Kale seedlings which were small enough to be maintained in a 9cm diameter petri-dish and old enough to have produced true leaves (Plate 1). All seedlings used were selected for uniformity of size and age and all had their roots lodged in cotton wool moistened with a water culture solution (van Emden, 1966a). The formula of this solution is noted in Appendix 1. This technique markedly increased the humidity within

PLATE 1: Culture chamber open and closed





the petri-dish and in order to minimise this the lid of the petri-dish was pierced with fine holes. The use of this culture chamber ensured the least possible disturbance to the developing aphids as the plants did not require to be changed, except in a very few cases. This would not have been possible had leaf discs been used.

A similar method was adopted to determine the developmental rate of the aphids' primary parasite Diaeretiella rapae.

A total of 40 young nymphs of Myzus persicae were transferred from a stock culture to the surface of an Asparagus/Kale leaf and allowed to settle. The leaf was placed in a watch glass, $4cm^2$, to which were added four virgin female parasites. The ovipositional chamber was sealed by means of a glass cover. The parasites originated from mummified aphids collected in the field and were allowed to feed on a ten per cent sucrose solution prior to introduction to the chamber. The parasites maintained contact with the aphids for a total period of four hours at room temperature to ensure that oviposition had occurred.

On completion of the contact period all the aphids were transferred to the culture chambers, described above, at a density of two per plant. Observations were made daily and records taken, at 5^{o}, 10^{o}, 15^{o}, $20^{o}C$ with a 12-hour photoperiod, consisted of:-

1. Time period to mummification.
2. Time period to adult parasite emergence.
3. Developmental stage of aphid at which mummification occurred.
4. Total production of nymphs by the aphid before mummification.
5. Colour of the parasite cocoon.
6. Proportion of non-emergent parasites.

R E S U L T S

SECTION A - FIELD POPULATION STUDIES

1. APHIDS

Of the three species of aphid infesting Brussels sprout crops, namely Myzus persicae (Sulzer), Macrosiphum euphorbiae (Thomas) and Brevicoryne brassicae (L), particular attention is paid to the species Myzus persicae.

Table 1 gives the numbers of aphids collected at each site during the complete study year. Identification of the aphid species was according to criteria provided by Theobald (1926-1927), Stroyan (1952) and Cottier (1953).

Total population trends of Myzus persicae

The mid-season peak in aphid numbers at sites A_1, A_2 and $B_1$73 occurred in the latter half of July. The population density at that time ranged from about five viable aphids per leaf at $B_1$73 to around 12 viable aphids per leaf at site $A_2$73. About seven viable aphids per leaf were sampled at site $A_1$73 at the mid-season peak.

All three populations declined rapidly in numbers during August although the population studied at site B_1 recovered slightly by the beginning of November. (Figures 4, 5 and Appendices 2, 3.)

At site A_3 during 1974 the aphid population increased in size to about 22 viable aphids per leaf at the end of August. Very few aphids were sampled three weeks after the mid-season peak. About 14 viable aphids per leaf were recorded at site $B_2$74 when the population was at its most dense towards the end of July. Zero population at this site was observed from mid November onwards (Figures 4, 5 and Appendix 4).

TABLE 1: Total number of live aphids sampled during the study period

Species of Aphid	SITES						
	1972	1973				1974	
	C	A_1	A_2	B_1	C	A_3	B_2
Myzus persicae	2,798	3,031	3,260	1,197	548	15,634	6,880
Macrosiphum euphorbiae	0	13	20	70	0	316	245
Brevicoryne brassicae	3,997	60	44	63	1,357	747	1,704
Total leaves sampled	1,350	1,952	1,898	990	900	3,501	3,889

Study period:

Site A_1 and A_2: 29. 5.73 → 4. 9.73
Site B_1 : 26. 6.73 → 20.11.73
Site C : 16.10.72 → 19.12.72
Site C : 30.10.73 → 29. 1.74
Site A_3 : 4. 6.74 → 24. 9.74
Site B_2 : 25. 6.74 → 3.12.74

TABLE 2: Percentage distribution in the age structure of the Myzus persicae population during the study period

Developmental Stage	SITES						
	1972	1973				1974	
	C	A_1	A_2	B_1	C	A_3	A_4
Ny1 + Ny2	52.75	60.26	63.95	56.20	63.12	58.74	56.25
Ny3 + Ny4	28.73	26.28	25.00	28.93	26.58	24.89	32.39
Ny4 alatae	0	1.28	2.91	3.30	1.66	6.73	3.41
Apterae adults	14.55	8.97	6.98	9.92	8.31	7.40	6.25
Alatae adults	4.00	3.21	1.16	1.65	0.33	2.24	1.70

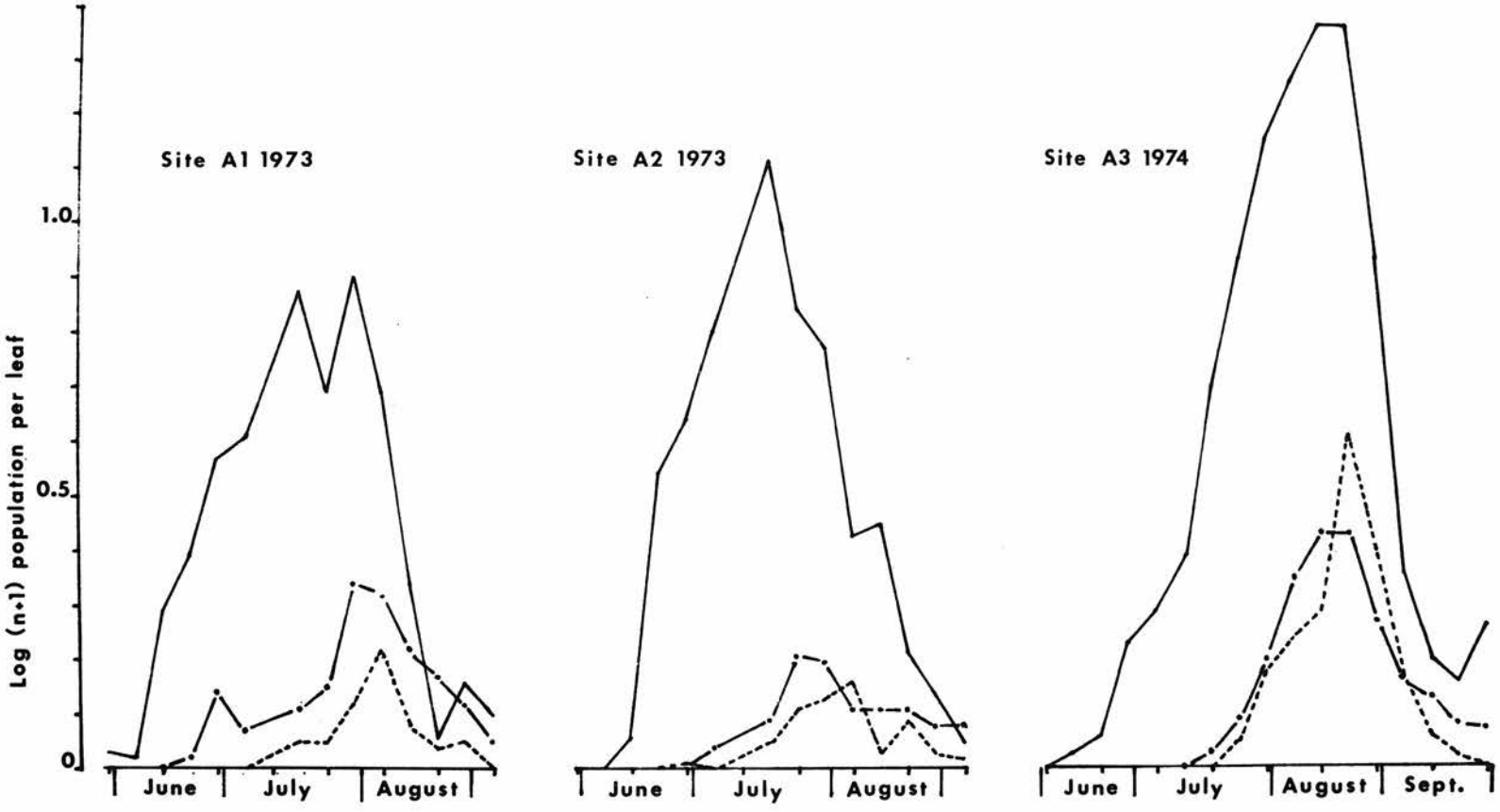


Figure4. Relationship between the trend of the viable Myzus persicae (Sulz.) population (——) and that number that were parasitised (——·) or attacked by fungi (----) per leaf.

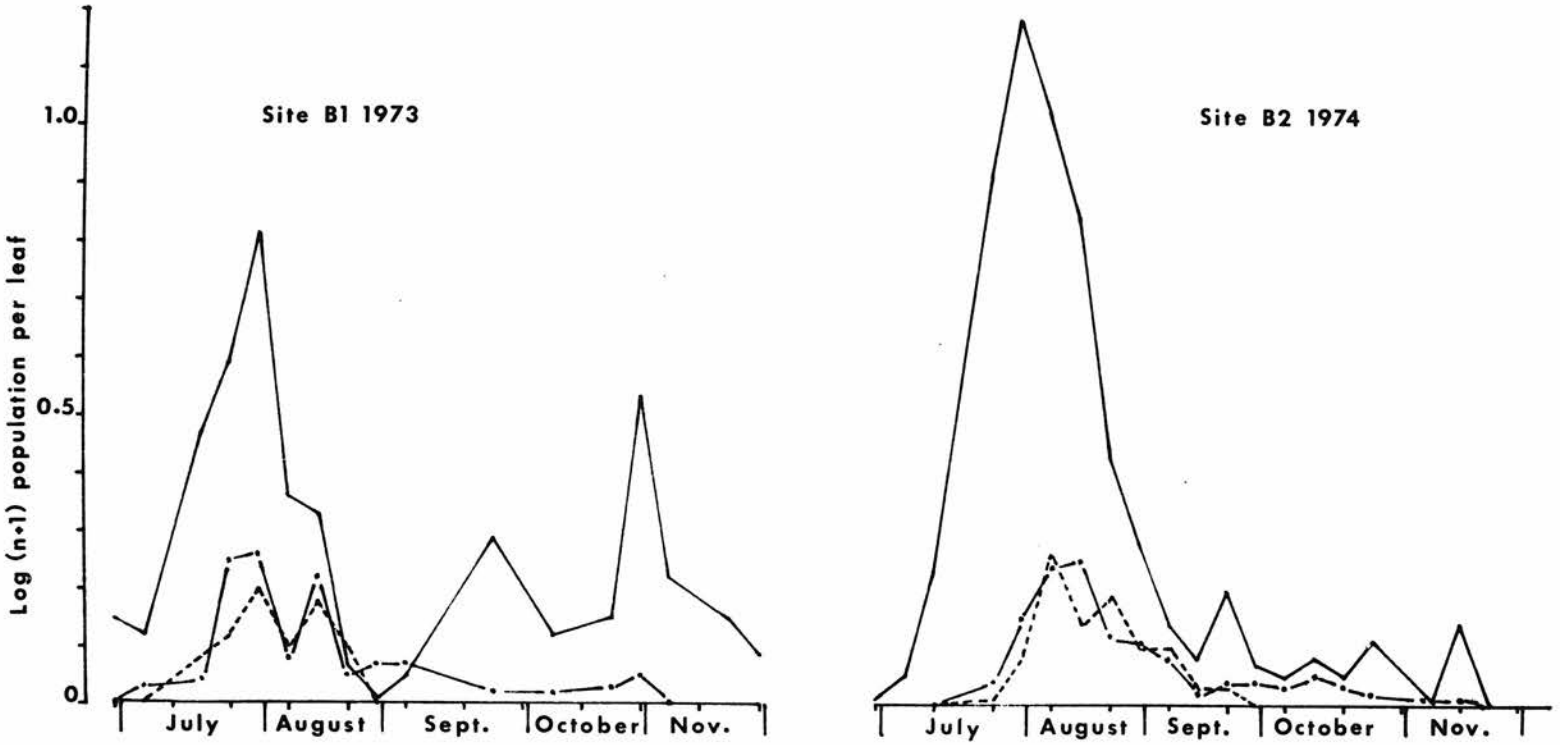


Figure 5. Relationship between the trend of the viable Myzus persicae (Sulz.) population (——) and that number that were parasitised (·—·) or attacked by fungi (·--·) per leaf.

Zero population was recorded at site C from mid December, 1972 and from mid January, 1974. The respective populations were declining in size from November onwards (Figure 6 and Appendix 5).

Age structure of the Myzus persicae populations

Table 2 details the percentage distribution in the age structure of the populations under study. In all populations studied the young nymphal stages (Ny1 + Ny2) accounted for more than half of the aphids sampled. The advanced nymphal stages (Ny3 + Ny4) only once exceeded 30 per cent of the aphid population and this was at site B_2 in 1974. Apterous adults were always few in number as were fourth stage alate nymphs and alate adults.

Age-specific population trends in Myzus persicae populations

Numbers of young and advanced stage nymphs at site $A_1$73 (Figure 7 and Appendix 6) reached a peak by the end of July but with advanced stage nymphs increasing and decreasing in number earlier than the young nymphs. Both stages were rare by mid August. The advanced stage alate nymphs (Ny4 al) were not detected until July in the sixth week of sampling. The percentage occurrence of this stage (Figure 10) reached its peak three weeks after the peak in the total aphid population only to disappear from the samples one week later.

Both winged and wingless adults were always few in number with the latter the slightly more common.

At site $A_2$73 (Figure 7 and Appendix 6) both the young and advanced stage nymphs reached a peak in the middle of July. However the number of young nymphs in the population declined at a slower rate to become

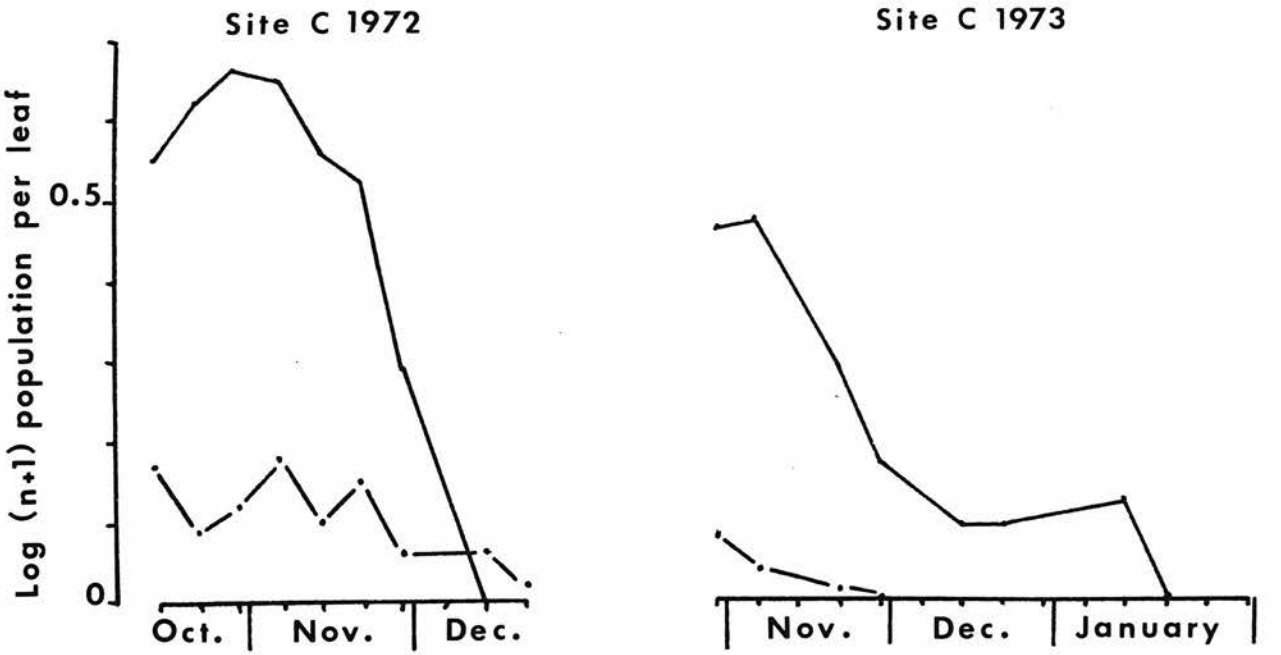


Figure6. Relationship between the trend of the viable Myzus persicae (Sulz.) population (——) and that number that were parasitised (·—·) per leaf.

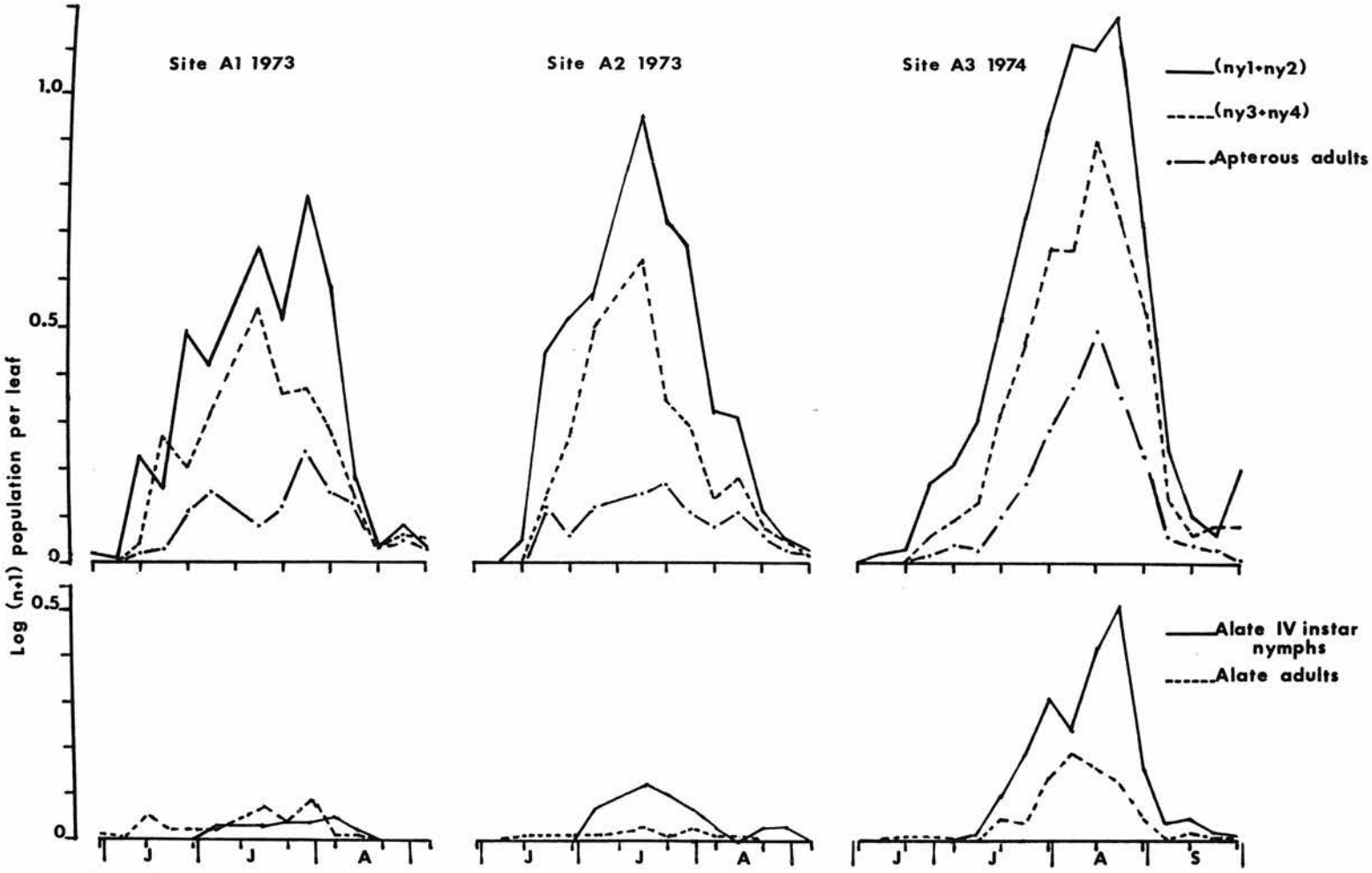


Figure 7. Age-specific population trends of Myzus persicae (Sulz.).

rare in the latter half of August compared to latter half of July in the case of advanced nymphs. The percentage occurrence of the Ny4 al (Figure 10) reached a peak six weeks after the peak in the total aphid population only to disappear from the samples one week later. This stage was first detected on the sixth week of sampling around the middle of July.

Both apterae and alatae adults were few throughout the sampling period with the alates disappearing from the population by mid August.

The young and advanced stage nymphs at site $B_1$73 (Figure 8 and Appendix 7) both displayed two peaks in density with those of the advanced nymphs slightly earlier than the young nymphs. Both stages were extremely rare at the bottom of the mid season decline.

Alate nymphs were first detected in the latter half of July only four weeks after the start of sampling. A rapid rise in the percentage occurrence of this stage occurred at the end of August four weeks after the total aphid population peak (Figure 10). These nymphs disappeared from the samples just as suddenly only to recover to fluctuate around ten per cent of total population during the remainder of the season.

The apterae adults also displayed two peaks in number during the season although they were not numerous. The alate adults disappeared from the samples by mid-August but were detected in low numbers during November after the second peak in the total aphid population.

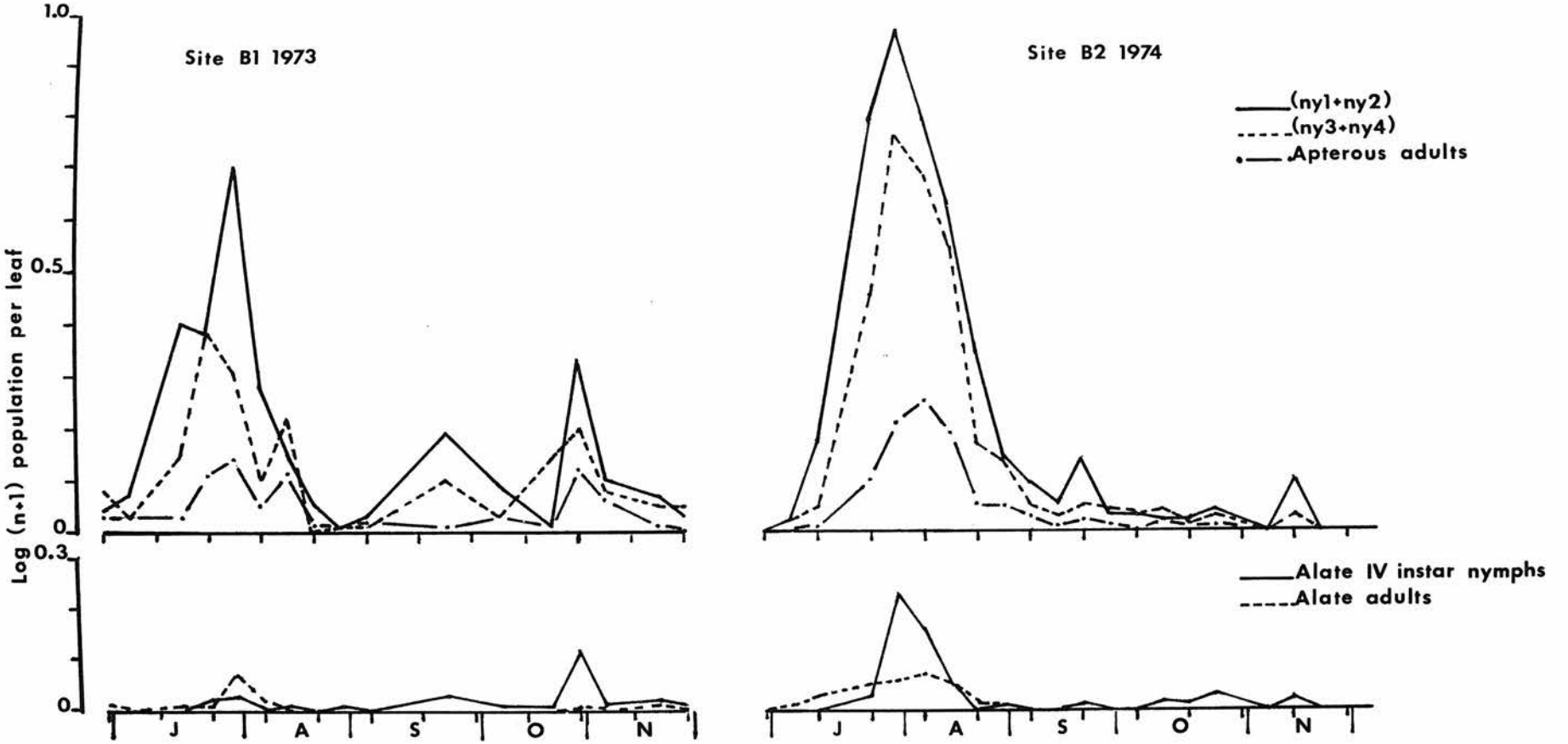


Figure 8. Age-specific population trends of Myzus persicae (Sulz.).

