ASPECTS OF THE BIOLOGY AND ECOLOGY

OF <u>ACYRTHOSIPHON</u> <u>KONDOI</u> SHINJI

(HOMOPTERA: APHIDIDAE)

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Nabis maoricus feeding on Acyrthosiphon kondoi.

ABSTRACT

The biology and ecology of the blue-green lucerne aphid, Acyrthosiphon kondoi Shinji, was studied in the Palmerston North area for one year.

Observations on the morphology of the developmental stages and morphs of A. kondoi are presented. Winter and spring peaks in the A. kondoi numbers occurred and the aphid can survive on lucerne all year round. The aphid colonies undergo a population cycle involving a population build up, high numbers, a decline in numbers, and a period of low numbers which persists until the next population build up. The stage of the cycle is apparent from the pattern of dispersion of the aphids on the plant and the number of alates present. A. kondoi appears to be continuously viviparous and parthenogenetic throughout the year, as no sexual forms were found.

High numbers of A. kondoi migrate by flying. A distinct spring peak in flight was observed with periods of lesser flight at other times. Some synchrony between the periods of flight and the number of aphids and alates on the plants was observed.

Factors controlling the A. kondoi population were studied. The predators, and an entomophthorous fungi which attacked A. kondoi were identified, but no evidence of parasitism of A. kondoi in the field was observed. The predators did not prevent the spring population peak of A. kondoi, because of the low predator numbers and their poor synchronisation with the aphid population. Predator exclusion cage studies indicated that predators, especially Nabis maoricus, prevented a summer-autumn A. kondoi population peak. N. maoricus consumed on average 11.25 A. kondoi per day in the laboratory.

The state of host plant growth is important in the occurrence of population cycles, and lucerne management practices can affect this considerably. Growing lucerne appears most suitable. Flowering of lucerne is not unfavourable to A. kondoi. A decline in the plant condition is partially involved in the population decline.

Cycles of the <u>A</u>. <u>kondoi</u> population occur independently of climate, though the maximum number of aphids reached in each cycle is probably dependent on climatic factors. Local, extreme weather conditions may temporarily affect <u>A</u>. <u>kondoi</u> numbers.

The population cycle involves self-regulation and can probably occur independently of extrinsic factors. It involves a rise and fall in the fecundity and reproductive rate, and the production of increasing numbers of alates as the cycle progresses. These changes could account for a considerable part of the population decline observed in a population cycle.

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CHAPTER ONE

INTRODUCTION

1.1. Background

The aphid <u>Acyrthosiphon kondoi</u> Shinji has recently become
a major pest on lucerne, (<u>Medicago sativa</u> L.), in New Zealand. It has
spread rapidly since it was first reported here in 1975, and was present
in all the major lucerne growing areas of the country by winter 1976. The
aphid reached epidemic proportions in February 1976 in the Manawatu
causing heavy losses of lucerne production. The present study was designed
to gain a preliminary understanding of the biology of the species.

1.2 The Identification of A. kondoi

<u>A</u>. <u>kondoi</u> was first described in 1938, but the original specimens
were subsequently destroyed by bombing during World War II (Dickson, 1975).
It was described by Takahashi (1965), a recognised authority on Japanese
aphids who was probably familiar with the specimens which Shinji used
(Dickson, 1975). A further description of <u>A</u>. <u>kondoi</u> is provided by Eastop
(1971) who also identified it as the aphid species recently discovered on
lucerne in areas of the USA (Nielson and Kodet, 1975). Unfortunately the
early descriptions were made from only a few specimens (e.g. one - Eastop,
1971; six - Takahashi, 1965; and apterous specimens only - Shinji, 1938),
hence the variability within the species was not described.

<u>A</u>. <u>kondoi</u> is also known by various common names including
'Blue alfalfa aphid, the 'Blue-green lucerne aphid' and the 'lucerne aphid'.
At the 1977 New Zealand Weed and Pest Control Conference, the name 'Blue
lucerne aphid' was suggested as the best term to distinguish <u>A. kondoi</u>
from other species which also infect lucerne.

1.3 The Host Plants of A. Kondoi

The major host plant of <u>A</u>. <u>kondoi</u> is <u>M</u>. <u>sativa</u>, 'alfalfa' or
'lucerne' (Shinji, 1938; Takahashi, 1965; Higushi and Miyazaki, 1971;
Eastop, 1971; Dickson, 1975). <u>M</u>. <u>sativa</u> is a crop of considerable
importance and potential in New Zealand (MacFarlane, 1970) and it is
recognised as one of the worlds most important forage crops because it

fixes nitrogen, improves soil structure, is higher in food value than all other commonly cultivated hay crops and it grows in extremely dry conditions.

All other known host plants of A. kondoi are also legumes. They include various Trifolium species (Takahashi, 1965; Miyazaki, 1971; Eastop, 1971; Cox and Dale, 1977) especially white clover (Trifolium repens L.) which may at times be an important secondary host in New Zealand (Trought, 1977). Dixon (1975) found six other legume host species while M.J. Esson (pers. comm.) has successfully bred A. kondoi on a variety of small seeded legumes. It has also been found on lupins (Burnett, 1977) and on sainfoin (Onobrychis vicifolia Scop.) which is a legume species of economic potential (P. Sheely pers. comm.).

It is not known why M. sativa is the preferred host of A. kondoi. Very high numbers of this aphid were found on T. repens in a glasshouse during the present study and there seems to be no nutritional reason why it does not always colonise this species. Possibly the preference for lucerne depends on an attractant which is unrelated to the nutritional value of the plant (Kennedy, 1958).

1.4 Occurrence of A. kondoi

Although A. kondoi is the most common aphid on lucerne in Japan in spring (Dickson, 1975) little was known about the species until it was discovered extensively damaging lucerne in Arizona in February, 1975. In October of the same year it was identified for the first time in New Zealand by Jennifer Cox (Cox and Dale, 1977). Its known distribution prior to these discoveries was Japan, Korea and Manchuria (Shinji, 1938; Takahashi, 1965; Miyazaki, 1971; Eastop, 1971), although Paik (1965) did not include it in his list of Korean aphids so it is presumably not common there. It is known to have been present in California in 1974 (Sharma et. al., 1975) and it is now also found in Arizona, Utah and Nevada (Nielson and Kodet, 1975; Nielson et al., 1976).

The widespread occurrence of A. kondoi in New Zealand when it was discovered indicates either multiple introduction (probably by wind), and/or that the aphid had been present and dispersing within New Zealand

for some time without being detected. High altitude dispersal of aphids does occur though the effective distance which can be covered by this means is not known (Johnson, 1967, 1969). Australia would appear to be be most likely source of flying aphids if wind was the means of introduction into New Zealand, but A. kondoi was not known to occur in Australia at the time of its discovery in New Zealand. Atmospheric global dispersal of aphids has been suggested by Johnson (1967) and Wolfenbarger (1975). The aphid may also have arrived by plane or have floated ashore on plant material dumped from a ship. It is unlikely though, that it can survive without food for longer than four days, and no eggs or other resting stages have been found.

1.5 The Economic Importance of A. kondoi

The damage caused by A. kondoi can be severe and result in high losses of production (Kain et al., 1976; Ford, 1976a; Kain et al.,1977; Wynn-Williams and Burnett, 1977). Although the economic threshold level is unknown it is undoubtedly low possibly because A. kondoi may inject a toxin into its host plant (Summers, 1975; Dunbier et al., 1977; Wynn-Williams and Burnett, 1977).

Following the discovery of A. kondoi in New Zealand, studies on the economic aspects of the species were quickly initiated. These largely involved insecticide trials which showed that most current aphicides were effective, though the recovery of A. kondoi population could be rapid (Kain et al., 1976; Sharpe and McDiarmid, 1976). The rapid reinfestation rates and the low numbers of aphids which can cause damage (Wynn-Williams and Burnett, 1977) means that chemical control can be expensive and the development of an integrated control approach therefore seems desirable from both an economic and ecological viewpoint. The use of resistant varieties of lucerne seems to provide some control potential (Lehman et al., 1975; Dunbier et al., 1977).

A.kondoi is one of a number of recent problems lucerne growers in New Zealand have been forced to combat including fungal and viral infections, various weevils, a spittle bug (MacFarlane and Pottinger, 1976) and recently the pea aphid, Acyrthosiphon pisum (Harris). The spotted alfalfa aphid, Therioaphis maculata (Buck), has been discovered in Australia (O'Loughlin and Berg, 1977) and it is therefore possible it will soon enter New Zealand.

1.6 The Present Study

A. kondoi seems to cause little economic damage in its regions of origin and therefore little was published concerning its biology. Immediately after its discovery in California, however, research on its biological and economic aspects was begun. This work was summarised in the Proceedings of the Fifth California Alfalfa Symposium but at the time of this symposium only six months had passed since the discovery of A. kondoi in the USA and therefore little information, especially quantitative data, was available.

The present study was started to find the aphid population pattern which emerged under New Zealand conditions (Chapters Three to Five) and to consider the factors affecting this pattern (Chapters Six to Ten). Even though somewhat similar work was begun in the USA it is useful to repeat such work since it is well known that the responses of one aphid species may vary from country to country. Biotypes, races and strains within one species have been described for many aphids (Eastop, 1973) and important aspects of the biology may vary between the different forms. Many biotypes have been described in A. pisum, a member of the same genus as A. kondoi.

Aphids are popular subjects for studies in population dynamics but they present many problems because of their high reproductive rate and overlapping generations (e.g. Hughes, 1962, 1963). Despite the enormous amount of information which has been collected on aphids as evidenced by the bibliographies of Sharma (1969, 1971 and 1972), no aphid species is completely understood and many generalisations concerning aphids have arisen from a few studied cases.

CHAPTER TWO

GENERAL METHODS AND STUDY AREA

2.1 Methods for Culturing Lucerne

The "Wairau" variety of M. sativa, a variety of lucerne
commonly grown in New Zealand, was used throughout this study. A
free draining potting mix of equal parts peat, perlite and pumice was
used together with the nutrient mixture described in Appendix One.
The plants were kept well watered.

Initially, established lucerne plants from the DSIR study plot
described in Section 2.3 were transplanted into pots 16-25 cm square
by 18.8 cm deep so that the first aphid culture could be started as soon
as possible. Subsequently, plants were grown from seed in seedling
trays and transplanted when about three cm high into "Five inch
Plastimatic"pots.

In the present investigation importance was attached to growing
lucerneplants which were as healthy as possible to ensure that the aphids
were in good physiological condition. Plants were grown in the Botany/
Zoology glasshouse at Massey until they were used for the aphid cultures.
Pritchett and Nelson (1961), Gist and Mott (1957) and Bula (1959) all
indicated that growth of lucerne was proportioned to light intensity,
with consequent high lucerne production in a glasshouse.

Once the plants had been used for aphid cultures, any remaining
aphids were removed by washing them off in water or fumigating them with
CO_2 or Shell Vapona Concentrate (1080 g/L dichlorvos). They were then
trimmed closely and allowed to recommence growth so that they could be
used again.

One lucerneplant was also cloned by floating cuttings of either
trifoliate leaves together with some of their stem or approximately four
cm sections of the growing tips of stems in a large plastic bowl of water.
They were then either illuminated with the Phillips Growth Lamp described
in Section 2.2 or placed in a glasshouse, but the success rate was not as
high in the latter situation. Once roots had grown the cuttings were
transplanted into the "Plastimatic" pots described above.

2.2 Methods for Culturing A. kondoi

A. kondoi was cultured so that it could be studied during the winter in case only eggs were present in the field at that time of year.

Aphids have usually been cultured by other workers under laboratory conditions which resemble those occurring at the time of their peak population in the field, with temperatures usually above $20^{o}C$ and with daylengths greater than 14 hours. These conditions are also generally favourable for the host plants.

In the present study the first cultures of A. kondoi were therefore maintained in a room thermostatically controlled as closely as possible to $20^{o}C$(range $17^{o}C - 28^{o}C$), with a photoperiod of 16 hours light and eight hours darkness. Lighting was provided by two 65W Mazda "Daylight" Fluorescent tubes and a Phillips HLRG 400W Horticultural Lamp. The latter was mounted 1.22 metres from the foliage and illuminated with 2500 lux at this distance. This also produced a light of high intensity over a wide spectrum and therefore increased the amount of red light necessary for plant growth and which was not provided by the fluorescent lights. Under these conditions the lucerne plants did not etiolate greatly.

The lucerne plants were placed individually in cages built to exclude aphid parasites since in some aphid cultures these constitute a considerable problem. Each cage was made of a wooden frame 30 cm by 46 cm by 60 cm high. The top was covered with glass to allow light to enter for plant growth whilst the sides and bottom were covered with organdie netting. This had a mesh size of 220μ and prevented aphids from escaping since the head widths of unborn larvae were found to range from 250μ to 320μ.

Ten adult A. kondoi with young visible within them were selected to start the first culture whilst also retaining some of the genetic variability of the field population. These insects appeared to be free from fungal infection and insect parasites.

Every 10 to 14 days a fresh lucerne plant was placed in each cage in contact with the old plant so that the aphids could move on to it. Providing fresh plants after this period was important because if plants were left for longer than this the aphids became dispersed over the plant, became smaller and yellower in colour, and alates formed. A similar

deterioration has been reported for <u>A</u>. <u>kondoi</u> cultures by Nielson and Kodet (1975).

Cultures were also started in other rooms, both with and without temperature control but provided that healthy plants were available the aphids grew successfully. Cages were not used in these later cultures as parasites were rare. In addition towards the end of the present study cultures were maintained in a glasshouse, a site which although preferred was initially unavailable in case <u>A</u>. <u>kondoi</u> spread to other susceptible legumes within it. The glasshouse proved to be an ideal environment since large colonies of healthy aphids were obtained.

2.3 The Study Area

Field studies were carried out in a paddock of lucerne (<u>M</u>. <u>sativa</u> var. Wairau) at the DSIR, Palmerston North (map reference NZMS 1 N149 095 320). The site is approximately 200 metres from the Manawatu River and is low lying so that the adjacent paddocks became flooded on one occasion during the present study. The area is, however an old riverbed and therefore freedraining so that in the past the lucerne has suffered from drought during the summer.

The lucerne in the study area has been subjected to varied agricultural management and experimental studies. It was planted eight years ago and until two years ago was maintained in good condition (P. Menalda, pers. comm.), but since then it has slowly become weed infested and was in poor condition compared to a commcercial lucerne plot. This is reflected in Table 1 which depicts the density of lucerne obtained using six inch and 12 inch square quadrats on the 12th and 25th April, 1976. The poor quality of the lucerne is attested to by the fact that some quadrats contained no lucerne and indeed areas greater than one metre square were often found without lucerne.

The area was subject to very little management except on the 22nd of October 1976 when it was grazed extensively by cattle for two days in an effort to remove weeds, and on the 15th of December when the lucerne was cut and left lying. No chemicals were applied at any stage.

Originally there was approximately two hectares of lucerne but most of this area was planted in maize in October 1976 leaving an area of lucerne approximately 30 by 90 metres.

The crops grown in the area surrounding the lucerne were varied. Immediately adjacent on the north side was a field of Paspalum dilatum Poir. while to the west and south were regularly grazed paddocks of mixed clover-grass sward. Whitcomb and Bell (1964), van Emden (1965), Hodek (1967) and other authors have noted that surrounding crops may greatly affect the aphid population because they form a reservoir of both aphids and predators.

Windbreaks are known to affect the distribution of aphids in crops by affecting windborne aphids (Taylor, 1962) but although no hedges bordered the lucerne field the maize crop to the east side may have performed such a role in February and March 1977 when it was fully grown.

The amount of lucerne grown in the Manawatu generally decreases from the coast to the Tararua Ranges, and since the prevailing winds also blow in this direction the study site seemed to be usefully placed for measuring the number of migratory aphids.

Additional observations were made on the farm of Mr H. Voss approximately ten km from Massey, at Flock House near Bulls, and at two sites south-west of Dannevirke.

Table 1   The density of lucerne at the DSIR study plot

Quadrat Size	6"x6"[a]	6"x6"[b]	12"x12"[a]	12"x12"[b]
Number of Samples	28	28	28	28
Mean	12.7 stems	6.7 stems	36.5 stems	29.6 stems
Standard Deviation	11.7	7.3	15.8	17.5
Range	0 to 43	0 to 31	9 to 78	1 to 65

[a] Sampled on the 12th April 1976

[b] Sampled on the 25th April 1976

CHAPTER THREE

PRELIMINARY INVESTIGATION OF THE MORPHOLOGY AND DEVELOPMENT

OF A. KONDOI

3.1   Introduction

This chapter contains the results of an initial investigation
to characterise the instars of A. kondoi, so that they could be recognised
during subsequent research. Also included here is the identification of
the morphs of A. kondoi, including some aspects of their morphology
which enabled me to distinguish A. kondoi from other aphid species. These
latter observations on the morphology of the species supplement those of
Takahashi (1965), Eastop (1966, 1971) and Kono (1975).

3.2   Materials and Methods

3.2.1 Determination of Instars

The number of instars of A. kondoi was determined from specimens
collected at the DSIR study plot described in Chapter Four, on the 9th,
10th and 19th May 1976, and on the 2nd June 1976. These were stored in
a mixture of two parts 90 - 95% ethyl alcohol to one part 75% w/w lactic
acid (Eastop and van Emden, 1972) until they were examined under a
binocular microscope.

Measurements were made of the following appendages of A. kondoi
which, being sclerotized, are of relatively unvarying dimensions within
any one stadium. The lengths of the cornicles and mesotibiae were
measured in all aphids. In the third and fourth instars and apterous
adults, measurements were made of antennal segments III, IV and VI
(terminal), whilst in the first and second instars antennal segment III
and the terminal segment were measured. This antennal nomenclature is
that of Cottier (1953). Both the left and right appendages of every
aphid were measured in case they were asymetrical since this has been
reported in other aphids (Bodenheimer and Swirski, 1957), or in case
the end of one antenna was lost.

Eastop and van Emden (1972) suggested that the greatest problem
when working with preserved material was recognising whether first instars
were present, and therefore to ensure that first instars were examined,
newly born larvae which had been bred in captivity were measured.
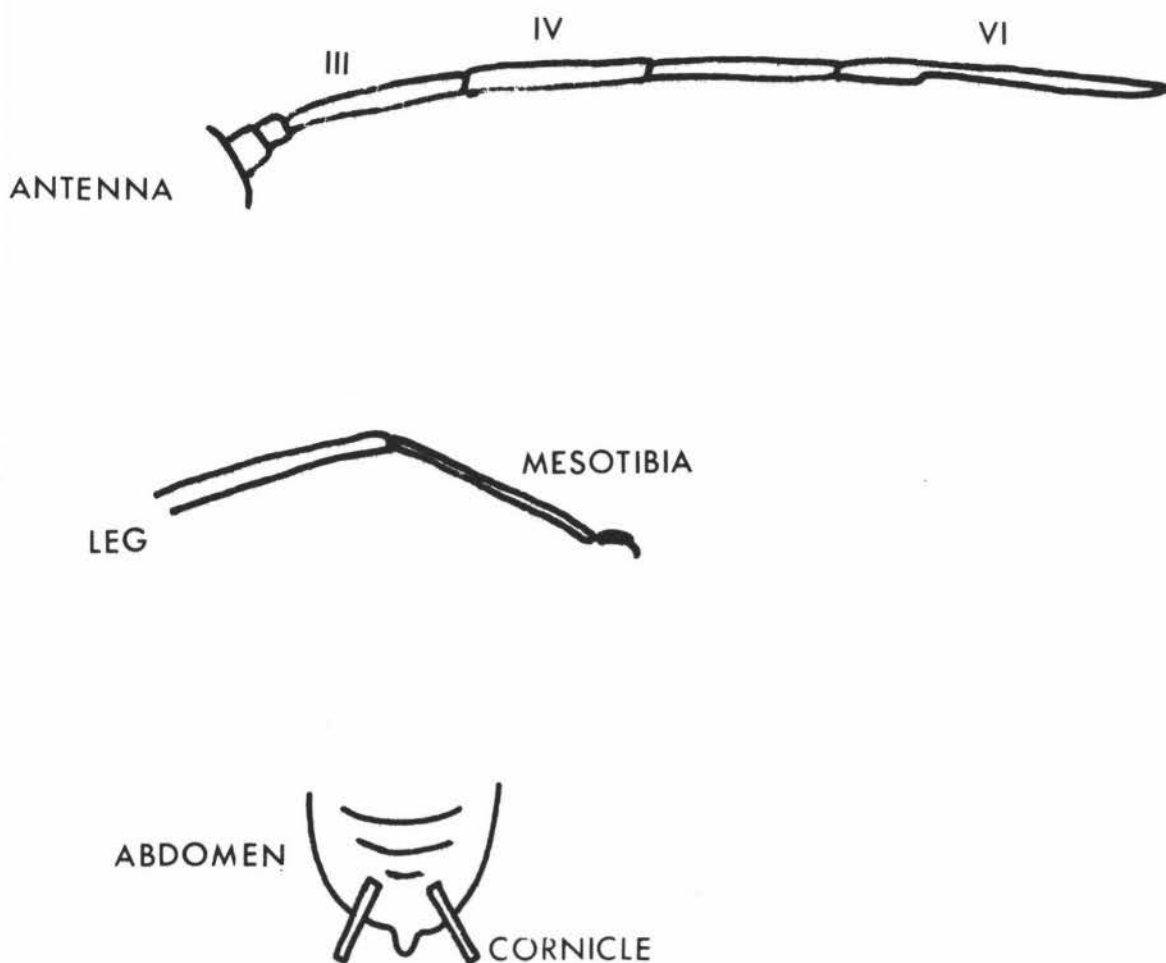
Fig. 1   The body parts of _A. kondoi_ which were measured
         to determine instars

3.2.2   The Search for Sexual Morphs

Adult alatae and apterae were regularly examined for the presence of sexual characteristics. Those aphids looked at included all the alate and apterous adults collected from the fortnightly plant samples described in Section 4.2, and all alate adults trapped on the yellow greased cylinders described in Section 5.2.

Initially the presence of larvae within the abdomen of the adults was noted. If these were not found then the apterous adults were examined for the presence of thickened metatibiae covered with pseudo-sensoriae which are characteristic of oviparae (Cottier, 1953; Imms, 1957), whereas the alate adults were examined for extra antennal sensoriae which are characteristic of males (Cottier, 1953; Imms, 1957).

3.3   Results and Discussion
3.3.1   The Instars of A. kondoi

A. kondoi was found to possess four nymphal instars and the adult. This is clearly shown in the scatter diagram of mesotibial length versus cornicle length (Fig.2). The presence of five instars was expected since most aphid species are known to possess that number (Baker and Turner, 1916; Baker, 1917; Takahashi, 1924).

The dimensions of all the morphological features used to disting-uish the instars of A. kondoi in the present study are given in Table 2. Many factors are known to affect the size of aphids (Murdie, 1969a), but since the measured A. kondoi were collected on different dates they should present a reasonable indication of the natural variation in size. It was noticed that the size of aphids decreased as the colony from which they were obtained became older.

No dimorphism, except that due to alateness or apterousness, or other striking morphological differences were noticed between or within instars of A. kondoi. In contrast, Hille Ris Lambers (1966) noted that in other aphids one instar may often be distinctly different from another or dimorphism within an instar may occur.

The most obvious change noted in specimens of A. kondoi as they grow is that the number of antennal segments increases from five in the first and second instars, to six in later instars. This is due to a division of segment III which corresponds to the second annulus of Imms (1940). The division takes place about halfway along the segment and the

Fig. 2   Plot of <u>A</u>. <u>kondoi</u> mesotibial length versus cornicle
length to show the four instars and adult size classes
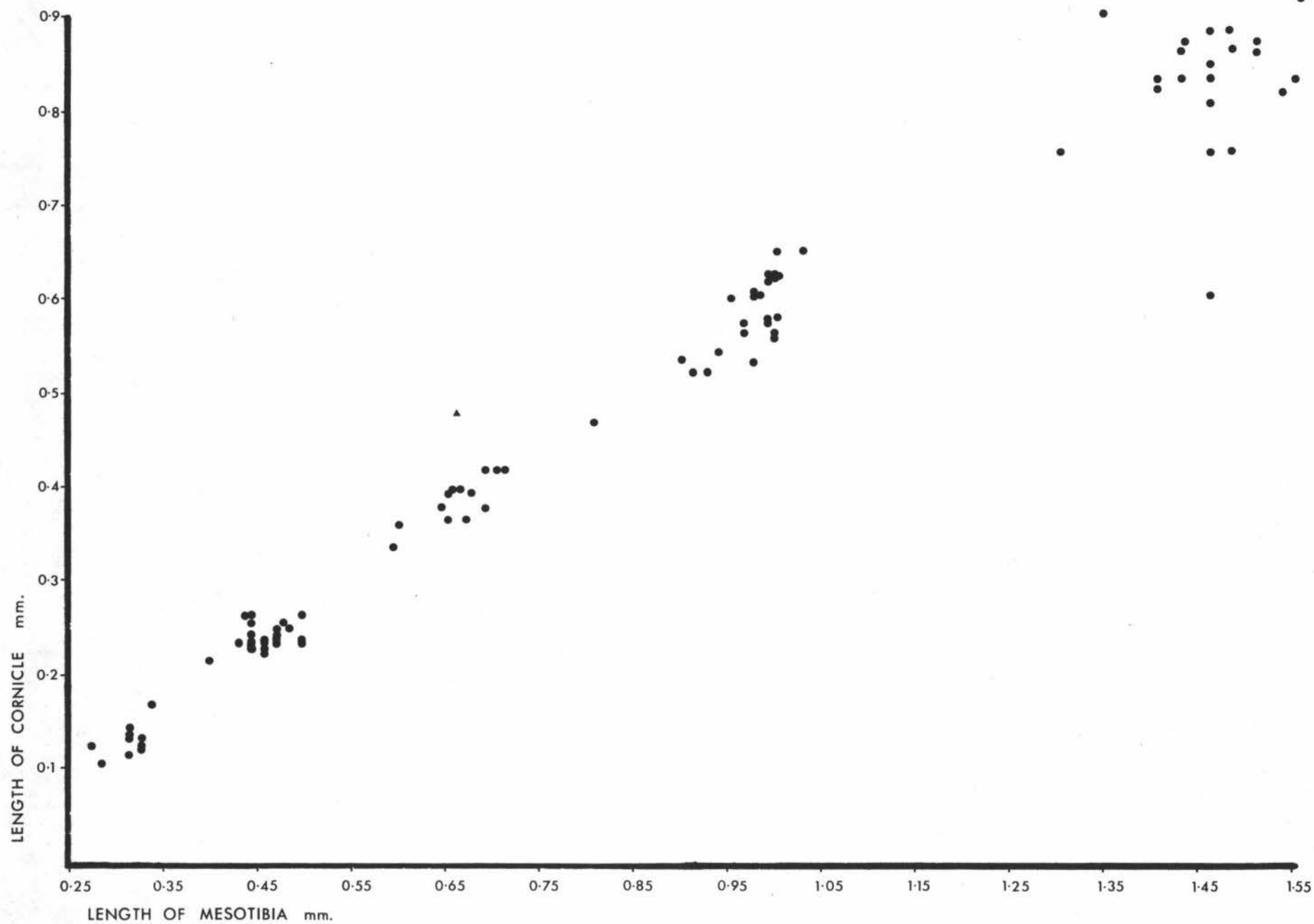
plane of division is visible in late second instar larvae. Division of the second annulus is usual in the great majority of Pterygota (Imms, 1940).

First and second instar larvae of A. kondoi may be readily distinguished from each other by the cornicles which are blunter in first instars and by the relative lengths of the antennae which often do not reach the proximal end of the cornicles in first instars, but extend almost to the distal end of the cornicles in second instars.

Second and third instar apterae can be separated by the presence of the additional antennal segment in the third instar which arises from the division of the second annulus as discussed above. Third and fourth instars of apterae can be distinguished by antennal segments III and IV which are of similar length in third instars whereas in fourth instars segment IV is noticeably larger than segment III.

No ready method of distinguishing whether a first or second instar larvae will become winged or wingless was discovered. However presumptive alatae and apterae can be distinguished in the third instar, since at this stage the wing buds although internal, are visible as distinct bulges in the dorsal region of the thorax. These wing buds, subsequently become external and clearly visible in the fourth instar.

In addition to the presence of fully developed wings in alate adults their dorsal thorax is orange-brown in colour in comparison to the bluish-green of apterous adults.

3.3.2 The Morphs of A. kondoi

Despite extensive searching only parthenogenetic viviparous alate and apterous A. kondoi were found in the present study. No oviparae or males were discovered and the probable reasons for this are discussed further in Chapter Seven.

3.3.3 Additional Notes on the Morphology of A. kondoi.

Apterous A. kondoi have no sensoriae on antennal segment III, whereas alate adults usually possess eight or nine, though this seems to vary between seven and eleven. Takahashi (1965) noted they only possess seven or eight, though he only examined one specimen. However it was always found difficult in the present study to be certain whether all the

sensoriae on a segment had been observed. The sensoriae of the alates are arranged linearly in the first half to two thirds of the segment and become slightly more spread out from each other towards the distal end of the segment (Fig. 3).

The pattern of markings on the dorsal abdominal surface of an alate adult A. kondoi is shown in Fig. 4. These are inconspicuous compared to those on many aphid species and are not readily observed even when viewed under a microscope.

Table 2　The Dimensions of the Instars of A. kondoi

| | Instar | Antennal Segment Number | Length (mm) | | Antennal Segment | | |
			Mesotibia	Cornicle	III	IV	Final
	One						
N		10	10	10	Absent	9	10
Mean		5	0.31	0.13		0.17	0.40
Range		0	0.27-0.34	0.10-0.14		0.15-0.21	0.38-0.44
	Two						
N		24	24	24	Absent	24	24
Mean		5	0.46	0.24		0.30	0.55
Range		0	0.42-0.50	0.22-0.26		0.27-0.37	0.52-0.59
	Three						
N		13	13	13	9	13	13
Mean		6	0.66	0.39	0.26	0.28	0.70
Range		0	0.59-0.72	0.33-0.42	0.21-0.28	0.25-0.31	0.65-0.74
	Four						
N		26	26	25	18	26	24
Mean		6	0.97	0.58	0.50	0.45	0.89
Range		0	0.82-1.04	0.46-0.66	0.43-0.52	0.32-0.57	0.71-1.02
	Five (Apterae)						
N		25	24	25	10	25	25
Mean		6	0.84	1.46	0.86	0.68	1.05
Range		0	0.76-0.93	1.35-1.57	0.77-0.92	0.47-0.97	0.93-1.12

Fig. 4

2·59 cm = 1mm
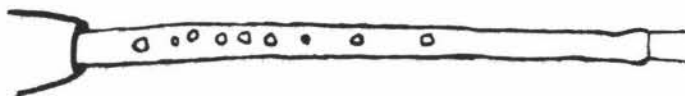
Fig. 3

LENGTH SEGMENT = 0·75mm

Fig. 3 Antennal segment III of an alate adult of A. kondoi
    showing sensoriae.

Fig. 4 The pattern of markings on the dorsal abdominal
    surface of an alate adult.

CHAPTER FOUR

SEASONAL CHANGES IN THE POPULATION

OF A. KONDOI

4.1 Introduction

The discovery of A. kondoi in New Zealand generated much speculation as to how the species would adapt to New Zealand conditions and how its numbers would vary during the year. Considering its origins it seemed likely that it would flourish during the cooler periods of the year. In order to eliminate this conjecture the present study was started to document the population variation during the one year period and to determine whether there was a change of aphid morphs during this period. The primary object was to determine the major trends of the population throughout the year, although it is known that the density of an aphid population may vary greatly within small areas (Stary, 1970; Heathcote, 1972) and over short intervals of only a few days. Therefore the number of samples, their distance apart, and the time interval between samples was selected to reduce this variability whilst still showing the overall population fluctuations.

Aphid numbers may change rapidly especially in favourable conditions because of the aphids' short generation time and high fecundity but the periods of rapid change usually only occur at particular times of the year and result from the aphids' ability to respond to many extrinsic factors such as climate, plant condition and predation together with its own intrinsic population regulating mechanisms.

Suction samplers are generally considered to be the most efficient method of sampling aphid populations (Johnson et al., 1955, 1957; Dietrick et al., 1959; Southwood and Pleasance, 1962) and therefore a modified vacuum cleaner was tested first. However this resulted in practical problems such as the difficulty of separating the aphids from the large amount of suctioned soil and litter. Also this method gives a measure of the number of aphids per weight of plant, yet it seemed that the number of aphids per stem was a more realistic biological unit and this was later found to be true. The vacuum sampler was therefore rejected in favour of collecting samples of individual stems by hand and

subsequently removing the aphids from these. The errors involved in this type of sampling have been discussed by Fenton and Howell (1957), Nielson (1957) and Heathcote (1972).

4.2 Materials and Methods

Samples were taken of individual lucerne stems at approximately fortnightly intervals. On each occassion 84 stems were collected from 28 randomised sample stations, three stems being taken at each sample station.

The sample stations were located by pacing out the distances between them, and the order of sampling was arranged in sequence so that the minimum possible distance between points was used, to avoid excessive trampling. An open bottomed box was placed on the ground one pace before the sampling station and this was used as a platform to stand on while sampling. These procedures resulted in much less than 10% of the sampling area, the maximum allowable (Hughes, 1972), being disturbed.

Initially a sampling device which consisted of a wooden pole with three paired lengths of wire protruding from it (Fig. 5) was used to select the three stems at each station. The two wires of each pair were at different heights and each lucerne stem was selected by aligning and sighting down the ends of a pair of wires. The furthermost stem was sampled last thereby avoiding disturbing the aphids on the nearer stems. Only stems greater than five cm tall were sampled to ensure a reasonable sample was obtained, though stems smaller than this were still visually checked to ensure that no anomalies occurred.

Each stem was cut as close to the ground as possible while it was held just above the point of cutting, a procedure recommended by Eastop and van Emden (1972) to avoid jolting the aphids from the plant or inducing their "drop-reaction". Cut stems were carefully placed into individually identified plastic bags which were held open very close to the plant.

In the first eight fortnightly samples the fresh weight of the stems was obtained then each sample was individually washed in water heated to $70^{o}C$ to remove aphids; a procedure used by Lowe and Dromgoole
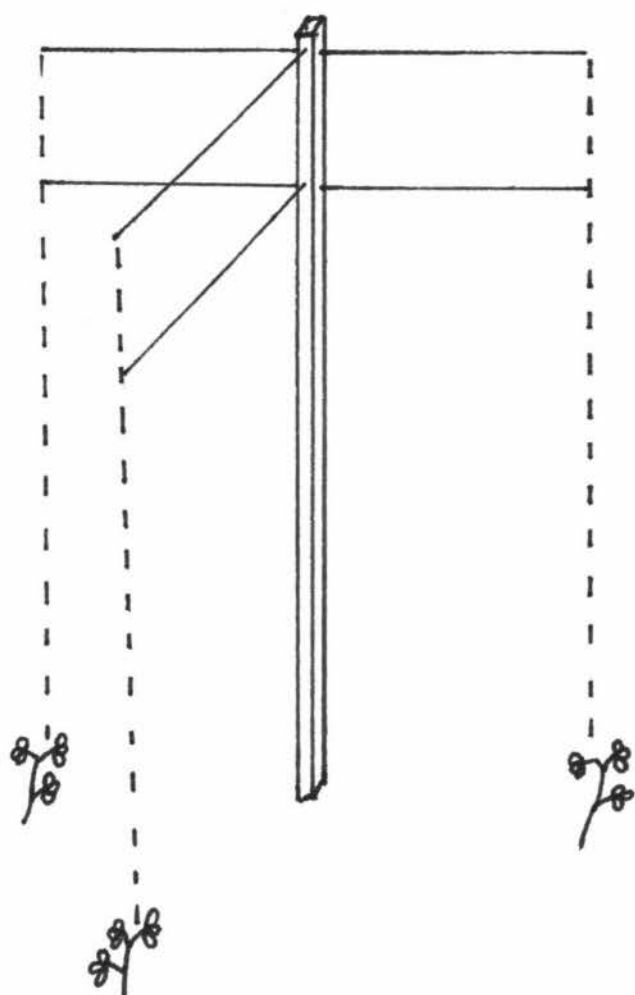
Fig. 5   Sampling device used for locating the lucerne stems to be
          sampled. (Approximate scale 10 cm = 1 m)

(1958). The entire contents of each bag were then poured into a white
plastic 'lily' cup so that the aphids were clearly visible. Normally
they were then removed with a Pasteur pipette, but if especially high
numbers were present they were filtered off through organdie mesh and
the stems were then removed from the 'lily' cup and dried to a constant
weight. Any aphids found remaining in the plastic bags were also
removed and all the aphids were stored in small plastic vials containing
the preservative described in Section 3.2.

After the third and fourth fortnightly samples had been
washed the stems were microscopically examined and found to have aphids
still adhering. Therefore in subsequent samples the lucerne stems were
washed vigorously in the 'lily' cup to dislodge all aphids.

The original intention was to measure both the fresh and dry
weights of the sampled stems to obtain a ratio of the proportion of live
and dead material per stem, but during the course of sampling it became
apparent that the amount of dead material was insignificant except during
a short period in winter when the plants died off. Fresh weights were
therefore no longer obtained after the eighth fortnightly sample. However
dry weights were obtained for the first 20 fortnightly samples to determine
whether there was any relationship between the plant weight (size) and
aphid numbers.

Ethyl acetate was added to the first eight fortnightly samples
to kill the aphids because the procedure involved in obtaining the fresh
weight of the stems meant that they often had to be left overnight in the
laboratory. If the aphids were not killed they could have increased
considerably in number during this period. In addition the first eight
fortnightly samples were collected in dry weather after 1000 hours each
day to avoid rain or dew upsetting the fresh weights.

After the eighth fortnightly sample no ethyl acetate was
added since fresh weights were not taken and the aphids were brought back
to the laboratory and washed off the stems immediately.

4.3   Results and Discussion

4.3.1 Preliminary Observations Concerning the Growth of an A.kondoi
       Population

An experienced observer can estimate the approximate age of an
aphid colony by noting the position of the colony and distribution of
aphids on the plant and the aphid morphs present. As the colony ages the
aphids become more dispersed over the plant, the inter-aphid distance and
the proportion of alates in the colony increases, while the total number
of aphids in the colony declines. This decline is relatively synchronised
in a field where most of the plants are colonised at the same time. Such
an event constitutes the "spontaneous" decline of an A. kondoi population
as observed by Richardson (1977). The decline is largely due to the
interactions between aphids and can be independent of predators, parasites,
entomophthorous fungi and climate. This pattern of increase and decrease
in aphid numbers is subsequently referred to in the present study as a
population "cycle", a term used by Stinner et al., (1977).

An A. kondoi population cycle can be divided into five phases
somewhat similar to those observed for Aphis nasturtii Kalt. and Aphis
fragulae Kalt. by Galecka (1966). These are an initial build up followed
by a rapid increase in numbers, maximal aphid abundance, decrease and low
population levels which persist until the next population build up.

4.3.2 Changes in the Population of A. kondoi

The numbers of A. kondoi found on lucerne throughout a one year
period at the DSIR study plot are shown in Figs 6 and 7. These changes in
the aphid numbers generally agreed with my subjective estimate of the
population levels. In brief two main periods of high aphid population
occurred, one in winter and one in spring.

This pattern showed certain similarities to those of other
aphid species in New Zealand since most populations reach their highest
numbers in spring as did A. kondoi. The numerical superiority of this
peak over the rest of the year's population is striking and undoubtedly
resulted from prevailing conditions being ideally suited for both
A. kondoi and the lucerne host plant. McSweeney (1976) reported that
the spring build up in numbers occurred throughout the Manawatu.

Fig. 6   The mean number of <u>A</u>. <u>kondoi</u> per lucerne stem found
during fortnightly sampling at the DSIR study plot
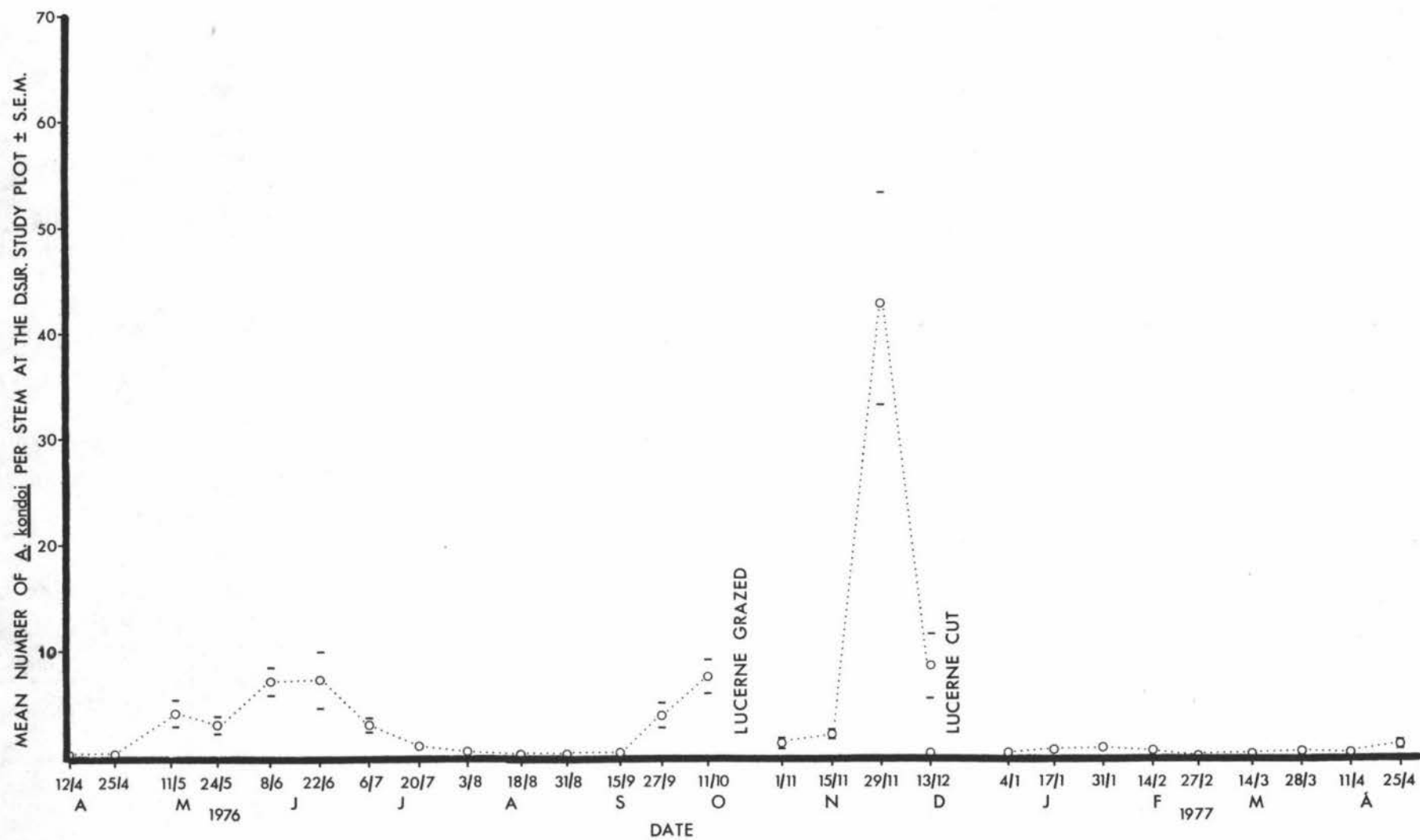
Fig. 7   The total number of $\underline{A}$. $\underline{kondoi}$ found during each sample
at the DSIR study plot.   On the 27th February 1977 no
aphids were found in the sample.
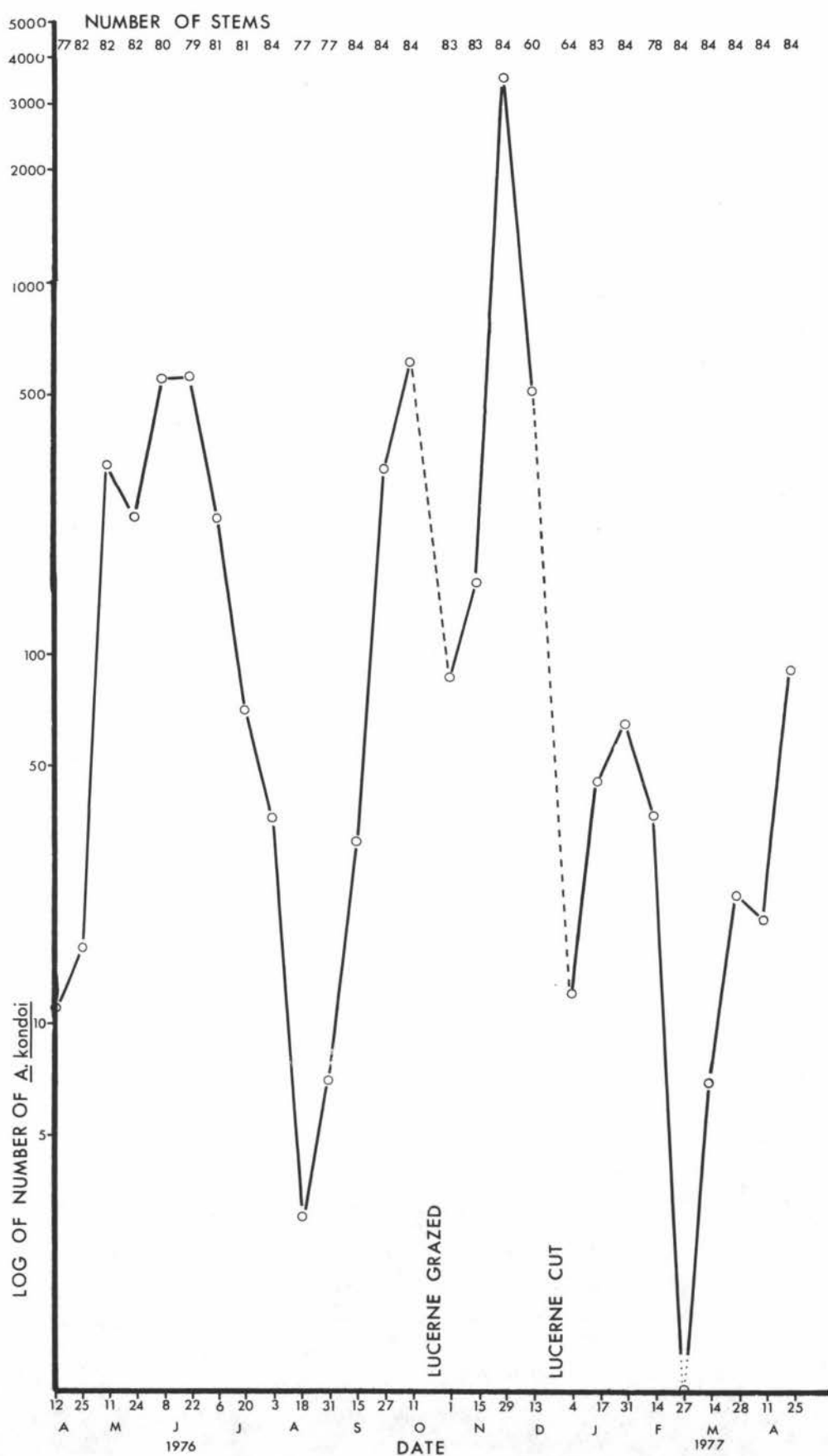
During summer the population of A. kondoi in the DSIR study
plot decreased to relatively low numbers. This effect is a feature of
many aphid populations and is generally attributed to the hot dry weather
at this time although it is highly likely that other influences such as
host plant condition or intraspecific population regulations may have
been important for A. kondoi as discussed further in Chapters Seven and
Ten.

