Factors Limiting the Efficiency of *Trioxys complanatus* (Quilis), A Parasitoid of the Spotted Alfalfa Aphid, *Therioaphis trifolii* (Monell) f. *maculata*, in South Australia.

by

D. Samoedi, Ir. (Bogor, Indonesia)

A thesis submitted for the degree of Doctor of Philosophy
in the Faculty of Agricultural Science
at the University of Adelaide

Department of Entomology
Waite Agricultural Research Institute
University of Adelaide

June, 1984

TABLE OF CONTENTS

SUMMARY

The effectiveness of the established parasitoid, *Trioxys complanatus*, in reducing the growth rate of the spotted alfalfa aphid (SAA), *Therioaphis trifolii*, was appraised by determining the relationship between SAA and its natural enemies in a lucerne field at the Waite Agricultural Research Institute. Studies were also done on some factors that possibly affect the effectiveness of *Trioxys*.

The population study was conducted in a 1 ha lucerne field at the Waite Institute between January 1981 and October 1982. The results suggest that the SAA was abundant in summer and autumn but was very scarce in winter and was not an economic problem in spring. In experimental colonies from which natural enemies were excluded, SAA grew at the rate (square root of aphids per day) of 1.59 in spring (November), 1.15 in summer (January) and 0.64 in autumn (May).

Trioxys was not detectable in winter and was very scarce in spring and it could only be regularly found at the beginning of mid-summer when the SAA had reached relatively high numbers. The numbers of *Trioxys* increased slowly during summer but more rapidly in April before gradually decreasing as the daily temperature got lower thereafter.

Other natural enemies that seemed to be important were the native predators *Coccinella repanda* and *Micromus tasmaniae*(hemerobiid) and their numbers were usually high in spring. The early build-up in numbers of these two predators seemingly depended on the numbers of pea aphid, *Acyrthosiphon pisum*, and blue green aphid, *Acyrthosiphon kondoi*, in early spring.

Parasitoid-predator exclusion studies were conducted between spring 1982 and autumn 1983 to determine the impact of *Trioxys* alone, *Trioxys* plus predators, and ants on the growth rate of SAA colonies. The results confirmed that natural enemies are a major cause of the scarcity of the SAA in spring. The total reduction in the growth rate of SAA that could be attributed to *Trioxys* plus predators (except ants) was estimated to be 71%.

Trioxys plus predators (mainly *Coccinella*) appeared to exert no influence on the SAA population in summer. The hot and dry climate during this period of the year probably exerted a more depressing effect on *Trioxys* rather than on the SAA. Other factors possibly affecting *Trioxys* effectiveness are discussed; one of these is the direct impact of competitors i.e. predators and secondary parasitoids. A direct reduction by predators of the number of *Trioxys* occurred because the predators consume some of the parasitoids as parasitized aphids which otherwise would yield new parasitoid that would reproduce (Figures 1.1 and 1.2). The total reduction in the number of *Trioxys* progeny that can be attributed to predation and secondary parasitism was estimated to be 43-56%, depending on the season.

Figure 1.1

A male adult *Coccinella repanda* (g) feeding on a mummy of *Trioxys complanatus* (f) which otherwise would yield a new parasitoid that would reproduce. Also showing the four nymphal stages of SAA i.e. 1st (a), 2nd (b), 3rd (c), 4th apterae (d) and 4th alatae nymphal stage (e).

Figure 1.2

Emerging *Trioxys complanatus*.

1.1

1.2

The reason for the poor performance of *Coccinella* in summer is not clear. Parasitism by *Dinocampus coccinellae* and *Tetrastichus* sp. is assumed to have been responsible.

Predation of SAA by ants (*Irridomyrmex* sp.) was significant; the total reduction in number of SAA in summer that could be attributable to predation by ants was estimated to be 94%. The ants, however, were ineffective in the wet autumn, particularly when heavy rain fell.

In the absence of natural enemies, the SAA grew more slowly in autumn than in either spring or summer. *Trioxys* and *Coccinella* which were common during autumn further suppressed the number of SAA. The estimated reduction of the SAA number that can be attributed to the impact of *Trioxys* plus predators during this season was 73%. These natural enemies, however, exerted no depressing effect on the SAA number if their appearance was delayed until the initial SAA density became higher. This result suggested that asynchrony between the appearance of SAA and its natural enemies in early autumn could have been partly responsible for the relatively high numbers of SAA in autumn. The results of further experiments supported this hypothesis and indicated that:

(i) *Trioxys* shows an inversely density-dependent behavioural response, i.e. each female of *Trioxys* tends to parasitize relatively fewer hosts as the host density increases. The possible reasons for this response are discussed.

(ii) The proportion of male progeny of *Trioxys* tends to increase with host density.

Evidence is given that the seasonal air temperatures seemed to affect the interaction between SAA and *Trioxys* in the field but it is not clear exactly how temperature affects the interaction. The appearant influence of high maximum summer temperatures on both SAA and *Trioxys* is discussed.

The use of aphid-resistant cultivar, grazing management (Allen 1984) and natural enemies will probably be the main control measures relied upon by livestock preoducers in South Australia. However, the occurrence of new biotypes of SAA that can thrive on the present resistant cultivars are likely to evolve in the future, so that natural enemies should always be an important component of integrated control for SAA in South Australia. The possibilities of augmenting the established natural enemies are discussed.

DECLARATION

This thesis contains no material which has been accepted for the award of any degree or diploma in any university and, to the best of my knowledge, contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

Consent is given for this thesis to be made available for photocopying and loan.

(D. Samoedi)

ACKNOWLEDGEMENTS

I wish to express sincere thanks to my 2 supervisors Dr D.A. Maelzer and Dr R. Laughlin for their constant guidance, profitable discussions and critical reading in the preparation of this thesis.

I would like to thank Dr P.W. Miles for his help and encouragement during early stages of this study.

I wish to thank Professor T.O. Browning, formerly Professor, Department of Entomology, Waite Agricultural Research Institute, for allowing me to conduct this study in the Department of Entomology.

I would like to thank Dr P.E. Madge, Head of the Entomology Unit, Department of Agriculture South Australia for giving me an opportunity to learn the breeding techniques of both SAA and *Trioxys* in the Department of Agriculture at the beginning of this study.

Thanks are due to my colleage Mr P.G. Allen for many profitable discussions.

I wish to thank the following for the identification of specimens: Dr I. Naumann, Dr. Mary Carver, and Dr R.W. Taylor of the Division of Entomology, C.S.I.R.O. Canberra; and Dr P.J.M. Greenslade of the Division of Soils, C.S.I.R.O. Adelaide.

I am indebted to members of various departments of the Waite Agricultural Research Institute, all of whom have helped me in many ways. Mr. N.C. Stewart helped by obtaining many pieces of equipment; Mr P.H. Mew and Mr B. Milligan helped by maintaining the study field; Ms Sally Wayte and Ms Alison Smith suggested appropriate analyses for my data; Mr B.A. Palk printed the black and white figures; Chroma colour printed glossy colour figures (Figures 1, 20 and 21) ; Mrs C. Schonfeldt made a multiple copy of this thesis. I wish to thank all these people, and others that I may have forgotten.

I would like to thank the Indonesian Government for awarding me the scholarship for making this study possible; and I am gratefull to the Indonesian Sugar Research Institute for granting me the period of leave required to carry out this study.

Finally, thanks are due to my wife, Utiek, and children, Monty and Sakty, for their unfailing patience and encouragement during the preparation of this thesis.

Chapter 1

General Introduction

1.1 Economic Importance

In Australia, lucerne (alfalfa)(*Medicago sativa* L.) is utilized throughout the year with over 80% of the area being grazed (Lodge *et al.* 1978). Before the spotted alfalfa aphid (SAA), *Therioaphis trifolii* (Monell) f. *maculata* (Hemiptera, Aphididae) arrived in 1977, South Australia had an area of about 829,000 ha of lucerne (Aust. Bur. Stats.) mainly for two purposes: irrigated lucerne for hay and seed production over 140,000 ha, and "dryland" (i.e. not irrigated) lucerne for grazing or livestock production over 689,000 ha, mainly in the upper south east of the state. The dryland lucerne alone was reported to be responsible for about 50% of the annual livestock production in South Australia (Allen 1982, Smith 1978). All the lucerne grown in South Australia was the cultivar Hunter River which is thought to have been selected from "Old Spanish" and "Old Flemish" lucerne (I.D. Kaehne, Department of Agriculture and Fisheries, Northfield Laboratory, South Australia, pers. comm.), and was very susceptible to SAA (LLoyd *et al.* 1980, Dunbier *et al.* 1978, Ridland and Berg 1978b).

The SAA swept very rapidly through the lucerne growing areas of the eastern States of Australia in 1977 causing much damage to "Hunter River" lucerne and annual medics, *Medicago* spp.(Passlow 1977). Dicovered in South Australia on the Adelaide plains in May 1977, SAA had spread to all South Australian lucerne growing districts within only 12 months (Wilson *et al.* 1982). The aphid caused a reduction of 95% in the area of grazed lucerne in the upper south east of South Australia and was the major contributor to the reduction of the stocking rate in the region, from an average of 3 dry sheep equivalents per hectare (hereafter denoted as DSE/ha) in 1977 down to 1 DSE/ha in 1981 (P.G. Allen pers. comm.). Similarly, Mohr (1978) estimated the losses to agriculture in 1977/1978 from infestation of exotic lucerne aphids (mainly SAA) in New South Wales (NSW) to be 41% of the annual production. Other authors reported that in NSW in the first 12 months of activity of the SAA alone caused an estimated $29 million damage (e.g. Reilly and Godyn 1979). The assessment of longer term damage to agriculture is complicated and difficult (Mohr 1978).

The type of damage done to lucerne by the SAA is essentially similar to that which has been recorded in the USA (Davis *et al.* 1978, Dickson *et al.* 1955, Randolph 1957). The aphid sucks the sap from the plants, at the same time injecting saliva which may or may not be phytotoxic to the plant (Diehl and Chatters 1956, Dickson *et al.* 1955, Hintz 1964). It also produces a copious amount of honeydew which is a medium for the growth of black moulds; lucerne with heavy deposits of honey dew can not be dehydrated properly and is very difficult to cut and bale. Severely damaged plants are almost defoliated and in some cases almost destroyed (Randolph 1957), and SAA attacks in autumn may especially kill seedlings. Attack in spring can kill mature plants, severely reducing hay yield and seed production (Brownlee *et al.* 1979). Allen (1982) has estimated that in dryland lucerne area of South Australia, 95% of all mature plants had been killed by SAA since 1977.

1.2 Current Methods of Control

Because of the rapidity of the invasion of SAA, the high susceptibility of Hunter River lucerne to SAA, and the scarcity of natural enemies in the early years after invasion by SAA, mean densities of SAA greater than 400 per stem were common (Allen 1982 , Forrester 1978) and the only possible means of controlling SAA was with insecticides. However, the cost/potential benefit ratio for SAA control in irrigated lucerne farming is much lower, and hence the willingness of grower to use insecticides was quite different for dry land grazing as opposed to irrigated hay or seed production.

Allen (1978,1982) studied the impact of SAA on the the production and persistence of "Hunter River" lucerne in the upper south east of South Australia and determined an economic threshold level of 40-60 SAA/lucerne stem. He believed that this low threshold level was virtually impossible to maintain over the majority of dryland farm because of the cost of chemical for control of SAA is relatively high in relation to the low profit margin from lucerne grazing. By contrast, the economic threshold level for seed production was taken as about 20 aphids per stem (D.A. Maelzer, pers. comm.) but the cost/potential benefit ratio in irrigated seed production is so much lower than in dryland farming that insecticidal control is profitable (Swincer *et al.* 1978, Reily and Godyn 1979). There are no data for insecticides for controlling SAA in South Australia since its introduction in 1977 but Maelzer *et al.* (1981) and Bailey *et al.* (1982) reported that 31% of the insecticides applied to lucerne seed crops in the Keith area in 1980 were applied for the control of SAA. Appart from being the only means of controlling SAA in the early years, insecticides were of course willingly used by farmers because of their rapid and uniform effectiveness and ease of application. However, insecticides often aggravate pest problems in the long term by, for example, inducing insecticide resistance or having toxic side effects on non-target organism (Batra 1982, Hagen and van den Bosch 1968, Huffaker 1970). Thus the occurrence of resistance by SAA to a wide range of insecticides in New South Wales were reported by Brownlee *et al.* (1979) just 2 years after the introduction of SAA into the area. The development of insecticide resistance in such a short period indicates the limitation of widescale sprays for long term control, and clearly the control of SAA by insecticides should only be regarded as an interim measure until other control techniques can be developed (Passlow 1977). Recent reports on the insecticidal control of SAA in Australia are to be found in Berg and Ridland 1978,1981, Brownlee *et al.* 1979, Franzmann and Rossiter 1981, Reilly and Godyn 1979, and Watt 1978.

In the long term, the use of aphid-resistant lucerne cultivars will probably be the only reliable control available to livestock producers. Native predators and introduced parasitoids did not usefully control SAA during periods of peak activity of SAA in dryland lucerne in South Australia (Allen 1982). More than 25 different resistant cultivars of lucerne are now being re-sown in the dryland grazing areas of South Australia (P.G. Allen pers. comm.).

The success rate of re-sowing has been about 50% and an estimated 170,000 hectares of former dryland lucerne pasture has been re-sown so far. About 80% of this area has been re-sown to resistant cultivars and about 20% has been re-sown with Hunter River again (T. Davidson, District Agronomist, Dept. Agric. Keith, South Australia, pers. comm.). However, the re-sowing of the former 689,000 hectares will take several years.

Finally, the development and use of SAA-resistant cultivars will not solve the SAA problem indefinitely because new biotypes of SAA that can thrive on the present resistant cultivars are likely to evolve in the future, as they have done in the USA, so that there will be a continuing need for the development of new resistant cultivars (Nielson *et al.* 1970, Nielson and Don 1974a, 1974b, Berg and Ridland 1981).

1.3 Evaluation of Natural Enemy Effectiveness

There are two related problems in the assessment of natural enemy effectiveness. They are (i) measurement of the beneficial result of colonization of newly imported exotic parasitoids or predators, and (ii) measurement of the degree of biological control exerted by already established natural enemies (DeBach and Huffafer 1971).

DeBach and Bartlett (1964) discuss various methods of evaluation of natural enemy effectiveness. They can be classified as

(i) quantitative methods of evaluation which are based on the analysis of population data, especially the correlation of population changes in numbers of both the host and of its natural enemies and (ii) experimental methods of evaluation which are based on comparisons of pest population levels in both the absence and the presence of natural enemies.

Assessment using any of the first methods alone is inadequate for rating the effectiveness natural enemies. Thus Hodek *et al.* (1972) believed that the weak point of these methods is that causal relationships are deduced in hindsight from a coincidence of events seen in the sampling data. The numbers of aphids and of their natural enemies are influenced by many factors which usually can not be controlled, such as heavy rain or high temperature. Also the aphids are influenced by changes in the physiological state of the host plant, suffer from fungal attack, and have their numbers diminished by the emigration of alatae. Periodic census and life table data provide much valuable information, but such methods, including regression techniques, are inadequate for the assessment of regulatory or controlling power of natural enemies (DeBach and Huffaker 1971, Huffaker and Kennet 1969). Those who question the evaluation of "success" in biological control programmes may argue that even if there is considerable justification for the conclusion that sucessful biological control has taken place, there is always a possibility, no matter how remote, that the lowering of population density of pest after the establishment of the enemy, was only a coincidence (Debach and Bartlett 1964).

What is really needed, therefore, for a convincing conclusion about the effect of introduced natural enemies is the use of direct (experimental) methods of evaluation whereby the effect of the natural enemy on the density of its host population can be satisfactorily measured.

1.4 The Scope and Nature of the Studies

It is not my objective in this thesis to provide an in-depth analysis of the biology and ecology of the SAA and its primary parasitoids, *Trioxys complanatus* (Quilis) f. *maculata*, since this has been extensively studied by several people elsewhere (Schlinger and Hall 1959,1961, Force and Messenger 1964a,1964b, Hughes and Roberts 1978). It is not my intention either to measure the beneficial result of colonization of *Trioxys complanatus* in South Australia because this has been adequately studied by Wilson *et al.* (1982). It is my purpose, rather, to provide an analysis of the factors which either promote or limit the predation capacity of *Trioxys complanatus*, which has recently been considered established permanently in South Australia (Wilson *et al.* 1982). It is hoped that this study, if combined with other information on the biology and ecology of the SAA and its natural enemies, will indicate why *Trioxys complanatus* and other natural enemies fail to control the SAA satisfactorily in South Australia, and hence will suggest (i) directions of research for improvement of their efficiency, and (ii) provide guidelines for the possible manipulation of the established natural enemies.

Chapter 2

General Materials and Methods

2.1 Growing lucerne plant in pots

The technique of growing lucerne plants in pots has been described by several people (Finney *et al.* 1960, Wilson *et al.* 1982). At the beginning of this study I tried to use a modification of the technique described by Finney which was employed by the Department of Agriculture and Fisheries Northfield Laboratory South Australia during 1977-1980 (Wilson *et al.* 1982). Soon, however, I found that growing lucerne by this technique was time consuming for a small number of plants because a 4 month minimum period of growth after seeding must ensue before the plant can be used for the culture of insects. What I needed was a method of growing lucerne plants in pots which required a shorter growth period than 4 months, and I achieved this by transplanting lucerne plants from the field. When using this method, however, care must be taken with the selection of plants to be transplanted to ensure a homogeneous regrowth. Plant selection is important if the plants are to be used for experiments. The method of transplanting is described below.

A one hectare block of two year old "Hunter River" lucerne provided a continous supply of plants at any time. However, the best time to transplants was (a) in spring when the ground was soft and (b) the plants had been mown 2-3 weeks earlier. Each plant was dug up with a pickaxe so as to cut the main root at a depth of about 15 cm below the ground. The plant with soil attached around the root was lifted carefully with both hands to ensure minimal damage to the rooting system. The foliage was cut back to a length of about 5 cm to prevent excess evaporation, and the plants were returned to the laboratory immediately where they were washed in running water to remove the soil. The main root was cut with a sharp cutter to a length of about 10 cm and the smaller roots were trimmed with scissors. Only those plants of an average size were selected for transplanting. Each was planted in a 5 litre black plastic pot containing a recycled University of California soil mixture. The planting rate was 1 plant per pot. A spoonful of slow-release compound granule fertilizer "Osmocote" containing 18% N, 4.8% P and 9.1% K, was spread onto the pot. The pot was then flooded with rain water and the plants were allowed to grow in the open under natural light and watered with rain water whenever necessary.

The young shoots were cut periodically to a height of about 10 cm. The pruning stimulated the rosetting of plant growth and caused the plant to produce vigorous, upright stems. During the warmer period of the year, the plants grew faster and were ready for use in insect cultures or in experiments about two months after transplanting.

To ensure that each plant was free of aphids before being used in the insect cultures or in experiments, it was fumigated. The fumigation took place in the shade in a cage measuring 200 x 90 cm (base) x 155 cm (height) and covered with clear plastic sheet. The lower surfaces of the cage frame rested on the floor and were lined with 20 mm thick plastic foam to provide a good seal. One "Shelltox Pest Strip" was hung on the wall inside the cage.

Fumigation lasted for 24 hours. Each plant was then left in the open for several hours to ensure that no chemical residue was left in the foliage. However, examination of the foliage for mummified aphids was still necessary before the plants could be used because a *Trioxys* larva or pupa inside an aphid mummy was unlikely to be killed by the fumigation.

2.2 Culture of *Therioaphis trifolii*

A stock culture maintained in an insectary provided a continous supply of insects for experiments. Such a culture is especially useful for studies throughout the year for an insect such as *Therioaphis trifolii* which is scarce in the field during winter, spring, and early summer in South Australia.

The culture was started by introducing several field-collected apterous adults of the SAA on a bouquet of excised lucerne stems in the laboratory. The adult aphids were allowed to produced progeny for 3 days and then removed. The leaves bearing the SAA nymphs were cut and transferred onto an aphid free potted "Hunter River" lucerne plant so as to provide a culture of the aphids that was free from disease and parasitism.

The rearing of aphids was based upon a modification of the technique described by Wilson *et al.* (1982). The aphids were reared in a cage measuring 45 x 45 cm (base) x 50 cm (height) which had a front and a top of clear plastic and other sides comprising fine voile. The bottom of the cage fitted over a metal tray and a strip of plastic foam 20 mm thick provided a seal between the cage frame and the tray. A potted lucerne plant which had been innoculated with nymphs of SAA as described above was placed inside the cage. The rearing was carried out in a 190 x 180 cm insectary cubicle under 14:10 h light-dark (L-D) photoperiod and at 24-26 ^{o}C. Lighting was provided by a bank of ten 65 watt flourescent tubes set 30 cm above the top of the cage, plus one 100 watt incandescent bulb. A humidifier was set to maintain 45-55% RH.

The foliage was cut as soon as the plants started to yellow and some aphids were transferred onto fresh potted plants for further continous rearing. The remainder were used for breeding the parasitoid, *Trioxys complanatus*. Finally, the used plants were flooded with water to wash the aphids off and then sprayed with insecticide "pyrethrum" to kill the remaining aphids before being used again.

This method of rearing provided an ample suply of aphids for stock and for parasitoid cultures as well as for experiments.

2.3 Culture of *Trioxys complanatus*

The rearing technique of *Trioxys* used was based on the technique employed by Wilson *et al.* (1982). Some modification, however, was made for a smaller scale of rearing.

The cage for rearing was the same as that used for rearing the aphids but the rearing took place in a growth cabinet measuring 105 x 60 cm (base) x 105 cm (height). The temperature of the cabinet was maintained at 23-27 ^{o}C and the relative humidity and photoperiod were kept at 45-55% and 14:10 h L-D respectively. Artificial lighting was provided by a bank of eight 40 watt cool white fluorescent tubes and five 100 watt incandescent bulbs. A built-in fan which provided a vertical down draught was always kept on. This air movement helped to prevent the humidity getting very high.

The culture was begun by placing one pot of lucerne in the cage and then innoculating it with several hundreds of SAA obtained from the aphid culture. The aphids were transferred onto the plants on a small piece of paper placed amongst the foliage. The aphids were allowed to settle down for 24 hours before 5 one-day old mated females of *Trioxys* were introduced into the cage. The *Trioxys* were obtained from field collected mummies. Honey solution was smeared on the sides of the cage for supplementary food of the adult parasitoids.

On the eighth day the foliage was cut off, placed in a tray and dried for 24 hours in the growth cabinet. The foliage was shaken gently to dislodge the live aphids which were then pooled and returned to fresh potted plants for continous rearing. The herbage, with many mummies attached, was placed in an emergence box. Adults of *Trioxys* usually started to emerge at day 12 after the initial *Trioxys* were introduced. The adults of *Trioxys* were removed every day as they emerged and were allowed to mate and fed on honey solution before being used for continous culture. This method of rearing provided an adequate number of parasitoids both for stock culture and experiments. Number of parasitoid produced could be manipulated, according to requirement, by providing different numbers of hosts.

The culture was renewed several times during the period of the project. Mummies of *Trioxys* were collected from the field in autumn (March-April) and adults that emerged were put in the same cage as insectary-reared individuals. These augmentations were done to minimize the loss of fitness (Boller 1972) or genetic decay (Mackauer 1972) of the species due to continous rearing in an artificial environment.

2.4 Preparation of stem cutting for laboratory experiment

One day before the start of an experiment (see sections 6.2 and 6.3) lucerne stems were obtained either from the field or from potted plants. The stems of 2-3 week old regrowth are desirable because they are quite hard and solid. Each stem was cut with a sharp surgical blade at its base and then the cut surface was immediately dipped into water in a 5-liter plastic bucket. Then in the laboratory each stem was cut again under water with a sharp surgical blade to minimize the occurrence of air bubbles which may have an effect on water imbibition by the excised stem. The leaves along 7 cm of the lower part of the stem were cut at the base of the petiole whereas the top part of the stem was cut to provive a stem length of about 15 to 20 cm depending on the experimental cage used (Figures 2.1 and 2.4). The foliage was examined for the presence of live or mummified aphids and any that were found were brushed off or destroyed.

Figure 2.

Types of experimental cages used in laboratory studies:

(1) Cage for experiments V and VI, measuring 25 x 25 cm (base) x 40 cm (height). In each cage there were 9 freshly lucerne stems placed in a 3 x 3 grid of 3-cm diameter holes in the floor of the cage;

(2) A typical excised lucerne stem used for experiments V and VI;

(3) and (4) cages used in experiments VIII and IX.

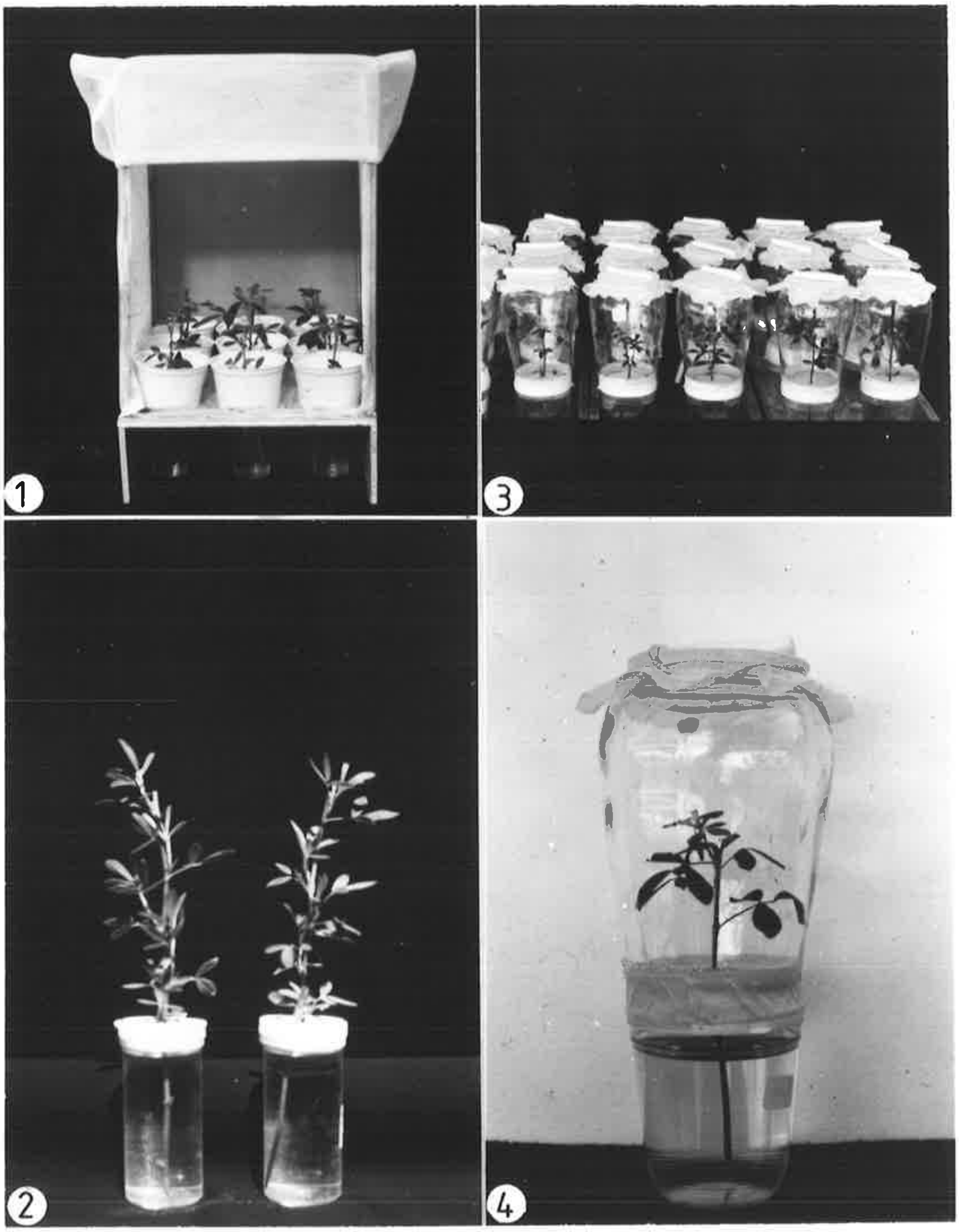


Fig. 2

Chapter 3

Seasonal Abundance

3.1 Introduction

To evaluate the impact of natural enemies, DeBach *et al.* (1976) suggest that population levels of both prey and natural enemies must be measured over a number of generations and on some common basis; and that information is further needed on the functional and numerical response of the enemies, on the degree of population fluctuations, on the economically acceptable level of the pest, on the capacity of the natural enemies to contain the pest population, and on the impact of other mortality factors. This chapter deals only with the seasonal abundance of SAA and its natural enemies in South Australia. The information about the interaction of the aphid and its natural enemies is given in Chapters 4 and 5.

The seasonal fluctuation of both the SAA and its natural enemies has been extensively observed elsewhere by many people (van den Bosch *et al.* 1959, Neuenschwander *et al.* 1975, Wilson *et al.* 1982), but detailed information was required on the size and fluctuation of local populations of SAA and the natural enemy complex under the conditions of this study. Such data are important not only for helping to evaluate the role of natural enemies but also for proper planning of future experiments to measure the degree of control exerted by natural enemies on the SAA population.