At site $A_3$74 (Figure 7 and Appendix 8) the advanced stage nymphs reached a peak one week earlier than the young nymph population during the latter half of August. Both populations declined rapidly in number during September.

Alate nymphs were detected on the sixth week of sampling only one month before the peak in the total aphid population. The percentage occurrence of this stage (Figure 10) reached its peak three weeks after the total aphid population peak only to decline rapidly prior to harvesting of the crop.

Apterae and alate adults were more common in 1974 than in 1973 reaching a peak in numbers prior to the total aphid population peak in the latter half of August.

At site $B_2$74 (Figure 8 and Appendix 8) both young and advanced stage nymph populations displayed similar growth patterns. Both reached a peak in the latter half of July and both disappeared from the samples in the latter half of November. Advanced stage alate nymphs were first observed on the fourth week of sampling. The percentage occurrence of this stage was not high during the mid-season peak and decline in the total aphid population but was the dominant stage in the samples during October and November (Figure 10). Alate adults were not observed in the samples after the end of August and the apterae, very few in number throughout, disappeared from the samples in November.

At site C72 (Figure 9 and Appendix 9) alates were present until December although no nymph alates were recorded. All other development stages disappeared from the samples by mid December.

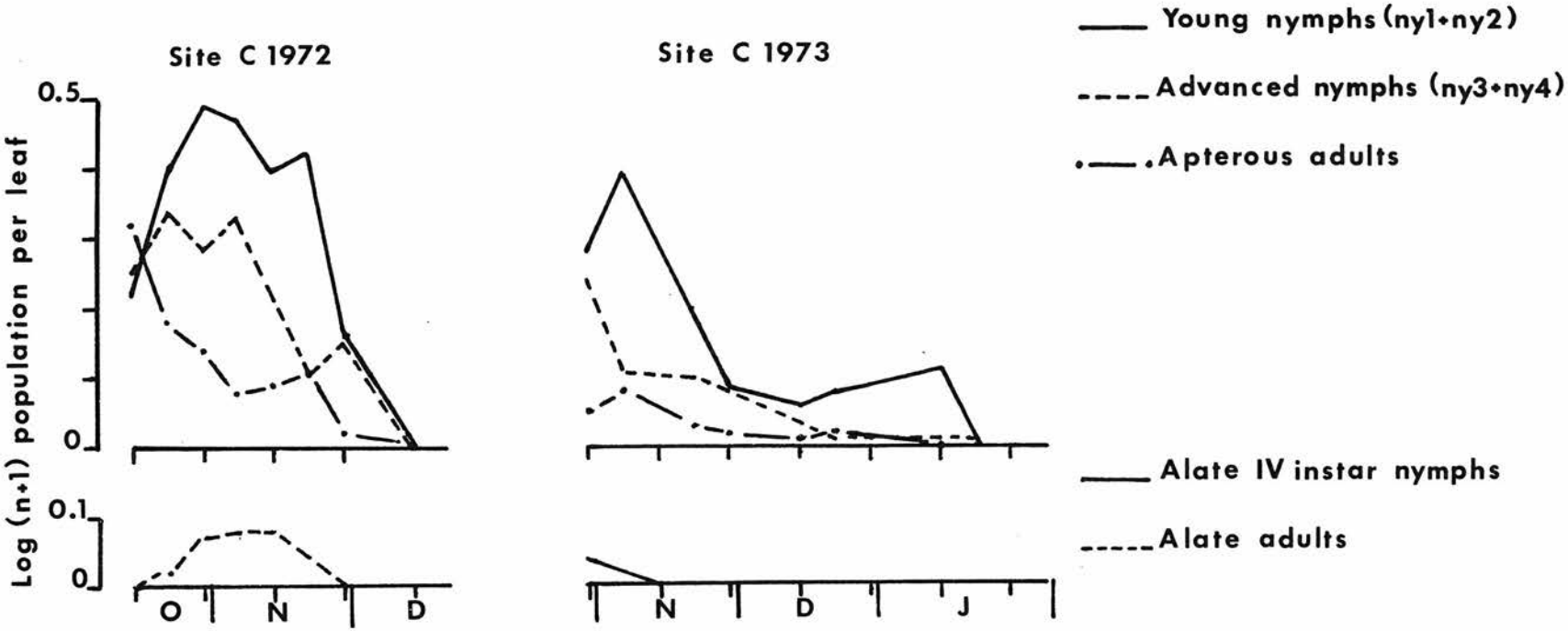


Figure 9. Age-specific population trends of Myzus persicae (Sulz.).

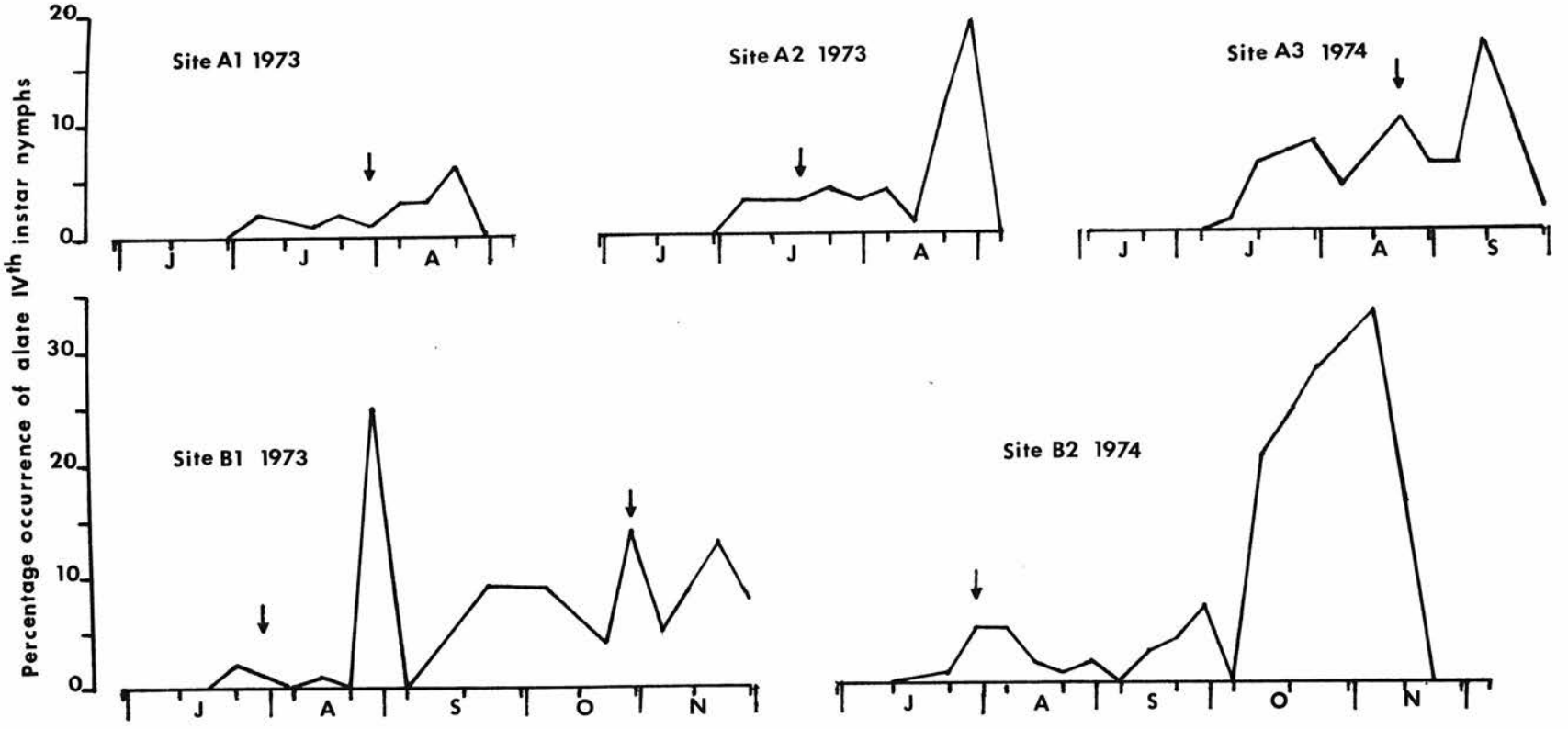


Figure10. Percentage occurrence of alate IV^th instar nymphs and its relationship to the peak of Myzus persicae (Sulz.) infestation (↓).

At the same site in 1973 (Figure 9 and Appendix 9) both alate nymphs and adults were sampled during November but only in very low numbers. The total population disappeared from the samples by mid January.

Distribution of Myzus persicae according to plant strata

Less than one per cent of the aphid population was sampled from the young Brussels sprout leaves at all sites except at sites $A_1$73 and $B_1$73.

At site $A_1$73 the distribution of the aphid population was such that 2.11 per cent infested the upper young regions and 62.38 per cent infested the lower senescing parts of the plants. At site $A_2$73 82.94 per cent of the aphid population was to be found on the senescing leaves and 16.98 per cent on the middle mature regions of the plants.

During 1974 as much as 90.90 per cent and 93.03 per cent of the aphid population inhabited the older region of the plants at sites B_2 and A_3 respectively with 0.54 per cent, at site A_3 and 0.46 per cent, at site B_2, to be found on the young leaves.

Predominately more aphids infested the middle region of the plants at site C73 than at site C72 (17.95 per cent compared to 7.58 per cent). Conversely 92.32 per cent of the aphid population occurred on the lower regions at site C72 compared to 81.68 per cent at site C73.

At site $B_1$73, where plants were subdivided into two growth regions, 94.66 per cent of the aphids infested the lower half and 5.34 per cent the upper half of the plants.

Aerial populations of Myzus persicae

1973

Analysis of the trapped alate aphids from sites A_1 and A_2 revealed that many more aphids were trapped at site A_1 than at site A_2. However those aphids identified as Myzus persicae accounted for 23.49 per cent and 26.78 per cent of the total alates trapped at site A_1 and A_2 respectively although numerically more common at site A_1 (Table 3a).

The percentage occurrence of this species over the season was such that two distinct peaks were obtained at site A_1. The first was reached in mid August and the second in mid September. Only one such peak was observed at site A_2 in the middle of August (Figure 11).

1974

Analysis of the trapped alate aphids during 1974 revealed that equal numbers were trapped at site A_3 and B_2. A small proportion of these aphids were identified as Myzus persicae, 9.73 per cent at site A_3 and 5.01 per cent at site B_2 (Figure 3b). At site A_3 the numbers of trapped Myzus persicae reached a peak in the latter half of July but at site B_2 this peak was not observed until the first half of August. Numbers of trapped alates of this species declined to zero by the end of September (Figure 11).

Discussion

During this study Myzus persicae was found to colonise the Brussels sprout crop as early as the end of May or the beginning of June. The variation in arrival date of the aphid in the crops may be due to

TABLE 3: The percentage of alate Myzus persicae within the total aphids trapped in the vicinity of Brussels sprout crops during 1973 and 1974 in East Lothian

(a) 1973

Fortnightly Totals	SITE A_1			SITE A_2			
	Total Myzus persicae	Total Aphids	% Myzus persicae	Total Myzus persicae	Total Aphids	% Myzus persicae	
2	13	39	33	3	10	30	MAY/JUNE
4	-	-	-	5	22	23	
6	-	-	-	1	6	17	JUNE/JULY
8	14	38	37	14	59	24	
10	94	249	38	62	179	35	
12	123	200	62	49	111	44	AUGUST
14	8	29	28	15	112	13	
16	6	15	40	1	7	14	SEPTEMBER
18	234	865	27	4	69	6	
20	70	970	8	0	0	0	SEPTEMBER/OCTOBER
TOTAL	565	2,405	23.49	154	575	26.78	

(b) 1974

Fortnightly Totals	SITE A_3			SITE B_2			
	Total Myzus persicae	Total Aphids	% Myzus persicae	Total Myzus persicae	Total Aphids	% Myzus persicae	
2	19	27	70	-	-	-	JUNE
4	6	135	4	-	-	-	
6	12	525	2	9	142	6	JULY
8	19	288	7	21	422	5	
10	178	753	24	56	1,371	4	JULY/AUGUST
12	84	912	9	77	1,051	7	
14	11	308	4	7	259	3	AUGUST/SEPTEMBER
16	3	350	1	1	100	1	
18	0	47	0	0	33	0	SEPTEMBER/OCTOBER
20	0	40	0	0	15	0	
22	0	24	0	0	13	0	
24	0	4	0	0	5	0	NOVEMBER
TOTAL	332	3,413	9.73	171	3,411	5.01	

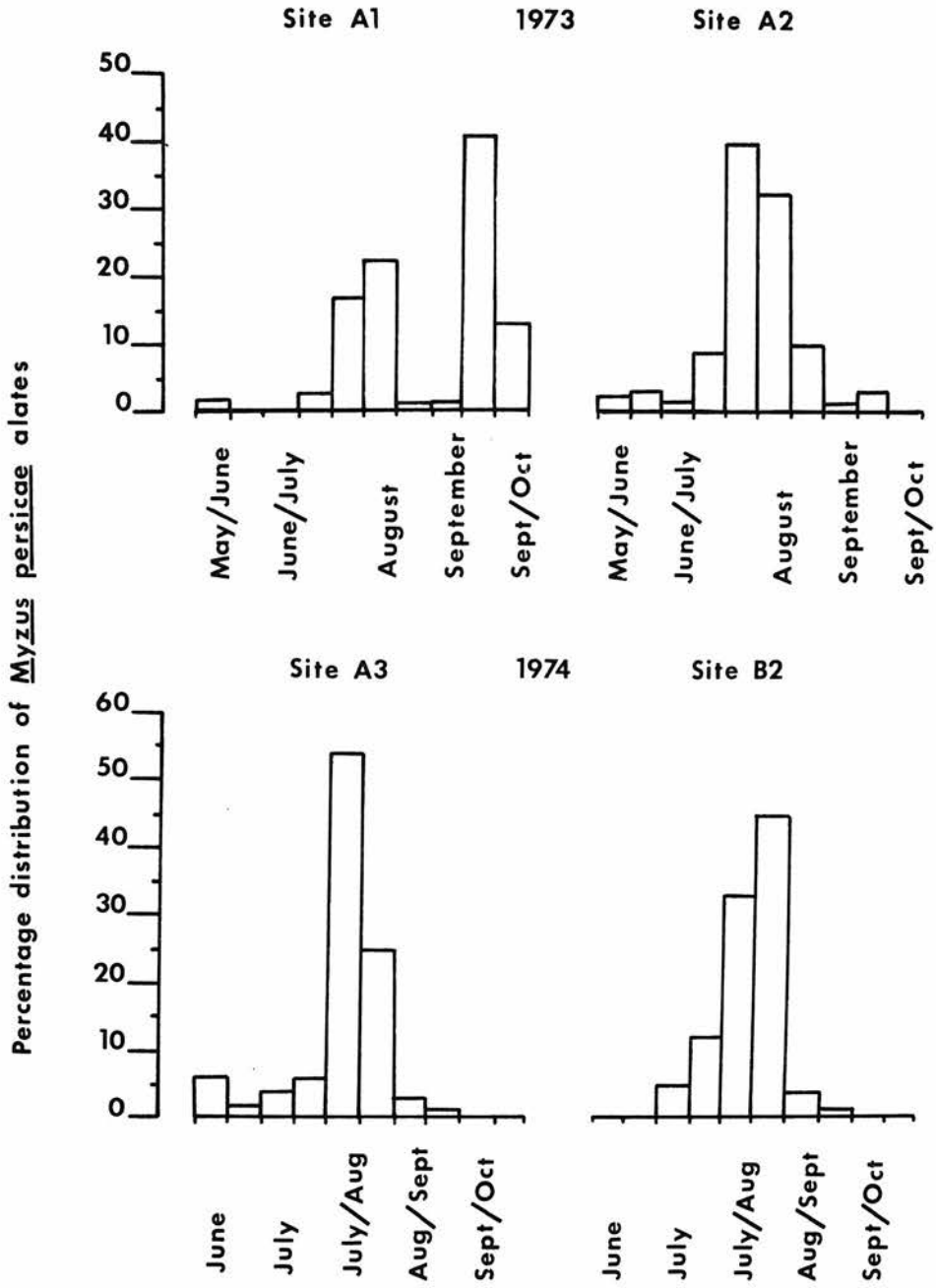


Figure 11. The percentage distribution of Myzus persicae (Sulz.) alates trapped at the specified sites during 1973 and 1974.

period at which the young plants were transplanted into the fields. These findings, supported by water trap catches are in contrast to that found by Agyen-Sampong (1972) who did not find this species of aphid on the crop until late June, in 1969, and early July, in 1970, although the sprout plants were to be found in the fields from mid May onwards in the Edinburgh area.

A pattern of numerical change was observed in the aphid populations but with two important differences between those observed in 1973 and those studied in 1974. Firstly the populations reached higher levels of density in 1974 than in 1973 and secondly those populations observed over long periods displayed two peaks of density in 1973 but not 1974.

The population growth patterns of this species were similar at most of the sites investigated in that the populations reached a mid-season peak within one month of colonisation and there appeared to be no change in the pattern of increase prior to the mid season decline in numbers.

However, at site $A_1$73 the population displayed a 'plateau effect' prior to the mid-season decline which may be partly due to the sheltered nature of this particular site. The population studied at site $A_3$74 appeared to increase rapidly at the start of the season but this increase diminished gradually prior to the mid-season peak. At both these sites the peaks were reached over a two month period.

No live Myzus persicae were to be found on Brussels sprout plants after mid-December, 1973 and mid-January, 1974. This supports the findings of Agyen-Sampong (1972) but differs from those of Fisken (1959a) who had found brassicas to be the most important overwintering host of this aphid species.

Analysis of the age structure of the aphid populations may have been confused by the presence of extensive overlapping of stages and of generations (Hafez, 1961) and perhaps through the difficulty in distinguishing various instars, especially at site C during 1972. Nevertheless it was apparent that the populations were heavily weighted towards the young nymphal stages. The large ratio of young nymphs to apterae clearly illustrates the reproductive potential of the adult Myzus persicase.

The occurrence of advanced stage alate nymphs within the aphid population would indicate that the colonies had become dense enough to promote the development of alatae which would then allow dispersion of the population within and between crops and the establishment of new colonies (Watson and Plumb, 1972). The results indicate that this stage was evident in the population about six weeks after colonisation in the end of May and about four weeks after colonisation in the end of June. Such information is useful with regard to the application of aphicides since it provides a timetable during which any application may result in a delay to the build up of the population thus preventing the production of alates in response to an increased density. This is important with regard to virus spread both within and between crops.

The host plant may itself affect changes in the aphid population. Although physiological studies were beyond the scope of this investigation it was found that the lower senescing regions of the plants were the most favourable habitat of Myzus persicae and normal defoliation must have had an effect on the seasonal fluctuations in the populations.

The influence of biotic and abiotic on seasonal population changes will be discussed more fully in Section C.

2. PRIMARY PARASITES AND HYPERPARASITES OF MYZUS PERSICAE

Table 4 shows those species of primary parasites and hyperparasites that emerged from mummified Myzus persicae during the present investigation. The criteria from which the Aphidius species were classified was that given by Eady (1969) and as a consequence Diaeretiella rapae is considered as a subgenus of the genus Aphidius. All other primary parasite identification was according to Starý (1966,1970) and the hyperparasites were classified from Hellén (1963) and Peck, Bouček and Hoffer (1964). Representatives of each identified species were checked for accuracy at the British Museum (Natural History), Cromwell Road, Kensington, London and by Dr. R. R. Askew, Department of Zoology, University of Manchester.

Relative abundance of parasites during 1973 and 1974

A total of 931 parasitised Myzus persicae were sampled during 1973 and early 1974. Of these 70.68 per cent were successfully reared to produce 531 adult primary parasites and 127 adult hyperparasites. During 1974 1,173 adult primary parasites and 60 adult hyperparasites were successfully reared from 1,634 parasitised Myzus persicae.

TABLE 4: Parasites and hyperparasites reared from aphid host *Myzus persicae* during the investigation

Primary Parasites			
	Ichneumonidea		
		Aphidiidae	Prainae
			Praon myzophagum Mackauer
			Praon volucre Haliday
			Aphidiinae
			Aphidius avenae Haliday
			Aphidius ervi Haliday
			Aphidius picipes group
			Aphidius rosae group
			Aphidius urticae group
			Diaeretiella rapae McIntosh
Hyperparasites			
	Chalcidoidea		
		Pteromalidae	Microgasterinae
			Coruna clavata Walker
			Asaphes vulgaris Walker
	Cynipoidea		
		Cynipidae	Charipinae
			Alloxysta ? ancylocera Cameron
			Phaenoglyphis ? spp. Foerster
	Proctotrupoidea		
		Ceraphrontidae	Ceraphrontinae
			Dendrocerus (=lygocerus) bicolor Kieffer

Table 5 details the above information and the numbers of each individual parasite species that emerged, together with the percentage occurrence of that species within the parasite species complex sampled from the specified sites.

Diaeretiella rapae at 67 per cent of the parasite complex was the most common species during 1973. The hyperparasites Alloxysta ? ancylocera Cameron and Asaphes vulgaris at seven per cent were the next most abundant species with the primary parasite Praon volucre Haliday accounting for six per cent of the total parasite population. In 1974 Diaeretiella rapae was still the commonest parasite although only about 28 per cent were identified as such. The Aphidius species all increased in abundance especially the Aphidius urticae group which accounted for about two per cent of the species complex in 1973 to about 23 per cent in 1974. Two Praon species were identified with Praon volucre much more common than Praon myzophagum Mackauer. Hyperparasites were few in number during 1974 with Alloxysta ? ancylocera the most common at about three per cent of the species complex. The remaining hyperparasite species accounted for less than one per cent of those parasites that emerged.

The relative abundance of each parasite species sampled at the individual sampling sites showed little variation from the overall situation except during the winter months. At site C73 the hyperparasites increased markedly in abundance with Alloxysta ? ancylocera accounting for about 30 per cent and Asaphes vulgaris composed 25 per cent of the species complex.