No true autumn peak occurred for A. kondoi at the DSIR study
plot, although most other aphid populations normally reach high numbers
again at this time. A small peak occurred in January 1977 but this was
too small and too early to be considered an autumn peak. The increase in
numbers which was occurring when sampling finished coincided with the
beginning of winter so this also cannot be regarded as an increase leading
to an aumtumn peak.

A summer-autumn peak occurred in Exclusion Cage One as
described in Chapter Nine, and this indicates that predation depressed a
summer-autumn peak in the field in 1977. Furthermore a summer-autumn
peak which coincided with the peak observed in Exclusion Cage One was
observed in a field population of A. kondoi on Voss's property from the
24th February 1977, when the aphid numbers were already high, until the
7th March 1977 by which time the population had declined. Very large
numbers of aphids were involved in this peak, probably greater than those
observed during the spring population peak at the DSIR study plot. This
may have been due to the high quality of lucerne at Voss's which was a
commercial plot.

A population peak was observed but not measured in late
March 1976 on the DSIR study plot before the present study commenced and
this presumably represented the first population increase after the intro-
duction of A. kondoi in the Manawatu. In this case also the numbers of
aphids rivalled the populations in spring 1976 probably because of the
suitability of the local ecosystem which was not yet adapted to the aphid.

A distinct winter peak was observed at the DSIR study plot in
June 1976 and a 1977 winter peak seemed to be commencing when sampling
terminated, although the latter began two weeks in advance of the winter
peak of 1976. The 1977 peak appeared to develop at the same time as cold

weather forced most of the remaining predators to leave the lucerne or become inactive.

This winter population increase is interesting for two reasons; the numbers of aphids was increasing while the temperature was dropping and a winter peak is not commonly reported for aphids. Summers (1975) however, described A. kondoi as a cool weather aphid and Kain et al. (1976) believed that populations could possibly develop in suitable areas in winter. Hughes (1977) stated that the lowest developmental temperature for A. kondoi is 4°C. Even during winter the daily temperature in the Manawatu rises above this so development of A. kondoi populations could occur.

High numbers of A. kondoi were also found on winter growing lucerne in a separate trial area of small plots at the DSIR, Palmerston North, in August 1976. The population cycles of the small plots were not followed because the plots were sprayed but the high numbers of aphids, their morphs present, and the aphid dispersion on individual plants (see Section 4.3.1) indicated that the population was still rising in mid-August and had been doing so for some time. This population was therefore reaching peak numbers when the numbers of A. kondoi at the main sampled DSIR study plot, only about 500 metres away, were very low. Richardson (1977) also found that populations of A. kondoi within very short distances of each other, could be in different stages of development. My observations therefore indicate that populations of A. kondoi are able to develop at virtually any time in the winter and at different sites may be in different stages of a population cycle. The environmental factors which enable sites to be independent of each other with respect to population cycles are not known but the size of the lucerne plots and their distance apart is probably important.

It therefore seems likely that a relatively undisturbed area of lucerne such as the DSIR plot will follow a pattern of three cycles per year and that these will approximately occur in spring, summer-autumn and winter. However the amplitude and duration of different cycles will vary between situations and depend on a variety of factors including any management methods used with the lucerne, and the presence or absence

of various biological control agents. These factors will also influence the precise time of year when a peak occurs, as was noted for the small plots at the DSIR.

The results of Richardson (1977) who studied a number of separate lucerne fields and who found a greater and more variable number of periods of A. kondoi population rise for any one field during the year may at first seem to contradict my results. The greater and more variable number of peaks can probably be explained by the cutting, spraying or grazing of the lucerne which occurred in her study when each peak was reaching its maximum level. These crop management practices reduced the aphid numbers considerably but at the same time induced a new aphid peak to develop rapidly on the lucerne which was recommencing growth. If the practice did not occur then a "spontaneous" decline in population took place and the population cycle was completed naturally as was observed in the present study. The period of recovery between natural cycles seems from the present study to be much longer (see Chapters Eight and Ten) than that between the truncated population cycles caused by the crop management practices.

The numbers of aphids found in the samples taken in the present study on the 24th May 1976 and on the 1st and 15th November 1976 appear to be anomalies in the general population trend. The population decline which occurred on 24th May involved a decrease in the number of first instars of A. kondoi and the possible reasons for this are discussed in Chapter Seven. The low number of aphids on 1st and 15th November resulted from the paddock being grazed on 22nd October.

4.3.3 Rate of Population Change

Fig. 8 shows the rate of population increase on an expanded time scale of sections of Fig.7 where the aphid population was rising. It can be seen that the rate of population growth is similar between the initial growth stages of both the 1976 and 1977 winter population cycles and of the initial spring population increase before grazing. The initial stage of the aborted summer-autumn peak had a lower rate of growth which can probably be attributed to predation.

Fig. 8   The rate of change of the population of <u>A. kondoi</u>
at the DSIR study plot showing sampling periods when
the population was increasing.

a.	25/4 - 11/5	1976
b.	24/5 - 8/6	1976
c.	15/9 - 27/9	1976
d.	15/11- 29/11	1976
e.	4/1 - 17/1	1977
f.	11/4 - 25/4	1977
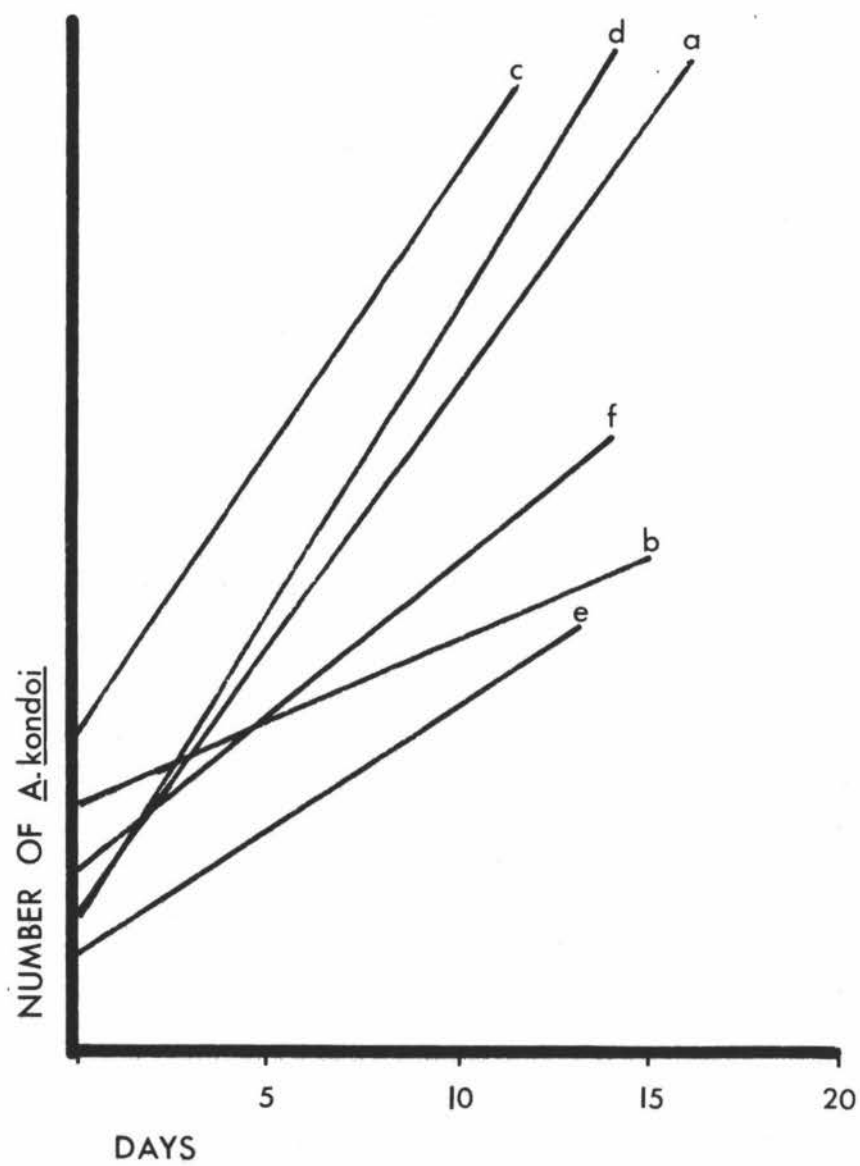
Richardson (1977) also observed that population developmental rates were very similar over a considerable period of time. It is of interest that the rate of population development appears, because of its constancy, to be independent of temperature. This indicates that there is some other limiting factor, possibly plant condition, or that, at this stage of the population cycle there is no external limiting factor, but that the rate of growth of the aphids is already at its maximum.

The apparent difference in maximum size between the winter and spring population peaks is because the rate of growth is maintained at a much higher population level in the spring peak between the 15th and 29th November. This may reflect the fact that the vegetation grows more rapidly in spring and it is therefore able to sustain the population growth for longer. Richardson's (1977) samples were only taken during the spring to autumn period and hence the growth rate was maintained to high population levels. In the present study the rate of population growth appeared to slow as the winter population peak was reached. This may indicate that the climate and plant condition then became limiting.

The rate of population decline is also slower during the winter peak than in spring. Although no definite explanation can be offered the apparent lack of flight by winter alates (Section 5.3.3) may be an important contributing factor.

4.3.4 The Numbers of A. kondoi

The numbers of <u>A</u>. <u>kondoi</u> sampled from the DSIR study plot did not seem to be as high as those reported from other areas. During the spring peak, when the number of aphids was at its greatest, one stem was found to have 679 aphids but the average number per stem during this peak was only 42. These relatively low numbers may have reflected the lack of management of lucerne at the DSIR study plot which resulted in a wide range in the age, and the general poor quality of the lucerne. The low and varied density of lucerne (Table 1) probably restricted migration by apterae between plants and this may have slowed the total population growth by retarding the rate of colonising of separate plants. Certainly the density of the host plant can affect the size of the total aphid population (Itô, 1960; Farrell, 1976).

The large variation in the numbers of A. kondoi per stem which often occurred within a fortnightly sample was probably due to factors such as the variable age and development rate of aphid colonies, and also the varied quality of the lucerne. The varied density of lucerne therefore resulted in aphid numbers per stem of lucerne being a more realistic population estimate than aphid numbers per unit area.

4.3.5 <u>Effect of Management Practices on the Population of A. kondoi</u>

My original intention was to follow the population of A. kondoi for one year on lucerne which was not subjected to any management practices. Although contrary to normal farming procedure this has definite advantages for population studies since sudden changes in vegetational quality such as those resulting from cutting or grazing do not occur. However this was not possible and it was necessary to graze the plot on 22nd October in order to remove the weeds which were threatening to dominate the lucerne and were making sampling difficult. The lucerne was also cut in error on 15th December without my prior knowledge.

The aphid population decreased considerably after both cutting and grazing. Similar decreases were found for A. pisum populations over each of several cuts by Dunn and Wright (1955), Stary (1970) and for A. kondoi by Richardson (1977). To some extent this was to be expected since aphids are knocked off and destroyed during cutting or grazing, and their source of food is removed.

The effect that these two changes in the lucerne had on the overall population development in the present study is less clear. In the absence of grazing the spring population peak would probably have reached much higher numbers than the winter peak, though probably not quite the numbers that it eventually did, since grazing allowed new growth of the lucerne to begin in ideal conditions.

Grazing also retarded the spring population cycle by four weeks and if this had not occurred then another population cycle may have taken place over summer. However after the high number of aphids which did occur the population would have taken some time to recover and with the less suitable summer lucerne growing conditions it is probable a similar growth pattern would have occurred. Also the cutting which took

place on 15th December only hastened the decline in aphid numbers which was already occurring and this would have compensated somewhat for the effects of grazing and allowed the population growth to "catch up" again. Therefore although cutting and grazing had some effect it is unlikely that they affected the overall population trends. A similar conclusion was arrived at by Stary (1970) for A.pisum populations on lucerne.

Grazing also indirectly affected the aphid population by decreasing the predator numbers (as shown in Chapter Nine) and probably cutting had a similar affect.

4.3.6 The Number of Generations of A. kondoi in One Year

The numbers of each instar of A. kondoi as found in each fortnightly sample are shown in Appendix Two. If it is assumed as was found by Hughes (1963) for the cabbage aphid Brevicoryne brassicae (L.) that the fourth instar development takes 1.2 times the average of the first three instars of A. kondoi, then the fourth apterous instar will have an instar duration of 65.75 day-degrees. Taking the pre-reproductive period of the adult as 24 hours at $23^{\circ}C$ (Appendix Three) then the period from birth to birth i.e. the generation time, for A. kondoi is 253 day-degrees. These calculations are discussed more fully in Appendix Three.

During a period of one year from the beginning of March 1976 to the end of February 1977, a total of 4529 day-degrees had accumulated and therefore 17.9 generations of A. kondoi could have occurred during this period. This figure is an upper estimate because lower or upper temperature threshholds for development are not taken into consideration, but the number of possible generations is realistic since Lowe (1967) stated that most economically important aphids in New Zealand undergo 15 generations per annum.

4.3.7 General Observations Concerning the Position of A. kondoi on the Host Plant

Young developing colonies of A. kondoi are found on the growing tips of the lucerne stems with the youngest aphids often being found between the unflurling leaves where presumably they are provided with some protection. This siting of the colony is characteristic of A. kondoi and provides a means of separating it from the closely related

A. pisum which forms colonies further down the stem (Summers, 1975).

As the A. kondoi colony grows it extends further down the main stem and on to the growing tips of lateral shoots and at its maximum size colonies have been observed with aphids thickly encrusting the upper 15 cm of a lucerne stem approximately 40 cm high. The colony then begins to deteriorate as the population cycle proceeds and the number of aphids begins to decline. They become less concentrated on the main growing tip and more dispersed over the plant and are found more frequently on the trifoliate leaflets than in the early stages of colony development.

This pattern of colony development with eventual dispersal over the plant has been noticed in four other aphid species by Itô (1960) and Wyatt (1965). This dispersal is possibly a response to or is in antici- pation of, a lowered nutritional condition and greater spatial competition and constitutes part of the population cycle.

The growing tip of a plant is a natural sink for nutrients and it is reasonable to suppose that A.kondoi exploits this by the siting of its colony. Formation of a colony probably involves active aggregation (Ibbotson and Kennedy, 1951; Way and Cammell, 1970) and this leads to the formation of an even more effective nutrient sink (Dixon and Wratten, 1971; Way, 1973) resulting in aphids which are larger and in better physiological condition (Way and Cammell, 1970).

4.3.8 Lucerne as a Year Round Host Plant

Lucerne seems to be the major host plant of A. kondoi during the entire year. This is probably partially attributable to lucerne being a perennial plant even though little growth may occur in winter. Hence A. kondoi can be found on an infected crop of lucerne throughout the year although often only in low numbers.

No aphids were taken on 27th February 1977 fortnightly sample but they were observed in the sample area at this time. In contrast Summers (1975) reported that there were times in the Californian summer when no A. kondoi were present.

4.3.9   The Future of A. kondoi in New Zealand

A. kondoi is still in in an introductory phase in New Zealand
and it may well be that the exact population pattern which will emerge
as it stabilises will vary from that observed in this study.

The introductory phase of most animals when introduced into a
new habitat which has not been previously occupied, is characterised by
excessively high numbers until the resident flora and fauna adapts to the
new species (e.g. Nielson and Barnes, 1961; Packer, 1975). It is likely
that parasites and predators already present will increase in number and
the times of their peak populations may change in response to the aphid
populations. Only those host plants which are resistant or tolerant to
the new pest will survive. These combined effects will result in lower
numbers of an introduced aphid, but in the case of a monocultural situation
which is inherently unstable due to its lack of species diversity, a
suitable balance may not be attained and the numbers of the new species
will continue to fluctuate.

However the diversification of the New Zealand aphid fauna by
the addition of a new species diversifies the food supply of existing
predators and hence creates the possibility of better control over other
species of aphids. A major problem in biological control is the provision
of supplementary foods for predators (Hagen, Sawall and Tasson, 1971;
Ben Saad and Bishop, 1976) during periods when the main prey species is
not abundant and diversification of the prey fauna may achieve this.

CHAPTER FIVE

THE FLIGHT OF A. KONDOI

5.1. Introduction

Nearly all species of aphid have a winged phase in their life cycle since much of the aphids mode of life is geared towards rapidly exploiting a transiently suitable habitat, then quickly dispersing to another site. In some instances flight is to a site, often on a different sort of host plant, where survival rather than immediate rapid reproduction is the main objective. The departure of alates may also constitute an important means of population regulation (See Section 10.3.4).

Alate aphids can be either sexual or parthenogenetic. The production of alate forms may be due to a number of factors the most notable of which are crowding effects (Hille Ris Lambers, 1966; Lees, 1966; Johnson, 1969) but other factors may also be involved including temperature, nutrition and photoperiod. All these factors are generally indicative of present or future unsuitable conditions.

A general review of insect migration and dispersal which includes recent theories on aphid flight has recently been published by C.G. Johnson (1969) who himself was a major contributor towards the development of many of these concepts.

The time of aphid flight, the numbers flying and the morphs of those flying, can provide much information on the biology of an aphid species, therefore a trapping programme was run to obtain information on these aspects of A. kondoi. Aphid migratory flight seems to conform to a regular pattern and some observations are presented on the pattern of flight in A. kondoi.

There are many types of traps for catching flying alate aphids. These are reviewed by Southwood (1966) and Taylor and Palmer (1972). It is generally recognised that the suction sampler is the most efficient (Johnson, 1950; Costa and Lewis, 1967; Taylor and Palmer, 1972) but none was available for the present study. Of the "impaction" traps which rely on the aphids colliding with the trap, those which are cylindrical are the

most efficient since they cause the least disturbance to the surrounding air flow. The use of grease covered cylindrical adhesive traps for catching aphids was first described by Broadbent et al. (1948) and since then such cylinders have been extensively used in aphid flight studies, including one of the main studies in New Zealand by Lowe (1968a).

Greased cylinders have four main advantages. They are cheap, easy to construct, have few maintenance problems and do not depend upon an external power supply. They also have the advantage of comparability of results since they have been used in many studies. Their disadvantages were studied by Johnson (1950), the major ones being that no reliable estimate of aphid density in the air can be made with them since they sample with varying efficiency and are especially inefficient at low wind speeds. Also when the traps are coloured it is difficult to separate attractant effects (which vary from species to species and in different light and weather conditions), from wind speed effects. These effects make a quantitative comparison between trapping periods difficult even when the wind run and velocity is known.

Within New Zealand studies on the flight periods of aphids in general have been conducted in Auckland by Lamb (1958a, 1958b) using Moericke yellow traps and more extensively in Canterbury by Lowe (1966a, 1968a) using yellow greased cylinders. The results of both authors indicate that the main periods of aphid flight are in spring and autumn. During these times the highest number and usually the greatest variety of aphid species are flying, but there are many minor variations between and within years and sites.

5.2 Materials and Methods

In the present study trapping was done at the DSIR study plot described in Section 2.3. The greased cylinder traps were placed ten metres from the north-west end of the lucerne field, at approximately four metre intervals. This placement minimised the catching of aphids which were leaving the lucerne crop in prevailing winds. Lowe (1966a) obtained a highly significant correlation between the numbers of aphids caught on three traps, two of which were placed in different crops with one between the crops. This indicates that the siting of a trap with respect to a crop does not affect the catch. The amount and type of crops

grown in the general area from which the trap is sampling can, however, affect both the number and species of aphids caught (Lowe, 1966a; Heathcote et al., 1969).

In the present study only two traps were used initially but three were used during the winter period to increase the chances of catching flying aphids. Each trap consisted of a metal cylinder 10.5 cm in diameter and 30 cm in length mounted on a metal stake with the base of the cylinder one metre above the ground. Heathcote (1957) has shown a cylinder of this diameter is suitable for trapping aphids.

The density of flying aphids can vary with height but evidence indicates that traps set at a height of one metre above ground will be close to the height of maximum aphid density (Heathcote, 1958; Coon and Pepper, 1968a; Wolfenbarger, 1975). Also there will be no effect on traps set at this height from aphids flying within the crop and most aphids trapped will be on their initial migratory flight (Johnson, 1954, 1969).

The traps were painted yellow since various authors (e.g. Heathcote, 1957; Heathcote et al., 1969; Roach and Agee, 1972) have reported that many aphid species are attracted to colours in the yellow region of the spectrum. However, aphids can only effectively control their flight at wind speeds below 1.5 m.p.h. (Haine, 1955) and therefore the attractant effect will steadily decrease at wind speeds above this.

A sheet of heavy clear plastic or a trimmed plastic bag was wrapped around each cylinder and fastened to it with paper clips. This plastic coating prevented damage to the yellow underpaint, and also it could be easily removed and taken to the laboratory when aphid numbers were high. If the sheets were taken to the laboratory the aphids were removed by washing in either xylol or a 50:50 mixture of isopropanol and benzene as recommended by Southward (1966). When few specimens were present they were removed in the field with a paint brush trimmed to only three or four millimetres of bristle. As much of the old grease as possible was then removed before a fresh layer was applied.

Three kinds of grease were used for trapping. "Stick-em Special" was used initially but this was observed to trap high numbers of large insects. Close (1959) found that trapping aphids using such a material was less efficient than using a 'cup' grease since he believed that the large insects shielded much of the trapping area, therefore, Mobil grease A No.0 was subsequently used in the present study. This grease also had other desirable properties because it was insoluble in water and of a suitable

consistency. Also weather did not greatly affect it although heavy rains
could cause it to peel off and it is possible that the orange colour of
this grease masked some of the attractant effects of the yellow cylinders
For these reasons 'Snow White' petroleum jelly was used for a three week
period in winter when very few aphids were flying. This also appeared to
be a suitable material since it had a relatively high melting point,was
insoluble in water, did not peel off, and gave a longer lasting smoother
and almost colourless covering. It did not, however, trap many insects
and therefore Mobilgrease was reverted to.

The traps were cleared away every four to eight days depending
on weather and all insects caught on the traps were kept to check for
A. kondoi as well as other aphids and aphid predators and parasites. The
catch was stored in a mixture of two volumes of 95% ethanol to one volume
of 75% W/W lactic acid (Eastop and van Emden, 1972). Any aphids were
examined under a dissecting microcscope and any possible A. kondoi were
stained and mounted, (see Appendix Four) and subsequently identified.

5.3.   Results and Discussion
5.3.1   The Flight Periods of A. kondoi

The flight periods of A. kondoi in relation to those of other
aphids trapped in the present study during the 1976-1977 period are shown
in Fig. 9. Results are given both as aphids per day per trap and as a
projected value of aphids per week on three traps, the latter being the
method of expression of Lowe (1966a, 1968a).

The spring flight peak was the most pronounced period of flight
involving many species of migrant aphid including A. kondoi and much
higher numbers of aphids than the period of flight which was considered to
be the autumn flight peak. This was probably due to the aphid populations
which are the source of the spring migrants, being larger and more synchro-
nised in their occurrence.

The autumn flight period contained no predominant peak with
flight occurring at a low but steady level during March-April 1977. Both
the beginning of trapping in 1976 and the end of it in 1977 may have
straddled the autumn peak and this may partially account for the low
numbers. Crop aphids in New Zealand generally have spring and/or autumn

Fig. 9   Aphids trapped on yellow cylinder adhesive traps
          at the DSIR study plot

AVERAGE NUMBER OF ALL APHID SPECIES PER DAY PER TRAP
AVERAGE NUMBER OF *A. kondoi* PER WEEK PER THREE TRAPS
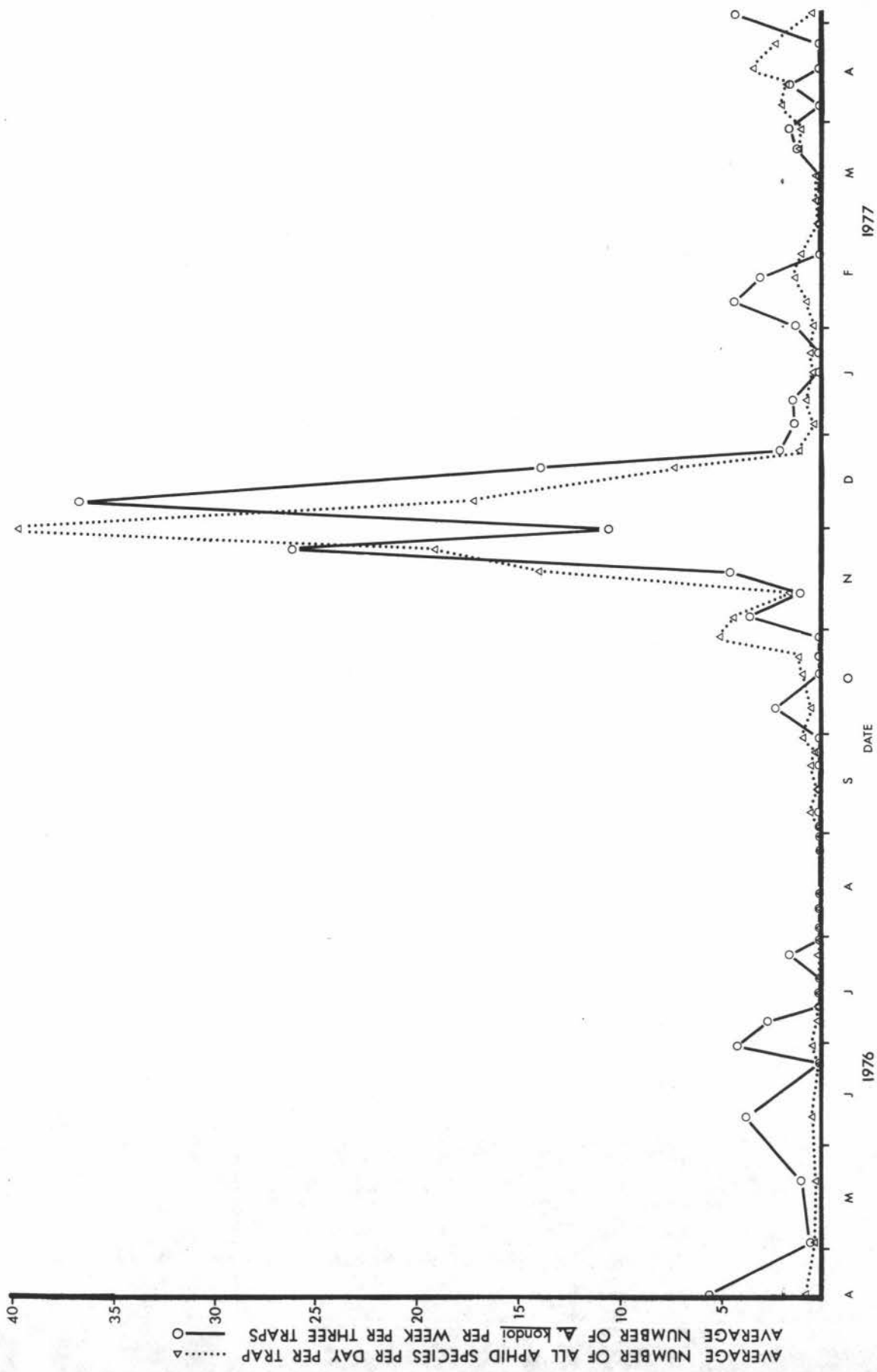
peak flights (Lowe, 1973b).

Flight by A. kondoi seemed to occur sporadically throughout summer though the number of aphids flying was very low. Flight during the winter months was also very low for species other than A. kondoi, but a small winter flight of A. kondoi did occur. Both Lamb (1958a, 1958b) and Lowe (1966a, 1968a) found that little aphid flight occurred in winter or summer.

The number of A. kondoi found per three traps places A. kondoi among the nine aphid species listed by Lowe (1966a) as major fliers. Other aphids which infest lucerne have also been classified as major fliers, especially A. pisum (Coon and Pepper, 1966a, 1966b) and T. maculata (Dickson and Laird, 1959) so this characteristic probably reflects some factor of the habitat. The maximum number of A. kondoi caught on the three traps in any one week was 37 although it is possible that the period from 8th to 15th December would have yielded even higher numbers but sampling did not occur then since the traps were destroyed when the crop was cut.

The maximum number of all species of aphid trapped was 833 per 3 trapsper week during the spring flight peak. This is lower than that reported by Lowe (1966a) and is probably accounted for by the fact that B. brassicae, the predominant aphid in Lowe's study, is not as significant in the Manawatu.

Some difficulty was encountered in interpreting the significance of small fluctuations and zero catches of flying aphids, especially when the errors of sampling with greased cylinders were considered (see Section 5.1) . Lowe (1966a) believed that catching no aphids does not necessarily mean none are flying, and has shown, using suction traps and greased cylinders operating together, that aphid flight can be occurring at a level which is not detected by the grease traps.

5.3.2   The Number of Flying A. kondoi In Relation to the Number on the Lucerne

The number of flying A. kondoi in relation to the population of A.kondoi on the plants is shown in Fig. 10. Since the source of the

Fig. 10   The number of <u>A</u>. <u>kondoi</u> trapped on yellow cylinder
           adhesive traps in relation to the total number of
           <u>A</u>. <u>kondoi</u> found on lucerne during fortnightly sampling
           at the DSIR study plot

NUMBER OF *A. kondoi* ON 84 STEMS ····●····

NUMBER OF *A. kondoi* PER WEEK PER THREE TRAPS ···○···

AVERAGE
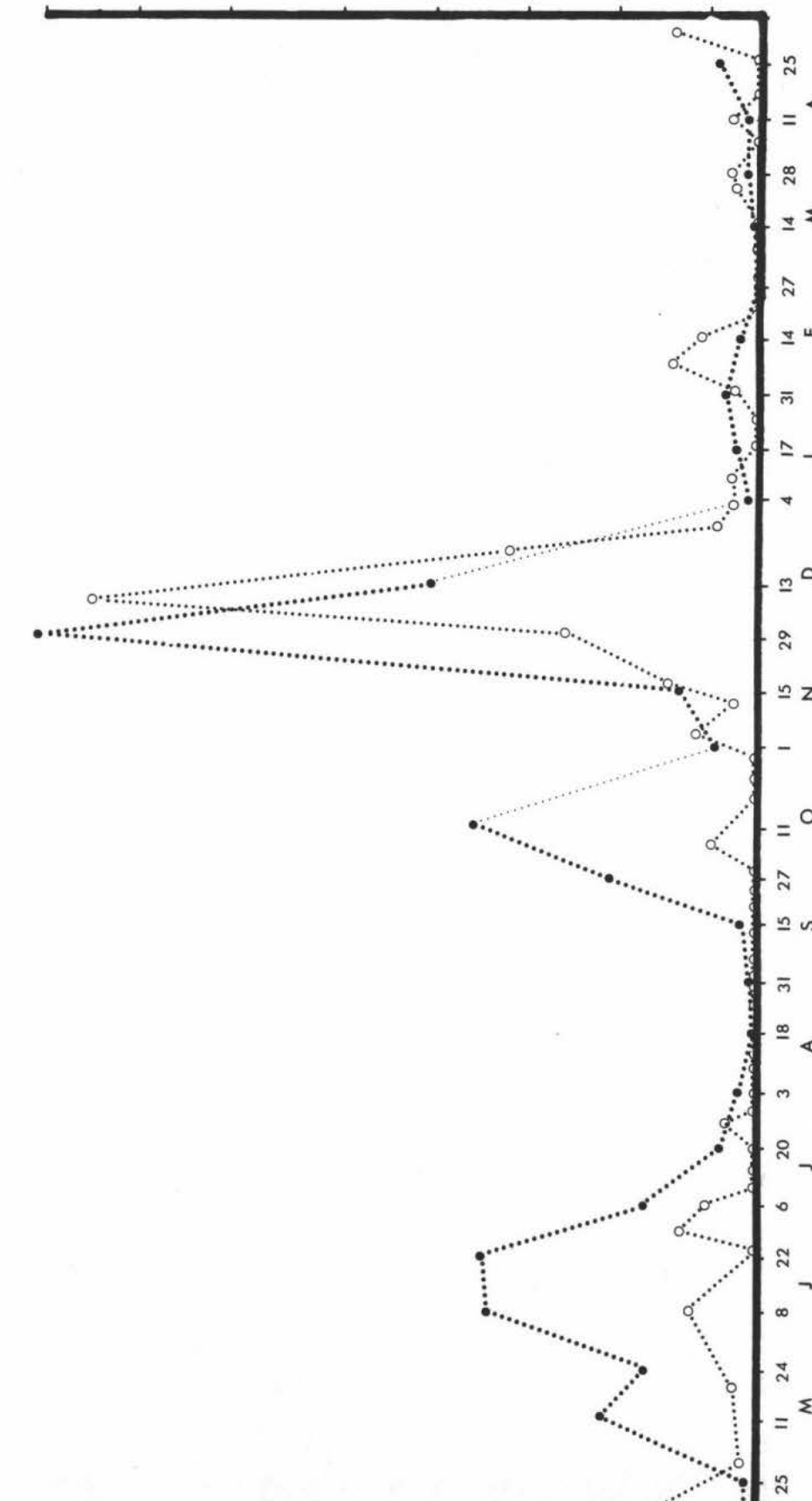
trapped <u>A</u>. <u>kondoi</u> is not known it is difficult to correlate the two factors
exactly but both periods of high <u>A</u>. <u>kondoi</u> populations at the DSIR study
plot, the winter and spring, coincided with aphid flight periods. Other
evidence (discussed in Section 10.3.4) indicates that alates are produced
as the aphid population density on the plants increase and hence flight
would be expected during these periods.

The major spring flight of <u>A</u>. <u>kondoi</u> coincided with the fall
off in the number of these aphids on lucerne in spring. The small June-
July flights were also presumably the result of the small increases and
consequent decreases in aphid numbers observed in winter. The smaller
population peak observed at the DSIR study plot at the end of January, but
more especially the high populations observed at Voss's at this time, and
which therefore presumably occurred in other local crops, were probably
the source of the alates trapped during the small February flight peak of
<u>A</u>, <u>kondoi</u>. The small flights in March and April 1977 again did not coincide
with any observed population rise at the DSIR study plot but other lucerne
plots in the Manawatu did contain high numbers of <u>A</u>. <u>kondoi</u> during this
period. Aphid populations were only beginning to build up during August-
September hence very little flight was recorded during this period.

Although Richardson (1977) showed that <u>A</u>. <u>kondoi</u> populations
on plants could build up to high numbers at any time in spring, summer or
autumn, in most cases these increases were prevented by management
practices from undergoing a "spontaneous" decline (see Section 4.3.2). It
is during the "spontaneous" population decline that alates are produced
(see Section 10.3.4) and if these declines are not allowed to occur then
this may partly account for the lack of more or less continuous flight
from October to April.

5.3.3 The Number of Flying A. kondoi in Relation to the Number
        of Alate A. kondoi on Lucerne

The presence of fourth instar alates rather than alate adults
is normally taken as evidence that a population is producing winged forms
because the presence of adult alates could mean that they were either
produced on the same plants or that they had flown there from another site.
Therefore the number of both fourth instar alates and adult alates in the
fortnightly population samples is shown in Fig. 11.

Fig. 11   The number of alate adult and alate fourth instar
           A. kondoi found during fortnightly population sampling
           at the DSIR study plot
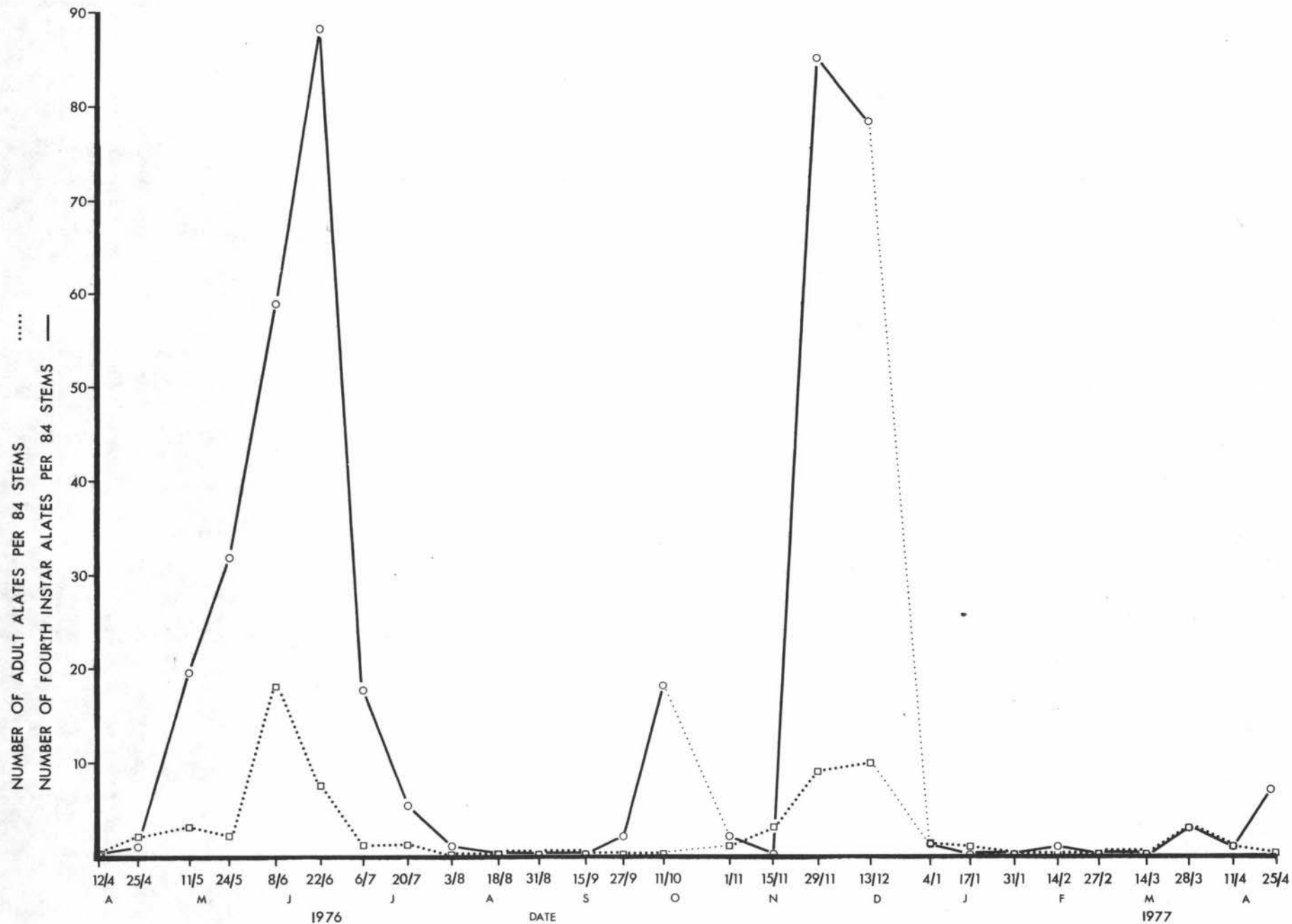
It can be seen that, in general, the occurrence of fourth instar alates on the plants coincided with the main flight periods of A. kondoi. Large numbers of fourth instar alates and adult alates occurred on the lucerne during May, June and July at the same time as the winter flight peak. These high numbers had declined by the 3rd August and this coincided with the drop off in the numbers of flying aphids. In addition, the small peak of fourth instar alates which occurred on 11th October also coincided with a small peak in the numbers of A. kondoi flying. Similar coincidences occurred between increased flight activity and the small increases in fourth instar alates on plants in early February and in late March and April.

The spring flight period also coincided with a peak of fourth instar alates on plants but there was a major discrepancy between the number of A. kondoi flying in November-December and in June-July, and the numbers which could have been expected to fly from the numbers of fourth instar alates observed on plants during these two periods. The number of fourth instar alates found on the plants on 22nd June was similar to that found on 29th November and 13th December and therefore flights of similar size could have been expected. In addition the number of adult alates observed on the plants was also similar so there was no reason to suspect that fourth instar alates were not maturing to adults in winter. There are a number of other possible explanations for the discrepancy: firstly, it is possible that the spring population numbers of fourth instar alates on plants was much higher than actually observed since the population samples on 29th November and on 13th December appear to have straddled a population peak. Secondly, many of the alates produced in the winter peak could have been 'non-flyers' (terminology of Shaw, 1967, 1968). This latter author showed that crowding increased the proportion of "migrant" alates in populations of Aphis fabae Scop., and possibly the required degree of crowding was lacking in the winter A. kondoi populations. Way (1973) believed that the stimulus for producing alates should not be confused with the stimulus required for them to fly. Thirdly, it is possible that alatae are much more active flyers in spring than in winter and hence they would have come from more distant sources. Such sources may also have produced a greater number of migrant alates than did the study paddock. Finally it is possible that temperatures were too low for flight to occur except on rare occasions in winter.

The overall pattern is that as the A. kondoi population increases the production of winged A. kondoi on plants also increasesand this coincides temporally, though not always numerically with an increase in the number of A. kondoi flying.

5.3.4 Alate Morphs of A. kondoi

All the specimens of A. kondoi caught on the flight traps were found to contain embryos and hence all were either sexuparae or virginoparae. However since no sexual forms of A. kondoi were ever observed on plants it is likely that all the alates were virginoparae.

5.3.5 Host Plants of the Alates of A. kondoi

It seems likely that because of the lack of a regular secondary host flights at all times of the year are to and from lucerne though occasionally many aphids may fly to lesser hosts such as white clover (T. repens).

The main flight periods occur before the periods of low aphid population on the plants, and this it would seem that few of the alate offspring survive these periods. The few that do survive along with those aphids which remain on the plants after population decline probably comprise the nucleus for the next population cycle.

5.3.6 General Comments

The correlation of aphid flight with weather factors has been an established practice (e.g. Davies, 1936; Thomas and Vevai, 1940; Kareem and Basheer, 1965) and most correlations resulted in the stating of specific weather conditions when aphid flight would occur. However, Johnson (1952a, 1952b, 1954, 1969) has argued that the particular weather conditions which are occurring when an aphid is trapped are not necessarily the same as those in which the aphid took off. The latter cannot be known without knowledge of the time and place of takeoff and even then the microenvironment within a crop may be quite different from the measured macroclimate. Johnson further believed that there was confusion between the weather factors which cause the production of alates and those which allow flight. It seems that most weather factors act primarily to affect

the general aphid population levels and hence the number of alates available for flight. Because of these criticisms no attempt was made to statistically correlate aphid flights with weather factors in the present study however it is apparent that no clear correlation exists. The general agreement with the A. kondoi plant population has been demonstrated in Section 5.3.2.

Because of the possible errors involved in calculating the density of flying aphids from greased yellow cyclinder trap catches (see Section 5.1) no attempt was made to do so. Lamb (1958a) transformed his catches in this manner, but the main reason for this seems to have been to impress on the reader the vast numbers of aphids which are flying even in periods when trap catches are relatively low.

5.3.7   The Flight Pattern of A. kondoi

Most aphid flight seems to follow a definite pattern which has been deduced from both field and laboratory observations (e.g. B. Johnson, 1958; Cockbain, 1961; Kennedy and Booth, 1963).

Aphids usually undergo an obligatory preparatory period after moulting to the adult alate form (Johnson, 1954, 1962) before flight can occur. Once this physiological barrier has been overcome and conditions are suitable, then the aphid takes off and begins an ascent phase due to a positive phototactic response and to the "irresistible" urge for persistent locomotion which characterises migration (Johnson, 1962, 1969). The combination of an obligatory preparatory period and the necessity for suitable conditions before takeoff occurs results in the observed diurnal peaks in aphid flight (Johnson, 1952a, 1962). The direction of the flight seems to be at the mercy of prevailing winds, and after a period of flight probably averaging one to three hours (Johnson, 1967,1969), with its consequent weakening of the migratory urge, the aphid will descend and is attracted to light of a yellow wavelength. Then by a series of usually increasingly shorter flights the aphid selects a suitable host plant using stimuli which are as yet poorly understood (van Emden, 1973). Some young may be deposited between these short flights but the majority are born after the aphid settles permanently.

There is evidence that A. kondoi conformed to this general pattern of flight behaviour. Alate A. kondoi were produced when the

density of aphids rose and they were frequently seen sitting close to the tops of stems often under the uppermost trifoliate leaves. Large numbers of alate adults were found on windows above cultures of A. kondoi and they are presumably responding to the light. Although the initial period of flight is not known, this may be quite long as evidenced by the rapid dispersal throughout New Zealand whereas at other times the initial flight was probably quite short, possibly only from one field to the next as was suggested for Rhopalosiphum padi L. by Lowe (1964). Short host-locating flights by A. kondoi also seem to occur since colonies consisting of a few first instars with or without an adult were found, especially during colonisation of a new growth of lucerne in the glasshouse by outside immigrants.

5.3.8   Conclusions

Only virginoparous alates of A. kondoi were found in the present study. Their major flight period in 1976 was in spring and no large autumn peak was observed. It is,however, known that the time and numbers of flying aphids may vary from year to year therefore further observations are required to establish the extent of variation. Sporadic flight occurred at other periods of the year, with some correlation being observed between the total number of aphids and the alates on the plant and the flight periods.Further study is required on the distance of aphid flight before the results can be more usefully interpreted.