3.2 Methods

3.2.1 Study site and climatological data

Population data were obtained from a periodic field census of aphids and natural enemies which was conducted on a 1 ha lucerne field at the Waite Agricultural research Institute, Adelaide, over a two year period. The field was first sown on 26th May (autumn) 1980 with 30 kg of "Hunter River" lucerne seed per hectare plus 125 kg of 9% Phosphate fertilizer. The plants were first irrigated on 28 November, 1980 and the crop was mown on 4 December, 1980 and shut off to produce a seed crop. The first 10 samples of insects were consequently taken from this first year seed crop (rather than a hay crop) in the period 8 January - 17 March 1981 (Table Appendix 2.1). Then the crop was mown again on 18 March and from then on, for the rest of 1981 and the whole of 1982 it was treated as a hay crop. For this latter purpose the lucerne was lightly mown at approximately regular intervals and grazed only when necessary for weed control. The mowing was always done o~~f~~n 2 half-field strips with an interval of 1-2 weeks between the cutting of the first strip and the cutting of the second strip. This strip mowing was adopted to allow the aphids and their natural enemies to persist in the field.

Adelaide lies within a broad region of South Australia whose climate is similar to that of Mediterranean countries, the cape region of South Africa, Chilie and California (Trumble 1948, Webber *et al.* 1976) with 7.3 months "effective rainfall" and 17% of drought frequency (Trumble 1948); summers are hot and dry while winters are cool and wet. The "effective rainfall" is defined as the period of rainfall which exceeds one third of the evaporation from a 36-inch standard evaporimeter, and percentage drought frequency is defined as the number of years in a hundred in which the season of continously effective rainfall is less than five months (Trumble 1948).

Climatic data were obtained from a meteorological station at the Waite Institute which was about 1 km from the study field. These data are presented in Table 1. These data show that the mean daily air temperatures (1925-1981) for the hottest month (January) and for the coldest month (July) vary between 16.4 °C(min.)-27.9 °C(max.) and between 7.8 °C(min.)-14.2 °C(max.) respectively; and the mean monthly relative humidity at 9.00 a.m. varies between 49.0% in January and 75.8% in July.

The mean annual precipitation (1925-1981) is 626.4 mms. The seasonal rains usually start in April (autumn) and concluded in October (spring) and most of the rain falls during June-August (winter)(see Table 1).

In South Australia, lucerne is sown in autumn (April-May) and in spring (September-October). Sowing in April-May is generally preferred (Walker 1959) because plants will have grown more by summer and will enter the dry period in summer with deeper roots than those plants sown in spring and therefore have a higher chance to survive.

The main factor restricting the growth of pasture plant during summer is lack of moisture because during these months eveporation exceeded rainfall (Table 1). After the top soil has dried, growth can only continue if the root system is capable of exploiting subsoil moisture. Deep-rooted perenials such as lucerne and phalaris are usually tolerant to drought.

Table 1. Mean monthly rainfall, evaporation, relative humidity (9.00 a.m.) and average daily maximum, minimum and mean air temperatures (1925-1981) at the Waite Agricultural Research Institute (WARI). These data were obtained from the WARI Biennial Report, 1980-1981.

Month	Rainfall (mm)	Evaporation (mm) A Class Pan	Relative Humidity 0900 hrs.	Average Daily Air temperatures (^{o}C)		
				Max.	Min.	Mean
January	23.8	236.4	49.0	27.9	16.4	22.1
February	26.6	201.5	52.4	27.6	16.5	22.0
March	21.8	170.4	53.7	25.5	15.3	20.4
April	55.0	107.5	60.8	21.5	12.9	17.3
May	79.0	64.9	68.8	17.8	10.7	14.2
June	74.8	46.3	74.2	15.1	8.6	11.9
July	86.2	48.7	75.8	14.2	7.8	11.0
August	73.4	65.6	71.7	17.1	8.1	11.7
September	62.5	95.0	64.4	17.6	9.4	13.5
October	54.7	140.9	58.9	20.3	10.9	15.6
November	38.7	175.0	54.2	23.3	12.8	18.0
December	29.9	212.0	50.9	25.8	14.7	20.2

There was an extensive drought during the period of this study (Figure 3). The lucerne was, therefore, watered for 6 hours for each of 7 nights after mowing in summer.

3.2.2 Sampling Techniques

The terminology of sampling that will be used is that of Cochran (1963) . At approximately seven-day intervals, a sample was taken to estimate: (i) the mean number of live aphids on the plants [see (1) below], (ii) the mean number of predators [see (2) below].

At certain other times during the aphid season different samples were also taken to estimate : (iii) the aerial population of the aphids [see (3) below], (iv) the mean number of immature stage of parasitoids on plants [see (4a) below], (v) the mean number of adult parasitoids on plants [see (4b) below, and (vi) the mean number of active adult parasitoids within the field [see (4c) below]. Samples were not taken on days when rain fell or when the field was being mown or grazed.

(1) Number of Aphids on Plants

From January (summer) 1981 to October (spring) 1982, samples were taken to estimate the mean numbers of aphids on plants. The stem sampling method described by Walden *et al.* (1978) was employed for use in this study. The relative precision and efficiency of this sample to the standard suction sample was 0.98

Figure 3.

Weather data of the study site - showing the mean daily maximum and minimum air temperature (^{o}C), total monthly rainfall (mm) and evaporation (mm) for 1981 - 1982.

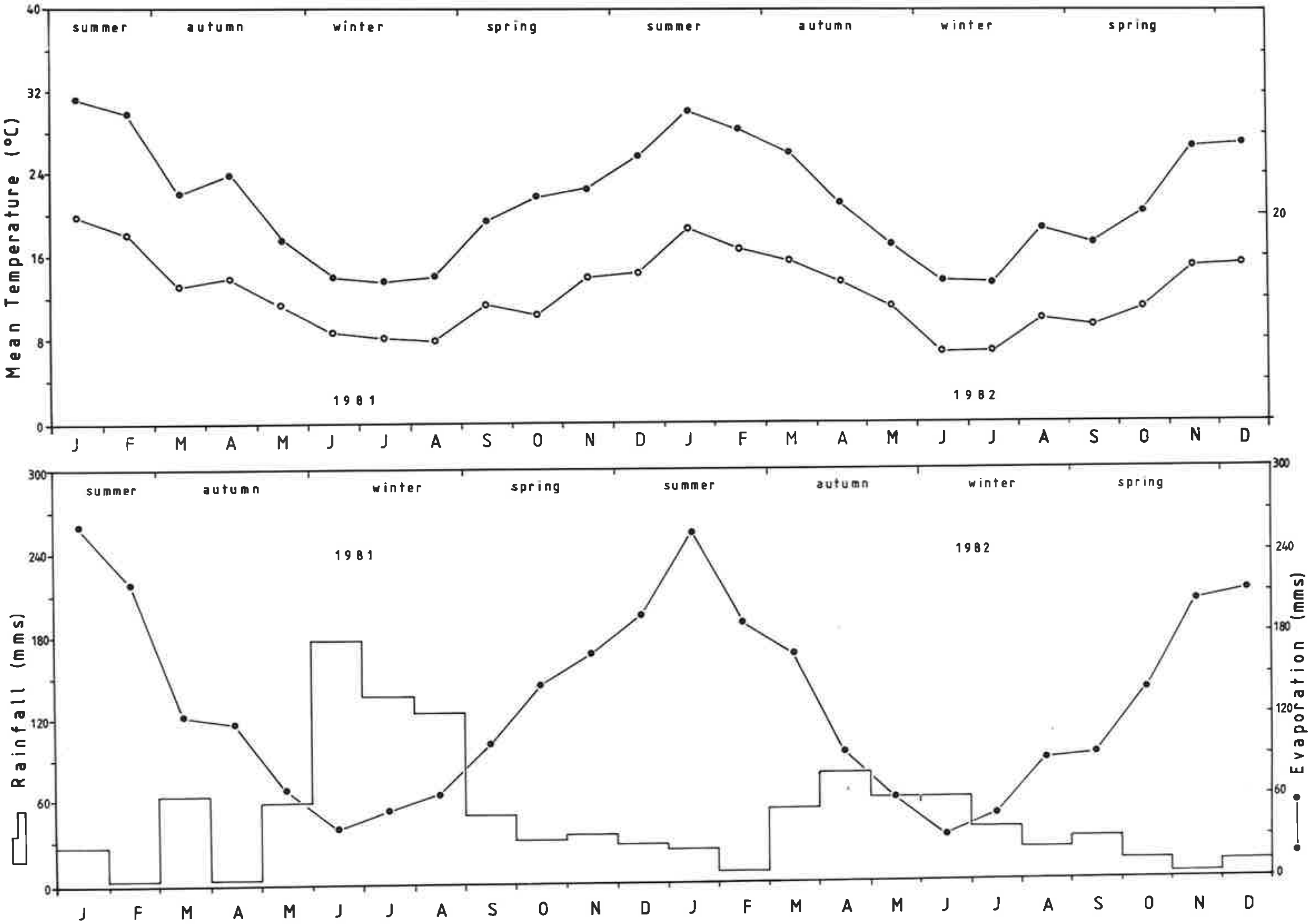

Mean Temperature (°C)
0
8
16
24
32
40
20
summer
autumn
winter
spring
summer
autumn
winter
spring
1981
1982
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
Rainfall (mms)
Evaporation (mms)
0
60
120
180
240
300

Fig. 3

and 85-88% respectively. Each sample comprised 30 randomly selected lucerne stems. To minimize aphids dropping from a stem that was sampled, each stem was sampled very carefully by cutting it off at base with sharp knife and putting it immediately into a 30 x 20 cm thick clear plastic bag. No stems were ever taken from a 5 m zone which was maintained around the field to reduce the edge effects.

Each sample was returned to the laboratory where aphids and mummies were removed by washing each stem and bag in water at about 70 °C. The water was then filtered through a series of gauzes of different mesh sizes. The coarse gauze separated the aphids from the debris and the fine gauze was fine enough to retain the first instar of SAA.

The aphids on the gauzes were then washed onto a counting tray marked with a grid, and the aphids from each sample stem were counted under a binocular microscope. If the number of aphids on a sample stem was greater than 500, a subsample was taken to reduce the time spent in counting. To take a subsample, all the aphids in a sample were spread out over a 7 cm petri dish in a minimum of alcohol. The disk was marked off in 8 equal sections. The aphids were then well stirred to get a distribution as even as possible over the petridish. Two sections of the dish were then chosen at random and the number of aphids in the resulting one quarter area of the dish was counted under a binocular microscope. This number was then multiplied by 4 to estimate the total number of aphids on the sample stem.

(2) Number of predators

At every sampling day the relative numbers of predators were estimated by taking a sample of 100 sweeps of a sweep net across half (0.5 ha) of the study field. The net had a diameter of 37.5 cm and each sweep was standardized as far as possible to sweep approximately 1.5 m of "row" of plants, always with the same type of sweeping action.

In practice, the 0.5 ha field was divided into 50 "plots" of 100 m^2 each. Ten of these plots were randomly chosen for sampling and in each one of them a subsample of 10 sweeps was taken and the resulting insects were inverted into a 45 x 30 cm clear plastic bag. In the laboratory the insects in the bag were then washed out with 70^oC water and rinsed through several sieves of decreasing mesh size to separate predators from the debris. The numbers of each species of predator were recorded for both young and adult stages.

(3) Number of Alate Aphids

From 15 August (winter) 1981 to 16 April (autumn) 1982, the aerial population of aphids was monitored by trapping them in 5 yellow water traps which were placed at permanent sites across the study field. Each trap was similar to that of Berg and Ridland (1978). It was held 80 cm above the ground in a metal ring which was attached to a steel post as in Figure 4.3.

Figure 4.

Types of traps used in this study:

(1) an electric suction trap (after Laughlin, et al 1978) for monitoring the field population of adult parasitoids;

(2) a "dark trap" measuring of 50 x 50 cm (base) x 75 cm (height) for monitoring the field population of adult parasitoids;

(3) a typical yellow water trap for trapping alate aphids;

(4) D-vac suction sampler used in experiment IV.

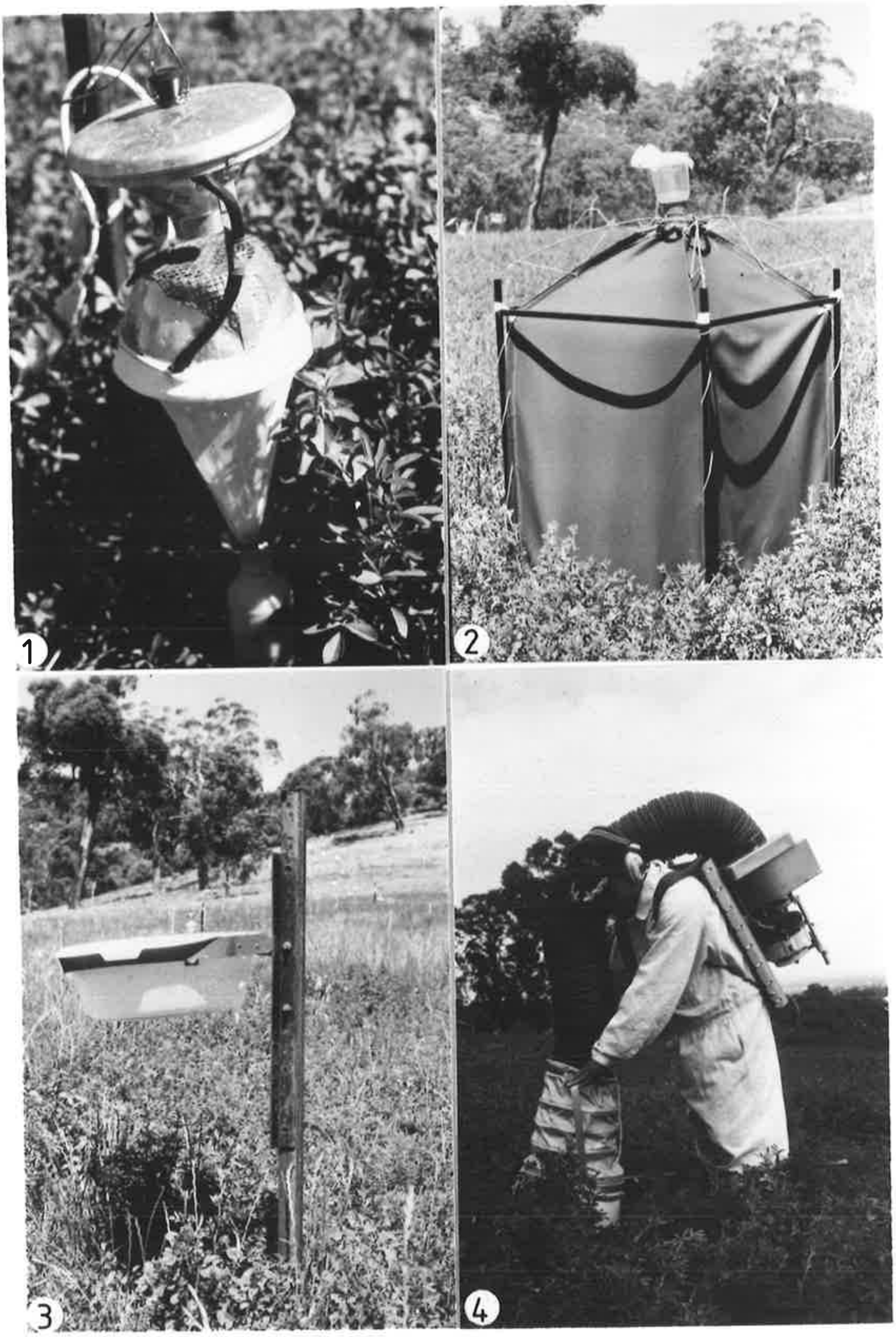


Fig. 4

The traps were serviced weekly. The caught insects were filtered through fine gauze material and the trap was cleaned and refilled with water plus a few drops of detergent to prevent fungal growth on the catches. The numbers of aphids and relevant insect species were recorded in the laboratory.

(4) Number of Primary and Secondary Parasitoids on Plants

The occurence of parasitoids on the plants is usually recorded as the percentage parasitization calculated as ratio of mummified aphids to live adult aphids in a sample (Hodek *et al.* 1972). According to van Emden (1963) this method involves the false assumption that adult aphids and mummies have equal persistence on plants.

More sensitive sampling methods for parasitoids involve the dissection of a certain number of aphids, or rearing aphids from the field on host plants in the laboratory and observing the number of aphids mummified. However such methods may not be accurate for estimating the number of searching adult parasitoids on the plants.

Most of the parasitoids of the SAA belong to the Order Hymenoptera. Their adult stage is highly mobile. A suction sampler or the "quick trap" of Turnbull and Nicholas (1966) are both ideal for collecting mobile insect parasitoids. On the other hand, form of leaf and stem sampling involves the risk of the adult parasitoids being disturbed and escaping.

In this study, three methods of parasitoid population sampling were employed to estimate (i) number of immature stage of parasitoids (in living or in mummified aphids) [see (4a) below], (ii) number of adult parasitoid on plants [see (4b) below], and (iii) number of active adult parasitoids within the crop [see (4c) below].

(4a) Number of Immature Stage of Parasitoids

The number of parasitized aphids which may either contain primary or secondary parasitoid species was estimated by sampling 30 stems taken at random adjacent to that of stems sampled for the aphid count [see 3.2.2 (1) above]. A separate sample was necessary because the method used to get the aphids off the stems for the aphids count is lethal to developing parasitoids.

Each stem sample was bulked into 3 groups of 10 stems each. Each group of stem was placed in a 5 litre plastic container whose top was covered with fine nylon gauze. The sample was then returned to the laboratory where all the aphids on the group of stems were transferred and reared on potted "Hunter River" lucerne plants growing on a 3-litre pot for 6 days. If the number of aphids was high they were divided into two or three subgroups and each of the subgroup was then reared separately on a 3-litre potted lucerne plant. It was expected that by day 6 the parasitized aphids on the sample were mummified. Any predator, parasitoid, and secondary parasitoid which may have been present in the sample was removed before putting the rearing "unit" into a nylon cage. The rearing took place under 14:10 h L-D photoperiod, at 22-24 °C and at 40-60% RH. Any parasitoid or secondary parasitoid which emerged before day 6 was caught in an aspirator and sexed. The number of each species which so emerged were recorded daily.

The stems and leaves bearing mummies were then transferred into plastic emergence box for a further 3-week observation period. Mummies that did not emerged were dissected to see whether they contained primary or secondary parasitoid species. The larva of *Trioxys* and of secondary parasitoids that died during rearing were not recorded.

(4b) Number of Adult Parasitoid on Plants

From 13 October (spring) 1981 to 16 April (autumn) 1982, the number of adult parasitoids and secondary parasitoids on the plants were estimated by trapping them with a "dark cage" trap as depicted in Figure 4.2. This trap had the same principle as that of the "quick trap" of Turnbull and Nocholls (1966). A preliminary test has been done to measure the temperature inside the cage during the first 2 hours of trapping. The result indicated that there was no obvious different between mean temperature inside the cage and that of outside. The trap was quickly placed over lucerne plants selected randomly. Any gap between the base of the trap and the ground was covered by sand bags to prevent trapped insects escaping. A 200 ml clear plastic container with a "lid" made of fine gauze was placed over the 3.5 cm "escape hole" at the top of the main portion of the trap. The container was removed after 2 hours trapping and returned to the laboratory. The caught insects were paralized by CO2 and killed in 70% alcohol, and their numbers were recorded according to the species and sexed. Three traps were employed across the study field and they were cleaned before being used especially from webs of spider.

(4c) Number of Active Adult Parasitoids within Field

From 13 October (spring) 1981 to 16 April (autumn) 1982, the within-field dispersal of primary and secondary parasitoids was monitored with three electric suction traps which were placed at permanent sites across the study field. Each trap was hung 40 cm above the ground on a steel post as shown in Figure 4.1. The trap was designed by Laughlin et al. (1978) originally for trapping mosquitoes. For the purpose of this study some modifications were made such as (i) the source of light was removed as this may attract some insects to the trap, (ii) the coarse net was replaced with a fine one, and (iii) the traps were run during day light only, from 6.00 a.m. to 6.00 p.m., because the primary as well as the secondary parasitoids of the SAA are diurnal species.

A plastic bottle, 5 cm diameter and 10 cm deep, was tied on the bottom of the net so the insects trapped would fall into the bottle. The bottle had two gauze covered 1 cm diameter overflow holes 7 cm above its base. The traps were serviced weekly. the bottle was removed and replaced with a clean one, filled with water plus few drops of detergent to prevent fungal growth on the caught insects. The number of primary and secondary parasitoids and other relevant insects trapped were recorded in the laboratory according to the species. The sexes of the parasitoids were also recorded.

3.3 Results and Discussion

In each of the subsequent sections I will first discuss the species involved and their relative abundance in the sample. The general evaluation of the aphid-natural enemy interactions which are based on these data will be discussed separately in Chapter 4. The parasitoids, secondary parasitoids, predators and the aphids observed on lucerne in the study field are listed in Appendix Table 1. Their numbers, especially of those associated with the SAA are presented in Appendix Table 2.

3.3.1 The Host Aphid and Natural Enemy Abundance

(1) The aphids on plants

There were 3 species of aphids observed, namely, the spotted alfalfa aphid (SAA) *Therioaphis trifolii* f. *maculata*, the blue green aphid (BGA) *Acyrthosiphon kondoi* Shinji and the pea aphid (PA) *A. pisum* (Harris). Their fluctuation in abundance throughout the study period is shown in Figure 5, in which the numbers of SAA and of (BGA+PA) per 30 stems are plotted against time of the year. Only the phenology of the SAA will be discussed in this section.

The mean number of SAA on 8 January 1981 when the study started was 34 aphids per stem. It reached a peak in March (213 SAA per stem)and again in April (413 SAA per stem) and decreased rapidly as the temperature got cooler thereafter. The plants were grazed on 9 June and no sample was taken until 10 July (winter) 1981. The numbers of SAA were very scarce and could not be detected in stem

Figure 5.

Seasonal abundance of the SAA (solid cirle) and BGA+PA (open circle) in a lucerne field at the Waite Institute during 1981-1982. The arrows mark the times at which the lucerne was mown.

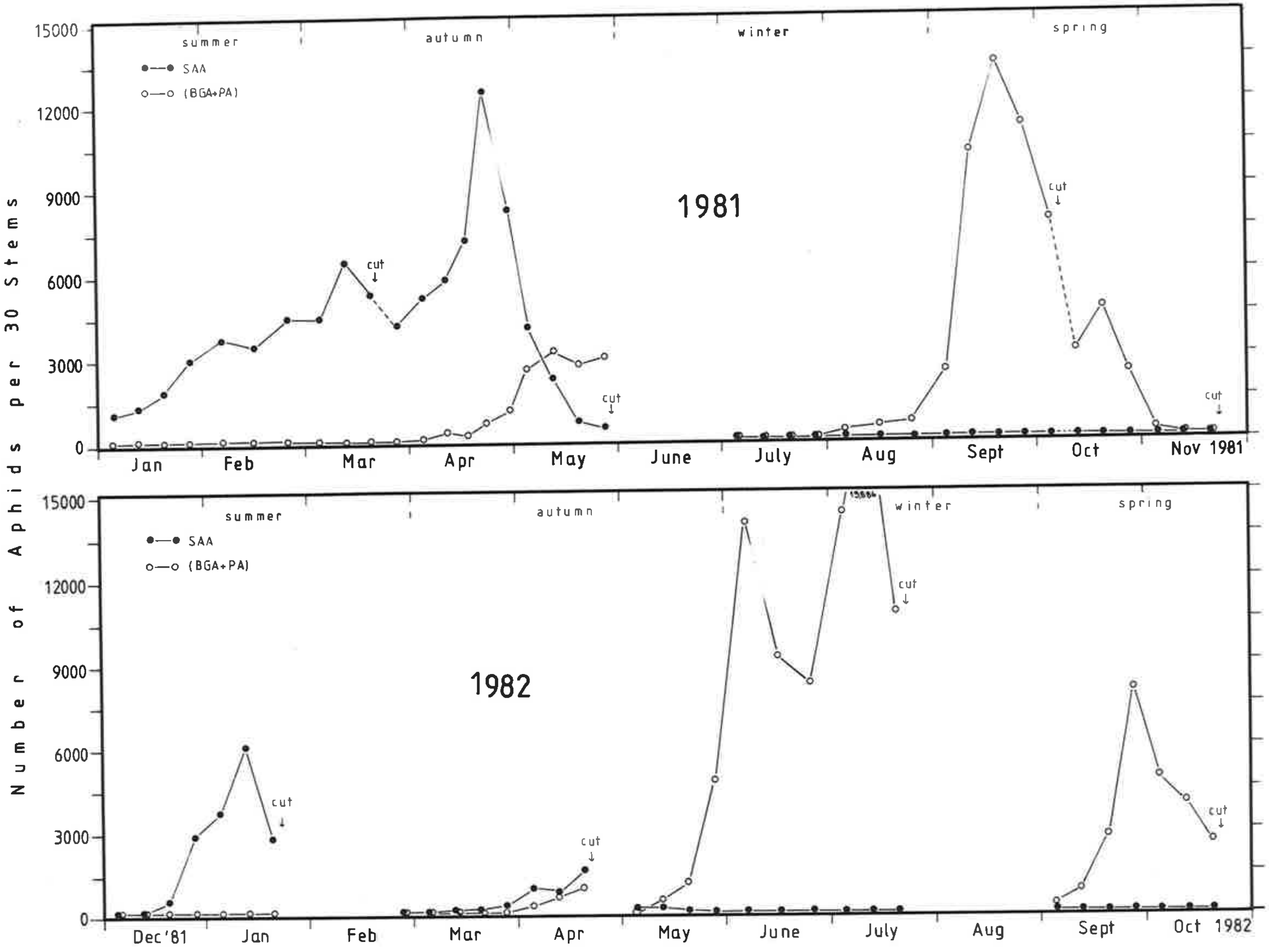

Number of Aphids per 30 Stems
15000
12000
9000
6000
3000
0
summer
autumn
winter
spring
●—● SAA
○—○ (BGA+PA)
1981
cut
cut
cut
cut
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov 1981
15000
12000
9000
6000
3000
0
summer
autumn
winter
spring
●—● SAA
○—○ (BGA+PA)
1982
15,884
cut
cut
cut
cut
Dec'81
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct 1982

Fig. 5

Figure 6.

Seasonal abundance of *Trioxys conplanatus* (solid circle) and its parasitoids (open circle): *Pachyneuron, Dendrocerus, Phaenoglyphis* and *Alloxista* in a lucerne field at the Waite Agriculture Research Institute during 1982-1982. The arrows mark the times at which the lucerne was mown.

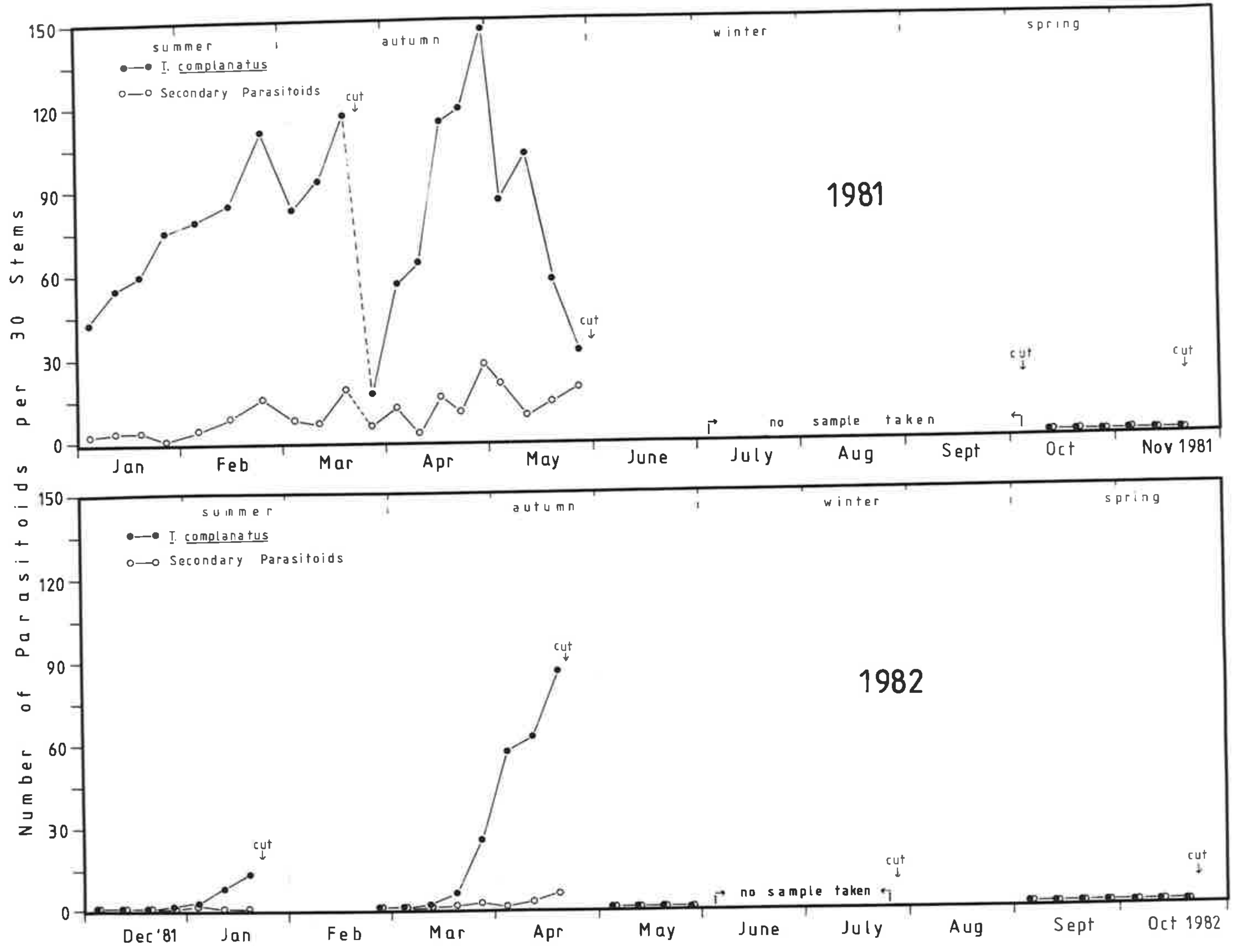

Number of Parasitoids per 30 Stems
150
120
90
60
30
0
summer
autumn
winter
spring
T. complanatus
Secondary Parasitoids
cut
cut
cut
cut
no sample taken
1981
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov 1981
150
120
90
60
30
0
summer
autumn
winter
spring
T. complanatus
Secondary Parasitoids
cut
cut
cut
cut
no sample taken
1982
Dec'81
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct 1982

Fig. 6

Figure 7.