TABLE 5: Total numbers of parasites that emerged from mummified Myzus persicae during the investigation (Numbers expressed as percentages given in parenthesis)

Species	SITES 1973				Total	SITES 1974		Total
	A_1	A_2	B_1	C		A_3	B_2	
Diaeretiella rapae	231(71.75)	107(62.57)	98(67.58)	5(25)	441(67.02)	240(29.16)	109(26.58)	349(28.30)
Praon volucre	20(6.21)	11(6.43)	8(5.51)	4(20)	43(6.53)	154(18.71)	59(14.39)	213(17.28)
Praon myzophagum	0	0	0	0	0	16(1.94)	0	16(1.30)
Aphidius avenae	0	0	0	0	0	67(8.14)	29(7.07)	96(7.79)
Aphidius ervi	4(1.24)	2(1.17)	6(4.14)	0	12(1.82)	48(5.83)	22(5.37)	70(5.68)
Aphidius picipes group	5(1.55)	8(4.68)	5(3.45)	0	18(2.74)	58(7.05)	52(12.68)	110(8.92)
Aphidius rosae group	2(0.62)	1(0.59)	1(0.69)	0	4(0.61)	27(3.28)	12(2.93)	39(3.16)
Aphidius urticae group	4(1.24)	8(4.68)	1(0.69)	0	13(1.98)	177(21.51)	103(25.12)	280(22.71)
Total Primary Parasites	266(82.61)	137(80.12)	119(82.07)	9(45)	531(80.70)	787(95.63)	386(94.15)	1,173(95.13)
Asaphes vulgaris	17(5.28)	15(8.77)	11(7.59)	5(25)	48(7.29)	1(0.12)	10(2.44)	11(0.89)
Coruna clavata	2(0.12)	2(1.17)	0	0	4(0.61)	0	0	0
Phaenoglyphis ? spp.	12(3.73)	6(3.51)	5(3.45)	0	23(3.49)	5(0.61)	4(0.98)	9(0.73)
Alloxysta ? ancylocera	22(6.83)	11(6.43)	10(6.90)	6(30)	49(7.45)	30(3.65)	10(2.44)	40(3.24)
Dendrocerus bicolor	3(0.93)	0	0	0	3(0.46)	0	0	0
Total Hyperparasites	56(17.39)	34(19.88)	26(17.93)	11(55)	127(19.30)	36(4.37)	24(5.85)	60(4.87)
Total Parasites emerging	322(71.56)	171(68.67)	145(71.78)	20(67)	658(70.68)	823(73.10)	410(80.71)	1,233(75.46)
Total Parasitised Aphids	450	249	202	30	931	1,126	508	1,634
Total non-emergence	128(28.44)	78(31.33)	57(28.22)	10(33)	273(29.32)	303(26.90)	98(19.29)	401(24.54)

Seasonal population trends of the common parasites

As outlined in the above section the common parasites that emerged from mummified Myzus persicae during 1973 were Diaeretiella rapae; Praon volucre; Allxoysta ? ancylocera; Asaphes vulgaris and Phaenoglyphis ? spp.

Appendix 10 provides the details of all parasites that emerged from the mummified aphids according to where and when the aphids were sampled.

It is evident that Diaeretiella rapae was found to infest the aphid population from around the middle of June and reached a peak by the end of July at all sites. According to the data obtained from samples at sites B_1 and C this species occurred in low numbers from the end of August until its disappearance from the samples in November. During that period this species constituted a very high proportion of the parasite species that emerged from the mummified aphids.

Praon volucre was more evident during August although it had been detected at the end of June at site A_1. This species was still evident during November at site C73.

The hyperparasites were most numerous during August with detection of Asaphes vulgaris and Alloxysta ? ancylocera occurring at the beginning of July. Phaenoglyphis ? spp. were found from early July to the beginning of September only but the other two species could still be found in the early part of November.

During 1974 the common parasite species were identified as Diaeretiella rapae; Aphidius urticae group; Praon volucre; Aphidius picipes group and Aphidius avenae.

With reference to Appendix 11 it can be seen that Diaeretiella rapae occurred from late June until the end of November. Praon volucre was not detected until mid July and was still in evidence during November. All three Aphidius species were detected from mid July although Aphidius avenae did emerge from an earlier sample of parasitised aphids. Only the occasional parasite that emerged from mummified aphids collected after mid September could be classified as belonging to one or other of these Aphidius species. All the primary parasites were most numerous during the period late July to the end of August.

The hyperparasites were few in number with Alloxysta ? ancylocera detected from late July at both sites although more common at site A_3. Asaphes vulgaris was more common at site B_2 and occurred primarily in the samples from late September to mid October. Equal numbers of Phaenoglyphis ? spp. emerged from samples taken from both sites over the same period.

Aerial populations of primary parasites and hyperparasites of Myzus persicae

The total number of each species of parasite trapped during the investigation are outlined in Table 6. Those species listed were also to be found in association with the Myzus persicae populations that were studied.

TABLE 6: Total numbers of parasites that were trapped during 1973 and 1974 (Numbers expressed as percentages given in parenthesis)

Species	SITES 1973		Total	SITES 1974		Total
	A_1	A_2		A_3	B_2	
Diaeretiella rapae	35(21.08)	7(12.28)	42(18.83)	52(13.68)	26(5.46)	78(9.11)
Praon volucre	7(4.22)	3(5.26)	10(4.48)	4(1.05)	15(3.15)	19(2.22)
Aphidius avenae	4(2.41)	5(8.77)	9(4.04)	22(5.79)	43(9.03)	65(7.59)
Aphidius ervi	18(10.84)	7(12.28)	25(11.21)	9(2.37)	26(5.46)	35(4.09)
Aphidius picipes group	28(16.87)	6(10.53)	34(15.25)	18(4.74)	17(3.57)	35(4.09)
Aphidius rosae group	7(4.22)	7(12.28)	14(6.28)	19(5.00)	25(5.25)	44(5.14)
Aphidius urticae group	21(12.65)	8(14.04)	29(13.00)	225(59.21)	277(58.19)	502(58.64)
Total Primary Parasites	120(72.29)	43(75.44)	163(73.09)	349(91.84)	429(90.13)	778(90.89)
Asaphes vulgaris	28(16.87)	3(5.26)	31(13.90)	6(1.58)	18(3.78)	24(2.80)
Phaenoglyphis ? spp.	2(1.20)	1(1.75)	3(1.35)	10(2.63)	17(3.57)	27(3.15)
Alloxysta ? ancylocera	16(9.64)	10(17.54)	26(11.66)	15(3.95)	12(2.52)	27(3.15)
Total Hyperparasites	46(27.71)	14(24.56)	60(26.91)	31(8.16)	47(9.87)	78(9.11)
Total Parasites	166	57	223	380	476	856

Analysis of the trapped parasites revealed that many more parasites were trapped in the vicinity of site $A_1$73 than site $A_2$73. Of those parasites that were trapped about 72 per cent at site A_1 and 75 per cent at site A_2 were primary parasites.

No one species accounted for more than 20 per cent of the total number of parasites trapped during the year. Diaeretiella rapae was the commonest with about 18 per cent, while the hyperparasite Phaenoglyphis ? spp. was the least common with about one per cent.

Diaeretiella rapae were more common in the vicinity of site A_1 where it accounted for about 21 per cent of the parasite complex. At site A_2 Diaeretiella rapae only accounted for 12 per cent of the numbers trapped and the hyperparasite Alloxysta ? ancylocera was the most common parasite species at around 18 per cent of the parasite species complex.

During 1974 more parasites were trapped in the vicinity of site A_3 than at site B_2. At both sites the primary parasites accounted for more than 90 per cent of the total number of parasites trapped.

The Aphidius urticae group were the most common species with about 59 per cent, at site A_3, and about 58 per cent, at site B_2, identified as such. Praon volucre was the least common species with about 2 per cent of the parasite complex. Asaphes vulgaris was the most common hyperparasite at site B_2 but the least common at site A_3. The occurrence of Alloxysta ? ancylocera showed the opposite to that.

The primary parasites were to be found in the traps during late July and early August in 1973 but were to be found slightly later in 1974 during August and early September.

The hyperparasites were found in the traps from the latter half of July through to October with the largest number trapped in September during 1973. In 1974 however the hyperparasites were not observed in the traps until mid August with the peak in number occurring in the latter half of September.

There is no record of active movement of adult parasites before July except at site A_1 in 1973. Here Diaeretiella rapae were found in high number during the last week of May and the first week of June. A single Aphidius ervi Haliday and a solitary parasite from the Aphidius urticae group were also trapped during that period (Appendix 12).

Discussion

Numerous reviews on the parasite species are to be found in the literature (Mackauer and Starý, 1967; Mackauer, 1968; Starý, 1970) and the records here complement and provide additional information to these.

Myzus persicae was found to be parasitised by at least eight species in two genera of primary parasites and by at least five species in five genera of hyperparasites. This was a more restricted range of species than that found previously in the Edinburgh area (Agyen-Sampong, 1972) who found at least eleven species in five genera of

primary parasites and at least eight species in five genera of hyperparasites to be in association with Myzus persicae.

All the parasite species with the exception of the Aphidius rosae group were also recorded by Agyen-Sampong. The Aphidius rosae group is new to the records of parasites of Myzus persicae in Britain although it had been found as a parasite of this aphid species in Canada (MacGillivray and Spicer, 1953) and also in the U.S.A. (Shands, Simpson, Roberts and Muesebeck, 1955).

Two distinct differences were apparent in the parasite species complex of 1974 compared to that of 1973.

Firstly there was a marked reduction in the percentage occurrence of Diaeretiella rapae. This reduction appeared to be due more to an increase in the number of other primary parasites rather than a reduction in the number of Diaeretiella rapae. Secondly the percentage occurrence of emerging hyperparasites was much lower in 1974 than in 1973.

Some variation in the percentage occurrence of the various species did occur from site to site in any one year. However this was not as great as the variation in numbers of parasites found in association with the aphid species particularly during 1974.

The pattern of distribution of the parasite species throughout the season was supported by the water trap records although there was a marked contrast in the values for percentage occurrence of each species trapped to those found in the crop. This may be due to a number of

factors such as placement of traps, presence or absence of windbreaks, windspeed and direction etc.

Since the effect of parasites on fluctuations in the Myzus persicae populations forms the main part of this study then elaboration of certain points and further discussion will be presented in Section C.

R E S U L T S

SECTION B - LABORATORY STUDIES

1 MYZUS PERSICAE (SULZER)

Effect of temperature on developmental rate

Table 7 and Appendix 13 detail the time taken, in days, for Myzus persicae to complete its development from birth to adult when reared under constant temperatures of 5^{o}, 10^{o}, 15^{o} and 20^{o}C together with high relative humidity and a 12-hour photoperiod.

This nymphal period ranged from 34.73 ± 1.65 days at 5^{o}C to 8.16 ± 0.49 days at 20^{o}C. At 10^{o} and 15^{o}C the nymphal period was of a similar duration with 13.50 ± 0.49 days and 12.14 ± 0.31 days taken respectively by the aphid to complete its development to adult stage. No significant difference was found between the time taken for each instar period to develop under the particular temperatures except at 5^{o}C where the fourth instar required a longer time to complete its development.

This relationship between temperature and the time taken to complete development describes an equilateral hyperbola (Andrewartha and Birch, 1954; Bodenheimer and Swirski, 1957). Over a range in temperatures this relationship can be represented by a straight line by regressing the reciprocal of the developmental rate with temperature.

The reciprocal of days taken for Myzus persicae to develop from birth to final moult were plotted against temperature. The regression of this plot is found on Figure 12 with slope $y = 0.002 \pm 0.0061x$. This straight line is best characterised biologically by the temperature threshold of development, t, which is the point where the straight line intercepts the x axis and by a time to adult, k, which is the

TABLE 7: Mean duration of instar periods (±s.e.) of Myzus persicae in days at constant temperature and high relative humidity with a 12-hour photoperiod

Temp. °C	Instar Period					Nymphal Period	Longevity
	I	II	III	IV	ADULT	Birth to Adult	Birth to Adult
5	6.76 ± 0.49	6.10 ± 0.51	8.17 ± 0.69	13.73 ± 1.25	25.87 ± 2.50	34.73 ± 1.65	60.60 ± 2.33
5*	6.25	8.50	11.00	17.67	8.67	42.33	51.00
10	2.25 ± 0.23	3.11 ± 0.33	3.68 ± 0.27	4.71 ± 0.57	9.29 ± 2.18	13.50 ± 0.49	22.79 ± 2.16
10*	2.33	3.33	2.67	15.00	7.00	25.00	32.00
15	2.13 ± 0.18	3.54 ± 0.22	3.29 ± 0.22	3.07 ± 0.28	16.54 ± 2.77	12.14 ± 0.31	28.68 ± 2.69
15*	3.00	3.00	4.00	5.00	12.50	15.00	27.50
20	1.31 ± 0.10	2.82 ± 0.26	2.62 ± 0.29	2.42 ± 0.22	8.90 ± 1.32	8.16 ± 0.49	17.05 ± 1.54
20*	No alate production						

* Development of aphid to alatae

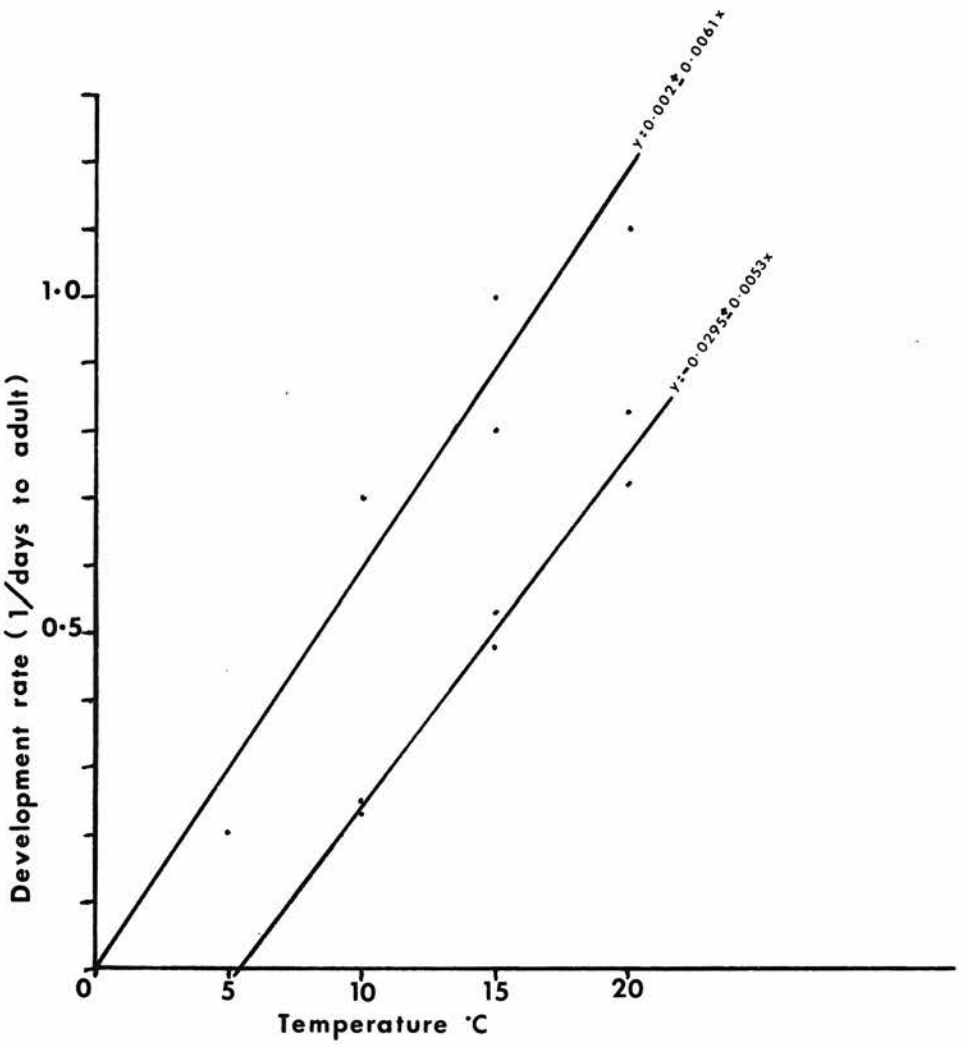


Figure 12. Constant temperature effects on development of Myzus persicae (birth to final moult) and Diaeretiella rapae (oviposition to adult emergence).

number of degree days above t required by the aphid to complete its development. k can be taken to be the reciprocal of the slope b of the straight line (Campbell, Frazer, Gilbert, Gutierrez and Mackauer, 1974). For Myzus persicae the value t was estimated to be $0^{o}C \pm 0.44^{o}C$ and k was estimated to be 163.93 ± 13.44 degree days above t .

Effect of temperature on longevity

Table 7 and Appendix 13 show the mean longevity of Myzus persicae at constant temperatures, high relative humidity and 12-hour photoperiod.

The mean total longevity, birth to death, ranged from 60.60 ± 2.33 days at $5^{o}C$ to 17.05 ± 1.54 days at $20^{o}C$ with longevity longer at $15^{o}C$ than at $10^{o}C$. Adult apterae survived for 25.87 ± 2.50 days at $5^{o}C$ compared to 8.90 ± 1.32 days at $20^{o}C$. The time period found at $20^{o}C$ did not differ significantly from that found at $10^{o}C$. At $15^{o}C$ the adult aphid survived with a mean longevity of 16.54 ± 2.77 days.

Figures 13, 14 and 15 show the changes in the daily survival rate of the aphid at the five different but constant temperatures. On these Figures the curve l_x describes the probability of an adult aphid being alive at age x ($l_0 = 100\%$).

From the graphs it can be seen that the adults remained alive for a longer period under constant conditions of 5^{o} and $15^{o}C$. The time taken to reach 50 per cent mortality was shorter at the three higher temperatures (10 - 14 days) in comparison to that found at $5^{o}C$ (25 days).

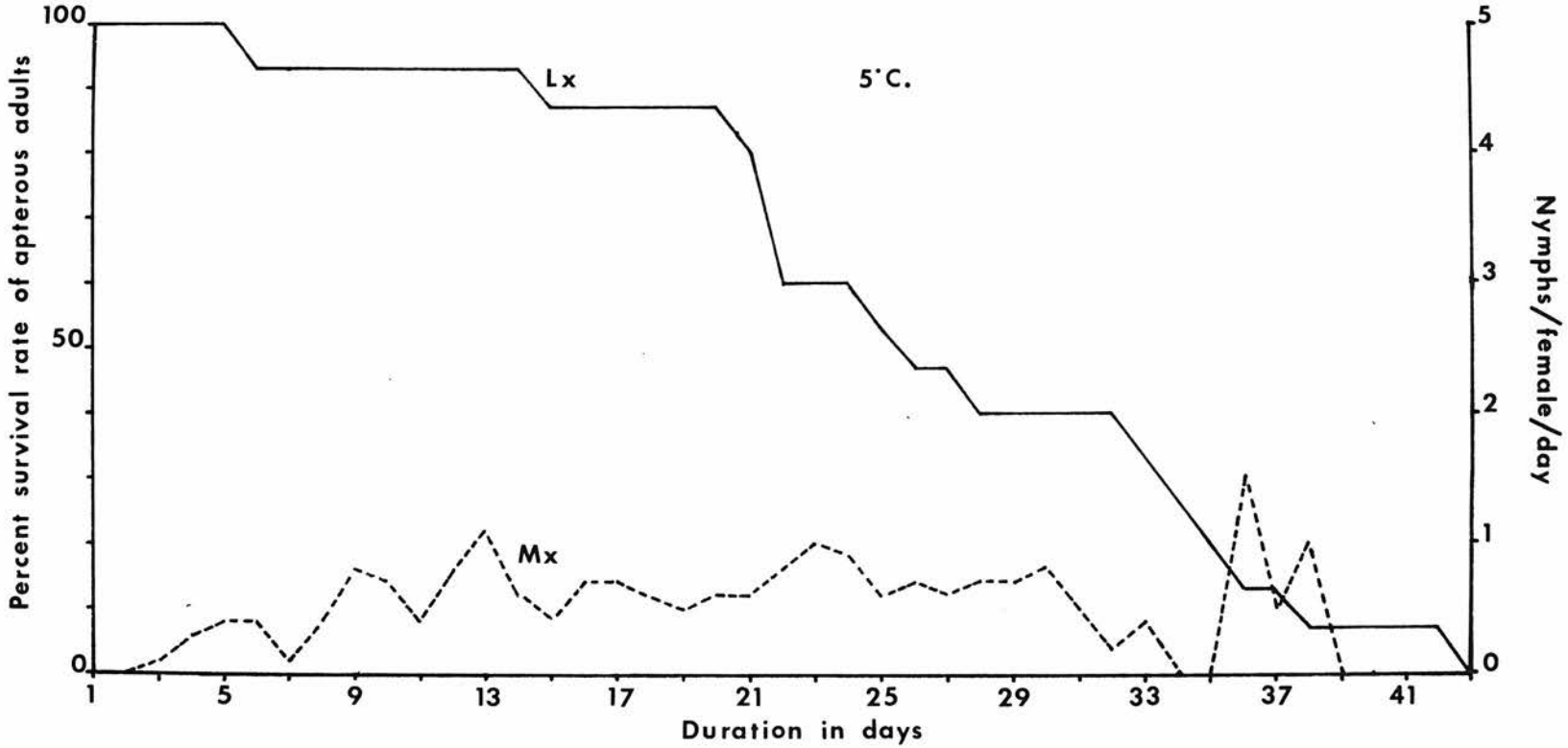


Figure 13. Age-specific survival and fecundity rates of Myzus persicae (Sulz.) reared on Asparagus Kale at constant temperature.

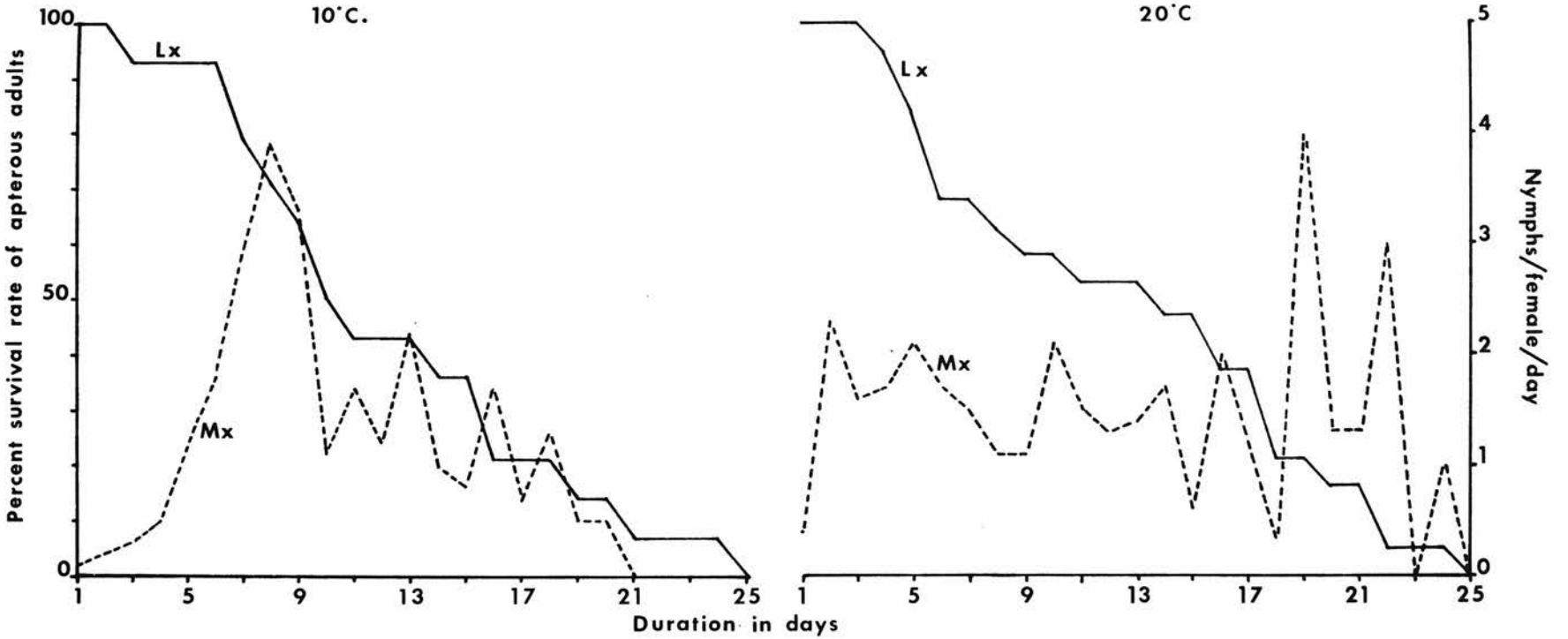


Figure 14. Age-specific survival and fecundity rates of Myzus persicae (Sulz.) reared on Asparagus Kale at constant temperature.