CHAPTER SIX

THE PREDATORS, PARASITES AND
FUNGI OF A. KONDOI

6.1   Introduction

A study of the biology of A. kondoi would be incomplete and
economically less useful without some indication as to which parasites,
predators and entomophagous fungi were influencing the aphid population
and their effectiveness in doing this. This chapter contains information
concerning the observed predators, parasites and fungi of A. kondoi while
their effectiveness in controlling the aphid population is considered in
Chapter Nine.

The main predators of aphids are confined to the Coleoptera,
Diptera, Neuroptera and Hemiptera, but in addition less important and
often non-aphid specific predators are found in other insect orders and
also amongst the arachnids and birds. Preliminary observations in the
late summer of 1976 at Flock House, Manawatu, showed that predation by
various insects on A. kondoi did occur. Also Kain et al., (1976) reported
predation by Micromus tasmaniae (Walk.), Coccinella undecimpunctata L. and
syrphid species at Massey University but they found that "predators" were
not as common at Dannevirke.

Information on biological control agents was obtained in the
present study to aid in interpreting the spring, summer and autumn popu-
lation fluctuations of A. kondoi since it was expected that predators and
parasites would be active in the warmer months.

At the conclusion of the present study the results of a
survey of biological control agents of A. kondoi in Canterbury were
published (Thomas, 1977). Except for the presence of Nabis capsiformis
Germar and the absence of Nabis maoricus Walker in Canterbury both the
species ocurring and their numbers were similar to those found in the
present study.

6.2   Methods

6.2.1 Predators of A. kondoi

There are four main methods of determining the predators of an
aphid species. These are: observation of the predator eating (Hodet et al.,
1972); gut content analysis of the predator (e.g. Vickerman and Sunderland,
1975); serological techniques (Franks, 1967); and the use of radioactive
tracers (Robertson, 1976). In the present study the first method was
used since the common predators of aphids in New Zealand are well known
and their number is limited. Practical considerations were also involved
in making this choice because the latter technqiues required more time
and effort than was justifiable. In addition it was unlikely that a new
predator species would have been introduced along with A. kondoi. Although
it was possible that a new parasite or fungal species could have become
introduced within the body/bodies of the first immigrating aphid/aphids.

A search was therefore made both in the field and amongst
collected samples for those predators of aphids noted by Cottier (1953),
Valentine (1967a), Miller (1971) and Kain et al., (1976). Each week this
involved: searching the yellow and white adhesive flight traps described in
Sections 5.2 and 9.2.1; fixed time searching (Hodek et al., 1972) on the
lucerne stems and on the ground; collecting 80 lucerne stems and washing
the predators off them; sweep netting; and beating (Heathcote, 1972; Hodek
et al., 1972) the predators from the plants on to a greased tray. These
methods are described in more detail in Section 9.2.1. In addition to the
above the fortnightly population samples were also examined for any
possible predators, parasites and fungi, and a note was also made of any
whenever I was in a position to observe them. It was felt that the use of
a wide variety of methods ensured that all such organisms would be found
even if only one stage of a lifecyle was present.

Whenever a possible predator was found live specimens were
collected and kept in a petri dish with approximately 20 to 40 live
A. kondoi. In each case a variety of instars and morphs of A. kondoi
was included to eliminate the possibility that the suspected predator may
have had a preference for a particular morph or was only able to feed on a
certain sized aphid. The petri dish was subsequently observed for signs
of predation. It must be emphasised however, that even if a predator was
found to attack A. kondoi, this did not indicate whether the prey was

essential for the predator to lay eggs, or was an alterantive food supply for bodily maintenance only (B.C. Smith, 1966).

6.2.2   Parasites of A. kondoi

A careful examination for the swollen parasitised aphid bodies, usually referred to as "mummies" was made during the fixed time plant searching, and by carefully examining all of the 80 stems collected each week before they were washed. In addition, samples of up to 100 live aphids, or as many as possible whenever aphid numbers were low, were collected each week and kept alive for three days before they were examined for the development of mummies.

Any aphid mummies that were found were placed in small vials sealed with cotton wool (method of Stary, 1970) and left at room temperature away from direct sunlight to allow the parasites to hatch. Further specimens of these parasites were obtained for identification by placing the adult parasites with 20 to 40 A. kondoi, again including various instars and morphs, in a modified cover-slip box. This box was provided with organdie covered holes in the side and a cotton wool padded notch through which the lucerne stem entered (Fig. 12).

6.2.3   Fungi Attacking A. kondoi

A search was made for fungally infected aphids during the fixed time plant searching and by checking the 80 lucerne stems collected each week before they were washed.

An attempt was made to identify the fungi on the 6th April 1977 by collecting seven A. kondoi which were infested with fungus and were at the stage where the fungal mycelium had not yet burst the aphid body. These were placed individually on glass microscope slides in a petri dish lined with moistened filter paper and placed in the dark at a constant temperature of 24^0C. Nineteen hours later mounts were made in Shears Mounting Fluid (see Appendix Five) of the aureole (or "halo") of ejected conidia, and of the aphid body separated from the aureole and teased out.

Fig. 12   A modified coverslip box used for rearing
           aphid parasites

On the 26th March 1977 ten randomly selected lucerne stems from Exclusion Cage One (see Section 9.4.3) were collected and the position of the fungally infected aphids on these stems was noted.

6.3.   Results and Discussion

6.3.1   The Neuroptera Attacking A. kondoi

Various members of the Neuroptera are well known for their aphid feeding habits and the juveniles of some species are popularly known as "aphid-lions". New (1975) presents a review of predaceous Neuroptera of the world.

In the present study two members of the family Hemerobiidae, Boriomyia maorica Till. and M. tasmaniae, were found to feed on A. kondoi. These two species were identified from the descriptions of Tillyard (1923) and Hilson (1964).

6.3.1.1 Predation by B. maorica

Only a single female of B. maorica was found on Voss's property on 24th February 1977. This was collected and placed in a petri dish with approximately 20 specimens of A. kondoi. It was not observed to feed but three clusters of two to five eggs were deposited on aphids which were either dying or which died soon afterwards. This does not necessarily indicate that the species oviposits in response to aphids. The petri dish was left at room temperature away from direct sunlight and four of the eggs hatched on 2nd March. These newly hatched young fed on live A. kondoi placed in the dish even though the aphids were much larger than themselves.

Hilson (1964) recorded greater numbers of B. maorica in Canterbury than were observed in the Manawatu present study, and he believed that this Neuropteran could be an effective biological control agent of aphids, but this certainly did not apply for A. kondoi in the Palmerston North area.

6.3.1.2 Predation by M. tasmaniae

This species has been studied intensively by Hilson (1964) who provides descriptions and drawings of all the lifestages. It is widely

distributed throughout New Zealand (Cumber, 1959a; Cumber and Eyles, 1961a;
Hilson, 1964) and was common as an adult at all localities visited in the
present study being the only Neuropteran present in any numbers. This
also appeared to be the situation in Canterbury (Thomas, 1977).

The number of adults found in the present study often suggested
that there should have been a much higher number of juveniles present than
was generally the case. Hilson (1964) however, reported that most of the
juveniles were found in the litter and therefore the possibility exists
that a similar occurrence took place in the present study, although
juveniles were not detected during the fixed time ground searching. If
they do inhabit the litter then they presumably do not exert much influence
on the aphid population. However the larvae of M. tasmaniae have been
recorded as feeding on ten species of aphid (Valentine, 1967a) and although
they feed on other soft-bodied insects, aphids make up the greatest
percentage of prey (Hilson, 1964).

Adult hemerobids are also considered to be aphidophagous and
to have similar feeding habits to the larvae (New, 1975). The adults of
M. tasmaniae were, however, never observed feeding on A. kondoi even in
conditions when many juveniles were feeding. Indeed if left in a petri
dish with a number of A. kondoi they usually died within two to three days
indicating that no feeding occurred although sporadic oviposition was
observed.

In conclusion although Hilson (1964) believed that M. tasmaniae
is probably an effective aphid predator, my observations do not support
this. Possible reasons are discussed in the section on the effectiveness
of A. kondoi predators (Chapter Nine).

6.3.2   The Coleoptera Attacking A. kondoi

The Coccinellidae are the best known aphid predators in the
Coleoptera (Hagen, 1962; Hodek, 1967) although many other beetles are
occassional aphid predators (e.g. Vickerman and Sunderland, 1975). A
great variety of aphid consuming species is found throughout the many areas
of the world and attempts have been made to introduce some exotic species
to New Zealand (Thomas, 1977). Coccinellids are often assumed to be the
most abundant of the aphid predators, though this may be partially due to

their readily noticeable colouration.

In the present study the only Coleoptera which were found to attack A. kondoi were two species of Coccinellidae, Adalia bipunctatata L. and C. undecimpunctata.

6.3.2.1 Predation by A. bipunctata ("Two Spotted Ladybird")

This species was relatively rare in terms of numbers but was present on lucerne at Dannevirke, Flock House and around Palmerston North. It has been found to be an important aphid predator by overseas authors (Iperti, 1966a, 1966b; Niemczyk, 1966; Savoikaya, 1966) and has been recorded as a predator of many aphid species in New Zealand (Valentine, 1967a).

A single female of A. bipunctata was collected on 24th February 1977 and placed in a petri dish. Eggs were deposited over the next two days in three main clusters of 10,17 and 23 eggs. The first juveniles hatched six days later on 2nd March and were observed to feed on live A. kondoi placed in the dish. However no larvae were observed in the field, and it therefore seems that the species is relatively unimportant as a predator of A. kondoi in the Manawatu. The species is also reported to be rare on lucerne in Canterbury (Thomas, 1977).

There are several possible reasons for the rarity of A. bipunctata. Firstly, Hodek (1966a) states that some Coccinellidae are unable to feed successfully on some aphid species because they are toxic to them, although Blackman (1966) reports A. bipunctata feeds on A. pisum which is closely related to A. kondoi. A second possibility is related to the habit coccinellids have of searching for their prey in a preferred type of habitat (Hodek et al., 1962; Hodek, 1966a; Dusek and Laska, 1966) and A.bipunctata is typically found in woody habitats, so lucerne may be unsuitable. Other factors may also be involved since Hodek (1967) records A. bipunctata as the most common coccinellid on beet and beans neither of which are woody plants.

6.3.2.2 Predation by C. undecimpunctata (The "Eleven Spotted Ladybird")

This species was introduced into New Zealand in 1884 (Dumbleton 1936) in one of the world's first attempts at biological control, and it

is now probably New Zealand's most common coccinellid. Aspects of the biology of this species have been studied by Hawkes and Marriner (1927) and Harpaz (1958) overseas, and in New Zealand by French (1966).

The eleven spotted ladybird was present at all sites visited and was extremely common compared to A. bipunctata, with all coccinellid juveniles observed being C. undecimpunctata. The species was observed to be active and conspicuous on warm days, especially in spring, but early instars were rarely observed or sampled on plants. It is unlikely this was due completely to their small size but was probably also because they were present only on the ground or in the litter and thus were not easily observed. French (1966) reported similar findings and stated that first instars do not live on exposed surfaces. The first instar ladybirds are therefore probably not important in controlling the A. kondoi population.

Attempts were made to induce the adults of C. undecimpunctata to oviposit in a petri dish by introducing specimens of A. kondoi, but this was never successful. French (1966) also observed a similar lack of response from C. undecimpunctata towards other aphid species and it is likely that some other stimuli is required to induce oviposition.

6.3.3   The Diptera Attacking A. kondoi

The Syrphidae were the main predators of A. kondoi amongst the Diptera and no Cecidomyidae, which are also reported to be predaceous on aphids were found. The larvae of two species of syrphid, Melangyna novaezealandiae (Macq.) and Melanostoma fasciatum Macq. were important.

The adults of the New Zealand species of syrphids have been described by Miller (1921), but adequate descriptions of the larvae do not appear to be readily available, although it is this latter developmental stage which is aphidophagous. The adults feed on nectar, pollen and honeydew (Hagen and van den Bosch, 1968).

6.3.3.1 Predation by M. novaezelandiae

This species was the less important of the two species of hoverfly at the DSIR study plot, but its larvae were more common at Dannevirke and on Voss's property near Palmerston North. High numbers

of M. novaezelandiae were found on the latter property during the period of high aphid numbers in February 1977. The larvae were observed feeding voraciously on A. kondoi both in the field and in the laboratory as well as attacking each other in the laboratory.

There was no obvious reason for the low numbers observed in the field in the present study. Chandler (1966) and Dusek and Laska (1966) have observed that it is not the food, but the habitat which initially attracts syrphids to an area. Possibly M. novaezelandiae prefers the pre-European wooded environment rather than a pasture or it may be that very high aphid numbers are required to induce oviposition. The latter possibility is discussed further in Section 9.3.1.

6.3.3.2   Predation by M. fasciatum

Cumber and Harrison (1959) recorded M. fasciatum as being distributed throughout the North Island, and in the present study it was often observed on lucerne in the Manawatu and Hawkes Bay. M. fasciatum was much more common than M.novaezelandiae and was present as the adult from the beginning of spring until sampling terminated at the beginning of winter.

The larvae of M. fasciatum have been observed feeding on A. kondoi in the field and in the laboratory, though in the latter situation they either did not survive for long, or underwent what seemed to be premature pupation, in petri dishes with A. kondoi present. Davidson (1922) expressed the opinion that Melonostoma spp. are both phytophagous and ento-mophagous.

There appeared to be few larvae of M. fasciatum present in the field in comparison to the number of adults as was the case with M. tasmaniae. Hamrum (1966) believes that Melanostoma larvae are nocturnal and this may partially account for the low numbers observed, but even if this is so it is still likely that they would have been found by some of the sampling methods used.

6.3.4   The Hemiptera Attacking A. kondoi

Although various Hemiptera are predaceous on aphids only two

members of the Nabidae, N. capsiformis and N. maoricus were found in the
present study. They were identified using DSIR collections and Walker's
(1878) description of N. maoricus. The identification of N. maoricus
was confirmed by Dr L. Deitz. Both species are reported to be beneficial
in controlling insect pests (Cumber, 1959b;Eyles, 1960; Somerfield and
Burnett, 1976).

Very little is known of the habits of the New Zealand species
but evidence obtained during the present study indicates that they have
similar lifecycles and habits to those described for overseas species
(Mundinger, 1922; Taylor, 1949; Werner and Butler, 1957;Fewkes, 1961;
Ridgway and Jones, 1968; Deitz et al., 1976). These latter species are
reported to lay their eggs in plant stems and go through six instars
including the adult. The developmental stages of Nabis roseipennis Reut.
and Nabis rufusculus Reut. are illustrated by Munchinger (1922). They are
known to feed on a wide range of aphids and other insect pest species
(Mundinger, 1922; Werner and Butler, 1957; Cumber, 1959b;Whitcomb and Bell,
1964; Deitz et al., 1976).

The full importance of nabids in aphid control is only now
being recognised and as yet little quantitative work has been carried out
as to their effectiveness.

6.3.4.1   Predation by N. capsiformis

This species was notable for its almost complete absence. It has
generally been accpeted as the more common Nabis species (Miller, 1971;
Thomas, 1977) but this was not found to be so in the present study. The
reason for its absence is not known but no live specimens were collected
to find if it did feed upon A. kondoi. Jessop (1963) reported that
N. capsiformis fed on apterous nymphs of B. brassicae but did not appear to
take them regularly and therefore it may act similarly towards A. kondoi.
Valentine (1967a) and Miller (1971) also reported that N. capsiformis fed
on "aphids" and Valentine (1976b) believes that their effectiveness in doing
this can be significant.

6.3.4.2 Predation by N. maoricus

This species was very common in the DSIR study plot and was the main predator present from January to April in 1977. In contrast, numbers were low at both Dannevirke and Voss's, although the reason for this is not known. It may be that the greater variety of edible invertebrates present in the more diverse vegetation of the DSIR study plot was necessary to supplement their diet. They may also be exceptionally sensitive to the insecticides used in commercial plots.

Both adult N. maoricus and nymphs with wing buds have been observed feeding in A. kondoi in the laboratory. After 24 hours' starvation N. maoricus will often commence feeding in a petri dish within two to three minutes of being provided with A. kondoi, but no instances of feeding in the field were observed.

During the fixed time searching N. maoricus was more commonly observed on the ground than on the plants although sweep netting and beating on to a tray demonstrated that large numbers were present on the plants. When disturbed they tend to run down the plant, and since the body colouration is the same as that of dead lucerne, these factors may account for them not being easily visible on plants.

The sudden appearance of large numbers of N. maoricus in the sweep net samples on 11th February 1977, and the fact that most of these were late instars or adults, indicated that either the early instars were not present in the sampled vegetation, that they were not being sampled adequately, or that the duration of the early instars was very short in comparison to the latter ones. Other studies of Nabis spp. indicate that the last possibility is unlikely and experiments showed that the early instars could not escape through the mesh of the sweep net, thus ruling out the second possibility. It was therefore concluded that the early N. maoricus instars live on, or in, the ground or litter, rather than on the plants. Such a behavioural pattern was also reported for Nabis ferus (L) (Werner and Butler, 1957) and Nabis alternatus (Parshley) (Wheeler, 1977). This implies that early instar N. maoricus do not feed on aphid colonies and probably only prey on aphids which drop off the plants.

The occurrence of N. maoricus adults and juveniles is shown in Fig. 13. Most specimens seemed to be mature by April and probably over-wintered in the adult stage as has also been found for Nabis spp. on lucerne in Arkansas by Whitcomb and Bell (1964). These authors also reported that the nabids overwintered in the litter and were active on warm days.

During the end of February and in March and April 1977 N. maoricus may have possessed food sources other than A. kondoi since the aphid numbers did not seem to be high enough to support the high N. maoricus population during this period. N. capsiformis has been reported by Jessop (1963) to feed on Pieris rapae L. and M. novaezelandiae larvae, and probably N. maoricus also feeds on soft bodied insects. Certainly on one occassion a N. maoricus specimen was observed attempting to feed on a M. novaezelandiae larvae in a petri dish.

The migratory 'behaviour' of N. maoricus is unknown. They do not seem to fly and none were ever found on the adhesive flight cylinders although other large Hemiptera were trapped. It is possible that the yellow and white colours of the traps were partly repellant to them. When dropped N. maoricus specimens fell directly to the ground and never flew. This was repeated many times, both deliberately in the laboratory and accidentally in the field. Also three specimens were fastened with non toxic glue to a pin on the ventral side of the thorax and held in various positions in front of a fan. Although the legs of the glued specimens were not in contact with any surface no wing motion was observed. The implic-ations of this apparent lack of dispersal in relation to the aphid controll-ing potential of the species is discussed in Chapter Nine.

Variation in body colouration was observed, some forms being a very dark grey-black whereas others appeared almost creamy yellow. Still other forms possessed red tinged abdomens. Werner and Butler (1957) have also reported colour variations in N. alternatus but they believe they are not biologically significant.

6.3.5. Parasitism of A. kondoi

Parasitism of A. kondoi or its consequences were never observed in the field. Considering the extent of the field observations, the many

Fig. 13 The occurrence of <u>Nabis</u> spp adults and juveniles at the
DSIR study plot. Results until the 10th December were
obtained from: 100 beats of the lucerne on to a greased
tray, 200 sweeps "above" the vegetation, collecting 100
lucerne stems, and searching the ground and the plants
for five minutes each per sample. From the 6th January
beating on to a greased tray was replaced by the results
from 50 sweeps "through" the vegetation.
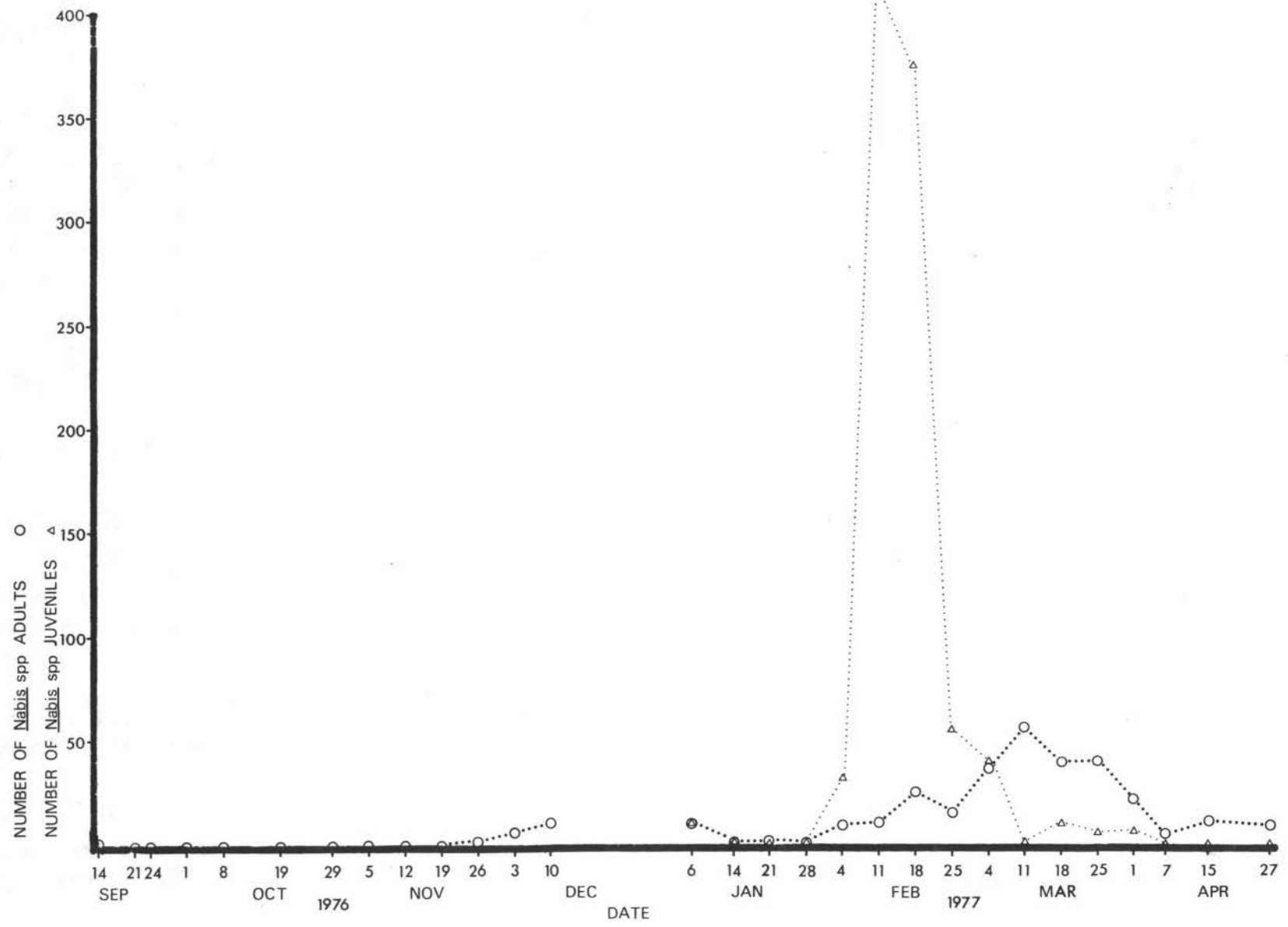
stems sampled, and the high numbers of aphids collected and held in "lily" cups, if parasitism was occurring it is highly likely it would have been detected. This complete absence of parasitism in the field conflicts with various reports from throughout the country. Only Thomas (1977) seems to have definitely detected parasitism in the field, and in this case the incidence was very low. Possibly the other reported cases were due to confusion between parasite mummies and fungally infected aphids. Parasites of A. kondoi also seem to be rare and restricted in distribution in Japan (Gonzalez et al., 1975).

In the present study parasitism was only observed in the laboratory and glasshouse. On the first occassion three parasitised aphids were collected from an A. kondoi colony kept in an insect culture room maintained above $20^{\circ}C$. Aphid mummies were also observed on two occasions in the glasshouse.

The parasite was identified as a member of the Hymenoptera family Aphelinidae by Mr Richard Hill. It is probably the same species as that found by Thomas (1977) and seems to prefer warm conditions.

6.3.6   The Arachnida Attacking A. kondoi

The Opilionidae (Harvestman) have been recorded as preying on small insects (Forster and Forster, 1973) and the Hunting Spiders probably also do this. Both were present in large numbers in the DSIR study plot especially in February and hence it is possible they were having some effect on the A. kondoi population. Hagen and van den Bosch (1968) reported that some spiders are known to prey upon aphids as a steady diet. Wheeler (1973) and Lopez and Teetes (1976) both state that spiders may be the first aphid predators present early in the season.

A large red mite, identified by Dr G. Ramsay as Anystis baccarum (L.) was common amongst glasshouse populations of A. kondoi and was observed to feed upon A. kondoi on a number of occasions. One mite was observed to feed for one hour on a second instar A. kondoi, resulting in almost complete evacuation of the aphid body. A. baccarum was reported to be one of the main causes of mortality of the aphids Schizolachnus pini-radiatae (Davidson) (Hagen and van dem Bosch, 1968), and Cinora palaestensis H.R.L. (Bodenheimer and Swirski, 1957).

6.3.7   Fungi Attacking A. kondoi

Fungally infected aphids were observed in high numbers in the spring of 1976 at the DSIR study plot, and in epidemic proportions in the autumn of 1977 in Exclusion Cage One (see Section 9.4). What appeared to be fungally infected aphids were also sporadically observed in much lower numbers on other occasions, mostly in areas of high aphid population. During many of the latter occasions the dead aphids were not microscopically examined, but they possessed the symptoms of infection by entomophthorous fungi, and other causes of death were unlikely since very few other microorganisms are known to infect aphids (Hagen and van den Bosch, 1968; Gustafson, 1971; Hall, 1973).

From the observations made on the large populations of A. kondoi at Voss's during February 1977, entomophthorous fungi never appeared to reach epidemic proportions at this locality. It is likely that this was due to unsuitable weather conditions especially dryness since high humidity seems to be an important factor promoting fungal attack. The more humid atmosphere inside the Exclusion Cages (see Section 9.4), where an epidemic of fungally infected aphids was also observed, was undoubtedly more conducive to fungal attack. It seems that Entomophthora spp. prefer warm moist conditions (MacLeod, 1955), though Hagen and van den Bosch (1968) and Gustafson (1971) both believe that it is difficult to generalise on this point. A suitably high aphid density is necessary for the spread of the infection throughout the aphid population (Grobler et al., 1962).

The fungus which caused the epidemic in Exclusion Cage One in autumn 1977 seems to have been a member of the genus Entomophthora and was probably Entomophthora planchoniana Cornu, though this identification is tentative.

Only three species of entomophthorous fungi have been recorded in New Zealand (Hall, 1973; Hall et al., 1976) and all are members of the genus Entomophthora (=Empusa) (Class Phycomycetes, Order Entomophthorales, Family Entomophthoraceae). This genus was first extensively described by Thaxter (1888) and the most recent work is that of Hall (1973).

In the present study fungally infected aphids were observed to turn a brick red to grey colour. The aphids became attached to the leaf

with a holdfast or rhizoid which emerged from the ventral thoracic region and terminated in a slight disc like expansion. As the infection pro- ceeded the aphids appeared to swell slightly and later short, thick, tubular and apparently unbranched conidiophore emerged from the dorsal surface of the abdomen (see Fig. 14), to form a relatively uniform growth. The conidia were then ejected to form an aureole or halo (Ingold, 1969) around the aphid, an effect which was easily observed when the aphids were placed on a glass slide. Under these conditions the conidia were observed to commence growth within 15 hours of their ejection. Later, presumably after the ejection of conidia was complete, the mycelium of the fungus broke down leaving a large hollow vent in the aphid's abdomen.

The condia which are shown in Fig. 15 are reminiscent of the "toupie d'Allemagne", or 'humming top'(Petch, 1938) of Cornu. The truncate, globose shaped with characteristic apical point conforms with the description of E. planchoniana in Petch (1938),Hall (1973) and Hall et al., (1976). They appeared to be surrounded by a mucilaginous layer which apparently attached them to the substrate (Alexopoulos, 1962). Thaxter's (1888) description of Entomophthora (=Empusa) planchoniana seems to be unreliable. This conclusion was also reached by Petch (1938).

E. planchoniana had been recorded in New Zealand on only four other aphid species (Hall et al., 1976) though it has been recorded overseas infecting other members of the genus Acyrthosiphon (Hall, 1973).

The sites on the plants where aphids infected with fungi were attached are shown in Table 3. The great majority of aphids were found on

Table 3   The site of attachment on plants of A. kondoi attacked by entomophthorous fungi

	Underside of leaflet	Topside of leaflet	Flower	Growing Tip	Flower Petiole	Leaf Petiole	Stems
No. of aphids	197	2	2	1	1	2	0

the completely opened leaflets and none were found on the main stem or auxiliary stems. The significance of these results is unclear. At the advanced stage of population growth, which these infected colonies of A. kondoi had reached, a great many of the aphids feed on the underside

Fig. 14 A. <u>kondoi</u> killed by E. <u>planchoniana</u>. The mycelium of the
fungus is growing from the abdomen of the aphid.

Fig.15   An ejected conidia of E. <u>planchoniana</u> showing the typical
"humming top" shape.
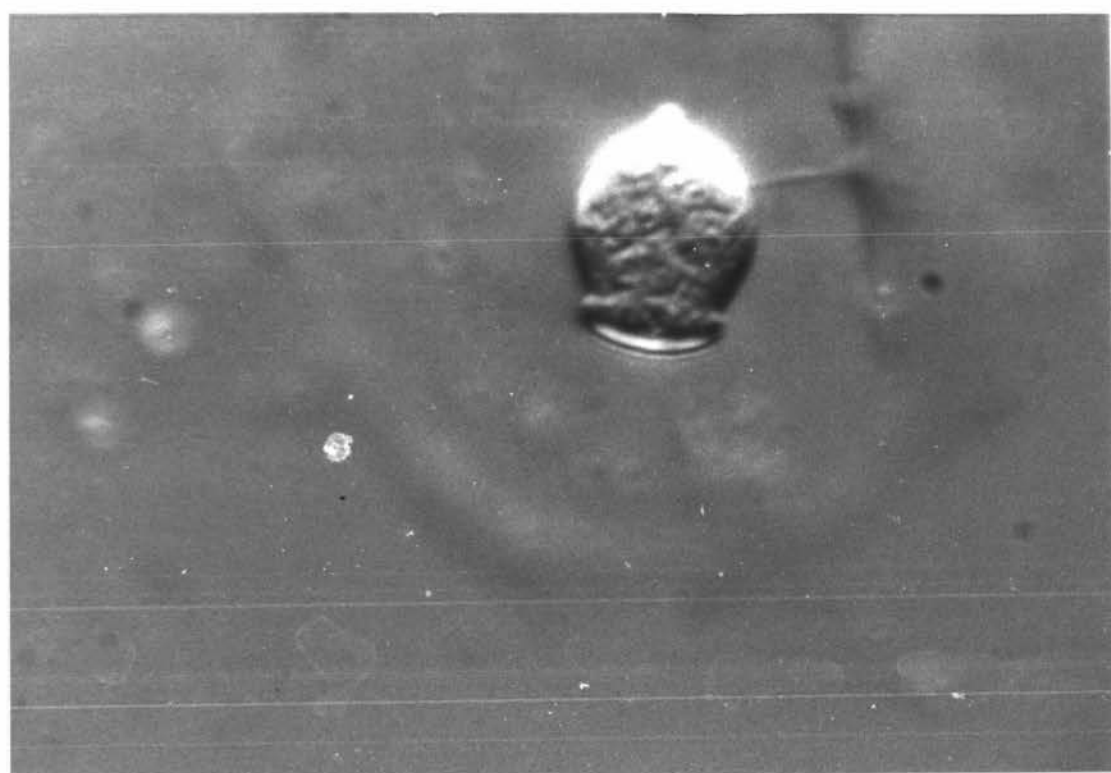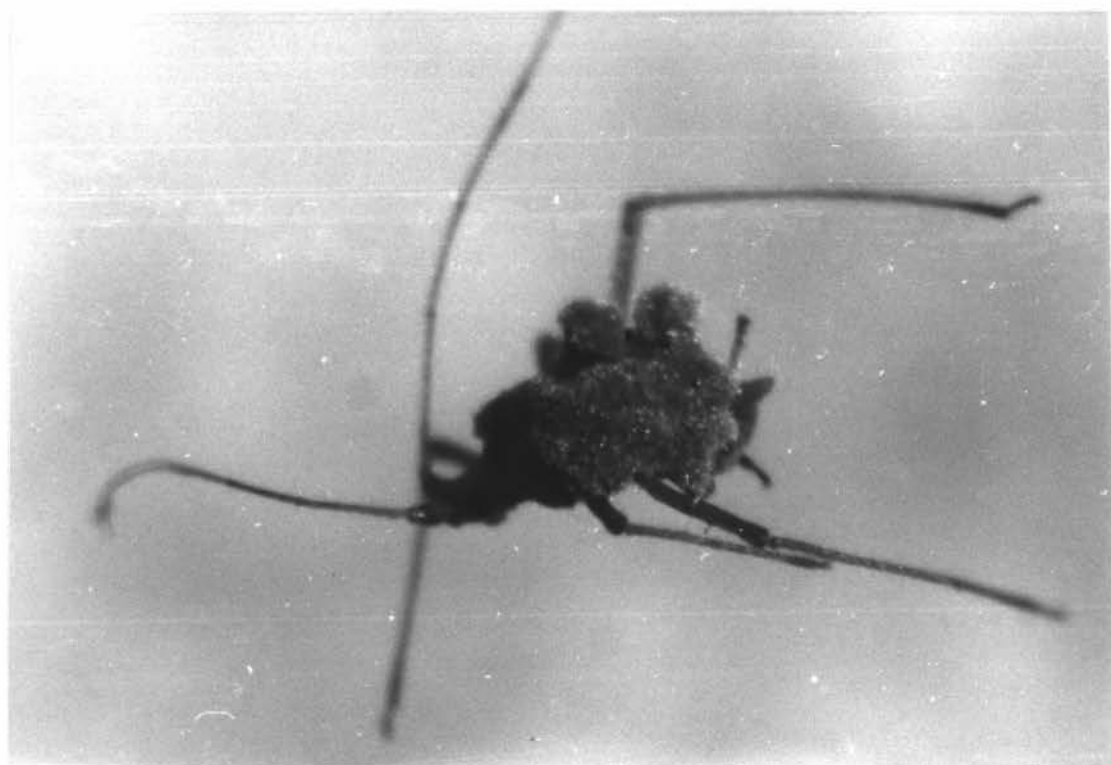
of leaflets. The site under the leaves may simply present a more suitable microclimate for the development of the fungus.

6.3.8 Conclusions

A large diversity of aphid predators and parasites seems to be lacking in New Zealand. Only one aphidophagous species in each of the four main aphidophagous orders seems to be present in large numbers. There also seem to be very few parasites, a conclusion also reached by Lowe (1968b) and Carver and Stary (1974).

Overseas studies usually show a greater variety of predators is present than is the situation in New Zealand. For example, Hamrum (1966) stated that 10 to 12 syrphid species are commonly found in Minnesota. Glumac (1966) noted there are 99 aphidophagous syrphid species in Yugoslavia, although six of these species make up 85% of the larvae found. Smith and Hagen (1966) reported that 19 species of coccinellid prey on lucerne aphids in California. Presumably the paucity of predators and parasites in New Zealand is due to the lack of a large native aphid fauna on which aphidophagous species could have evolved.

The implications of this lack of diversity in the predator fauna are great (e.g. Hodek, 1967). Each predaceous species is only effective in certain microenvironment conditions (Chiang, 1966; Ewert and Chiang, 1966) and since a large variety of microenvironments occur in a particular crop, predators are needed which are successful in each of these to effectively control the number of aphids. This microenvironment effect has been demonstrated in three species of coccinellid by Ewert and Chiang (1966) and in syrphids (Dusek and Laska, 1966).

Biological differences between predator species may also be important. Sluss (1967) has demonstrated that two coccinellids, Hippodamia convergens Guerin-Meneville and Olla abdominalis (Say) require different densities of aphids for them to stay in an area, and hence O. abdominalis remained and fed on Chromaphis juglandicola (Kalt.) when aphid numbers were below the critical level required to retain H. convergens.

CHAPTER SEVEN

THE EFFECTS OF WEATHER

ON A. KONDOI

7.1.1 Factors Controlling the Population of A. kondoi

It has been estimated that if one aphid was allowed to breed in ideal conditions its progeny after 300 days would number 210^{15} (Imms, 1957). Obviously this situation never occurs since the aphid population is part of a system in which various extrinsic factors interact with the aphids' homeostatic mechanisms to control the population.

Few efforts have been made to study a population of aphids with respect to all the factors influencing it because of the formidable logistical problems involved but some studies have successfully considered a number of aspects (e.g. Hughes, 1963; Sluss, 1967; Foster, 1975; Perrin, 1976). Most studies however are restricted to the effect of one factor, though obviously an intensive study of each factor, and a comprehensive study of all the factors and their interactions, are both useful and necessary.

One of the main reasons for studying aphid populations is to identify the controlling factors and determine how these interact (Hughes, 1972). This must be done both qualitatively and quantitatively before a model can be developed which enables accurate predictions to be made on the aphids' future population. Ideally the models describing lucerne aphids and their controlling factors should be synthesized with the models of other lucerne pests to provide a model of the complete lucerne eco-system such as is presently being attempted in the USA (Armbrust and Gyrisco, 1975).

The present study necessarily falls far short of any such comprehensive model and for the most part only a verbal model (Clarke et al. 1967; Hughes, 1972) which lacks quantitative data can be presented. This is to be expected if little is known of the insect, as was the situation with A. kondoi in New Zealand, since the first year must be spent in the planning stage gaining basic information (Hughes, 1972). Five

years is considered the minimum period required to obtain useful inform-
ation on the population dynamics of any insect in a temperate climate
(Richards, 1961) and even longer term cycles may exist in an aphid
population (Dixon, 1970).

There are four main factors affecting any population of aphids.
These are climate, predators, parasites and fungi, the host plant and the
aphids themselves. In this study the effects of each of these factors on
the population of A. kondoi over the one year study period is considered.

7.1.2 Introduction - the Effects of Weather on A. kondoi

Climatic variation may account for up to 60% of the fluctuation
in numbers observed in some insect populations (Richards, 1961). Aphids
are poikilothermic, soft bodied and fragile insects which often live in
positions which expose them to the full force of the elements. It follows
then that weather often plays a major part in their population dynamics
and largely determines their recurring annual population ryhthms. Climate
may also indirectly influence the aphid population by affecting many
other factors which interact with the population, the most important of
which are the entomophagous fungi.

There are two important aspects when considering the effects
of climate on aphid populations. Firstly there may be especially large,
usually severe effects resulting from a limited period of exceptional
weather such as very low or high temperatures or heavy rain. These are
usually restricted in their occurrence and hence are referred to as the
local weather effects. Secondly, there is the climatic effect on aphids,
which extends beyond the local weather effects. It is a long term effect
and is due to the annually recurring seasons.

The conclusions drawn in this chapter are mostly the result of
correlations between the observed numbers of A. kondoi and the various
climatic factors. Such correlations can indicate but do not prove cause
and effect. The situation is further complicated in that the climatic
factors themselves are interrelated. Laboratory experimentation is
usually needed to isolate and determine the effect of each particular
factor, and a comprehensive knowledge of the effect of weather on aphids

would require many years of data collection and experimental analysis
(Lowe, 1966b).

The present study was limited to investigating the effect of
macroclimate on A. kondoi, however it is recognised that the microclimate
effect on aphids may be substantial (e.g. Lewis and Siddorn, 1972), and
certainly may occasionally influence A. kondoi (see Section 7.3.1.2).

7.2 Methods

All meteorological data was obtained from Climate Recording
Station 19 at the DSIR in Palmerston North. This station is sited
approximately 400 metres from the A. kondoi study area. Both sites are
equally exposed, though the study area is lower by ten metres and is
closer to the Manawatu River.

The wind run was measured with a recording cup anemometer;
the evaporation with a raised pan evaporimeter; the grass minimum was
recorded at a height of one inch above the ground; and the daily maximum
and minimum, and nine a.m. air temperature in a Stevenson screen.

7.3. Results and Discussion
7.3.1 Local Extreme Weather Effects
7.3.1.1 Rainfall

The effects of heavy rain in removing aphids from plants was
observed in February 1977, when A. kondoi colonies were examined before
and after a period of exceptionally heavy rain. On the latter examination
the colonies were found to have rain drop sized "holes" in them. The
aphids had apparently not moved to a more protected place on the plant,
and the holes in the colonies therefore indicated that it was the actual
physical impact of the drops which had dislodged them. A. kondoi would
be especially exposed to this form of mortality because of its habit of
feeding on the growing tips of the plants.

Studies by Miskimen (1970) on Siphaflava (Forbes), the Yellow
Sugarcane aphid, have shown that heavy rain may be a major factor in
population control, but this species occurred in a tropical rain zone,
and such heavy rain at Palmerston North is infrequent. In the temperate

zones occasional reports indicate the detrimental effects of heavy rain on aphids (e.g. Le Roux, 1959; Nielson and Barnes, 1961; Dunn, 1965; Way and Banks, 1967; Hughes and Gilbert, 1969) and though such rain can have a severe effect it is sporadic in occurrence, and is rarely a major factor in long term aphid population change.

7.3.1.2 Wind

Strong winds blew for long periods during parts of November and December 1976. These winds were probably dehydrating to both the plants and aphids at a time when water stress is normally high.

On 2nd December 1976 the colonies of A. kondoi at the DSIR are thought to have changed their positions on the plants since after this date fewer aphids were present around the growing tips, than were found on side shoots and around the intersection of side shoots and the main stem. These latter positions were more within the shelter of the crop microenvironment and were subject to noticeably less rapid wind movement than the growing tips. The pattern of aphid distribution and the numbers of aphids involved indicated that their movement was not entirely dependent on aging of the colony (see Section 4.3.7).

It is possible that the aphid movement occurred because the continuous erratic movement of the growing tip was disturbing feeding rather than because of direct moisture stress on the aphids, but it is also likely that water stress on the plant plays a significant part in determining its suitability for A. kondoi, and therefore a combination of both factors may be involved.

Preliminary experiments using wind tunnels were unsuccessful in inducing a similar movement of aphids but it was difficult to simulate exactly the crop microenvironment within the wind tunnel for a long enough period of time.

7.3.1.3 Frost

On the 24th May 1976, the A. kondoi population at the DSIR study plot was observed to have decreased from that measured on 11th May 1976 and this was apparently due to abnormally low numbers of first instar A. kondoi (see Appendix Two). These low numbers may have been due to the selective deaths of this instar, or to a decrease in the reproductive rate

of adults. It is however, significant that on 23rd and 24th May immediately before the low numbers of first instars were observed, the first two major frosts of the year were recorded. A similar decline in the ratio of first to second instars occurred in the population sample of 25th April 1977, four days after the first frost of 1977.

Mortality due to frosts has also been demonstrated to occur in Aphis pomi DeG. by Le Roux (1959).

7.3.2 Long Term Climatic Effects
7.3.2.1 General

The meteorological factors that appeared most likely to influence the aphid population were daily maximum temperature, daily grass minimum temperature, daily nine a.m. temperature, daily nine a.m. relative humidity, daily rainfall and daily evaporation. The wind run was not considered because it would affect the aphids mainly via evaporation. All values recorded were averaged over the interval between samples.

It can be seen from Figs 16 and 17 that there is no strong correlation between the numbers of A. kondoi and the above climatic factors, and this is in agreement with the results of Richardson (1977). The relationship between climate and population need not however be consistent, for example the climate factor may have a limited range within which the correlation is strong whereas outside this range the correlation may change or may not exist. Figs 18 and 19 were plotted to show whether this occurred, but it can again be seen that no such obvious partial correlation exists. The effects of the individual climatic factors are considered in more detail below.

7.3.2.2 Temperature

Temperature is the main climatic component affecting aphids since their metabolic rate is heavily dependent on it. The "classical" picture of the effect of temperature on aphids is that low winter temperatures falling beyond a developmental threshhold temperature results in low aphid numbers and consequently no population increase. With the rising temperatures of spring, an increase in aphid numbers and developmental rates occurs, which falls off when the temperature passes the optimum, and stops when the upper developmental threshhold temperature is exceeded.