Seasonal abundance of predators: *Coccinella repanda* (solid circle) and *Micromus tasmaniae* (open circle) in a lucerne field at the Waite Agricultural Research Institute during 1981-1982. The arrows mark the times at which the lucerne was mown.

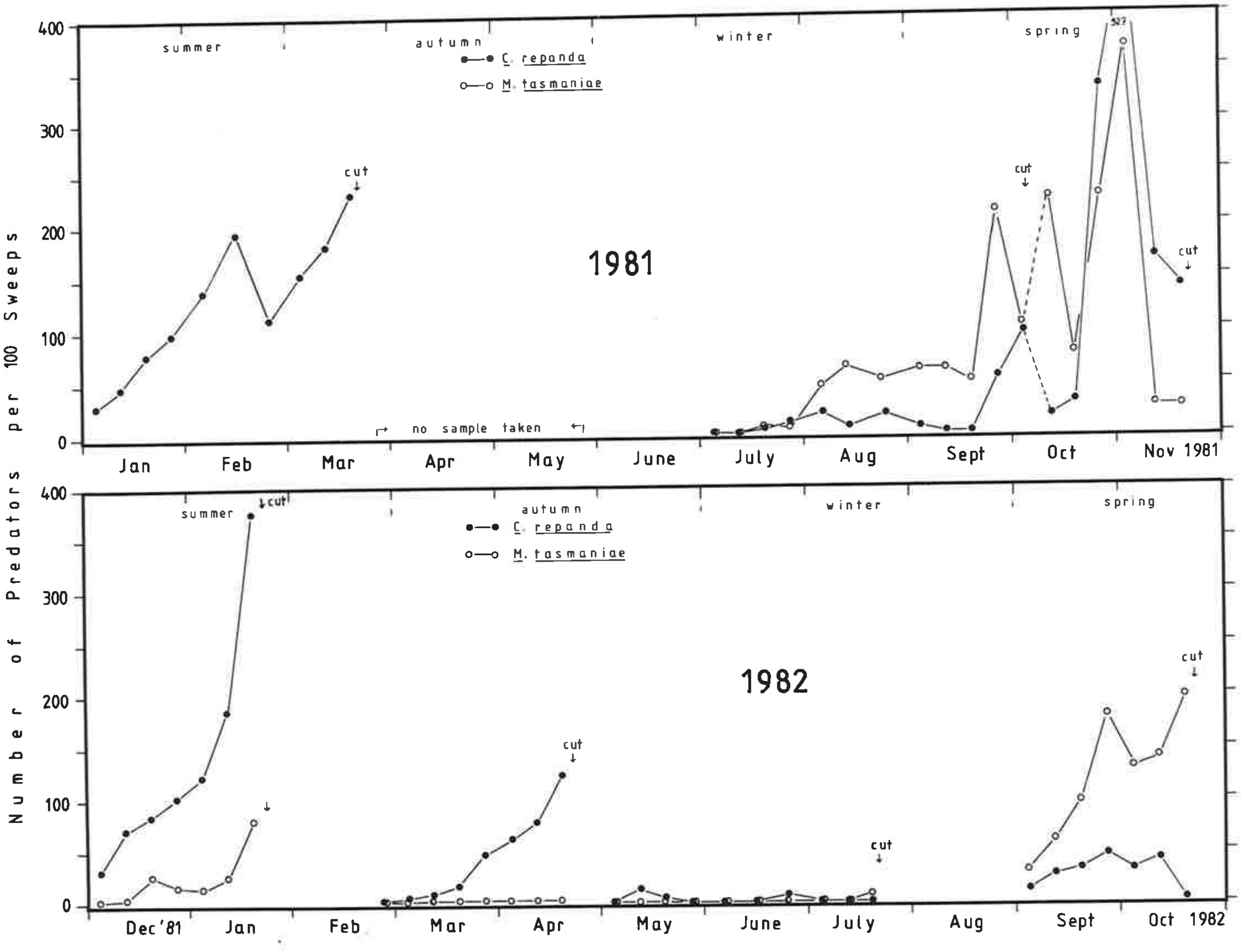

Number of Predators per 100 Sweeps
400
300
200
100
0
summer
autumn
winter
spring
●—● C. repanda
○—○ M. tasmaniae
1981
cut
cut
cut
527
no sample taken
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct
Nov 1981
1982
cut
cut
cut
Dec'81
Jan
Feb
Mar
Apr
May
June
July
Aug
Sept
Oct 1982

Fig. 7

samples until the middle of October (spring) when they fluctuated at low densities until the second week of December. Then the SAA numbers increased rapidly, reaching a peak of about 200 aphids per stem in the middle of January (summer) 1982. The plants were mown at the end of January but then the plants grew very slowly even though they were watered for 6 hours every night during the first week after mowing. The next sample was taken on 23 February and very few aphids were recorded. The autumn population then grew rapidly and reached a peak (53 SAA per stem) in April just before the plants were mown on 23 April 1982. Thereafter the numbers of SAA decreased, but a small peak (7 SAA per stem) occurred in May before the aphids gradually disappeared in winter again.

In general, the SAA numbers in January (summer) 1982 were approximately double those of summer 1981 but the autumn (April-May) 1982 numbers were much lower than those of autumn 1981.

The spring (September-October) population in 1982 started to develop at the beginning of October, about 2 weeks earlier than the 1981 populations. Very low numbers were observed. Their number increased to average 1 SAA per stem before the plants were cut at the end of October.

(2) The abundance of alates

The log numbers of winged aphids per trap and the log numbers of aphids per stem during the trapping period are plotted against time of the year in Figure 8. The first alate aphid of SAA trapped was in the middle of November 1981 which was about 3 weeks after the presence of SAA nymphs was detected in the stem samples (Figures 5 and 8). This indicates that the alates trapped were unlikely to be new emigrants. The next alate was caught at the end of December 4 weeks after the plants being cut. Number of SAA on the plants at that time was 19 aphids/stem. The trapped alates reached a peak in the middle of January 1982 which appeared to coincide with the peak of the SAA population on the plants. In March and April 1982, the numbers of alates trapped were much lower compared to that of January 1982, presumably because either the aphids were less crowded or the host plants were in better condition than in the period previously mentioned.

(3) The primary parasitoids

(3a) The abundance of species.

Three imported species of primary parasitoids of the SAA namely *Trioxys complanatus* , *Praon exsoletum* (Nees.), and *Aphelinus asychis* Walker were released in South Australia against the SAA (Woolcock 1978). At the time of the study *Trioxys* was the only parasitoid which had established (Wilson *et al.*1982) and it was the only parasitoid found attacking the SAA in the study field. Its identification was confirmed by Dr. Mary Carver, Division of Entomology, CSIRO Canberra.

Figure 8.

Number of alates of SAA (open circle) trapped in the yellow water traps and number of aphids per stem (solid cirle) at times of sampling during October 1981 to April 1982. Data shown in log scale.

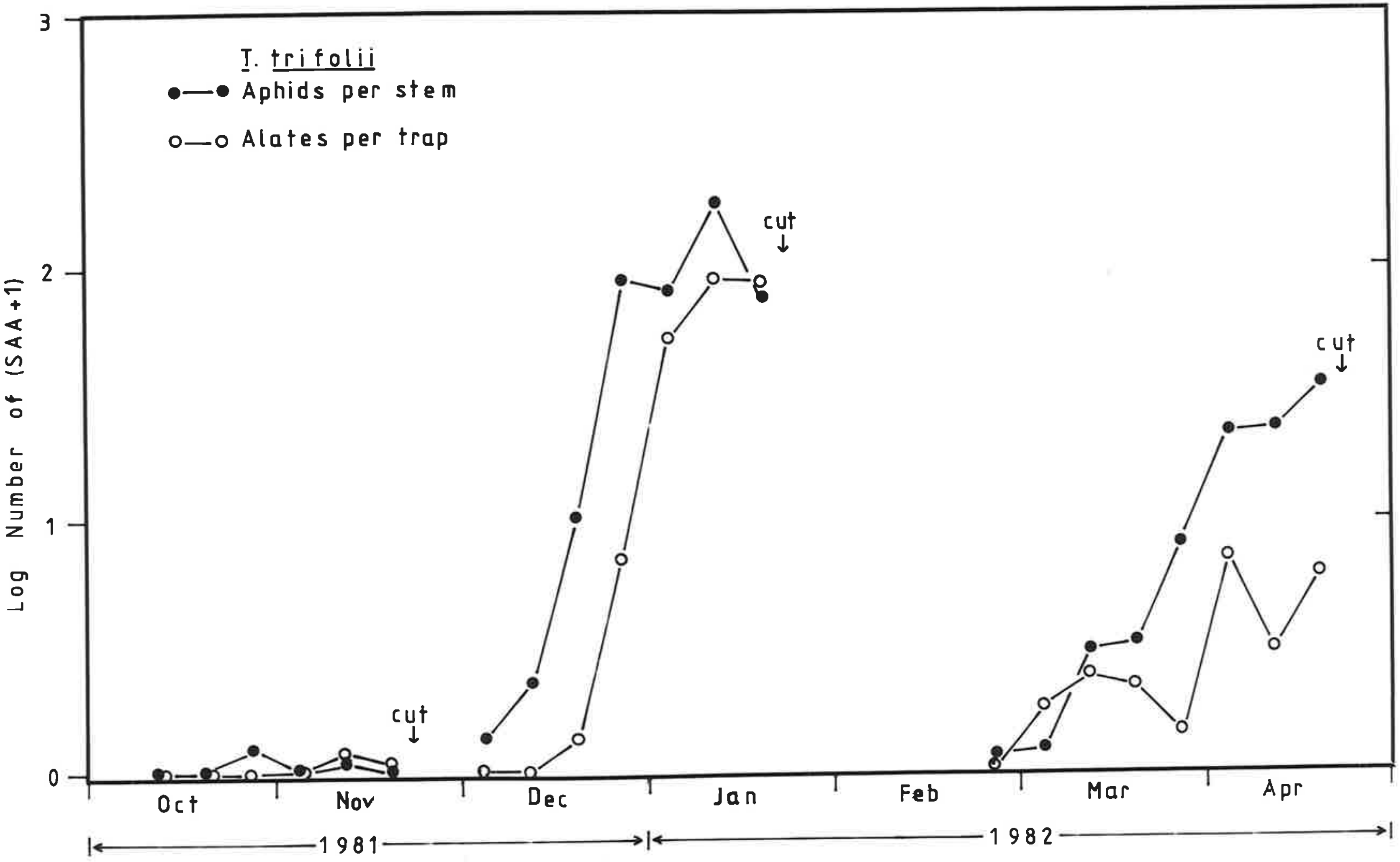

T. trifolii
●—● Aphids per stem
○—○ Alates per trap
Log Number of (SAA+1)
3
2
1
0
cut
cut
cut
Oct
Nov
Dec
Jan
Feb
Mar
Apr
1981
1982

Fig. 8

The mean numbers of *Trioxys* per 30 stems are plotted against time of the year in Figure 6. The number of *Trioxys* in the first week of January 1981 was about 42 parasitoids per 30 stems. It increased slowly, reached the peaks in February and March and again in April (149 parasitoids per 30 stems) before gradually decreasing thereafter, apparently in relation to the decline of the SAA. *Trioxys* adults were occasionally caught in sweepnet samples in winter (June-August) and spring (September-November) but parasitized SAA were never found in the stem samples during these times.

The summer 1981/1982 population started to develop at the end of December 1981. Its numbers remained low during the hot period in January to the middle of March 1982, ranging from only 0 to 14 *Trioxys* per 30 stems. *Trioxys* then began to increase and reached the peak of 85 parasitoids per 30 stems in the middle of April which seemed to be related to SAA population peak (Figure 5). In general, however, the *Trioxys* population in 1981 was much higher compared to that of 1982.

Similar trends were observed in the data for trapped adult parasitoids (see Figures 10(A) and 11(A)).

(3b) Parasitism

The percentage parasitism, expressed as the ratio of total *Trioxys* emerging from the stem sample for parasitoids [Subsection 3.2.2 (4a)] to the number of total adults SAA in the

Table 2. Percentage parasitism of SAA by *Trioxys complanatus*; expressed as the ratio of total *Trioxys* emerging from stem sample for parasitoids (column 5) (see Appendix Table 2 columns 8 + 9) to the number of total adults SAA in the stem sample for the aphids (columns 2+3+4); field survey data 8 January-17 March 1981 and 10 December 1981-16April 1982.

Date of sampling	Numbers of SAA/sample			Total	Total numbers of *Trioxys*	Parasitism (%)
	Adults		Mummies			
	Apterae	Alatae				
1	2	3	4	(2+3+4)	5	6
8/1	122	147	9	278	43	15.5
15/1	166	74	39	229	65	28.4
22/1	58	144	25	227	70	30.8
30/1	227	265	35	527	85	16.1
9/2	146	238	23	407	89	21.9
17/2	121	428	30	579	101	17.5
24/2	150	189	56	395	134	33.9
3/3	170	264	52	486	98	20.2
10/3	343	178	64	585	107	18.3
17/3	245	284	57	586	144	24.6
10/12	2	0	0	2	0	0
17/12	7	0	0	7	0	0
24/12	33	3	0	36	0	0
31/12	69	200	0	269	1	0.4
7/1	106	258	1	365	4	1.1
14/1	205	518	1	724	13	1.8
21/1	258	565	10	823	15	1.8
23/2	0	1	0	1	0	0
2/3	2	0	0	2	0	0
10/3	8	1	2	11	2	18.2
17/3	12	1	3	16	7	43.8
24/3	34	19	9	62	27	43.6
1/4	30	9	40	79	58	73.4
9/4	32	16	47	95	63	66.3
16/4	47	45	55	147	90	61.2

stem sample for the aphids [Section 3.2.2(1)], is presented in Table 2. The degree of parasitization by *Trioxys* during January-February 1981 ranged from 15% to 34 %, but in approximately the same period in 1982 the percentage of parasitism was less than 2%. The percentage parasitism began to increase in the middle of March, 1982 and reached a peak of 66-73% in April 1982.

(3c) Sex ratio

Sex ratio of *Trioxys* was estimated from different methods of sampling: (i) stem samples , (ii) dark and suction traps [see 3.2.2 (4) above]. The proportions of male *Trioxys* that emerged from stem samples (Appendix Table 3) are plotted against dates of sampling in Figures 9.1 and 9.2. The males of *Trioxys* were predominant than females on every sampling occasion from January to May 1981 (Figure 9.1) with the percentage of males ranging from 52 to 81% . There was no clear peak in January-March but there was an ovious peak in April-May. In January 1982 (Figure 9.2), when the number of *Trioxys* was low, females became dominant but as soon as the number of parasitoids increased in April, the number of males exceeded the number of females. As has been mentioned in Section 3.3.1(3a) above, similar trends in *Trioxys* number of stem samples and those of trapped were observed (see Figures 9.1A, 9.2A 10A and 11A; Appendix Table 4). However, when the number of parasitoids caught was high, the proportion of males was much higher compared to that emerging from stem samples (see Figures 9.1B, 9.2B, 10B and 11B).

Figure 9.1.

Numbers of *Trioxys complanatus* emerging from each stem sample (A), and the sex-ratio of *T. complanatus* within each sample (B) during January to May 1981.

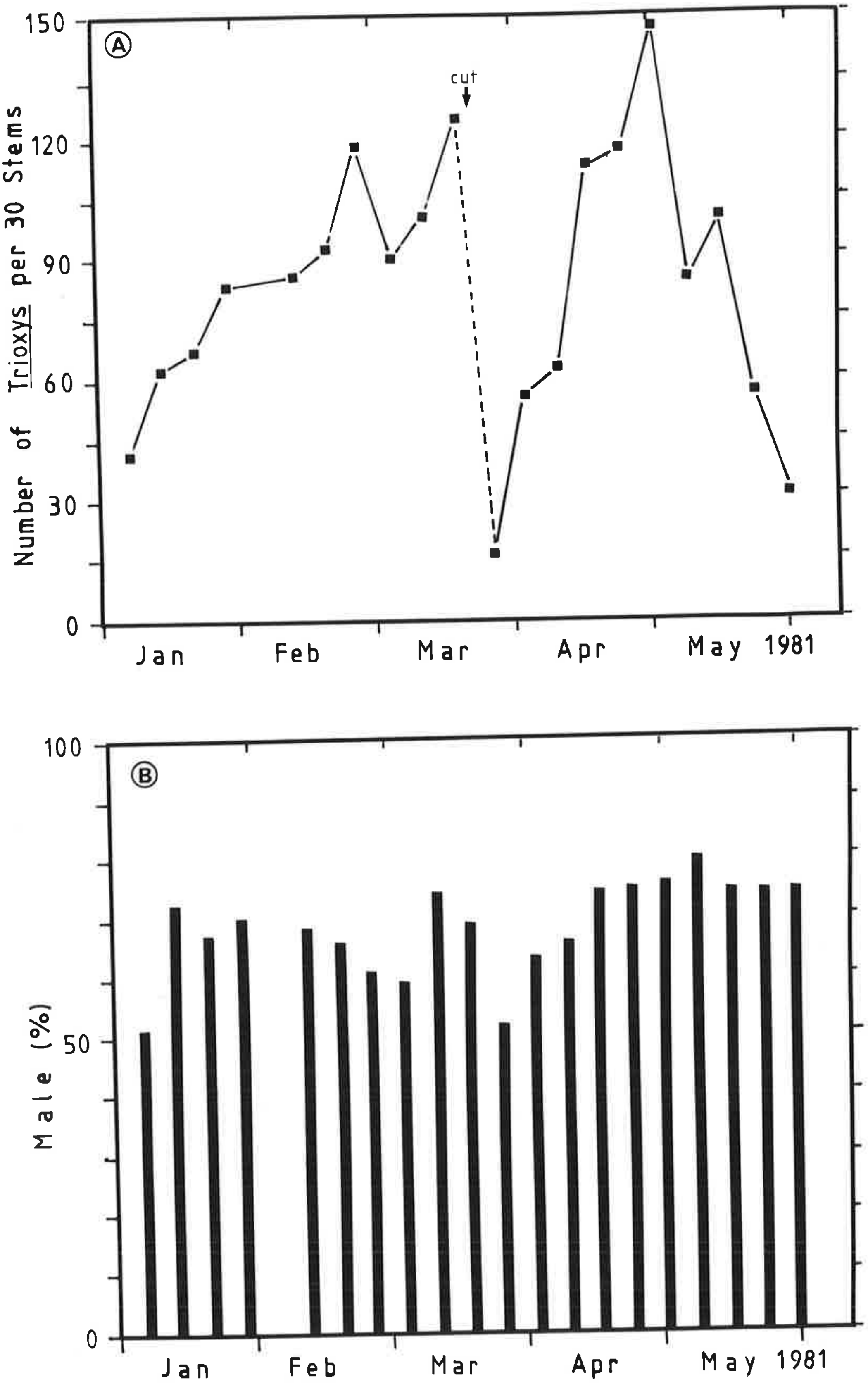

Ⓐ
150
120
90
60
30
0
Number of Trioxys per 30 Stems
cut
Jan
Feb
Mar
Apr
May 1981
Ⓑ
100
50
0
Male (%)
Jan
Feb
Mar
Apr
May 1981

Fig. 9.1

Figure 9.2.

Numbers of *Trioxys complanatus* emerging from each stem sample (A), and the sex-ratio of *T. complanatus* within each sample (B) during January to April 1982.

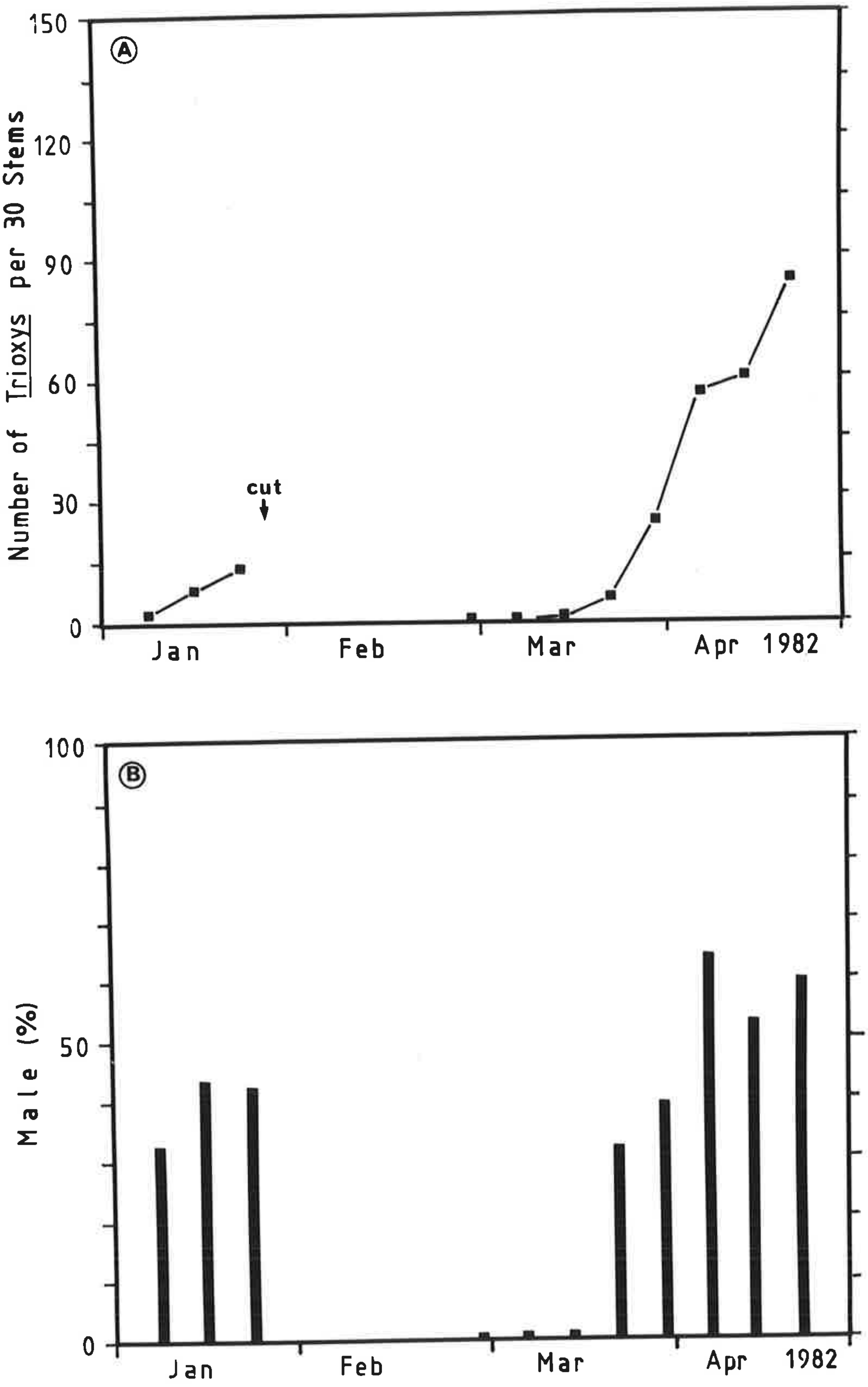
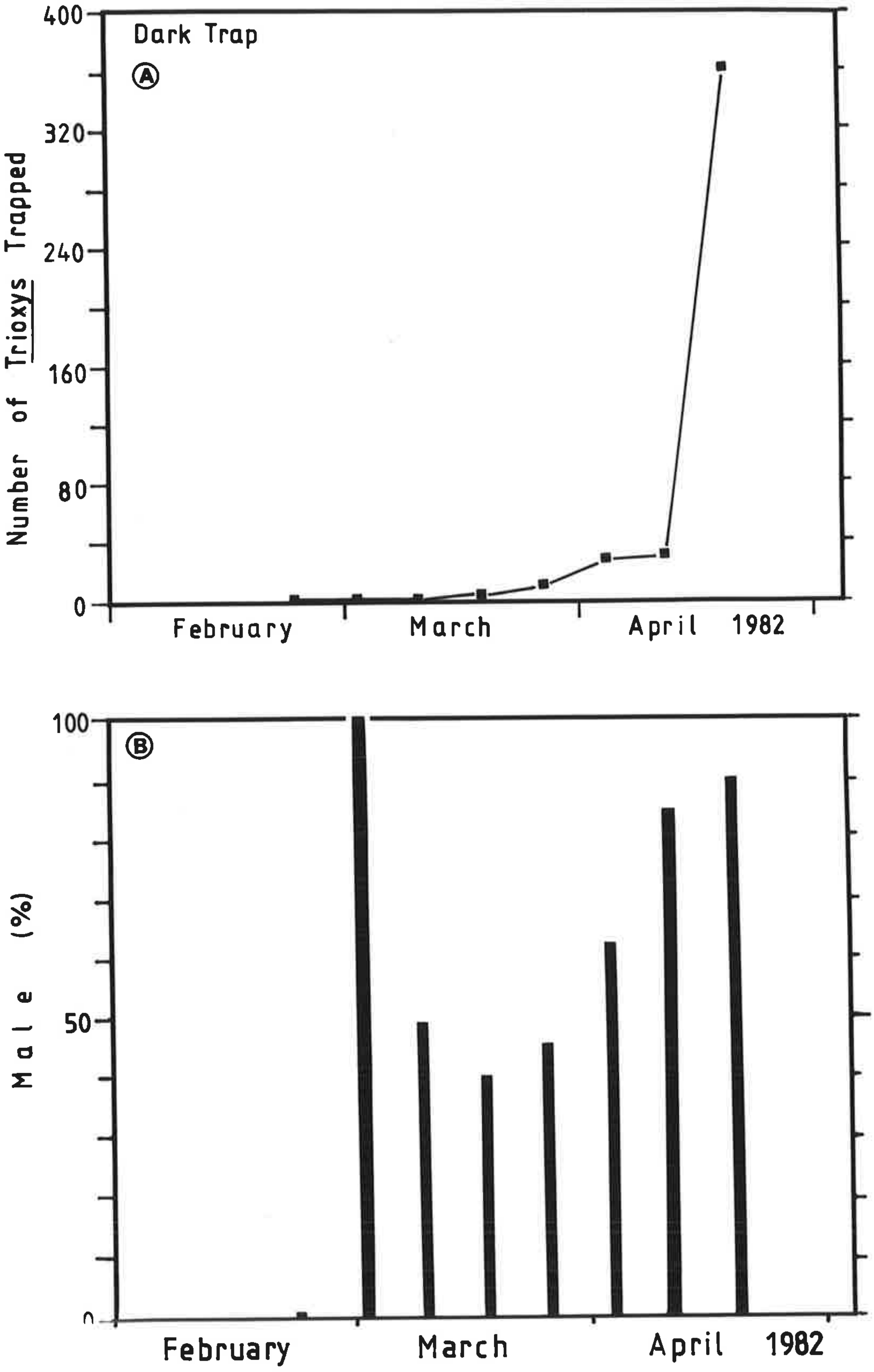

Ⓐ
150
120
90
60
30
0
Number of Trioxys per 30 Stems
cut
Jan
Feb
Mar
Apr 1982
Ⓑ
100
50
0
Male (%)
Jan
Feb
Mar
Apr 1982

Fig. 9.2

Figure 10.

Numbers of *Trioxys complanatus* trapped in "dark traps" at each sampling date (A), and the sex-ratio of *T. complanatus* within each sampling date (B) during February to April 1982.