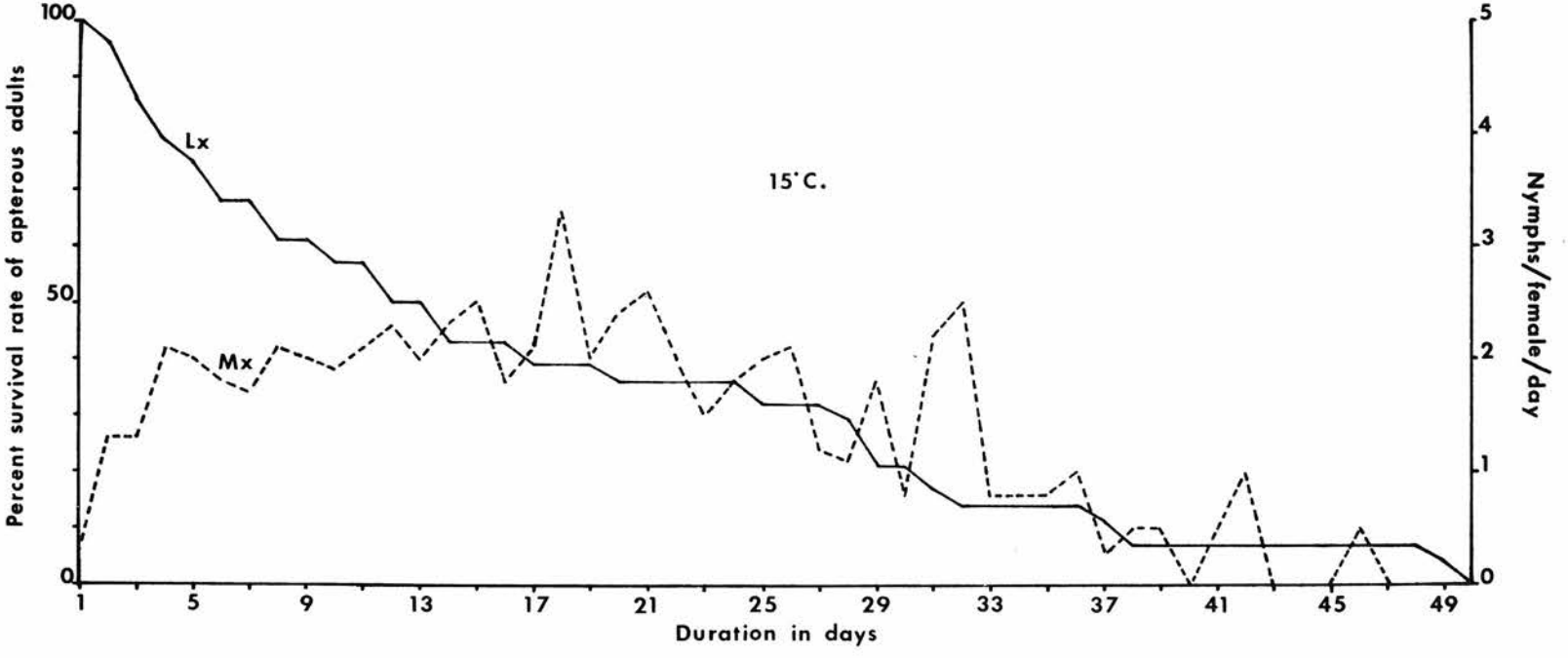


Figure 15. Age-specific survival and fecundity rates of Myzus persicae (Sulz.) reared on Asparagus Kale at constant temperature.

The percentage survival rate at 5°C declined rapidly after the 50 per cent mortality point whereas the decline remained relatively constant at the higher temperatures although occurring over a much longer period at 15°C.

Effect of temperature on fecundity

Table 8 outlines the reproductive capacity of apterous Myzus persicae under the constant temperature conditions.

No significant difference in the mean number of progeny produced per female at constant conditions of 5°, 10° and 20°C was observed. However, between 10° and 15°C there was a highly significant increase in mean progeny per female ($P < 0.001$) and between 15° and 20°C there was a highly significant decrease in mean progeny per female ($P < 0.001$).

The daily age-specific fecundity rates (Mx) of the apterous Myzus persicae are illustrated as the mean number of young born per day per female alive each day in Figures 13, 14 and 15. Production of nymphs occurred within the first day of an adult's life in all but conditions of 5°C. At this temperature production of young was maintained at a low level throughout. At 10°C the number produced increased sharply to a peak of about four nymphs per female per day before declining to zero. Under constant conditions of 15°C the production of young increased steadily to fluctuate around two nymphs per female per day over most of the developmental period before declining to zero in the latter stages of the experiment. At 20°C the level of production was maintained below two nymphs per female per day over a short time period with only two increases above this rate observed.

TABLE 8: Reproductive capacity of Myzus persicae at specified constant temperature, high relative humidity and 12-hour photoperiod

Temp. °C	Total Adult Aphids	Total Progeny	Progeny/Female Range	Progeny/Female Mean ± s.e.
5	15	200	3 - 29	15.33 ± 2.12
5*	3	6	0 - 6	2.00
10	14	216	0 - 30	15.43 ± 3.07
10*	1	10	10	10.00
15	28	799	0 - 84	28.54 ± 5.14
15*	2	32	1 - 31	16.00
20	19	336	0 - 34	17.68 ± 2.40
20*	No alate production			

Effect of temperature on production of alates

As can be seen from Table 8 and Appendix 13 very few alates were produced under the experimental conditions used, with zero production at 20°C.

Although the effects of temperature on the development, fecundity and longevity of these alates are recorded no significance is placed on these except to say that the alates tended to have a longer nymphal period than did the apterae and that total longevity was of a similar duration with adult alates surviving for a shorter time period than did apterous adults.

2. DIAERETIELLA RAPAE M^{C}INTOSH

Effect of temperature on developmental rate

Table 9 describes the developmental period of Diaeretiella rapae under constant temperature conditions of 5°, 10°, 15° and 20°C.

The results show that as temperature increases the time taken to develop from oviposition to adult emergence decreases. This period ranged from zero development at 5°C to 13.12 ± 0.41 days at 20°C. A similar situation was observed for development from oviposition to mummification with a range of zero development at 5°C to 7.71 ± 0.19 days at 20°C.

As with Myzus persicae the reciprocal of the days taken for Diaeretiella rapae to develop from oviposition to adult emergence was plotted against time. The regression of this plot is found on Figure 12 with slope $y = -0.0295 \pm 0.0053x$. The values of t, the temperature

TABLE 9: Mean duration (±s.e.) of development of *Diaeretiella rapae* at constant temperature, high relative humidity and 12-hour photoperiod

Temp. °C	Original Aphids	Premature death of aphid	Number Mummified	Time to Mummification (days)		Time to adult emergence (days)		Per cent non-emergence
				Range	Mean ±s.e.	Range	Mean ±s.e.	
5	40	zero development of parasite						
10	40	14	19	19 - 37	23.79 ± 0.87	34 - 50	41.68 ± 0.90	0
15	40	11	22	9 - 15	11.00 ± 0.31	18 - 23	20.47 ± 0.37	13.64
20	40	14	17	7 - 9	7.71 ± 0.19	11 - 16	13.12 ± 0.41	0

threshold of development, and k, the number of degree days above t required to complete development could then be estimated in the manner described for Myzus persicae.

For Diaeretiella rapae the value of t was estimated to be $5.5^{o}C \pm 0.18^{o}C$ and k was estimated to be 188.68 ± 7.49 degree days above t.

Effect of temperature on development of parasitised Myzus persicae

Apart from four parasitised aphids all development of the aphids ceased in the fourth instar period at which mummification occurred. Of those four aphids that continued to develop three were mummified at $15^{o}C$ and one at $20^{o}C$ in the adult stage. One of those developing to adult stage at $15^{o}C$ produced one nymph before mummification occurred. No significant difference was found between the number of aphids mummified in the fourth instar period at constant temperatures of 10^{o}, 15^{o} and $20^{o}C$ with zero development of the parasite at $5^{o}C$ (Table 10).

Effect of temperature on colouration of mummified Myzus persicae

Three colours of mummified aphid were observed. These were light brown or straw coloured, brown and dark brown (Table 11). The proportion of straw coloured mummies increased with increase in temperature. The opposite was true for brown coloured mummies. Dark brown mummies were observed at 10^{o} and $15^{o}C$ with those at $15^{o}C$ remaining unemerged.

TABLE 10: Effect of parasitism by Diaeretiella rapae on the development of Myzus persicae at constant temperature, high relative humidity and 12-hour photoperiod

Temp. °C	Mummified aphids	Development stage of aphid		Nymphs produced by adult aphid
		IV instar	Adult	
5	0	0	0	0
10	19	19	0	0
15	22	19	3	1
20	17	16	1	0

TABLE 11: Effect of temperature on morphology of mummified Myzus persicae attacked by Diaeretiella rapae

Temp. °C	Colour of mummified aphid		
	Light Brown	Brown	Dark Brown
5	0	0	0
10	5	12	2
15	14	5	3 (non-emerged)
20	16	1	0

3. DISCUSSION

Constant temperature conditions have had a direct effect upon the development of both Myzus persicae and its primary parasite Diaeretiella rapae. The time taken to complete development by both species decreased with increased constant temperature.

The rates of development for Myzus persicae estimated during this particular investigation differed from that obtained in other studies. Weed (1927) in America and Agyen-Sampong (1972) in the Edinburgh area obtained significantly lower rates of development at the lower temperatures of 5° and $10^{\circ}C$ but at 15° and $20^{\circ}C$ the rates were comparable.

The rates obtained here resulted in a lower theoretical threshold of development of $0^{\circ}C \pm 0.44^{\circ}C$ with 163.93 ± 13.44 degree days above the threshold required to complete development to adult stage. This compares to a threshold of $3.5^{\circ}C$ estimated by Agyen-Sampong (1972) for Myzus persicae although he found this species to reproduce at $1^{\circ}C$ to $2^{\circ}C$. Indeed active stages of Myzus persicae have been found to survive undercooling down to $-20^{\circ}C$ (Solomon, 1967).

The effect of temperature upon the development of Diaeretiella rapae has been reported previously but when in association with Brevicoryne brassicae, the cabbage aphis. In that relationship Hafez (1961) found both the aphid and the parasite to have the same threshold of development of $6.5^{\circ}C$ with the number of degree days above this threshold required to complete development to be slightly longer for the parasite (188 compared to 182 degree days). Hughes (1963) found Diaeretiella

rapae to cease development at 7°C with 97 ± 3 degree days above this required to complete development. He found the host Brevicoryne brassicae to have a theoretical threshold of development at 5°C with 127 degree days above this required to develop to adult form. In both situations the parasite species was shown to have a slight disadvantage over its aphid host at these low temperatures.

This study shows that Diaeretiella rapae, when in association with Myzus persicae, had a threshold of development at 5.5°C ± 0.18°C with 188.68 ± 7.49 degree days required to complete its development. Although the threshold of development is a full degree lower these results compare favourably to those found by Hafez (1961). If these findings were to hold true for the field situation then the build up of the parasite population in the spring would be delayed until the average temperatures increased by which time the Myzus persicae population would have become well established since its threshold was found to be 5C° lower than its primary parasite. This would be of benefit to the parasite population since an adequate host supply would ensure the parasites survival as a species.

The reproductive capacity of the aphid was at its best at a temperature of 15°C compared to 25°C as found by Agyen-Sampong (1972). If this was also reflected in the field population then the species would be at an advantage in the early part of the season when temperatures are of this order (Section C1).

Constant temperature conditions resulted in the production of very few alates. The reasons for such low numbers are not known although it is known that the use of leaf discs would tend to promote the production

of alates (Johnson and Birks, 1960). High temperatures and long photoperiod would also suppress alate development although the development of the winged adult could proceed in the presence of other factors such as overcrowding and poor host plant conditions (Johnson, 1969).

Diaeretiella rapae, when reared under the conditions described above, appeared to induce mummification of the aphid before that aphid reached the adult form. This will obviously have the effect of reducing the reproductive capacity of the aphid (Section C2). This effect may not be a direct consequence of the temperature conditions but more probably due to oviposition in the young nymphal stages.

Temperature may have been important in the determination of mummy colouration. The production of lighter coloured mummies increased as the temperature increased. Starý (1970) recognised two aspects of colouration. Firstly the specific colouration and secondly colouration due to age. It would appear from the results here that temperature conditions acting on the parasite via the host could also determine the colouration of the cocoon. This may also determine whether or not the parasite is hibernating but evidence here is inconclusive and further physiological studies may provide some useful data.

R E S U L T S

SECTION C - ANALYSES OF SEASONAL FLUCTUATIONS IN *MYZUS PERSICAE* POPULATIONS

1. WEATHER

A full record of the climatic conditions from the end of May, 1973 to the end of May, 1975 is to be found in Appendix 14.

(a) Temperature

Figure 16 illustrates the changes in the weekly mean of maximum and minimum temperature recorded during the investigation.

From the end of May, 1973 until the end of May, 1974 the maximum temperature ranged between a weekly mean of 22.6°C, at the end of July, and 3.4°C, at the beginning of December. Over the following year the weekly mean of maximum temperature ranged between 22.8°C, at the beginning of August, 1974, and 3.9°C, in the second week of February, 1975. The slightly higher weekly mean in maximum temperature was recorded over a longer period in the summer of 1974 than in the summer of 1973.

Regression analysis showed no significant relationship between maximum temperature and changes in the aphid population size at any site studied during 1973. However a significant relationship did occur in 1974 (site A_3, $P < 0.05$ and site B_2, $P < 0.01$).

Minimum temperatures recorded between June, 1973 and May 1974 ranged from a weekly mean of 13°C, at the end of July to - 6.7°C, at the beginning of December. Over the same period, 1974 to 1975, the temperature ranged between 10.7°C, in mid July, and - 1.1°C, in the second week of February, 1975. During both years the weekly mean only once went below 0°C with the minimum temperatures maintained at a low level during the winter of 1973/1974.

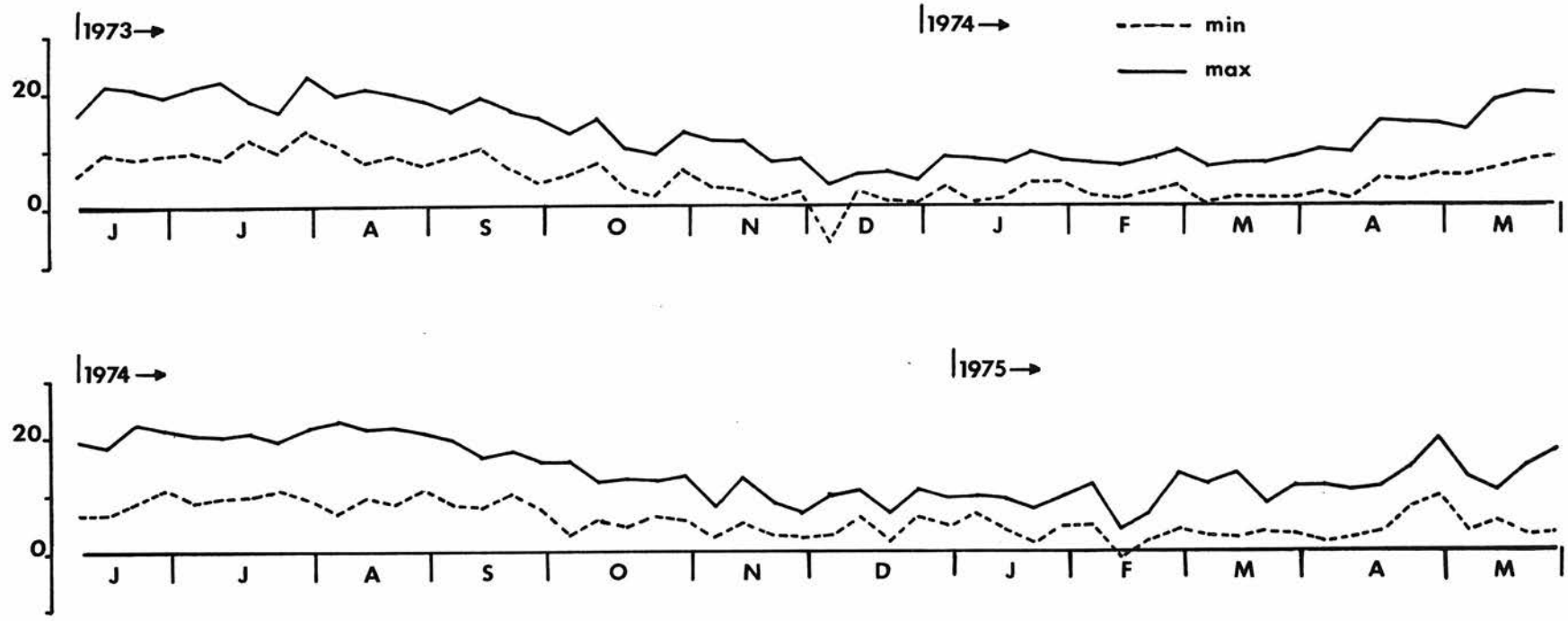


Figure 16. Temperature record: June 1973 to May 1975

Regression analysis revealed no significant relationship between minimum temperatures and changes in the aphid population size except for site A_1, 1973 ($P < 0.001$) and site B_1, 1973 ($P < 0.02$).

Discussion

The direct effect of constant temperature conditions upon the development and performance of Myzus persicae was reported in Section B. It was shown that as temperature increased then the rate of turnover of successive generations (the time taken to develop to adult form) also increased and that for this aphid species a theoretical temperature threshold of development was estimated to be $0^{o}C \pm 0.44^{o}C$.

Temperature records in the field show that only on two occasions were the minimum temperatures so low as to produce a weekly mean below $0^{o}C$. Temperatures experienced by the aphids were therefore not low enough to either cause excessive mortality or to prevent development taking place, if the theoretical value obtained in the laboratory holds true for the field situation. The aphid population would therefore be able to both survive and develop over the winter period, albeit at a slow rate (estimated to take 34.73 ± 1.65 days for completion of one generation at $5^{o}C$).

Summer temperatures did not reach the upper thermal death point of $38.5^{o}C$ for Myzus persicae (Broadbent and Hollings, 1951). Instead maximum temperatures tended to fluctuate around a weekly mean of $20^{o}C$. In the laboratory it was estimated (Section B) that at this temperature the rate of turnover of successive generations would take 8.16 ± 0.49 days and each adult female would produce on the average 17.68 ± 2.40 nymphs during its life span of 8.90 ± 1.32 days.

If temperatures are the important factor in influencing the population growth pattern of Myzus persicae then it could be expected that the populations would tend to increase faster and over a longer period in 1974 than in 1973. The higher maximum temperatures were maintained over a longer period in the summer of 1974 than in 1973.

Investigations in the field (Section A) show that the Myzus persicae populations tended to increase over a longer period and to a greater density in 1974 compared to 1973. Analyses showed that maximum temperatures appeared to be a significant variable in this development of the aphid populations.

Temperatures in 1973 were not excessively lower compared to 1974 and were still within the range for rapid development of the aphid populations. This suggests that other factors could have suppressed the aphid populations during 1973 and that those factors were either missing or that their degree of action was less in 1974. Howell (1973) suggested that temperature regimes found in April may affect the build up in the aphid population that year. Temperature records showed that the mean maximum temperature for April, 1973 was 10.25^{o}C and the mean minimum temperature was 2.9^{o}C. During April, 1974 the mean maximum temperature was 13.17^{o}C with a mean minimum temperature of 3.5^{o}C. If Howell's premise holds true then the temperature conditions experienced in April, 1974 would tend to benefit the development of the aphid population in that year and that those experienced in April, 1973 would have been of less benefit in comparison. This would appear so (Section A).

(b) Rainfall

The pattern of rainfall, recorded in mm per week, from June, 1973 until May, 1975 is detailed in Figure 17.

The first half of this period was found to be the driest with weekly rainfall ranging between 25.9 mm, at the beginning of June to 0 mm in mid November, 1973 and mid April, 1974. From June, 1974 until May, 1975 the weekly rainfall ranged from 66.9 mm in the second week of May, 1975 to 0 mm at the end of June and October, 1974.

Regression analysis revealed no significant relationship between rainfall and changes in the aphid population size.

Discussion

Rainfall is a natural factor which may at times exert an influence on the aphid population in a number of ways. Firstly the direct action of rain may reduce the aphid population by physically washing the aphids from the surface of the leaf. This may be difficult since the majority of Myzus persicae were to be found on the lower leaves (Section A) and on the undersurface of those leaves (Agyen-Sampong, 1972). The greater the amount of rain that occurred in the months of September, October and November, 1974 compared to the same period in 1973 may therefore have been a causative factor in the prevention of a resurgence in the aphid population in 1974 as was observed in 1973 (Figure 5). Since no record was made of the intensity of this rainfall then no significant conclusion can be drawn as to the importance of rainfall as a mortality factor in this sense.

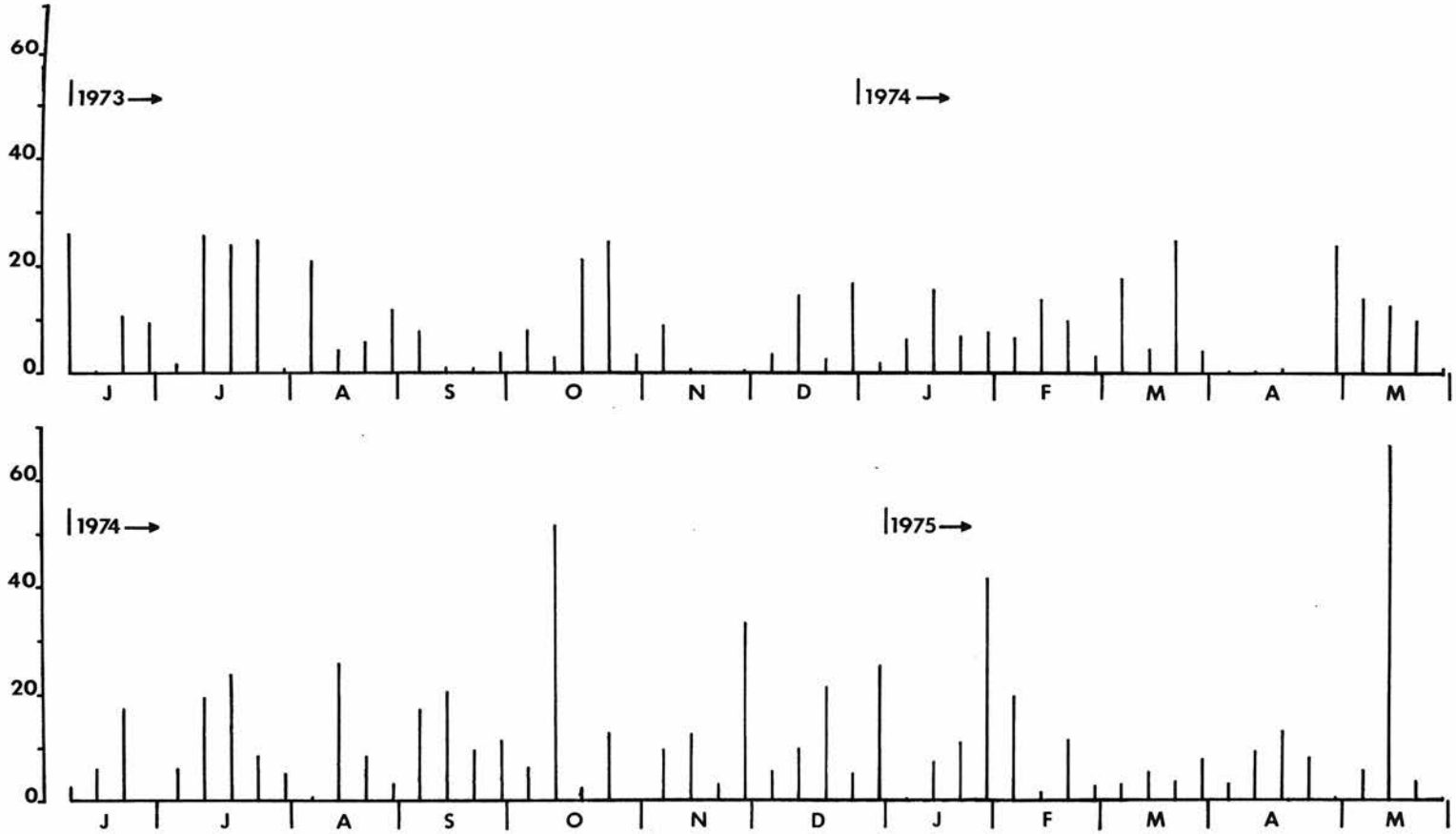


Figure 17. Rainfall record in mms. per week: June 1973 to May 1975

Secondly the lack of moisture in the soil due to drought conditions would result in a lowering of the water content of the plant and leaves would become less turgid. A lack of turgidity in the leaves may result in a reduction of the aphid population feeding on those leaves (Banks, 1965). On the other hand reduced watering of plants has been reported to result in an increase in Myzus persicae populations (Wearing and van Emden, 1967).