Fig. 16   The relationship between the population of <u>A. kondoi</u>
           at the DSIR study plot and temperature related factors
           of the climate
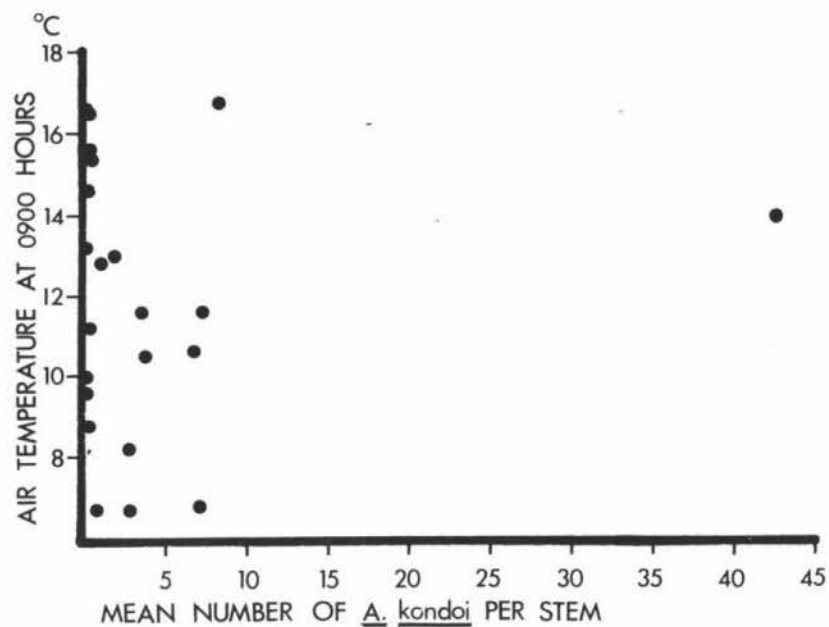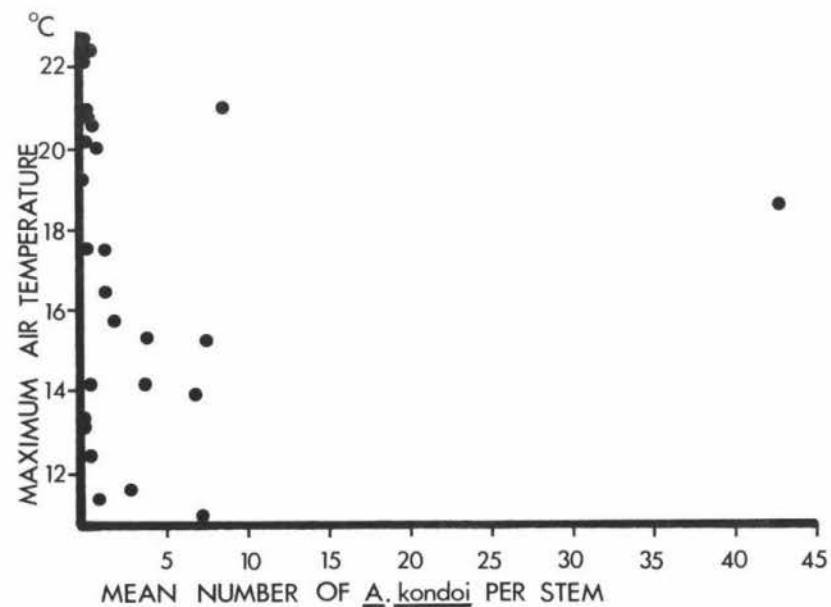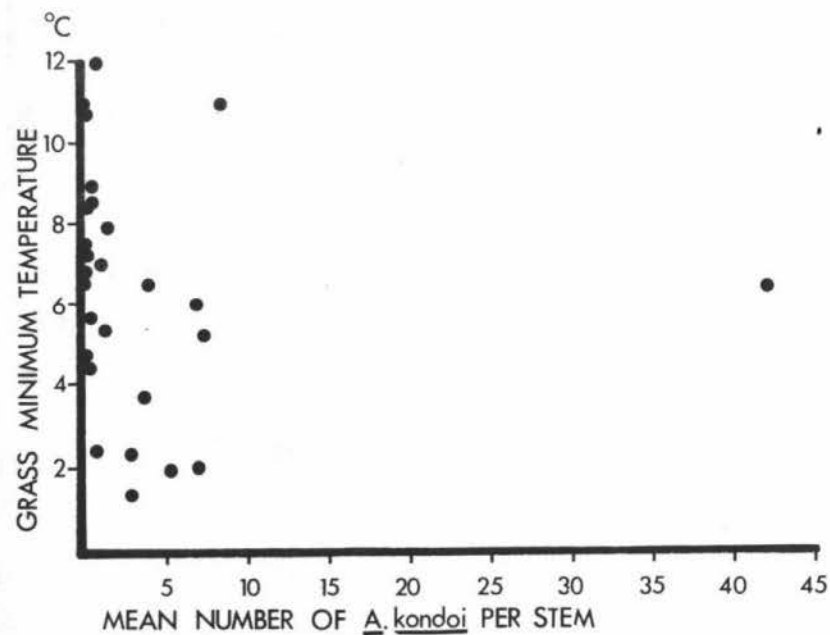
Fig. 17   The relationship between the population of A. kondoi
           at the DSIR study plot and moisture related factors
           of the climate
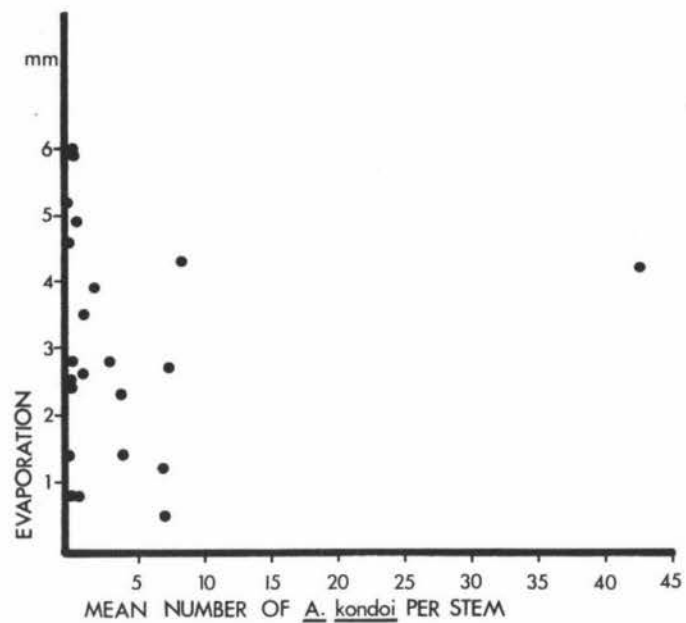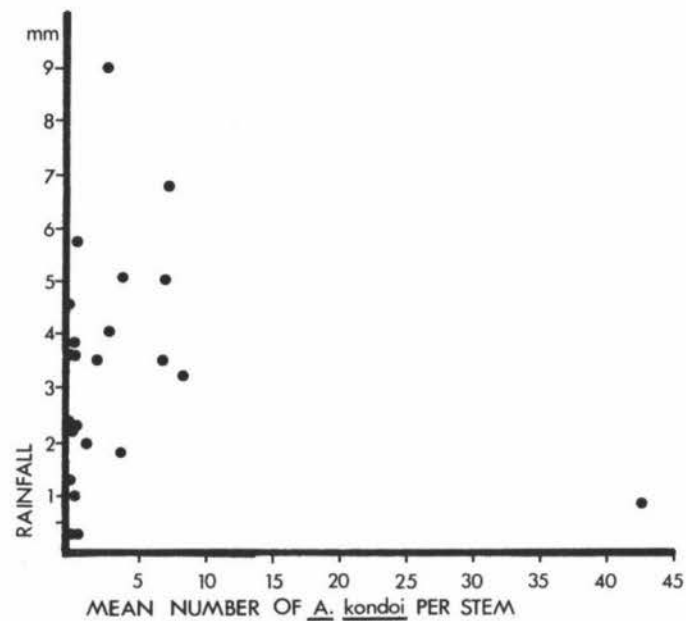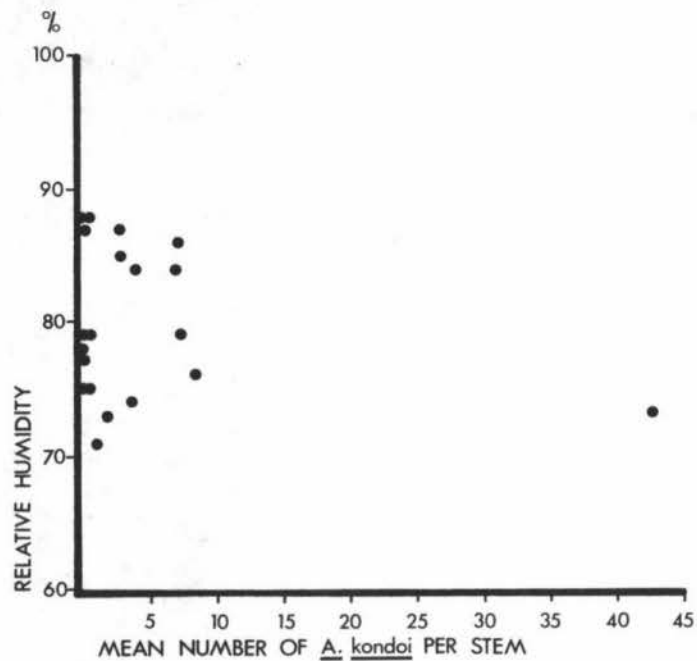
Fig. 18   The population of A. kondoi at the DSIR study plot
           in relation to the variation in temperature related
           factors of the climate

NUMBER OF *A. kondoi* PER 84 STEMS ●⋯●

1977

DATE

1976

°C

DAILY GRASS MINIMUM TEMPERATURE ▽⋯▽
DAILY MAXIMUM AIR TEMPERATURE □⋯□
DAILY AIR TEMPERATURE AT 0900 HOURS ▼⋯▼
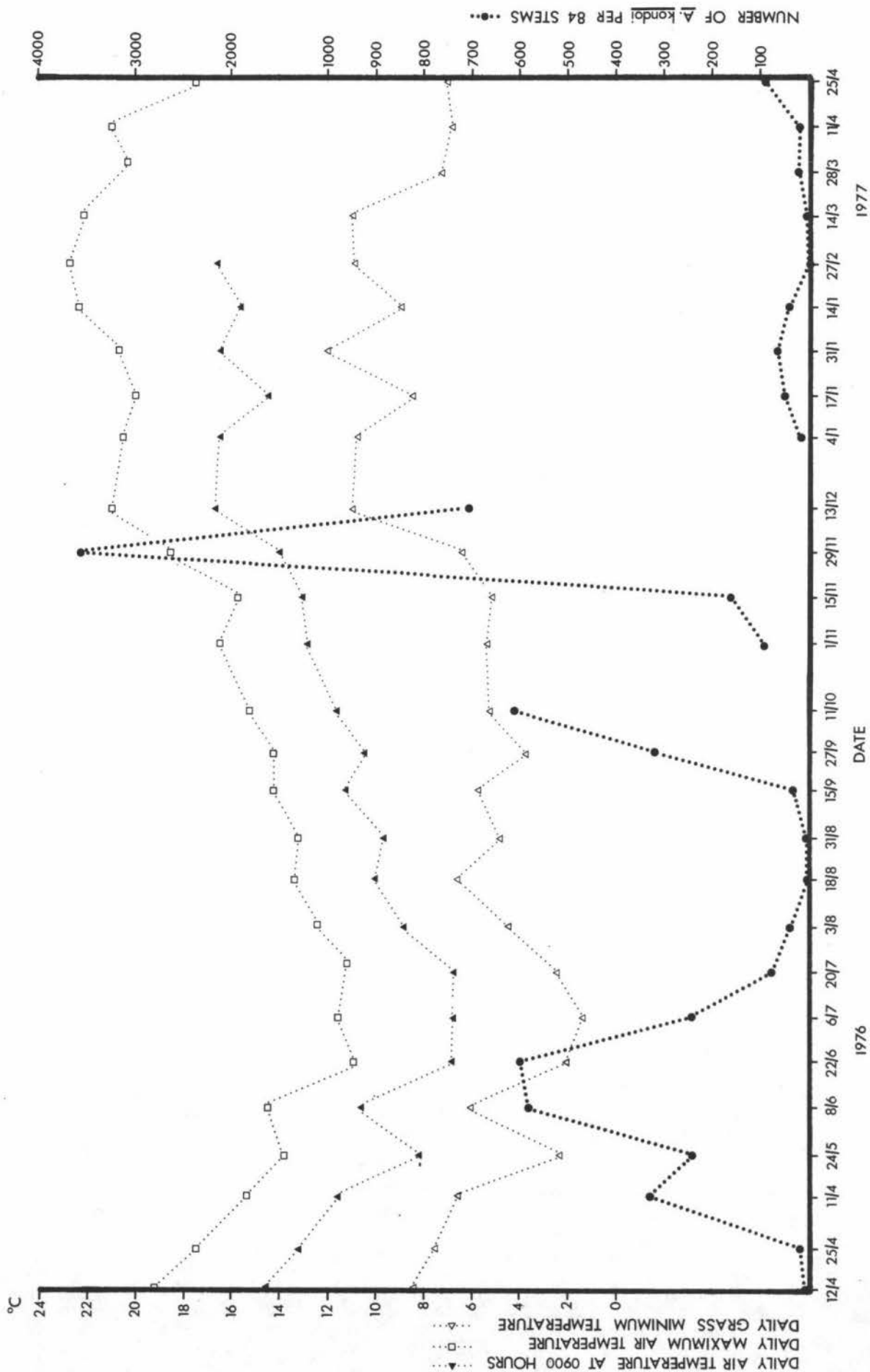
Fig. 19   The population of $\underline{A}$. kondoi at the DSIR study plot in
           relation to the variation in moisture related factors
           of the climate
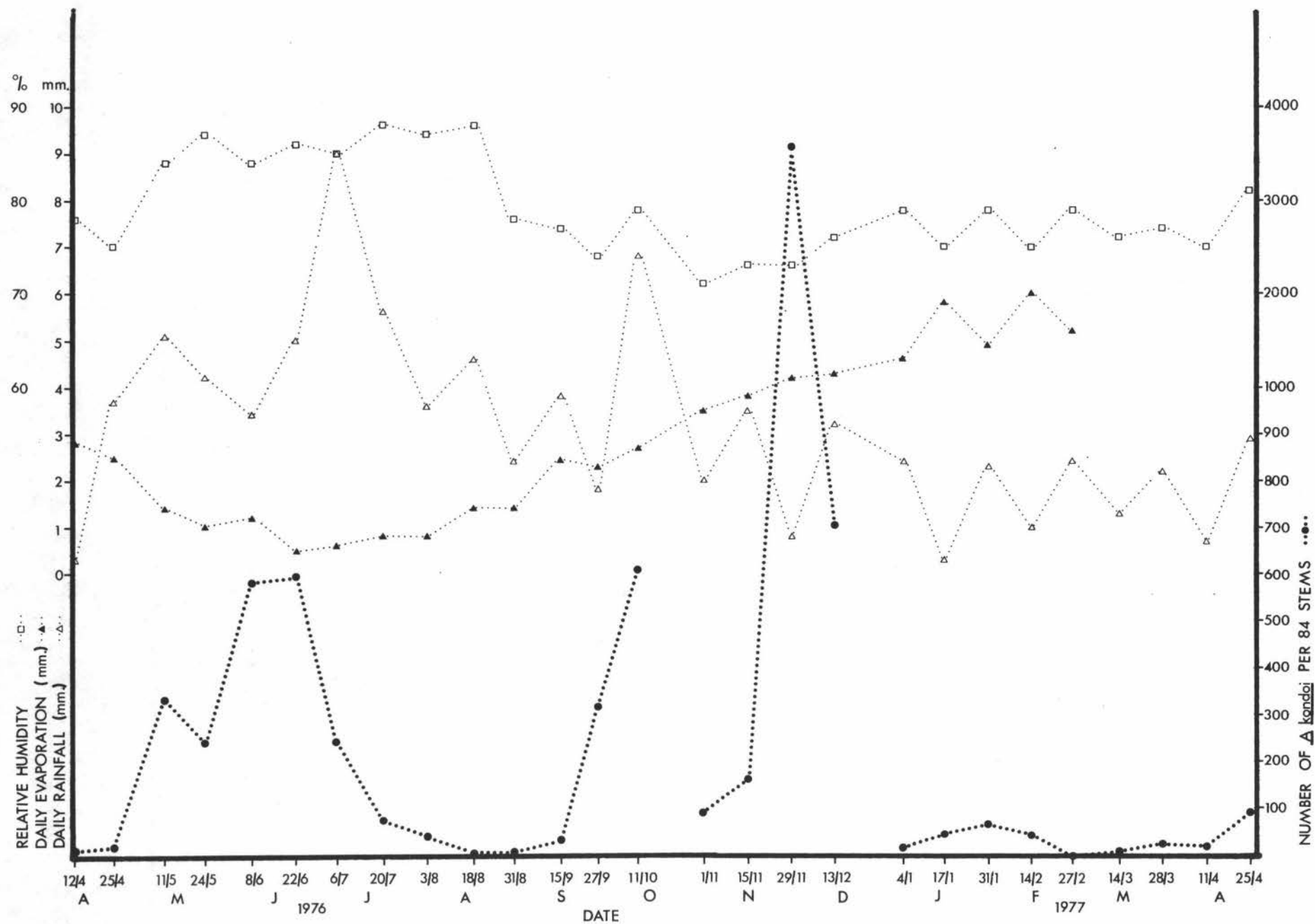
In autumn the temperature again passes through the suitable temperature range resulting in another increase in aphid numbers. The lower development threshhold temperature for $\underline{A}$. $\underline{kondoi}$ is $4^{o}C$ (Hughes, 1977) and the upper developmental temperature is probably around $24^{o}C$ (Lowe, 1966b).

In winter the numbers of $\underline{A}$. $\underline{kondoi}$ increased while the temperatures were decreasing. Indeed the aphid population seems to have been developing to its winter peak in numbers when the lowest average daily maximum temperature and average daily nine a.m. temperature occurred (see Fig. 18). The low temperatures of winter in the Manawatu do not therefore seem detrimental to $\underline{A}$. $\underline{kondoi}$ and the main effect of low temperatures during the winter period seems have been in decreasing maximum population size of the winter cycle and extending the duration of the cycle. The effect on the maximum population size would have occurred partially through a vegetational effect since during the low temperatures the host plants would only have been growing very slowly if at all and hence could only have supported a low aphid population. The effect on duration of the cycle can be seen by comparing the winter peak which extended from 25th April 1976 to the end of July, approximately three months, whereas the spring peak began in early November and probably would have ended in late December, a period of about two months.

The population of $\underline{A}$. $\underline{kondoi}$ began to rise after the 31st August paralleling the rise in temperature which had, however, started sometime previously. This again indicates that the pattern of aphid population cycles was not determined by low temperatures. This increase in numbers continued up to a maximum when the daily maximum temperature rose to within a range of $18.6^{o}C$ to $21^{o}C$ in early December and after this a rapid decline in numbers occurred. It is tempting to attribute this rapid decrease, and the low numbers of aphids which were found from January to April 1977, to high temperatures and although this may be partially true, the hypothesis that high temperatures cause low numbers of $\underline{A}$. $\underline{kondoi}$ is not consistent with all the facts. Although the situation concerning the low numbers of $\underline{A}$. $\underline{kondoi}$ which occurred during January to April 1977 was confused by the presence of predaceous nabid bugs exclusion cage experiments indicated that the aphid populations would have undergone a period of high numbers during the hottest part of the year. Indeed the highest

number of A. kondoi in Exclusion Cage One coincided with the occurrence of the highest maximum temperature, 22.8°C. If the drop off in aphid numbers after the spring population peak and the subsequent period of low aphid numbers had been due entirely to high temperatures then it is difficult to explain the population peak at Voss's which was close to its highest numbers when the highest temperatures of summer were recorded. Similarly, the occurrence of high numbers of A. kondoi on white clover in a glasshouse was observed at this time and this again indicates that high temperatures did not control the aphid population especially since temperatures in the glasshouse were even higher than outside.

It can therefore be concluded that at no time were high temperatures alone responsible for determining the pattern of A. kondoi population observed from December to April and although A. kondoi was considered a cool weather aphid by Summers (1975), large populations appear able to develop in situations where very high temperatures occur. The reputation of A. kondoi being a cool weather aphid is possibly explained by three factors: firstly, the effects of crop microclimate are often not considered. Secondly, often only extremes of daily weather are considered, but so long as A. kondoi can survive these extremes it can develop rapidly at other periods of the day when conditions are more suitable. Lastly, weather factors are usually considered in isolation, mainly for practical reasons, and yet a combination of factors may be more important. For example, it appears probable that A. kondoi is capable of withstanding much higher temperatures if it is not subject to water stress.

It is likely that the upper threshhold temperature for development was never effectively reached and that the decline in aphid numbers in the study plot after the spring population peak was due to intrinsic population regulating mechanisms of A. kondoi (see Chapter Ten), and/or plant conditions (see Chapter Eight), while the low numbers observed outside the exclusion cages over the January to March period was largely due to predators (see Section 9.4).

Attributing low aphid numbers over summer to high temperatures has often not been supported with corroborating evidence. Frazer and

van den Bosch (1973) demonstrated this when they artificially released
C. juglandicola in summer in areas which had not had high aphid numbers
in spring. The rapid increase in the numbers of this aphid which then
occurred indicated that it was not high temperatures which had previously
kept aphid numbers low in summer, but that leaves were normally rendered
unacceptable to the aphids by sooty mould and debris from the spring peak.
Sluss (1967) also noticed that high temperatures did not always stop the
population growth of C. juglandicola and Miskimen (1970) believes excess-
ive emphasis has been placed on high temperatures controlling aphids in
summer. This does not mean that temperature is unimportant in all aphid
populations because in some it obviously does exert a large effect (e.g.
Richards, 1961; Sluss and Hagen, 1966; Sluss, 1967; Perrin, 1976), rather
it is difficult to attribute critical population effects to temperature
without corroborating evidence.

It seems likely that the lower temperature threshhold for
development in A. kondoi was never effectively reached in the present
study. Although the temperature did fall below $4^{\circ}C$, the lowest average
maximum daily temperature reached was $10.9^{\circ}C$ and this occurred at a time
when aphids were observed in very high numbers on winter growing lucerne
on a small study plot at the DSIR.

The population seemed to expand most rapidly in the period
between the 1st and 15th November when the average maximum temperature
was $15.7^{\circ}C$ and the average nine a.m. temperature was $13^{\circ}C$ and these
temperatures can therefore be assumed to be close to the optimum develop-
mental temperature. As optimum temperatures these seem to be relatively
low and this may also explain in part why A. kondoi is considered a cool
weather aphid.

7.3.2.3 Moisture

There is little obvious relationship between the moisture
related factors and aphid numbers (see Figs 17 and 19). Exceptionally
high rainfall occurred in 1976, but it is doubtful whether this signifi-
cantly affected the observed aphid population. Except for the situation
discussed in Section 7.3.1, it is probable that moisture was never a
limiting factor.

7.3.3   Overall Effect of the New Zealand Climate

New Zealand's climate is relatively mild, with few extremes, and most introduced aphids can take advantage of this by remaining as parthenogenetic viviparous females throughout the year (Cottier, 1953). In a useful discussion of the effects of weather on aphids, Lowe (1966b) has observed that this absence of sexual forms is "the dominant effect of climate on aphids under New Zealand conditions".

A. kondoi appears to overwinter as a parthenogenetic viviparous female (see Chapter Four) and the presence of this mode of reproduction throughout the year is the main effect of New Zealand climate on A. kondoi.

CHAPTER EIGHT

THE EFFECT OF PLANT CONDITION ON A. KONDOI

8.1. Introduction

The aphid-plant relationship can be considered as a parasite and its host (Kennedy and Stroyan, 1959). The plant manufactures all the nutrients which aphids tap and can be considered a "veritable widow's cruse" (van Emden, 1973). Indeed aphids do not fully utilise all the plant sap they imbibe and much is excreted as honeydew (Auclair, 1963). The only work required to be done by the aphid is to penetrate a suitable plant cell, usually a phloem cell (Blackman, 1974). However, despite this outward simplicity, the plant and aphid relationship is complex. For example, aphids are able to alter the physiology of the plant, the most visible manifestation of this being galling (Forrest, 1971; Forrest and Dixon, 1975) which is probably caused by the injection of salivary substances, possibly indole acetic acid (IAA) (Miles, 1968). Also large colonies of aphids are able to create "sinks" for nutrients (Kennedy and Stroyan, 1959; Canny and Askham, 1967; Way and Cammell, 1970).

Conversely, the condition of the plant can affect the aphid numbers considerably since the plant must provide suitable nutrients both quantitatively and qualitatively for the aphids but cannot continuously support the drain on these nutrients which a large aphid population imposes. Nitrogen compounds have often been suggested as a limiting factor in aphid colonisation on plants. The stage of plant development is also known to affect the suitability of the plant for the aphids and this is probably linked to the availability of different compounds at different stages of plant growth. In this respect, young and senescent plants are generally considered more suitable than mature plants (van Emden et al., 1969).

During the present study flowering of the lucerne was observed to coincide with a decline in A. kondoi numbers and therefore an attempt was made to see if this physiological change in the plant was the cause of the decline in aphid numbers or whether it was merely coincident with it. Also the A. kondoi population on lucerne was observed to fluctuate throughout the year and an attempt was made to discover whether this was partly due to a change in plant condition and possible exhaustion of the

nutrients available to the aphids, or whether there was a simple
proportional relationship between the size of a plant and the number
of aphids which fed upon it.

8.2   Methods
8.2.1 Methods for Studying the Effects of Flowering on A. kondoi.

On 5th January 1977, sixteen five inch "Plastimatic" pots of
approximately three month old lucerne were trimmed closely to ensure
that no flowering buds already initiated would continue to grow, then
eight of these pots were assigned to each of two treatments. In one
treatment the plants were induced to flower whereas in the other they
were made to remain vegetative.

Lucerne can be classified as a Long Day Plant and appears to
have a critical daylength for flowering of 12 hours (Thomas, 1967).
Flowering was induced by following the recommendations of Thomas (1967).
Plants which were to flower were grown in a 24 hour light regime consist-
ing of a period of eight hours in the glasshouse during the daytime to
supply the period of "relatively high intensity light" required followed
by 16 hours under two 60W incandescent bulbs placed approximately 35 cm
above the plants in a light-proof room. The glasshouse temperature was
uncontrolled but the dark room temperature was thermostatically controlled
to the recommended range of 20 to $24^{\circ}C$. These treatments resulted in the
first flowers appearing on 27th January.

The only light to which the plants which were to remain
vegetative were exposed was that during the eight hour period in the glass-
house. This ensured that both the flowering and non-flowering plants
received the same amount of photosynthetically important light, and there-
fore were of comparable quality. In addition the non-flowering plants were
placed in the same room although shielded from light, as the flowering
plants to ensure that both received equal temperature treatments. All the
plants were checked each night during this growth period and any stray
aphids found were washed or blown off them.

On 30th January three flowering and three non-flowering plants
were placed in a room with light being supplied by two 65W four foot
Cool White fluorescent tubes. Although this provided identical conditions
for both plant treatments it should not have significantly affected their

flowering or non-flowering state. It was important to provide identical conditions for both treatments so that any observed effect on the aphids could not be attributed to environmental variation other than the flowering state of the plant.

A total of 11 cages of the type described in Appendix Three were placed so that each contained one flowering stem tip on the flowering plants and a similar number of cages were placed on the non-flowering plants so that each contained a vegetative stem tip. All the cages were attached to stakes in seed trays containing peat and pumice alongside the potted plants to avoid breaking the tall flowering stems.

A single third or fourth instar apterous A. kondoi was placed in each cage. These cages were then ckecked periodically and the survival of adults and the number of offspring was noted. All the offspring were removed during each check.

In the present study the survival of the adult aphids and their fecundity was measured. The problem of which aphid parameter to use to estimate the suitability of the host plant has been discussed by Adams and van Emden (1972).

As a further check on the effect of flowering on the aphids the number of aphids was determined on 40 non-flowering and 40 flowering stems collected from the DSIR study plot on 3rd February 1977. All the stems were collected in the same area to prevent any error due to non-random aphid distribution.

8.2.2. Methods for Obtaining the Weight of Plants

The fresh and dry weights of the lucerne stems collected in the fortnightly population samples was found by the methods described in Chapter Four.

8.3. Results and Discussion
8.3.1. The Effects of Flowering

As a measure of the suitability of the flowering and non-flowering lucerne for A. kondoi the survival and fecundity of the caged aphids were measured. The results of this trial are given in Table 4.

Table 4   Survival and fecundity of A. kondoi on flowering (F)
           and non-flowering (NF) lucerne stems.

Date	30 Jan F	30 Jan NF	1 Feb F	1 Feb NF	3 Feb F	3 Feb NF	7 Feb F	7 Feb NF	9 Feb F	9 Feb NF	11 Feb F	11 Feb NF	14 Feb F	14 Feb NF
No. of live aphids	11	11	11	10	11	2	6	0	2	0	1	0	0	0
No. aphids producing young	0	0	0	1	7	4	10	1	4	0	2			
Total young produced	0	0	0	1	54	36	102	14	13	0	7			
Average No. of offspring of each parent	0	0	0	0.09	7.7	9	17	14	3.25	0	3.5			

It can be seen from this table that aphids reared on non-flowering stems had better adult survival though there was no significant difference in fecundity in terms of the average production of offspring of each parent. Colonies of aphids were observed to develop on both flowering and non-flowering plants placed in the same room.

Fifty-one aphids were found on the 40 non-flowering stems collected from the DSIR study plot, and 74 from a similar number of flowering stems. The flowering stems were therefore supporting fractionally more aphids per stem.

When lucerne was grown in the glasshouse in the present study, A. kondoi seemed to be removed from both flowering and non-flowering shoots with equal frequency. This indicated that the alates depositing these aphids were selecting the sites without bias and this presumably occurred in the field situation.

On the 9th February 1977 A. kondoi was observed feeding in very high numbers on white clover in a glasshouse. The clover was flowering and the aphids were on both the petioles and the flowers including the petals themselves. Trought (1977) reports that this is a common situation in Canterbury.

The results show that flowering stems are at least as suitable for supporting A. kondoi as non-flowering stems and it is concluded that flowering was not the cause of the decline in aphid numbers observed in the field in December 1976.

Previous authors have also noted that inflorescences can provide a suitable habitat for aphids. Dahms and Painter (1940) found that the numbers of A. pisum (=Illinoia pisi (Kalt.)) when caged on flowering and vegetative lucerne plants increased more rapidly on the flowering shoots. Tambs-Lyche (1958) demonstrated that the flower buds of field beans were as attractive to A. fabae as the vegetative buds. Wyatt (1965) demonstrated that Myzus persicae (Sulz.) on glasshouse chrysanthemums would migrate to the inflorescences and Ito (1960) also mentioned an upward movement to the inflorenscences of three species of aphids.

8.3.2 The Effect of Plant Size and Age on the A. kondoi Population

The relationship between plant weight and the numbers of A. kondoi is shown in Fig. 20. This shows that the numbers of A. kondoi vary considerably in relation to the plant weight. The relationship of the aphid to the plant is therefore not simply dependent on the available surface area of the plant nor on the increasing amount of nutrient which the plant can produce as its size increases. Stary (1970) found that lucerne growth was not always coincident with the increase in numbers of A. pisum.

This data and other observations also indicated that plant age is not the critical factor in determining the occurrence of A. kondoi since fluctuations in the aphid population could occur relatively independently of the age of the plants. This is not to say however that plants of a particular age are not more or less suitable for A. kondoi.

Other factors, especially whether the plant is growing rapidly may also be important. Although not enough situations were observed for the results to be conclusive it appeared that young rapidly growing lucerne was very suitable for supporting an increasing A. kondoi population a conclusion which is supported by the results of Richardson (1977) (see Chapter Four).

Fig. 20   The population of <u>A</u>. <u>kondoi</u> at the DSIR study plot
and the weight of lucerne stems from which they were
obtained

NUMBER OF *A. kondoi* PER 84 STEMS ●⋯

MEAN DRY WEIGHT OF LUCERNE PER STEM ■⋯
MEAN FRESH WEIGHT OF LUCERNE PER STEM ▼⋯

LUCERNE CUT

LUCERNE GRAZED

DATE
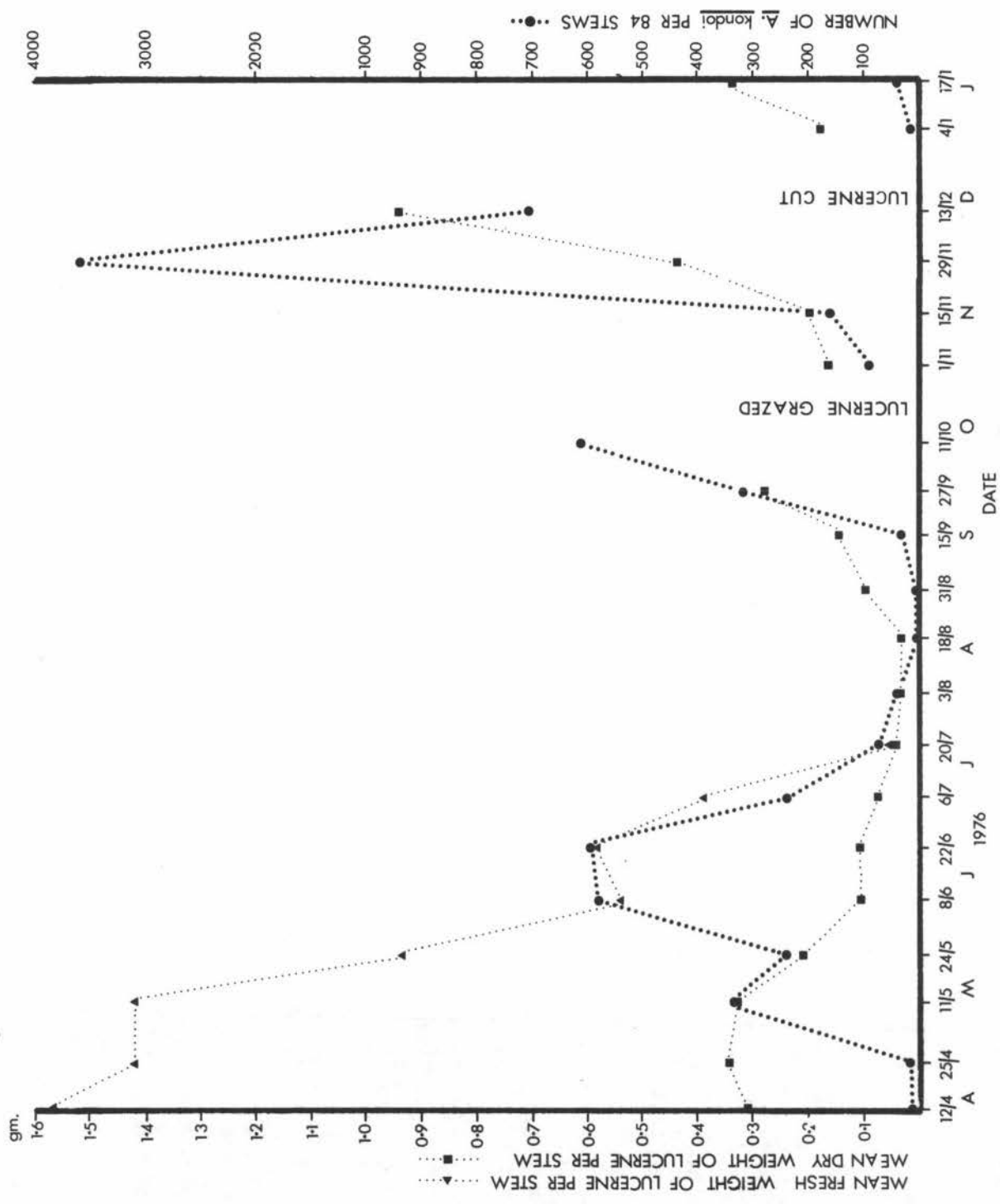
1976

This was certainly the situation after the lucerne was grazed in October 1976 and, but for predators, a similar situation would have occurred after the lucerne was cut in December. The initial A. kondoi spring population build up before the lucerne was grazed was also on predominantly young growing lucerne since most of the older lucerne had died off over winter. Older lucerne such as that during autumn-winter 1976 and March-April 1977 also supported A. kondoi population growth. At these times of year (autumn), this lucerne was growing rapidly.

8.3.3 The Effect of a Decline in Plant Condition on the A. kondoi Population

On a small host plant such as lucerne the effect of many aphids may be severe and often result in the death of the plant. As with any parasite-host relationship this is disadvantageous for the parasite (the aphid), because it limits the chances for future aphid colonisation. The population of A. kondoi on lucerne follows a regularly fluctuating cyclical pattern (see Section 4.3.1) incorporating a 'spontaneous' decline in aphid numbers and hence presumably a decline in the death rate of plants. It is difficult to distinguish whether the decline in aphid population is caused by (i) a decline in the condition of the plant, and therefore the number of aphids it can support, and/or (ii) whether it is due to some intraspecific aphid mechanism which anticipates the plant condition becoming limiting. The actual methods by which the aphids reduce their population are discussed in Chapter Ten.

After a decline in the A. kondoi population the plants, although not dead, did not support a large aphid population for some time afterwards until the increase stage of the next aphid population cycle. The low numbers of aphids in the intervening period between cycles may have resulted (i) because the plant was nutritionally incapable of supporting a large aphid population and/or (ii) because a plant factor, possibly formed by the plant as a defensive reaction or by the aphids themselves, inhibited recolonisation and/or (iii) because of some other aphid mechanism. The latter possibility involves the period required for the aphid condition to return to its optimum after a population cycle and is discussed further in Chapter Ten. Again it is difficult to distinguish between the possibilities.

Although not all the factors could be ruled out an indication
as to which was at least partially active in both the 'spontaneous'
population decline, and in retaining the aphids at low population levels
between cycles was obtained in a culture of A. kondoi. Recolonisation
of plants, and production of offspring by adult alates was observed to
occur when an A. kondoi culture was kept in a room from which the alates
could not escape, and on which a population cycle with its decline in
aphid population had occurred. Although the offspring were in poor
condition and few in number they did grow slowly indicating that the
plants were not totally depleted as a source of food for the aphids.
This means there was some at least partially anticipatory aphid mediated
mechanism involved in the decline of the aphid population. However, as
the aphids were in such poor condition it is probable the plants were
also in poor condition. Even if the aphid mechanism was anticipatory it
would take some time to act and the plant condition would decline
rapidly during this time. In the field the plants would have supported
many hundreds of aphids, and it is reasonable to expect that at least
some plant "conditioning" by the aphids would occur. The period of low
aphid population between cycles will therefore be partially due to poor
plant condition.

Franz (1958), Sluss and Hagen (1966) and Sluss (1967) have
shown that high numbers of aphids can "exhaust" or "condition" (alter)
a plant or parts of a plant so that high numbers of aphids cannot survive
on them for some time afterwards.

Observations in the present study, and the results of Richardson
(1977) both indicate that cutting or grazing of the lucerne removes the
factor(s) inhibiting a build up in the aphid population, and that a new
population cycle will begin on new growth.

CHAPTER NINE

THE EFFECTS OF PREDATORS, PARASITES AND

FUNGI ON A. KONDOI

9.1   Introduction

In the broad ecological sense, any lowering of aphid numbers
by biological control agents indicates that they are "effective", but in
the agricultural sense "effectiveness" entails maintaining the aphids
below an economically damaging population level (Hodek et al., 1972).
Since few non-economically important aphid populations have been studied
the latter sense is the one which is normally referred to.

Two approaches to considering the effectiveness of predators,
parasites and fungi were used in the present study. Firstly a quantita-
tive value of the overall effectiveness of the biological control agents
was found by excluding all predators, and secondly the effects of individ-
ual predators was sought by investigating different aspects of their
"effectiveness" as the latter term was defined by van Emden (1966).

Instances of the effective biological control of aphids are not
common, or at least do not seem to be common. Instead it may be that
ineffective biological control results in large numbers of aphids which
are more noticeable. However as Kennedy and Stroyan (1959) and Hagen and
van den Bosch (1968) indicate, unequivocally proven instances of bio-
logical control are rare.

A number of models have been proposed for considering predator
effectiveness e.g. Bombosch (1963, van Emden (1966), Tamaki et al., (1974).
van Emden (1966) divided the aphid-predator relationship into three major
parts; voracity of the predators, synchronisation of predator and prey
populations, and the prey's reproductive rate.

"Synchronisation" refers to the temporal and spatial occurrence
of predators and prey, while "voracity" includes the "abundance" and
"activity" of predators and the number of prey consumed by predators.

By integrating these factors it was possible to find what effect the biological control agents may have had, and a similar division of predator traits was used in the present study.

Before a biological or integrated control programme can be developed in New Zealand, and this seems essential in view of the rapid reinfestation rate after insecticide spraying (Kain et al., 1976), the extent of the effects and interactions of the existing biological control agents must be known. The introduction of a new predator or parasite species may affect many other species (e.g. Frazer and van den Bosch, 1973).

Entomophagous insects generally require more components in the ecosystem than phytophagous insects (Hagen et al., 1971). Existing predators must be encouraged by suitable agricultural practices, such as the provision when necessary of suitable alternative food, both artificial (Hagen et al., 1971) and natural (B.C. Smith, 1966; Way, 1966), and suitable alternative habitats (Galecka, 1966).

9.2   Methods
9.2.1   Methods for Studying the "Synchronisation" of Predators and Prey

Sweep netting for predators, beating the predators on to a greased tray, greased flight cylinders, fixed time searching for predators, and collecting predators off vegetation samples were all used to determine the synchronisation in temporal and spatial occurrence of predators and the aphids. A variety of sampling methods were used both because of their intrinsic interest and because no one method can be applied equally efficiently to all predators, parasites and fungi, and to all of their developmental stages. Also a truly representative picture of the community can only be obtained by using several methods (Hodek et al., 1972). Useful summaries of predator sampling techniques have been discussed by Southwood (1966), Hodek at al., (1972) and Ruesink and Kogan (1975).

There are three habitats to be considered when trapping predators; the ground, the vegetation and the air. This distinction is not usually made but can provide useful ecological information about the predators. The youngest Nabidae and Coccinellidae for example, appear

to dwell only on the ground, while later non-adult stages climb on the plants. Also the adult Coccinellids migrate by flying whilst N. maoricus adults do not appear to do so.

Two methods were used for sampling flying predators. Firstly, three yellow and three white grease covered flight cyclinders were used and set up as described in Section 5.2. Three white cylinders of the same dimensions as the yellow cylinders were also used to allow for the predators possibly being repelled by the yellow colour. Hilson (1964) used similar yellow cylinders for trapping M. tasmaniae and reported them to be effective. White traps were reported to be attractive to Syrphidae (Sol, 1966), though the attractiveness varied with the crop and the stage of syrphid development. Way and Banks (1968) and Hodek et al., (1972) state that sticky traps are also suitable for Coccinellids.

The greased cylinder flight traps provided some useful information though the numbers of most species caught was never high and some syrphids were observed to settle on the traps and then fly off. For future studies it is suggested that a grease which more effectively traps heavier insects than does Mobil grease A No. 0, be used.

Secondly a net 30 cm in diameter with a mesh size of 0.66 mm was used for sweep netting predators. Sweeps through 180 degrees were taken one step apart while walking into the wind so specimens would be blown into the net. Up until 10th December 1976 sweeping was done at such a height as to touch and therefore sample approximately the top 10 cm of vegetation and also trap any insects taking off after being disturbed. From 14th September until 10th December 200 such sweeps were taken on each sampling occasion. After 6th January 1977 this was decreased to 100 on each occasion. Henceforth the method described above will be referred to as sweeping "above" the vegetation, while that described below as sweeping "through" the vegetation.

Predators on the vegetation were sampled using four methods; sweeping through the vegetation, fixed time searching, collecting plant samples, and beating the animals from the vegetation on to a greased tray with a piece of wood.

Fixed time searching was carried out by searching the vegetation, especially around the growing tip which the aphids inhabit, for two five minute periods, and then searching the ground surface especially that beneath the litter for a further two five minute periods. Many nabids especially were found under the litter which was formed when the lucerne was cut. Ground and vegetation searching was carried out in two different areas of the paddock to allow for possible differences in predator densities, and searching always took place from the middle of the paddock to the outside of the field. During each five minute search of the vegetation 20 to 30 stems of lucerne would be examined. The main problems associated with visual sampling techniques are that some species and different life stages of species are more visible than others and there is also the possibility that predators may occupy different places in different weather conditions for example, in adverse weather some predators tend to move down the plants (French, 1966). The first problem was overcome to some extent by randomly selecting stems to be searched and only counting predators on those stems. The second problem was partially overcome by searching both the ground and the vegetation. A further unavoidable source of error was the efficiency at detecting predators increased with experience.

To obtain an estimate of predator density on plants 80 lucerne stems were also sampled on each sampling occasion by collecting the closest undisturbed stem to the tip of my boot at every second step during a random walk across the sample area. The stems were carefully cut at ground level and placed into a plastic bag held as close to the stem as possible. The stems were taken back to the laboratory and carefully searched for parasite mummies and fungally infected aphids. To check for any further development of mummies live aphids from these stems were placed in a plastic lily cup lined with moistened filter paper on which were placed excised trifoliate leaves. The dish was covered with organdie mesh and placed at room temperature away from direct sunlight. This latter method provides a more reliable estimate of percentage parasitism than noting the ratio of parasite mummies to live aphids collected from the fields because the latter is based on the assumption that the duration of mummies is the same as that of the unparasitised aphid (Stary, 1970). After searching the stems for mummies and fungally infected aphids they were then washed twice in water heated to 70°C to ensure that

all predators were removed. These were then collected by sieving through organdie mesh.

Samples from beating the vegetation were obtained until the 10th December by beating the vegetation with a 35 cm by 26 cm piece of 4 cm thick hardboard on to 36 cm by 28.5 cm by 5 cm deep tray smeared with Mobilgrease A No. 0, and held at approximately a 45 degree angle downwind from the plant. A beating sample was taken by making one stroke each step for 100 steps, care being taken not to damage the vegetation. The grease covered insects were later recovered by dissolving the grease in xylol, or a 50:50 mixture of isopropyl alcohol and benzene (Southwood, 1966).

Beating the vegetation is analagous to sweeping it and subject to the same errors(Hodek et al., 1972). A disadvantage was that it took a relatively long time to remove the grease, while sweeping "through" the vegetation was less time consuming overall and the specimens taken were easier to handle and in better condition. Therefore on each sample occasion from the 6th January onwards 50 sweeps were made "through" the vegetation and in these the sweep net was held so as to sweep as closely as possible to the base of the vegetation.

It should be noted that some changes in methods occurred between 1976 and 1977 but that stem sampling, fixed time sampling and sweeping above the vegetation were retained as similar for comparative purposes.

All the samples were obtained weekly between 9 a.m. and 11 a.m. to avoid any possible comparative errors caused by the diurnal rhythms of predators (Stary, 1970). The errors in searching for predators just during the daytime or at one particular time of the day have recently been discussed by Sunderland and Vickerman (1975) who demonstrated that many predators are nocturnal. Certainly Hamrum (1966) stated that Melanstoma spp are nocturnal and Hilson (1964) found that M.tasmaniae is most active during or just after dusk. Fewkes (1961) also notes that more nabids are caught at night. These factors, along with weather conditions, must be taken into consideration when considering the over-all abundance of predators.

9.2.2   Methods for Studying the "Voracity" of Predators

9.2.2.1 General Experimental Plan

The term "voracity" as used by van Emden (1966) includes the "abundance" and "activity" of predators, and the number of prey consumed by predators. Information on the first two aspects was gained by the same means as described above for "synchronisation" of the predators and their aphid prey.