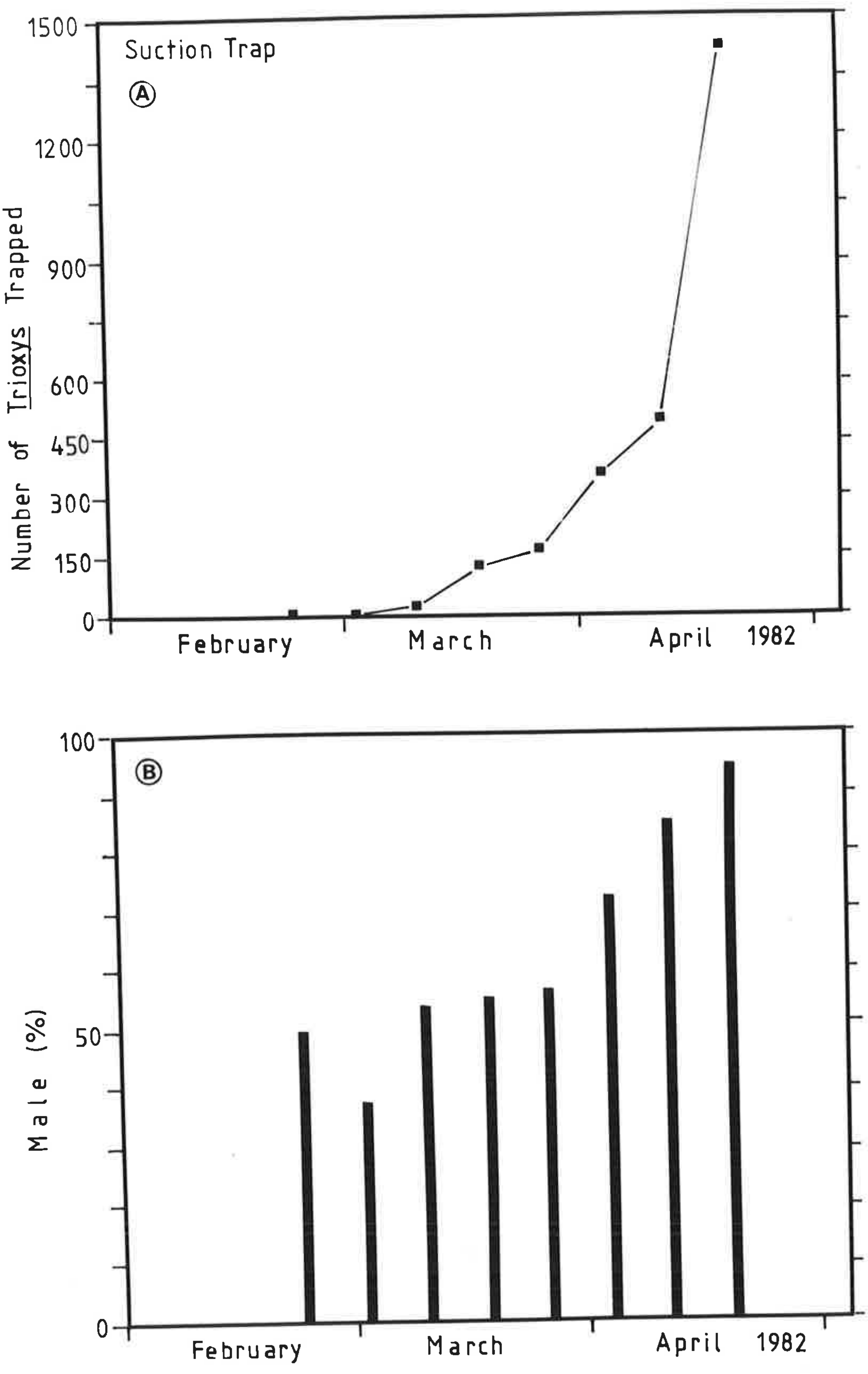


Dark Trap
Ⓐ
400
320
240
160
80
0
Number of Trioxys Trapped
February
March
April 1982
Ⓑ
100
50
0
Male (%)
February
March
April 1982

Fig. 10

Figure 11.

Numbers of *Trioxys complanatus* trapped in "suction traps" at each sampling date (A), and the sex-ratio of *T. complanatus* within each sampling date (B) during February to April 1982.



Suction Trap
A
1500
1200
900
600
450
300
150
0
Number of Trioxys Trapped
February
March
April
1982
B
100
50
0
Male (%)
February
March
April
1982

Fig. 11

The indication that the sex ratio of *Trioxys* was influenced by its own density will be discussed in Chapter 6.

(4) Secondary parasitoids

(4a) The species composition

The secondary parasitoids found attacking *Trioxys* mummies in the study plot were *Dendrocerus* spp. (Ceraphronidae), *Pachyneuron* sp. (Pteromalidae), *Alloxista* sp. and *Phaenoglyphis* sp. (Cynipidae). Their identification was confirmed by Dr. I. Naumann, Division of Entomology, CSIRO Canberra. The species present were similar to those found by Wilson *et al.* (1982). The numbers of each species which emerged from the field mummy collection on each sampling date are given in Table 3.1. In Table 3.1 are also given (i) the total number of each species and (ii) on the last line , the "species composition", expressed as the proportion x 100 of the total of each species to the total all species. The "species composition" of the parasitoids from stem samples is given in Table 3.2

The data show that *Pachyneuron* was the most abundant species and comprised about 70% and 56% respectively of the total number of field mummy collection and of stem samples. The second most abundant species emerging from the stem samples was *Dendrocerus*, followed by *Phaenoglyphis* and *Alloxista* (Table 3.2). However, the mummy collection data has indicated that *Dendrocerus* was the least abundant among the four species (Table 3.1). One possible explanation of this phenomenon is as follows. The endo-parasitoids

Table 3.1. Species composition of secondary parasitoids emerging from mummy collected from 31 December 1981 to 16 April 1982.

Date of sampling	Number of mummies	*Trioxys* ♀	♂	total	Secondary parasitoids *Pachy.*	*Dendr.*	others	total
31/12	4	2	2	4	0	0	0	0
7/1	13	5	4	9	4	0	0	4
14/1	18	7	5	12	5	1	0	6
21/1	10	2	4	6	4	0	0	4
23/2	8	5	3	8	0	0	0	0
2/3	14	6	7	13	1	0	0	1
10/3	19	10	7	17	2	0	0	2
17/3	27	18	8	26	1	0	0	1
24/3	53	31	15	46	4	0	3	7
1/4	104	61	32	93	6	0	5	11
9/4	98	38	31	69	24	0	5	29
16/4	95	33	48	81	4	2	8	14
Total	463	218	166	384	55 (69.6%)	3 (3.8%)	21 (26.6%)	79

Table 3.2. Species composition of secondary parasitoids emerging from 30-stem samples.

	1981*		1982**	
Secondary parasitoids	Total number of each species	%of total of all species	Total number of each species	%of total of all species
Pachyneuron sp.	118	58.7	10	55.6
Dendrocerus sp.	75	37.3	6	33.3
Phaenoglyphis sp.+ *Alloxista* sp.	8	4.0	2	11.1
Total of all species	201		18	

* obtained from 20 sampling occasions from 8 January to 28 May 1981.

** obtained from 11 sampling occasions from 7 January to 16 April 1982.

such as *Phaenoglyphis* and *Alloxista*, oviposit in the larva of *Trioxys* when the aphid is still alive, while the ecto-parasitoids such as *Dendrocerus* and *Pachyneuron*, oviposit on the late instar larva or pupa of *Trioxys* when the aphid has been mummified (Schlinger and Hall 1959). By removing mummies from the field, (in the mummy field collection), the ecto-parasitic *Dendrocerus* may have a smaller chance attacking the mummies of *Trioxys* compared to that of the endo-parasitic, *Alloxista* and *Phaenoglyphis*. Another possibility is that relatively more endo-parasitoids died during the rearing of parasitized aphids in the stem samples.

Data of *Trioxys* mummy collection in autumn 1983 revealed a different result. Of 266 mummies collected on 8 May 1983, 90 did not yield parasitoids. Most of the mummies seemed to have a much thicker and darker cocoon compared to those mummies collected in summer and in early autumn. Similarly, Schlinger and Hall (1961) found that mummies containing parasitoids in aestival diapause were contructed with tougher, thicker walls than those with parasitoids not in diapause. However, dissection of the 90 mummies 4 weeks after the date of collection revealed dead larvae rather than dead pupal or adult parasitoids.

Of the other 126 mummies from which parasitoids emerged 30% were *Trioxys*, 67% were *Dendrocerus* and 3% were *Phaenoglyphis* plus *Alloxista*. No *Pachyneron* was found. This species composition is not understood. It is possible, that as the season advances, the species composition is shifted towards *Dendrocerus* because, compared to the other species of secondary parasitoids, *Dendrocerus* has a stronger preference for SAA (Mary Carver, pers. Comm.) and SAA is usually more abundant during autumn (see Figure 5).

(4b) The abundance of species

The numbers of primary and secondary parasitoids emerging from stem samples are plotted against the time of the year in Figure 6. Low numbers of secondary parasitoids were observed during January 1981. Their numbers increased slightly at the end of February (summer) and reached a peak (19 parasitoids per 30 stems) in the middle of March which appeared to coincide with the peak of *Trioxys* on the plants. In autumn 1981 their number fluctuated between a minimum of 4 to a maximum of 28 per 30 stems with a peak at the end of April. Secondary parasitoids persisted in the study field in winter and spring attacking mummies of *Aphidius* sp., a parasitoid of BGA and PA. In November (spring) 1981 adults of secondary parasitoids were trapped either in "suction traps" or in "dark traps", which was about 2 months before they were detected by stem samples (see Appendix Table 5).

In general, the numbers of secondary parasitoids in 1982 were lower compared to those in 1981, presumably because there were relatively fewer *Trioxys* in 1982.

(4c) Secondary parasitism

The percentage of secondary parasitism, expressed as the proportion X 100 of the number of secondary parasitoids to the total

Figure 12.

Percentage of secondary parasitism between January and May in 1981 (A) and 1982 (B). The values are derived as the proportion x 100 of number of secondary parasitoids to the total parasitoids (primary and secondary) that emerged from the stem samples. The arrows mark the time at which the lucerne was mown.

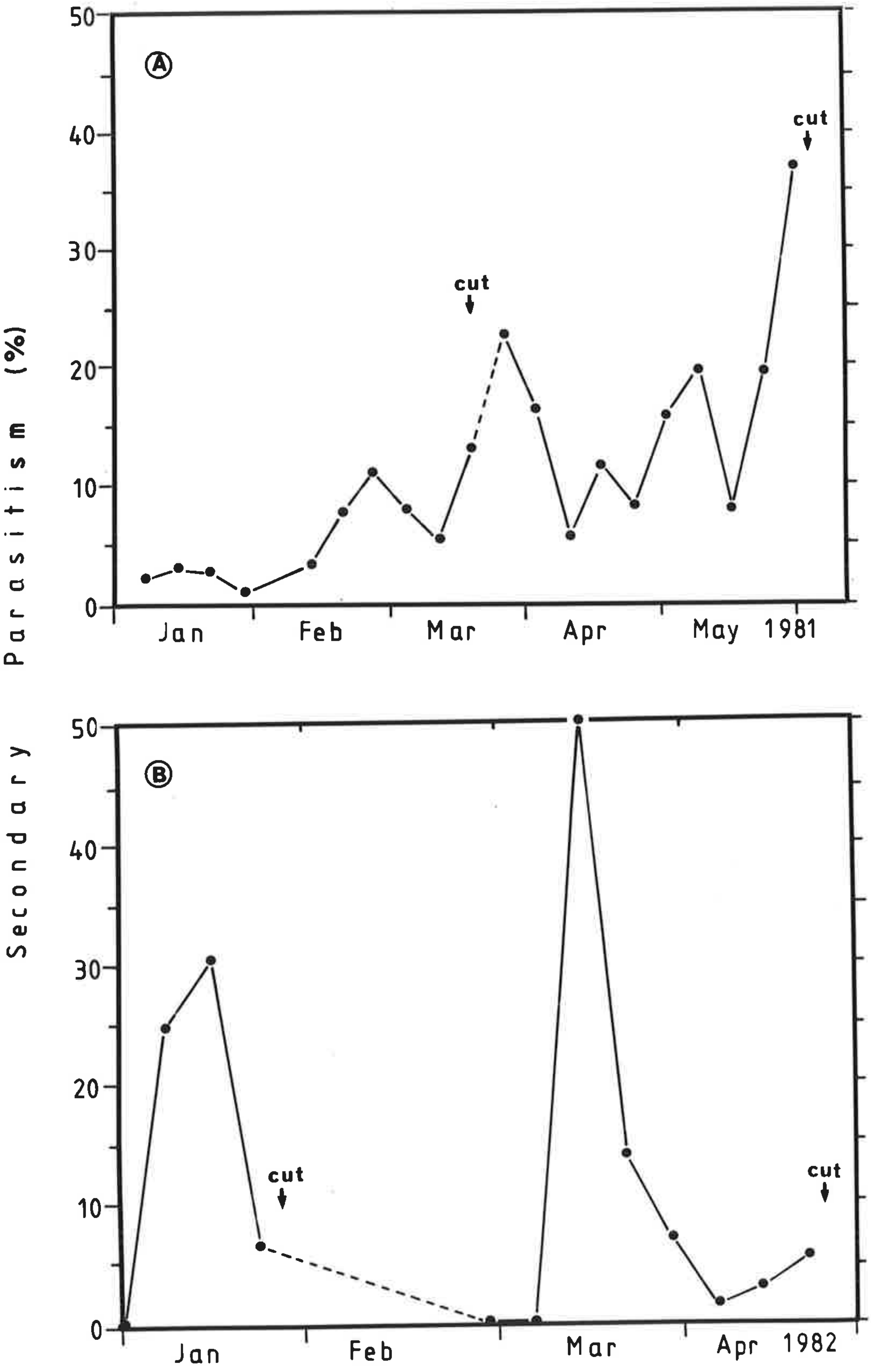

Secondary Parasitism (%)
Ⓐ
50
40
30
20
10
0
cut
cut
Jan
Feb
Mar
Apr
May
1981
Ⓑ
50
40
30
20
10
0
cut
cut
Jan
Feb
Mar
Apr
1982

Fig. 12

number of secondary parasitoids plus *Trioxys* that emerged from the stem samples is presented graphically in Figure 12. The mean percentage of secondary parasitism was 10.8% (1.2 to 37.3%) and 6.5% (0 to 50%) respectively for 1981 and 1982 observations. The dotted line in Figures 12B representing that there was no observation between 21 January and 23 February 1982 as has been mentioned above in Subsection 3.3.1(1).

(5) Predators

The common predators found attacking aphids in the study field were *Coccinella repanda* Thunberg (Coccinelidae) and *Micromus tasmaniae* (Walker)(Hemerobidae). These species of predators are predacious in both the adult and the larval stages. Other predator species which were occasionally abundant for short periods were the syrphids *Melangyna viriceps* (Macquart) and *Simosyrphus grandicornis* (Macquart), and the chrysopid, *Chrysòpa signata* Schnieder. Spiders were found almost the year around but their numbers were low and they were presumed to have a negligible impact on the population of aphids. The other coccinellid predator which is common in South Australia, namely *Leis conformis* (Boisd.) (Coccinellidae) was rarely observed. It is usually found feeding on aphids of trees and shrubs (Maelzer 1978). From now on, therefore, only *C. repanda* and *M. tasmaniae* will be discussed further. Their numbers are plotted against time of the year in Figure 7.

(5a) *Coccinella repanda*

Figure 7 indicates that in 1981 *C. repanda* was abundant in March (early autumn). Its numbers were low during early winter (June) when the prey population was quite abundant. However, its numbers slightly increased during September (spring) and reached a peak (96 larvae per 100 sweeps) at the beginning of October, about a 2 week time lag after the population peak of the aphids. Most of the *Coccinella* population at that time consisted of larvae (Appendix Table 2.3). Those larvae of *Coccinella* probably did not starve in the lucerne crop when the plants were mown lightly in October because there was still quite a high number of prey remaining (Figure 5). Samples taken at about 10 days after cutting revealed that larvae of *Coccinella* were still found on the lucerne. The numbers of *C. repanda* then increased very rapidly in October and reached a peak (927 adults plus larvae per 100 sweeps) at the beginning of November which seemed to be related to the collapse of the population of the aphids, BGA and PA. Even though these aphids became scarce, a relatively large number of *C. repanda* adults were observed in the field until the middle of November 1981 (2 weeks after the peak). These adult *Coccinella* are likely to have emerged from pupae in the field.

A similar trend in *Coccinella* numbers was observed in the summer 1981-1982 (i.e. December 1981-January 1982). No larvae were found for the first few weeks in December, and when the adult population increased thereafter it seemed to have an obvious relation to the decrease in the SAA population. *Coccinella* numbers reached a peak (372 adults plus larvae per 100 sweeps) in the third week of January, which was about one week after the peak of the SAA population.

The autumn 1982 population was low and comprised adults only. As in winter 1981, very low *Coccinella* numbers were observed in winter 1982 even though prey was abundant. The number increased slightly in spring and reached a peak on 24 September wich appeared to coincide with the peak of aphid numbers. In comparison, however, the peak number of *Coccinella* in 1982 was lower than that of 1981.

(5b) *Micromus tasmaniae*

Micromus was first sampled in July (winter) 1981 when its numbers were low (Figure 7) and comprised adults only (Appendix Table 2.3). Its numbers increased faster than those of *C. repanda* and reached a small peak (60 adults/100 sweeps) in the middle of August 1981. For several weeks then, its number did not increase further even though BGA and PA were abundant (Figure 5); probably because it was still winter and mean daily temperatures were too low (Figure 3.1). Only after daily temperatures had increased and after the aphid population had reached a peak in mid-September, did *Micromus* increase substantially; and both larval and adult stages were observed then. Relatively high numbers of adults of *Micromus* were observed in October, preying on the abundant BGA and PA. Peak numbers of the species were reached at the same time as those of

C. repanda namely, at the beginning of November, which was about two weeks behind the peak of aphid populations.

Following peak numbers in spring, most aphid species are scarce over the long hot and dry Australian summer and aphid predators are usually scarce then (Maelzer 1981). So, too, in this study, *Micromus* -especially larvae- were scarce in the summer 1981-1982. But low numbers of adults were found until a small peak was reached in the 3rd week of January 1982. Then, after the lucerne crop was mown, and the numbers of SAA had dropped markedly (Figure 5). *Micromus* then practically disappeared from the study field. It could not be detected in sweep net samples until the middle of July (winter) 1982 when 5 adults were caught. The lucerne plants were then cut and grazed in August, so no further samples were taken during August. However, *Micromus* was again fairly common in September-October 1982 and, as in the previous spring, both adult and larval stages were found. Peak number observed in September and October which seemed to be related to the drop of the aphids numbers.

Chapter 4

Host-Natural Enemies Associations

4.1 Introduction

This chapter discusses the interactions between *Trioxys* and SAA and between predators and aphids (SAA, BGA+PA) that may be inferred from the field survey data described in Chapter 3. The purpose is to examine the general magnitude of host- or prey-natural enemy interactions rather than to estimate it precisely from the field data. The host-natural enemy interaction in the field is too complicated to allow precise analysis in this type of study, but a general evaluation of trends in number will at least provide an indication of the sort of follow-up experiments that can be done to shed more light on the more precise form of the association.

It seems to be generally agreed that the effective species of natural enemies affecting an insect population are likely to be those that show density-dependent responses (DeBach and Smith 1941a, DeBach *et al.* 1976, Morris *et al.* 1958). Such a response can take either one or both of two forms, namely (i) the population density of natural enemies may change as a result of changes in host (or prey) density; this is the so called "numerical" response of Solomon (1949) and (ii) the population density of the host (or prey) may change because of a differential attack rate of the natural enemies (Hassell 1978, Holling 1961, Morris *et al.* 1958).

Hassell (1966) suggests that the responses of parasitoids or predators to their host or prey densities should be considered in term of change in the percentage parasitism or predation. In the field, however, the direct recording of percentage parasitism or of predation of aphids on plants is not easy. Parasitism is probably easier to record than predation but even for parasitism, each of the common methods of assessment described in Section 3.2.2(4) involves false assumptions and is hence subject to bias. Therefore, in this section, the responses of parasitoids and predators to changing host densities is expressed in terms of changes in the density of enemies as the numbers of hosts rise or fall (Solomon 1949, Holling 1959, 1961, Morris *et al.* 1958).

It was hypothesized that the responses to host (or prey) density of parasitoids such as *Trioxys* or predators such as *Coccinella* and *Micromus* may not be the same in different seasons or in different years; each response may be expected to be a function of the mean temperatures during the period of association of natural enemy and host (or prey) and also of the initial host density at which the association started. This hypothesis was examined by comparing the slopes of the regression of log (density of parasitoids or predators) on the log (density of the aphids) of various sets of data as has been done by Wright and Laing (1982). These authors (ibid) ~~as~~ and DeBach *et al.*(1976) believe that the slope which represents the response of natural enemies to host (or prey) is a partial measure of the regulation potential of the natural enemies.

4.2 *Trioxys*-SAA association

The numbers of both *Trioxys* and SAA in any one season of about 10 weeks were transformed to logarithms because (i) for both variates, the variance increased as the variate increased in value, and (ii)a log-log transformation of similar field data was used by Wright and Laing (1982) to analyse the relationship between coccinellids and aphids in corn in Canada. Because of the relationship found by Wright and Laing, a simple linear regression of log (density of parasitoids or predators) on the log (density of the aphids) was expected.

Tables 4.1 and 4.2 show the mean log numbers of *Trioxys* per 10 stems (Y) and the mean log SAA per stem (X) on each sampling occasion during January-March (summer) 1981 and March-May (autumn) 1981 respectively; and the apparent numerical responses of *Trioxys* to the changing of SAA population in summer an in autumn 1981 are plotted in Figure 13.

In the last column of both Tables 4.1 and 4.2 is presented the deviation of each point (XY) from the estimated regression line. Note that the first point of the "autumn data" (Table 4.2) with X = 2.05, Y = 0.8937, the deviation $d_{y.x}$ = 0.5368 is twice as large as any other deviation. No good reason can be thought of for this large deviation which occurred on the first date of sampling in the small plot after the rest of the study field have been mown and grazed and it is likely that it was simply a "bad" sample.

A test of significance was therefore applied to determine whether the deviation of this first point of the "autumn data" was within sampling error. The test was taken from Snedecor and Cochran

Table 4.1. Deviation from regression of mean log number of *Trioxys* per 10 stems on mean log number of SAA per stem; field survey of aphids and natural enemies during January - March (summer) 1981.

Date of sampling	Mean log number of SAA/stem (X)	Mean log number of *Trioxys* per 10 stems (Y)	Estimate of μ $(\hat{Y})$	Deviation from regression d_{yx} $(Y - \hat{Y})$
8/1	1.38	1.1285	1.2338	- 0.1053
15/1	1.46	1.3445	1.2676	0.0769
22/1	1.59	1.3733	1.3226	0.0507
30/1	1.86	1.4571	1.4369	0.0202
9/2	1.94	1.4684	1.4707	- 0.0023
17/2	1.95	1.5431	1.4749	0.0682
24/2	2.00	1.6136	1.4961	0.1175
3/3	1.98	1.2079	1.4876	- 0.2797
10/3	2.26	1.5419	1.6061	- 0.0642
17/3	2.12	1.6651	1.5469	0.1182

Table 4.2. Deviation from regression of mean log number of *Trioxys* per 10 stems on mean log number of SAA per stem; field survey of aphids and natural enemies during 25 March to 28 May (autumn) 1981.

Date of sampling	Mean log number of SAA/stem (X)	Mean log number of *Trioxys* per 10 stems (Y)	Estimate of μ $(\hat{Y})$	Deviation from regression d_{yx} $(Y - \hat{Y})$
25/3	2.05	0.8937	1.4305	- 0.5368
1/4	2.16	1.2896	1.4534	- 0.1638
8/4	2.20	1.3400	1.4618	- 0.1218
15/4	2.33	1.6114	1.4889	0.1225
23/4	2.56	1.6180	1.5369	0.0811
29/4	2.41	1.7488	1.5056	0.2432
5/5	2.00	1.5232	1.4200	0.1032
13/5	1.79	1.5612	1.3762	0.1850
21/5	1.20	1.3540	1.2531	0.1009
28/5	1.12	1.2234	1.2364	- 0.0130

Figure 13.

Regression, in differen~~ce~~t seasons, of log number of *Trioxys* per 10 stems on log number of the SAA per stem.

A: 8 January to 17 March (summer) 1981;
$Y = 0.649 + 0.423 X$ ($r = 0.703$; $P<0.05$),

B: 1 April to 28 May (autumn) 1981;
$Y = 1.024 + 0.228 X$ ($r = 0.656$; $P<0.10$).

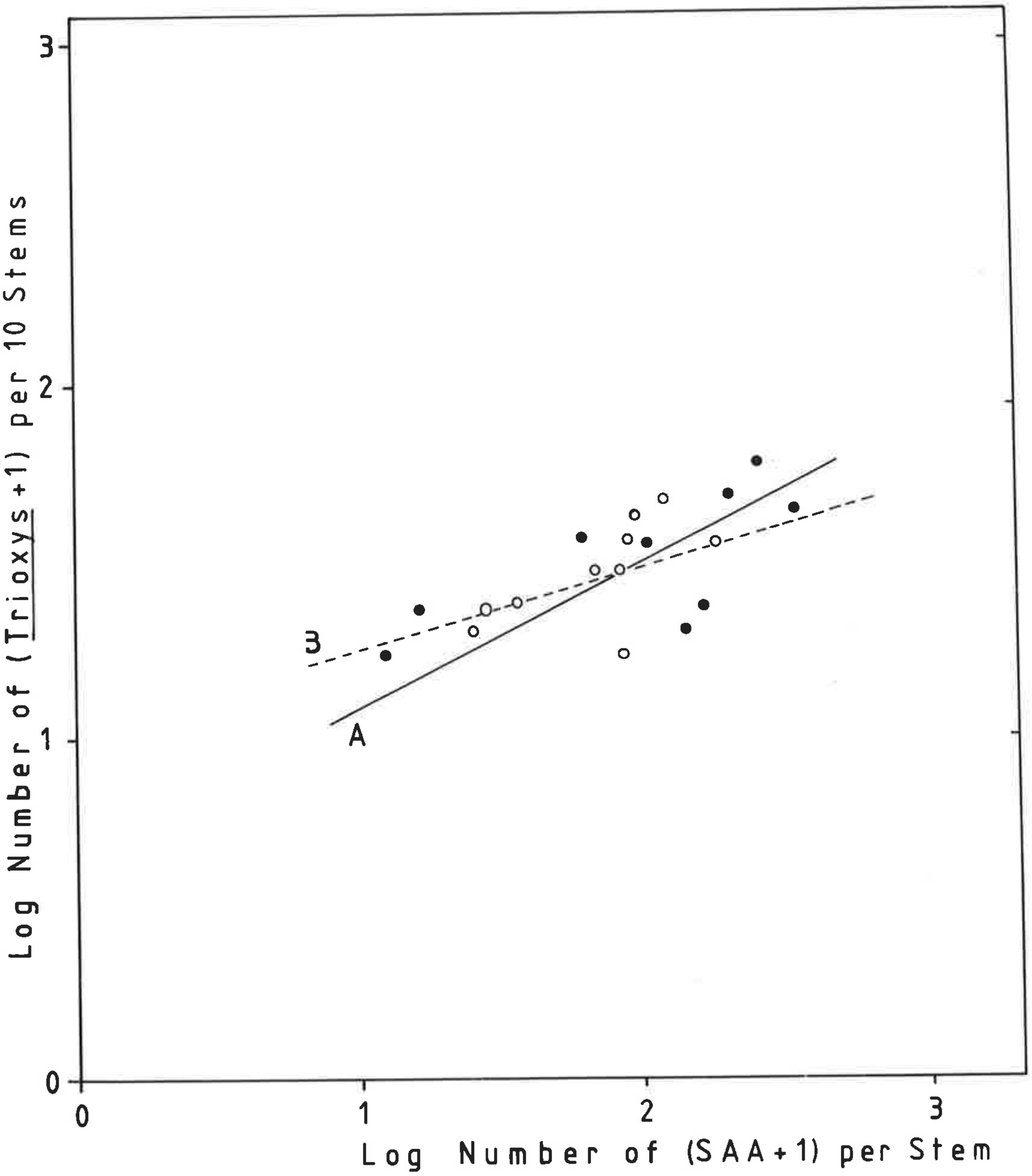

3
2
1
0
0
1
2
3
Log Number of (Trioxys+1) per 10 Stems
Log Number of (SAA+1) per Stem
A
B

Fig. 13

(1967; p 157-158) and the results are presented in Appendix 6 which shows that P = 0.0547 and therefore the null hypothesis should not be rejected at the usually accepted 5% probability level. However, if the first point is included in the autumn data, the regression of *Trioxys* numbers on aphid numbers is not significant (P>0.15) but if the first point is excluded from the data set, then the regression is significant (P<0.05). Since the other data sets show a significant regression of *Trioxys* numbers on SAA numbers (see Figure 13 line A and Figure 14 line B) it more likely than not that the regression for the autumn data is also significant and that therefore the first data point should be omitted as a bad sample. When this is done, the regression line was estimated as Y = 1.024 + 0.227 X (see Figure 13, line B).

The test of null hypothesis that the linear regression of the response of *Trioxys* to SAA in January-March (summer) and in March-May (autumn) are similar is taken from Snedecor and Cochran (1967); page432-436. The regression may differ in the residual variances, in the slopes or in the intercepts and will be tested in that order. The appropriate variances etc. are given in Table 5, which corresponds to Table 14.6.2. of Snedecor and Cochran (1967); and have been used as follows:

(i) The residual variances

The variances etc. for fitting seperate lines to "summer" and "autumn" data are given in the first and the second lines of Table 5. The ratio of the regression mean squares (= residual

Table 5. Comparison of regression lines of the responses of *Trioxys* to the changing of SAA numbers in summer 1981 (8 January-17 March) and in autumn 1981 (25 March-28 May).

L	Within season	d.f.	Sxx	S.P	Syy	Coef. Reg.	Deviation from regression		
							d.f	SS	MS
1	summer	9	.7390	.3127	.2671	.4231	8	.1348	.0169
2	autumn	8	2.1088	.4807	.2543	.2279	7	.1447	.0207
3							15	.2795	.0186
4	Pooled	17	2.8478	.7934	.5214	.2781	16	.3004	.0188
5	Difference between slopes						1	.0209	.0209
6	Combined	18	2.9166	.8182	.5290	.2798	17	.3006	
7	Difference between intercepts						1	.0002	.0002

Test of hypoteses:

(a) Residual variances are homogenous:

F = 0.0207/0.0169 = 1.22 ; d.f.= 7,8 ; P>0.05 ; N.S.

(b) Homogenity of slopes;

F = 0.0209/0.0186 = 1.12 ; d.f.= 1,15 ; P>0.05 ; N.S.

Eccept null hypothesis.

(c) Homogenity of intercepts:

F = 0.0002/0.0188 = 0.01 ; d.f = 1,16 ; P>0.05 ; N.S.

Eccept null hypothesis.

variances) can be tested by an F test; F = 0.0207/0.169 = 1.22 with 7 and 8 degrees of freedom (d.f.), which is not significant. So the residual variances may be assumed to be homogeneous and the test can now be applied to compare the slopes.

(ii) Comparing the slopes

(a) The d.f. and the SS for the deviation from the individual regressions are summed in line 3; and the new residual MS (= .2795/15 = .0186) is the residual mean square obtained when seperate regression lines are fitted to "summer" and "autumn" data.