The young plants present in the sites towards the end of May and into June, 1973 did display a degree of flabbiness which could be attributed to the dry conditions prevailing in the region at that time although no measurement of soil moisture content was carried out. The condition of the host plant may therefore have reduced the suitability of the crop as a site for colonisation of the aphid species compared to that of 1974. Differences in the variety of Brussels sprout may also be important when regarding lack of turgidity as a mortality factor (Agyen-Sampong, 1972).

Rainfall may also be important when, in the presence of high temperatures, the relative humidity of the atmosphere is raised. Such conditions are suitable for the initiation of fungal growth (Hafez, 1961; Gustafsson, 1965, 1969). The importance of fungal disease in the bionomics of Myzus persicae populations will be discussed below.

(c) Sunshine

It is apparent from Figure 18 that the summer of 1974 was sunnier than the corresponding period in 1973. From June, 1973 until May, 1974

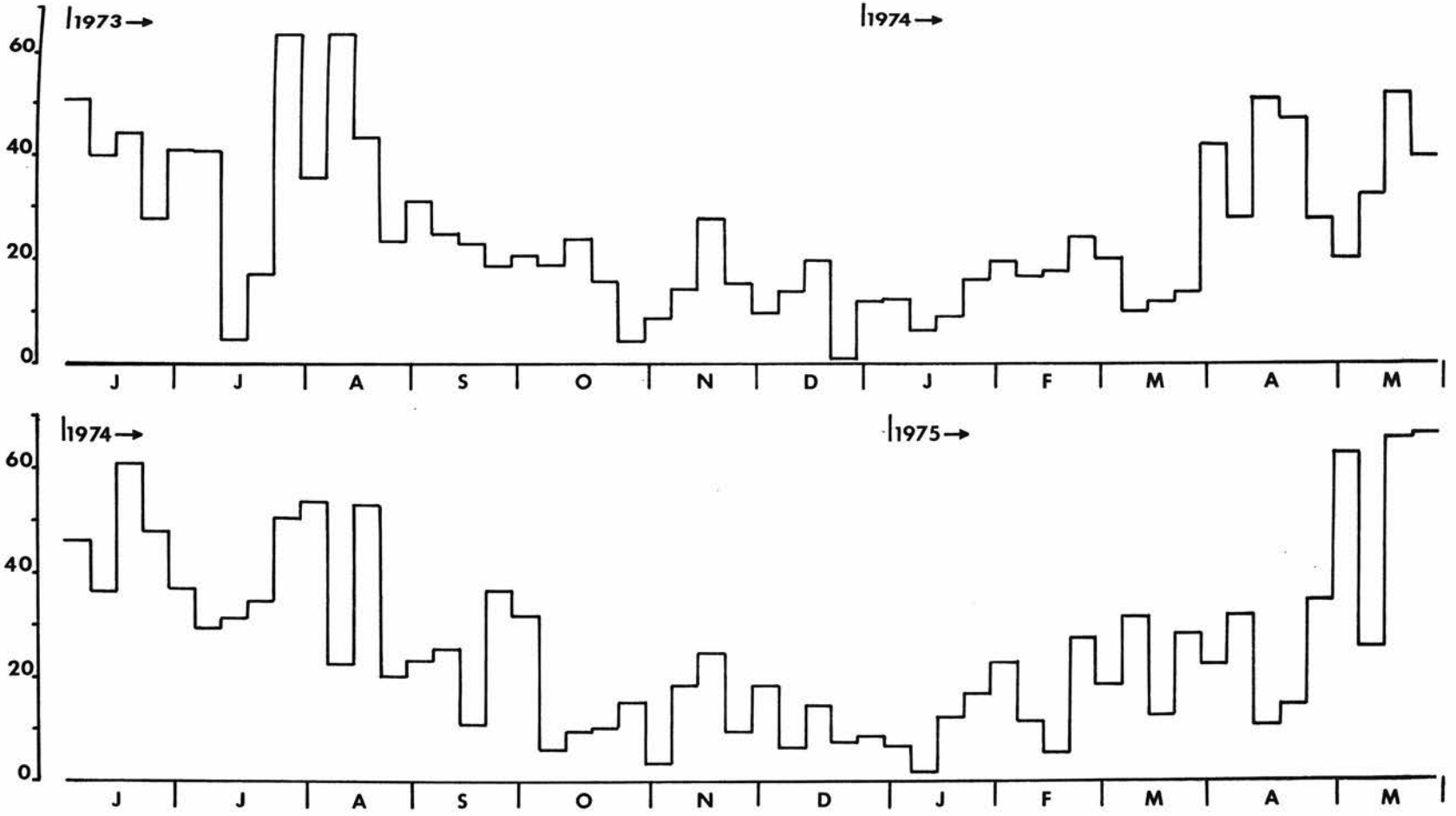


Figure 18. Duration of sunshine in hours per week: June 1973 to May 1975

the highest recorded amount of sunshine in any one week was 63.5 hours in the second week of August, 1973. The lowest was 0.4 hours at the end of December, 1973. In the same period, 1974 to 1975, weekly sunshine ranged from 66.6 hours at the end of May, 1975 to 1.3 hours in the second week of January, 1975.

Regression analysis revealed a significant relationship between sunshine and changes in the aphid population size at site B_2 ($P < 0.01$). No significant relationship was found at any of the other sites.

Discussion

Todd (1961) believed the earliness and amount of sunshine to be an important factor in controlling the direction of spread of the aphid, Myzus persicae, in south-east Scotland. This natural factor may also inhibit the reproductive processes of the aphid during the mid season peak in numbers (Broadbent, 1953). Light intensity is also thought to affect the activity of alate Myzus persicae (Broadbent, 1949) and short day length is thought to promote the production of alates within the aphid population (Johnson, 1969). No detailed study on the effect of sunshine was carried out in this survey but it is suggested as an important area for future study.

2. PREDATORS

Crop sampling revealed that the dipteran family Syrphidae was the most common predator found in association with Myzus persicae colonies. A record of the distribution and abundance of the developmental stages of the various predators was kept (Appendix 15).

During 1973 the Syrphidae were found from the middle of June until early September although most abundant towards the end of July. The presence of predators was more obvious at sites A_1 and A_2 than at site B_2 where, in addition to the Syrphidae, the occurrence of Chrysopa (lacewing) eggs was observed.

The presence of Syrphidae was not detected until the middle of August in 1974. At both sites they reached a peak towards the end of August and early September and gradually disappeared from the samples by the end of October.

An attempt was made to rear predator stages to the adult form for identification purposes. Only four out of five pupae and 10 out of 49 larvae successfully completed development in 1973. These were identified as Syrphus balteatus Degeer (according to Coe, 1953). The same species was reared successfully from two out of three pupae and 14 out of 43 larvae collected in 1974.

Aerial sampling realised a catch of 1,310 and 815 adult Syrphidae at site A_1 and A_2 respectively during 1973 with the majority trapped in the latter half of August (Appendix 16). Of those Syrphidae trapped at site A_1 only four genera were identified as those whose larvae were known to be aphidophagous (Coe, 1953). These were Platychirus St. Fargeau and Serville, Melanostoma Schiner, Sphaerophora St. Fargeau and Serville together with the most common genus Syrphus Fabricus. At site A_2 only the aphidophagous genera Syrphus and Platychirus were found.

Fewer Syrphidae were trapped during 1974 with 530 caught at site A_3 and 619 at site B_2 (Appendix 16). Only the aphidophagous genera Syrphus and Platychirus were found with the peak in numbers reached in the latter half of September.

Discussion

The influence that predators have on the seasonal fluctuations in Myzus persicae populations did not form an integral part of this study. However their presence during the period of the aphid population peak in number must signify that they are an important part of the community mechanism. It is a recommendation that an in-depth study on the significance of this group in the area should be carried out in order that the overall effect of biotic factors may be quantitatively analysed.

3. FUNGAL DISEASE

The effect of entomophagous fungi as a mortality factor of Myzus persicae populations was evident at all sites except those studied at site C (Figures 4, 5 and 6).

During 1973 diseased Myzus persicae were detected as early as the end of June at site A_2 but its effects were more general from the second week in July. At site A_1 in 1973, where 4.23 per cent of the aphid population was destroyed by fungi (Appendix 2), the relationship between the total aphid population and those attacked by fungi was shown by regression analysis to be slightly significant ($P < 0.05$). At site A_2 in the same year 4.15 per cent of the aphid population was destroyed by fungi (Appendix 2) but no significant relationship to the changes in the aphid population was found.

The aphid population studied at site B_1 in 1973 displayed a level of fungal attack that ranged from 8 per cent to 47 per cent but with an overall mortality of 8.89 per cent (Appendix 3).

Regression analysis revealed a highly significant relationship between fungal disease and the total aphid population ($P < 0.001$). In 1974 a highly significant relationship between the total aphid population and those attacked by fungi was also found by regression analysis ($P < 0.01$ at site A_3 and $P < 0.001$ at site B_2). 6.54 per cent and 5.35 per cent mortality for the season was recorded at site A_3 and B_2 respectively (Appendix 4). At these two sites fungal disease was not detected until the latter half of July and reached a peak in August. The diseased aphids disappeared from the samples by the end of September.

Discussion

Entomophagous fungus outbreaks are thought to be partly responsible for the mid-season decline in aphid populations. Hafez (1961) found an abundance of infected Brevicoryne brassicae towards the end of July and the beginning of August and attributed the abrupt decline in aphid numbers to this. Dunn and Kempton (1971) noted that Brevicoryne brassicae were severely affected by fungal disease over that same period and also found that the time coincided with a period of high atmospheric humidity which had followed the rain. They also found that the strong colonial habit of this aphid species was an important factor in rapid spread of the disease.

Reports of epizootics in Myzus persicae are not so evident, perhaps because the species is not so colonial as Brevicoryne brassicae, although a number of studies cite fungal disease as playing a major role in the control of this species even although relatively few diseased aphids were found (van Emden, Eastop, Hughes and Way, 1969).

In this study it would appear that the incidence of fungal disease varied from site to site, perhaps due to differences in microclimate although no evidence exists for this here. The high levels of mortality such as 47 per cent at site B_1 in 1973 and 32 per cent at site B_2 in 1974 provide evidence of an epizootic. However, the influence of these epizootics would have occurred too late in the season to have prevented a build up in the aphid population. This is of particular importance when dealing with a virus vector such as Myzus persicae.

Gustafsson (1969) emphasized that the development of an epizootic was dependent upon temperature, rainfall, high relative humidity and light. He also found that epizootics often occurred long after the aphids infested a crop in the spring because the probability of infection by an overwintering form of the fungus was low. It was only at sites B_1 and B_2, where evidence of epizootics existed, that correlation analysis revealed a significant relationship between fungal disease outbreaks and amount of sunshine ($P < 0.001$ at site B_1, and $P < 0.01$ at site B_2) and between fungal disease outbreaks and maximum temperature ($P < 0.02$ at site B_1 and $P < 0.01$ at site B_2). The development of an epizootic will also be dependent upon the density of the host species being large enough to initiate a natural epizootic.

This density level may very often be higher than that which can be tolerated by plants and farmers (van Emden et al., 1969). This appeared to be the case here (Figures 4 and 5).

It is recommended that an amplified study of this particular aspect of aphid control be initiated in this area.

4. INTERACTION BETWEEN PARASITES AND MYZUS PERSICAE IN THE FIELD

Extent of parasitism

Parasitised aphids were detected in the population as early as the middle of June at site A_1 during 1973 (Figure 4 and Appendix 2). A peak was reached towards the end of July and the start of August with numbers declining steadily after this time. The level of parasitism within the aphid population at this site ranged from 1.02 per cent on detection to 65.62 per cent in the middle of August. 13.04 per cent of the total aphids sampled were destroyed by parasitism with the peak reached about three weeks after the peak in the aphid population (Figure 19 and Appendix 2).

The number of parasitised aphids sampled from site A_2 remained low with a peak reached in the latter half of July (Figure 4 and Appendix 2). 6.93 per cent of the aphid population was destroyed by parasitism over the season although the level of parasitism ranged from 1.85 per cent on detection, in the first week of July, to 51.52 per cent, in the first week of September, at least seven weeks after the aphid population peak (Figure 19).

Sampling at site B_1 during 1973 showed that two peaks in the number of parasitised aphids within the population was reached. The first

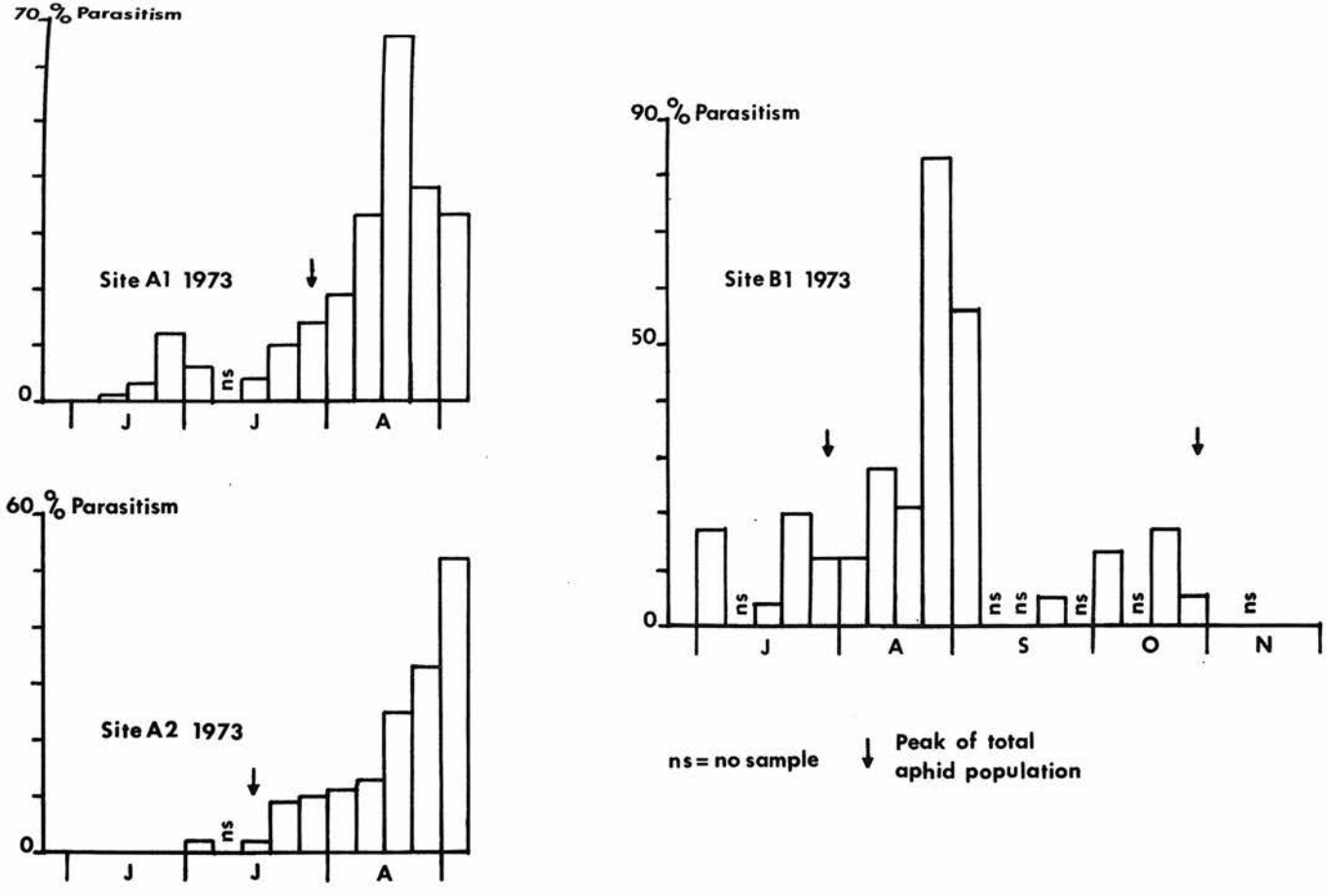


Figure 19. Trend in percentage parasitism of Myzus persicae (Sulz.) over the specified sampling period.

peak at the end of July and the second at the end of October (Figure 5 and Appendix 3).

Mortality by parasitism increased from 17.39 per cent on detection in the first week of July to 83.33 per cent at the end of August at least one month after the aphid population had reached a peak. At the end of August the aphid population was at its lowest density during the mid-season decline. The level of parasitism declined rapidly through September but recovered to reach a second peak of 16.67 per cent at least one week before the October peak in the aphid population. Overall 13.82 per cent of the total aphid population had been destroyed by parasitism (Figure 19 and Appendix 3).

During 1974 only 6.43 per cent of the aphid population was destroyed by parasitism at site A_3 (Appendix 4). Parasitism was detected at the end of June and reached a peak in the middle of August and declined to a low level during September (Figure 4).

At the end of June only 0.79 per cent of the population was parasitised but this increased to 8.72 per cent by the end of August. There followed a marked increase in the level of parasitism with 29.11 per cent recorded two weeks later and at least one month after the peak in the aphid population (Figure 20).

In the same year, at site B_2, 6.75 per cent of the total aphid population was destroyed by parasitism (Appendix 4). Parasitism was detected at this site from the middle of July and reached a peak by the middle of August which was about two weeks after the peak in the aphid

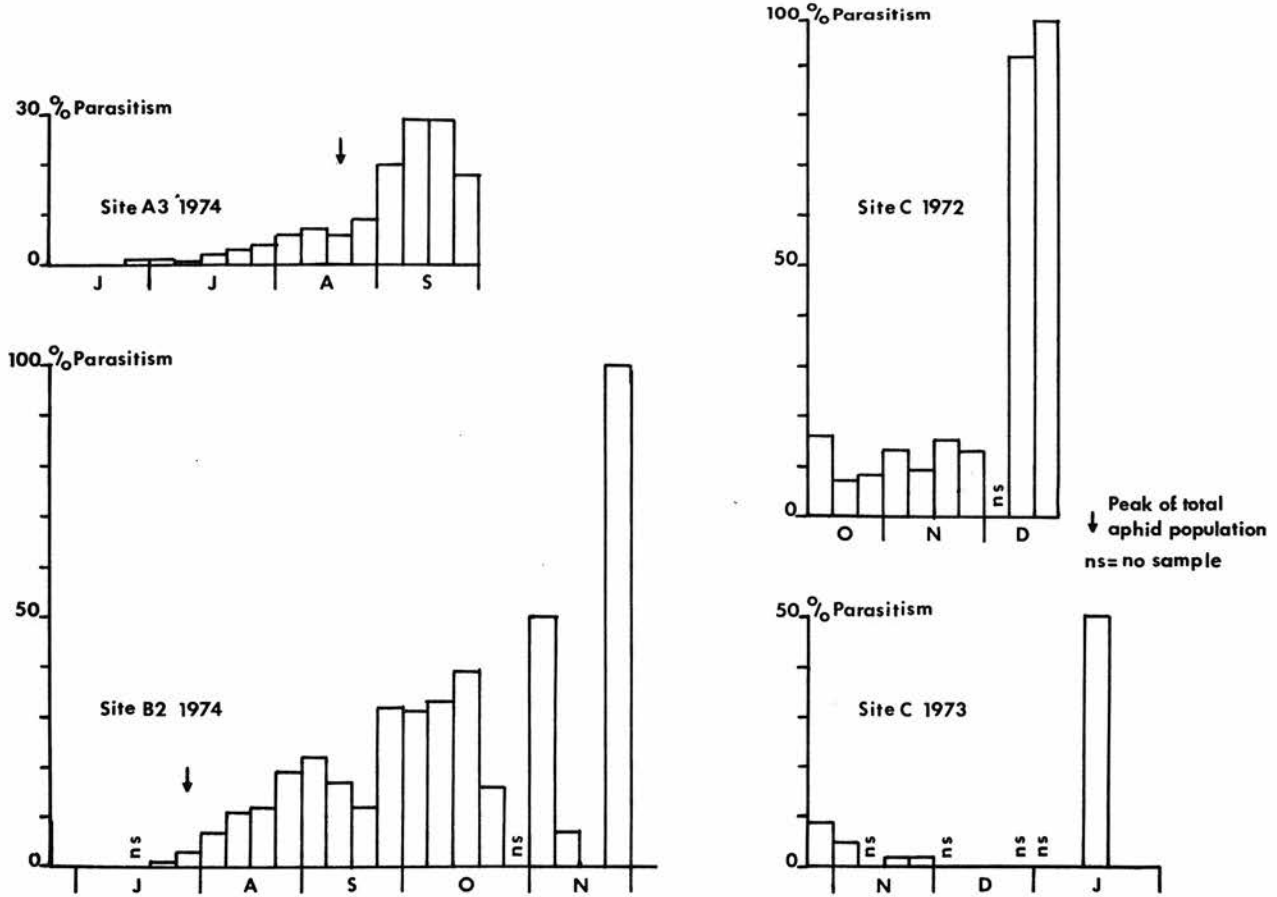


Figure 20.Trend in percentage parasitism of Myzus persicae (Sulz.) over the specified sampling period.

population. No second peak was observed as in 1973 with the numbers of parasitised aphids remaining few until the cessation of sampling in the first week of December (Figure 5).

From a level of 1.37 per cent in the middle of July parasitism increased to 22.22 per cent in the first week of September, at least five weeks after the peak in the aphid population. A slight decline to 11.61 per cent was observed after which the level of parasitism rose and was maintained at a reasonably high level within the population until sampling stopped in December (Figure 20).

During 1972 at site C the number of parasitised aphids in the sample declined from the first week in November until the middle of December after which no live aphids were detected. During 1973 at the same site the parasitised aphids declined to zero in the samples by the end of November and, apart from one mummified aphid in the middle of January 1974, parasitism remained undetected in the population (Figure 6 and Appendix 5). The levels of parasitism were such that 12.66 per cent of the population in 1972 and 5.21 per cent in 1973 were destroyed (Figure 20).

Approximately twice as many aphids that were sampled in the field were parasitised and mummified at all sites except C, in 1973 and B_2, in 1974. At site C about 14 times as many aphids sampled in the field were parasitised and mummified but at site B_2 equal numbers of mummified aphids and non-mummified but parasitised aphids were sampled (Table 12).

TABLE 12: The ratio of mummified to non-mummified but parasitised Myzus persicae that were present in the population on the day of sample

Site	Mummified Aphids		Ratio	Percentage Occurrence	
	Day 0	Day 3 + 6	Day 0 : Day 3 + 6	Day 0	Day 3 + 6
A_1	274	176	1.6 : 1	60.89	39.11
A_2	183	66	2.8 : 1	73.49	26.51
B_1	135	67	2.0 : 1	66.83	33.17
C	28	2	14 : 1	93.33	6.67
A_3	724	402	1.8 : 1	64.30	35.70
B_2	244	264	0.9 : 1	48.03	51.97

TABLE 13: The statistical relationship between parasitism and the density of Myzus persicae populations

Site	Correlation coefficient (r)	Degrees of freedom	Probability level (P)
C72	+ 0.7829	8	< 0.02
A_1	+ 0.7294	13	< 0.01
A_2	+ 0.0918	13	NS
B_1	+ 0.8482	15	< 0.001
C73	+ 0.9055	8	< 0.001
A_3	+ 0.9577	15	< 0.001
B_2	+ 0.7958	20	< 0.001

Parasitism and host density

To determine if any relationship existed between the parasitised aphid population and the total aphid population a correlation analysis was carried out for each site according to Bailey (1969). Analysis of the data from all sites except site A_2 showed that a significant relationship between the density of the total aphid population and that proportion that was parasitised did exist. At site A_2 however no significant relationship existed (Table 13).

Distribution of parasitism according to plant strata

During 1973 at site A_1 approximately 55 per cent of the parasitised aphids were sampled on the lower leaves of the sprout plants compared to 41 per cent on the middle regions and 4 per cent on the young leaves. At site A_2 parasitism was restricted to the aphids that inhabited the older and mature regions of the plants with about 86 per cent found on the former. At site B_1 however, where plants sub-divided into upper and lower halves, 94.47 per cent of the parasitised population were recorded on the lower half. Approximately 94 per cent of the parasitised aphids were found on the old leaves at site A_3 during 1974 with 5 per cent on the middle leaves and very few on the young, upper leaves. At site B_2 in the same year the distribution of parasitism was such that about 89 per cent occurred on the lower regions and zero on the upper leaves.