The number of A. kondoi consumed by N. maoricus was specifically studied since the exclusion cage experiments described in Section 9.4 indicated that this predator was very effective in controlling A. kondoi but very little was known of its habits. To obtain this data the nabids were confined individually with either 20 or 30 second and third instar A. kondoi in tissue culture dishes of 35 mm diameter and 10 mm depth. Each dish contained an excised trifoliate leaf sellotaped to the lid. These dishes were placed in a thermoststically controlled modified fridge cabinet at a temperature of $18.0 \pm 1.5^{\circ}C$ and in a light regime which included ten hours of darkness. The exact ratios of light and dark experienced by the nabids varied as different experiments were begun at different times of the day. Light was provided by a 13W Tropical Daylight fluorescent tube. Each trial was run for 24 hours and one or more dishes in each trial was always left without a nabid as a control.

9.2.2.2 Preliminary Studies in Determining the Number of Prey Consumed by N. maoricus

This experimental plan described above evolved from a number of early trials. The first trials showed exceptionally high aphid mortality and it was difficult to distinguish whether an aphid had been killed by the nabid or whether the death was due to some other cause. Trials were therefore conducted to find the extent of "background" mortality. On the 11th March 1977, 18 dishes were set up with 20 A. kondoi per dish. The aphids were all second and third instars collected from white clover in a glasshouse. This was done by breathing gently on the aphids which caused a drop reaction hence ensuring that the aphid stylets were unbroken and no mortality due to such damage would occur. By using second and third instars the problem of any additional aphids being born and possibly fed upon, was avoided. No predators were added to these

dishes and after 24 hours the dishes were removed from the constant temperature cabinets and the number of live aphids was counted. The average survival was exceptionally low (Table 5).

It had previously been noted that aphid survival was much higher if a trifoliate leaf of lucerne was present. The reason for this is not known since presumably feeding cannot occur, although the aphids do congregate on the leaflet. Hence further "background" mortality trials were set up in culture dishes to which excised trifoliate leaves were added. The petiole of the leaf was selotaped to the roof of the dish in such a way that the apices of the leaflets just touched the floor of the dish. This ensured that in the feeding trials all the aphids would be accessible to the nabids though in practice the leaflet edges could curl up providing a shelter for a few aphids. The effect of the presence or absence of lucerne trifoliates on aphid survival is shown below.

Table 5   The effect of the lucerne leaf on the survival of A. kondoi

	Trifoliate Leaf Not Present	Trifoliate Leaf Present
Number of dishes	18	18
Number of aphids alive in each dish at beginning of trial	20	20
Average number of aphids per dish alive after 24 hours ± S.D.	3.77 ± 4.15	19.72 ± 0.46*

* This figure is the basis for the background mortality of A. kondoi

Using this information further trials were conducted and on 17th March 20 second and third instar aphids and a trifoliate leaf of lucerne were placed in individual dishes. Adult N. maoricus collected from the DSIR study plot within the previous half hour were placed, one per dish and the dishes were put in the constant temperature cabinet. After 24 hours all the dishes were removed and the number of live aphids counted. The results are shown in Table 6. It was found that some nabids consumed all 20 aphids presented to them, hence two further trials were carried out with 30 aphids per culture dish and the results of these trials are also shown in Table 6.

Table 6   The consumption of A. kondoi by N. maoricus

Trial	17 March	25 March	30 March
Initial number of aphids per dish	20	30	30
Number of dishes	10	10	10
Background mortality per dish (Number of aphids)*	0.28	0.42	0.42
Average number of aphids per dish dead after 24 hrs	13.8	17.0	10.7
Average number of aphids dead per dish minus background mortality	13.52	16.58	10.28
Range of numbers of aphids dead	3.72 - 19.72	10.58 - 25.58	1.58 - 20.58
SD	6.118	4.202	6.75
SEM	1.934	2.135	2.135
Number of A. kondoi dead in control dish with no nabid present	0	9	2.66
Average number of A. kondoi per dish which appeared to have died naturally	Not Done	Not Done	2
Average number of A. kondoi dead per dish minus number dead in control dish	13.8	8	8.04
Average number of A. kondoi dead per dish minus number found naturally dead	Not done	Note Done	11.25
Average of Trials 17 March and 30 March	11.25		

* Obtained from earlier trials

It is probable that the results of the 17th of March trial
are the most realistic since the results from the control dish with
no nabid present agree almost exactly with the earlier calculated back-
ground mortality. The reason for the nine deaths in the control dish on
the 25th March is unknown but this trial was discounted in the final
calculation because the value is so high. However, it is interesting to
note that if the nine aphids observed dead in this control dish is a
true average value for this trial, then the average number of A. kondoi
consumed per nabid was eight, this being very similar to the result
of the 30th March trial.

On the 30th March the three control dishes indicated an average
natural mortality of 2.66 aphids per dish and to check this the dead
aphids in all the dishes which contained feeding nabids were studied to
see if feeding occurred. In some cases this was difficult to distinguish
but the maximum number of aphids found dead due to non-predatory causes
was four, and the average was two. Hence the control dishes seemed to
present a realistic picture and the results obtained by this method were
also used.

9.2.2.3 Methods Used for Determining the Voracity of Entomophthorous
Fungi

The voracity of fungi was measured by collecting nine lucerne
stems from Exclusion Cage One on the 23rd March 1977 and counting the
number of infected aphids since at this time the epidemic seemed close to
its peak. On the 26th March a further ten stems were randomly selected,
and collected in a plastic bag and the instars of the infected aphids
were noted.

9.3   Results and Discussion
9.3.1.1   Synchronisation of the Predators and Prey
The term "synchronisation" refers to to the temporal and spatial
relationship of the predators, parasites and fungi, and the aphid popu-
lation on which they are preying. This relationship was studied by
following the occurrence of the predators and aphidophagous fungi, (no
parasites were found in the field - see Section 6.3.5), and the popu-
lation of A. kondoi in the DSIR study plot. The results are shown in
Figs 6, 7, 13, 21, 22 and 23.

Fig. 21   The occurrence of C. undecimpunctata at the DSIR study
          plot. Results until the 10th December were obtained
          from: 100 beats of the lucerne on to a greased tray,
          200 sweeps "above" the vegetation, collecting 100 stems,
          and searching the ground and the vegetation for five
          minutes each per sample. From the 6th January beating
          on to a greased tray was replaced by the results from
          50 sweeps "through" the vegetation.

NUMBER OF *Coccinella undecimpunctata* JUVENILES ···▽···

NUMBER OF *Coccinella undecimpunctata* ADULTS ···○···
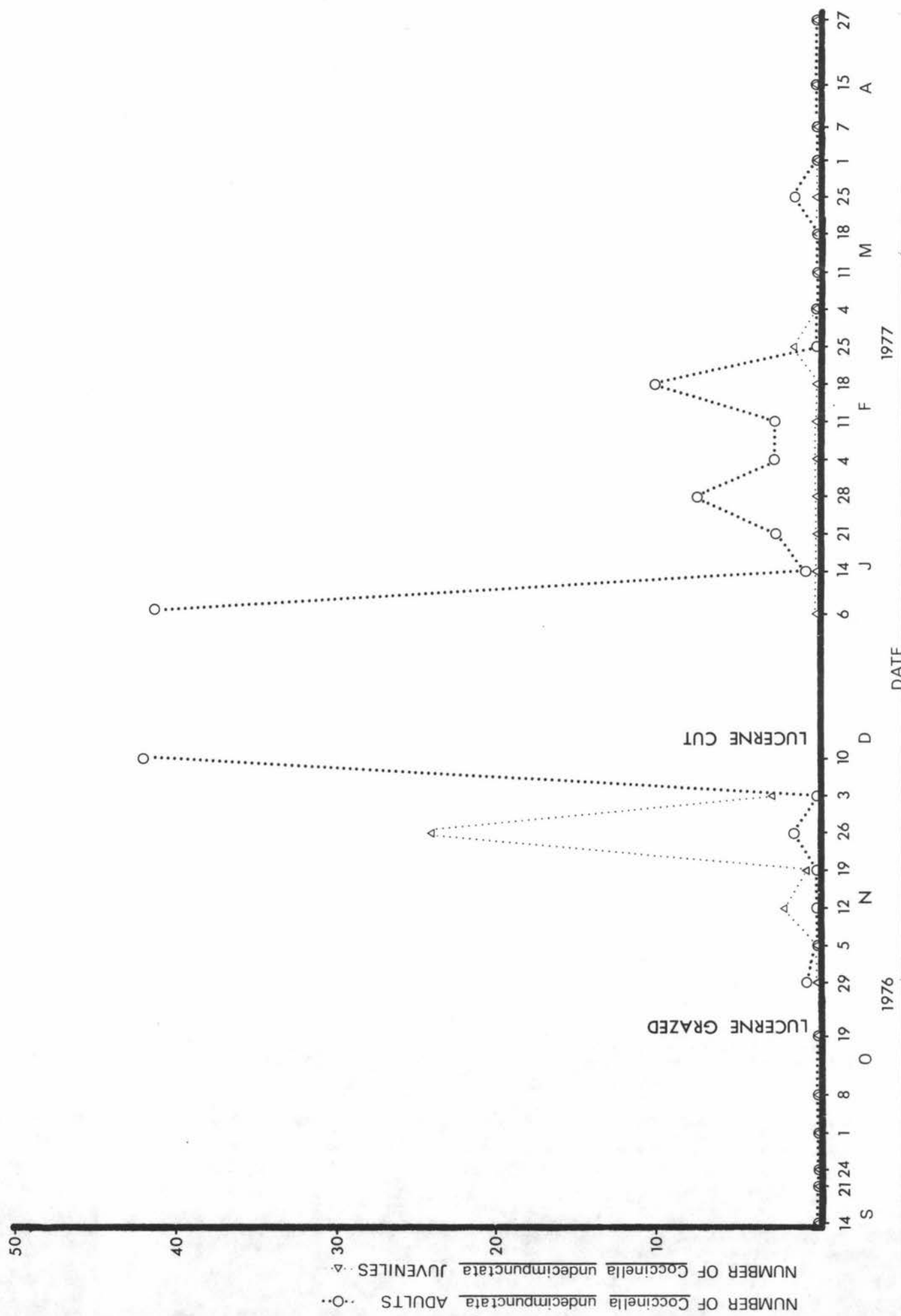
Fig. 22   The occurrence of syrphids at the DSIR study plot.
          Results until the 10th December were obtained from:
          100 beats of the lucerne on to a greased tray, 200
          sweeps "above" the vegetation, collecting 100
          lucerne stems, and searching the ground and the
          vegetation for five minutes each per sample. From
          the 6th January beating on to a greased tray was
          replaced by the results from 50 sweeps "through"
          the vegetation.
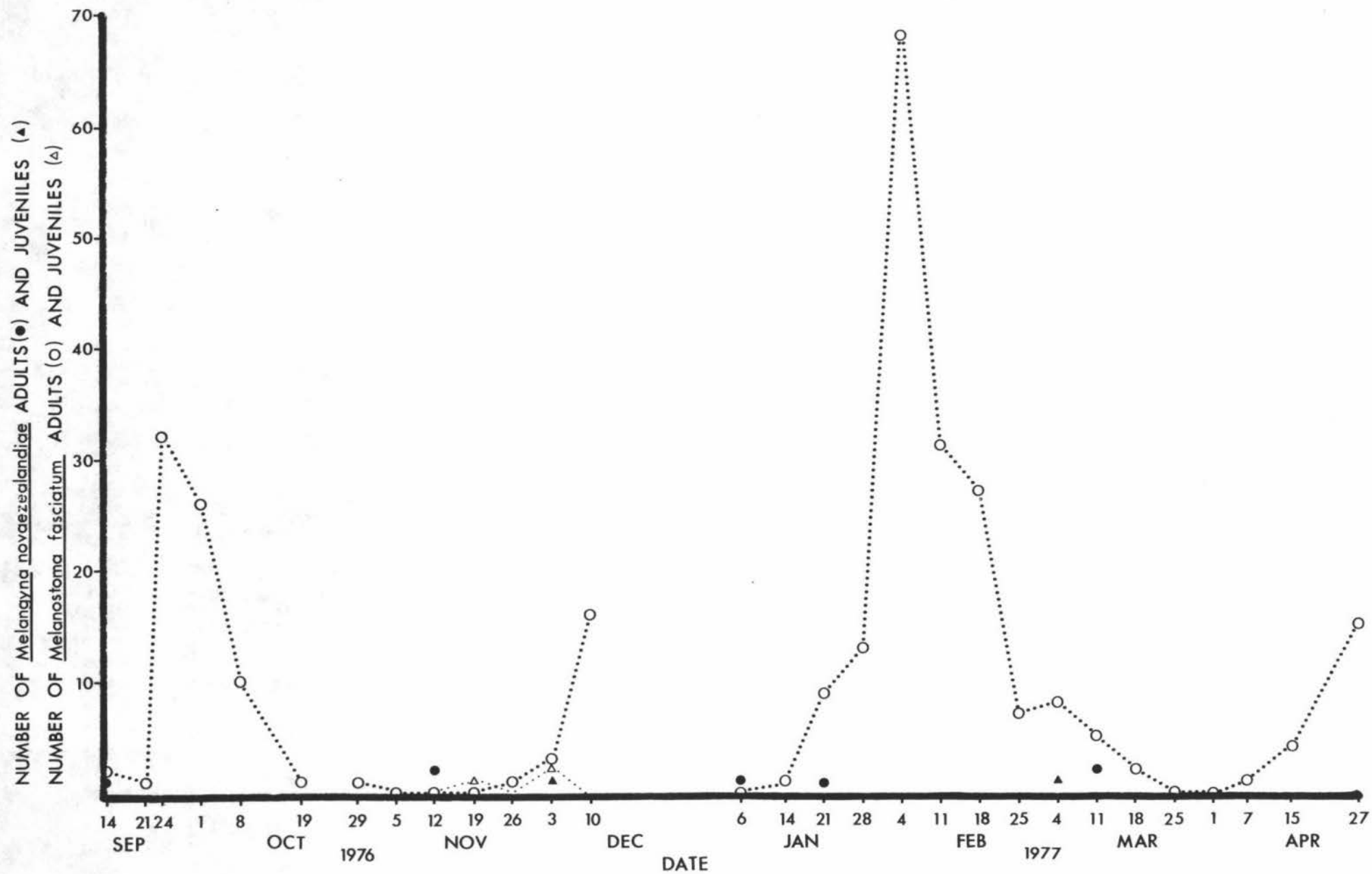
Fig. 23   The occurrence of **M. _tasmaniae_** at the DSIR study plot.
Results until the 10th December were obtained from:
100 beats of the lucerne on to a greased tray, 200
sweeps "above" the vegetation, collecting 100 lucerne
stems, and searching the ground and the vegetation for
five minutes each per sample. From the 6th January
beating on to a greased tray was replaced by the
results from 50 sweepes "through" the vegetation.
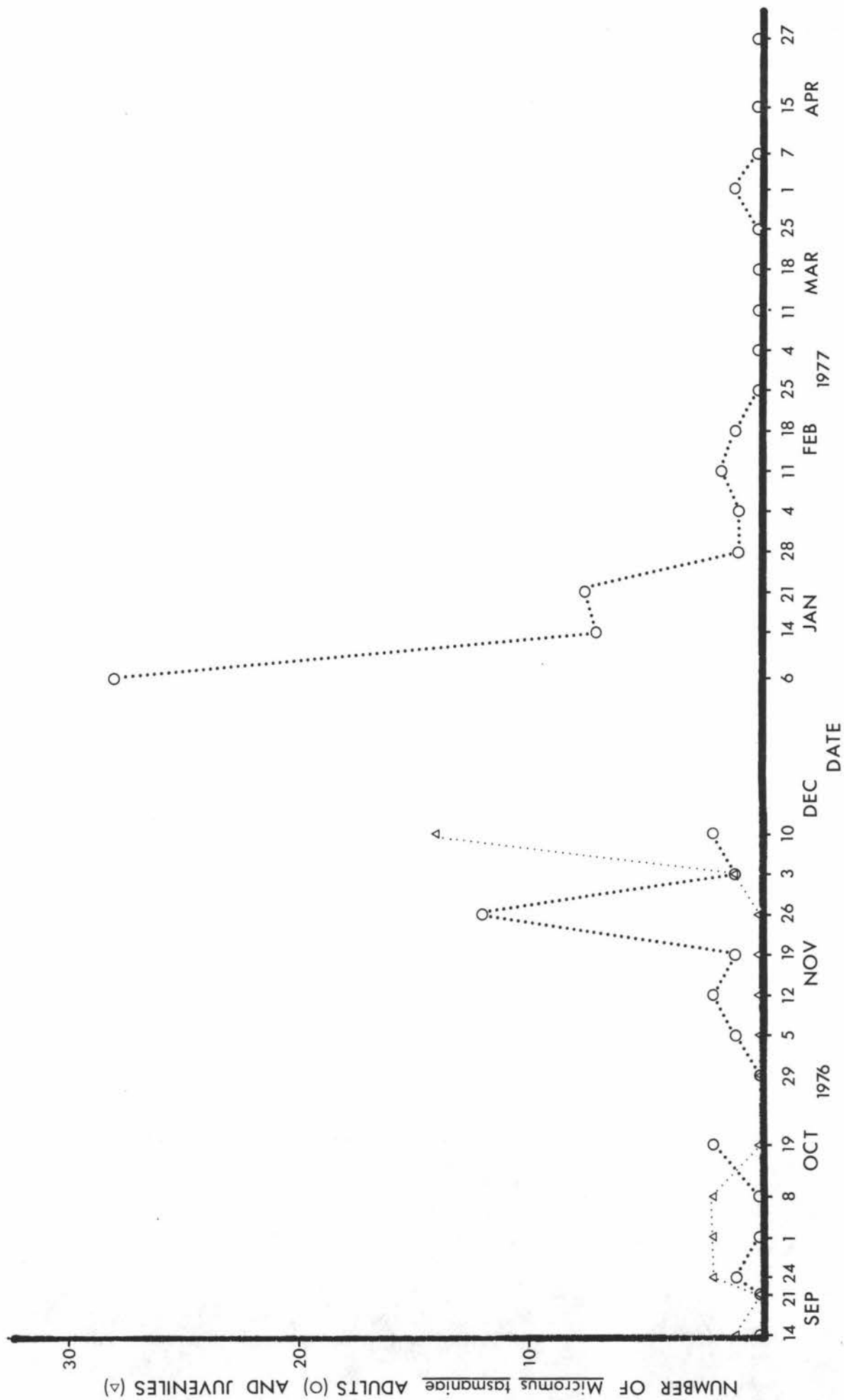
The population of A. kondoi in the spring at the DSIR study plot began to build up during early September 1976 and the rate of increase became even greater after the middle of September (Fig. 7). This trend continued until the plot was grazed on 22nd October. After the 15th September the aphid population was almost certainly at a high enough level to attract predators.

Predator sampling commenced on 14th September but the only predator present in any numbers up to the time the plot was grazed was the syrphid M. fasciatum. Even for this species no larvae, which constitute the predaceous stage of the lifecyle, were found. During this period larvae of the lacewing M. tasmaniae were also present though the adults were rare, very few nabids were present and coccinellids were entirely absent. Hence until 2nd November there was little effective predation on A. kondoi which therefore escaped the influence of predators at this critical stage. It is concluded the synchronisation of predators with the aphids early in the season was poor.

The aphid numbers decreased considerably after the plot was grazed on 22nd November, and grazing seems to have been detrimental to the predators as well. Lacewing larvae disappeared possibly because of the short period of reduced food and suitable habitat. If eggs were laid by the high numbers of syrphids present at the beginning of November then these too could have been destroyed by cutting. No coccinellids and very few nabids had been observed by the time the paddock was grazed so no effect was noticed on their populations.

Nabids were absent from 24th September to 26th November and hence have a similar occurrence to coccinellids during the spring aphid peak only increasing when the aphid population was at its peak.

The aphid population remained low after grazing until the period of 15th to 29th November when it underwent a high increase in numbers. This corresponded to a similar rapid increase in the numbers of most predators. Nabids showed a sudden rapid increase presumably in response to the abundance of aphids, although higher temperatures may also have been important. Nevertheless nabid numbers during the spring were never as high as later in summer. The number of adult M. fasciatum

also increased, though again larvae were rare probably due to the low number of adults during the previous four to five weeks. Since the adults are nonpredaceous then this increase in number would not have directly affected A. kondoi until the larvae hatched when the aphid population was very close to declining. M. tasmaniae adults also responded to the high aphid numbers and also decreased very rapidly after 29th November with the decline in aphid numbers. However, as with syrphids, their larvae did not increase significantly until 3rd December when the aphid population was already declining. The situation was similar for C. undecimpunctata adults.

Although their numbers did not appear to rise until after the 3rd December they were increasing rapidly at the last sample on 10th December. Since it is probable that the aphid population was declining by this time very poor synchronisation is indicated. The larvae of C. decimpunctata seem to be better synchronised with the A. kondoi population than the adults since both the aphid and the eleven spotted ladybird juveniles increased rapidly after the 19th November.

Normally an increase in adult ladybird numbers before an increase in juveniles would be expected but an apparent reversal of this situation was observed in the present study. The first C. undecipunctata adult was actually seen on 29th October, and so enough eggs may have been laid to produce the increase observed in juvenile numbers, whereas the low aphid numbers during the intervening period was possibly not sufficient to retain the adults. Specimens collected from the flight traps (Fig. 24) support this suggestion of the late arrival of the eleven spotted ladybird adults. The numbers flying increased rapidly in early December reaching a peak on the day when the plot was cut.

All other predator species were already present by the time C. undecimpunctata arrived. The late arrival of coccinellids at aphid populations has been noted previously by, for example, Eichmann and Webster (1940) and Hilson (1964). French (1966) found that in New Zealand the movement of adult occinellids was common on 7th September and that the larvae were present by 9th October but in the present study the adults arrived more than a month later on 29th October. It is possible that if higher numbers of aphids were present by this date then higher numbers of ladybirds would have been recorded. However it is unlikely that the

Fig. 24   The predators of <u>A</u>. <u>kondoi</u> trapped on adhesive traps
at the DSIR study plot. The results are from three
white and three yellow cylcinder adhesive traps. The
numbers of <u>C</u>. <u>undecimpunctata</u> in spring and the
response of <u>M</u>. <u>fasciatum</u> to the 1977 winter <u>A</u>. <u>kondoi</u>
population rise are plotted.
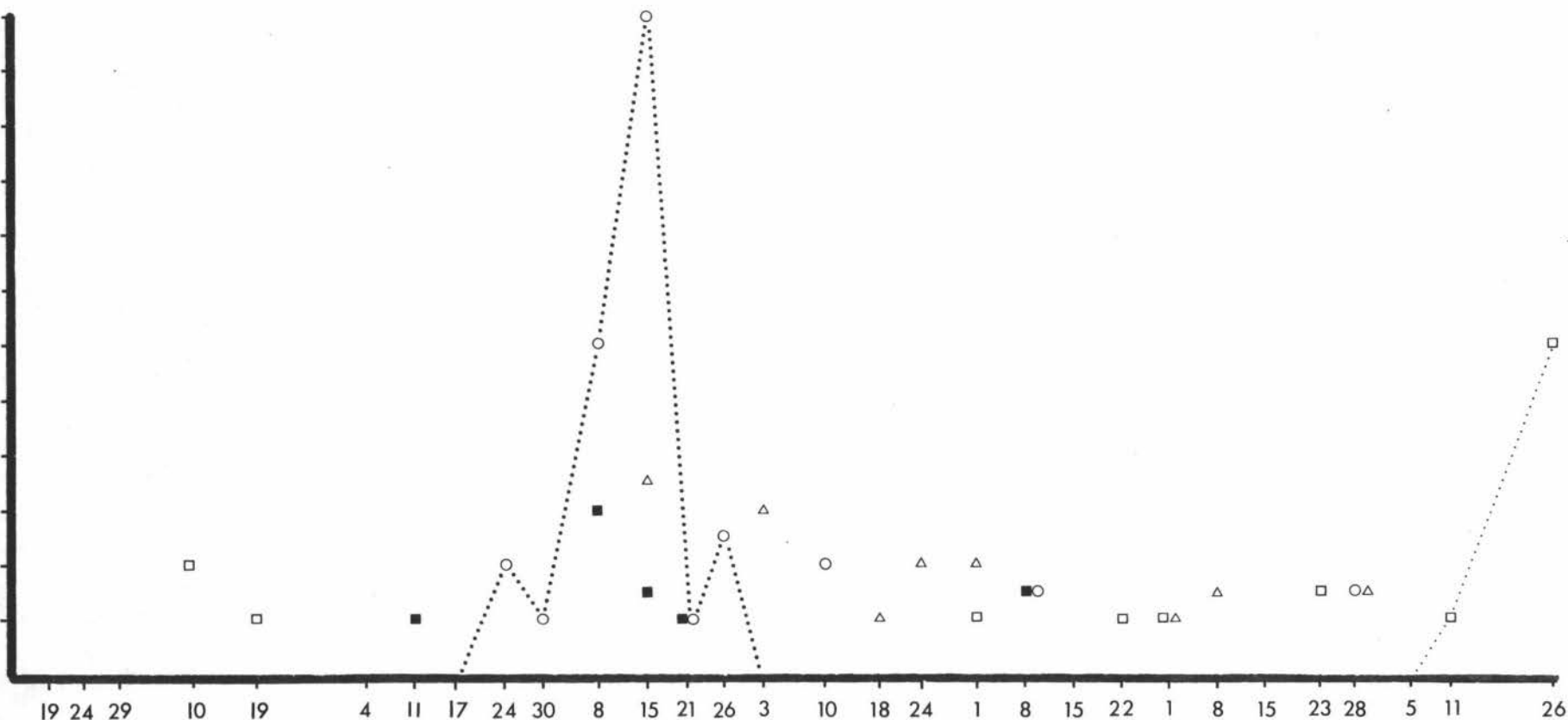
coccinellids would have affected an uninterrupted aphid spring peak
since the aphid population was already increasing rapidly when grazing
took place.

It can be noted that, after grazing, the increase in the
populations of all predators coincided with or actually occurred slightly
later than the aphid population increase. The "classical" situation is
similar with the predator population "chasing" the aphid population,
usually peaking in numbers slightly later and dropping off slightly later
as predators compete for limited resources and consequently disperse
(Way, 1966). Unfortunately in the present study due to the lucerne being
cut, the drop off in the predator population, except for lacewing adults,
was not demonstrated since cutting the lucerne meant comparable samples
could no longer be taken. However, inspection of the sample area indicated
that few predators remained.

Since the predator numbers seem to follow the aphid numbers it
can be assumed they were not effective except during the aphid population
decline when they may have exerted an effect on the alate aphids being
produced in high numbers at this time. Even though grazing of the field
reduced the aphid population to low numbers until 15th November, the
predators were still not able to gain the ascendancy. This conclusion
supports the results of the exclusion cage experiments (see Section 9.4)
which showed that predators were unable to control the spring population
build up of A. kondoi.

Sampling resumed at the beginning of January as the lucerne
began to grow again after cutting. After the 1976 spring peak, the aphid
population remained at low fluctuating levels until winter 1977.

Both M. tasmaniae adults and C. undecimpunctata adults were
present in high numbers at the beginning of January and they may have
been responding to the low number of aphids until competition for aphids
from N. maoricus increased. Only two eleven spotted ladybird larvae were
sampled in 1977. The small peak in adult ladybird numbers on 28th January
coincided with the small aphid population peak but there is no similar
explanation for the peak on 18th February. C. undecimpunctata adults may
have been partially responsible along with N. maoricus for controlling

the A. kondoi population in this period. After the end of February
C. undecimpunctata virtually disappeared. French (1966) also observed
lower numbers of this species in autumn. A similar pattern of population
with very low numbers in autumn was observed for the lacewing M. tasmaniae.
The absence of the two species can be explained partly by the low numbers
of aphids found at the DSIR study plot in 1977 since both species were
observed in other areas.

The numbers of the hoverfly M. fasciatum coincided exception-
ally well with the aphid population, with all four peaks of aphid numbers
from spring 1976 to autumn 1977 coinciding with peaks in the number of
adult M. fasciatum. In April M. fasciatum was the only predator species
to respond to the beginning of the 1977 winter peak in aphid numbers, and
it can be seen that the A. kondoi population and the numbers of M. fasci-
atum caught in the final flight trap sample indicates there was rapid
migration by this hoverfly into the plot. No other predator responded
to this winter rise in aphid population.

M. fasciatum seems to be unique amongst the predators of
A. kondoi firstly in its ability to withstand cold temperatures, since it
was the first predator present in spring and the last in autumn, and
secondly in its ability to respond to small increases in aphid population.
This is probably due in part to its superb flying ability being the
strongest and most agile of all the predators of A. kondoi. It must also
be able to detect very low populations of aphids, but the lack of larvae
is difficult to explain. The stimulus for oviposition may be entirely
different from that for prey detection or it may be that a much higher
number of aphids is required than was present. Oviposition was slight
during the spring aphid population peak and therefore if the number of
aphids present is the stimulus for oviposition, then an aphid population
close to the average of 42 per stem observed on 29th November may be
needed. Certainly syrphid larvae were common at Voss's where the average
number of aphids per stem was much higher than this. Because of the
good "synchronisation" ability of M. fasciatum this species may be worth
further study, especially of the factors which affect oviposition.

The low numbers of M. novaezelandiae observed may be due to
this species requiring a high aphid population to retain it in an area
and induce it to oviposit. The larvae of M. novaezelandiae at Voss's
did not seem to be present until late in the aphid population development
and they seemed to be present in their highest numbers after the aphid
population had "crashed" and virtually disappeared.The absence of
of M. novaezelandiae at the DSIR study plot where aphid numbers were
relatively low throughout the study compared to other areas, supports the
earlier contention that a high density of aphids is needed to attract and
retain the adult and induce oviposition. Since the populations of
M. novaezelandiae seem to be poorly synchronised with A. kondoi it is
likely that very high mortality of the larvae occurs as the aphid popu-
lation crashes, and the nondispersing predator juveniles are forced to
compete for limited resources. In this respect, R.F. Smith (1966)
stated that insufficient attention had been given to the effects of food
shortages at critical times in the lifecycle of aphidophagous insects.
French (1966) noted that during December when aphid numbers had declined
the number of juvenile C. undecimpunctata decreased and those remaining
seemed underfed.

The population of N. maoricus was the most outstanding feature
of the predator population in this period. The number of juvenile nabids
increased rapidly together with the aphid population at the end of January.
After this peak nabid numbers steadily and slowly declined to the low
overwintering numbers with the population becoming adult in composition and
not responding to the rise in aphid numbers in April.

The nabid population seemed to be relatively independent of the
A. kondoi population compared to other predators. However this was not
altogether true since exclusion cage experiments (see Section 9.4) showed
that the low aphid numbers during the period from February to April 1977
were due to nabid feeding, and therefore the two populations were very much
related.

The apparent stability and the long period of high numbers of
the N. maoricus population is probably due to the wide variety of prey
species which the nabids consume, and the apparent lack of adult flight.
The apparent absence of flight means that synchronisation between nabids

and aphids is dependent on sufficient numbers of nabids being present
in an area when the aphid population begins to increase there. If this
does not occur then the nabids do not "synchronise" at all with the aphid
populations because they do not "follow" them as do other predators.

It seems that the synchronisation ability of predators ranges
from an apparent lack of this in N. maoricus, through the moderate ability
of M. tasmaniae and C. undecimpunctata to the good synchronisation ability
of M. fasciatum. In the particular instance studied it seems that
N. maoricus was the most effective predator partially because, by chance,
it was highly synchronised with the potentially high February-March aphid
population at the DSIR study plot.

The two fungal epidemics observed were poorly synchronised with
the aphid population and neither occurred until the aphid population was
already declining. This may indicate that a critical aphid density is
required before the fungus can spread (Grobler et al., 1962). In the
present study the critical aphid density seemed to occur just before the
crash of the aphid population when the aphid density was already above
the economic threshhold, a situation also noted by Hagen and van den Bosch
(1968), and van Emden et al., (1969). The level of the critical aphid
density may depend on many factors especially weather. Lowe (1963)
believed that given suitable weather conditions Entomophthora aphids
Hoff. could control aphid populations in autumn.

9.3.1.2 Conclusion

As a generalisation the mobile predators and fungi, often
especially the aphidophagous stages of their lifecyles, occurred too late
to prevent the aphid population from reaching damaging proportions. Their
main effect was probably in hastening the decline of the aphid population
and such an effect has been noticed by other authors (e.g. Bodenheimer
and Swirski, 1957; R.F. Smith, 1966; Way and Banks, 1968; Perrin. 1976).
More importantly they may decrease the number of alate adults which fly
to new hosts, but considering the high mortality which normally occurs
during the flight of adult alatae it is possible that even the latter
effect is not important. Observations in other areas indicate that the
situation is similar in most areas and aphid populations "chase" but do
not control, the aphid population.

9.3.2.   Voracity of Predators

Of the characteristics of "voracity" as defined by van Emden
(1966), the number of prey consumed by N. maoricus and the abundance of
all the predator species were considered in detail in the present study.
The former was considered since it seemed that N. maoricus was responsible
for controlling the summer-autumn population of A. kondoi (see Section 9.4).
Although some observations were made on the activity, searching behaviour and
rate of multiplication of predators, these factors were not considered in
detail since time did not allow it, and in some respects they are less
important, and in some cases information is already available.

9.3.2.1 Activity

The term activity refers to the actual feeding periods of the
predator. Other studies indicate this is mainly a function of weather,
especially temperature and of daily rhythms if they occur. As expected
fewer predators seemed to be active and visible on cold days than on
warm days.

9.3.2.2 Searching Behaviour

The searching behaviour of coccinellids has already been
described by Hagen (1962), that of neuropterous by New (1975), that of
syrphids by Schneider (1969) and some observations on nabids have been
made by Mundinger (1922). In the present study casual observations were
made on the searching behaviour of N. maoricus. These were active on
plants, but mostly seemed to be found on the underside of leaves and were
rarely observed on the growing tip where the aphids were most dense. They
may remain motionless, seemingly awaiting prey and intersperse this with
short bursts of activity. Observations in petri dishes indicated that
N. maoricus is not especially efficient at searching for prey. They often
ignored aphids very close to them yet attacked others further away.
Presumably their general searching behaviour is related to the wide variety
of prey species they will accept and they do not appear to have any
behavioural patterns for searching specifically for aphids as is found in
syrphids and coccinellids.

9.3.2.3   Rate of Multiplication

In the present study N. maoricus was found to multiply most
rapidly in the summer, rather than during the spring.

The rate of multiplication of C. undecimpunctata has been
investigated by French (1966), and that of M. tasmaniae by Hilson (1964).
Less information is available for M. fasciatum and N. maoricus, though
information on other syrphid species can be found in Schneider (1969)
and on other Nabis species in Mundinger (1922) and Taylor (1949).

9.3.2.4   Abundance

The abundance of predators was studied in more detail and the
results are seen in Figs 13, 21, 22 and 23.

Of all the predators only N. maoricus attained very high
numbers for an extended period. The numbers of this nabid sampled at
the DSIR were exceptionally high compared to observations and samples
made in fields at Dannevirke and Voss's. This undoubtedly reflects the
wide variety of vegetation and the lack of agricultural practices at the
DSIR study plot.

On 11th February 1977 at the DSIR study plot 338 N. maoricus
were collected during 50 sweeps with a 12 inch diameter net, and this
number is very high. Simpson and Burkhardt (1960) reported an average of
8.3 N. ferus were collected per 75 sweeps of a 15 inch diameter net and they
considered the species to be relatively abundant. Taylor (1949) found
N. alternatus to be the most numerous predator in Utah lucerne fields in
spring, and Werner and Butler (1957) found N. ferus and N. alternatus
were common in Arizona crops. In New Zealand nabids, especially
N. maoricus, are commonly regarded as minor predators both in abundance
and importance (Cumber, 1959b; Eyles, 1960).

At the DSIR study plot nabids were the most abundant predator in
a single sample. Considering sweeping above the vegetation the maximum
numbers of nabid found by this method was 172 on 18th February 1977,
while the maximum number of coccinellids found was 11 on 10th December
1976 and the maximum number of M.tasmaniae was eight adults on the 26th
November 1976. The maximum number of M.tasmaniae larvae found was two.

<u>M</u>. <u>fasciatum</u> is more difficult to compare by this method since it is more likely to evade the sweep net, but 48 adults were found on 4th February although larvae were very rare.

In terms of the total number of a species found by all sampling methods during the period from September 1976 to April 1977 again <u>N</u>. <u>maoricus</u> was dominant. The relative abundance during this period was <u>N</u>. <u>maoricus</u> ˃ <u>M</u>. <u>fasciatum</u> ˃ <u>C</u>. <u>undecimpunctata</u> ˃ <u>M</u>. <u>tasmaniae</u> ˃ <u>M</u>. <u>novae-zelandiae</u>. During spring from the 14th September to the cutting of the lucerne on 15th December the relative abundance was <u>M</u>. <u>fasciatum</u> ˃ <u>C</u>. <u>undecimpunctata</u> ˃ <u>M</u>. <u>tasmaniae</u> ˃ <u>N</u>. <u>maoricus</u>. The situation was the same in summer and autumn except that nabids were the most abundant predators. When only the predaceous stages of each species are considered the effectiveness of predators in relation to their abundance over spring, summer and autumn was <u>N</u>. <u>maoricus</u> ˃ <u>C</u>. <u>undecimpunctata</u> ˃ <u>M</u>. <u>tasmaniae</u> ˃ <u>M</u>. <u>fasciatum</u>.

<u>M</u>. <u>fasciatum</u> was the second most abundant predator in terms of the maximum numbers observed but its larvae were rarely found at the DSIR study plot. However they were abundant at Voss's and the possible reasons for this have been discussed previously.

<u>M</u>. <u>tasmaniae</u> never attained very high numbers either as an adult or juvenile. Both <u>M</u>. <u>tasmaniae</u> and <u>C</u>. <u>undecimpunctata</u> were notable for their relative absence in the autumn of 1977 and especially for the absence of larvae of both species during this time. Hyperparasitism may have been an important factor in this (Hilson, 1964; French, 1966).

In overseas studies coccinellids are generally reported as the most common aphid predators, while the relative numbers of syrphid, neuropteron and hemipteran predators seems more variable. Except for the occurrence of high numbers of nabids, the situation at the DSIR study plot would have been similar.

The pattern of abundance of the predators is important. The extended peak of numbers of <u>N</u>. <u>maoricus</u> compared to the sharp population peaks of the other predators is indicative of a sustained effect on the aphid population. The long duration of predation presumably due to the nabids' relative immobility means they can exert pressure on any population

of aphids which begins to build up. There may be value in conceptually separating non-aphid specific predators and mobile, more aphid specific predators which follow the aphid populations. While attempts are made to encourage the mobile aphid specific predators, it would seem that little is specifically attempted to encourage the other predators which, as found in the present study, can be highly successful.

A number of factors may be acting to reduce the abundance of the predators. Cannibalism occurs amongst aphidophagous coccinellid, neuropteran and syrphid juveniles (Hagen, 1962; Schneider, 1969; New, 1975) and also in nabids (Mundinger, 1922). The effect of cannibalism on predator abundance is unclear although it is known to have an adaptive function in that it ensures the survival of at least some of the predators (New, 1975).

Hyperparasitism is common and may be the major factor reducing the abundance of predators. Syrphid species worldwide are parasitised, often in high numbers by <u>Diplazon</u> spp. (Bodenheimer and Swirski, 1957; Evenhuis, 1966; Hagen and van den Bosch, 1968; Schneider, 1969). Hudson (1884) and Cumber and Eyles (1961b) record <u>Diplazon</u> <u>laetatorius</u> F. (=<u>Bassus</u> <u>laetatorius</u> F.) as being common in New Zealand. High numbers of this species were also found at the DSIR study plot in the present study. Of 11 <u>M</u>. <u>fasciatum</u> larvae which pupated in the laboratory, four hatched out specimens of <u>D</u>. <u>laetatorius</u> and another one was found on dissection to contain the parasite. Of seven <u>M</u>. <u>novaezelandiae</u> larvae which pupated in the laboratory, <u>D</u>. <u>laetatorius</u> specimens hatched from two, and on dissection a further four were found to contain the parasite.

<u>C</u>. <u>undecimpunctata</u> is parasitised by a Braconid wasp <u>Perilitus</u> <u>coccinellae</u> (Schrank). Gourlay (1930) attributes the low summer numbers of the ladybird to parasitism and French (1966) states that up to 85% parasitism may occur in late spring.

<u>M</u>. <u>tasmaniae</u> is parasitised by at least one Figitid <u>Anachris</u> <u>zealandica</u> Ashmead and possibly two other species. It is also fed upon by various predators and infected by a virus (Hilson, 1964).

The predators and parasites of nabids, if any, are unknown
(Valentine, 1967a), although parasites are reported for American Nabis spp
(Taylor, 1949; Whitcomb and Bell, 1964).

It is therefore possible that nearly all the common predators of
A. kondoi are parasitised and often at high levels. Even at low levels
the effect of hyperparasites may be important if they reduce the abundance
of predators below the level necessary for adequate control of the aphids.

9.3.2.5 Number of Prey Consumed

The number of aphids consumed by predator species has been
studied by many authors but comparisons are difficult because of the
different types and sizes of aphids (often this information not being
given), the varied conditions under which the experiments are done, and
the difficulty of relating laboratory studies to natural conditions.

The aphid consumption of the predators found in the present study
and/or closely related species is shown in Table 7. In general syrphids
seem to be the most voracious, and in this study they were observed to be
rapid feeders on A. kondoi though no specific data was found for M. tasmaniae
or M.novaezelandiae. The New Zealand neuropterans and coccinellids
appear to be less voracious than their overseas counterparts (French, 1966;
Thomas, 1977) and the situation may be similar with syrphids. Even overseas
C. undecimpunctata is considered to be a relatively unvoracious species of
coccinellid (Harpaz, 1958).

The number of A. kondoi consumed by N. maoricus adults is shown
in Table 6. From this figure it can be seen that an adult consumes an
average of 11.25 second and third instar A. kondoi per day in the conditions
specified, though the maximum number can be as high as 26. There is some
variability present in the results but it appears that the number of A. kondoi
consumed by N. maoricus was normally in the range of eight to fourteen aphids
per day, and probably closer to the latter.

There are many possible sources of error in doing predator
feeding experiments in the laboratory and attempting to relate them to
the natural situation. For example, the searching time of the predator

Table 7   The predators (or closely related species) of $\underline{A}$. $\underline{kondoi}$
and the number of prey they consume.

Predator Species	Number of Aphids Consumed Per Day Per Predator	Reference
Coleoptera		
$\underline{C}$. $\underline{undecimpunctata}$	16.2 aphids at $30^{\circ}C$ in constant dark	French (1966)
$\underline{A}$. $\underline{bipunctata}$	19 - 35 medium sized $\underline{Myzodes}$ $\underline{persicae}$ at $25^{\circ}C$ and 75% R.H.	Iperti (1966b)
$\underline{C}$. $\underline{undecimpunctata}$	15 - 16 $\underline{A}$. $\underline{kondoi}$	Thomas (1977)
Neuroptera		
$\underline{M}$. $\underline{tasmaniae}$	2.11 $\underline{R.padi}$ adult equivalents (by December larvae)	Hilson (1964)
Diptera		
$\underline{Syrphus}$ $\underline{corollae}$ F.	86.7 medium sized $\underline{A}$. $\underline{fabae}$ and $\underline{Myzus}$ $\underline{persicae}$ Sulz. at 22oC and 55% R.H.	Schneider (1969)
$\underline{Allograpta}$ $\underline{obliqua}$ Say.	33.2 large $\underline{T}$. $\underline{maculata}$ at temperatures averaging $22.5^{\circ}C$	Simpson and Burkhardt (1960)
Hemiptera		
$\underline{N}$. $\underline{ferus}$	18.5 large $\underline{T}$. $\underline{maculata}$ at temperatures averaging $21.2^{\circ}C$	Simpson and Burkhardt (1960)
$\underline{N}$. $\underline{ferus}$	22.6 $\underline{T}$. $\underline{maculata}$	Nielson and Henderson (1959)
$\underline{N}$. $\underline{americoferos}$	4-23 aphids	Hendrick (1967)
$\underline{Nabis}$ $\underline{flavo-}$ $\underline{marginatus}$ Scholtz.	3.1 first to third instar $\underline{Acyrthosiphon}$ $\underline{spartii}$ (Koch.)	B.D. Smith (1966)

in the dishes is almost nil, and the predator's hunting behaviour is probably unimportant. The small size of the tissue culture dishes used makes all aphids easily accessible and the aphids have little opportunity to escape from the predator. Also the microclimate within the dishes may vary greatly from that measured in the constant temperature cabinet. French (1966) and Way (1966) have noted that coccinellids consume more aphids in varying temperatures than at constant temperatures and therefore N. maoricus may also act in this manner.

The only comparative data available concerning the number of aphids consumed by nabids is on Americam Nabis species. Neilson and Henderson(1959) found that N. ferus consumes 22.1-22.6 T. maculata per day at an unspecified temperature while the same species feeding on "large" T. maculata consumed 18.5 aphids per day at temperatures averaging 22.5°C (Simpson and Burkhardt, 1960). Hendrick (1967) found that nabids (presumably Nabis americoferus Carayon) consumed 4-23 aphids per day. The consumption of aphids by these species is therefore similar though slightly higher in the first two cases, to that of N. maoricus. The higher and more varied, or unspecified, temperatures of the experiments may partly explain the difference and it can be concluded that Nabis spp are moderate aphid feeders, but since they are polyphagous predators it is unlikely that, at any one time, their diet would be composed totally of aphids.

Simpson and Burkhardt (1960) provide information on the number of aphids consumed by N. ferus instars, and it appears that there is a steady increase in consumption as a nabid grows. From observations on N. maoricus instars' feeding habits, and the size of the instar in comparison to the adult, it is probable that there is a similar pattern for this species and that fourth and fifth instar N. maoricus would consume eight to ten A. kondoi per day. Even the first instar of N. ferus was found by Burkhardt and Simpson to consume 5.1 large aphids per day but this was in artificial conditions and although first instar A. kondoi could possibly consume this number of A. kondoi they are apparently rare on plants (see Section 6.3.4.2) and therefore may not eat many aphids.

Using the information presented above supporting evidence for the results of the exclusion cage studies can be gained assuming fourth and fifth instar N. maoricus larvae consume on average eight aphids per day.