(b) In line 4 the sum squares and the products are added and used to calculate a pooled slope (= 0.2781) and a pooled SS (= 0.3004) which represents deviations from a model in which a single pooled slope is fitted. The different between this SS and that given in in line 3 (i.e 0.3004 - 0.2795 = 0.0209), with 1 d.f. measures the contribution of the difference between the two regression coefficients to the sum of squares of deviations (see line 5).

(c) Finally, the slopes are compared with an F test, with F being obtained in Table 5, as 0.0209/0.0186 = 1.12 with 1 and 15 d.f. ($P > 0.05$) supporting the assumption that the slopes do not differ.

(iii) Comparing the intercepts

(a) Comparison of the intercepts is necessary because the variances are homogeneous [see (i) above] and the lines are parallel [see (ii) above]. The regression of summer data and that of autumn data were combined and a deviation SS, 0.3006, is obtained (Table 5 line 6). This SS and that of Deviation SS in line 4 is substracted to give 0.0002, the SS between intercepts. I find F = 0.0002/0.0188 = 0.01 with d.f. = 1,16 and P>0.05 supporting the null hypothesis that the intercepts do not differ.

(b) It can be concluded that the responses of *Trioxys* to the changing of SAA numbers are the same for summer and autumn 1981 with a combined regression fuction of log Y = 0.9185 + 0.2798 log X (r = 0.66, P<0.005).

The plotted response of *Trioxys* to SAA for summer-autumn 1982 is shown in Figure 14 (line B). The regression was again significant and the the line log Y = - 0.1274 + 1.0296 log X (r=0.98, P<0.05) was fitted to the data. The analysis of variance for comparison of *Trioxys* responses to SAA in summer-autumn of 1981 and of 1982 is presented in Appendix Table 7; it shows that the residual variances are homogeneous with F = 0.0185/0.0177 = 1.05 (d.f. = 6,17) (P>0.05); and the mean residual variation about the joint fit is significantly worse than that of the individual fits with F = 0.7582/0.0179 = 42.36 (d.f. = 1,23) (P<0.001). Therefore, the responses of *Trioxys* to the changing of SAA numbers may be considered to be different for the two years. This difference can probably be attributed to the different host density at the beginning of each aphid "season". The difference in response of the parasitoid to the density of SAA in the two years suggest that *Trioxys* responds faster, as indicated by the much steeper slope of line B in Figure 14, when the initial aphid number is low. The difference in the response of *Trioxys* in the two years could

Figure 14.

Regression, in different years, of log number of *Trioxys* per 10 stems on log number of the SAA per stem.

A: 8 January to 28 May 1981;
$Y = 0.919 + 0.280 X$ ($r = 0.657$; $P<0.005$),

B: 23 January to 16 April 1982;
$Y = -0.127 + 1.030 X$ ($r = 0.980$; $P<0.001$).

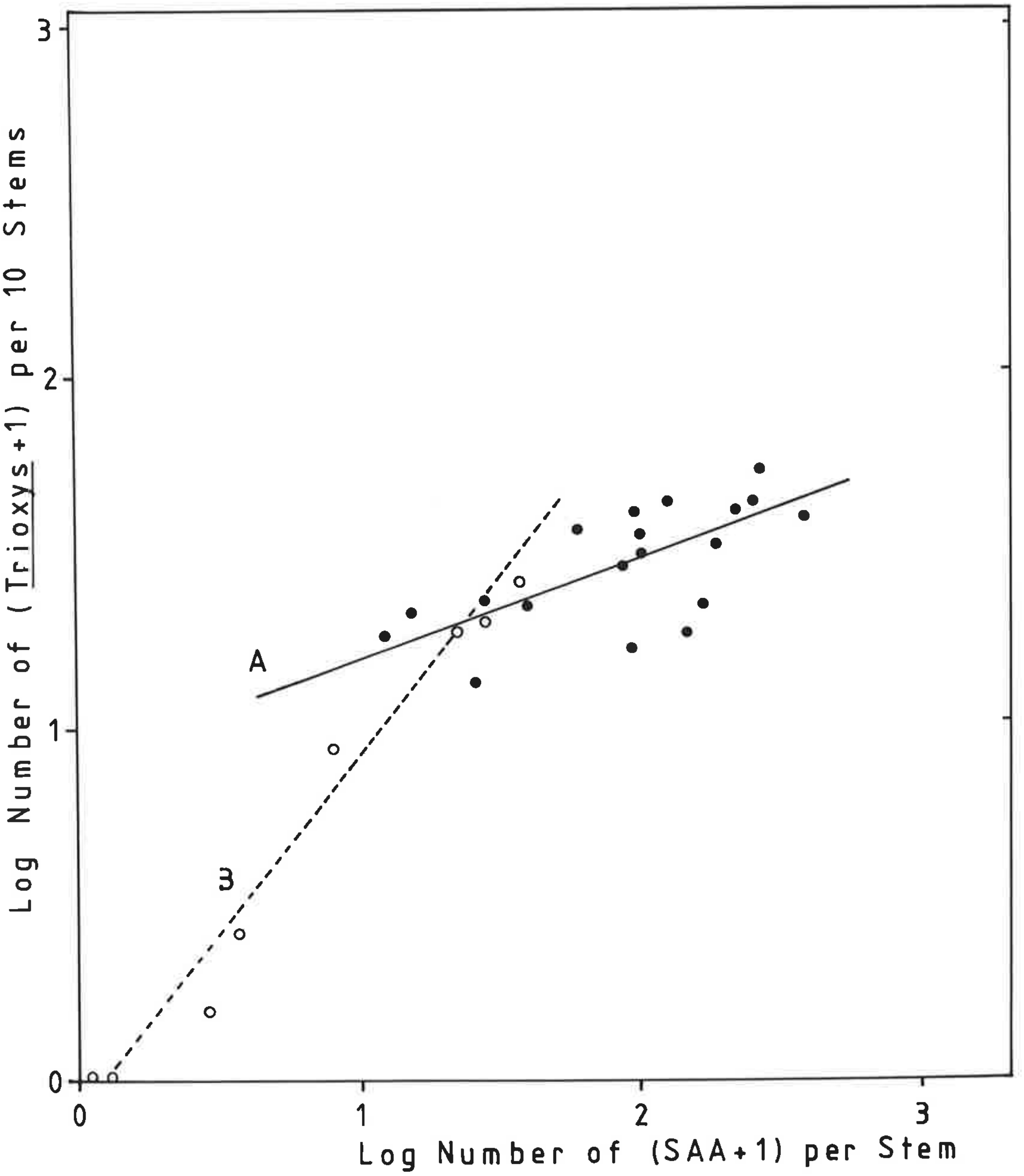

3
2
1
0
0
1
2
3
A
B
Log Number of (Trioxys+1) per 10 Stems
Log Number of (SAA+1) per Stem

Fig. 14

have been due to a difference in mean temperature, or in the initial parasitoid/aphid ratio or simply in the number of aphids. The mean temperatures in the two periods being compared were 24.0 °C and 21.9 °C, and the initial parasitoid/aphid density ratios were 43/1027 (see Appendix Table 2.1) and 2/118 (see Appendix Table 2.4) respectively. The evidence indicates therefore that the difference in response was probalbly due to both host density and the initial parasitoid/aphid density ratio.

The indication of the effect of host density and of parasitoid/host ratio on the response of the parasitoid will be tested experimentally in Chapter 6.

4.3 Predator-prey association

4.3.1 Predator-(BGA and PA) association

The responses of *C. repanda* and *M. tasmaniae* will also be examined at different times of the years, and especially when the predators were most abundant. This examination will allow the measurement of the predators' responses to different mean temperatures and also to different aphid species populations, because the aphid populations in the winter-spring period are dominated by BGA and PA whereas SAA is the dominant species in the summer-autumn period.

The apparent numerical responses of *Coccinella* and *Micromus* to the changing aphid population in the winter-spring period of 1981 (from 10 July to 1 October) are shown in Figure 15.1 and 15.2 respectively. The fitted regression lines of the plotted response are shown in Figure 16. Examination of the slope of the regression of line (A) in Figure 16 indicates that *Coccinella* has no response to the increasing prey numbers between 10 July and 1 October 1981. Its numbers increased rapidly only when the aphids reached very high numbers (Figure 15.1). A similar trend in number was observed with the *Micromus* population (Figure 15.2), although *Micromus* appeared to respond much more rapidly than did *Coccinella*, especially during the first six weeks of the association (Figure 16, line B).

Both *Coccinella* and *Micromus* numbers increased even more rapidly after 13 October and seemed to be related to the collapse of BGA+PA populations thereafter (see Figures 5 and 7). However, at the same time, many alates were caught in water traps as can be seen in Figure 17. So if the predators did contribute to the rapid decrease of aphid populations during that period they were unlikely to be the only contributor. The data of Figure 17 show that a large number of alates was trapped in the water traps between the middle of September and the end of October 1981 during which period the number of aphids in the crop was highest. The number of aphids in the crop then decreased to near zero at the midle of November and the number of winged aphids caught in the traps also felt to near zero. The number of aphids in the crop then fluctuated in low level until January but the number of alates caught in the traps rose again probably either because the increasing photoperiods and higher temperatures induced

Figure 15.

Relationships of the log numbers of *C. repanda* (1) and *M. tasmaniae* (2) to log number of BGA plus PA. The raw numbers of the predators are per 10 sweeps and those of the aphids are per stem. Data were obtained from field census from 10 July to 19 November 1981.

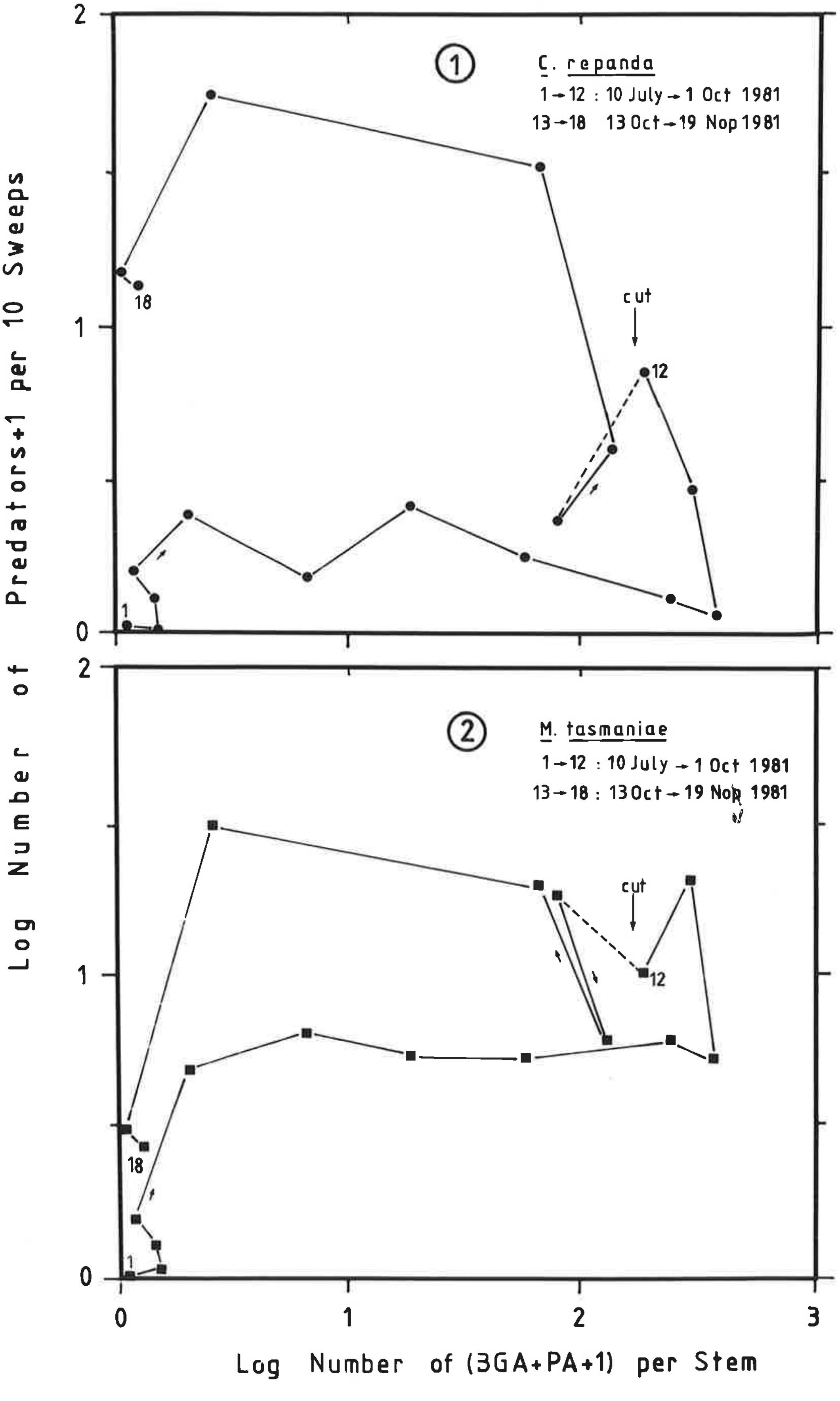

①
C. repanda
1→12 : 10 July→1 Oct 1981
13→18 13 Oct→19 Nop 1981
cut
12
18
1
②
M. tasmaniae
1→12 : 10 July→1 Oct 1981
13→18 : 13 Oct→19 Nop 1981
cut
12
18
1
2
1
0
2
1
0
0
1
2
3
Log Number of Predators+1 per 10 Sweeps
Log Number of (3GA+PA+1) per Stem

Fig. 15

Figure 16.

Regression of *C. repanda* (A) and *M. tasmaniae* (B) to log number of BGA plus PA.

A: $Y = 0.1486 + 0.094\ X$ ($r=0.400$; $P<0.25$),
B: $Y = 0.2160 + 0.329\ X$ ($r=0.814$; $P<0.005$).

Data were obtained from field census during 10 July to 1 October 1981.

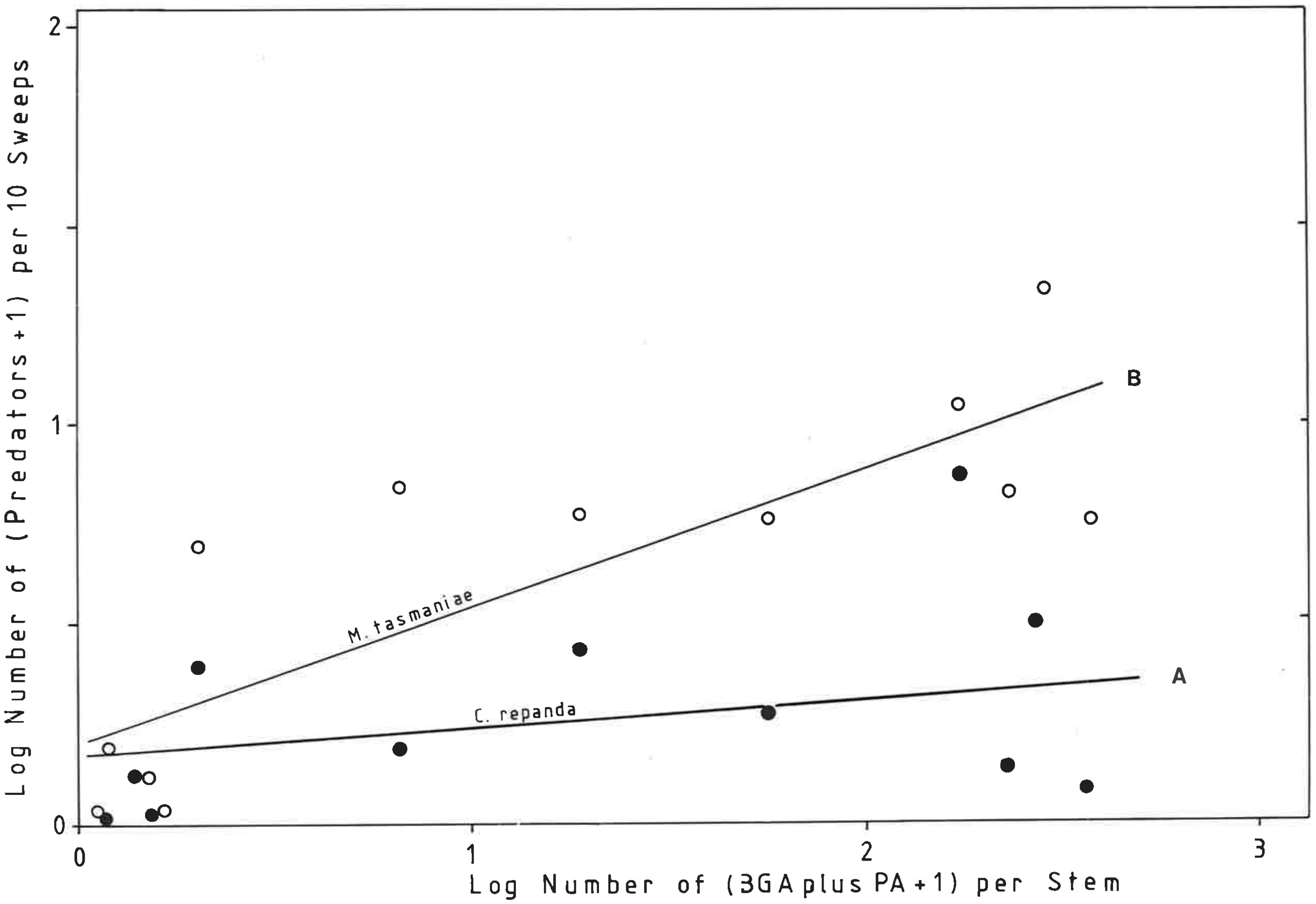
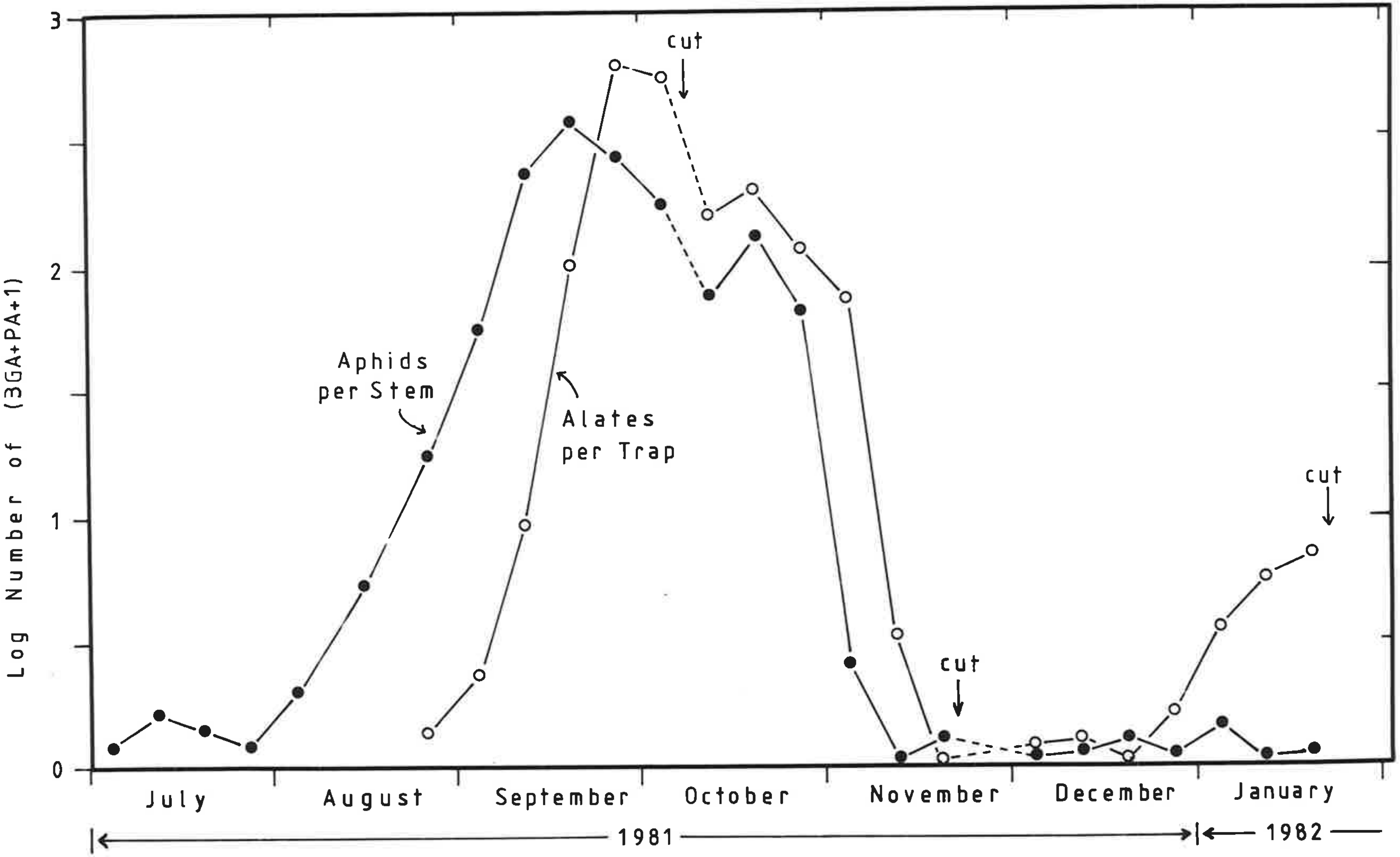

Log Number of (Predators + 1) per 10 Sweeps
2
1
0
0
1
2
3
Log Number of (3GA plus PA + 1) per Stem
M. tasmaniae
B
C. repanda
A

Fig. 16

Figure 17.

Numbers of alates of BGA plus PA (open circle) trapped in yellow water traps and the numbers of aphids per stem (solid circle) at times of sampling during July 1981 to January 1982. Data shown in log scale.



3
2
1
0
Log Number of (3GA+PA+1)
Aphids per Stem
Alates per Trap
cut
cut
cut
July
August
September
October
November
December
January
1981
1982

Fig. 17

alate formation of BGA and PA. This finding is not in agreement with that of Johnson (1965,1966) who worked with the cowpea aphid, *Aphis craccivora* Koch (Hemiptera, Aphididae). This inagreement was likely to be due to differential flight behaviour between the aphid species (Johnson 1954).

4.3.2 Predator-SAA association

Coccinella repanda was the most abundant predator found in the study field during the summer-autumn period . Figure 18A shows the response of *Coccinella* to the changing SAA numbers during December 1981-January 1982 (summer) and during March-April 1982 (autumn). The fitted regression lines are shown in Figure 18B. They suggest a direct positive response of *Coccinella* to the increases in SAA populations. A test of significance for a comparison of the two regression lines (Appendix Table 8) indicates no difference between responses for the two seasons.

Figure 18A.

Relationship of log numbers of *C. repanda* to log numbers of SAA. The raw numbers of the predators are per 10 sweeps and those of the aphid are per stem. Data were obtained from field census during 10 Decemcer 1981 to 16 April 1982.

Figure 18B.

Regression of log numbers of *C. repanda* to log numbers of the SAA; data were the same as those in Figure 18A:

line 1 (10 December 1981 - 21 January 1982):
$Y = 0.597 + 0.296 X$ ($r = 0.745$; $P<0.10$),

line 2 (2 March - 16 April 1982):
$Y = 0.027 + 0.611 X$ ($r = 0.947$; $P<0.005$).

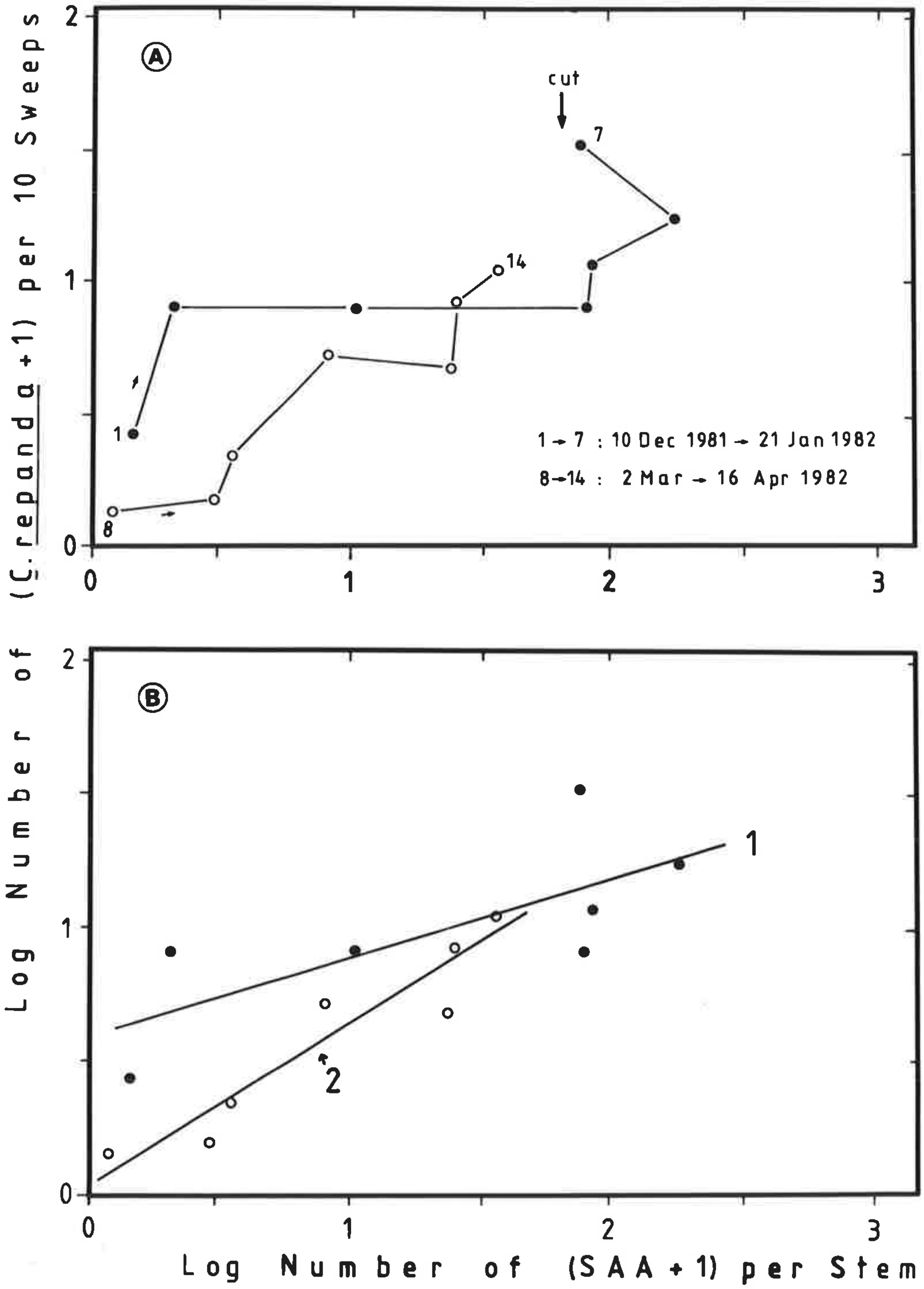

Log Number of (C. repanda + 1) per 10 Sweeps
Log Number of (SAA + 1) per Stem
A
cut
7
14
1
8
1 → 7 : 10 Dec 1981 → 21 Jan 1982
8 → 14 : 2 Mar → 16 Apr 1982
B
1
2
0
1
2
3

Fig. 18

Chapter 5

The Impact of *Trioxys*
and
Naturally Occurring Predators

5.1 Introduction

The regression analysis of field population data in the previous chapter indicated that there were significant positive associations between *Trioxys complanatus* or *Coccinella repanda* and the spotted alfalfa aphid. However the regression method cannot demonstrate that either *Trioxys* or *Coccinella* was responsible for regulating the aphid numbers at some particular population density.

Much indirect evidence of the regulatory control of SAA by *Trioxys* or coccinellids has been obtained from field population census data of other workers, e.g.(van den Bosch *et al.* 1959, Wilson *et al.* 1982). However, De Bach and Bartlett (1964) and many other writers believe that any evaluation of natural enemy effectiveness based on census data usually is inadequate for determining the importance of any one or a combination of natural enemies in the regulation of an insect's average population density. They believe that a more convincing method of evaluation is the experimental comparison of plots with natural enemies against plots with natural enemies excluded. So I have used the experimental method in this study to determine the role of natural enemies in regulating the density of the SAA population.

For determining the role of natural enemies experimentally, natural enemies can be eliminated in a number of ways, e.g. mechanically, chemically, or biologically (DeBach 1946, DeBach and Bartlett 1951, 1964, DeBach *et al.* 1949, 1951, DeBach *et al* 1976, Doutt *et al.* 1976, Huffaker and Messenger 1964, Maelzer 1977, Smith and DeBach 1942). Although the purpose of all methods is the same, each method has certain advantages and disadvantages. The cage exclusion technique, for example, may exclude 100% of natural enemies but it may alter the microenvironment inside the cage. A chemical exclusion technique usually does not create such a problem but, on the other hand, it usually can not exclude all natural enemies. Both cage exclusion and insecticidal-check methods were therefore used in this study to determine the degree of control exerted by natural enemies, especially that of *Trioxys complanatus*, on the trends in the rate of change of SAA populations.

5.2 Cage Exclusion of Natural Enemies

5.2.1 Materials and Methods

Three identical experiments were conducted in the study field during spring, summer, and autumn when both the SAA and its natural enemies are active in the field.

The "treatments" were different sorts of cages. The type of the cages and the natural enemies that each type of cage was expected to exclude are given in Tabel 6 for each of the 3 experiments. In more detail, the cages plus aphids (see below) gave the following treatments.

(A) Plant plus aphids caged with fine nylon gauze (242holes/cm^2) to exclude parasitoids and predators; ants excluded by smearing "fluon" around the wall of the pot (see below).