At site C there were marked contrasts in the distribution found in 1973 compared to 1972. Parasitised Myzus persicae were equally abundant on the lower and middle regions with zero on the upper leaves during 1973 whereas in 1972 about 10 per cent occurred on the young

leaves and 68 per cent on the senescing leaves with remainder distributed throughout the larger middle, mature regions.

Effect of parasitism on the reproductive rate of Myzus persicae

To have an effect on the reproductive capacity of an aphid then mummification must occur before the aphid reaches maturity. If mummification was to occur in the adult stage then the aphid might reproduce before mummification takes place (Hafez, 1961; Starý, 1970). Those aphids that were parasitised during this investigation were examined to determine the developmental stage of the aphid at which mummification occurred. By means of Chi-square analysis any significance between the number of nymphs mummified and the number of adults mummified was detected. Figure 21 and Figure 22 detail the periods in the season at which the number of mummified nymphs were significantly more numerous than the number of mummified adults during 1973 and 1974.

At site A_1 in 1973 significantly more nymphs were mummified in July ($P < 0.001$) particularly on the two weeks prior to the decline in the aphid population. During these two weeks the ratio of live young nymphs to live adult aphids (a guide as to the reproductive rate of the aphid population in the field) declined from 9.76 nymphs per adult to 5.34 and 5.31 per adult (Table 14).

At site A_2 the number of mummified nymphs only differed significantly on the last week in July which was one week after the peak in the aphid population ($P < 0.01$). The reproductive rate of the population dropped from 16.53 nymphs per adult, at the peak in the aphid population, to 8.11 per adult on the last week of July (Table 14).

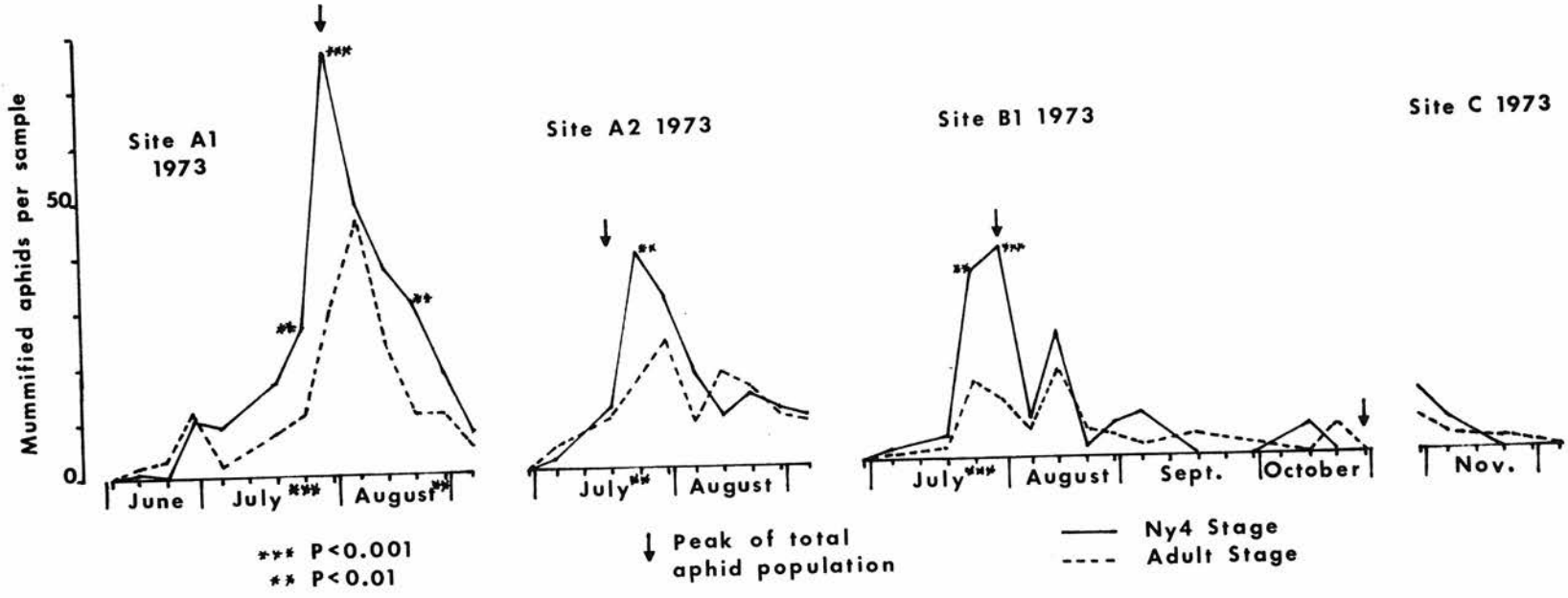


Figure21. Relationship between developmental stage of Myzus persicae (Sulz.) mummified and the peak of aphid infestation. (Development to apterae only.)

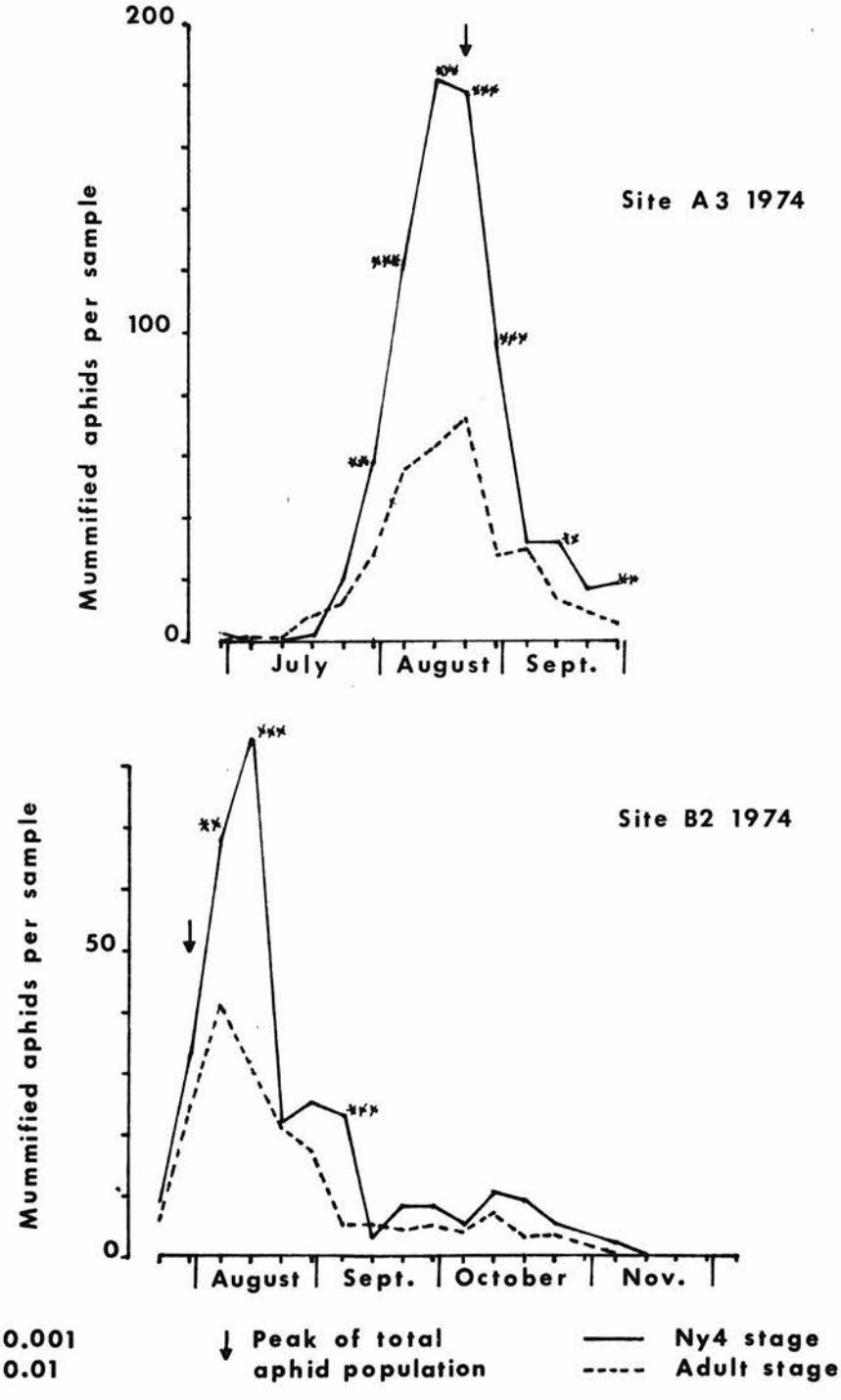


Figure22. Relationship between developmental stage of Myzus persicae (Sulz.) mummified and the peak of aphid infestation. (Development to apterae only.)

TABLE 14: The proportion of young nymphs to adult Myzus persicae before and during the mid-season decline in 1973 and 1974

	Reproductive rate of Myzus persicae population (Young nymphs per adult)		
Date	Site A_1	Site A_2	Site B_1
17.7.73	9.76	16.53	15.33
24.7.73	5.34	8.11	4.72
31.7.73	5.31	10.00	3.84
7.8.73	6.84	5.21	5.40
14.8.73	1.34	3.39	1.33
21.8.73	1.20	2.08	2.67
28.8.73	1.55	2.00	1.00
4.9.73	1.50	1.75	1.33
Date	Site A_3	Site B_2	
23.7.74	7.63	13.30	
30.7.74	5.82	10.40	
6.8.74	6.39	5.80	
13.8.74	4.57	4.80	
20.8.74	8.86	2.50	
27.8.74	4.97	3.80	
3.9.74	4.83	4.00	
10.9.74	1.90	7.40	
17.9.74	1.71	2.30	

At site B_1 significantly more nymphs were mummified in July ($P < 0.001$) particularly in the last two weeks of that month just prior to the decline in the aphid population. The reproductive rate during this period declined from 15.33 young nymphs per adult in the middle of July to 4.72 and 3.84 per adult in the last two weeks of that month (Table 14).

During 1974 at site A_3 significantly more nymphs were found to be mummified from the last week in August until the end of September ($P < 0.001$). However no significant change in the reproductive rate was evident during this period (Table 14). At site B_2, however, significantly more mummified nymphs ($P < 0.001$) were found after the peak in the aphid infestation which occurred in the last week of July. At this stage the reproductive rate was 10.4 nymphs per adult which was reduced to 5.8 per adult one week later when significant differences in the stage of development at which aphid mummification was observed (Table 14).

Effect of parasitism on alate production

There appeared to be no effect on the production of alate Myzus persicae and therefore no effect on the migration rate of the aphid populations during 1973. At site A_1 only three alate nymphs and one alate adult were found to be parasitised. None were found at site A_2 and only one alate adult was parasitised at site B_1.

During 1974 however, three alate nymphs and 32 alate adults were parasitised at site A_3 together with 10 alate adults at site B_2.

Effect of hyperparasitism on primary parasites

Hyperparasites were more common in 1973 than in 1974 when they destroyed 12.44 per cent of the primary parasites at site A_1; 13.66 per cent at site A_2; 12.87 per cent at site B_1 and 36.67 per cent at site C. In 1974 the level of hyperparasitism was as low as 3.20 per cent at site A_3 and 4.72 per cent at site B_2 (Table 5).

During 1973 the effect of hyperparasitism was detected as early as the first week of July (Figure 23) and reached a peak from mid August until mid September (Figure 24). In 1974, however, hyperparasitism was not recorded until the end of July (Figure 23) and did not reach a peak until the end of September (Figure 24).

Effect of weather on primary parasites

Regression analysis between the climatic data (Appendix 14) and the parasitised aphid population revealed no significant relationship at either site A_2 in 1973 or site A_3 in 1974. At site A_1 in 1973 the minimum temperatures appeared to have some significance in determining the level of parasitism in the aphid population ($P < 0.05$). At site B_1 in 1973 both maximum and minimum temperatures were significant ($P < 0.05$) together with the amount of sunshine ($P < 0.02$) in determining the activity of parasites as estimated by the number of parasitised aphids in the population. In 1974 at site B_2 the parasitised aphid population could only be related to maximum temperatures and the amount of sunshine ($P < 0.01$).

During the winter period of 1973 and 1974 temperature, particularly maximum temperature, ($P < 0.02$) appeared to be significant although minimum temperature could also have been important ($P < 0.05$).

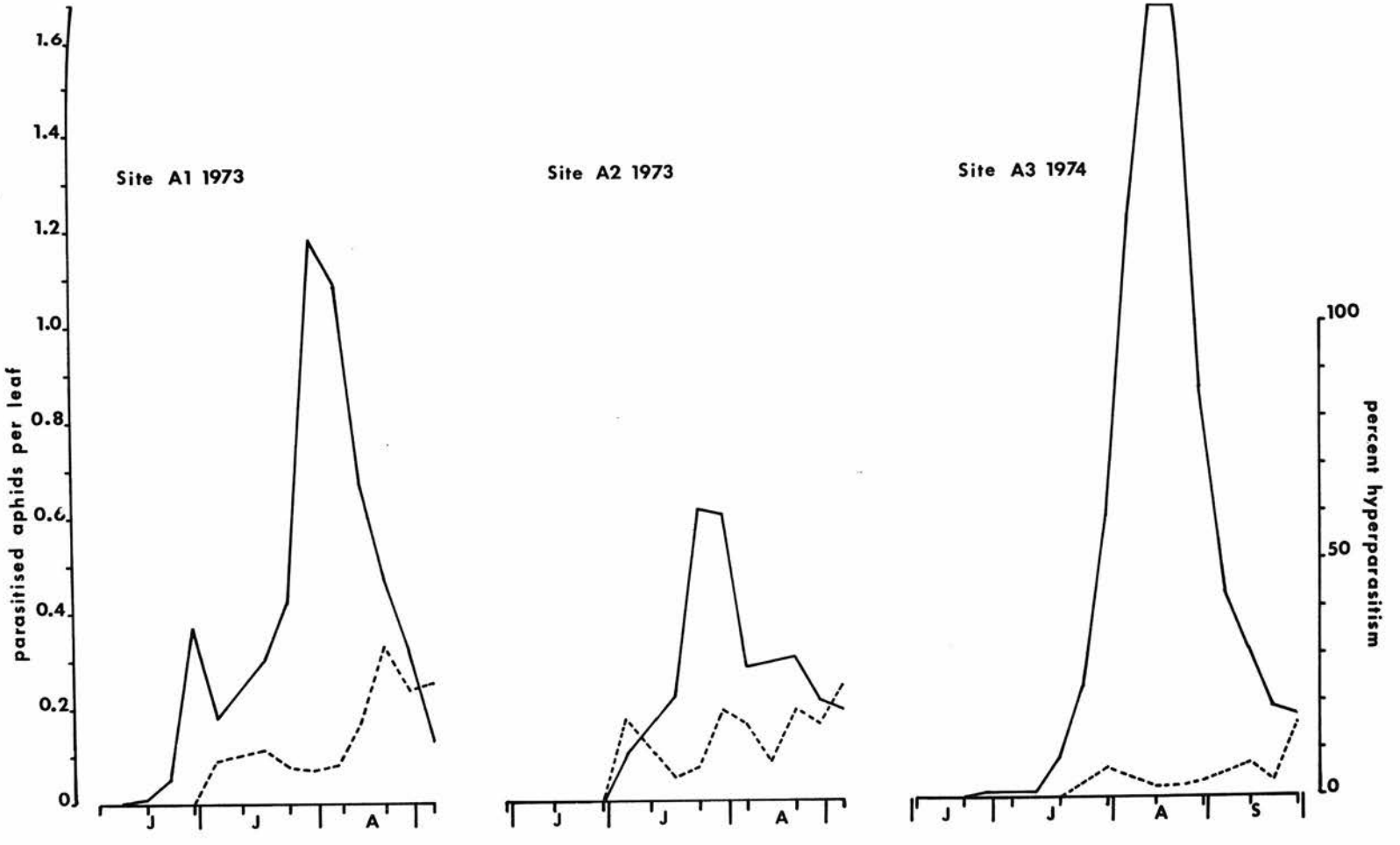


Figure23. Relationship between parasitised Myzus persicae (Sulz.) per leaf and the degree of hyperparasitism occurring each week at the specified sites.

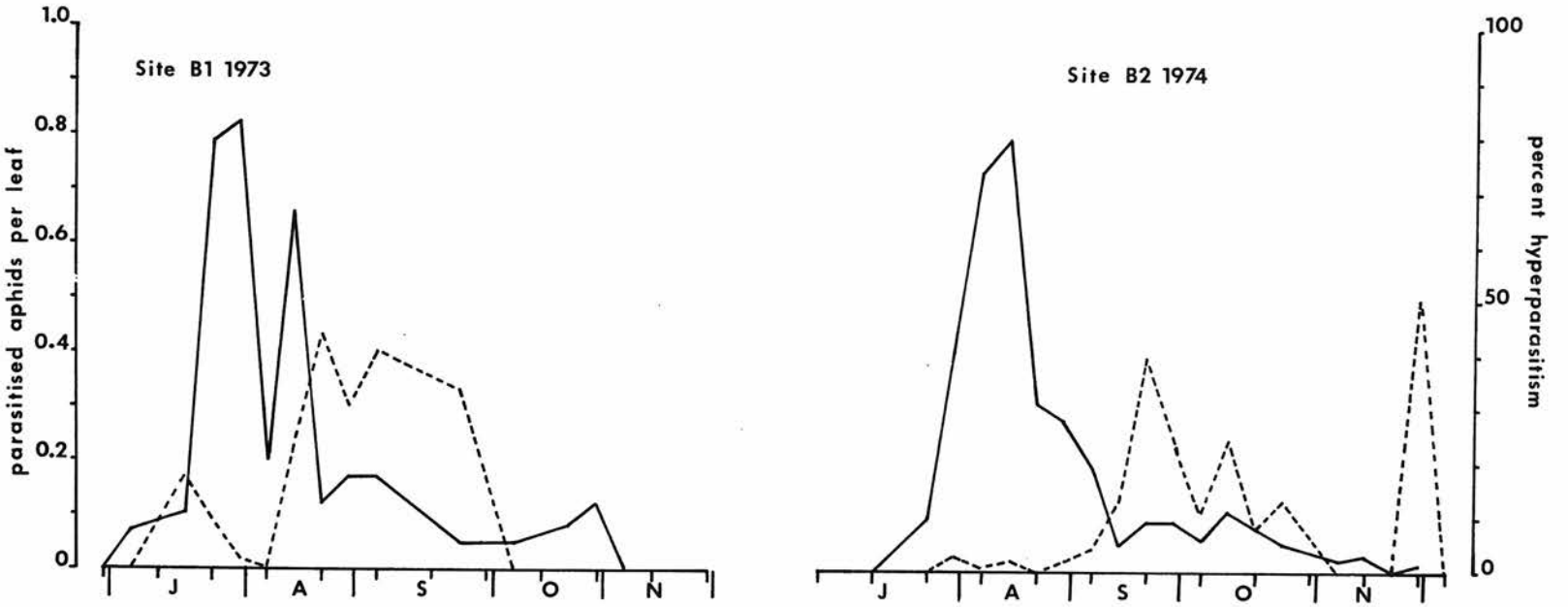


Figure 24. Relationship between parasitised Myzus persicae (Sulz.) per leaf and the degree of hyperparasitism occurring each week at the specified sites.

Discussion

The overall effect of the parasite species complex upon the Myzus persicae population, as estimated by percentage parasitism, was greater in 1973 than in 1974. But, although greater in 1973 the overall levels of parasitism found that year were not excessively high with less than 15 per cent mortality recorded.

In June, which was probably the most significant month with regard to the establishment and build up of the aphid population, the effects of parasitism were either absent or occurred at low levels. The effect of parasitism appeared only to have an effect upon the population from mid July onwards when significantly more nymphs were found mummified thus reducing or slowing up the rate of reproduction of the aphid population but having little effect on the migration rate. The avoidance of alatae as an ovipositional site may also affect the synchronisation of parasites with a new population of aphids on a crop since the immigrant alatae would be parasite free (van Emden, 1966b).

Mortality, expressed as percentage parasitism, only tended to increase after the peak in the aphid population even although the parasites appeared to affect the population prior to this point. This delayed influence of the parasite upon the aphid population (reciprocal oscillations) tends to signify that parasitism as a mortality factor was effective but it would appear from the results that this effectiveness was not economically significant since their action was too late to prevent either the build up in the aphid population or the spread of the population. The latter is important when considering the

spread of virus disease by the alate aphids from one plant or from one crop to another (Watson and Plumb, 1972).

The correlation of the changes in the Myzus persicae population with that proportion showing symptoms of parasitism does indicate that the action of parasites was a response to a change in density. This response was not evident in one population (site A_2) which may be partly explained by the topography of the area. This site was situated in a very exposed area of the crop and this may have resulted in the reduction in the activity of the adult parasites by, for example, the wind blowing over the site. The colonisation site should, in fact, have a maximum protective cover for the parasite (van den Bosch and Telford, 1964). It would therefore appear that in order not to limit the effectiveness of the parasite complex any degree of exposure must be undesirable.

The presence of hyperparasites are also thought to limit the effectiveness of the primary parasites (Dunn, 1949; Hafez, 1961). Although the levels of hyperparasitism recorded in 1973 were high compared to 1974 the levels themselves were much lower than those recorded by Agyen-Sampong (1972) in the Edinburgh area. He recorded levels of 39.4 per cent and 46.9 per cent hyperparasitism in Myzus persicae populations during 1969 and 1970 respectively.

Such variation in the levels of hyperparasitism may be significant when looked at in relation to the increases in the aphid populations that have occurred in recent years (Scottish Agricultural Colleges Technical Note No.3, 1975). It is well known that when

hyperparasitism is severe then it may annihilate primary parasite populations in subsequent generations (Hafez, 1961). The high levels of hyperparasitism recorded by Agyen-Sampong may then have been contributory to the increase in the Myzus persicae populations by reducing the primary parasite populations and their effectiveness in subsequent generations. This would then have the effect of reducing the availability of primary parasitised aphids for the hyperparasites to oviposit in thus reducing hyperparasitism to the levels recorded during this investigation.

This line of argument may be supported by the effect of hyperparasitism over the season as recorded in 1973 and 1974. The earlier effect of hyperparasitism in 1973, together with the much higher overall effect, may have reduced the number of overwintering primary parasites. This would have the dual effect of reducing the number of primary parasites that would attack the aphid population in the spring as well as reducing the number of ovipositional sites for next year's hyperparasites thus lowering the level of hyperparasitism within the aphid population. Aphid populations would therefore become well established in the spring although climate may also be of importance with regard to overwintering and early season development of the Myzus persicae population (Section B and Section C 1.).

The effects of temperature on the development of parasite populations are of interest since it was determined from laboratory studies (Section B) that constant temperature conditions had a direct effect on the development of Diaeretiella rapae, a common primary parasite of Myzus persicae populations in this study. The effect of

temperature was particularly pronounced in the lower regimes when cessation of development occurred when conditions dropped below a theoretical temperature threshold of $5.5^{o}C \pm 0.18^{o}C$.

The weekly mean in minimum temperature remained below this level from November, 1973 until mid May, 1974 (Figure 16 and Appendix 14). This suggests that if the laboratory findings are true to the field situation then Diaeretiella rapae would rarely develop to adult stage before mid May and even then at a slow rate with the generation time, k, estimated to be 188.68 ± 7.49 degree days above the threshold of $5.5^{o}C \pm 0.18^{o}C$.

Temperature conditions in the field were not constant and the effect of increasing maximum temperatures may initiate sporadic development and emergence of the parasite throughout the winter period which would die without reproducing if aphid hosts could not be found (Hafez, 1961). Other species of parasite that attack Myzus persicae will have different thresholds of development (Starý, 1970; Agyen-Sampong, 1972; Campbell, Frazer, Gilbert, Gutierrez and Mackauer, 1974). But the maintenance of low temperatures must however delay their development and consequently delay the arrival of parasites as an effective mortality factor in the aphid population in the spring. Therefore since the aphid appeared to be more adapted to lower temperature regimes (Section B) then the aphid population would become well established on its host plant. This would result in the lag period that was found, before the arrival of parasitism in the aphid population (Figure 5 and Figure 6).