On 11th February 1977, the time of the highest nabid population, seven
N. maoricus larvae were found on 80 lucerne stems at the DSIR study plot
and on 14th February the number of A. kondoi per stem was 0.46. It is
therefore quite feasible that N. maoricus was effectively controlling the
A. kondoi population. Further supporting evidence is provided by Tamaki
and Weeks (1972) who found that one specimen of N. americoferus per
plant was sufficient to control populations of up to 14 Myzus persicae
Sulz) per sugarbeet plant. On this basis with seven N. maoricus per 80
stems the A. kondoi population would have been uncontrollable at a
population of 7 x 14 = 98 aphids on 80 stems or 1.225 aphids per stem.
The A. kondoi population was actually less than half this. Indeed it is
possible that, even while N. maoricus was controlling the A. kondoi
population, it was also resorting to supplementary foods.

The number of A. kondoi destroyed by entomophthorous fungi was
determined by sampling Exclusion Cage One (see Section 9.4) close to the
peak of the fungal epidemic. On nine lucerne stems 141 aphids were
heavily infected with fungus and 218 were unifested or only slightly so.
MacLeod (1955), Grobler et al. (1962), Lowe (1968) and Smirnoff and
MacLeod (1973) all reported a high percentage of infection, up to 100%
by various fungal species. The mortality caused by fungi can be very
high and very rapid compared to that caused by predators.

In March 1977 a further ten stems of lucerne were collected and
a note was made of which instars were infected. The results presented
in Table 8 show that all the instars of A. kondoi were infected, though
late instars especially alate adults made up the highest proportion.
Possibly this was because they move on the plant more than feeding aphids,
or possibly because of their age they were exposed to infection for a
longer time allowing the fungus time to develop. The fourth instar alates
and adult alates are normally present in large numbers in the population
at this stage of its development and therefore this does not necessarily
mean they are more susceptible to infection. These results support the
possibility suggested earlier that one of the main effects of fungus is to
decrease the number of alates available for colonising new crops.

Table 8   The numbers of each instar of <u>A</u>. <u>kondoi</u> attacked
by entomophthorous fungi on ten lucerne stems.

Stem	1	2	3	4	5	6	7	8	9	10
Adult Alatae	1	1	3	32	6	2	6	10	3	50
Adult Apterae	0	0	0	2						
4th instar alatae	3	0	3	8						
4th instar apterae	1	0	0	3						
3rd instar	1	0	1	5						
2nd instar	0	0	0	3						
1st instar	0	0	0	4						
Uncertain instar	0	0	1	1						
Total number aphids on each stem	6	1	8	58	11	8	10	43	5	63

9.3.2.6 Summary - Synchronisation and Voracity of Predators

By considering all the individual components of predator
effectiveness some conclusions can be drawn. Overall there was no
effective biological control of A. kondoi which prevented the aphid
reaching economically damaging levels during the spring of 1976. This
was mainly due to the predators arriving too late to prevent the aphids
with their rapid multiplication rate increasing their population numbers
beyond the possibility of effective control. Only one non-aphid specific
predator, N. maoricus, served as an effective controlling agent during
part of summer 1977.

The adults of M. fasciatum were notable for their early
arrival when the A. kondoi population began building up, but this
synchrony with the aphid population did not seem to extend to the larvae.
The larvae probably consume a large number of aphids per day, but because
they were rare at the DSIR study plot they were almost totally ineffective.

C. undecimpunctata was poorly synchronised with the A. kondoi
population, although it was the second most abundant predator, whilst
M. tasmaniae was also poorly synchronised but was not present in any
numbers.

Since N. maoricus apparently does not fly it must rely on being
present at the start of an aphid population build up. Thus, although this
nabid will normally not possess any control over its synchronisation with
the aphid population, they were abundant and voracious enough to control
the population of A. kondoi at the DSIR study plot during late summer.

Entomophthorous fungi were also too poorly synchronised to
prevent damage by A. kondoi and their main effect seemed to be in reducing
the number of migrating alates.

9.4 Overall Efficiency of Predators

9.4.1 Introduction

The most natural and convincing test of the effectiveness of
natural enemies would be the comparison of an aphid population along with
predators and parasites, with a completely analogous situation where
natural enemies are absent (Hodek et al., 1972). Such situations are

difficult to find in nature and hence it is necessary to attempt to artificially create them by excluding predators.

In the present study two trials, one in spring and one in autumn, in which predators were excluded from the aphids were therefore carried out because of the need to distinguish the overall effects of predators from other factors acting on the A. kondoi population and they also place a quantitative value on this effect. This value is a composite result which is due to all the individual components of predator effectiveness discussed previously. Various techniques have been developed for excluding predators (Pollard, 1969; Hodek et al., 1972) but in a densely growing field crop such as lucerne exclusion cages are the most suitable.

9.4.2   Methods
9.4.2.1 Exclusion Cage Design

Two box shaped exclusion cages were built (Fig. 25a) with frames made of No. 8 wire, and dimensions of 104 cm by 104 cm by 62 cm high. The cages were covered with terylene with a mesh size of 0.9 x 0.4 mm which was sewn on to the cages. The seams were sealed with four cm wide masking tape and this was also placed around the base of the cage to prevent the terylene decomposing. Both the exclusion cages and the microclimate control cages described below were painted with green paint in Trial I but the new exclusion cages made for the second trial were not painted.

A number of exclusion cage designs and materials have been described these depending on the situation where the cage is to be used. Cages in field crops have usually been box-like (e.g. Bombosch and Tokmakoglu, 1966; Sailor, 1966; Sparks et al., 1966) and this design was adopted in the present study.

A variety of materials for covering exclusion cages have been used by other workers. These include for example organdie (De Bach et al., 1949), perlon (Bombosch and Tokmakoglu, 1966), 16 mesh metal screen (Sparks et al., 1966) and terylene (Way and Banks, 1968; Woodford, 1973). Terylene was chosen for the present study because it does not decompose easily and is relatively inexpensive.

Fig. 25   The exclusion cage and microclimate control cages
          used at the DSIR study plot.

                    a. exclusion cage
                    b. microclimate control cage
                    c. microclimate control cage (Over page)
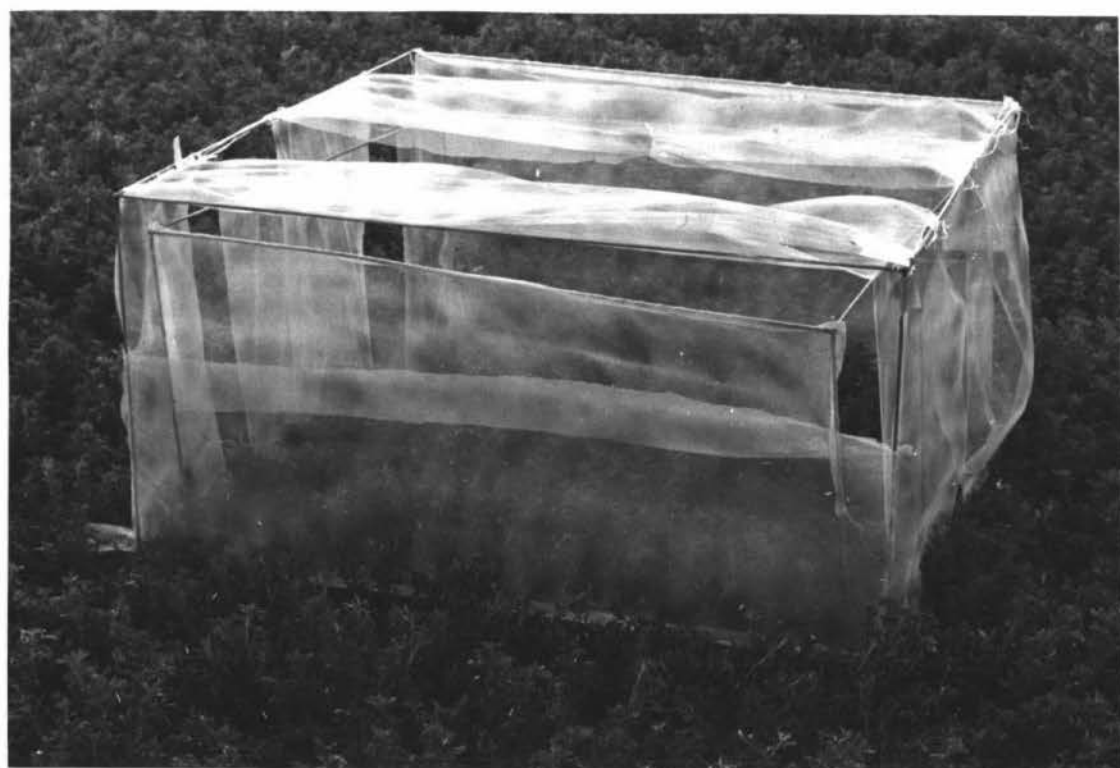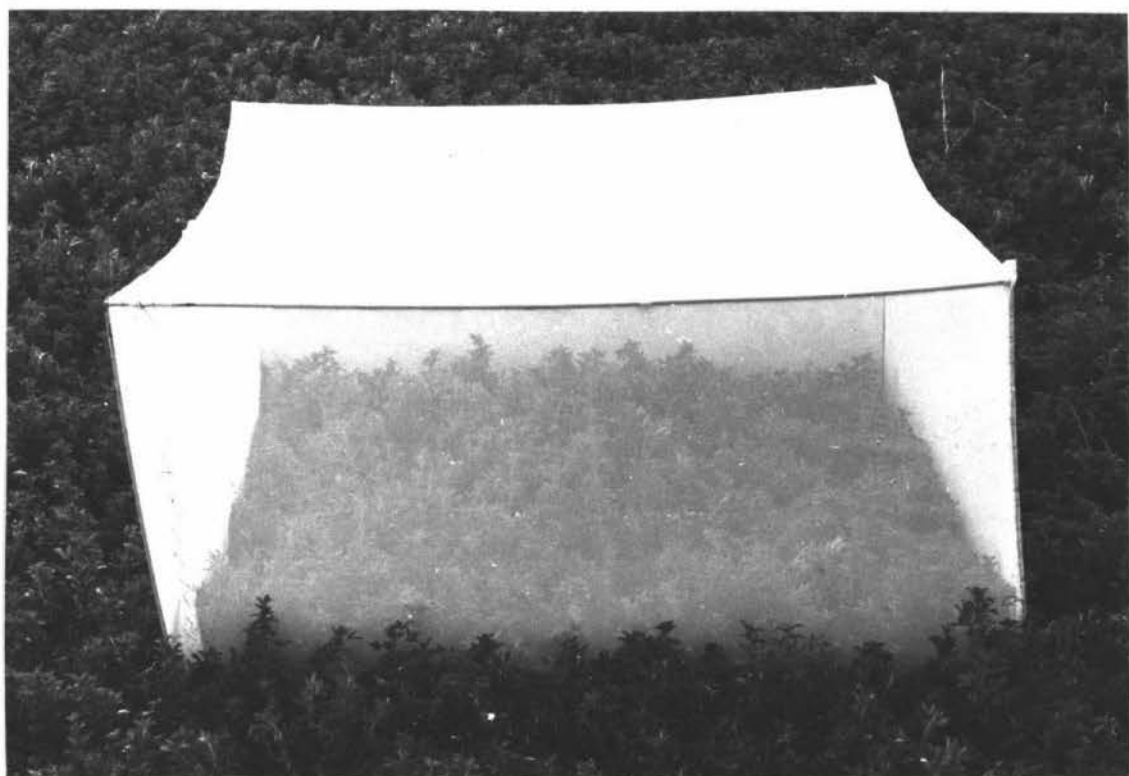
c. Microclimate control cage

There were two opposing considerations in choosing a mesh size. Firstly there was the need to limit the entry of predators while allowing alate aphids to escape, and secondly it was important to avoid significantly altering the microclimate within the cages since this can affect both the plants and animals (Woodford, 1973). The mesh size chosen seemed to meet these requirements.

The cages were painted with green paint to ensure that they were neither highly attractive nor repellant to predators. Large numbers of aphids in a cage can cause the deposition of predator eggs on the outside of the cage or parasitism of those aphids on the cage walls. It was found, however, that the painted terylene became brittle and ripped easily, hence the new exclusion cages for the second trial were not painted.

9.4.2.2 Microclimate Control Cage Design

Two microclimate control cages were constructed, each consisting of two cages, one fitting inside the other. The outer cages were of the same size as the exclusion cages while the inner cages were ten cm smaller in all dimensions.

The terylene in the first type of microclimate cage (Fig. 25b) consisted of alternating strips both on the roof and sides, whereas the second type (Fig. 25c) had a solid outer roof. To allow for the reduced exit area through the roof, the number of vertical strips was increased to provide a greater opportunity for the entry and exit of predators.

Both the microclimate control cages and exclusion cages were fastened to the ground with metal stakes.

The design of the two microclimate control cages was broadly based on that of Sparks et al., (1966). With the notable exception of Franz (1956) and Way and Banks (1968), very few authors have used microclimate control cages and hence their results are always open to the criticism that the differences in prey numbers observed between the inside and outside of exclusion cage are due to microclimate differences, and certainly their results cannot be considered quantitative.

Again there were two opposing considerations in designing the control cage. The surface area of the cages must be great enough so that

their microclimate is the same as in the exclusion cages, but aphids and predators must be able to enter and leave freely. The gap between the inner and outer cages in the present study was 2.5 cm greater than that used by Sparks et al., (1966) and this increased clearance, and also the painting of the cages was an attempt to decrease the trapping of parasites and predators within the cages as this was observed by Sparks et al. A lesser problem was that predators which did enter the cages may have been more effective due to an improved microclimate.

Peterson (1945) was the first to quantify the climate in exclusion cages and show how they differed from the outside. This has been repeared by various authors and all have found the greatest differencesto be in light intensity and wind speed. For example, Way and Banks (1968) recorded an 18% decrease in light intensity and a 24% decrease in wind speed in their terylene cages, while Woodford (1973) recorded a decrease of as much as 58% in light intensity and up to 85% decrease in wind speed. Obviously the mesh size and percentage open area of the mesh is important. Temperature and humidity were found to differ much less by Way and Banks (1968) and Woodford (1973), but Sparks et al., (1966) found that the temperature could be 8-10°F less in the cages than in the open, on a sunny day. The temperature does not tend to fluctuate as much in the cages as outside (Sparks et al., 1966; Woodford, 1973) nor does the humidity (Sparks et al., 1966).

Recordings made during the present study showed that the temperatures were within 1°C of each other in both microclimate and exclusion cages. The maximum temperature recorded was 2.5°C higher outside the cages than inside. Humidities were very similar with the microclimate control cages being 2-3% lower than the exclusion cages and the outside being 4-5% lower than the microclimate cages. These differences in temperature and humidity are probably for the most part unimportant and are in the order of magnitude of the differences observed by Sparks et al., (1966), Way and Banks (1968) and Woodford (1973).

Although recording anemometers were not available to measure differences in wind velocity, there did not appear to be a great difference between the cages. Slatted windbreaks such as in the microclimate control cages are usually found to be as effective as solid windbreaks such as in the exclusion cages. The amount of light entering the microclimate control

and exclusion cages is similar with the areas in the microclimate control cages which received direct sunlight being compensated for by the areas which were doubly shaded by the overlapping of the terylene slats.

9.4.2.3 Experimental Procedure

Two trials were carried out using the exclusion cages at the DSIR study plot. Trial I was begun on 4th November 1976 while Trial II was started on 28th January 1977. In both trials, three control areas, each four feet by four feet were pegged out, in addition to the two exclusion cages and the two microclimate cages.

For Trial I the four cages and three pegged areas were laid out randomly in an area of approximately equal lucerne density. The areas were close to the middle of the field and grouped with about two metres between each to avoid any variation in aphid numbers over the paddock. Both areas to be covered by the exclusion cages were prepared by closely examining them for predators and any found were removed. An approximately 10 cm wide strip of vegetation was removed from around the perimeter of the exclusion cages to deter predators which may have entered the caged area while the cage was lifted for sampling. The exclusion cages were placed over these prepared areas and the perimeter of the cages was sealed with soil.

The other five areas were also examined for predators but these were not removed. This ensured that the "drop reaction" of the aphids occurred in all areas. It is known that after a drop reaction many aphids do not survive and their fecundity may be affect (Niku, 1975). After this procedure all the areas were left for 24 hours before the initial sampling to allow the aphids time to climb back on the plants.

Various methods have been used for the initial removal of predators from exclusion cages and a review of these has been published by Hodek et al. (1972). In Trial I, predators were removed by hand and although this has the disadvantage of disturbing the aphids it does not affect the environment as insecticides do. Also some predators will not be found but the cages were set up soon after the paddock was grazed and hance both predator and aphid numbers were very low at this time.

To ensure that the cages were effectively excluding predators, the exclusion cage walls were checked for visible predators before the cages were lifted for each sample. The vegetation inside the cages was also carefully examined visually at each sample and any predators found were removed. All predators found in the collected stem samples were noted. A record was also made at each sample of all predators visible inside microclimate control cages to discover any trapping effects, although no such effect was ever noticed.

Samples were taken at weekly intervals by removing nine stems from each of the seven areas. Each stem was randomly chosen, then care-fully held, cut at its base, and placed inside a plastic bag. Limiting the samples to nine stems avoided depleting the vegetation. Each stem was washed with water heated to $70^{o}C$ in the laboratory and the numbers of aphids and predators were counted.

Trial II was intended to measure the effectiveness of predators on the anticipated autumn aphid population peak. The cages and control plots were dispersed randomly in a new area approximately ten metres from the area of Trial I and two to three metres from each other to prevent insecticide from one plot contaminating others. The exclusion cages were set up in a similar way to Trial I. Stem samples were taken as before except for the stems being collected singly and the number of aphids on each stem was counted.

In Trial II insecticide was spread on the ground to ensure that the exclusion cages were maintained predator free since some problems were experienced with Trial I in this respect. Lindane (Gamma - BHC) was used because it has a high contact toxicity, an almost non existent systemic action, is non phytotoxic, and has a low fumigant action (v.p. 9.4×10^{-6}mm Hg at $20^{o}C$) (Martin, 1971). It was applied in the prill form to avoid wind movement of the insecticide and especially its deposition on plants. The prills were spread throughout the cage and on the soil piled around the cage perimeter. Although the sample areas had been set up on 28th January the lindane was not applied until the 1st February to allow adequate time for the aphids to climb back on the plants. Laboratory experiments during the present study indicated that lindane did not appear

to affect A. kondoi on lucerne, although Koeler and Gyrisco (1957) have reported a systemic and fumigant effect of this insecticide on Meadow Spittlebugs.

Since large numbers of nabids were present during Trial II in Exclusion Cage Two as shown by those found in samples and those observed during sampling, a second examination of this cage was carried out on 8th March when the cage was thoroughly searched twice and 14 adult and 14 juvenile N. maoricus were found and removed. The presence of the nabids could indicate that the initial searching was inefficient, but as noted in Section 6.3.4.2, it would seem that the earliest nabid instars live in placed not easily searched, presumably in the ground and litter.

After the nabids were removed Exclusion Cage Two, the micro-climate control cages and the control areas were reinoculated with A. kondoi. Exclusion Cage One which was excluding predators successfully was not touched.

9.4.3 Overall Efficiency of Predators - Results of Exclusion Cage Trials and Discussion

9.4.3.1 Trial I

The results of this spring trial are given in Table 9 and show that there were much higher numbers of A. kondoi in the exclusion cages on 25th November than in the predator control areas and microclimate control cages. The numbers were still high on 2nd December and therefore it can be concluded that lack of predators allowed the aphids to reach their population peak earlier and extend its period. The peak of the aphid population is also more distinct due to the more rapid growth up to the peak.

The relative increases in aphid population for the exclusion cages between 19th and 25th November is significantly higher than for all other areas. Without predators the populations of aphids seem to be closer to an exponential growth, characteristic of a growing population which is not inhibited.

It can be assumed that most of the aphid populations reached their peak numbers between 25th November and 2nd December, hence the

Table 9   The results of exclusion cage Trial I

Numbers of A. kondoi present per nine stems of lucerne

Date of Sample (1976)	Exclusion Cages		Microclimate Control Cages		Predator Control Areas		
	One	Two	One	Two	One	Two	Three
5/11	1	8	5	4	4	34	4
12/11	33	54	43	71	21	99	15
19/11	79	155	121	202	119	147	74
25/11	961	1276	339	635	443	754	374
2/12	1009	1071	607	507	697	1173	2329
9/12	632	114	200	97	128	242	704
16/12	0	0	0	0			

timing of the maximum of the population peak does not seem to be greatly affected, though samples at closer time intervals would be needed to verify this.

Nothing definite can be concluded as to the effect of predators on the number of aphids present at the maximum of the population peak, since Predator Control Area One was lower than either of the exclusion cages, whereas Predator Control Area Three was almost 100% higher. However both microclimate control areas were very much lower than either of the exclusion cages or predator control areas. If this lowering of the maximum population is a microclimate effect, then such an effect would decrease the maximum numbers of aphids in the exclusion cages by half. Also it is reasonable to expect the peak of Exclusion Cages One and Two, to have occurred between the 25th November and 2nd December and if an almost exponential growth rate had occurred up to the peak between this period then the peak numbers may have been even higher than those of Predator Control Area Three. Further investigation is required to verify whether the difference in numbers is a microclimate effect and if so then it can be concluded that predators decreased the maximum size of the aphid population.

Although a predator effect is usually most notable after the aphid population peak, in this study there were two complicating factors in interpreting the results obtained when the aphid population was declining. The first of these was the occurrence of entomophthorous fungi in the exclusion cages at this time. This would have increased the the rate of decline and may account for no predator effect being apparent during the population decline. It is noticeable that the fungus did not occur in the microclimate control cages, and this provides supporting evidence for the necessity of a critical aphid density before an epidemic will occur. The second complicating factor is the retention of alate adults in the exclusion cages. Sailor (1966) found thousands of winged Macrosiphum euphorbiae(Thomas) on the interior walls of the cage he was using, and the writer noted a similar occurrence in the present study. These alates were released each week during sampling since the cages were upturned, but between samples they may have larviposited on leaves and retarded the rate of decline of the aphid population. No conclusions can therefore be drawn as to the effects of predators on the declining aphid population because of these opposing factors.

Overall the major effect of predators seemed to be on the rate of growth of the aphid population and on the extent and maximum size of the peak, but even though the predators were active the aphid numbers in all areas were above the level of economic importance. The failure of predators to effectively control spring populations of aphids seems to be a common occurrence.

Some value can be placed on the results obtained since, although Table 10 shows that some predators were still present in the exclusion cages in this trial their numbers would undoubtedly have been lower than outside the cages.

9.4.3.2 Trial II

This second trial was run to study the effect of predators on the anticipated population peak in summer and autumn, and the results are given in Fig. 26 and Table 11. The summer-autumn aphid peak did not eventuate in the field and this trial indicated that this was at least partially due to the effect of predators mainly N. maoricus.

Only in Exclusion Cage One did the aphid population progress and this indicated predators were effective outside the cages since both visual sampling and stem sampling (Table 12) showed that predators were successfully excluded from this cage.

Exclusion Cage Two showed the opposite trend and this was undoubtedly due to the nabids present, which being trapped in a confined area, undoubtedly fed intensively. This observation in Exclusion Cage Two supports the observations in Exclusion Cage One and indicates that N. maoricus was the main predator component.

Once the possible importance of predation by N. maoricus had been indicated it was decided to confirm this by removing N. maoricus from Exclusion Cage Two. After the removal of 28 N. maoricus from the cage the aphid population proceeded to build up whereas the aphids failed to survive in the other areas which had been innoculated with aphids at the same time. This clearly showed that N. maoricus was the main predator species responsible for the depletion of the aphid population in the field at this time. This result, along with the build up of aphids in

Table 10   The predators found in exclusion cage Trial I

Number of predators present per nine lucerne stems.

Date of Sample (1976)	Exclusion Cages		Microclimate Control Cages		Predator Control Areas		
	One	Two	One	Two	One	Two	Three
5/11	0	0	0	0	0	0	0
12/11	0	0	0	0	0	0	0
19/11	0	0	0	0	0	0	0
25/11	0	0	0	0	1c	0	0
2/12	0	0	0	1a,1b	2b	3b	0
9/12	2a	1a	3a,2b	1b	0	1a,1e	0
16/12	1b	0	0	0	1d	0	0

a = M. tasmaniae juvenile

b = Syrphid juvenile

c = C. undecimpunctata juvenile

d = M. tasmaniae adult

e = N. maoricus juvenile

Fig. 26   The result of excluding predators from A. kondoi
          in Trial II.   The effect of removing N. maoricus
          from Exclusion Cage Two can be clearly seen.

NABIDS REMOVED

DATE

MAR 1977

APR 1977

FEB

600
500
400
300
200
100
80
60
40
20

EXCLUSION CAGE ONE

EXCLUSION CAGE TWO

PREDATOR CONTROL AREA ONE
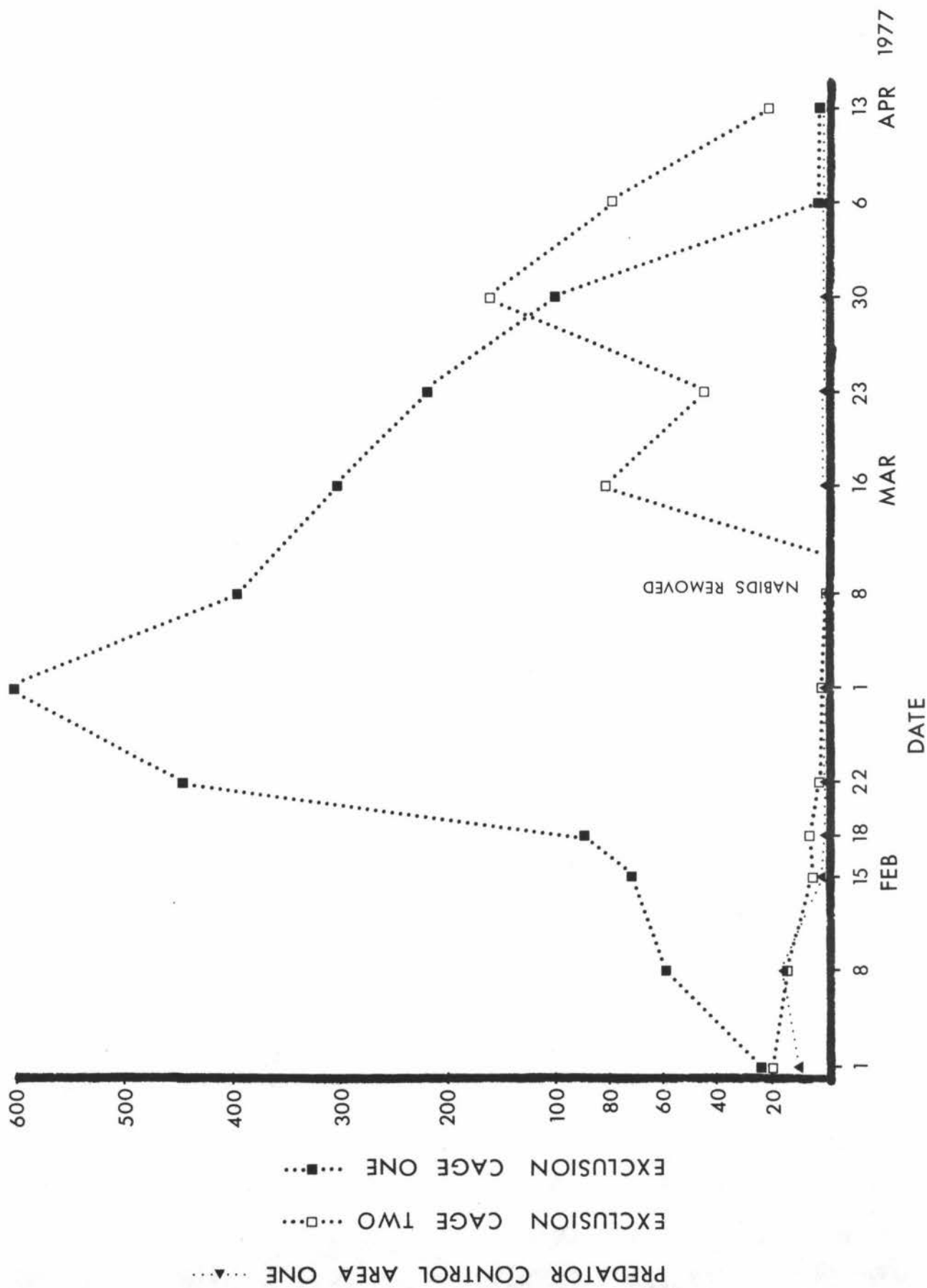
Table 11   The results of exclusion cage Trial II

Numbers of <u>A</u>. <u>kondoi</u> present per nine stems of lucerne.

Date of Sample (1977)	Exclusion Cages		Microclimate Control Cages		Predator Control Areas		
	One	Two	One	Two	One	Two	Three
1/2	24	20	4	4	9	12	8
8/2	56	14	1	7	16	15	11
15/2	72	6	6	8	1	3	2
18/2	89	6	1	0	0	3	0
22/2	445	3	0	3	0	0	1
1/3	601	2	0	0	0	0	0
8/3	393	0	0	3	0	0	0
Nabids Removed							
16/3	303	83	0	0	0	0	3
23/3	216	49	0	0	1	0	0
30/3	100	158	0	0	2	0	-
6/4	4	76	0	3	1	0	3
13/4	3	22	0	0	0	0	0

Table 12   The predators found in exclusion cage Trial II

Number of predators present per nine lucerne stems.

Date of Sample (1977)	Exclusion Cages		Microclimate Control Cages		Predator Control Areas		
	One	Two	One	Two	One	Two	Three
1/2	O	O	O	O	O	O	O
8/2	O	1b	O	O	O	O	O
15/2	O	O	O	1b	O	O	1b
18/2	1a	2b	O	1b	O	1b	O
22/2	O	1b	O	3b	O	O	O
1/3	O	2b	O	O	O	2b	3b
8/3	O	O	O	O	O	O	O
	Nabids Removed						
16/3	O	O	O	O	1c	1b	O
23/3	O	1b	O	1b	O	O	O
30/3	O	O	O	O	O	O	O
6/4	O	O	O	O	O	O	O
13/4	O	O	O	O	O	O	O

a = C. undecimpunctata

b = Nabis sp.

c = M. tasmaniae

Exclusion Cage One also demonstrated that throughout the duration of Trial II the predators controlled the A. kondoi population. Figure 27 shows the aphid population observed in Exclusion Cage One superimposed on the population pattern obtained from fortnightly plant samples. Hence it shows the A. kondoi population pattern which may have been observed were it not for N. maoricus and it can now be seen that the small aphid population build up which occurred in late January was the beginning of an aborted summer-autumn peak.

It is of interest that such an effect on the aphid population could occur when aphid specific predators were absent and that just one predator species, rather than the complexes of predators which are often reported, could be so effective. Attributing the entire effect to N. maoricus may be an oversimplification but of the aphid specific predators only the eleven spotted ladybird was sporadically present and this was mainly as the adult with only two larvae being found during the trial. "Miscellaneous" predators, especially spiders, which in February were present in large numbers, may also have had some effect.

The effect of "miscellaneous" or non-aphid specific predators on aphids has only recently been recognised (e.g. Whitcomb and Bell, 1964; Vickerman and Sunderland, 1975). The former authors attributed the prevention of many pest outbreaks to the combined effect of miscellaneous predators. It is possible that the lack of reports of effective aphid control is due to the lack of recognition of the importance of the non aphid specific predators and the attributing of this effect to some other controlling factor such as weather (Frazer and van den Bosch, 1973).

Bombosch and Tokmakoglu (1966) found, using exclusion cages, that aphids increased their numbers by 360 fold in the absence of predators, whereas with predators the increase was much lower. In the present study the effect of predators was even higher with a 600 fold difference on 1st March between areas which lacked or possessed predators.

In Trial II lindane was used in the exclusion cages to prevent the predator problems experienced in Trial I, but the effectiveness of this is doubtful. Certainly Exclusion Cage Two contained high numbers of nabids until they were removed on 8th March. Exclusion Cage One in this

Fig. 27   The population of A. kondoi in Exclusion Cage One
           (Trial II) superimposed on the population of A. kondoi
           found during fortnightly samples at the DSIR study
           plot. The population peak sampled in Exclusion Cage One
           may have occurred as a summer-autumn population cycle
           throughout the entire study plot, but for predation
           by N. maoricus

LUCERNE CUT

LUCERNE GRAZED

MEAN NUMBER OF A. kondoi PER STEM AT THE DSIR STUDY PLOT

········ MEAN NUMBER OF A. kondoi PER STEM IN EXCLUSION CAGE ONE

DATE

12/4 A 25/4 11/5 M 24/5 8/6 J 22/6 1976 6/7 20/7 J 3/8 18/8 A 31/8 15/9 S 27/9 11/10 O 1/11 15/11 N 29/11 13/12 D 4/1 17/1 J 31/1 14/2 F 1977 27/2 14/3 M 28/3 11/4 A 25/4

70 60 50 40 30 20 10
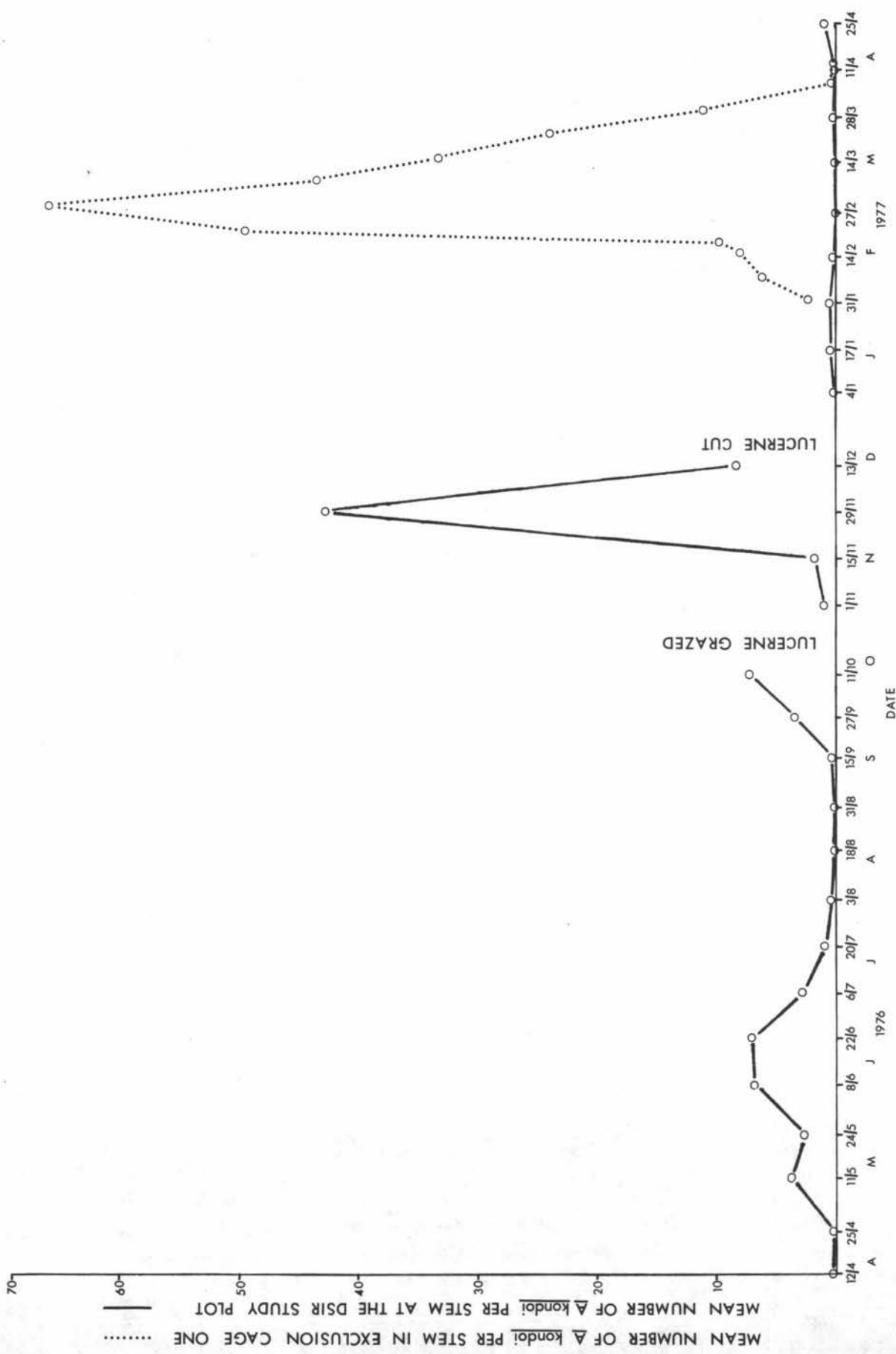
trial seemed from all observations and samples to have successfully
excluded predators and the occurrence of the single coccinellid adult
was probably due to it flying in while the cage was lifted for sampling.
The removal of nabids by hand in Exclusion Cage Two on 8th March also
seems to have been successful.

9.4.3.3 Conclusions

Predators had a slight effect on the spring A. kondoi population
but were unable to control it. They did however prevent the build up of
the numbers of A. kondoi in February and March and retained the population
below economically damaging levels at this time. This effect was mainly
attributed to the presence of N. maoricus.

The results of Thomas (1977) also suggest that predators may
have been more effective in autumn and it may be that predator control
of aphid numbers is more common on potential aphid peaks which occur after
the high spring populations. This is probably due to a build up in the
numbers of the predators on the spring and subsequent aphid populations.
Since the A. kondoi population cycles seem to occur continuously through-
out spring to autumn (Richardson, 1977) shortage of food should not be a
problem.

CHAPTER TEN

INTRASPECIFIC REGULATION OF
THE A. KONDOI POPULATION

10.1 Introduction

In an environment free from climatic effects and predators
an aphid population will increase rapidly on a suitable host plant. Indeed
this increase will almost be exponential until intraspecific competition
for space or food begins. If no regulation of the population occurs the
population will rapidly exhaust its resources by killing the host plant
resulting in a population "crash" with large aphid mortality. Such
mortality is a waste of the resources of both the host plant and the
aphids because the host plant is killed and is therefore unavailable for
future colonisation, while the aphids on the plant also die when it dies
without replacing or increasing the numbers of their species (Way and
Banks, 1967; Dixon and Wratten, 1971). The latter is important since the
"success" of an aphid can be considered in terms of the number of viable
offspring it produces (Way and Banks, 1967; Hughes and Gilbert, 1969).

Some aphid species seem to have developed beyond this
simple relationship with the host plant to one in which the aphids by
their interactions with each other can control their population growth
(e.g. Way and Banks, 1962, 1967; Way, 1968, 1973; Blackman, 1974). The
self induced population homeostatic mechanisms ensure that the resources
available are utilised to produce viable aphids without undue aphid mortal-
ity or death of the host plant. For this self regulation to occur the
aphids must monitor their own numbers and tactile, olefactory, visual
(e.g. Ibbotson and Kennedy, 1951) and possibly oral (Forrest and Noordink,
1971) communication may be involved in this.

Aphids could affect the production of the number and type
of viable adults in a variety of ways. These could include:
  (a) having a higher or lower fecundity
  (b) producing offspring at a higher, lower or varying rate
  (c) producing dispersive forms
  (d) altering the morph(s) of their offspring
  (e) possessing a longer or shorter life span
  (f) varying the period of offspring production in adult life.

The first four of these especially, have frequently been
implicated in aphid population regulation.

An "optimum" population density with respect to aphid
condition and hence fecundity and reproductive rate is known to exist for
at least two aphid species, A. fabae and B. brassicae (Way and Banks, 1967;
Way, 1968). This optimum population density seems to be relatively low,
approximately 8 - 100 aphids in an aggregate. At densities less than the
optimum the aphids mutually benefit through effects on food caused by the
presence of other aphids (Way and Banks, 1962, 1967; Way and Cammell,
1970; Dixon and Wratten, 1971). Above the optimum interaction between
aphids results in a decrease in population growth, a decline in general
aphid condition, and the population becoming more dispersive. These
developments are induced by increased interaction, probably mainly tactile,
between the aphids rather than by poor plant condition, though certainly
a decline in the latter may lead to an increase in aphids wandering on the
plant and hence more contact between aphids and therefore more tactile
stimulation. Also the "active aggregation" of aphids in a colony
(Kennedy and Ibbotson, 1951) ensures that aphid interaction occurs norm-
ally (Way, 1968). The aphids response is therefore predictive, and self-
regulatory (Way and Banks, 1967; Way, 1973).

In the present study the A. kondoi population was observed
to undergo a cyclical growth pattern, with each cycle involving an increase
and decrease in numbers. Since the population decrease may have been due
to intraspecific regulation by the aphids themselves by the methods listed
above (a - f), or may simply have been due to increased aphid mortality
due to competition between aphids, or a combination of both factors, an
attempt was made to elucidate which of these was causing the observed
effects. Special attention was paid to possible changes in fecundity,
reproductive rate, aphid morphs, and the production of dispersive forms
(a,b,c,d), since preliminary observations and the reports of other authors
suggested these were most likely to be important in population regulation.

10.2 Experimental Procedure and Results

A variety of approaches were taken to determine possible
changes in the fecundity and/or reproductive rate of A. kondoi during a

population cycle.

An initial attempt was made to study the changes in these characteristics during the anticipated autumn cycle. Hence, at approximately two week intervals from 10th January, adult apterae were collected from the DSIR study paddock by beating the aphids from the vegetation on to a tray and collecting them with an aspirator. In the laboratory the adults were placed in plastic disposable petri dishes with one aphid in each dish. Each dish was lined with moistened filter paper and one trifoliate lucerne leaf was placed in it. A single plant was used as the source of all the leaves. The dishes were then left for 24 hours at a temperature of $20^{\circ}C \pm 2^{\circ}C$ with 24 hours continuous light provided by one 13W, 48 cm Thorn Tropical Daylight Lamp. The offspring were counted after 24 hours and the results are shown in Fig. 28. Counting the number of nymphs produced in 24 hours gives a direct measure of reproductive rate. In this case the reproductive rate seems to be inversely proportional to the aphid population. Not enough adults were collected for an adequate sample after the 9th February, and since it seemed unlikely by then that an autumn population peak would occur, further studies were undertaken in the laboratory.

The body size of an aphid reflects the conditions of the aphid and its environment (e.g. Bodenheimer and Swirski, 1951; Way and Banks, 1962; Dixon and Wratten, 1971). Murdie (1969b) and Dixon and Wratten (1971) have shown that the size of an adult aphid is proportional to its fecundity in a linear manner. An increase in body size also indicates a change in reproductive rate since Dixon and Wratten (1971) found that the heavier adults had a higher reproductive rate earlier in their lives. Therefore to gain further data on fecundity and reproductive rate the abdominal length and width, and the length of the mesotibia was measured on apterae fourth instars and adults collected in the population samples on 11th May 1976 and 6th July 1971 i.e. an increasing and decreasing population respectively. Abdominal length and width were measured because the abdomen is important as the storage region for growth materials, and hence reflects general body condition. Tibial length was also measured as this length can be clearly demarcated, and it is believed that it is proportional to the size of the aphid as indicated by

Fig. 28   The number of offspring produced by apterous adult
_A_. <u>kondoi</u> collected from the DSIR study plot in
relation to the total population of _A_. <u>kondoi</u> found
in the fortnightly population samples

NUMBER OF A. kondoi ON 84 STEMS •••••

AVERAGE NUMBER OF OFFSPRING PRODUCED
PER ADULT IN 24 HOURS ± S.E.M. ···O···

DATE   1977
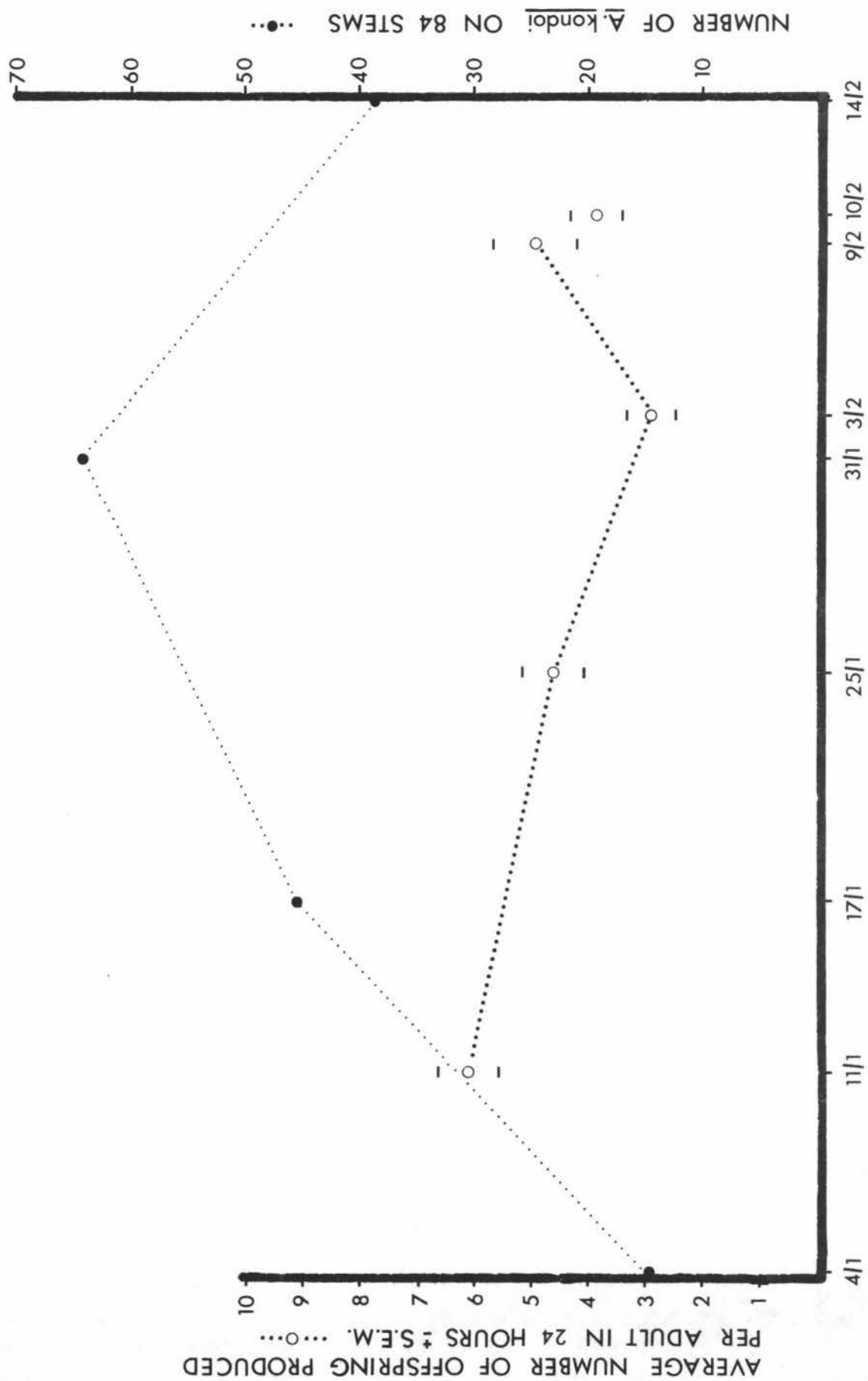
its positive correlation with the abdominal measurements. The measure-
ments are shown in Table 13. There is a highly significant decrease in
the length of the mesotibia and the abdominal length between the adults
collected on the 11/5 and those collected on the 6/6. Although a decline
in the size of the measured characteristics, in keeping with a decline in
aphid size with an increasing aphid population, was found for field
collected fourth instar apterae, the difference was not significant. This
is undoubtedly due to the small numbers sampled and does not indicate a
decrease in difference in size between fourth instar apterae and adult
apterae.