Table 6. Summary of the treatments used in one or more of the parasitoid-predator cage exclusion experiments, and a list of the particular treatments used in each of the 3 experiments.

Treatments: Treatments were different sorts of cages of a potted plant seeded with aphids. The cages were covered with:		The expected effects		
		Parasitoids	Predators (except ants)	Ants
(A)	fine nylon gauze + fluon	-	-	-
(B)	coarse nylon gauze + fluon	+	-	-
(C)	partly open cage + fluon	+	+	-
(D)	fine nylon gauze	-	-	+
(E)	fine nylon gauze + fluon;	-	-	-
	then no fluon and partly opened at day 18	+	+	+
(F)	fine nylon gauze + fluon;	-	-	-
	then partly opened at day 18, still with fluon	+	+	-

Experiments	Time Done	Treatments
I	26 Oct. - 25 Nov. 1982	(A),(B),(C)
II	4 - 29 January 1983	(A),(B),(C),(D),(E),(F)
III	28 April - 23 May 1983	(A),(B),(C),(D),(E),(F)

(B) Plant plus aphids caged with coarse nylon gauze (16holes/cm^2) to exclude predators but not parasitoids; ants excluded as in (A).

(C) Plant plus aphids in a partly open cage to provide ingress and egress of both parasitoids and predators; ants excluded as in (A).

(D) Plant plus aphids caged with fine nylon gauze (242holes/cm^2) to exclude both parasitoids and predators but ants allowed to enter.

(E) Plant plus aphids caged with fine nylon gauze (242holes/cm^2) to exclude all parasitoids and predators and ants, but only until day 18 from the beginning of the experiment. By day 18, when the number of aphids was expected to be high, the cage was partly opened and fluon was removed so that parasitoids and predators and ants were able to reach the aphids;

(F) As for treatment (E) except that ants were prevented from reaching the aphids on plants throughout the course of the experiment.

Treatment (A) was expected to estimate the rate of change in numbers of SAA in the absence of natural enemies and various comparisons of treatments were expected to give estimates of the effects on the rate of increase of SAA as follows:

(i) (B) versus (A) - the influence of parasitoids only.

(ii) (C) versus (A) - the influence of parasitoids and predators other than ants.

(iii) (D) versus (A) - the influence of ants only.

(iv) (E) versus (F) - the influence of ants only, at initially higher prey densities.

(v) (F) versus (A) - the influence of parasitoids and predators other than ants at initially higher host (or prey) densities.

(vi) (E) versus (A) - the influence of parasitoids and predators and ants at initially higher host (or prey) densities.

The type of cage used in this study is shown in Figure 19. The cage was 50 X 50 X 75 cm; it had a solid wooden floor and wooden frames for the sides which were covered with nylon gauze. The sides of the cage of treatment (A) were covered with fine gauze (242holes/cm^2) to exclude natural enemies whereas the sides of cage of treatment (B) were covered with coarse nylon gauze (16holes/cm^2) to exclude predators but allow parasitoids to enter. Half of each side of cage of treatment (C) was covered with coarse nylon gauze as in treatment (B); the other half of the side was left open.

The top of each cage was closed with a wooden frame covered with fine nylon gauze (242holes/cm^2) and served as the door of the cage. The cage was firmly positioned within the lucerne field with flexible "octopus" straps attached to steel pegs in the ground, and a potted lucerne plant was placed in each cage. The plants used were chosen to be as homogeneous as possible and consisted of about 15 stems with approximately 100 trifoliate leaves. Each potted plant was fumigated with a "shelltox" pest strip to ensure that it was initially free of aphids (see Section 2.1). Each of the treatments was replicated three times.

Figure 19.

Types of experimental cages used in field exclusion experiments.

(1) and (2): cage and a double potted lucerne plant used in spring 1982 exclusion experiment (expt.-I);

(3) and (4): cage and a double potted lucerne plant used in summer 1982/1983 exclusion experiment (expt.-II). Note that there was more vermiculite provided to the outer pot to absorb the excess water because plants needed more frequent watering during this experiment;

(4) and (6): cage and a double potted lucerne plant used in autumn 1983 exclusion experiment (expt.-III). Note that the top of the cages were covered with a clear plastic sheet to minimized the effect of rain on the aphids in the cage (see Maelzer 1977).

The wall of the outer pot was smeared with "fluon" to prevent ants from reaching the aphids on the plant.

Fig. 19

The initial host density per potted plant at the beginning of the experiment (day zero) was 100 apterae SAA of different development stages: 40 1st and 2nd instar nymphs plus 30 3rd and 4th instar nymphs plus 30 reproductive females. The aphids were obtained from the laboratory culture and were seeded onto the plants by the technique described in section 2.2.

The number of aphids in each treatment during the course of the experiment was estimated by sampling 9 trifoliate leaves, 3 each being taken randomly from the top, middle, and bottom parts of the plants. The number of ahpids in the sample was recorded under a binocular microscope; the aphids were returned to the plants immediately after recording. The samples were taken at day 7, 14, 18, 21 from the initiation of the experiment until further sampling was considered to be inappropriate because in some treatments at least the number of aphids was so high that the host plants were deteriorating.

The impact of ants was not originally intended to be included in this study until I learnt that they had removed many SAA from the plants in pilot experiments conducted in January and April 1982 using caged field plants. I made numerous attempts to start the colonies of aphids for these experiments but they failed because of the action of ants. So in the later experiments, described here as experiments I, II, and III, I used potted plants instead of field plants. Moreover I initially tried various methods of excluding ants that were not succesfull. Finally I tried "fluon" (polytetrafluoroethylene) grade 1 and found it worked well. So in all later experiments each potted plant was placed inside another outer pot which acted as the barrier (Figures 19.2, 19.4, 19.6). All the outlets of the outer pot were sealed with sticky tape from both sides and a 20 cm band of fluon was then smeared around its outer wall. A preliminary test with fluon for this purpose of excluding ants indicated that a number of ants could escape from a plastic container which had a band of fluon less than 10 cm wide on its vertical sides but none escape when the band was 20 cm wide.

During the periods of the experiments the plants were watered regularly. To absorb the excess water a layer of vermiculite was spread in the base of the outer pot.

Weather data during the experiment were obtained from the meteorological station at the Waite Institute.

5.2.2 Analysis of Data

The relationships between the number of SAA per sample (expressed in square roots) and time of sampling for each treatment were derived from regression analysis. The square root (sqrt) transformation was applied to the data to obtain homogeneous variances.

Only data from the first sampling date onward were subject to regression analysis. Numbers of aphids on day zero were excluded from the analyses for the following reasons: (i) the rate of change in numbers of SAA from day zero to day 7 (first sampling) is not equal to the rate of change in numbers after day 7, (ii) The first sampling is the more realistic point at which to begin treatment comparison because it reflects differences between treatments, whereas at time zero the treatments are artificially constrained to be the same. There is no treatment comparison at time zero (Sally Wayte, Biometric Section, Waite Institute, pers. comm.).

The rate of change in numbers of SAA in each treatment is measured from day 7 to day 25 and derived from the linear function $Y = a + bX$ where $Y = \text{sqrt}$ (number of aphids per sample), and $X =$ number of days after the start of the experiment.

5.2.3 Results and Discussion

Each of the experiments will be discussed separately. I shall first discuss the rate of change in numbers of SAA in the absence of natural enemies and then evaluate the degree of control exerted by *Trioxys* alone, by *Trioxys* plus predators, and by ants. For the purposes of discussion, the term "parasitoid" is replaced with *Trioxys* since *Trioxys* was the only parasitoid found attacking the SAA in the study field (Section 3.3.1.3a); and the term "predator" is used for any predator except ants. The terms "fine cage" and "coarse cage" and "partly open cage" are used to refer to the treatments (A),(B) and (C) respectively (Table 6).

(1) Experiment I

(26 October-21 November, spring 1982)

The total numbers of aphids in each of the different sorts of cages are given in Table 7.1, the mean numbers of aphids per each treatment are shown in Table 7.2 and the conditions of the plants are illustrated in Figure 20. The transformed data are plotted in Figure 22 against number of days after the start of the experiment. The subsequent analyses of variance for testing the significance of both linear and curvilinear regression for each treatment are given in Appendix Tables 9 and 10 which indicate that the regressions are significantly linear for each treatment. Table 8 gives the relevant statistics of each regression line.

(A) The Growth Rate of SAA (treatment A)

In the absence of natural enemies (i.e. in the fine gauze cages), the SAA increases in number very rapidly (Tables 7.1, 7.2; Figure 22.1). The observed mean number of SAA per sample of 9 lucerne leaves was 1594 on day 25 after the start of the experiment (Table 7.2) and the rate of change in numbers from day 7 to day 25 was 13.9 times, derived from the fitted line sqrt Y = $-0.6629 + 1.5902$ X ($r = 0.942$, $P<0.01$) (Table 8). However the rate of increase was probably reduced earlier than day 25 by deterioration of the plant because the lower leaves started to yellow by day 18 from the beginning of the experiment (Figure 20.1) and by day 28 the plant was defoliated.

Table 7.1. Numbers of aphids per 9 leaves of lucerne plants of different treatments (cages) on each date of sampling; parasitoid-predator exclusion experiment I, 26 October - 21 November 1982; spring. See Section 5.2.1 for detail of the treatments.

Days	Treatments (A-C) and Replicates (I-III)								
*	(A) Fine cage			(B) Coarse cage			(C)Partly open cage		
	I	II	III	I	II	III	I	II	III
7	124	87	101	60	89	78	43	45	62
14	667	271	553	298	628	285	60	191	25
18	1134	816	678	426	1039	527	108	190	125
21	1257	751	789	513	1049	521	144	497	91
25	1985	1571	1226	556	1110	469	183	262	177

*"Days" = numbers of days after the start of the experiment.

Table 7.2. Means of data in Table 7.1.

Days *	Treatments		
	Fine cages	Coarse cages	Partly open cages
7	104	76	50
14	497	404	92
18	876	664	141
21	932	694	244
25	1594	712	207

N.B.Economic threshold density of SAA = 45 aphids per 9 leaves.
*"Days" = numbers of days after the start of the experiment.

Figure 20.

The condition of plant at 18 days after the start of the experiment I (spring 1982).

(1) in fine gauze cage from which natural enemies were expected to be excluded. Ants were also excluded by smearing "fluon" around the wall of the pot;

(2) in coarse gauze cage from which predators but not parasitoids were expected to be excluded. Ants were excluded as in (1);

(3) in partly open cage, in which both predators and parasitoids were expected to find the aphids. Ants were excluded as in (1).

Figure 21.

The condition of plants at 27 days after the start of the experiment II (summer 1982/1983).

(1) in fine gauze cage from which natural enemies were expected to be excluded. Ants were excluded by smearing "fluon" around the wall of the pot;

(2) in coarse gauze cage from which predators but not parasitoids were expected to be excluded. Ants were excluded as in (1);

(3) in partly open cage in which both predators and parasitoids were expected to find the aphids. Ants were excluded as in (1);

(4) in fine gauze cage as in (1) but ants were allowed to reach the aphids on plants;

(5) in fine gauze cage but only until day 18 from the start of the experiment when the cage was partly opened and "fluon" was removed so that the parasitoids and predators and ants were then able to reach the aphids;

(6) as for treatment (5) except that ants were prevented from reaching the aphids on plants throughout the course of the experiment.

20.1

20.2

20.3

21.1

21.2

21.3

21.4

21.5

21.6

Figure 22.

Growth rates of SAA in different type of cages:

(1) fine gauze cages;

(2) coarse gauze cages;

(3) partly open cages.

The numbers of live aphid SAA per sample of 9 trifoliate leaves (expressed as square roots) are regressed on the numbers of days of sampling. The horizontal dotted lines denote the economic threshold density for SAA (= 45 aphids per 9 leaves)(Hanson 1961, Nielson and Barnes 1961).

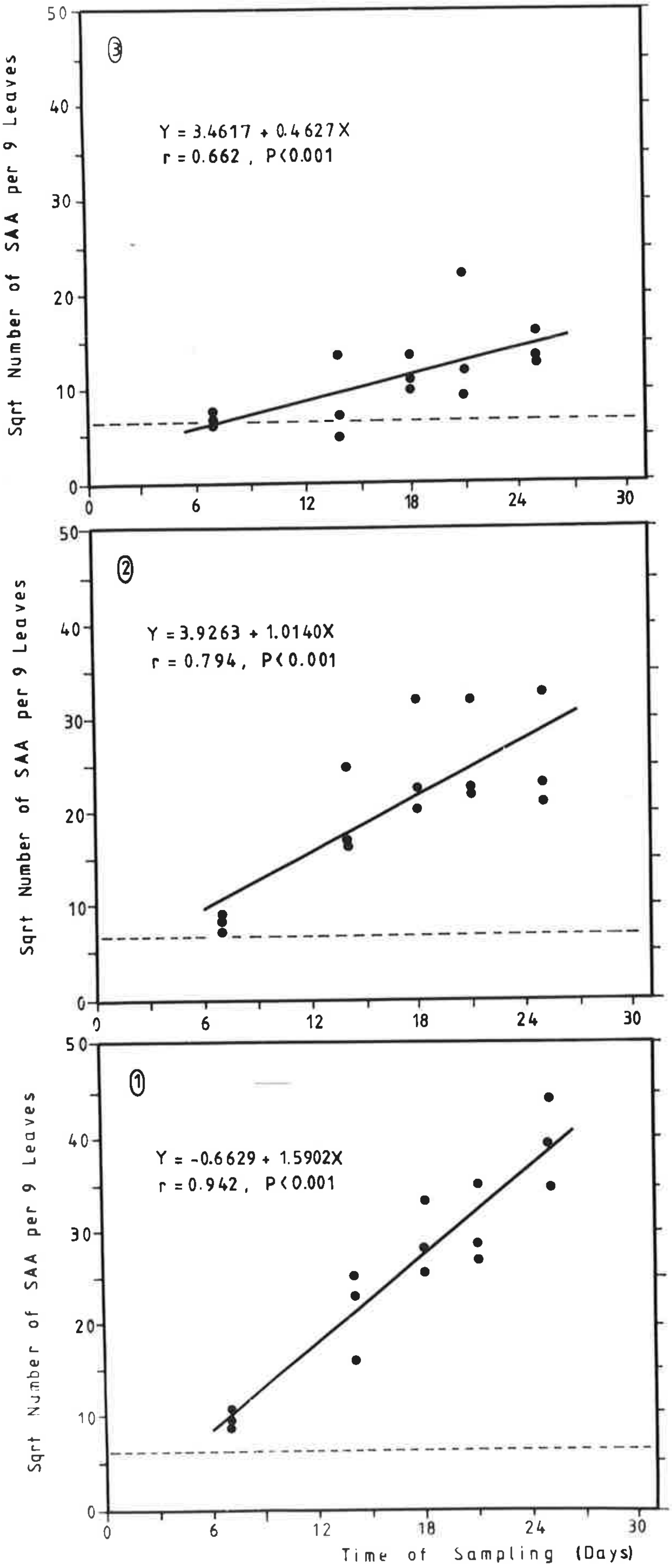
③
Y = 3.4617 + 0.4627X
r = 0.662 , P<0.001
Sqrt Number of SAA per 9 Leaves
0
10
20
30
40
50
0
6
12
18
24
30
②
Y = 3.9263 + 1.0140X
r = 0.794, P<0.001
Sqrt Number of SAA per 9 Leaves
0
10
20
30
40
50
0
6
12
18
24
30
①
Y = -0.6629 + 1.5902X
r = 0.942, P<0.001
Sqrt Number of SAA per 9 Leaves
0
10
20
30
40
50
0
6
12
18
24
30
Time of Sampling (Days)

Fig. 22

Table 8. Statistics for linear regression of the growth rate of SAA in different sorts of cages on the numbers of days after the start of the experiment; parasitoid-predator exclusion experiment I; 26 October to 21 November 1982.

Treatments	Intercepts	Slopes	(r)	(P)
(A) Fine gauze cages	-0.6629	1.5902	0.942	<0.001
(B) Coarse gauze cages	3.9263	1.0140	0.794	<0.001
(C) Partly open cages	3.4627	0.4627	0.662	<0.001

(B) The Impact of *Trioxys*
(treatment B versus treatment A)

At the beginning of the experiment, *Trioxys* was not commonly seen in the study field but adults were frequently caught in sweep net samples taken during this time of the year. In the experiment, the presence of *Trioxys* was indicated by observing either its adults or its mummies on the experimental plants. A *Trioxys* mummy was first found at day 14, indicating that an adult *Trioxys* had discovered and parasitized the aphids about a week before.

The impact of *Trioxys* in this experiment can be inferred from a comparison of the rate of increase in numbers of aphids in the coarse cages as opposed to those in the fine cages (Figure 22.2 vs Figure 22.1). When the numbers of aphids were transformed to square roots and regressed on the numbers of days from the start of the experiment, the trend in numbers in each type of cage could be expressed as sqrt Y = 3.9263 + 1.0140X (r = 0.794, P<0.001) (Appendix Tables 9B and 10B); and an analysis of variance (ANOVA) to compare the slopes of the two regression lines indicated that they were statistically different (Appendix Table 11).

The percentage reduction in the rate of increase of SAA in the coarse cages that can be attributed to *Trioxys* can be estimated from the regression coefficients (Table 8) as [(1.5902 - 1.0140)/1.5902] x 100 = 36% . However, the mean number of aphids on day 25 from the start of the experiment was 712 per 9 leaves.

So *Trioxys* could not prevent the SAA populations from reaching the economic threshold density of 45 per 9 leaves (Nielson and Barnes 1961, Hanson 1961) and damage to the lower leaves was seen on day 18 (Figure 20.2) when an average count of 694 SAA per 9 leaves was recorded. It is possible that a combination of factors, such as a low *Trioxys*-SAA ratio at the beginning of the interaction and secondary parasitism (see Section 6.4 below), was responsible for the failure of *Trioxys* to keep the SAA population below the economic threshold density.

(C) The Impact of Predators plus *Trioxys*
(treatment C versus treatment A)

C. repanda and *M. tasmaniae* were the most abundant predators in the field during spring (September-November) (Appendix Table 2.3). The early buildup in numbers of these two predators seemingly depended on the numbers of pea aphids and blue green aphids in early spring (Figure 5) and in this experiment they were probably responsible for a portion of the huge reduction of aphid numbers in the partly open cages (Table 7.2) as opposed to that of the fine gauze cages. Again, when the sqrt of numbers of aphids (Y) in the partly open cages were regressed on numbers of days (X) from the start of the experiment in Figure 22.3, the linear regression of $Y = 3.4627 + 0.4627\ X$ was significant ($r = 0.662$, $P<0.001$) (Appendix Tables 9C and 10C). The slope of this line was then compared to that of the coarse cages to compare the impact of predators plus *Trioxys* with the impact of *Trioxys* alone in the reduction of the growth rate of the aphids (Appendix Table 12). The slope of the line for the partly open cages was significantly smaller than that of the coarse cages. So predators plus *Trioxys* caused a significantly greater reduction in the growth rate of the aphids than did *Trioxys* alone and the total reduction attributable to predators plus *Trioxys* (in the partly open cages) can be eastimated from the regression coefficients as [(1.5902 - 0.4627)]/1.5902] x 100 = 71% . Then, since *Trioxys* alone was estimated to cause a 36% reduction, the predators can be eastimated to have been responsible for another 71 - 36 = 35% . This further great reduction in the numbers of aphids in the partly open cages was reflected by the condition of the plants in this treatment (Figure 20.3) which was markedly better than those in the other treatments.

The actual contribution of predators to the reduction in the rate of increase in aphid numbers in the open cages may have been greater than the 35% reduction estimated above because the reduction due to *Trioxys* in the partly open cages may have been less than the 36% estimated from the coarse cages. When predators and parasitoids are both present, the actual rate of parasitism is usually underestimated because the predators consume some of the parasitoids as parasitized aphids. Thus Hagen and van den Bosch (1968) point out that the true extent of parasitization by *Trioxys* is often masked by coccinellid predation because the bulk of aphids, parasitized as well as healthy, may be destroyed before *Trioxys* pupates. Observations on the numbers of *Trioxys* mummies found on plants of the coarse and partly open cages support this hypothesis. Thus Table 9

Table 9. Numbers of mummy of *Trioxys* on a 9 leaf sample taken from plants of "coarse gauze" and "partly open"cages; parasitoid-predator exclusion experiment, January (summer) 1983.

Days *	Treatments	Replicates			
		I	II	III	Total
7	Coarse cages	0	0	0	0
	Partly open cages	0	0	0	0
14	Coarse cages	1	3	13	17
	Partly open cages	0	0	1	1
18	Coarse cages	1	1	13	15
	Partly open cages	0	0	2	2
21	Coarse cages	1	2	14	17
	Partly open cages	1	6	2	9
25	Coarse cages	3	1	14	18
	Partly open cages	1	7	0	8
Total:	Coarse cages				67
	Partly open cages				20

* "Days"=numbers of days after the start of the experiment.

shows that the number of *Trioxys* mummies found in the partly open cages was much smaller than that in the coarse cages from which the predators were excluded. So it is likely that *Coccinella* and *Micromus*, which are abundant in numbers during that period, did indeed destroy a number of larvae of *Trioxys* in the partly open cages. In the laboratory, I have seen an adult *Coccinella* squeeze a larva of *Trioxys* from a mummified SAA and eat it (Figure 23.B).

(2) Experiment II ; 4-29 January (summer) 1983

Methods

There were 6 treatments of different sorts of cages (Table 6) in this experiment which were conducted in January (summer) 1983. Three other treatments were added to those in experiment 1, namely D-F (see Table 6) to determine the impact of predation on SAA by ants and by other natural enemies at initially higher host or prey density and comprising:

A : fine gauze cages plus fluon on the pots to exclude parasitoids and predators and ants.

B : coarse gauze cages plus fluon on the pot to exclude predators and ants but not parasitoids.

C : partly open cages plus fluon on the pots to exclude ants.

D : fine gauze cages and no fluon on the pots to exclude parasitoids and predators but not ants.

E : fine gauze cages plus fluon to exclude all natural enemies

Figure 23A.

Mummies of *Trioxys* at different stages of development.

Figure 23B.

A male adult *Coccinella repanda* feeding on a mummy of *Trioxys*.

Figure 23C.

A skin of a mummy of *Trioxys* left by *C. repanda*.

Figure 23D.

A scarred mummy of *Trioxys* caused by mandibles of *C. repanda*; however a normal adult *Trioxys* emerged from this mummy a few days later.

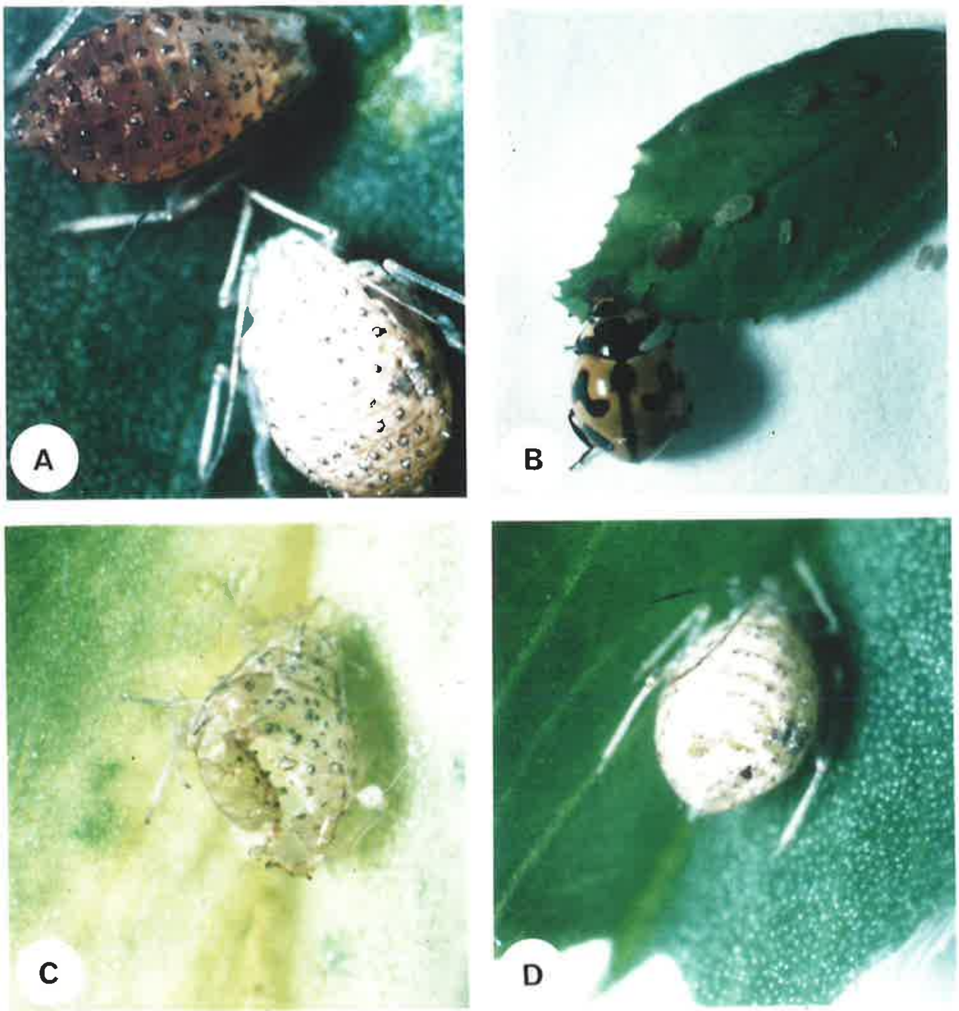


Fig. 23

until day 18 from the begining of the experiment when the cage was partly opened and fluon was removed so that all natural enemies were able to reach the aphids.

F : fine gauze cage plus floun to exclude all natural enemies until day 18 from the start of the experiment when the cage was partly opened but floun was not removed so that all natural enemies except ants were able to reach the aphids.

The details of the methods of the experiment are described in Section 5.2.1.

It was expected that during this experiment the plants would need more frequent watering and therefore more vermiculite was provided to the outer pot to absorb the excess water (compare the pots in Figure 19.4 with those in Figure 19.2).

Results and Discussion

The total numbers of aphids per sample for each treatment on each of a number of days after the start of the experiment are shown in Tables 10.1 and the mean numbers per treatment are given in Table 10.2, and the conditions of the plants are illustrated in Figure 21. The data were transformed to square roots and then plotted against numbers of days after the start of the experiment in Figure 24.1 to 24.6, and in Appendix Tables 13 and 14 are given the analyses of variance of the transformed data for testing the

Table 10.1. Numbers of aphids per 9 trifoliate leaves on plants of different treatments (cages) on each date of sampling; parasitoid-predator exclusion experiment II,4-29 January (summer) 1983.

Days **	Treatments (A-F)* and replicates(I-III)																	
	A			B			C			D			E			F		
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
7	111	79	86	62	81	84	71	33	50	27	32	15	126	67	98	84	68	107
14	94	281	227	144	262	225	232	70	184	7	3	2	337	143	n.a.	264	309	71
18	408	607	663	390	531	384	334	184	229	1	1	17	709	603	n.a.	725	709	585
21	658	799	874	388	479	681	648	587	262	53	11	4	3	3	n.a.	909	938	399
25	738	735	789	513	398	980	685	377	183	145	1	1	3	2	n.a.	758	552	187

(*) "Treatments":
A = fine cages + fluon;
B = coarse cages + fluon;
C = partly open cages + fluon;
D = fine cages with no fluon;
E = fine cages + fluon until day 18 and then were opened to natural enemies; and
F = fine cages + fluon until day 18 and then were opened to natural enemies other than ants (see Section 5.2.1 for details).
(**) "Days" = numbers of days after the start of the experiment.
n.a. = data not available because plants were dying.

Table 10.2. Means of data in Table 10.1

Days	Treatments*					
	A	B	C	D	E	F
7	92	76	51	25	97	86
14	201	210	162	4	240	215
18	559	435	249	6	653	673
21	777	516	499	23	3	749
25	754	630	415	49	3	499

N.B. Economic threshold density of SAA = 45 aphids per 9 leaves.

* Treatments:

A = fine cages plus fluon;

B = coarse cages plus fluon;

C = partly open cages plus fluon;

D = fine cages with no fluon;

E = fine cages plus fluon until day 18 from the start of the experiment then were opened to natural enemies;

F = fine cages plus fluon until day 18 after the start of the experiment and then were opened to natural enemies (except ants).

Table 11. Statistics for the linear regression of the growth rate of SAA on the number of days from the start of the experiment; parasitoid-predator exclusion experiment II, 4 to 29 January (summer) 1983.

Treatments *	Intercept	Slope	(r)	(P)
(A)	0.9385	1.1488	0.922	<0.001
(B)	2.2752	0.9375	0.895	<0.001
(C)	1.6538	0.8061	0.792	<0.001
(D)	"no linear regression"			
(E)	"no linear regression"			
(F)	4.2156	0.9018	0.705	<0.005

* The treatments were :

(A) = Fine cages + fluon;

(B) = Coarse cages + fluon;

(C) = Partly open cages + fluon;

(D) = Fine cages with no fluon;

(E) = Fine nylon cages + fluon until day 18 and then were opened to ants and natural enemies; and

(F) = Fine gauze cages until day 18 then were opened to natural enemies except ants. See Section 5.2.1 for details.

significance of linear and curvilinear regression respectively for each treatment. No curvilinear regressions were significant (Appendix Table 14) but 4 of the 6 linear regressions were sgnificant (Appendix Table 13) and their statistics are given in Table 11.