The host specificity of parasites may also be a major factor that would limit the effectiveness of those parasites although differences in opinion on the factors that have determined the host specificity of the aphidiids (the parasites that attack only aphids) still occur (Starý, 1970).

Diaeretiella rapae was the most common parasite of Myzus persicae in 1973 (Table 5). In fact, this species accounted for 67.02 per cent of all emerging parasites reared from this aphid species in that year. All other parasite species were less than 7 per cent each of the total parasite emergence. During 1974, however, Diaeretiella rapae only accounted for 28.30 per cent of the total parasite complex. This reduction was reflected in an increase in the other parasite species particularly Praon volucre and the Aphidius urticae group (Table 5).

This distribution is of interest when looked at with respect to the presence of species of aphid other than Myzus persicae, in particular, Brevicoryne brassicae - the cabbage aphid, which occurred on the plants during the study.

Diaeretiella rapae is known to prefer Brevicoryne brassicae as a host species (Hafez, 1961). Hafez demonstrated that this parasite would attack the cabbage aphid in preference to Myzus persicae in the laboratory and his field findings tended to collaborate this. George (1957) had not found this in the laboratory where Myzus persicae was the preferred host although he did find the cabbage aphid to be preferred in the field. Pimentel (1961) found that

differences in the degree of parasitism caused by Diaeretiella rapae was not the direct result of host attraction but was more a consequence of the density searching relationship so that the most abundant aphid species on the plant would exhibit the highest degree of parasitism.

During this study 167 Brevicoryne brassicae were sampled in 1973 compared to 2,451 during the same period in 1974 (Table 1). Of those aphids that were parasitised Diaeretiella rapae accounted for 100 per cent of all emerging primary parasites (unpublished data). If the findings of these other studies are taken into account and the fact that Myzus persicae appears more able to defend itself better against parasite attack than do some other aphid species (Wilbert, 1967) then it would appear that the high density of Brevicoryne brassicae in 1974 'competed' with Myzus persicae as an ovipositional site for Diaeretiella rapae. This would be particularly so from the end of June onwards when the cabbage aphid was more common (unpublished data). The resultant effect of this 'competition' would be to lower the overall effectiveness of the parasite complex in controlling Myzus persicae populations in 1974 compared to 1973.

It could be argued that the loss in effectiveness of the parasite complex may have been compensated by the increase in the other parasite species. The Aphidius urticae group, which includes the species matricariae Haliday (Eady, 1969), was more common in 1974 than in 1973 but species in this group have not been shown to contribute significantly in the reduction of aphid populations except under

favourable conditions as found in greenhouse environments (McLeod, 1937; Hussey, 1965; Wyatt, 1970).

The other parasite species to increase dramatically in number from 1973 to 1974 was Praon volucre. This species was studied by Agyen-Sampong (1972) as the common parasite of Myzus persicae but discounted its effectiveness due to a higher threshold of development compared to that of the aphids.

Harvesting of the crop and early ploughing of the fields must also count, in addition to the above, as a limiting factor in the effectiveness of parasites in regulating aphid abundance because a number of mummies must be destroyed in the physical process that takes place and this would reduce the number that would overwinter successfully.

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APPENDICES

APPENDIX 1: Water Culture Nutrient Solution (van Emden, 1966a)

Complete Feed	Stock Solution g/l	Final Solution ml stock solution /l
$Ca(NO_3)_2.4H_2O$	236.16	7.5
KNO_3	101.10	7.5
$MgSO_4.7H_2O$	246.50	3.0
KH_2PO_4	136.09	1.5
Fe(EDTA)	36.40	1.5
Micronutrients:		
$MnSO_4.4H_2O$	11.20	1.5
$CuSO_4.5H_2O$	1.20	1.5
$ZnSO_4.7H_2O$	1.50	1.5
H_3BO_3	0.18	1.5

K E Y

TO APPENDICES 2; 3; 4; 5.

Symbol

A	Total aphids per leaf
B	Parasitised aphids per leaf
C	Total aphids attacked by fungal disease per leaf
D	Total leaves sampled
E	Parasitism per cent
F	Fungal attack per cent
G	Total viable aphids per leaf
——	No sampling occurred

APPENDIX 2: Details of *Myzus persicae* population per leaf at Sites A_1 and A_2, 1973

Week		A	B	C	D	E	F	G	
(29.5.73)	1	0.08	0	0	313	0	0	0.08	
	2	0.05	0	0	426	0	0	0.05	
	3	0.94	0.01	0	313	1.02	0	0.93	JUNE
	4	1.48	0.05	0	60	3.37	0	1.43	
	5	3.07	0.37	0	60	11.96	0	2.70	
	6	3.30	0.18	0	60	5.56	0	3.12	
	7	-	-	-	-	-	-	-	
SITE	8	6.83	0.30	0.11	90	4.39	1.63	6.42	
A_1	9	4.41	0.42	0.11	90	9.57	2.52	3.88	JULY
1973	10	8.46	1.18	0.32	90	13.93	3.81	6.96	
	11	5.64	1.08	0.67	90	19.09	11.81	3.90	
	12	2.03	0.67	0.20	90	32.79	9.84	1.17	
	13	0.71	0.47	0.09	90	65.62	12.50	0.16	AUGUST
	14	0.86	0.32	0.11	90	37.66	12.99	0.43	
(4.9.73)	15	0.40	0.13	0.01	90	33.33	2.78	0.26	
TOTAL		1.77	0.23	0.07	1,952	13.04	4.23	1.46	
(29.5.73)	1	0.004	0	0	285	0	0	0.004	
	2	0.01	0	0	413	0	0	0.01	
	3	0.14	0	0	300	0	0	0.14	JUNE
	4	2.47	0	0	60	0	0	2.47	
	5	3.38	0	0.02	60	0	0.49	3.37	
	6	5.42	0.10	0	60	1.35	0	5.32	
	7	-	-	-	-	-	-	-	
SITE	8	12.32	0.22	0.13	90	1.80	1.08	11.97	JULY
A_2	9	6.82	0.61	0.30	90	8.96	4.40	5.91	
1973	10	5.89	0.60	0.34	90	10.19	5.85	4.94	
	11	2.43	0.28	0.46	90	11.42	18.72	1.70	
	12	2.20	0.29	0.07	90	13.13	3.03	1.84	AUGUST
	13	1.21	0.30	0.24	90	24.78	20.18	0.67	
	14	0.64	0.21	0.06	90	32.76	8.62	0.38	
(4.9.73)	15	0.37	0.19	0.04	90	51.52	12.12	0.13	
TOTAL		1.89	0.13	0.08	1,898	6.93	4.15	1.68	

APPENDIX 3: Details of Myzus persicae population per leaf
Site B_1 in 1973

Week		A	B	C	D	E	F	G	
(29.5.73)	1	NO PLANTS							
	2	NO PLANTS							
	3	NO PLANTS							JUNE
	4	NO PLANTS							
	5	0.40	0	0	30	0	0	0.40	
	6	0.38	0.07	0	60	17.39	0	0.32	
	7	-	-	-	-	-	-	-	
	8	2.27	0.10	0.20	60	4.41	8.82	1.97	JULY
	9	3.98	0.78	0.33	60	19.67	8.37	2.87	
	10	6.82	0.82	0.60	60	11.98	8.80	5.40	
	11	1.72	0.20	0.25	60	11.65	14.56	1.27	
	12	2.32	0.65	0.52	60	28.06	22.30	1.15	AUGUST
	13	0.57	0.12	0.27	60	20.59	47.06	0.18	
	14	0.20	0.17	0	60	83.33	0	0.03	
SITE	15	0.30	0.17	0	60	55.56	0	0.13	
B_1	16	-	-	-	-	-	-	-	SEPTEMBER
1973	17	-	-	-	-	-	-	-	
	18	0.98	0.05	0	60	5.08	0	0.93	
	19	-	-	-	-	-	-	-	
	20	0.38	0.05	0	60	13.04	0	0.33	
	21	-	-	-	-	-	-	-	OCTOBER
	22	0.50	0.08	0	60	16.67	0	0.42	
	23	2.48	0.12	0	60	4.70	0	2.37	
	24	0.65	0	0	60	0	0	0.65	
	25	-	-	-	-	-	-	-	NOVEMBER
	26	0.40	0	0	60	0	0	0.40	
(28.11.73)	27	0.22	0	0	60	0	0	0.22	
TOTAL		1.48	0.20	0.13	990	13.82	8.89	1.14	

APPENDIX 4: Details of Myzus persicae population per leaf at Sites A_3

Week		A	B	C	D	E	F	G
(4.6.74)	1	0	0	0	296	0	0	0
	2	0.07	0	0	353	0	0	0.07
	3	0.14	0	0	354	0	0	0.14
	4	0.69	0.01	0.002	548	0.79	0.26	0.69
	5	0.96	0.01	0	150	0.69	0	0.95
	6	1.43	0.01	0.01	150	0.46	0.46	1.42
	7	4.05	0.08	0.01	150	1.98	0.16	3.96
SITE	8	7.77	0.23	0.12	150	2.92	1.54	7.42
A_3	9	14.11	0.59	0.53	150	4.20	3.78	12.99
1974	10	19.33	1.22	0.74	150	6.31	3.83	17.37
	11	24.53	1.69	0.96	150	6.90	3.91	21.87
	12	26.71	1.69	3.07	150	6.34	11.48	21.95
	13	9.86	0.86	1.52	150	8.72	15.42	7.48
	14	2.20	0.43	0.47	150	19.70	21.21	1.30
	15	1.05	0.31	0.15	150	29.11	14.56	0.59
	16	0.67	0.19	0.05	150	29.71	6.93	0.43
(24.9.74)	17	0.99	0.17	0.01	150	18.12	0.67	0.81
TOTAL		5.00	0.32	0.33	3501	6.43	6.54	4.47

and B_2 , 1974

Week		A	B	C	D	E	F	G	
(4.6.74)	1	NO PLANTS							
	2	NO PLANTS							JUNE
	3	NO PLANTS							
	4	0.02	0	0	242	0	0	0.02	
	5	0.12	0	0	362	0	0	0.12	
	6	0.71	0	0	435	0	0	0.71	
	7	-	-	-	-	-	-	-	JULY
	8	7.32	0.10	0.02	150	1.37	0.27	7.20	
	9	14.57	0.40	0.20	150	2.74	1.37	13.97	
	10	11.10	0.73	0.84	150	6.55	7.57	9.53	
	11	7.12	0.79	0.37	150	11.14	5.15	5.96	AUGUST
	12	2.57	0.31	0.54	150	11.95	21.04	1.72	
SITE	13	1.44	0.28	0.27	150	19.44	18.52	0.89	
B_2	14	0.84	0.19	0.27	150	22.22	31.75	0.39	
1974	15	0.31	0.05	0.06	150	17.39	21.74	0.19	SEPTEMBER
	16	0.75	0.09	0.08	150	11.61	10.71	0.58	
	17	0.27	0.09	0.01	150	32.50	2.50	0.17	
	18	0.19	0.06	0.01	150	31.03	3.45	0.13	
	19	0.34	0.11	0.02	150	33.33	5.88	0.21	OCTOBER
	20	0.21	0.08	0	150	38.71	0	0.13	
	21	0.33	0.05	0	150	16.00	0	0.28	
	22	-	-	-	-	-	-	-	
	23	0.04	0.02	0	150	50.00	0	0.02	
	24	0.40	0.03	0	150	6.67	0	0.37	NOVEMBER
	25	0	0	0	150	0	0	0	
	26	0.01	0.01	0	150	100.00	0	0	
(3.12.74)	27	0	0	0	150	0	0	0	
TOTAL		1.94	0.13	0.10	3,899	6.75	5.35	1.70	

APPENDIX 5: Details of Myzus persicae population per leaf at site C in 1972 and 1973

Week		A	B	C	D	E	F	G	
(16.10.72)	1	3.01	0.49	0	150	16.19	0	2.52	
	2	3.44	0.23	0	150	6.59	0	3.21	OCTOBER
	3	3.85	0.32	0	150	8.30	0	3.53	
	4	4.02	0.52	0	150	12.94	0	3.50	
SITE C 1972	5	2.89	0.27	0	150	9.47	0	2.61	NOVEMBER
	6	2.72	0.41	0	150	14.95	0	2.31	
	7	1.09	0.15	0	150	13.41	0	0.95	
	8	-	-	-	-	-	-	-	
	9	0.17	0.16	0	150	92.31	0	0.01	DECEMBER
(19.12.72)	10	0.05	0.05	0	150	100.00	0	0	
TOTAL		2.29	0.29	0	1,350	12.66	0	2.07	
(30.10.73)	1	2.08	0.19	0	90	9.09	0	1.89	
	2	2.06	0.10	0	90	4.86	0	1.96	
	3	-	-	-	-	-	-	-	NOVEMBER
	4	0.96	0.02	0	90	2.33	0	0.93	
	5	0.50	0.01	0	90	2.22	0	0.49	
	6	-	-	-	-	-	-	-	
SITE C 1973	7	0.22	0	0	90	0	0	0.22	DECEMBER
	8	0.24	0	0	90	0	0	0.24	
	9	-	-	-	-	-	-	-	
	10	-	-	-	-	-	-	-	
	11	0.31	0	0	90	0	0	0.31	
	12	0.02	0.01	0	90	50.00	0	0.01	JANUARY
	13	0	0	0	90	0	0	0	
(29.1.74)	14	0.01	0	0	90	0	0	0.01	
TOTAL		0.64	0.33	0	900	5.21	0	0.61	

APPENDIX 6: Age-specific analysis of the Myzus persicae population per leaf at Sites A_1 and A_2, 1973

Week		Ny1 + Ny2	Ny3 + Ny4	Apterae	Ny4al	Alatae
(29.5.73)	1	0.05	0	0	0	0.02
	2	0.02	0.01	0.01	0	0.005
	3	0.69	0.09	0.04	0	0.11
	4	0.45	0.87	0.07	0	0.05
	5	2.12	0.60	0.30	0	0.05
	6	1.65	1.08	0.42	0.07	0.05
SITE	7	-	-	-	-	-
A_1	8	3.69	2.49	0.20	0.08	0.18
1973	9	2.26	1.28	0.33	0.10	0.09
	10	5.08	1.32	0.72	0.09	0.23
	11	2.89	0.90	0.40	0.12	0.02
	12	0.52	0.41	0.36	0.04	0.03
	13	0.07	0.07	0.06	0.01	0
	14	0.19	0.14	0.11	0	0.01
(4.9.73)	15	0.10	0.11	0.07	0	0
TOTAL		0.94	0.41	0.14	0.02	0.05
(29.5.73)	1	0.004	0	0	0	0
	2	0.005	0	0	0	0.002
	3	0.11	0	0.003	0	0.03
	4	1.73	0.38	0.32	0	0.03
	5	2.33	0.85	0.15	0	0.03
	6	2.72	2.15	0.33	0.18	0.02
SITE	7	-	-	-	-	-
A_2	8	7.90	3.34	0.40	0.31	0.08
1973	9	4.23	1.19	0.49	0.26	0.03
	10	3.56	0.97	0.29	0.17	0.07
	11	1.10	0.38	0.19	0.07	0.02
	12	1.06	0.53	0.29	0.01	0.02
	13	0.30	0.19	0.14	0.08	0
	14	0.13	0.12	0.07	0.08	0
(4.9.73)	15	0.08	0.04	0.04	0	0
TOTAL		1.10	0.43	0.12	0.05	0.02

APPENDIX 7: Age-specific analysis of the Myzus persicae population per leaf at Site B_1, 1973

Week		Ny1 + Ny2	Ny3 + Ny4	Apterae	Ny4al	Alatae
(29. 5.73)	1	NO PLANTS				
	2	NO PLANTS				
	3	NO PLANTS				
	4	NO PLANTS				
	5	0.10	0.20	0.07	0	0.03
	6	0.18	0.07	0.08	0	0
	7	-	-	-	-	-
	8	1.53	0.40	0.08	0	0.02
	9	1.42	1.40	0.28	0.05	0.02
	10	4.03	1.05	0.38	0.05	0.17
	11	0.90	0.25	0.12	0	0.05
	12	0.40	0.65	0.30	0.02	0
SITE B_1	13	0.13	0	0.05	0	0
	14	0.02	0.02	0.02	0.02	0
1973	15	0.07	0.03	0.05	0	0
	16	-	-	-	-	-
	17	-	-	-	-	-
	18	0.55	0.27	0.03	0.08	0
	19	-	-	-	-	-
	20	0.22	0.07	0.07	0.03	0
	21	-	-	-	-	-
	22	0.02	0.37	0.02	0.02	0
	23	1.15	0.60	0.33	0.33	0.02
	24	0.27	0.20	0.15	0.03	0
	25	-	-	-	-	-
	26	0.17	0.13	0.03	0.05	0.02
(28.11.73)	27	0.07	0.13	0	0.02	0
TOTAL		0.68	0.35	0.12	0.04	0.02

APPENDIX 8: Age-specific analysis of the Myzus persicae population per leaf at Sites A_3 and B_2, 1974

Week	SITE A_3 1974					SITE B_2 1974				
	Ny1 + Ny2	Ny3 + Ny4	Apterae	Ny4al	Alatae	Ny1 + Ny2	Ny3 + Ny4	Apterae	Ny4al	Alatae
1	0	0	0	0	0	NO PLANTS				
2	0.05	0.01	0	0	0.01	NO PLANTS				
3	0.06	0.03	0.01	0	0.03	NO PLANTS				
4	0.47	0.15	0.05	0	0.02	0.004	0.004	0.004	0	0.01
5	0.63	0.22	0.10	0	0	0.04	0.04	0.003	0	0.02
6	0.99	0.35	0.06	0.02	0.01	0.48	0.12	0.03	0	0.07
7	2.33	1.08	0.26	0.23	0.11	-	-	-	-	-
8	4.43	1.97	0.48	0.55	0.10	5.05	1.79	0.25	0.06	0.13
9	7.37	3.61	0.89	1.03	0.38	8.15	4.66	0.63	0.70	0.15
10	11.93	3.60	1.32	0.73	0.55	5.06	3.79	0.77	0.46	0.17
11	11.54	6.82	2.09	1.62	0.43	3.15	2.46	0.55	0.13	0.11
12	14.23	4.27	1.25	2.23	0.36	1.17	0.49	0.11	0.01	0.02
13	4.07	2.35	0.69	0.46	0.13	0.39	0.39	0.13	0.02	0.03
14	0.74	0.39	0.15	0.09	0	0.23	0.12	0.06	0	0
15	0.25	0.15	0.09	0.11	0.05	0.11	0.07	0.03	0.01	0
16	0.16	0.19	0.07	0.05	0.03	0.39	0.12	0.05	0.03	0.01
17	0.58	0.21	0.03	0.02	0.01	0.06	0.09	0.03	0.01	0
18	-	-	-	-	-	0.06	0.07	0	0	0
19	-	-	-	-	-	0.05	0.10	0.04	0.05	0
20	-	-	-	-	-	0.05	0.03	0.03	0.03	0
21	-	-	-	-	-	0.10	0.08	0.03	0.08	0
22	-	-	-	-	-	-	-	-	-	-
23	-	-	-	-	-	0	0.01	0.01	0.01	0
24	-	-	-	-	-	0.25	0.08	0	0.06	0
25	-	-	-	-	-	0	0	0	0	0
26	-	-	-	-	-	0	0	0	0	0
27	-	-	-	-	-	0	0	0	0	0
TOTAL	2.62	1.11	0.33	0.30	0.10	0.99	0.57	0.11	0.06	0.03

(4.6.74 ≡ Week 1)

(24.9.74 ≡ Week 27)

APPENDIX 9: Age-specific analysis of the Myzus persicae population per leaf at Site C in 1972 and 1973

Week		Ny1 + Ny2	Ny3 + Ny4	Apterae	Ny4al	Alatae
(16.10.72)	1	0.66	0.77	1.07	0	0.01
	2	1.49	1.21	0.47	0	0.05
	3	2.07	0.89	0.39	0	0.17
	4	1.95	1.16	0.21	0	0.19
SITE C 1972	5	1.54	0.62	0.24	0	0.21
	6	1.65	0.29	0.28	0	0.09
	7	0.49	0.41	0.05	0	0.01
	8	-	-	-	-	-
	9	0	0	0	0	0.01
(19.12.72)	10	0	0	0	0	0
TOTAL		1.09	0.59	0.30	0	0.08
(30.10.73)	1	0.92	0.74	0.13	0.09	0.01
	2	1.46	0.28	0.19	0.04	0
	3	-	-	-	-	-
	4	0.58	0.27	0.08	0.01	0
	5	0.23	0.20	0.04	0	0.01
SITE C 1973	6	-	-	-	-	-
	7	0.14	0.06	0.02	0	0
	8	0.19	0.02	0.05	0	0
	9	-	-	-	-	-
	10	-	-	-	-	-
	11	0.29	0.02	0	0	0
	12	0.01	0	0	0	0
	13	0	0	0	0	0
(29. 1.74)	14	0	0	0.01	0	0
TOTAL		0.38	0.16	0.05	0.01	0.002

APPENDIX 10: Details of the parasite species emerging from parasitised Myzus persicae during 1973

Species of Parasite \ Week of Sample	SITE A_1 1973														SITE A_2 1973											
	JUNE			JULY					AUGUST						JULY						AUGUST					
	3	4	5	6	7	8	9	10	11	12	13	14	15	Total	5	6	7	8	9	10	11	12	13	14	15	Total
Diaeretiella rapae	0	1	4	9	-	16	30	70	60	19	13	7	2	231	0	3	-	8	37	27	11	7	11	1	2	107
Praon volucre	0	0	3	0	-	0	0	3	10	1	0	1	2	20	0	0	-	0	0	1	2	3	2	2	1	11
Aphidius ervi	0	0	0	0	-	0	1	1	1	0	1	0	0	4	0	0	-	0	0	2	0	0	0	0	0	2
A. picipes group	0	0	0	0	-	2	0	1	1	0	1	0	0	5	0	0	-	3	1	0	0	2	1	1	0	8
A. rosae group	0	0	0	0	-	0	0	0	0	0	1	1	0	2	0	0	-	0	0	0	0	0	1	0	0	1
A. urticae group	0	0	0	0	-	0	0	1	2	1	0	0	0	4	0	0	-	1	0	3	0	1	3	0	0	8
Total Primary Parasites	0	1	7	9	-	18	31	76	74	21	16	9	4	266	0	3	-	12	38	33	13	13	18	4	3	137
Asaphes vulgaris ex Praon	0	0	0	0	-	0	0	0	0	1	0	1	0	2	0	0	-	0	0	0	0	0	0	0	1	1
Asaphes vulgaris ex Diaretus	0	0	0	1	-	0	1	2	0	0	8	2	1	15	0	0	-	0	0	6	2	0	0	3	3	14
Coruna clavata ex Praon	0	0	0	0	-	0	0	0	0	0	0	1	0	1	0	0	-	0	0	0	0	0	1	0	0	1
Coruna clavata ex Diaretus	0	0	0	0	-	0	0	0	0	0	0	1	0	1	0	0	-	0	0	0	0	1	0	0	0	1
Phaenoglyphis ? spp. ex Diaretus	0	0	0	0	-	1	1	3	2	2	1	1	1	12	0	0	-	1	1	4	0	0	0	0	0	6
Alloxysta ? ancylocera ex Diaretus	0	0	0	0	-	2	1	2	6	5	4	1	1	22	0	1	-	0	3	0	2	1	4	0	0	11
Dendrocerus bicolor ex Diaretus	0	0	0	0	-	0	0	0	0	2	1	0	0	3	0	0	-	0	0	0	0	0	0	0	0	0
Total Hyperparasites	0	0	0	1	-	3	3	7	8	10	14	7	3	56	0	1	-	1	4	10	4	2	5	3	4	34
Total Parasites	0	1	7	10	-	21	34	83	82	31	30	16	7	322	0	4	-	13	42	43	17	15	23	7	7	171
Total Parasitised Aphids	3	3	22	11	-	27	38	106	97	60	42	29	12	450	0	6	-	20	55	54	25	26	27	19	17	249
% emergence	0	33	32	91	-	78	89	78	85	52	71	55	58	72	0	67	-	65	76	80	68	58	85	37	41	69

APPENDIX 10: (cont.)