A further indication of changes in fecundity and repro-
ductive rate was found by studying these parameters in glasshouse colonies
of aphids. On the 14th April 1977, lucerne plants were removed from pots,
trimmed heavily and planted in a seedling tray using the peat:perlite:
pumice mix described in Section 2.1 and the nutrients described in
Appendix One. The plants were grown in a glasshouse with a daily bench-
flood watering system. Natural infestation by $\underline{A}$. kondoi was observed on
27th April and so on this date most of the aphids were removed, then the
population was allowed to grow from those few remaining. On 4th May 17
adults were collected from these plants and placed individually in tissue
microculture dishes along with a trifoliate lucerne leaf and moistened
filter paper. These were placed in a constant temperature cabinet at
$20^{\circ}C \pm 2^{\circ}C$ and after 24 hours the adults and offspring were separated, the
adults were weighed, and the offspring counted. A similar procedure was
carried out on 12th May. The two samples were taken from an expanding and
a declining population respectively. The criterion used for selecting the
two sampling dates were, for the first sample, a virtual absence of alate
adults but enough apterous adults for a reasonable sample, and for the
second sample high numbers of alate adults and the dispersion of aphids
over a plant. The results are shown in Table 14 and indicate that both
the size of the aphids, and the number of offspring they produce in 24
hours decreases significantly as the colony ages.

The ratio of apterous adults to the sum of first and/or
second instars can also be used as an indicator of fecundity assuming that
the mortality rate of both adults and juveniles remains constant. The

Table 13   The size of <u>A</u>. <u>kondoi</u> at two stages of colony development at the DSIR study plot

Aphid Instar	Date of Sample	No. of Aphids	Length Meso-tibia ± SEM (mm)	No. of Aphids	Abdomen width ± SEM (mm)	No. of Aphids	Abdomen length ± SEM (mm)
Fourth Apterae	11/5	11	38.9±1.7	9	35.4±0.7	10	79.9±2.4
Fourth Apterae	6/7	3	37.7±3.2	3	35.8±1.2	3	82.2±2.5
Adult Apterae	11/5	18	53.9±0.9	15	48.9±3.6	14	97.7±2.7
Adult Apterae	6/7	10	46.7±0.8[a]	10	42.8±0.7[b]	10	91.2±1.5[c]

a = Significant at P = 0.001

b = Significant at P = 0.05

c = Significant at P = 0.01

Table 14   The weight of adults and number of offspring of <u>A</u>. <u>kondoi</u>
             at two stages of colony development in a glasshouse.

Sample Date	No. of Adults	Average Weight of Adult (gm)	SEM	No. of offspring Produced per Adult in 24 hrs	SEM
5/5	17	0.00122	0.00005	5.76	0.67
13/5	21	0.00069	0.00003	3.57	0.40

t = 9.7608   t = 2.9247

Difference is significant   Difference is significant
at P = 0.001   at P = 0.01

proportion of first instar A. kondoi to adult apterae for one year at the
DSIR study plot is shown in Fig. 29. There are two peaks in this ratio
on the 15th September and the 15th November. Both occur just before a
significant aphid population build up. The 15th September build up
occurred just at the beginning of the initial spring peak (which was
destroyed by grazing) and its high value probably reflects the ideal
conditions for aphid growth at this time. In the next sample on 27th
September although the total aphid population had increased considerably
the fecundity as determined by the ratio of first instars to adults had
declined. A similar decline occurred despite a total population increase
on 29th November. An increase in fecundity also appeared to occur on 31st
January 1977 and this would have been at the beginning of a February
population cycle, but this increase was prevented by nabid bugs.

As an indication of the importance of aphid dispersal to
the A. kondoi population the proportion of alates in the population for
one year at the DSIR study plot was noted. The results are shown in Fig.
30 and indicate that the production of alates generally increased as the
colony aged. The absolute numbers of alates sampled are shown in Fig. 11.
A more intensive study with closer sampling intervals was made during the
spring exclusion trial, and the changes in the proportion of fourth instar
alates are shown in Fig. 31. This shows that the proportion of fourth
instar alates in the population continued to increase after the population
began to decline, usually at a more rapid rate. The proportion of fourth
instar alates in Microclimate Control Cage Two then began to decline,
but the results from Exclusion Cage Two differed. However the other areas
were not sampled for a long enough period after the population decline to
decide which trend was the most common.

10.3 Discussion
10.3.1 A Change in Fecundity

Two measures of fecundity were obtained in the present
study; the body size (or 'condition') of the aphids, and the ratio of
first instars to adults in the population.

Results from the present study showing a change in the
average size of adult A. kondoi as a colony ages are presented in Tables

Fig. 29   The ratio of first instar _A. kondoi_ to fifth instar
(apterous adult) _A. kondoi_ and the total _A. kondoi_
population

FIRST INSTARS : FIFTH INSTARS *A. kondoi* ---●---
FIRST INSTARS : TOTAL *A. kondoi* ···○···

MEAN NUMBER OF *A. kondoi* PER STEM ± SEM ·······
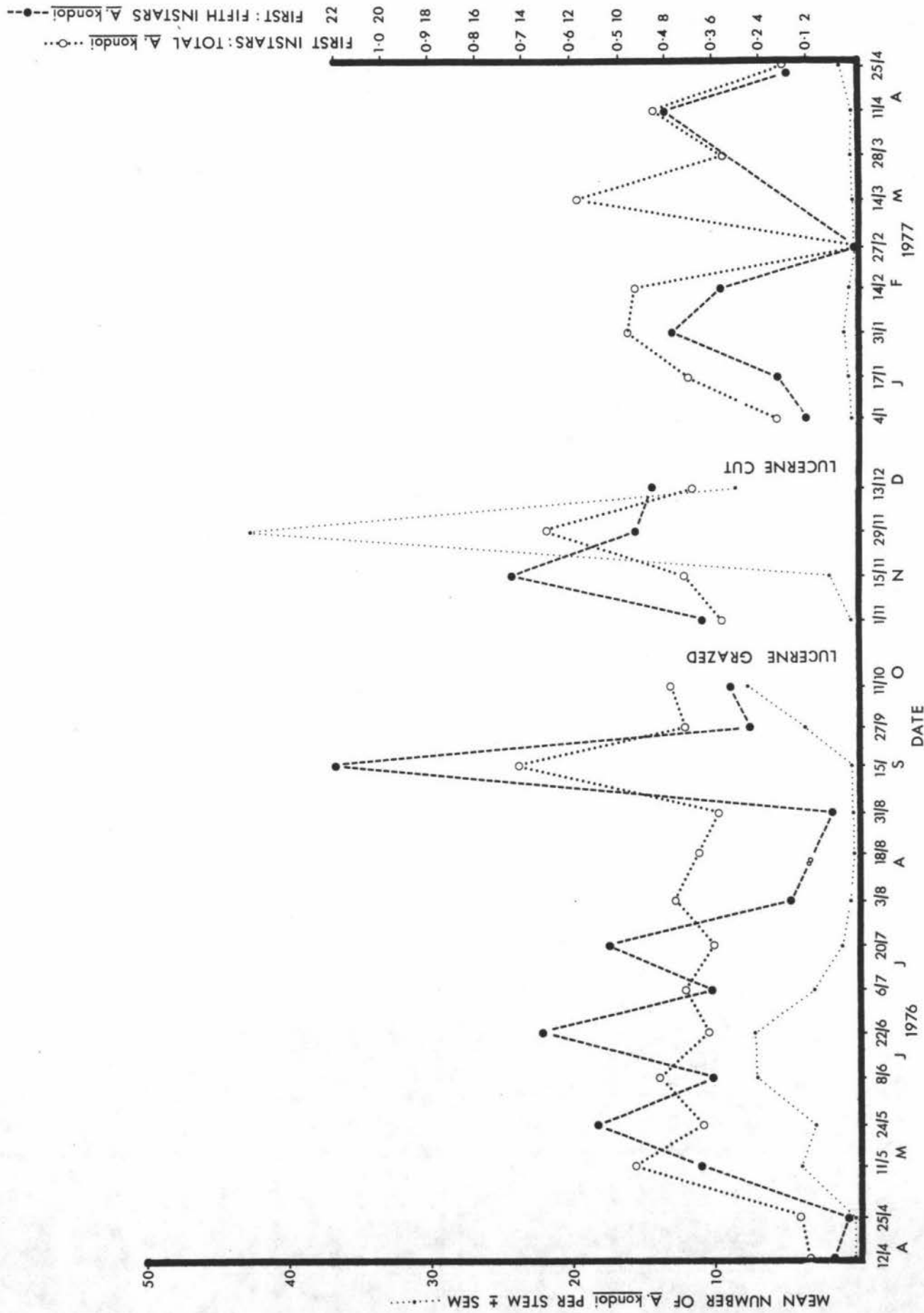
Fig. 30   The production of alate morphs in the fortnightly
           population samples at the DSIR study plot

RATIO OF FOURTH INSTAR ALATAE TO FOURTH INSTAR APTERAE

PROPORTION OF FOURTH INSTAR ALATES IN THE _A. kondoi_ POPULATION
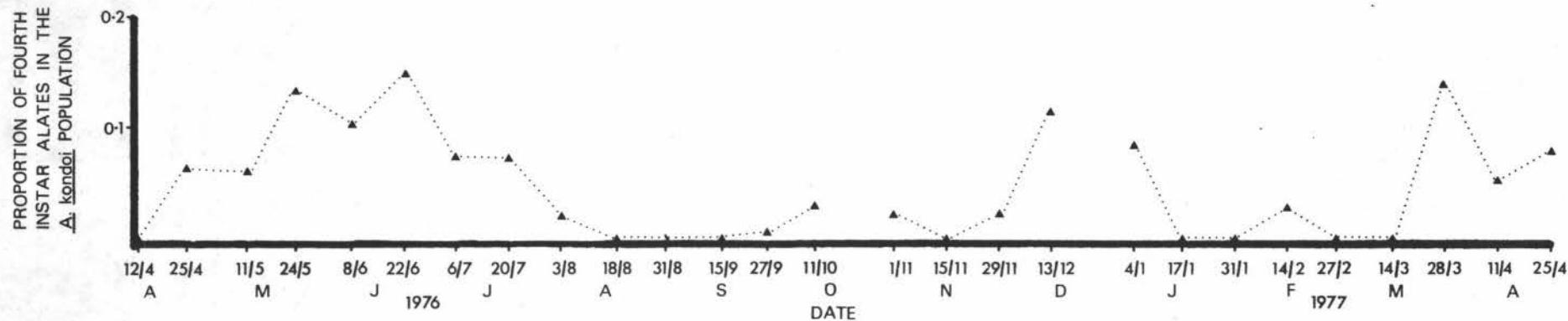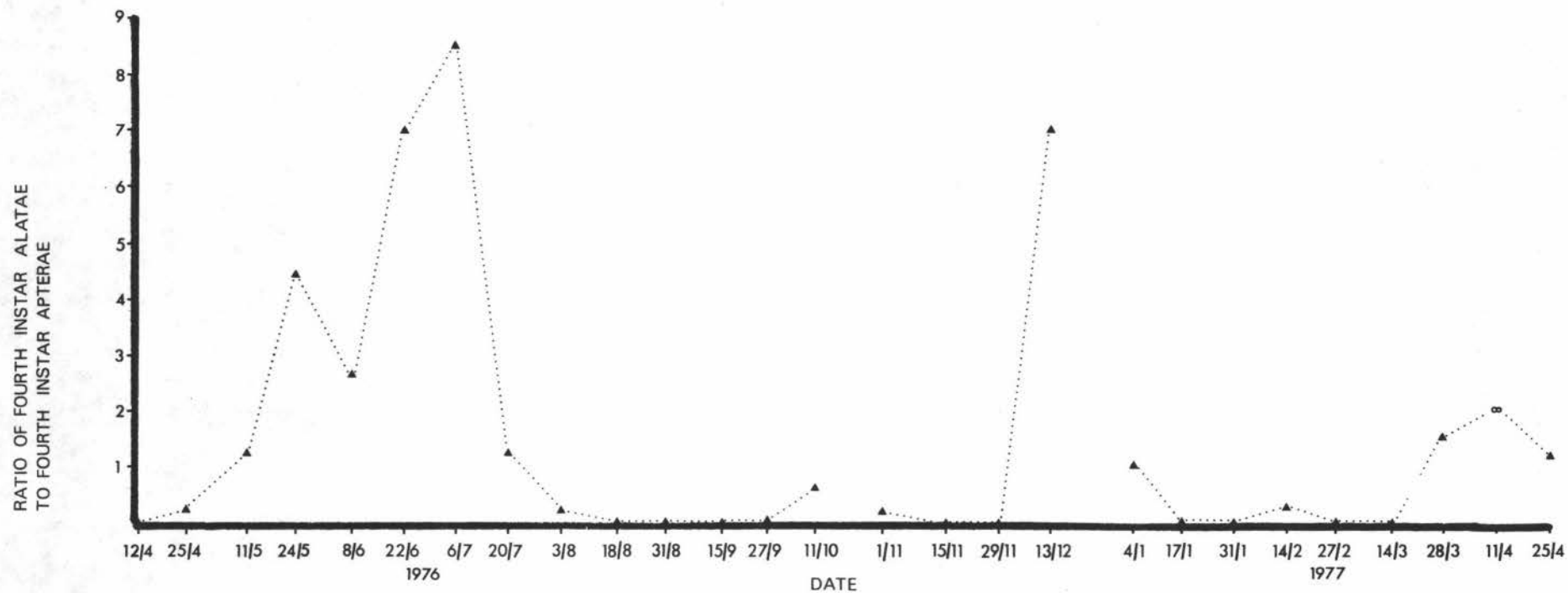
Fig. 31   The production of fourth instar alates during
          predator exclusion Trial I
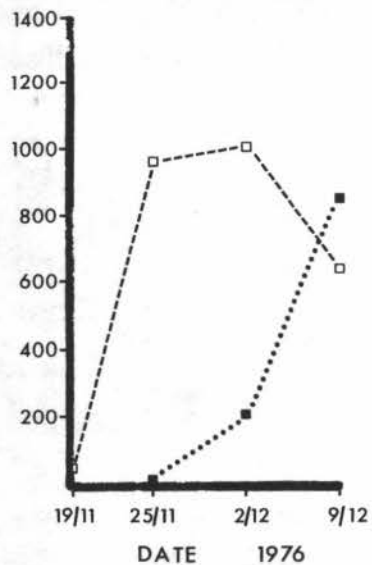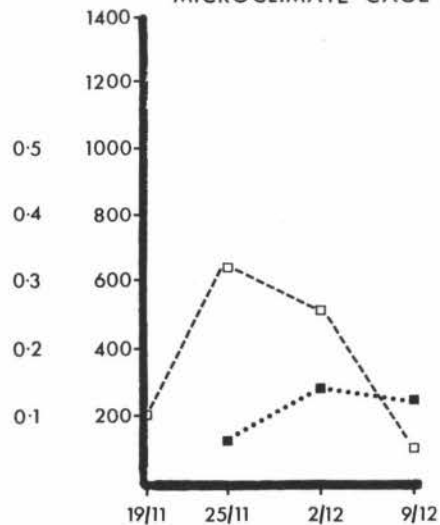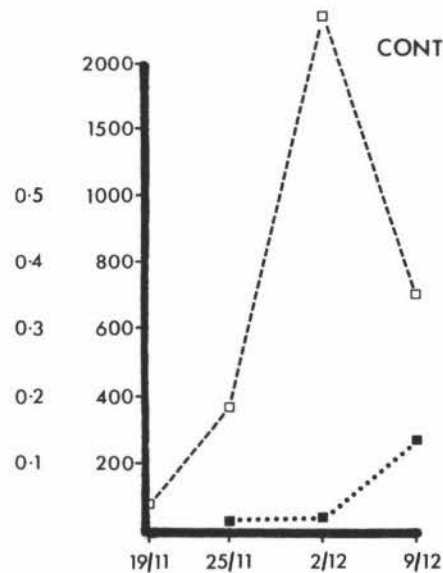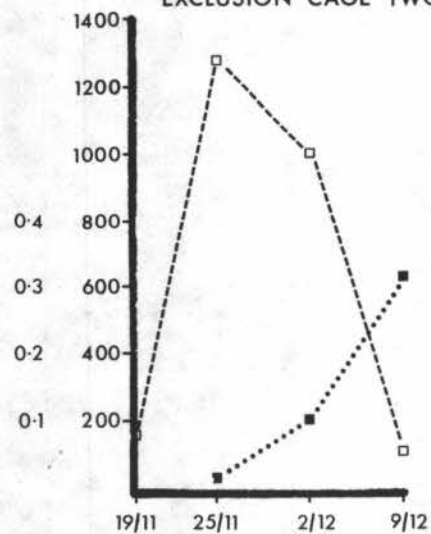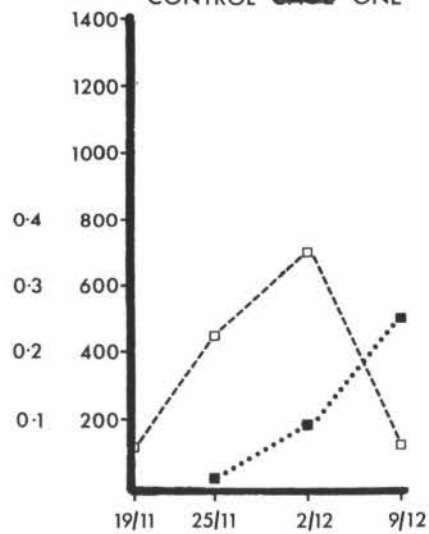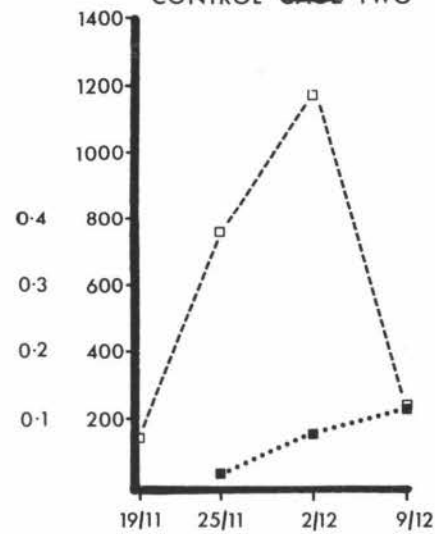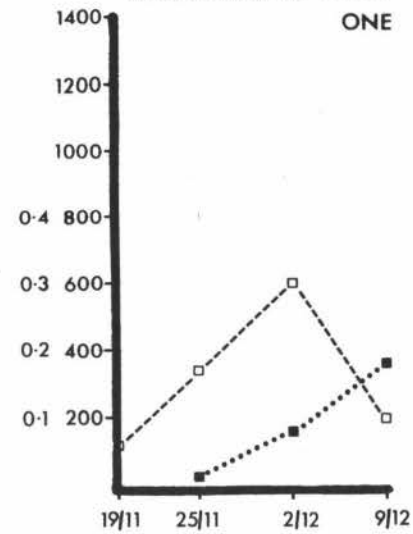
13 and 14. It seems that the age of an aphid colony is inversely proportional to the aphid size indicating that a decline in fecundity is occurring as the colony ages.

Way and Banks (1967) demonstrated that a decrease occurred in the size of adult A. fabiae after the optimum population size was reached. The optimum size was low (eight adults and their offspring) and so the fecundity of aphids in the colony declined from a very early stage and a similar trend is indicated for A. kondoi.

The proportions of adult aphids and their offspring indicated the occurrence of high fecundities at the early stage of the population cycles. A subsequent decline in each instance indicated that for all three potential or actual aphid population cycles there was an initial increase in aphid fecundity followed by a decrease, presumably after an optimum population size was reached. This decrease in fecundity occurred despite the increasing aphid population and indicated that the optimum population size for A. kondoi is relatively low.

The winter population cycle during May to mid-August 1976, does not conform to this pattern, but the reason is not clear. Possibly poor weather, and the lower number of aphids present affected the attainment of the optimum population size in any one colony. The decline in the ratio of first instars to adults on 25th April 1977 presumably just before the winter population cycle can be attributed to first instar mortality caused by frosts (see Chapter Seven).

On the 15th September and 15th November the mean number of A. kondoi per stem was 0.4 and 1.9 respectively. However when attempting to determine an optimum colony size it is probably more realistic to consider only the colonies in which adult apterae were found. On the 15th September the number of aphids in this type of colony averaged 13, and 19.4 on the 15th December. These values are likely to be close to the optimum population size for A. kondoi colonies. As found in other studies (Way and Banks, 1967; Way, 1968; Way and Cammell, 1970) the optimum size of the colony is therefore quite small in comparison to the size the colony may reach.

10.3.2 A Change in Reproductive Rate

The data indicating a change in reproductive rate is, in part, similar to that used to indicate a change in fecundity and generally the reproductive rate seems to decrease as the colony ages.

Observations on the repdocutive rate of aphids during the anticipated autumn population peak showed that the reproductive rate decreased as the population increased and this was to be expected with a low optimum aphid population (assuming the optimum was achieved). The reversal of the trend in the reproductive rate as the aphid population began to decline in February may reflect improved conditions as competition from other aphids decreased becase of their removal by predators especially nabids. The reversal may also indicate an effect of the aphid density on reproductive rate mediated by communication between aphids. Way and Banks (1967) and Way (1973) believe that such self-regulation allows an increase in reproductive rate to combat the destruction of aphids by natural enemies.

The decline in the reproductive rate in the field during the anticipated autumn population cycle was from 6.1 to 2.9 offspring per 24 hours for each adult (Fig. 28) an approximate halving of the reproductive rate over a relatively short period. Table 14 shows that the average size of the aphids decreased by half between the two samples and therefore the fecundity would be approximately halved. A reduction by half of both the fecundity and the reproductive rate over an aphid population cycle would cause a considerable decrease in the growth rate of the population.

Dixon and Wratten (1971) have shown that the decreasing size of an aphid, A. fabiae, can have a considerable effect on the intrinsic rate of increase of the aphid population. They showed that it can take four generations or forty days in favourable conditions for the adult weight to increase from 300 μg to 460 μg and therefore to reach a higher level of fecundity and reproductive rate. Thus, when considering the cyclical pattern of population development observed for A. kondoi in the present study, it is apparent that the period between cycles could be accounted for by the time required for the aphid size, and hence fecundity and reproductive rate, to recover. This explanation is probably partially

correct and certainly accounts for why those aphids which remain on the crop after a population decline do not begin a rapid new population build up, but this does not explain why alatesfrom other populations do not rapidly recolonise the crop. In Chapter Eight it was postulated that the period of low aphid numbers between peaks in aphid population cycles could be accounted for by a loss of plant condition or by a plant factor preventing population growth and it still seems these effects might play some part.

10.3.3 A Change of Morph

The production of different morphs of A. kondoi was restricted to the production of alate virginoparae or apterous virginoparae and no sexual forms were ever found. The two morphs are adapted to the environment they are to exploit and the apterae can be considered a super-parasitic form (Kennedy and Stroyan, 1959; Hille Ris Lambers, 1966; Hughes, 1972) adapted to most efficiently exploit the highly suitable conditions which exist early in a colony's development. In A. kondoi the apterae are usually larger than the alatae and it is generally found that alatae are smaller and less fecund than apterae (Dixon and Wratten, 1971).

The causes of alate production in A. kondoi were not determined and the situation is complex although it is acknowledged that tactile stimulation between aphids acting via density is important for some species (Lees, 1966; Hille Ris Lambers, 1966; Way, 1973) rather than food quality. It has recently been considered possible that aphid population growth is directed towards producing high quality alates (Mittler, 1973; Way, 1973) and this may explain some of the apparent anomalies observed in nutrition studies. Also there is some evidence indicating that ancestral forms of aphids were all winged and that it may be more correct to ask what factor(s) promotes the production of apterae rather than what promotes alate production (Mittler, 1973).

10.3.4 Dispersal

Migration of aphids from a plant serves to both reduce intra-specific competition and hence allow better aphid survival on the plant, and to disperse the species. Way and Banks (1967) showed that as the population of A. fabiae increased beyond the optimum size, dispersal firstly of apterae and then of alatae occurs. The initial dispersal by

apterae is to less favoured sites on the 'mother' plant and then to
other plants where a similar pattern may occur(Ito, 1960). The apterae
only disperse over short distances, often from one plant to the next,
whereas alate dispersal ensures colonisation over a much wider area. As
the mother plant nears complete exhaustion all the remaining aphids on
it may migrate.

Such a pattern of dispersal appears to occur in A. kondoi.
The initial dispersal from the growing tip to less favoured sites on a
plant with its consequent reduction in food quality has already been
noted in Chapter Four and dispersing apterous aphids can be seen on the
ground moving away from the plant.

Observation of the proportion of alate aphids at the DSIR
study plot (Fig. 30) showed that the production of alate aphids occurred
even while the aphid population was increasing, but it reached a maximum
shortly after the population peak was reached. This could also be readily
seen by observing single colonies. It is probably adaptive for A. kondoi
to produce migrants at an early stage while the plant is still highly
suited to aphid production since the migratory aphids produced at this
time will be in good condition to undertake long flights. In contrast
if alates were only produced when the host plant was nearing exhaustion,
many would not survive, and those that did would be in poor condition. The
early production of alates also means that at least some aphids will have
dispersed even if some disaster should befall the colony.

The migration of alate A. kondoi is obviously an important
factor in the decline of a colony, and it is necessary to consider how
much influence they have. Even at the times of maximum alate production
there was still some fourth instar apterae present, although the numbers
were very low. This was to be expected since the aphid population in the
field never disappeared completely. However since the ratio of fourth
instar alatae to fourth instar apterae may be greater than eight to one
migration by alate forms must play a major part in the population decrease.
Even if the fourth instar alates have a greater instar duration than
fourth instar apterae as Hughes (1963) found for B. brassicae then taking
his correction factor into account the ratio of fourth instar alates to
fourth instar apterae is still five to one.

Noting the production of alates during predator exclusion
trials (Fig. 31) showed that in all trial areas the proportion of fourth
instar alates in the population continuned to increase after the popula-
tion began to decline, usually at a more rapid rate. Up to the stage of
the population maximum, the proportion of fourth instar alates in the
population was usually less than 10% and in most cases was in the range
5 to 7.5%. After this the proportion increased rapidly to 42% in the
case of Exclusion Cage One. Exclusion Cage Two also had a high proportion
(31.5%) of alates and it is possible that enclosing the aphids led to more
contact between aphids and therefore higher numbers of alates. A high
proportion such as 42% was greater than would be expected even if all the
aphids being produced were alates. This therefore indicates that there
was probably an abnormally low number of the lower instars due to the
decreased fecundity and reproductive rate of apterous adults as discussed
previously. Table 9 shows that between the 2nd and 9th December the
A. kondoi population in Exclusion Cage One decreased by 37% and such a
decline is easily accounted for if 42% of the population migrated.

In most of the other areas of Trial One the proportions
of alatae in the populations are lower and it is difficult to account for
the observed rate of population decline entirely by the migration of
winged adults. For example, Control Area Three declined in population by
69% between the 2nd and 9th November, yet the proportion of fourth instar
alates in the population was only 13% and even allowing for the possible
development of two generations of alate aphids during this period, the
decline in population can still not be totally account for by emigration.
In Control Area Three, predators may have been more important than in the
exclusion cages.

There is no constant relationship between the rate of
population decline and the proportion of alates in the field situation
at the DSIR study plot, and this indicates that the role of alate migration
in population declines is variable. This supports the evidence of
variability observed in the proportion of alates between the different
areas of Trial One.

O'Connor and Hart (1977) and Palmer (1977) have presented
information on the proportion of "winged" A. kondoi in field populations

in the Manawatu and Canterbury, but these proportions involved alate adults and as already noted such data is difficult to interpret. O'Connor and Hart found a ratio of one winged to ten wingless aphids in Canterbury and assuming all these winged adults developed on the plant they were found on, then this ratio could account for a considerable decline in the population.

The importance which the production of alates play in aphid population declines has been disputed. For example Hughes and Gilbert (1969) found that the production of winged forms did not greatly affect absolute numbers in a population of B. brassicae. On the other hand Wyatt (1965) B.D. Smith (1966), Sluss (1967) and Dixon (1973) believed that alates may have been important in the population declines of the aphid species they were studying, though the evidence for this was not always conclusive (e.g. Sluss, 1967).

10.3.5   Life span and period of offspring production in adult life.

In the present study information was not obtained on the possession by A. kondoi of a longer or shorter life span. However, since A. kondoi seems to possess an optimum population density when numbers are low, and since the adults seem to be in peak condition as indicated by their size at this time, it is likely that these adults live for the longest period. Way and Banks (1967) found that the adults of A. fabiae lived longest at an optimum population of about eight adult aphids and their offspring but a change in longevity is probably not one of the most important factors controlling the A. kondoi population.

Also no information was obtained on any possible variation in the period of offspring production in A. kondoi but Dunn (1959) has demonstrated this occurs in Pemphigus bursarius (L) and Dixon and Wratten (1971) noted that the heavier A. fabiae produced a greater proportion of their offspring in their early adult life.

10.4   Conclusion

The present study has demonstrated that a decline in both fecundity and the reproductive rate of A. kondoi takes place as a population cycle proceeds. The optimum fecundity and reproductive rate

occurred when the aphid numbers were still relatively low. A considerable
loss to declining aphid populations was also shown to occur by the emigra-
tion of alate aphids. It seems that aphid population growth patterns are
directed towards the lowering of mortality but, although no information
was collected on mortality rates in the present study, it is apparent
that a halving of the fecundity and reproductive rate of A. kondoi along
with the production of many dispersing aphids could account for a
considerable portion of the population declines.

The effect of the decrease in aphid size on the intrinsic
rate of population increase may also partially account for the periods
of low aphid numbers observed between each population peak.

CHAPTER ELEVEN

Concluding Remarks

Some initial uncertainty was involved in determining a suitable approach for the present research because A. kondoi had only recently arrived in New Zealand when the present study began and its reaction to local conditions was unknown. Since most studies were directly involved in methods of controlling the pest, a more basic biological approach seemed useful, the data gained being potentially useful for some of the less direct methods of pest control.

As the present study evolved the identification and understanding of the population cycles of A. kondoi became the central area of research. It became apparent that early observations of the transient nature of the populations of this aphid could be explained in terms of intraspecific regulation. Such regulation in an undisturbed situation at any particular site, results in the population going through three of four cycles a year, and aphid mortality due to uncontrolled Malthusian growth does not occur. Each cycle involves a period of increase and decrease in aphid numbers; the latter is caused by a decline in the fecundity and reproductive rate of the aphids and the production of an increasing number of alate aphids. In the present study one complete winter and one complete spring cycle were measured at the DSIR study plot and exclusion cage experiments indicated that a further cycle would have occurred during the summer or autumn period in the absence of predators. The period of low aphid numbers may be due to a plant factor, or it may represent the recovery period of the aphids in relation to such characteristics as fecundity and reproductive rate.

The "spontaneous" declines of the A. kondoi populations observed by Richardson (1977) appear from the present study to be the decline stages of the cycle. Aphid induced population declines have also apparently resulted in misinterpretation by other authors of the importance of predators since the declines may have been attributed to them erroneously. In the present study exclusion cage experiments in spring 1976 demonstrated that although high numbers of predators coincided with the peak aphid population and the decline stage they did not cause the decline. Indeed the rapid growth of aphid numbers during the stage of a

cycle when the population is increasing, and the transient occurrence of the cycles undoubtedly serves to disrupt predator populations. Predators did not appear to be effectively synchronised with the spring aphid population, but the synchronisation and adequate numbers of N. maoricus in late summer-autumn enabledthis predator to control the A. kondoi population and depress a potential cycle.

It appears to me that the cyclical nature of aphid populations may also have resulted in climatic effects sometimes being miscredited with causing population declines. The high temperatures of early summer have often previously been proposed as the reason for the decline of spring aphid populations whereas in A. kondoi the real cause appeared from the present study to be an at least partially self-induced population decline. Possibly the favourable conditions in early spring have some synchronising effect on population cycles over a wide area resulting in the population declines also coinciding and thereby making them appear attributable to temperature. The occurrence of A. kondoi population cycles in the Manawatu was not limited by weather and they occurred all year round, although the maximum size of such cycles was influenced by prevailing weather conditions. This independence from climate was supported by the observations of different field populations which could be at different stages of a population cycle at any one time although within short distances of each other.

It would be useful if future studies were directed towards obtaining a more detailed understanding of the intraspecific mechanisms which regulate population cycles of A. kondoi using, for example, methods such as those developed by Hughes (1963) for B. brassicae. By linking these studies to field observations the effects of lucerne management practices could be elucidated. In particular, it could be important to understand why a rapid aphid population build up may occur after such practices (Richardson, 1977). The effects of the aphids on the plants and the recovery of good aphid condition could be important in this. It may also be useful for farmers to undertake certain management practices at specific times in a population cycle. For example little would be gained from spraying the aphid population when it is already undergoing a population decline.

Future studies should also provide a greater understanding of the biology and ecology of local aphid predators because the information available on some species is very limited.

Three reasons were initially advanced for the severe effect of A. kondoi immediately after its introduction to New Zealand. Firstly, it was believed that A. kondoi preferred the cooler moist conditions (Summers, 1975). Secondly, parasites and predators had not had time to increase in numbers and thereby affect the aphid population, and thirdly the local lucerne varieties only possessed a low level of natural resistance. However, the problems may not continue at the early severe level. Kain et al., (1976) believe that the pest status of A. kondoi could change in the future. Nielson and Barnes (1961) demonstrated that there was a reduction in the severity of damage by the Spotted Alfalfa Aphid T.maculata in Arizona over the five year period after the aphid's introduction due to the increased effects of various man made and natural ecosystem factors. In New Zealand such an adaption of the native ecosystem can be partially expected, and there is some evidence that lucerne crops did not seem to have suffered as severely in spring 1976 as in spring 1975 (Anon, 1976).

Appendix One   Nutrients for growing lucerne.

To one bushel of potting mix was added:
  80 cc Slow Release "Osmocote" (Sierra Chemical Co.)
  20 cc Quick Release "Osmocote" (Sierra Chemical Co.)
  70 cc Superphosphate (Yates "Gro-Plus")
  17 cc Uramite
  400 cc Dolomite Lime
  Trace element mixture (Fetrilon Comboi. Henry York and Co.)

No short term Osmocote was added to the initial lucerne plants in March, 1976.

Appendix Two.

The Instars of A. kondoi at the DSIR Study Plot

Date of Sample	Number of Instars						
	1st	2nd	3rd	4th Alatae	4th Apterae	5th Alatae	5th Apterae
12/4	1	1	4	0	4	0	1
25/4	1	2	4	1	4	2	2
11/5	153	61	48	19	15	3	23
24/5	76	62	49	31	7	2	7
8/6	225	84	114	56	21	17	37
22/6	173	180	92	3	12	7	13
6/7	84	66	48	17	2	1	14
20/7	21	15	22	5	1	1	2
3/8	14	6	5	1	5	0	5
18/8	3	1	1	0	1	0	0
31/8	2	1	1	0	1	0	2
15/9	22	2	5	0	1	0	1
27/9	116	88	58	2	24	0	26
11/10	245	179	93	18	31	0	47
1/11	25	26	19	2	10	1	4
15/11	58	50	30	0	13	3	4
29/11	422	101	56	0	24	9	45
13/12	172	137	101	56	8	7	20
4/1	2	3	2	1	1	1	2
17/1	16	16	3	0	4	1	5
31/1	31	12	15	0	2	0	4
14/2	17	7	5	1	3	0	3
27/2	0	0	0	0	0	0	0
14/3	4	3	0	0	0	0	0
28/3	6	2	6	2	3	3	0
11/4	8	5	3	1	0	1	1
25/4	14	7	30	7	6	0	5

Erratum

Appendix Two p. 153 The 29/11 A. kondoi population sample is
a subsample of the instars of all the aphids collected
from 15 randomly selected stems. Only the number of 4th
instar and adult alates was determined for all 84 stems.
In total 3587 aphids were found including 85 fourth
instar alates and nine adult alates.

Appendix Three   Laboratory investigations concerning the longevity,
                  pre-reproductive period and instar duration of
                  A. kondoi.

Introduction

An attempt was made to gain data on the logevity, pre-
reproductive period and instar durations of A. kondoi because this
information would have been exceptionally useful in interpreting
population data, especially the proportions of instars (e.g. Hughes,
1962, 1963). These investigations were however not successful though
some data was obtained.

Materials and Methods

Various methods of caging aphids have been attempted
(MacGillivray and Anderson, 1957; Adams and van Emden, 1972). It was
decided to cage A. kondoi on an intact plant since excised plant material
is known to affect the aphid performance (Thomas et al., 1966; Adams and
van Emden, 1972). The cultivation of plant material is described in
Section 2.1.

Considerations taken into account when making cages for aphids
include: (a) size and visibility - the cages must localise the aphid
enough to make it easily found and clearly seen. (b) Microclimate - since
the aphid is ostensibly "performing" in the conditions outside the cage
it is best to reduce the microclimate effect as much as possible. The
cage must have adequate ventilation. (c) Toxicity - recent studies have
indicated that some synthetic polymers can exert a considerable toxic
effect on living organisms (Kieckhefer and Medler, 1960; Chada, 1962;
Markkula and Rautapaa, 1963). (d) Expense.

Each cage was constructed from a glass cylinder, 22 mm high and
25 mm in diameter. One end was covered with cloth (pore size 220µ) while
the other end was left open. To set up each cage a small bottle, 40 mm
tall and 25 mm in diameter was placed upside down in the potting mix in
the plant pot. A layer of cotton wool approximately five mm thick was
placed on top of these and covered with two squares of muslin large enough
to extend beyond the edges of the cage. The youngest fully open trifoliate
leaf on a stem was then extended across the muslin and a small piece of

cotton wool was placed over the stem where it entered the cage. The glass cage was placed down on this and held in place by an elastic band and a stake. Five cages could be set up per pot (see Fig. 32).

After seven days the plant was replaced with as minimal disturbance to the aphid as possible. Aphids were always transferred with brushes moistened with distilled water (Adams and van Emden, 1972).

The experiments were conducted in a modified Frigidaire "cylamatic" cabinet, thermostatically controlled to $23^{\circ}C \pm 2^{\circ}C$. Lighting was provided by four 13W "Tropical Daylight" lamps and a 24W Tungsten bulb to supplement the red light. Humidity was maintained by placing a beaker of water near the fan.

In order to determine longevity and the pre-reproductive period, one or two adults were placed per cage and allowed to give birth, then the adults and all except one progeny were removed.

During the instar duration trial of the 27th July, four adults per cage were placed in 12 cages at 6 p.m. and the adults were removed at 9 a.m. on 28th July. In the November trial approximately 100 adult aphids were placed in a petri dish on excised trifoliate leaves on moistened filter paper. After three hours all first instars were removed and placed ten per cage. In both experiments, cages were checked daily with one to three cages being checked per day. The cages were alternated to avoid excessive disturbance to the aphids. The time when 50% of the aphids had moulted at the end of each instar was calculated by assumming that the proportion of aphids which had moulted increased in a linear manner during 24 hours.

Results and Discussion.
Longevity and Pre-Reproductive Period.

Three alate aphids born about two a.m. on 19th July gave birth to their first nymphs on 30th July and the 1st and 2nd August respectively. The pre-reproductive period is not known exactly but other observations indicate that it can be less than 24 hours. In cases where fourth instars were placed in petri dishes and checked the next day, a moult skin and first instar nymphs were noted.

Fig. 32   Cages used for holding A. kondoi during aphid fecundity,
          instar duration, longevity trials, and to examine the
          effects of lucerne flowering on A. kondoi

Assuming a pre-reproductive period of 24 hours then the period from birth to the final moult was 11, 13 and 14 days respectively. Two apterous adults in the same experiment gave birth on the 30th and 31st July giving a developmental period to the final moult of 11 and 12 days respectively.

An adult apterae and adult alatae which were born at 2 a.m. on 28th July both moulted to adulthood on 8th August, hence these both had a developmental period of 11 days.

The longer period of development observed for the alates, although not significant may be due to a possible longer duration of the fourth instar alates as opposed to the fourth instar apterae (Hughes, 1963).

The average period of the adult life of the alates was six days. (Range four to seven days).

Instar Duration.

Two experiments yielded information on the instar duration. The results are shown below.

Table 15   The instar duration of A. kondoi

	Experiment commenced on 8th July	Experiment commenced on 11th November
First instar	61.5 hrs (1414 hr degrees)	60.5 hrs (1391 hr degrees)
Second instar	56.5 hrs (1299 hr degrees)	
Third instar (apterae)	57 hours	54 hrs (1242 hr degrees)
Third instar (alatae)	51 hours	

The results are presented in hour degrees since the rate of development of an aphid is dependent on the prevailing temperature. This developmental period on a physiological time scale is a relatively constant value whether or not the temperature is fluctuating (Hughes, 1963).

Within the limits of the assumptions of this experiment it is reasonable to presume that the instar durations of the first, second and third instars are approximately similar as found by Hughes (1963) for B. brassicae.

Hughes (1963) obtained a duration for the first three instars of B. brassicae of 1336 hour degrees per instar and the values for A. kondoi are in a similar range.

Appendix Four   Method of preparing, staining and mounting aphids

The following method was modified from that of McKenzie (1967) (p. 34).

The body contents of the aphid were removed under a dissecting microscope, while the aphid was floating in 70% ethyl alcohol. The cleared specimen was then placed in three ml of Essigs Aphid Fluid (see below) in a Syracuse watch glass, and heated at 52°C for approximately 30 minutes. Nine drops of staining solution were then added and the aphid was left for a further 20 minutes. It was then removed from the hot plate and placed in Tetrahydrafuran (C_4H_8O) solution for a half to one minute and finally mounted in Canada balsam or Eukitt.

All aphids were handled with a small paint brush or Watchmakers forceps.

Essigs Aphid Fluid

Lactic Acid	20 parts
Phenol saturated in distilled water	2 parts
Glacial Acetic Acid	4 parts
Distilled Water	1 part

Stain
Essigs Aphid Fluid	15 ml
Acid Fuchsin (2%aq.sol.)	20 drops
Lignin Pink (2%aq.sol.)	20 drops
Erythrosin (2%aq.sol)	20 drops

Appendix Five   Shears Mounting Fluid

The following formula is taken from Tuite (1969).

Potassium acetate	10 g	
H_2O	500 ml	"standard"
95% ethyl alcohol	300 ml	"mycological"
Glycerine	200 ml	mounting media

<u>Appendix Six</u>   <u>The attractiveness of yellow and white flight traps to flying aphids.</u>

As a generalisation the great majority of aphids are attracted to yellow coloured traps (e.g. Roach and Agee, 1972). In addition, aphids which feed on docotyledonous plants are reported to be more attracted to the yellow-green wavelengths of the spectrum, than species that feed on grasses or sedges (Heathcote <u>et al</u>., 1969).

In the present study some information was gathered as to the effect of yellow versus white traps on aphids since the white traps were used in predator studies and the results are presented in Table 16.

Table 16   The catches of aphids on yellow and white adhesive traps

	Total Aphid Catch		<u>A. kondoi</u> Catch	
	Three White Traps	Three Yellow Traps	Three White Traps	Three Yellow Traps
Number of Samples	23	23	23	23
Average Catch per Sample	22.3	24.4	1.15	1.30
SEM	5.66	6.19	0.45	0.55
	t = 1.2		t = 0.4175	

Since the catches were not normally distributed a paired t test was used to compare catches and as the results are highly non-significant (t = 2.074 at P = 0.05) then the test was deemed to be valid. Overall the yellow traps caught more aphids but the difference is not significant. Of the total aphids caught in the 23 samples the yellow traps caught more in 12 samples and the white more in nine samples. Of <u>A. kondoi</u> caught the yellow traps caught more in six samples while the white traps caught more in seven samples. The results were unexpected, and the reasons for the apparent non significant attractiveness to yellow traps are not known.

The equal attractiveness as shown by the total catches is unlikely to be due to a large number of monocotyledon preferring aphids, although no aphid identifications were made. The period the results cover does not include the main spring flight peak and although there is no reason to believe the attractiveness of colours may change with season, the higher numbers flying during the main flight periods could make any attraction to the yellow traps more oustanding. Many of the samples were taken during periods of exceptionally high winds, and in such winds aphids would have little control over flight. The yellowish tinge provided by the trapping grease may also have been important.

Appendix Seven   The catches of flying predators in yellow and white
                  adhesive traps.

Table 17 The catches of flying predators in yellow and white adhesive
          traps.