(A) The Growth Rate of SAA (treatment A)

In the absence of natural enemies (i.e. in the fine cages) the SAA increased very rapidly (Figure 24.1). The mean number of SAA per sample of 9 leaves was 754 on day 25 after the start of the experiment (Table 10.2) and the rate of increase in numbers from day 7 to day 25 was 10.9 times, derived from the fitted line: sqrt Y = 0.9385 + 1.1488 X (r = 0.902, P<0.001)(Table 11). However the rate of increase was again probably reduced earlier than day 25 by deterioration of the plants because the lower leaves started to yellow by day 18. By day 27, 2 days after the experiment was terminated, some of the leaves were drying and a copious amount of honey dew was seen on the leaves and on the lip of the pot (Figure 21.1); most of the aphids were on leaves as well as on stems.

(B) The Impact of *Trioxys*
(treatment B versus treatment A)

The sqrts of numbers of SAA (Y) in the coarse gauze cages (treatment B) are plotted against the numbers of days (X) after the start of the experiment in Figure 24.2. The regression was

Figure 24.

Growth rates of SAA in different types of cages in summer 1982/1983 exclusion experiment (expt.-II):

(1) fine gauze cages,

(2) coarse gauze cages,

(3) partly open cages,

(4) fine gauze cages but ants were allowed access to aphids on plants,

(5) fine gauze cages as in (1) but only until day 18 from the start of the experiment. Then the natural enemies (parasitoids, predators and ants) were allowed access to the aphids,

(6) as for treatement (5) except that ants were prevented from reaching the aphids on plants.

The regression lines were obtained by plotting the numbers of live SAA (expressed as square roots) per sample of 9 trifoliate leaves against the numbers of days of sampling. The horizontal dotted lines denote the economic threshold density of SAA (= 45 aphids per 9 leaves of lucerne)(Hanson 1961, Nielson and Barnes 1961).

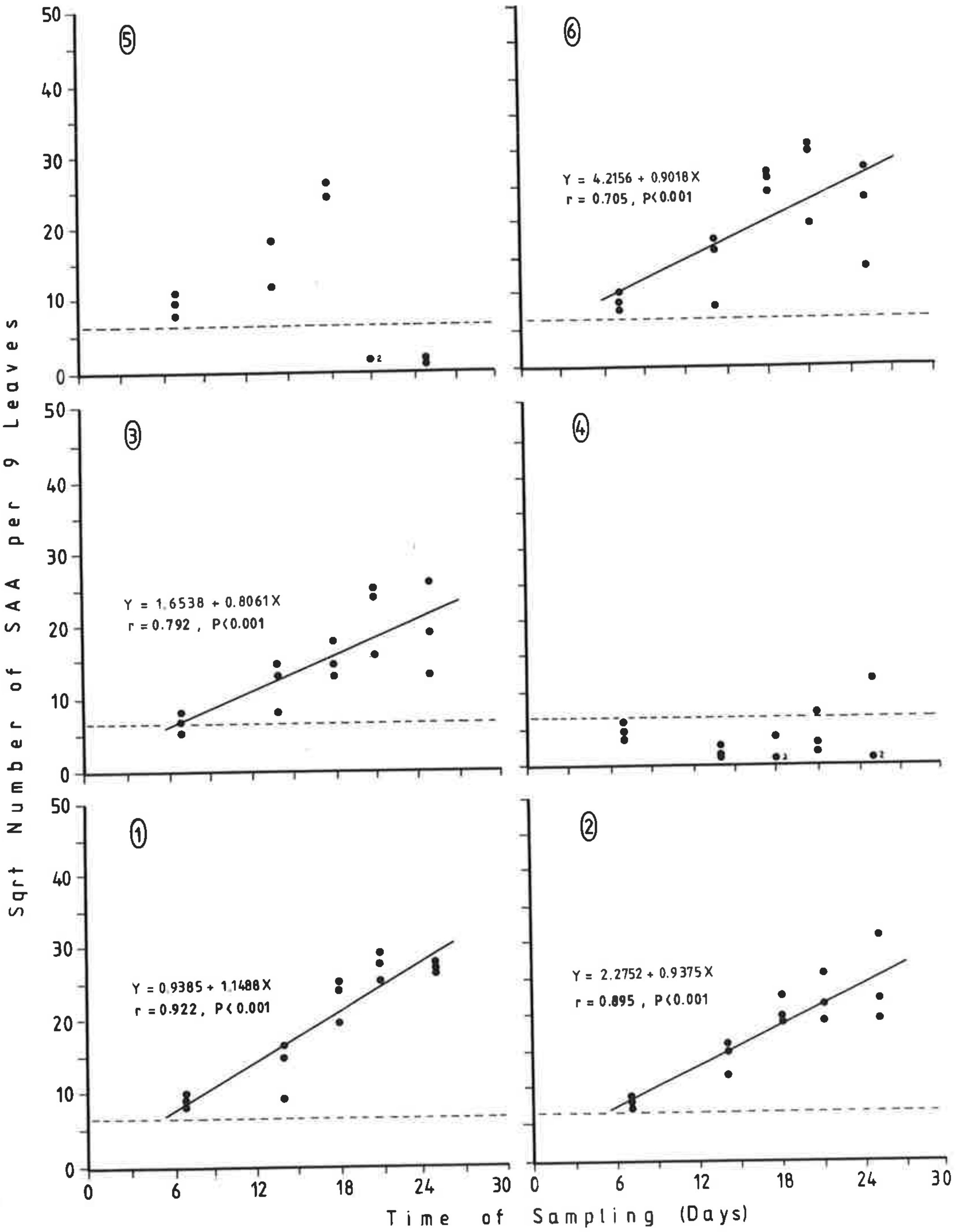

⑤
⑥
Y = 4.2156 + 0.9018X
r = 0.705, P<0.001
③
Y = 1.6538 + 0.8061X
r = 0.792, P<0.001
④
①
Y = 0.9385 + 1.1488X
r = 0.922, P<0.001
②
Y = 2.2752 + 0.9375X
r = 0.895, P<0.001
2
2
2
50
40
30
20
10
0
0
6
12
18
24
30
Sqrt Number of SAA per 9 Leaves
Time of Sampling (Days)

Fig. 24

significantly linear (Appendix Tables 13B and 14B) and was described by the line sqrt Y = 2.2752 + 0.9375 X (Table 11). The slope of this regression was then compared to that of the fine cages (treatment A) (Appendix Table 15) and found to be not significantly different.

Obviously, however, *Trioxys* exerted little, if any, influence on the SAA numbers during the period of this experiment. A mean number of aphids of 630 per 9 leaves was recorded on day 25 after the start of the experiment and it was reflected by the poor condition of the plants of this treatment. Notice that the condition of the plants in the fine cages was similar to those in the coarse cages (Figure 21.1 vs Figure 21.2).

The poor performance of *Trioxys* in this period is due to be attributed to the prevailling high temperatures in the period of this experiment with the daily maximum temperature going above 30 °C on several days (Appendix Table 18). To my knowledge there is no information about the effect of daily high temperatures on biology of *Trioxys* but some indication of the effect of temperature on the interaction of *Trioxys* and SAA can be obtained from Force and Messenger's (1964a) studies at constant temperatures in the laboratory. They found (ibid) that the innate capacity for increase (r_m) of *Trioxys* was highest (0.48 per day) at 26.7 °C; it then decreased to 0.43 at 29.4 °C and it was negative at 32.2 °C. By contrast, the values of r_m for SAA were lower than those of *Trioxys* at all temperature under 30 °C but at about 30 °C, the values for the two species were equal and the trend line of r_m plotted against temperature was still increasing for SAA at 30 °C but it was dropping sharply for *Trioxys*.

The field census data (Tables 5, 6, and 7) have also indicated that even with abundant predators, *Trioxys* did not prevent the SAA numbers in this period of the year to reach far above economic threshold density of 1200-1800 aphids per 30 stems (Allen 1978,1982).

(C) The Impact of Predators plus *Trioxys* (treatments C and F versus treatment A)

C. repanda plus *T. complanatus* were the commonest natural enemies observed in the study field during the period of this experiment. The other natural enemies were syrphids and chrysopids which were present in small numbers.

To test the impact of predators and *Trioxys* on SAA the sqrts of numbers of aphids (Y) in the partly open cages (treatment C) are regressed on the numbers of days (X) from the start of the experiment. The points are plotted in Figure 24.3 and the analysis of regression, which was significant, is given in (Appendix Tables 13C). The line: sqrt $Y = 1.6538 + 0.8061 X$ ($r = 0.792$, $P<0.001$) was fitted to the data and its slope of this regression was then compared to that of the regression for fine gauze cages with no natural enemies (treatment A) (Appendix Table 16) and found to be not significantly different. So predators plus *Trioxys* can be inferred to have had no significant influence on the SAA population during the period of this experiment (summer). The number of aphids in treatments (C and F) increased above that of economic threshold density of 45 aphids per 9 leaves (Nielson and Barnes 1961, Hanson 1961) (Table 10.2); a mean count of 415 and 499 SAA per 9 leaves being recorded in treatment C and in treatment F respectively on day 25 after the start of the experiment.

The lack of influence of predators plus *Trioxys* in the partly open cages (treatment C) was reflected again by the poor condition of the plants of this treatment which seemed to be only slightly better than those in the fine gauze cages (Figure 21.3 vs Figure 21.1). The plant condition of treatment F (Figure 21.6) also reflects the lack of influence of predators and *Trioxys* at initially higher aphid density; it shows that the conditions of plants of treatment F are very similar to those of treatment A (Figure 21.6 versus Figure 21.1).

The low impact of *C. repanda* (the most common predator species during the period of this experiment) on the increasing SAA population in this period of the experiment is not fully understood since the species is usually most active at the higher temperatures of summer. One possible reason for the low impact of *C. repanda* in this period of the season was perhaps the activity of their hymenopterous parasitoids, *Dinocampus* (=Perilitus) *coccinellae* (Schrank) (Braconidae) and *Tetrastichus* sp. (Eulopidae), which are usually active from late spring (November) to mid summer (January). *Dinocampus* and *Tetrastichus* are adult and pupal parasitoids, respectively, of many coccinellids species; their identification was conformed by Dr I. Naumann, C.S.I.R.O. Canberra).

The biology and ecology of these two parasitoids of coccinellids in South Australia are not known but a parasitized adult *C. repanda* is gradually less active so the reduction of its predation capacity is expected. Wright and Laing (1978) reported that, in Canada, *Dinocampus* is thelytokous, has several generations per year, and overwinters as first-instar larvae within adult coccinellids.

The impact of the parasitoids on *C. repanda* populations in South Australia is not clear. But Ridland and Berg (1978a) reported that about 25% of pupae of *C. repanda* collected in February in Victoria were parasitized by *Tetrastichus* and in New Zealand the incidence of parasitism by *Dinocampus* on overwintering *C. unidecimpunctata* has been estimated to be as high as 95% (J.A. Wightman, DSIR, Chrischurch, N.Z., pers. comm.).

(D) The Impact of Ants
(treatments D and E versus treatment A)

There were at least 3 species of ants in the study field during the period of this experiment. They were all native to

Australia and identified (to genus level) by R.W. Taylor and P.J.M. Greenslade of CSIRO Canberra and Adelaide respectively as *Iridomyrmex* sp. (Dolichoderinae), *Paratrechina* sp. (Formicinae), and *Pheidole* sp (Myrmicinae). *Iridomyrmex* (Figure 25) was found to be the most abundant species, and *Pheidole* was the least common.

(i) From the start of the experiment (treatment D)

The ants were seen removing the aphids from the experimental plants and were primarily or totally responsible for the great reduction of aphid numbers on the plants of treatment (D) (Table 10.2). The sqrt of number of aphids (Y) in this treatment was plotted against the number of days (X) from the beginning of the experiment in Figure 24.4; the linear regression was not significant (Appendix Table 13D). So the reduction in the growth rate of the SAA in this treatment that can be attributable to the impact of ants could not be estimated from regression coefficient. However, the reduction in numbers of aphids in this treatment by ants can be estimated roughly from the mean number of aphids on day 25 after the start of the experiment (Table 10.2) as [(754-49)/754] x 100 = 94% . This huge reduction in the potential numbers of aphids was reflected by the condition of the plants of this treatment (Figure 21.4) which were markedly better than those of the other treatments.

A few ants were continually present on plants of this treatment at any sampling occasion (Table 12). They were such good

Figure 25.

Irridomyrmex sp. found in the study field in summer 1982/1982 (1) and in autumn 1983 (2).

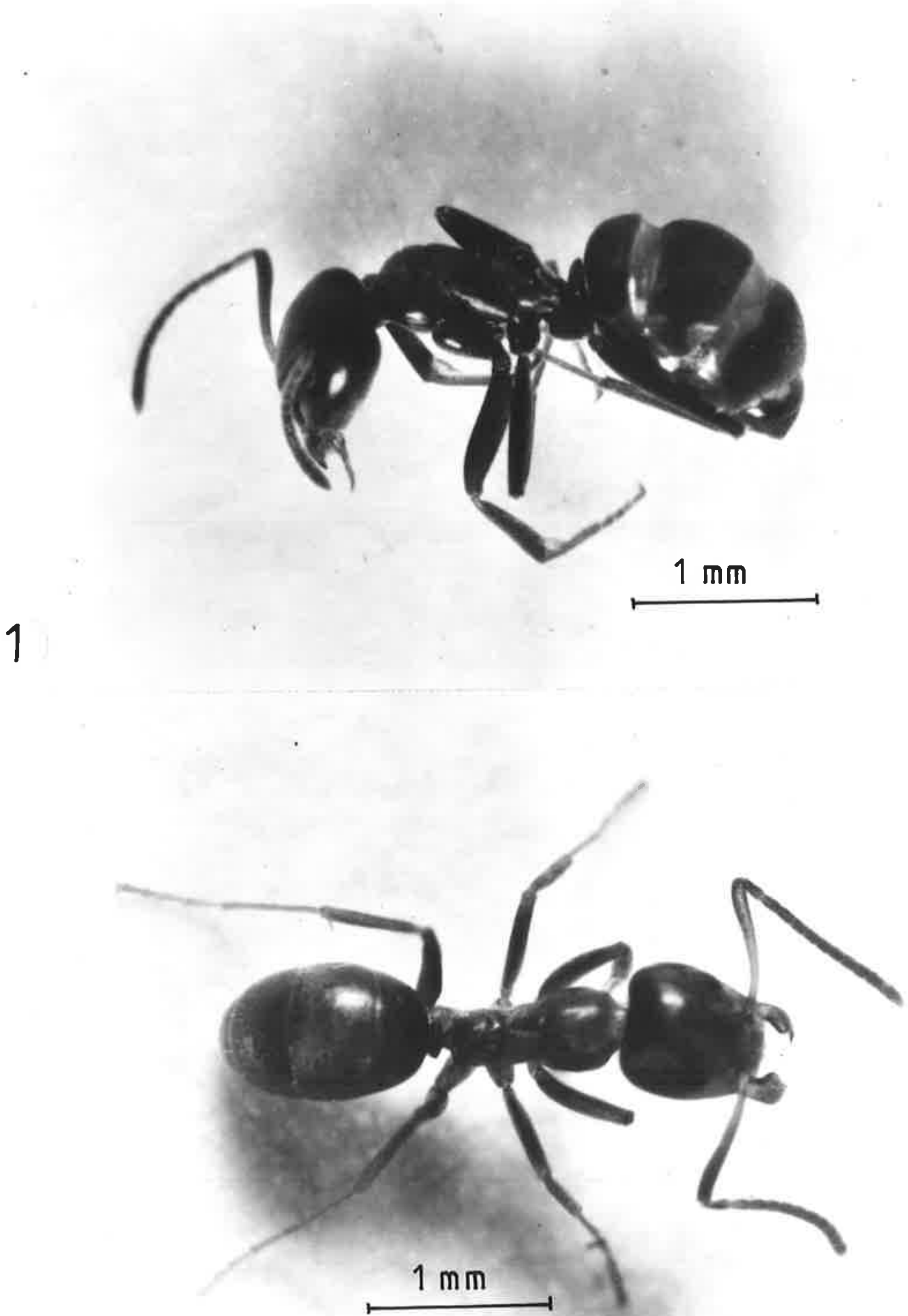


Fig. 25

Table 12. Total numbers of ants in 3 replicates observed on plants of treatments (D) and (E); parasitoid-predator exclusion experiment II, 4-29 January (autumn) 1983.

Days *	Treatments **	
	(D)	(E)
7	3	0
14	4	0
18	3	0
19	few	hundreds
21	2	2
25	10	2

* "Days"=numbers of days after the start of the experiment.

** Treatments:

(D)= Fine cages with no fluon, and

(E)= Fine cages plus fluon until day 18 and by day 18 the fluon was removed and the cages were partly opened to allow the natural enemies to be able to reach the aphids.

predators that the mean SAA numbers on day 14 after the start of the experiment was less than half of that initially seeded on the plants (Table 10.2). However, when the SAA numbers became very low, the ants seemed to reduce their activity so that the aphids could increase slightly in numbers. It is shown in Table 12 that the number of ants on treament (D) was less than 5 when the mean number of aphids on this treatment was below 25 (Table 10.2) but when the mean number of aphids increased 2 fold from 23 to 49 the number of ants increased 5 times from 2 to 10 (see subsection (ii) below for other evidence). Such activity of ants reflected the activity of an effective species of natural enemy since it regulates its own average numbers at low level by regulating the prey numbers at low density.

(ii) after exposure to ants on day 18 (treatment E)

In treatment E, ants were excluded for the first 18 days so that no ants were seen on the plants (Table 12). The cages were then manipulated to allow predation by ants when the mean number of aphids per 9 leaves on the plants had increased to 653 (Table 10.2). The following day (day 19) hundred of ants were seen on the plants (Table 12) and by day 21 a mean of only 3 aphids per 9 leaves was left. This vast reduction in aphid numbers occurred whilst the aphid numbers in the fine gauze cage (treatment A) and in treatment F (exposed to all natural enemies except ants after day 18) were still increasing (Table 10.2), so there can be no doubt that the ants were solely responsible for the predation in treatment E. And again, after the aphid numbers had dropped to a ~~very~~ low number, very few ants were seen on the plant on days 21 and 25 (Table 12).

The huge reduction in the numbers of aphids in treatment (E) was reflected again by the condition of the plants of this treatment (Figure 21.5) which was better than those of all other treatments except that of treatment (D) in which ants were allowed to prey on the aphids from the beginning of the experiment.

The influence of ants can further be evaluated by comparing the plant conditions in treatment (E) and those of treatment (F) in which the aphids were protected from ants and other natural enemies until day 18 and then were exposed to predators plus *Trioxys* but were still protected against ants; they show that the plant conditions of treatment F was markedly worse than those of treatment E (Figure 21.5 versus Figure 21.6). Thus it can be concluded that there was no effect of predators plus *Trioxys* after day 18 and so that the reduction in aphid numbers must have been due to ants.

(3) Experiment III ; 28 April-23 May (autumn) 1983.

Methods

The methods of this experiment were the same as those of "experiment II" described in Section 5.2.4(2) except that the top of each cage was covered with a clear plastic sheet, as shown in Figures 19.5 and 19.6, because more rain falls in autumn than in either spring or summer. Rain has been reported to cause high mortality of adults and older nymphs of the rose aphid, *Macrosiphum rosae* (L.) (Maelzer 1977), and the plastic cover was intended to minimize the effect of rain on the aphids in the cage.

The treatments in this experiment were the same as in experiment II, namely the treatment A to F described in Table 6 and comprising:

A : fine gauze cages plus fluon on the pots to exclude parasitoids and predators and ants.

B : coarse gauze cages plus fluon on the pot to exclude predators and ants but not parasitoids.

C : partly open cages plus fluon on the pots to exclude ants.

D : fine gauze cages and no fluon on the pots to exclude parasitoids and predators but not ants.

E : fine gauze cages plus fluon to exclude all natural enemies until day 18 from the beginning of the experiment when the cage was partly opened and fluon was removed so that all natural enemies were able to reach the aphids.

F : fine gauze cage plus fluon to exclude all natural enemies until day 18 from the start of the experiment when the cage was partly opened but fluon was not removed so that all natural enemies except ants were able to reach the aphids.

The details of the methods of the experiment are described in Section 5.2.1.

Results and Discussion

The total numbers of SAA per replicate for each treatment on each of the numbers of days after the start of the experiment are shown in Tables 13.1 and the mean numbers per treatment are given in Table 13.2. The data in Table 13.1 were transformed to square roots and then are plotted against the numbers of days after the start of the experiment in Figure 26 ; and in Appendix Tables 19 and 20 are given the analyses of variance for testing the significance of linear and curvilinear regression respectively for each treatment. As in experiment II none of the relationships were significantly curvilinear (Appendix Table 20) but all were significantly linear (Appendix Table 19). The statistics for the linear regressions are given in Table 14.

In this experiment, the comparison of the condition of plants of all treatments will not be described because they all looked the same, i.e. there were no differences in condition.

Table 13.1. Numbers of aphid per 9 trifoliate leaves of lucerne plants ofdifferent treatments (cages) on each date of sampling; parasitoid-predator exclusion experiment III, 28 April-23 May (autumn) 1983.

Days *	Treatments (A-F)** and Replicates (I-III)																	
	A			B			C			D			E			F		
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
7	62	56	49	31	34	66	43	67	30	58	55	51	75	59	43	45	77	31
14	157	101	111	87	80	71	70	61	137	69	47	89	119	126	71	219	105	59
18	221	181	158	183	119	107	102	95	112	199	181	157	211	253	134	265	117	173
21	190	161	269	173	104	94	103	69	120	116	221	199	259	203	106	168	168	177
25	399	341	444	322	224	92	98	97	95	249	354	222	302	421	109	374	250	154

*"Days" = numbers of days after the start of the experiment.

**Treatments:
(A) = fine cages + fluon;
(B) = coarse cages + fluon;
(C) = partly open cages + fluon;
(D) = fine cages with no fluon;
(E) = fine cages + fluon until day 18 and then were opened to natural enemies;
(F) = fine cages + fluon until day 18 and then were opened to natural enemies other than ants. See for details in Section 5.2.1.

Table 13.2. Means of data in Table 13.1

Days *	Treatments **					
	(A)	(B)	(C)	(D)	(E)	(F)
7	56	44	47	55	59	51
14	123	79	89	68	105	128
18	187	136	103	179	199	185
21	206	124	97	179	189	185
25	394	213	97	275	277	259

N.B. Economic threshold density of SAA = 45 aphids per 9 leaves.

*"Days" = numbers of days after the start of the experiment.

** Treatments:

(A) = fine cages + fluon;

(B) = coarse cages + fluon;

(C) = partly open cages = fluon;

(D) = fine cages with no fluon;

(E) = fine cages + fluon until day 18 and then were opened to natural enemies;

(F) = fine cages + fluon until day 18 and then were opened to natural enemies other than ants.

Table 14. Statistics for linear regression of the growth rate of SAA on the number of days after the start of the experiment ; parasitoid-predator exclusion experiment III, 28 April-23 May (autumn) 1983.

Treatments*	Intercepts	Slopes	(r)	(P)
(A)	2.3471	0.6413	0.938	<0.001
(B)	3.5273	0.4064	0.784	<0.001
(C)	6.2340	0.1723	0.652	<0.001
(D)	2.8075	0.5254	0.888	<0.001
(E)	4.2260	0.4747	0.759	<0.001
(F)	4.0330	0.4718	0.792	<0.001

* Treatments :

(A) = Fine gauze cages + fluon;

(B) = Coarse gauze cages + fluon:

(C) = Patrly open cages + fluon;

(D) = Fine gauze cages with no fluon;

(E) = Fine gauze cages + fluon until day 18 and were then opened to natural enemies; and

(F) = fine gauze cages + fluon until day 18 and were then opened to natural enemies other than ants.

(A) The Growth Rate of SAA (treatment A)

Even in the absence of natural enemies (i.e. in the fine gauze cages) SAA did not increase as rapidly as in the summer experiment (Figure 26.1). The mean number per sample of 9 leaves was 394 on day 25 after the start of the experiment (Table 13.2) and the growth rate in numbers from day 7 to day 25 after the start of the experiment was 4.0 times, derived from fitted line sqrt Y = 2.3471 + 0.6413 X ($r = 0.938$, $P<0.001$) (Table 14)). In the summer (experiment II), the rate of increase was estimated as 10.9 from day 7 to day 25 (Section 5.2.4 (2A)).

The relatively slow growth rate of SAA numbers during this autumn experiment was due of course to the low temperatures during the the experiment when the mean daily temperature was 15.2 °C in contrast to the spring experiment with a mean temperature of 19.1 °C (Appendix Table 23) and the summer experiment with a mean temperature of 21.1 °C (Appendix Table 25). As with other aphid species the mean productivity of SAA declines as the temperature decreases (Messenger and Force 1963, Hughes and Roberts 1978).

(B) The Impact of *Trioxys*
(treatment B versus treatment A)

Both mummies and adults of *Trioxys* were common in the study field from the beginning of the experiment. A mummy of *Trioxys* was first recorded in treatment B on day 14 from the start

Figure 26.

Growth rates of SAA in different types of cages in autumn 1983 exclusion experiment (expt.-III):

(1) fine gauze cages,

(2) coarse gauze cages,

(3) partly open cages,

(4) fine gauze cages but ants were allowed access to aphids on plants,

(5) fine gauze cages as in (1) but only until day 18 from the start of the experiment. Then the natural enemies (parasitoids, predators and ants) were allowed access to the aphids,

(6) as for treatament (5) except that ants were prevented from reaching the aphids on plants.

The regression lines were obtained by plotting the numbers of live SAA (expressed as square roots) per sample of 9 trifoliate leaves against the numbers of days of sampling. The horizontal dotted lines denote the economic threshold density of SAA (= 45 aphids per 9 leaves of lucerne)(Hanson 1961, Nielson and Barnes 1961).

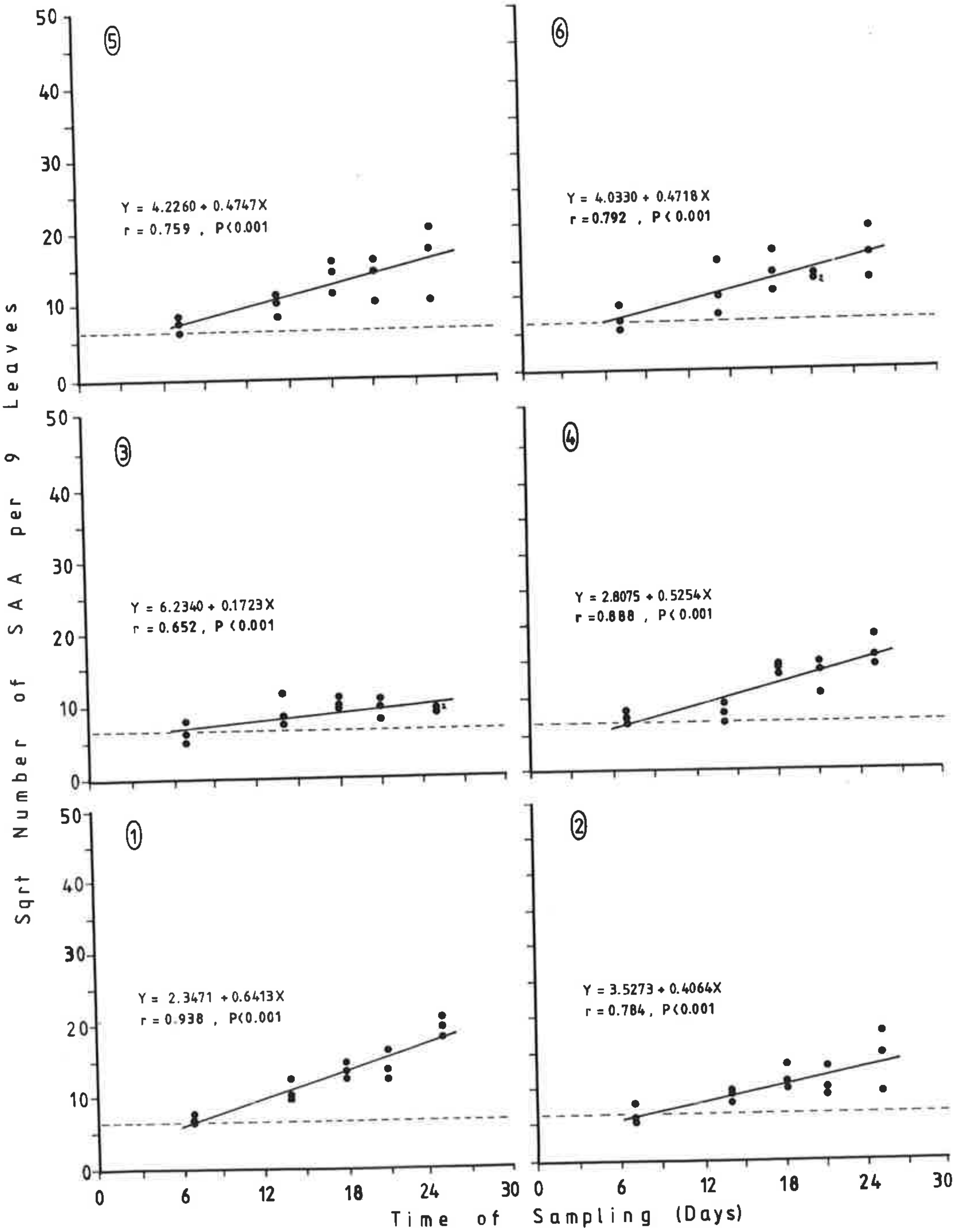

⑤
Y = 4.2260 + 0.4747X
r = 0.759 , P<0.001
⑥
Y = 4.0330 + 0.4718X
r = 0.792 , P<0.001
③
Y = 6.2340 + 0.1723X
r = 0.652 , P<0.001
④
Y = 2.8075 + 0.5254X
r = 0.888 , P<0.001
①
Y = 2.3471 + 0.6413X
r = 0.938 , P<0.001
②
Y = 3.5273 + 0.4064X
r = 0.784 , P<0.001
50
40
30
20
10
0
0
6
12
18
24
30
Sqrt Number of SAA per 9 Leaves
Time of Sampling (Days)

Fig. 26

of the experiment. However the female of *Trioxys* may have discovered and parasitized the aphid soon after the experiment started because it always develops more slowy at lower temperatures (Force and Messenger 1964b). By day 21 mummies of *Trioxys* were very common in treatment B.