Species of Parasite \ Week of Sample	SITE B_1 1973																					SITE C 1973/1974																
	JULY					AUGUST				SEPTEMBER				OCTOBER					Total		NOVEMBER					DECEMBER				JANUARY				Total
	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23		23	24	25	26	27	28	29	30	31	32	33	34	
Diaeretiella rapae	4	-	3	31	31	5	15	1	3	0	-	-	0	-	0	-	3	2	98	3	2	-	0	0	-	0	0	-	-	0	0	5
Praon volucre	0	-	0	1	0	0	4	0	2	0	-	-	1	-	0	-	0	0	8	2	1	-	0	1	-	0	0	-	-	0	0	4
Aphidius ervi	0	-	0	1	4	0	1	0	0	0	-	-	0	-	0	-	0	0	6	0	0	-	0	0	-	0	0	-	-	0	0	0
A. picipes group	0	-	0	0	1	2	2	0	0	0	-	-	0	-	0	-	0	0	5	0	0	-	0	0	-	0	0	-	-	0	0	0
A. rosae group	0	-	0	0	1	0	0	0	0	0	-	-	0	-	0	-	0	0	1	0	0	-	0	0	-	0	0	-	-	0	0	0
A. urticae group	0	-	0	0	1	0	0	0	0	0	-	-	0	-	0	-	0	0	1	0	0	-	0	0	-	0	0	-	-	0	0	0
Total Primary Parasites	4	-	3	33	38	7	22	1	5	0	-	-	1	-	0	-	3	2	119	5	3	-	0	1	-	0	0	-	-	0	0	9
Asaphes vulgaris ex Praon	0	-	0	0	0	0	0	0	0	0	-	-	0	-	0	-	0	0	0	0	3	-	0	0	-	0	0	-	-	0	0	3
Asaphes vulgaris ex Diaretus	0	-	0	2	0	0	6	1	1	1	-	-	0	-	0	-	0	0	11	1	1	-	0	0	-	0	0	-	-	0	0	2
Coruna clavata ex Praon	0	-	0	0	0	0	0	0	0	0	-	-	0	-	0	-	0	0	0	0	0	-	0	0	-	0	0	-	-	0	0	0
Coruna clavata ex Diaretus	0	-	0	0	0	0	0	0	0	0	-	-	0	-	0	-	0	0	0	0	0	-	0	0	-	0	0	-	-	0	0	0
Phaenoglyphis ? spp. ex Diaretus	0	-	0	0	0	0	0	1	1	3	-	-	0	-	0	-	0	0	5	0	0	-	0	0	-	0	0	-	-	0	0	0
Alloxysta ? ancylocera ex Diaretus	0	-	1	2	1	0	3	1	1	0	-	-	1	-	0	-	0	0	10	6	0	-	0	0	-	0	0	-	-	0	0	6
Dendrocerus bicolor ex Diaretus	0	-	0	0	0	0	0	0	0	0	-	-	0	-	0	-	0	0	0	0	0	-	0	0	-	0	0	-	-	0	0	0
Total Hyperparasites	0	-	1	4	1	0	9	3	3	4	-	-	1	-	0	-	0	0	26	7	4	-	0	0	-	0	0	-	-	0	0	11
Total Parasites	4	-	4	37	39	7	31	4	8	4	-	-	2	-	0	-	3	2	145	12	7	-	0	1	-	0	0	-	-	0	0	20
Total Parasitised Aphids	4	-	6	47	49	12	39	7	10	10	-	-	3	-	3	-	5	7	202	17	9	-	2	1	-	0	0	-	-	0	1	30
% emergence	100	-	67	79	80	58	79	57	80	40	-	-	67	-	0	-	60	29	72	71	78	-	0	100	-	0	0	-	-	0	0	67

APPENDIX 11: Details of the parasite species emerging from parasitised

	SITE A_3 1974														
	JULY						AUGUST				SEPTEMBER				
	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
Diaeretiella rapae	2	1	1	5	26	22	21	44	39	30	16	10	11	12	240
Praon volucre	0	0	0	1	0	2	27	29	35	22	11	16	4	7	154
Praon myzophagum	0	0	0	0	0	0	4	2	6	4	0	0	0	0	16
Aphidius avenae	1	0	0	0	1	4	8	23	19	6	2	1	2	0	67
A. ervi	0	0	0	0	0	2	25	10	7	3	1	0	0	0	48
A. picipes group	0	0	0	0	2	8	14	14	9	6	3	1	1	0	58
A. rosae group	0	0	0	0	0	1	6	10	8	1	0	1	0	0	27
A. urticae group	0	0	0	3	0	34	48	51	29	5	5	2	0	0	177
Total Primary Parasites	3	1	1	9	29	73	153	183	152	77	38	31	18	19	787
Asaphes vulgaris															
ex *Praon*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ex *Diaretus*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Phaenoglyphis ? spp.															
ex *Praon*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
ex *Diaretus*	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4
Alloxysta ? *ancylocera*															
ex *Diaretus*	0	0	0	0	1	5	7	3	3	4	3	3	1	0	30
Total Hyperparasites	0	0	0	0	1	5	7	4	4	4	3	3	1	4	36
Total Parasites	3	1	1	9	30	78	160	187	156	81	41	34	19	23	823
Total Parasitised Aphids	3	1	1	12	34	89	183	254	254	129	65	46	29	26	1126
% Emergence	100	100	100	75	88	88	87	74	61	63	63	74	66	88	73

Myzus persicae during 1974

SITE B_2 1974																							
		AUGUST				SEPTEMBER				OCTOBER					NOVEMBER								
8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	Total
9	8	14	18	10	16	4	4	1	4	3	6	5	3	-	1	2	0	1	0	109
0	2	5	20	5	4	2	0	5	4	3	2	4	1	-	0	2	0	0	0	59
0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
0	2	5	10	5	2	3	1	0	0	0	1	0	0	-	0	0	0	0	0	29
0	2	10	6	1	2	1	0	0	0	0	0	0	0	-	0	0	0	0	0	22
1	14	5	13	4	7	7	0	0	0	0	0	1	0	-	0	0	0	0	0	52
0	0	6	5	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	12
5	27	48	15	6	0	1	0	0	0	0	0	0	1	-	0	0	0	0	0	103
15	55	93	87	32	31	18	5	6	8	6	9	10	5	-	1	4	0	1	0	386
0	0	0	0	0	0	0	0	1	1	1	3	0	0	-	0	0	0	0	0	6
0	0	0	0	0	0	0	0	2	1	0	0	0	0	-	0	0	0	1	0	4
0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0
0	0	0	0	0	0	0	1	1	0	0	1	1	0	-	0	0	0	0	0	4
0	2	1	2	0	1	1	0	1	1	0	0	0	1	-	0	0	0	0	0	10
0	2	1	2	0	1	1	1	5	3	1	4	1	1	-	0	0	0	1	0	24
15	57	94	89	32	32	19	6	11	11	7	13	11	6	-	1	4	0	2	0	410
15	60	109	119	46	42	28	8	13	13	9	17	12	8	-	3	4	0	2	0	508
100	95	86	75	70	76	68	75	85	85	78	76	92	75	-	33	100	0	100	0	81

APPENDIX 12: Fortnightly totals of primary parasites and secondary parasites that were trapped in the vicinity of the specified sites during 1973 and 1974

Species of Parasite \ Fortnightly Totals	SITE A_1 1973											SITE A_2 1973										
	May/June		June/July			August		September		Sept/Oct	Total	May/June		June/July			August		September		Sept/Oct	Total
	2	4	6	8	10	12	14	16	18	20		2	4	6	8	10	12	14	16	18	20	
Diaeretiella rapae	24	-	-	0	0	5	6	0	0	0	35	0	0	0	0	1	1	5	0	0	0	7
Praon volucre	0	-	-	0	1	3	3	0	0	0	7	0	0	0	0	0	3	0	0	0	0	3
Aphidius avenae	1	-	-	0	0	3	0	0	0	0	4	0	0	0	0	0	3	2	0	0	0	5
A. ervi	0	-	-	0	2	11	5	0	0	0	18	0	0	0	0	0	5	2	0	0	0	7
A. picipes group	0	-	-	1	1	22	3	0	1	0	28	0	0	0	0	0	4	2	0	0	0	6
A. rosae group	0	-	-	0	0	7	0	0	0	0	7	0	0	0	0	0	0	7	0	0	0	7
A. urticae group	1	-	-	0	4	11	4	0	0	1	21	0	2	0	0	2	2	2	0	0	0	8
Total Primary Parasites	26	-	-	1	8	62	21	0	1	1	120	0	2	0	0	3	18	20	0	0	0	43
Asaphes vulgaris	0	-	-	0	1	0	1	10	14	2	28	0	0	0	0	0	0	1	1	1	0	3
Phaenoglyphis ? spp.	0	-	-	0	0	0	0	0	2	0	2	0	0	0	0	0	0	1	0	0	0	1
Alloxysta ? *ancylocera*	0	-	-	0	0	2	5	8	0	1	16	0	0	0	0	0	0	9	1	0	0	10
Total Hyperparasites	0	-	-	0	1	2	6	18	16	3	46	0	0	0	0	0	0	11	2	1	0	14
Total Parasites	26	-	-	1	9	64	27	18	17	4	166	0	2	0	0	3	18	31	2	1	0	57

APPENDIX 12: (cont.)

Species of Parasite / Fortnightly Totals	SITE A_3 1974													SITE B_2 1974								
	June		July		July/Aug		Aug/Sept		Sept/Oct				November		June		July		July/Aug		Aug/Sept		Sept/Oct	
	2	4	6	8	10	12	14	16	18	20	22	24	Total	2	4	6	8	10	12	14	16	18	Total
Diaeretiella rapae	0	0	0	0	0	0	26	20	3	2	0	1	52	0	0	0	0	0	13	5	7	1	26
Praon volucre	0	0	0	0	0	0	3	1	0	0	0	0	4	0	0	0	0	1	12	0	2	0	15
Aphidius avenae	0	0	0	0	5	2	12	3	0	0	0	0	22	0	0	0	0	3	0	39	1	0	43
A. ervi	0	0	0	0	1	0	8	0	0	0	0	0	9	0	0	0	1	2	13	9	1	0	26
A. picipes group	0	0	0	0	0	0	18	0	0	0	0	0	18	0	0	0	0	1	14	2	0	0	17
A. rosae group	0	0	0	0	4	14	0	1	0	0	0	0	19	0	0	0	1	2	6	7	9	0	25
A. urticae group	0	0	0	1	19	82	112	11	0	0	0	0	225	0	0	0	7	24	162	74	9	1	277
Total Primary Parasites	0	0	0	1	29	98	179	36	3	2	0	1	349	0	0	0	9	33	220	136	29	2	429
Asaphes vulgaris	0	0	0	0	0	1	1	0	4	0	0	0	6	0	0	0	0	0	3	3	1	11	18
Phaenoglyphis ? spp.	0	0	0	0	0	0	0	4	2	3	1	0	10	0	0	0	0	0	1	0	4	12	17
Alloxysta ? ancylocera	0	0	0	0	0	1	3	6	1	2	2	0	15	0	0	0	0	0	1	3	7	1	12
Total Hyperparasites	0	0	0	0	0	2	4	10	7	5	3	0	31	0	0	0	0	0	5	6	12	24	47
Total Parasites	0	0	0	1	29	100	183	46	10	7	3	1	380	0	0	0	9	33	225	145	41	26	476

APPENDIX 13: Duration in days of the developmental stages of *Myzus persicae* at specified constant temperatures, high relative humidity and 12 hour photoperiod

Temp °C	NYMPH 1				NYMPH 2			
	No. Aphids	Total days	Range	Mean ±s.e.	No. Aphids	Total days	Range	Mean ±s.e.
5	25	169	2-11	6.76 ± 0.49	21	128	2-10	6.10 ± 0.51
5*	4	25	3- 8	6.25	4	34	5-11	8.50
10	20	45	1- 4	2.25 ± 0.23	18	56	2- 6	3.11 ± 0.33
10*	3	7	1- 4	2.33	3	10	2- 5	3.33
15	39	83	1- 5	2.13 ± 0.18	35	124	1- 7	3.54 ± 0.22
15*	2	6	2- 4	3.00	2	6	2- 4	3.00
20	32	42	1- 3	1.31 ± 0.10	28	79	1- 7	2.82 ± 0.26
	NYMPH 3				NYMPH 4			
5	18	147	3-13	8.17 ± 0.69	15	206	6-24	13.73 ± 1.25
5*	4	44	7-16	11.00	3	53	13-26	17.67
10	16	59	2- 7	3.69 ± 0.27	14	66	2- 9	4.71 ± 0.57
10*	3	8	2- 3	2.67	1	15	15	15.00
15	31	102	1- 6	3.29 ± 0.22	28	86	1- 6	3.07 ± 0.28
15*	2	8	2- 6	4.00	2	10	5- 5	5.00
20	21	55	1- 6	2.62 ± 0.29	19	46	1- 4	2.42 ± 0.22
	ADULT				NYMPHAL PERIOD			
5	15	388	5-42	25.87 ± 2.50	15	521	21-43	34.73 ± 1.65
5*	3	26	1-22	8.67	3	127	37-49	42.33
10	14	130	0-28	9.29 ± 2.18	14	189	10-17	13.50 ± 0.49
10*	1	7	7	7.00	1	25	25	25.00
15	28	463	1-49	16.54 ± 2.77	28	340	10-16	12.14 ± 0.31
15*	2	25	3-22	12.50	2	30	15-15	15.00
20	19	169	2-20	8.90 ± 1.32	19	155	5-11	8.16 ± 0.49
	TOTAL LONGEVITY							
5	15	909	43-75	60.60 ± 2.33				
5*	3	153	38-63	51.00				
10	14	319	13-41	22.79 ± 2.16				
10*	1	25	25	25.00				
15	28	803	14-60	28.68 ± 2.69				
15*	2	55	18-37	27.50				
20	19	324	8-31	17.05 ± 1.54				

* Alate development

No alates developed at 20°C

APPENDIX 14: Climatic record from June 1973 to May 1975

Week Ending	Mean Temperature °C Max	Min	Total Rainfall (mm)	Total Sunshine (hrs)
5. 6.73	16.2	5.8	25.9	50.5
12. 6.73	21.2	9.3	0.1	39.7
19. 6.73	20.4	8.3	10.4	44.0
26. 6.73	19.2	9.0	9.6	27.6
3. 7.73	20.4	9.5	1.8	40.7
10. 7.73	21.6	8.1	25.3	40.3
17. 7.73	18.3	11.4	18.7	4.6
24. 7.73	16.5	9.7	24.5	16.8
31. 7.73	22.6	13.0	0.4	63.4
7. 8.73	19.1	10.8	20.9	35.3
14. 8.73	20.2	7.4	4.1	63.5
21. 8.73	19.7	8.5	5.5	43.0
28. 8.73	18.1	7.1	11.8	23.2
4. 9.73	16.8	8.4	7.9	30.8
11. 9.73	18.6	10.0	1.0	24.2
18. 9.73	16.8	6.7	0.9	22.6
25. 9.73	15.3	4.0	3.9	18.1
2.10.73	12.4	5.1	7.7	20.1
9.10.73	15.0	7.3	3.0	18.3
16.10.73	9.9	3.0	21.0	23.3
23.10.73	9.0	1.8	24.4	15.3
30.10.73	12.9	6.2	3.2	4.0
6.11.73	11.3	3.5	8.7	8.5
13.11.73	11.3	2.5	0.7	14.0
20.11.73	7.9	1.0	0	27.1
27.11.73	8.1	2.1	0.2	15.0
4.12.73	3.4	-6.7	3.3	9.3
11.12.73	5.3	2.4	14.2	13.3
18.12.73	5.6	0.8	2.3	19.3
25.12.73	4.3	0.4	16.8	0.4
1. 1.74	8.4	3.1	1.9	11.7
8. 1.74	8.0	0.5	6.3	12.0
15. 1.74	7.5	1.2	15.7	6.0
22. 1.74	9.0	4.0	6.8	8.9

(cont.)

APPENDIX 14: Climatic record from June 1973 to May 1975 (cont.)

Week Ending	Mean Temperature °C Max	Min	Total Rainfall (mm)	Total Sunshine (hrs)
29. 1.74	7.9	4.0	7.4	15.7
5. 2.74	7.1	1.9	6.5	19.1
12. 2.74	7.0	1.3	13.5	16.2
19. 2.74	8.0	2.1	9.7	17.3
26. 2.74	9.3	3.4	8.3	23.9
5. 3.74	6.7	0.4	17.6	19.8
12. 3.74	7.1	1.4	4.4	9.6
19. 3.74	7.4	1.4	24.5	11.4
26. 3.74	8.4	1.3	4.0	13.4
2. 4.74	9.8	2.0	0.1	41.3
9. 4.74	9.1	1.3	0.1	27.7
16. 4.74	14.6	4.8	0.6	50.3
23. 4.74	14.4	4.1	0	46.6
30. 4.74	14.3	5.1	23.5	27.5
7. 5.74	13.1	5.1	14.0	20.0
14. 5.74	18.4	6.1	12.2	32.0
21. 5.74	19.8	7.5	9.9	51.6
28. 5.74	19.3	8.2	0.6	39.4
4. 6.74	19.5	6.5	2.4	46.0
11. 6.74	18.7	6.7	6.0	36.4
18. 6.74	22.2	8.9	17.4	60.7
25. 6.74	21.7	10.4	0	47.8
2. 7.74	20.4	8.6	6.0	36.9
9. 7.74	20.0	9.5	19.3	29.0
16. 7.74	20.4	9.8	23.7	31.0
23. 7.74	19.6	10.7	8.8	34.8
30. 7.74	21.4	9.2	5.2	50.2
6. 8.74	22.8	6.8	1.0	53.5
13. 8.74	21.1	9.5	25.7	22.6
20. 8.74	21.4	8.4	8.7	52.8
27. 8.74	20.8	10.7	3.5	20.0
3. 9.74	19.6	8.1	17.0	23.1
10. 9.74	16.3	7.9	20.4	25.2
17. 9.74	17.5	10.0	9.7	10.9

(cont.)

APPENDIX 14: Climatic record from June 1973 to May 1975 (cont.)

Week Ending	Mean Temperature °C Max	Min	Total Rainfall (mm)	Total Sunshine (hrs)
24. 9.74	15.8	7.4	11.7	36.7
1.10.74	15.8	3.0	6.5	31.8
8.10.74	12.1	5.6	51.6	6.0
15.10.74	12.7	4.1	2.4	9.6
22.10.74	12.5	6.0	12.1	10.1
29.10.74	13.0	5.4	0	15.0
5.11.74	7.8	2.5	9.5	3.4
12.11.74	12.5	4.9	12.3	18.2
19.11.74	8.4	2.8	3.4	24.7
26.11.74	6.8	2.1	33.5	9.6
3.12.74	9.5	2.8	5.9	18.1
10.12.74	10.4	5.9	9.7	6.3
17.12.74	6.7	1.7	21.2	14.3
24.12.74	10.4	5.9	5.1	7.2
31.12.74	9.5	4.1	25.0	8.4
7. 1.75	9.8	6.4	0.1	6.6
14. 1.75	9.0	3.6	7.4	1.3
21. 1.75	7.4	1.6	10.8	12.0
28. 1.75	9.5	4.1	41.8	16.4
4. 2.75	11.7	4.4	19.7	22.4
11. 2.75	3.9	-1.1	1.6	11.5
18. 2.75	6.8	1.8	11.1	5.3
25. 2.75	13.2	3.7	2.4	27.1
4. 3.75	11.9	2.6	3.0	18.2
11. 3.75	13.2	2.4	5.1	31.6
18. 3.75	8.1	3.1	3.7	12.3
25. 3.75	11.1	2.9	7.8	28.1
1. 4.75	11.1	1.6	3.1	22.3
8. 4.75	10.9	2.4	9.4	31.7
15. 4.75	11.1	3.2	13.0	10.4
22. 4.75	14.6	7.7	18.0	14.6
29. 4.75	19.6	9.4	0.7	34.6
6. 5.75	12.7	3.3	5.6	62.8
13. 5.75	10.3	5.0	66.9	25.9
20. 5.75	14.9	2.7	3.6	65.7
27. 5.75	17.6	3.0	0.1	66.6

Monthly record prior to June 1973:

	Mean Temperature °C Max	Min	Total Rainfall (mm)	Total Sunshine (hrs)
March	10.80	1.7	9.4	134.2
April	10.25	2.9	34.0	125.7
May	13.60	6.2	79.0	132.1

APPENDIX 15: Details of the predators sampled during 1973 and 1974

Sampling Period		SITE A_1 1973				SITE A_2 1973				SITE B_1 1973			
		L	E	P	Total	L	E	P	Total	L	E	P	Total
(29.5.73)	1	0	0	0	0	0	0	0	0	———			
	2	0	0	0	0	0	0	0	0	———			
	3	0	0	0	0	0	0	0	0	———			
	4	0	0	0	0	0	5	0	5	———			
	5	1	0	0	1	0	1	0	1	1	0	0	1
	6	0	0	0	0	1	7	0	8	0	0	0	0
	7	———				———				———			
	8	1	0	0	1	4	0	0	4	0	0	0	0
	9	2	6	1	9	3	9	0	12	1	0	0	1
	10	9	9	0	18	5	8	0	13	0	0	0	0
	11	7	0	0	7	9	0	0	9	0	0	0	0
	12	1	4	1	6	3	4	0	7	0	0	0	0
	13	0	2	0	2	1	8	2	11	2 lacewing eggs			
	14	1	2	1	4	1	6	0	7	1	0	0	0
(4.9.73)	15	0	0	0	0	0	2	0	2	0	0	0	0
TOTAL		22	23	3	48	27	50	2	79	3	0	0	3
										+2 lacewing eggs			

Sampling Period		SITE A_3 1974				SITE B_2 1974			
		L	E	P	Total	L	E	P	Total
4.6.74	1	0	0	0	0	———			
	2	0	0	0	0	———			
	3	0	0	0	0	———			
	4	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0
	7	0	0	0	0	———			
	8	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0
	11	3	0	0	3	0	0	0	0
	12	8	6	0	14	0	1	0	1
	13	25	7	0	32	0	0	0	0
	14	3	1	1	5	0	8	0	8
	15	2	2	0	4	0	0	0	0
	16	0	0	1	1	0	0	0	0
	17	0	5	1	6	1	0	0	1
	18	———				0	8	0	8
	19	———				0	0	0	0
	20	———				0	0	0	0
22.10.74	21	———				1	1	0	2
TOTAL		41	21	3	65	2	18	0	20

Key: L = Syrphid larvae
E = Syrphid eggs
P = Syrphid pupae
——— = No sample

APPENDIX 16: Details of the Syrphidae genera trapped during 1973 and 1974

GENERA	SITE A_1 1973											SITE A_3 1974											
	2	4	6	8	10	12	14	16	18	20	Total	2	4	6	8	10	12	14	16	18	20	22	Total
Syrphus Fabricus	0	-	-	11	47	74	704	358	31	3	1,228	10	12	0	1	0	13	18	169	82	79	34	418
Platychirus St. Fargeau & Serville	2	-	-	0	0	4	12	13	9	2	42	5	3	0	0	0	1	0	5	1	4	1	20
Melanostoma Schiner	0	-	-	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Sphaerophora St. Fargeau & Serville	0	-	-	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Non-Aphidophagous Genera	0	-	-	0	1	2	10	6	14	5	38	0	2	0	0	0	5	8	30	23	18	6	92
TOTAL	2	-	-	11	48	80	726	378	55	10	1,310	15	17	0	1	0	19	26	204	106	101	41	530
	SITE A_2 1973											SITE B_2 1974											
Syrphus Fabricus	9	1	6	16	29	39	383	240	9	0	732	-	-	0	0	0	22	15	151	114	71	55	428
Platychirus St. Fargeau & Serville	0	0	0	0	0	2	12	43	4	0	61	-	-	0	0	1	0	2	5	1	5	4	18
Non-Aphidophagous Genera	1	0	0	0	0	0	10	5	6	0	22	-	-	1	0	3	18	19	68	29	15	20	173
TOTAL	10	1	6	16	29	41	405	288	19	0	815	-	-	1	0	4	40	36	224	144	91	79	619
FORTNIGHTLY TOTALS →	M/J		J/J			AUG			SEPT		S/O		JUNE		JULY		J/A		A/S		S/O		OCT	