Catches of Micromus tasmaniae

Trapping Period (Days)	White Traps		Yellow Traps	
	Number of Traps	Number of Predators	Number of Traps	Number of Predators
7	3	2	2	0
6	3	2	2	0
5	2	1	2	1
7	3	1	2	0
8	3	1	2	0
5	3	0	2	1
7	3	0	2	1
7	3	0	2	1
7	3	0	2	1
8	3	0	2	1
8	3	7	2	2
Total Catch	32	7	22	8

Catches of Coccinella undecimpunctata

6	3	1	1	0
5	3	1	2	1
7	3	2	2	0
7	3	0	3	2
6	3	0	3	1
8	3	0	1	2
7	3	0	2	8
7	3	0	2	1
5	3	0	2	1
Total Catch	27	4	18	16

Catches of Melanostoma fasciatum

11	3	2	3	0
9	3	1	3	0
7	3	2	2	0
7	3	1	2	0
7	3	1	2	0
8	3	1	2	0
8	3	1	2	0
8	2	0	2	1
Total Catch	23	9	18	1

Catches of Melangyna novaezelandiae

7	3	0	3	1
8	3	0	1	1
7	3	0	2	1
6	3	1	1	0
Total Catch	12	1	7	3

To determine whether there was a difference in attractiveness between the different coloured traps significance tests were performed firstly for all the trapping periods from 19th September 1976 to 26th April 1977 whether the particular predator was caught or not, and secondly for only those trapping periods when at least one specimen of the particular predators was caught on either coloured trap. The latter test therefore indicates the effectiveness of trapping when the predator was definitely flying. The results are shown below.

Table 18   The significance of trap colour to the effectiveness
            of the trap.

	Micromus tasmaniae	Coccinella undecimpunctata	Melanostoma fasciatum
All trappings	t = 0.8323	t = 1.5931	t = 2.0039*
Only trappings in which a specimen was caught comparing numbers per three traps	t = 0.3030	t = 1.8224**	t = 2.4962*

        * = significant at P = 0.05
       ** = significant at P = 0.10

M. fasciatum appears to be attracted to white traps or repelled by yellow traps, but the catches of other predators do not appear to be affected by trap colour. However the predator catches were not large and with more sampling the eleven spotted ladybird may have been found to be more efficiently caught by yellow traps than white ones.

Sol (1966) reported that white traps were attractive to syrphids and the catches of M. fasciatum support this.

REFERENCES

ADAMS, J.B. and VAN EMDEN, H.F., 1972. The biological properties of aphids and their host plant relationships. p.47 - 104. In VAN EMDEN, H.F., 1972.

ALEXOPOULOS, C.J., 1962. Introductory mycology. John Wiley and Sons Inc, New York, 613 p.

ANON., 1976. No marked effect yet of wilt, aphids on lucerne. Hawkes Bay Tribune, December 10.

ARMBRUST, E.J. and GYRISCO, G.G., 1975. Forage crops insect pest management. p.445 - 469. In METCALF, R.L. and LUCKMAN, W.H., 1975.

AUCLAIR, J.L., 1963. Aphid feeding and nutrition. Annual Review of Entomology 8: 439 - 490.

BAKER, A.C., 1917. Life history of Macrosiphum illinoisensis, the grapevine aphis. Journal of Agricultural Research 11: 83 - 90.

BAKER, A.C., and TURNER, W.F., 1916. Rosy apple aphid. Journal of Agricultural Research 7: 321 - 344.

BANKS, C.J., and MACAULEY, E.D.M., 1970. Effects of varying the hostplant and environmental conditions on the feeding and reproduction of Aphis fabae. Entomologia Experimentalis et Applicata 13: 85 - 96.

BEN SAAD, A.A. and BISHOP, G.W., 1976. Effect of artifical honeydews on insect communities in potato fields. Environmental Entomology 5: 453 - 457.

BLACKMAN, R.L., 1966. The development and fecundity of Adalia bipunctata L. and Coccinella septempunctata L.feeding on various species of aphids. p. 41-43 In HODEK, I., 1966b.

BLACKMAN, R., 1974. Aphids. Ginn and Co. Ltd.,London, 175 p.

BOMBOSCH, S., and TOKMAKOGLU, O., 1966. The efficiency of aphidophagous insects in control of Aphis fabae Scop. p 271 - 275. In HODEK, I., 1966b.

BODENHEIMER, F.S., and SWIRSKI, E., 1957. The Aphidoidea of the Middle East. The Weizmann Science Press of Israel, Jerusalem, 378 p.

BROADBENT, L., DONCASTER, J.P., HULL, R., and WATSON, M.A., 1948. Equipment used for trapping and identifying alate aphides. Proceedings of the Royal Entomological Society of London (A) 23: 57 - 58.

BULA, R.J., RHYKERD, C.L., and LANGSTON, R.G., 1959. Growth responses of alfalfa seedlings under various light regimes. Agronomy Journal 51: 84 - 86.

BURNETT, P., 1977. New Zealand Weed and Pest Control Conference, Johnsonville 1977.

CANNY, M.J., and ASKHAM, M.J., 1967. Physiological inferences from the
    evidence of translocated tracer : a caution. Annals of Botany 31:
    409 - 416.

CARVER, M., and STARY, P., 1974. A preliminary review of the Aphidiidae
    (Hymenoptera: Ichneumonoidea) of Australia and New Zealand. Journal of
    the Australian Entomological Society 13: 235 - 240

CHANDLER, A.E.F., 1966. Some aspects of oviposition responses in aphido-
    phagous Syrphidae. p. 113 - 115 In HODEK, I., 1966b.

CHIANG, H.C., 1966. Distribution of entomophagous insects in their habitats.
    p 157 - 159. In HODEK, I., 1966b.

CLARK, L.R., GEIER, P.W., HUGHES, R.D., and MORRIS, R.F., 1967. The ecology
    of insect populations in theory and practice. Methuen and Co. Ltd.,
    232 p.

CLOSE, R., 1959. Sticky traps for winged aphids. New Zealand Journal of
    Agricultural Research 2: 375 - 379.

COCKBAIN, A.J., 1961. Fuel utilisation and duration of tethered flight in
    Aphis fabae Scop. Journal of Experimental Biology 38: 163 - 174.

COON, B.F., and PEPPER, J.O., 1968a. Alate aphids trapped in air traps
    arranged at different heights. Journal of Economic Entomology 61:
    1473 - 1474.

COON, B.F. and PEPPER, J.O., 1968b. Alate aphid species captured in yellow
    pans. Journal of Economic Entomology 61: 1472 - 1473.

COSTA, C.L., and LEWIS, T., 1967. Comparison of water traps, sticky traps
    and suction traps for assessing aphid migration. Rothamsted Experi-
    mental Station Report for 1966: 201.

COTTIER, W., 1953. Aphids of New Zealand. New Zealand Department of
    Scientific and Industrial Research Bulletin 106, 382 p.

COX, J., and DALE, P., 1977. New records of plant pests in New Zealand. II.
    New Zealand Journal of Agricultural Research 20: 109 - 111.

CUMBER, R.A., 1959a. The insect complex of sown pastures in the North Island
    VI The Psocoptera and Neuroptera as revealed by summer sweep sampling.
    New Zealand Journal of Agricultural Research 2: 898 - 902.

CUMBER, R.A., 1959b. The insect complex of sown pastures in the North Island
    II The Hemiptera as revealed by summer sweep sampling. New Zealand
    Journal of Agricultural Research 2: 1 - 25.

CUMBER, R.A., and EYLES, A.C., 1961a. Insects associated with the major
    fodder crops in the North Island. VI Odonata, Orthoptera, Isoptera,
    Psocoptera, Thysanoptera, Neuroptera, Lepidoptera. New Zealand
    Journal of Agricultural Research 4: 426 - 440.

CUMBER, R.A., and EYLES, A.C., 1961b. Insects associated with the major
    fodder crops in the North Island IV Hymenoptera. New Zealand Journal
    of Agricultural Research 4: 390 - 408.

CUMBER, R.A., and HARRISON, R.A., 1959. The insect complex of sown pastures in the North Island. III The Diptera as revealed by summer sweep sampling. New Zealand Journal of Agricultural Research 2: 741 - 762.

DAHMS, R.S., and PAINTER, B.H., 1940. Rate of reproduction of the pea aphid on different alfalfa plants. Journal of Economic Entomology 33: 482 - 485.

DAVIDSON, W.M., 1922. Cited in Hamrum, C.L., 1966.

DAVIES, W.M., 1936. Studies on the aphids infesting the potato crop. Laboratory experiments on the effect of wind velocity on the flight of Myzus persicae (Sulz.) Annals of Applied Biology 23: 401 - 408.

DEBACH, P., DIETRICK, E.J., and FLESCHNER, C.A., 1949. A new technique for evaluating the efficiency of entomophagous insects in the field. Journal of Economic Entomology 42: 546 - 547.

DEITZ, L.L., RABB., R.L., VAN DUYN, J.W., BROOKS, W.M., BRADLEY Jr., J.R., and STINNER, R.E., 1976. A guide to the identification and biology of soybean arthropods in North Carolina. North Carolina Agricultural Experiment Station Technical Bulletin 238: 264 p.

DICKSON, R.C., 1975. Identity, origin and host range of the blue alfalfa aphid. p. 22 - 23. In Fifth Californian Alfalfa Symposium.

DICKSON, R.C., and LAIRD, E.F., 1959. Californian desert and coastal populations of flying aphids and the spread of lettuce-mosaic virus. Journal of Economic Entomology 52: 440 - 443.

DIETRICK, E.J., SCHLINGER, E.I., and VAN DEN BOSCH, R., 1959. New method for sampling arthropods using a suction collecting machine and modified Berlese funnel separators. Journal of Economic Entomology 52: 1085 - 1091.

DIXON, A.F.G., 1970. Stabilisation of aphid populations by an aphid induced plant factor. Nature 227: 1368 - 1369.

DIXON, A.F.G., and WRATTEN, S.D., 1971. Laboratory studies on aggregation size and fecundity in the black bean aphid Aphis fabae Scop. Bulletin of Entomological Research 61: 97 - 111.

DUNBIER, M.W., KAIN, W.M., and MCSWEENEY, K.B., 1977. Performance of lucerne cultivars resistant to blue-green lucerne aphid in New Zealand. Proceedings of the 30th New Zealand Weed and Pest Control Conference: 155 - 159.

DUNN, J.A., 1959. The effect of temperature on reproduction by the alatae of Pemphigus bursarius (L.) Annals of Applied Biology 47 (4): 772 - 777.

DUNN, J.A., 1965. Studies on the aphid, Cavariella aegopodii Scop. I On willow and carrot. Annals of Applied Biology 56: 429 - 438.

DUNN, J.A., and WRIGHT, D.W., 1955. Population studies of the pea aphid in East Anglia Bulletin of Entomological Research: 46: 369 - 387.

DUSEK, J., and LASKA, P., 1966. Occurrence of syrphid larvae on some aphids. p. 37 - 38. In HODEK, I., 1966.

EASTOP , V.F., 1966. A taxonomic study of Australian Aphidoidea (Homoptera). Australian Journal of Zoology 14: 399 - 592.

EASTOP , V.F., 1971. Keys for the identification of Acyrthosiphon (Hemiptera : Aphididae). Bulletin of the British Museum (Natural History) Entomology 26: 1 - 115.

EASTOP, V.F., 1973. Biotypes of aphids. p 40 - 51. In LOWE, A.D., 1973a.

EASTOP, V.F., and VAN EMDEN, H.F., 1972. The insect material. p.1 - 45. In VAN EMDEN, H.F. 1972.

EICHMANN, R.D., and WEBSTER, R.L., 1940. The influence of alfalfa on the abundance of the pea aphid on peas grown for canning in Southeastern Washington Agricultural Experiment Station Bulletin Number 389 36p.

EVENHUIS, H.H., 1966. Syrphid predators of apple aphids and their parasites p. 191 - 193 In Hodek, I., 1966b.

EWERT, M.A., and CHIANG, H.C., 1966. Effect of some environmental factors on the distribution of three species of Coccinellidae in the microhabitat. p.195. In HODEK, I., 1966b.

EYLES, A.C., 1960 - Insects associated with the major fodder crops in the North Island II Hemiptera. New Zealand Journal of Agricultural Research 3: 994 - 1008.

FARRELL, J.A.K., 1976 Effects of groundnut crop density on the population dynamics of Aphis craccivora Koch (Hemiptera, Aphididae) in Malawi. Bulletin of Entomological Research. 66: 317 - 329.

FENTON, F.A., and HOWELL, D.E., 1957. A comparison of five methods of sampling alfalfa fields for arthropod populations. Annals of the Entomological Society of America 50: 606 - 611.

FEWKES, D.W., 1961. Diel vertical movements in some grassland Nabidae (Heteroptera).

FORD, M., 1976. Lucerne needs aphid control. Evening Standard, October 14.

FORREST, J.M.S., 1971. The growth of Aphis fabae as an indicator of the nutritional advantage of galling to the apple aphid Dysaphis devecta. Entomologia Experimentalis et Applicata 14: 477 - 483.

FORREST, J.M.S., and DIXON, A.F.G., 1975. The induction of leaf-roll galls by the apple aphids Dysaphis devecta and D. plantaginea Annals of Applied Biology 81: 281 - 288.

FORREST, J.M.S., and NOORDINK, J. Ph. W., 1971. Translocation and subsequent uptake by aphids of ^{32}P introduced into plants by radioactive aphids. Entomologia Experimentalis et Applicata. 14: 133 - 134.

FORSTER, R.R., and FORSTER, L.M., 1973. New Zealand spiders; an introduction. Collins, Auckland, 254 p.

FOSTER, W.A., 1975. The life history and population biology of an
        intertidal aphid, <u>Pemphigus trehernei</u> Foster. Transactions of the
        Royal Entomological Society of London <u>127</u>: 193 - 207.

FRANKS, J.H., 1967. A serological method used in the investigation of the
        predators of the pupal stage in the winter moth, <u>Operophtera brumata</u>
        (L.) (Hydriomenidae). Quaestiones Entomologicae <u>3</u>: 95 - 105.

FRANZ, J.M., 1958. The effectiveness of predators and food in limiting
        graduations of <u>Adelges</u> (<u>Dreyfusia</u>) <u>piceae</u> Ratz. in Europe.
        Proceedings of the 10th International Congress of Entomology,
        Montreal 1956 <u>4</u>: 781- 787.

FRAZER, B.D., and VAN DEN BOSCH, R., 1973. Biological control of the walnut
        aphid in California: the interrelationship of the aphid and its
        parasite. Environmental Entomology <u>2</u>: 561 - 568.

FRENCH, R.A., 1966. The biology and ecology of <u>Coccinella undecimpunctata</u>
        L. M. Agr. Sc. Thesis, University of Canterbury.

GALECKA, B., 1966. The effectiveness of predators in control of <u>Aphis</u>
        <u>nasturtii</u> Kalt. and <u>Aphis frangulae</u> Kalt. on potatoes. p. 255 - 258.
        <u>In</u> HODEK, I., 1966b.

GIST, G.R., and MOTT, G.O., 1957. Some effects of light intensity, temper-
        ature and soil moisture on the growth of alfalfa, red clover and
        birdsfoot trefoil seedlings. Agronomy Journal <u>49</u>: 33 - 36.

GLUMAC, S., 1966. Syrphid larvae as aphid predators in Yugoslavia.
        p. 163 - 164 <u>In</u> HODEK, I., 1966b.

GONZALEZ, D., WHITE, W., DICKSON, R., and VAN DEN BOSCH, R., 1975. The
        potential for biological control of the blue alfalfa aphid. p.35-37. <u>In</u>
        Fifth Californian Alfalfa Symposium.
GOURLAY, E.S. 1930. Some parasitic hymenoptera of economic importance in
        New Zealand. New Zealand Journal of Science and Technology <u>11</u>: 339-343.

GROBLER, J.H., MACLEOD, D.M., and DE LYZER, A.J., 1962. The fungus <u>Empusa</u>
        <u>aphidis</u> Hoffman parasitic on the wooly pine needle aphid, <u>Schizolachnus</u>
        <u>pini</u> - <u>radiatae</u> (Davidson). The Canadian Entomologist 94: 46 - 49.

GUSTAFSON, M., 1971. Microbial control of insects and scales. p. 375 - 384.
        <u>In</u> BURGES, H.D., and HUSSEY, N.W., (ed). Microbial control of insects
        and mites. Academic Press, London, 861 p.

HAGEN, K.S., 1966. Biology and ecology of predaceous Coccinellidae. Annual
        Review of Entomology. <u>7</u>: 289 - 326.

HAINE, E., 1955. Aphid take-off in controlled wind speeds. Nature <u>175</u> : 474

HAGAN, K.S., SAWALL, E.F., and TASSAN, R.L., 1970. The use of food sprays to
        increase effectiveness of entomophagous insects. Proceedings of the
        Tall Timbers Conference on Ecological Animal Control by Habitat
        Management <u>1</u>: 59 - 81.

HAGEN, K.S., and VAN DEN BOSCH, R., 1968. Impact of pathogens, parasites and predators on aphids. Annual Reviews of Entomology 13: 325 - 384.

HALL, I.M., 1973. Pathogens of aphids. p. 30 -39 In LOWE, A.D., 1973a.

HALL, I.M., LOWE, A.D., and GIVEN, B.B., 1976. New records of aphid hosts of Entomopthora aphidis and E. planchoniana in New Zealand. New Zealand Journal of Zoology. 3: 111 - 112.

HAMRUM, C.L., 1966. Food utilisation of the common Minnesota Syrphinae. p. 71 - 73. In HODEK, I., 1966b.

HARPAZ, I., 1958. Bionomics of the 11-spotted Ladybird Beetle, Coccinella undecimpunctata L. in a subtropical climate. Proceedings of the 10th International Congress of Entomology, Montreal, 1956 2: 657 - 659.

HAWKES, O.A.M., and MARRINER, T.F., 1927. A preliminary account of the life history of Coccinella 11-punctata L. Transactions of the Royal Entomological Society of London 75: 47 - 53.

HEATHCOTE, G.D., 1957. The optimum size of sticky aphid traps. Plant Pathology 6: 104 - 107.

HEATHCOTE, G.D., 1958. Effect of height on catches of aphids in water and sticky traps. Plant Pathology 7: 32 - 35.

HEATHCOTE, G.D., 1972. Evaluating aphid populations on plants. p. 105 -145. In VAN EMDEM, H.F., 1972.

HEATHCOTE, G.D., PALMER, J.M.P., and TAYLOR, L.R., 1969. Sampling for aphids by traps and by crop inspection. Annals of Applied Biology 63 : 155 - 166.

HENDRICK, R.D., 1967. Field and laboratory studies on the ecology and morphology of Nabis americoferus Carayon and its parasites in California. Ph. D. Thesis, University of California. Cited in TAMAKI, G. and WEEKS, R.E., 1972.

HIGUSHI, H., and MIYAZAKI, M., 1969. A tentative catalogue of host plants of Aphidoidea in Japan. Insecta Matsumurana, Supplement Five. 66 p.

HILLE RIS LAMBERS, D., 1966. Polymorphism in Aphididae. Annual Review of Entomology 11: 47 - 78.

HILSON, R.J.D., 1964. The ecology of Micromus tasmaniae (Walker). M. Sc. Theis in Zoology, University of Canterbury.

HODEK, I., 1966a. Food ecology of aphiophagous Coccinellidae p. 23 - 30. In HODEK, I., 1966b.

HODEK, I., (ed), 1966b. Ecology of aphidophagous insects. Academia, Prague 360 p.

HODEK, I., 1967. Bionomics and ecology of predaceous Coccinellidae. Annual Review of Entomology 12: 79 - 104.

HODEK, I., HAGEN, K.S., and VAN EMDEN, H.F., 1973. Methods for studying effectiveness of natural enemies. p. 147 - 188. In VAN EMDEN, H.F., 197]

HODEK, I., STARY, P., and STYS, P., 1962. The natural enemy complex of
    Aphis fabae and its effectiveness in control. Proceedings of the
    11th International Congress of Entomology, Wien, 1960: 747 - 749.

HUGHES, R.D., 1962. A method for estimating the effects of mortality in
    aphid populations. Journal of Animal Ecology. 31: 389 - 396.

HUGHES, R.D., 1963. Population dynamics of the cabbage aphid Brevicoryne
    brassicae (L.) Journal of Animal Ecology 32: 393 - 424.

HUGHES, R.D., 1972. Population dynamics. p. 275 - 293 In VAN EMDEN, H.F.,
    1972.

HUGHES, R.D., 1977. 30th New Zealand Weed and Pest Conference, Johnsonville,
    New Zealand.

HUGHES, R.D., and GILBERT, N., 1969. A model of an aphid population - a
    general statement. Journal of Animal Ecology 37: 553 - 563.

IBBOTSON, A., and KENNEDY, J.S., 1951. Aggregation in Aphis fabae Scop. I
    Aggregation on plant. Annals of Applied Biology. 38: 65 - 78.

IMMS, A.D., 1940. On growth processes in the antennae of insects. Quarterly
    Journal of Microscopical Science 81 581 - 593.

IMMS, A.D., 1957. A general textbook of entomology. Ninth ed. Methven and Co.
    Ltd. London, 886 p.

INGOLD, C.T., 1969. The Biology of Fungi. Hutchinson Educational Limited
    London. 147 p.

IPERTI, G., 1966a. Some components of efficiency in aphiophagous coccinellids.
    p. 253. In HODEK, I., 1966b.

IPERTI, G., 1966b. Comparison of voracity of five coccinellids p. 61. In
    HODEK, I., 1966b.

ITO, Y., 1960. Ecological studies on population increase and habitat
    segregation among barley aphids. Bulletin of the National Institute
    of Agricultural Science, Tokyo, Series C. Phytopathology and Ento-
    mology 11: 45 - 130.

JESSOP, C.T., 1963 A note on the feeding habits of Nabis capsiformis Germar.
    The New Zealand Entomologist 3 (3): 23.

JOHNSON, B., 1958. Factors affecting the locomotor and settling responses of
    alate aphids. Animal Behaviour 6: 9 - 26.

JOHNSON, C.G., 1950. The comparison of suction trap, sticky trap and townet
    for quantitative sampling of small airborne insects. Annals of
    Applied Biology 37: 268 - 285.

JOHNSON, C.G., 1952a The role of population level, flight periodicity and climate in the dispersal of aphids. Transactions of the Ninth International Congress of Entomology 1: 429 - 431.

JOHNSON, C.G., 1952b. The changing numbers of Aphis fabae Scop. flying at low level in relation to current weather and to the population on the crop. Annals of Applied Biology 39: 525 - 547.

JOHNSON, C.G., 1954. Aphid migration in relation to weather. Biological Reviews 29: 87 - 118.

JOHNSON, C.G., 1957. A new method of extracting arthropods and molluscs from grassland and herbage with suction apparatus. Bulletin of Entomological Research 48: 211 - 218.

JOHNSON, C.G., 1962. Aphid migration. New Scientist 305: 622 - 625.

JOHNSON, C.G., 1967. International dispersal of insects and insect-borne viruses. Netherlands Journal of Plant Pathology, Supplement 1: 21 - 43.

JOHNSON, C.G., 1969. Migration and dispersal of insects by flight. Methuen and Co. Ltd,. London, 763 p.

JOHNSON, C.G., SOUTHWOOD, T.R.E., and ENTWHISTLE, H., 1955. A method of sampling arthropods and molluscs from herbage by suction. Nature 176: 559.

KAIN, W.M., ATKINSON, D.S., MARSDEN, R.S., OLIVER, M.J., and HOLLAND, T.V., 1977. Blue-green lucerne aphid damage in lucerne crops within southern North Island. Proceedings of the 30th New Zealand Weed and Pest Control Conference: 177 - 181.

KAIN, W.M., ESSON, M.J., HOLLAND, T.V., and ATKINSON, D.S., 1976. Preliminary studies of chemical control of blue-green lucerne aphid. Proceedings of the 29th New Zealand Weed and Pest Control Conference: 23 - 27.

KAREEM, A.A., and BASHEER, M., 1966. Correlation studies in the effects of weather factors on the possible dispersal of aphids. Indian Journal of Entomology 27: 455 - 459.

KENNEDY, J.S., 1958. Physiological condition of the host plant and suscept-ibility to aphid attack. Entomologia Experimentalis et Applicata 1: 50 - 65.

KENNEDY, J.S., and BOOTH, C.O., 1963. Free flight of aphids in the laboratory. Journal of Experimental Biology 40: 67 - 85.

KENNEDY, J.S., and STROYAN, H.L.G., 1959. Biology of aphids. Annual Review of Entomology 4: 139 - 160.

KIECKHEFER, R.W., and MEDLER, J.T., 1960. Toxicity of cellulose acetate sheeting to leguminous plants. Journal of Economic Entomology 53: 484.

KOEHLER, G.S., and GYRISCO, G.G., 1957. The sytemic action of lindane in alfalfa upon the meadow spittlebug. Journal of Economic Entomology 50: 346 - 347.

KONO, T., 1975. Distribution and identification of the blue alfalfa aphid, p. 24 - 27 In Fifth Californian Alfalfa Symposium.

LAMB, K.P., 1958a. Aphid sampling. The New Zealand Entomologist 2 (3): 6 - 11

LAMB, K.P., 1958b. Alate aphids trapped in Auckland, New Zealand using Moericke colour traps. New Zealand Journal of Science 1: 579 - 589.

LEES, A.D., 1966. The control of polymorphism in aphids. Advances in Insect Physiology 3: 207 - 277.

LEHMAN, W.F., HUNT, O.J., and STANFORD, E.H., 1975. Possibilities of varietal resistance to the blue-alfalfa aphid (Acyrthosiphon kondoi) p 31 - 34 In Fifth Californian Alfalfa Symposium.

LE ROUX, E.J., 1959. Effects of frost, rainfall and aestival temperature on populations of the apple aphid, Aphis pomi DeG. (Homoptera: Aphididae) on apple in Quebec. Annals of the Entomological Society of Quebec. 5: 49 - 52.

LEWIS, T., and SIDDORN, J.W., 1972. Measurement of the physical environment p. 235 - 273 In VAN EMDEN, H.F., 1972.

LOPEZ, E.G. and TEETES, S.L., 1976. Selected predators of aphids in grain sorghum and their return to cotton. Journal of Economic Entomology 69: 198 - 204.

LOWE, A.D., 1963. The fungus Entomophthora aphidis Hoffman parasitic on the cabbage aphid (Brevicoryne brassicae L.) in New Zealand. New Zealand Journal of Agricultural Research 6: 314 - 317.

LOWE, A.D., 1964. The ecology of the cereal aphid in Canterbury. Proceedings of the 17th New Zealand Weed and Pest Control Conference: 175 - 182.

LOWE, A.D., 1966a. Aphids trapped at 3 sites in Canterbury, New Zealand over four years with flight patterns for nine main species. New Zealand Journal of Agricultural Research 9: 771 - 807.

LOWE, A.D., 1966b. Some effects of weather on aphids in crops and pastures in Canterbury, New Zealand. Proceedings of the New Zealand Ecological Society 13: 86 - 90.

LOWE, A.D., 1967. Aphids on crops in New Zealand. Proceedings of the 20th New Zealand Weed and Pest Control Conference: 185 - 196.

LOWE, A.D., 1968a. Alate aphids trapped over eight years at two sites in Canterbury, New Zealand. New Zealand Journal of Agricultural Research 11: 829 - 848.

LOWE, A.D., 1968b. The incidence of parasitism and disease in some population of the cabbage aphid in New Zealand. New Zealand Journal of Agricultura Research 11: 821 - 828.

LOWE, A.D., (ed.), 1973a. Perspectives in aphid biology. Bulletin Number 2, Entomological Society of New Zealand. 123 p.

LOWE, A.D., 1973b. Aphid biology in New Zealand. p.7 - 19 In LOWE, A.D., 1973a.

LOWE, A.D., and DROMGOOLE, M.V., 1958. The development of an electronic aphid counter. New Zealand Journal of Agricultural Research 1: 903-912.

MACFARLANE, R.P., 1970. A preliminary study of the fauna associated with lucerne (Medicago sativa L., variety Wairau) in New Zealand with special reference to pests, sampling methods and lucerne seed production. M. Agr. Sc. Thesis, Lincoln College.

MACFARLANE, R.P., and POTTINGER, R.P., 1976. Insects affecting lucerne seed production. Proceedings of the 29th New Zealand Weed and Pest Control Conference: 19 - 22.

MACGILLIVRAY, M.E., and ANDERSON, G.B., 1957. Three useful insect cages. The Canadian Entomologist 89: 43 - 46.

MCKENZIE, H.L., 1967. Mealybugs of California. University of California Press, Berkeley. 525 p.

MACLEOD, D.M., 1955. A fungus enemy of the pea aphid Macrosiphum pisi (Kaltenbach). The Canadian Entomologist 87: 503 - 505.

MCSWEENEY, B.J., 1976. Aphid pest has been hibernating. In FORD, M., Evening Standard, September 16, 1976.

MARKKULA, M., and RAUTAPAA, J., 1963. PVC rearing cages for aphid investigations. Annales Agriculturae Fenniae 2: 208 - 211.

MARTIN, H., (ed.), 1971. Pesticide manual. British Crop Protection Council, 495 p.

METCALF, R.L., and LUCKMAN, W.H., 1975. Introduction to insect pest management. John Wiley and Sons, New York, 587 p.

MILES, P.W., 1968. Studies on the salivary physiology of plant-bugs: experimental induction of galls. Journal of Insect Physiology 14: 97 - 106.

MILLER, D., 1921. Material for a monograph on the Diptera fauna of New Zealand: Part II, Family Syrphidae 53: 289 - 333.

MILLER, D., 1971. Common insects in New Zealand. A.H. and A.W. Reed, Wellington, 178 p.

MILLER, D., CLARK, A.F., and DUMBLETON, L.J., 1936. Biological control of noxious insects and weeds in New Zealand. New Zealand Journal of Science and Technology 18: 579 - 593.

MISKIMEN, G.W., 1970. Population dynamics of the yellow sugarcane aphid, Sipha flava in Puerto Rico as affected by heavy rains. Annals of the Entomological Society of America. 63: 642 - 645.

MITTLER, T.G., 1973. Aphid polymorphism as affected by diet p.65 - 75 In LOWE, A.D., 1973a.

MIYAZAKI, M., 1971. A revision of the Tribe Macrosiphini of Japan. (Homoptera: Aphididae, Aphidinae). Insecta Matsumurana 34: 1 - 247.

MUNDINGER, F.G., 1922. The life history of two species of Nabidae (Hemip. Heterop.) Nabis roseipennis Reut. and Nabis rufusculus Reut. Syracuse University New York State University College of Forestry Technical Publication 16: 149 - 167.

MURDIE, G., 1969a. Some causes of size variation in the pea aphid. Acyrthosiphon pisum Harris. Transactions of the Royal Entomological Society of London. 121: 423 - 442.

MURDIE, G., 1969b. The biological consequences of decreased size caused by crowding or rearing temperatures in apaterae of the pea aphid, Acyrthosiphon pisum Harris. Transactions of the Royal Entomological Society of London 121: 443 - 455.

NEW, T.R., 1975. The biology of Chrysopidae and Hemerobiidae (Neuroptera) with reference to their usage as biocontrol agents: a review. Transactions of the Royal Entomological Society of London 127: 115-140.

NIELSON, M.W., 1957. Sampling technique studies on the spotted alfalfa aphid. Journal of Economic Entomology 50: 385 - 389.

NIELSON, M.W., and BARNES, O.L., 1961. Population studies of the spotted alfalfa aphid in Arizona in relation to temperature and rainfall. Annals of the Entomological Society of America 54: 441 - 448.

NIELSON, M.W., and HENDERSON, J.A., 1959. Biology of Collops vittatus (Say.) in Arizona and feeding habits of seven predators of the spotted alfalfa aphid. Journal of Economic Entomology. 52: 159 - 162.

NIELSON, M.W., and KODET, R.T., 1975. The blue alfalfa aphid in Arizona. p. 39 - 40 In Fifth California Alfalfa Symposium.

NIELSON, M.W., LEHMAN, W.F., and KODET, R.T., 1976. Resistance in alfalfa to Acyrthosiphon kondoi. Journal of Economic Entomology 69: 471 - 472.

NIEMCZYK, E., 1966. Predators of aphids associated with apple orchards. p. 275 - 276 In HODEK, I., 1966.

NIKU, B., 1975. Behaviour and fecundity of apterous pea aphids (Acyrthosiphon pisum) after a drop-reaction. Entomologia Experimentalis et Applicata 18: 29.

O'CONNOR, B.P., and HART, R.I.K., 1977. Primicarb for the control of blue-green lucerne aphid. Proceedings of the 30th New Zealand Weed and Pest Control Conference: 170 - 172.

PACKER, J.S., 1975. Insect immigrants. Insect World Digest July/August 1975: 4 - 9.

PAIK, W.H., 1965 Aphids of Korea. Seoul National University, Seoul, 160 p.

PALMER, T.P., 1977. Aphids on lucerne sown with insecticides and cover crop. Proceedings of the 30th New Zealand Weed and Pest Control Conference: 173 - 176.

PERRIN, R.M., 1976. The population dynamics of the stinging nettle aphid _Microlophium carnosum_ (Bukt.). Ecological Entomology 1: 31 - 40.

PETCH, T., 1938. Notes on entomogenous fungi. The British Mycological Society Transaction 21: 35 - 67.

PETERSON, A., 1945. A manual of entomological equipment and methods. Cited in SPARKS et al., 1966.

POLLARD, E., 1969. The effect of removal of arthropod predators on an infestation of _Brevicoryne brassicae_ (Hemiptera : Aphididae) on brussel sprouts. Entomologia Experimentalis et Applicata. 12: 118 - 124.

PRITCHETT, W.L., and NELSON, L.B., 1951. The effect of light intensity on the growth characteristics of alfalfa and bromegrass. Agronomy Journal 43: 172 - 177.

RICHARDS, D.W., 1961. The theoretical and practical study of natural insect populations. Annual Review of Entomology 6: 147 - 162.

RICHARDSON, C.A., 1977. Population dynamics of blue-green lucerne aphid in the lower North Island. Proceedings of the 30th New Zealand Weed and Pest Control Conference: 149 - 151.

RIDGEWAY, R.L., and JONES, S.L., 1968. Plant feeding by _Geocoris pullens_ and _Nabis americoferus_. Annals of the Entomological Society of America 61: 232 - 233.

ROACH, S.H., and AGEE, H.R., 1972. Trap colours: preference of alate aphids. Environmental Entomology 1: 797 - 798.

ROBERTSON, G., 1976. Marking aphids and their parasites with ^{14}C in field studies. Entomologia Experimentalis et Applicata 19: 65 - 76.

RUESINK, W.G., and KOGAN, M., 1975. The quantitative basis of pest management: sampling and measuring. p. 309 - 351. In METCALF, R.L., and LUCKMAN, W.H., 1975.

SAILOR, R.I., 1966. An aphid predator exclusion test. p. 263. In HODEK, I., 1966b.

SAVOISKAYA, G.I., 1966. The significance of Coccinellidae in the biological control of the apple-tree aphids in the Alma Ata fruit-growing region. p. 317 - 319 In HODEK, I., 1966b.

SCHNEIDER, F., 1969. Bionomics and physiology of aphidophagous Syrphidae. Annual Review of Entomology 14: 103 - 124.

SHARMA, M.L., 1969, 1971, 1972. Bibliography of Aphidoidea. (3 Tomes). L'Universite de Sherbrooke, Quebec. 293 p., 221 p., and 207 p. respectively.

SHARMA, R.K., STERN, V.M., and HAGEMANN, R.W,, 1975. Blue alfalfa aphid
     damage and its chemical control in the Imperial Valley, California
     p. 29 - 30. In Fifth Californian Alfalfa Symposium.

SHARMA, R.K., STERN, V.M., and HAGEMANN, R.W., 1976. Blue alfalfa aphid:
     a new pest in the Imperial Valley. California Agriculture 30: 14 - 15.

SHARPE, C.J., and MACDIARMID, B.N., 1976. Control of brassica aphid
     and blue-green lucerne aphid with chlorpyrifos. Proceedings of the
     29th New Zealand Weed and Pest Control Conference: 189 - 192.

SHAW, M.J.P., 1967. The flight behaviour of alate Aphis fabae . Rothamsted
     Experimental Station Report for 1966: 200 - 201.

SHAW, M.J.P.,1968 . Field studies on flight behaviour. Rothamsted Experi-
     mental Station Report for 1967: 192.

SIMPSON, R.G., and BURKHARDT, C.C., 1960. Biology and evaluation of certain
     predator of Therioaphis maculata (Buckton). Journal of Economic
     Entomology. 53: 89 - 94.

SLUSS, R.R., 1967. Population dynamics of the walnut aphid Chromaphis
     juglandicola (Kalt.) in Northern California. Ecology 48: 41 - 58.

SLUSS, R.A., and HAGEN, K.S., 1966. Factors influencing the dynamics of
     walnut aphid in Northern California. p. 243 - 248. In HODEK, I.,
     1966b.

SMIRNOFF, W.A., and MACLEOD, D.M., 1973. Une epizootié d'Entomophthora
     sp. dans une population du puceron du sapin (Cinara curvipes)
     (Hemiptera: Aphididae).

SMITH, B.C., 1966. Food ecology of aphidophagous insects. p 19 - 22. In
     HODEK, I., 1966b.

SMITH, B.D., 1966. Effects of parasites and predators on a natural popu-
     lation of the aphid Acyrthosiphon spartii (Koch.) on broom
     (Sarothamnus scoparius L.) 35: 255 - 267.

SMITH, R.F., 1966. Summing up of section V. p. 285 - 287. In HODEK, I.,
     1966b.

SMITH, R.F., and HAGEN, K.S., 1966. Natural regulation of alfalfa aphids in
     California. p. 297 - 315. In HODEK, I., 1966b.

SOL, R., 1966. The occurrence of aphidivorous syrphids and their larvae
     on different crops, with the help of coloured water traps. p.181 - 184.
     In HODEK, I., 1966b.

SOMERFIELD, K.G., and BURNETT, P.A., 1976. Lucerne insect survey. Proceed-
     ings of the 29th New Zealand Weed and Pest Control Conference: 14-18.

SOUTHWOOD, T.R.E., 1966. Ecological methods. Methuen and Co. Ltd., London, 391 p.

SOUTHWOOD, T.R.E., and PLEASANCE, H.J., 1962. A hand operated suction apparatus for the extraction of arthropods from grassland and similar habitats with notes on other models. Bulletin of Entomological Research 53: 125 - 128.

SPARKS, A.N., CHIANG, H.C., BURKHARDT, C.C., FAIRCHILD, M.L., and WEEKMAN, G.T., 1966. Evaluation of the influence of predation on corn borer populations. Journal of Economic Entomology. 59: 104 - 107.

STARÝ, P., 1970. Biology of aphid parasites with respect to integrated control. Dr. W. Junk, The Hague, 642 p.

STARÝ, Y., 1970. Routine alfalfa (Medicago sativa) cutting program and its influence on pea aphid (Acyrthosiphon pisum Harris) populations. Oecologia (Berl.) 5: 374 - 379

STINNER, R.E., JONES, T.W., TUTTLE, C., and CARON, R.E., 1977. Population mortality and cyclicity as affected by intraspecific competition. The Canadian Entomologist 109: 879 - 890.

SUMMERS, C.G., 1975. The 'Blue alfalfa aphid' - biology and economic thresholds. p. 28. In Fifth Californian Alfalfa Symposium.

TAKAHASHI, R., 1924. On the nymphs of the Aphidinae. Proceedings of the Entomological Society of Washington 26: 1 - 11.

TAKAHASHI, R., 1965. Some new and little-known Aphididae from Japan (Homoptera). Insecta Matsumurana 28: 19 - 61.

TAMAKI, G., MCGUIRE, J.U., and TURNER, J.E., 1974. Predator power and efficacy: a model to evaluate their impact. Environmental Entomology 3: 625 - 630.

TAMAKI, G., and WEEKS, R.E., 1972. Efficiency of three predators Geocoris bullatus, Nabis americoferus, and Coccinella transversoguttata, used alone or in combination against three insect prey species, Myzus persicae, Ceramica picta, and Mamestra configurata in a greenhouse study. Environmental Entomology 1: 258 - 263.

TAMBS-LYCHE, H., 1958. Unpublished. In KENNEDY, J.S., 1958.

TAYLOR, C.E., 1962. Factors influencing the infestation of a bean field by Aphis fabae Scop. Entomologia Experimentalis et Applicata 5: 105 - 113.

TAYLOR, E.J., 1949. A life history of Nabis alternatus. Journal of Economic Entomology 42: 991.

TAYLOR, L.R., and PALMER, J.M.P., 1972. Aerial sampling. p 189 - 234. In VAN EMDEN, H.F., 1972.

THAXTER, R., 1888. The Entomophthoraceae of the United States. Memoirs of the Boston Society of Natural History 4: 133 - 201.

THOMAS, I., and VEVAI, E.J., 1940. Aphis migration. An analysis of the results of five seasons trapping in North Wales. Annals of Applied Biology 27: 393 - 405.

THOMAS, J.G., SORENSON, E.L., and PAINTER, R.H., 1966. Attached vs. excised trifoliates for evaluation of resistance in alfalfa to the spotted alfalfa aphid. Journal of Economic Entomology 59: 444-448.

THOMAS, R.G., 1967. Flowering and reproductive development in lucerne p. 195 - 204. In R.H.M. LANGER (ed.) The lucerne crop. A.H. and A.W. Reed, Wellington.

THOMAS, W.P., 1977. Biological control of the blue-green lucerne aphid. The Canterbury situation. Proceedings of the 30th New Zealand Weed and Pest Control Conference: 182 - 187.

TILLYARD, R.J., 1923. Descriptions of new species and varieties of lace-wings (Order Neuroptera Planipennia) from New Zealand, belonging to the families Berothidae and Hemerobiidae. Transactions and Proceedings of the New Zealand Institute 54: 217 - 225.

TROUGHT, T.E.T., 1977. Control of blue-green lucerne aphid on white clover seed crops. Proceedings of the 30th New Zealand Weed and Pest Control Conference: 188 - 191.

TUITE, J., 1969. Plant Pathological Methods Fungi and Bacteria. Burgess Publishing Co., Minneapolis. 239 p.

VALENTINE, E.W., 1967a. A list of the hosts of entomophagous insects in New Zealand. New Zealand Journal of Science 10: 1100 - 1209.

VALENTINE, E.W., 1967b. Biological control of aphids. Proceedings of the 20th New Zealand Weed and Pest Control Conference: 204 - 207.

VAN EMDEN, H.F., 1965. The effect of uncultivated land on the distribution of the cabbage aphid (Brevicoryne brassicae) on an adjacent crop. Journal of Applied Ecology 2: 171 - 176.

VAN EMDEN, H.F.,1966. The effectiveness of aphidophagous insects in reducing aphid populations. p. 227 - 235. In HODEK, I., 1966b.

VAN EMDEN, H.F.,(ed.), 1972. Aphid technology. Academic Press, London and New York. 344 p.

VAN EMDEN, H.F., 1973. Aphid host plant relationships some recent studies. p. 54 - 64 In LOWE, A.D., 1973a.

VAN EMDEN, H.F., EASTOP, V.F., HUGHES, R.D., and WAY, M.J., 1969. The ecology of Myzus persicae. Annual Review of Entomology 14: 197-270.

VICKERMAN, G.P., and SUNDERLAND, K.D., 1975. Arthropods in cereal crops: nocturnal activity, vertical distribution and aphid predation. Journal of Applied Ecology 12: 755 - 766.

WALKER, F.B., 1873. Catalogue of the specimens of Heteropterous Hemiptera in the collection of the British Museum 7: 145.

WAY, M.J., 1966. Summing up of section I. p. 91 - 94 In HODEK, I., 1966b.

WAY, M.J., 1968. Intra-specific mechanisms with special reference to aphid populations p. 18 - 36. In SOUTHWOOD, T.R.E., (ed.), Insect abundance, Royal Entomological Society, London.

WAY, M.J., 1973. Population structure in aphid colonies. p 76 - 84. In LOWE, A.D., 1973a.

WAY, M.J., and BANKS, C.J., 1962. Significance of competition in the natural control of aphids. Proceedings of the 11th International Congress of Entomology, Wiens: 746.

WAY, M.J., and BANKS, C.J., 1967. Intraspecific mechanisms in relation to the natural regulation of numbers by Aphis fabae Scop. Annals of Applied Biology 59: 189 - 205.

WAY, M.J., and BANKS, C.J., 1968. Population studies on the active stages of the black bean aphid Aphis fabae Scop. on its winter host Euonymus europaeus L. Annals of Applied Biology 62: 177 - 197.

WAY, M.J., AND CAMMELL, M., 1970. Aggregation behaviour in relation to food utilisation by aphids. p. 229 - 247. In WATSON, A., ed. Animal Populations in relation to their food resources. Symposium Number 10 of the British Ecological Society.

WERNER, F.G., and BUTLER Jr., G.D., 1957. The Reduvids and Nabids associated with Arizona crops. Arizona Agricultural Experiment Station Bulletin 133: 13 p.

WHEELER Jr., A.G., 1973. Studies on the arthropod fauna of alfalfa V Spiders (Araneida). The Canadian Entomologist 105: 425 - 432.

WHEELER Jr., A.G., 1977. Studies on the arthropod fauna of alfalfa VII Predaceous insects. The Canadian Entomologist 109: 423 - 425.

WHITCOMB, W.H., and BELL, K., 1964. Predaceous insects, spiders and mites of Arkansas cotton fields. Arkansas Agricultural Experiment Station Bulletin 690. 83 p.

WOLFENBARGER, D.O., 1975. Factors affecting dispersal distances of small organisms. Exposition Press, Hicksville, N.Y. 230 p.

WOODFORD, J.A.T., 1973. The climate within a large aphid proof field cage. Entomologia Experimentalis et Applicata 16: 313 - 332.

WYATT, I.J., 1965. The distribution of <u>Myzus persicae</u> (Sulz) on year round chrysanthemums. Annals of Applied Biology <u>56</u>: 439 - 459.

WYNN-WILLIAMS, R.B., and BURNETT, P.A., 1977. Effect of blue-green lucerne aphid on seedling lucerne in a glasshouse. Proceedings of the 30th New Zealand Weed and Pest Control Conference: 152 - 154.

Minor Emendations

Page	Section	Emendations
20	Methods	From this period the colony was observed 2-3 days a week from one primary site, and several secondary locations with binoculars and a 27x telescope.
20	Methods	All statistical analysis was done using SAS analysis of variance (ANOVA) 6.12.
37	Methods	All statistical analysis was done using SAS analysis of variance (ANOVA) 6.12.
55	Table: 5.2	Equations for the derivation of length and mass of fish prey from otolith measurements, where x = otolith length.