The sqrts of aphid numbers (Y) in the coarse gauze cages (treatment B) are plotted against the numbers of days (X) after the start of the experiment in Figure 26.2. The relationship was linear (Appendix Tables 19B and 20B) and was described by the line sqrt Y = 3.5273 + 0.4064 X (Table 14) The slope of this line was then compared to that of the fine gauze cages and was found to be significantly smaller (Appendix Table 21). So *Trioxys* could be inferred to have reduced the growth rate of the SAA.

The percentage reduction in the rate of increase of the aphids numbers in the coarse gauze cages that can be attributed to the impact of *Trioxys* can be estimated from the regression coefficients (Table 14) as [(0.6413 - 0.4064)/0.6413] x 100 = 37% . Despite this reduction, *Trioxys* was again unable to keep the SAA numbers below economic threshold density (45 aphids per 9 leaves). An average of 213 SAA per 9 leaves was recorded on day 25 after the start of the experiment and had caused the lower leaves of the plants to yellow. The failure of *Trioxys* during the course of this experiment may have been due to the prevailing low temperature in the period of this experiment during which the minimum temperatures almost always dropped below 15 °C and even below 10 °C on several occasions (Appendix Table 25). Force and Messenger (1964a) reported that in temperature under 15 ^{o}C, the SAA may be capable of surpassing the innate capacity of *Trioxys*. These authors also reported that low temperature was able to increase larval mortality of *Trioxys* (Force and Messenger 1964a).

(C) The Impact of Predators plus *Trioxys* (treatments C and F versus treatment A)

(i) From the start of the experiment;

treatment C versus treatment A

The sqrts of numbers of aphids (Y) in the partly open cages were regressed on the numbers of days (X) after the start of the experiment in Figure 26.3. The relationship was linear (Appendix Tables 19C and 20C) and line sqrt Y = 6.2340 + 0.1723 X ($r=0.652$, $P<0.001$) was fitted to the data. The slope of this line was then compared to that of the fine gauze cages (Appendix Table 22) and shows that the slope of this line was significantly smaller than that of the fine gauze cages.

C. repanda and *T. complanatus* were the commonest natural enemies found in the study field during the period of this experiment; a few *M. tasmaniae* were also observed but only in the third week after the beginning of the experiment, and may have been responsible for a small fraction of the reduction of aphid numbers.

The percentage of reduction of the aphid growth rate in the partly open cages that can be attributed to the impact of predators plus *Trioxys* can be estimated from the two regression coefficients (Table 14) as ((0.6413 - 0.1723)/0.6413) x 100 = 73% . Then, since *Trioxys* alone was estimated to cause a 37% reduction (see Subsection (B) above), the predators can be estimated to have been responsible for another 73 - 37 = 36% .

(ii) After day 18 (treatment F versus tretamnet A)

The impact of predators plus *Trioxys* in the cages that were protected from all natural enemies until day 18 and were exposed thereafter to natural enemies other than ants can be estimated by comparing the slope of the fitted regression line of treatment (F) to that of treatment A (fine gauze cages). The analysis (Appendix Table 23) shows that the slopes were not statistically different. The lack of significant reduction may have due to the predators and *Trioxys* not being allowed a sufficient time to act upon the aphid population.

(D) The Impact of Ants
(treatments D and E versus treatment A)

(i) From the start of experiment;
treatment D versus tretament A

The sqrts of numbers of aphids (Y) in treatment (D) (i.e. fine gauze cages with no fluon, to exclude all natural enemies except ants) are plotted against the numbers of days after the start of the experiment in Figure 26.4. Again, the relationship was linear

(Appendix Tables 19D and 20D) and the line sqrt Y = 2.8075 + 0.5254 X was fitted to the data. The slope of this line was then compared to that of the fine gauze cages (Appendix Table 24) and found to be not statistically different. So unlike experiment II in which ants caused a huge reduction in aphid numbers, ants in this experiment seemed to have had no influence on SAA numbers.

(ii) After exposure to ants on day 18;
treatment E versus treatment A

The impact of ants can also be estimated from the comparison of numbers of aphids in treatment (E) with those of treatment (F) in which the aphids were protected from the ants and other natural enemies until day 18 and then exposed to predators and *Trioxys* but were still protected against ants. The slopes of the regression lines are so similar (Table 14) that no test is necessary to tell they are not different, and the similarity of the slopes supports the conclusion above that ants exerted no influence on SAA numbers.

Direct observation supported the conclusion from the treatment above that, in contrast to experiment II [Section 5.2.4.(2D)], there were very few ants in the study field during the period of this experiment. The reason for this scarcity of ants is not understood. One possible factor that reduced the number of ants in the study field was heavy rains that fell in March and April 1983, i.e. in the 2 months before the the start of the experiment. Thus Table 15 shows the month in which each experiment was done,

Table 15. Relative occurrence of ants in relation to rainfall before each of the parasitoid-predator exclusion experiments; November 1981 to May 1983.

Sort of Experiments	Month and year	Monthly rainfall (mm)	Occurrence of ants
	November 1981	35.6	
	December	26.8	
Pilot experiment I	January 1982	24.6	(+)
	February	7.0	
	March	54.2	
Pilot experiment II	April	81.2	(+)
	May	63.2	
	June	62.6	
	July	38.6	
	August	24.6	
	September	32.0	
	October	16.0	
Experiment I	November	3.4	(+)
	December	13.2	
Experiment II	January 1983	22.4	(+)
	February	1.8	
	March	105.6	
	April	99.0	
Experiment III	May	76.6	(-)

the monthly rainfall over the period of the experimentation and the relative occurrence of ants during the course of each experiment. As mentioned above ants were rare in May 1983 after 214.6 mms rains in the previous 2 months. By contrast, the total rainfall during the 2 months before the start of each of the other experiments was never greater than 62.4 mms in November and December 1981. The high rainfall in March-April 1983, before the start of experiment III, may reduced the numbers of ants by either causing high mortality through drowning or by causing the ground to be unsuitably wet for nesting (Greenslade 1979).

5.3 Chemical Exclusion of Natural Enemies

Experiment IV; 8 March-19 April (autumn) 1983

5.3.1 Introduction

The insecticidal-check method has been used widely for demonstrating natural enemy effectiveness. If applied stringently enough, it might serve as an exclusion method (DeBach *et al.* 1976). As used, it differentially kills and so reduces the efficiency of natural enemies, resulting in an increase to a higher number of the pest species, and thus shows that the natural enemies were responsible for controlling the pest..

The chemical selected must exhibit a marked differential adverse effect upon the pest species as contrasted to the natural enemy. DDT, due to its usual relative innocuousness to red spider mites, scale insects, aphids, and mealybugs, and its great toxicity to many hymenopterous parasitoids and ladybird beetles (DeBach and Bartlett 1951), has been most widely used in this context (DeBach 1946,1955, Huffaker *et al.* 1962, DeBach and Huffaker 1971). For the same reason ~~DTT~~ DDT was, therefore, selected for use in this experiment to determine the effectiveness of the natural enemies attacking SAA.

5.3.2 Materials and Methods

There were 3 treatments namely (i) 1000 g a.i. DDT/ha, (ii) 500 g a.i. DDT/ha, and (iii) untreated check; each treatment was replicated 3 times. The plot size was 10 x 10m with a 5 metre wide buffer zone seperating each plot to reduce cross-contamination by spray drift and to provide easy access for sampling etc. All sprays were applied in 300 litres water per hectare with a "SOLO" mistblower. The sampling and spraying intervals are shown in the diagram below. The first spray was made on 9 March 1983 one day after the first sample was taken.

Weeks

	0	1	2	3	4	5	6
Sprays:	↑	↑	↑	↑	↑	↑	
Samples:	↑	↑	↑	↑	↑	↑	↑
Dates:	8/3		22/3		5/4	12/4	19/4

The numbers of SAA and its natural enemies on each plot were estimated from a sample taken by a "D-vac" suction sampler (Figure 4.4) (Dietrick 1961). Aphids and natural enemies were vacuumed from 9 spots selected randomly across the plot. The catches were pooled in a plastic bag and returned to the laboratory where aphids and natural enemies were removed by washing in 70 °C water. The water was then filtered through 4 series of brass sieves of decreasing mesh sizes. A piece of fine voile was placed at the end of the finest seive to retain the first instar nymphs of SAA and other small insects species such as secondary parasitoids. If the number of aphids in the catches was too high, a subsample, as decribed in section 3.2.2(1), was taken to reduce time of counting.

Only the number of aphids was counted from subsamples; the number of parasitoids, secondary parasitoids and predators were recorded from the whole samples.

The experiment was conducted in a "Hunter River" lucerne field at the Waite Institute from 8 March to 19 April (autumn) 1983 during which time both the aphids and their natural enemies were expected to be common in the field (see Figures 5,6, and 7).

5.3.3 **Results and discussion**

Numbers of SAA, primary and secondary parasitoids, and predators at each sampling date are presented in Tables 16.1 and 16.2 below. The data show that the aphids increased very rapidly on the untreated plots. Their numbers reached 25,132 per sample at 6 weeks after the start of the experiment. By contrast, there were only 51 and 21 aphids on 500 g DDT and 1000 g ~~DTT~~ DDT plots respectively. This result was the opposite of that expected and the opposite of those cases where ~~DTT~~ DDT has been applied to horticultural crops infested with pest and natural enemies e.g. Ebeling (1945) on red mite and aphid-infested citrus trees, Griffiths and Thompson (1947) on scale-infested citrus trees, DeBach (1955) on cottony-cushion scale-, mealy bug-, yellow scale-, and two-spotted mite-infested citrus trees, Huffaker *et al.* (1962) on olive scale-infested olive trees. In all those cases pest numbers on the DDT-treated trees increased more rapidly and to higher numbers than those on

Table 16.1. Estimated numbers of SAA (A) and *Trioxys* (B & C) and secondary parasitoid (D) on untreated and DDT-treated plots in 3 replicates. Chemical exclusion experiment, 8 March to 19 April (autumn) 1983.

Date of sampling	Untreated plots	DDT/ha		Untreated plots	DDT/ha	
		500g	1000g		500g	1000g
	(A) The SAA			**(B) *Trioxys* (adults)**		
8/3	0	1	0	0	7	0
22/3	541	43	12	1	1	0
5/4	9512	496	6	33	2	1
12/4	15697	190	16	41	4	0
19/4	25132	51	21	24	3	8
	(C) *Trioxys* (mummies)			**(D) *Dendrocerus***		
8/3	0	0	0	0	1	0
22/3	6	1	0	40	4	2
5/4	29	13	0	320	2	0
12/4	112	8	0	208	2	2
19/4	126	1	3	290	1	2

Table 16.2. Estimated numbers of secondary parasitoids (E) and predators (F, G, H, and I) on untreated and DDT-treated plots in 3 replicates. Chemical exclusion experiment, 8 March to 19 April (autumn) 1983.

Date of sampling	Untreated plot	DDT/ha		Untreated plot	DDT/ha	
		500g	1000g		500g	1000g
	(E)*Pachyneuron+Alloxista*			(F) *C.repanda*		
8/3	0	0	0	0	3	1
22/3	4	0	0	2	1	0
5/4	16	0	0	1	0	0
12/4	5	1	0	0	0	0
19/4	6	1	1	2	0	0
	(G) *M. tasmaniae*			(H) Spiders		
8/3	0	0	0	8	14	7
22/3	0	1	0	31	14	5
5/4	0	1	1	34	11	6
12/4	1	1	1	29	15	8
19/4	1	0	0	25	6	5
	(I) Ants					
8/3	23	23	16			
22/32	25	17	1			
5/4	19	4	7			
12/4	10	7	8			
19/4	37	15	7			

the untreated trees.

The results indicate a hugely reduced numbers of SAA (A in the table) in the DDT-treated plots as compared to the untreated plot. So, too, the numbers of *Trioxys* adults (B) and mummies (C) were much lower in the DDT-treated plots, as were also the numbers of secondary parasitoids (D and E) and of spiders (H) and ants (I). The numbers of *C. repanda* (F) and *M. tasmaniae* (H) were too low in all plots to compare.

The results clearly indicate therefore that DTT drastically reduced the numbers of SAA and also significantly reduced the numbers of parasitoids, spiders and ants. It is also of interest to note that an almost total suppression of the parasitoids was achieved with the lower dosage of DDT, and that the larger dosage of DDT clearly depressed further the numbers of aphids and of spiders but not ants.

Tables 16.2 and 16.2 also indicate that DDT aplications, even at the higher dose, did not eradicate natural enemies from the treated plots.

Chapter 6

Some Biotic Factors Affecting *Trioxys* Effectiveness

6.1 Introduction

It is generally agreed that the quantification of parasitoid effectiveness is not simple because it is a dynamic phenomenon which is influenced by many interacting factors. As Stary (1970) has pointed that "...the effectiveness of a parasite in nature is no constant or even a specific feature: potential rate of increase is surely specific, but it depends on the environmental forces whether the parasite may realize this rate".

Factors affecting the effectiveness of a parasitoid have been described by many people (Doutt 1964, Hodek *et al.* 1972, Huffaker *et al.* 1976,1977, Knipling 1977, Stary 1966, Ullyett 1949, van den Bosch and Telford 1964). Perhaps the best description is given by van den Bosch and Telford (1964) and then completed by Stary (1970). The latter author believes that parasitoid effectiveness is a result of the interaction of the intrinsic features of the parasitoid species with the physical and biological properties of the environment and its stability and relative permanence.

Much information about the intrinsic features of *Trioxys complanatus* has been obtained from laboratory studies (Force and Messenger 1964a, 1964b, 1965, 1968, Hughes 1978, Messenger 1964, Schlinger and Hall 1959,1961). It appears to indicate that *Trioxys* could be an effective biological agent for the SAA. However, evidence given in Chapters 3 and 5 suggests that during the course and time of this study *Trioxys* failed to keep SAA population under the economic threshold density. Could both biotic and abiotic factors have then contributed in some degree to the reduction of *Trioxys* effectiveness?

The field census data as well as the field experimental data (Chapters 3, 4 and 5) have indicated that the following factors may have contributed to the reduction in the effectiveness of *Trioxys*:

(a) the host and parasitoid density at the beginning of the aphid "season".

(b) the parasitoid sex-ratio

(c) the action of competitors, i.e. predators and secondary parasitoids.

However, there are no published experimental reports of the quantitative impact of any of these factors on the effectiveness of *Trioxys*. Some experiments were therefore done both in the laboratory and in the field to corroborate the earlier results and to further explore the following aspects:

(i) the response of *Trioxys* to host density (see Section 6.2 below);

(ii) the effect of host and parasitoid density on the sex-ratio of *Trioxys* progeny (see Section 6.3 below);

(iii) the impact of predation and secondary parasitism on *Trioxys* abundance. (see Section 6.4 below).

6.2 The Response of *Trioxys* to Host Density

Host and parasitoid densities per unit area are believed to be important variables affecting parasitoid effectiveness (Knipling 1977, Stary 1966). Thus the number of parasitoids present in a given area will determine the proportion of the area that can be searched for host individuals and, in turn, will determine the proportion of the host population in that area that will be parasitized. Furthermore, the number of hosts that are parasitized governs the number of parasitoids in the next parasitoid generation (the so-called numerical response).

There are two contrasting ways of investigating the response of a parasitoid to different host densities (Hassell 1971). Firstly, one or more parasitoids can be confined to each different host density for a constant period of time to determine the importance of factors such as the handling time and egg limitation. Secondly, the parasitoids can be exposed to hosts so that they have a choice of a range of different host densities at the same time. This latter method assesses the response of the parasitoid to different host densities which are distributed unevenly in discrete units. Hassell (1971) emphasized the importance of host distribution when evaluating the searching efficiency of *Nemeritis canescens* (Grav.), a parasitoid of the larva of the almond moth, *Ephestia cautella* (Walk.). He stated that ".... the outcome of a parasite searching for hosts which are more-or-less continously distributed in space is likely to be very different than when hosts are distributed discontinuously in "clumps". A discontinuous distribution of hosts in the field is to be expected for SAA because of the variation of SAA within and between plants, and it is more realistically represented in the laboratory experiments by allowing a parasitoid to have a choice of many host densities at the same time. So this method of varying host density was used in this study.

The aim of the first experiment described here as experiment V, was to determine whether *Trioxys* possesses the ability of a regulatory species as described by DeBach and Smith (1941b), that is, if it had, within certain limits, the ability to destroy a greater portion of the host population when the density of the host is high than when it is low.

6.2.1 Experiment V

Response of *Trioxys* to Host Density and Distribution

(1) Materials and Methods

The host aphid and parasitoid used in this experiment were obtained from the laboratory culture described in Sections 2.2 and 2.3. *Trioxys complanatus* is an arrhenotokous endoparasitoid; superparasitsm is common (Force and Messenger 1965, Schlinger and Hall 1961) but only one parasitoid reaches maturity. Supernumerary larvae are apparently killed by physical combat or adverse physiological conditions (Schlinger and Hall 1961).

The treatments were different *Trioxys* densities varying from 1 to 16 females per cage. In each cage the *Trioxys* were presented with 240 aphids of 1st and 2nd instar nymphs which were distributed unevenly within the cage on 9 stems of lucerne as follows:

- 4 stems initially with 10 aphids;
- 2 stems initially with 20 aphids;
- 2 stems initially with 40 aphids; and
- 1 stem initially with 80 aphids.

The position of each stem in the cage was chosen ramdomly.

The type of cage used in this experiment is shown in Figure 2.1. The cage was 25 x 25cm (base) x 40cm (height); it had a wooden floor and metal rod frames for the sides which were covered with fine nylon gauze (242 holes/cm^2). The top of the cage was covered with a piece of clear perspex. Nine holes, each 3 cm diameter, were drilled in the floor of the cage in a 3 x 3 pattern and an excised "Hunter River" lucerne stem was put through each hole into a vial of water below (Figures 2.1 and 2.2). Each stem plus vial was then placed within a wider 50 ml plastic cup which acted as an aphid trap because some of the aphids tend to drop when disturbed by *Trioxys*. A 1 cm band of "fluon" was smeared around the inner top side of each cup to prevent the escape of any SAA that fell. The SAA nymphs were transferred onto each lucerne stem using the method described in Section 2.3.

After emergence, *Trioxys* females from the culture were allowed to mate and to feed on honey solution for one day. Only those females which moved actively and were about an average size were selected for use in the experiment. The parasitoids were then randomized to obtained the different required densities of 1, 2, 4, 8, and 16 and each lot of parasitoids was placed within a cage and allowed to parasitize the aphids for 24 hours. There were 5 replicates of each treatment.

The highest density of 16 parasitoids per cage was higher than one would expect under field conditions. However, trap data from the "dark trap" in Appendix Table 4 show that in the field *Trioxys* density reached 121 adults per trap which is probably equivalent to 15 parasitoids per cage of this experiment. The details of the experimental design are given in Table 17.

The experiment was conducted in an insectary at 22-26 °C with 50%-60% RH and a 14-10 h L-D phothoperiod. Illumination was provided from a bank of 10 white flourescent tubes set about 40cm above the top of the cages.

After the parasitoids had been removed, the aphids from each stem were reared for several days until mummies were formed and

Table 17. Details of experiment V

	Treatments	Within Treatment:					
Size of cage (cm)	*Trioxys* density per cage	Total aphids per cage	Aphid distribution No of stems with:				Replicates
			10	20	40	80	
25x25x40	1,2,4,8,16	240	4	2	2	1	3

could be counted. Fresh excised lucerne stems were provided for the aphids every alternate day.

The number of hosts that were parasitized in each treatment was estimated from the number of hosts that were mummified. This value is probably an underestimate because of mortality of early stages of *Trioxys* larvae due to either superparasitism or natural causes during the rearing.

(2) Data analysis

Hassell (1982) discussed a variety of subtly different measures of searching efficiency of a natural enemy. He believes that for precise evaluation of natural enemy effectiveness, it is necessary to gather the following information: (i) the host distribution, (ii) the actual number of searching parasitoid, (iii) the actual searching time per parasitoid, and (iv) the number of host parasitized. In this present experiment, however, I have gathered only the first and the last information because of technical difficulty in observing the numbers of *Trioxys* searching and the searching time of *Trioxys* without disturbing the aphid and parasitoid involved. The searching effeciency of *Trioxys* was, therefore, estimated by using the equation below in which searching time "Ts" is replaced by total period available for search, T = 1 (see Hassell,1982).

$$a = a' T = (\ln N - \ln N')/p$$

where, a = area of discovery of Nicholson (1933)

a' = searching efficiency of Hassel (1969)

T = searching time = 1

N = the initial host density, and

N' = the surviving host density

p = the parasitoid density.

(3) Results and Discussion

The number of hosts mummified at each initial host density (=treatment) is presented in Table 18. The calculated area of discovery per parasitoid density based on these data is shown in Appendix Table 26 and in Figure 27 the log area of discovery is plotted against log *Trioxys* density. The response is obviously linear with a strong slope (or mutual interference constant as called by Hassell, 1969), m = -0.8181. It is clear that an increase in the number of female *Trioxys* in the cage could result a decrease in the searching effeciency per individual parasitoid. This response is probably due to the incidence of physical interference between searching *Trioxys* which increases with parasitoid density.

An inverse association between searching efficiency of a parasitoid and its population density has also been demonstrated in

Table 18. Numbers of mummified SAA on each of 9 lucerne stems with initial densities of 10, 20, 40, or 80 aphids together in a cage (replicate) when exposed to 1, 2, 4, 8, or 16 *Trioxys* for 24 hours. Each cage had an initial total number of 240 aphids (N). Also given is the number of aphids that survive (i.e. were not parasitized) at each treatment (N'; see text).

Reps. (cage)	*Trioxys* density	Initial host density									Total per cage	Number of surviving
		10	10	10	10	20	20	40	40	80	N = 240	host : N'
I	1	10	9	7	8	16	15	24	21	24	134	106
	2	9	9	9	9	14	11	25	26	51	163	77
	4	8	10	8	8	12	20	28	26	56	176	64
	8	8	9	9	10	16	15	31	36	61	195	45
	16	9	10	9	9	14	18	30	38	59	196	44
II	1	7	9	7	9	19	16	29	27	47	170	70
	2	6	9	6	7	16	13	26	30	49	162	78
	4	7	7	9	10	12	18	33	32	58	186	54
	8	9	8	5	7	18	17	30	31	59	184	56
	16	8	8	8	8	14	20	32	39	68	204	36
III	1	9	10	8	10	19	16	30	28	45	175	65
	2	9	10	8	10	18	16	29	30	54	184	56
	4	10	9	7	10	18	19	29	31	56	189	51
	8	10	10	10	8	18	17	33	34	59	200	40
	16	9	10	10	9	18	17	37	33	58	201	39

Figure 27.

Relationship between searching efficiency of *Trioxys* (expressed as log area of discovery) and log density of searching females of the parasitoid.

Figure 28.

Interference test for *Trioxys*-SAA relationship (after Hassel 1969). The log k-values for parasitism are plotted against the log density of searching parasitoids as iether an independent or a dependent variable.

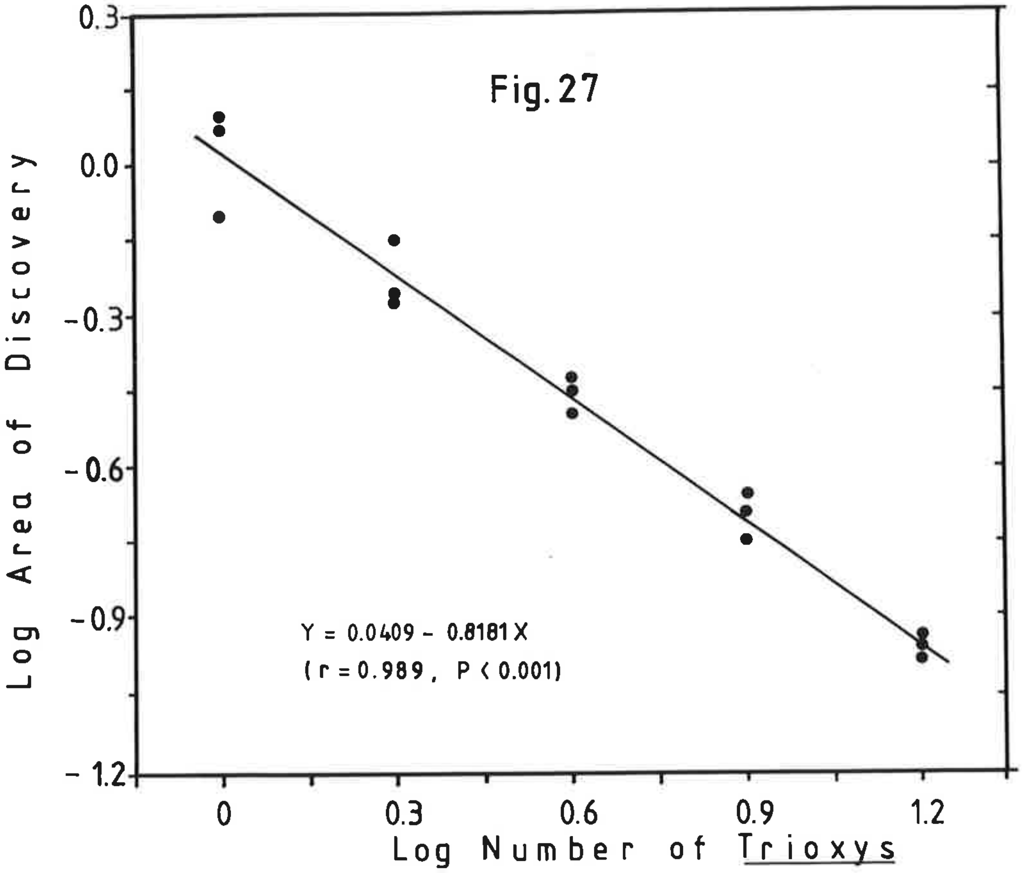


Fig. 27
Y = 0.0409 - 0.8181 X
(r = 0.989, P < 0.001)
Log Area of Discovery
0.3
0.0
-0.3
-0.6
-0.9
-1.2
0
0.3
0.6
0.9
1.2
Log Number of Trioxys

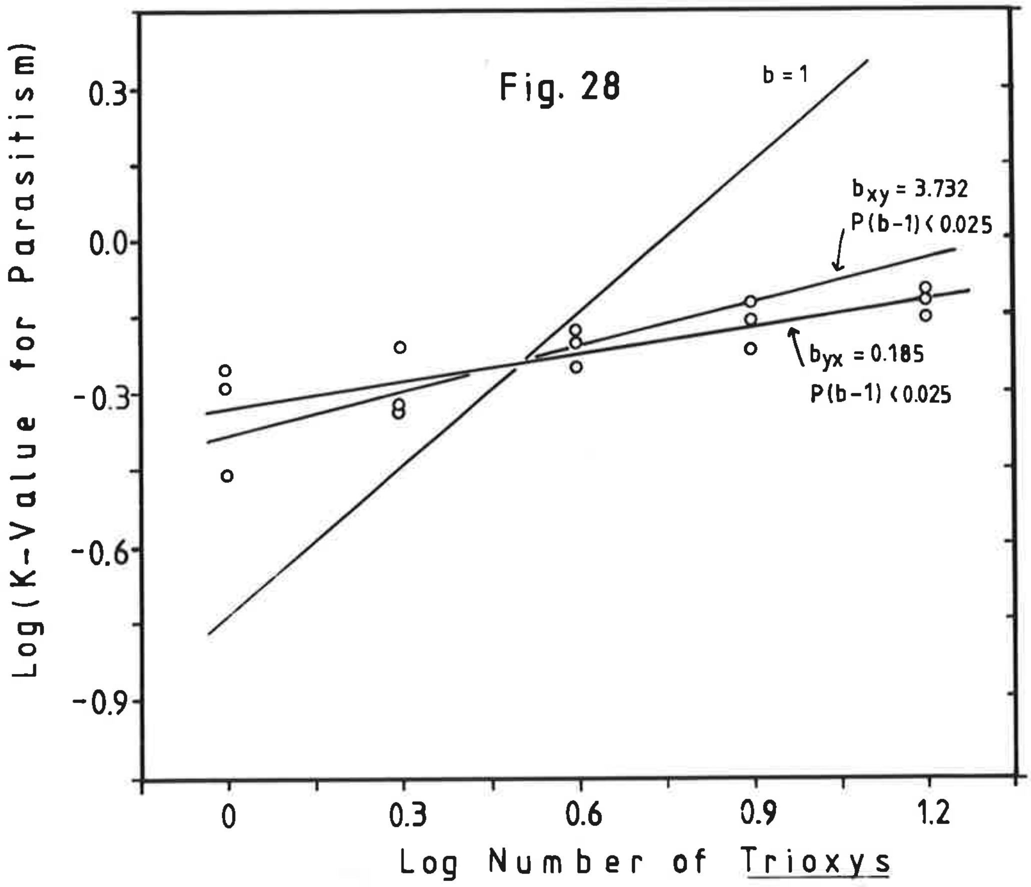


Fig. 28
b = 1
b_xy = 3.732
P(b-1) < 0.025
b_yx = 0.185
P(b-1) < 0.025
Log(K-Value for Parasitism)
0.3
0.0
-0.3
-0.6
-0.9
0
0.3
0.6
0.9
1.2
Log Number of Trioxys

a wide range of insect parasitoids (Huffaker and Kennett 1969 on *Nemeritis* (Venturia) *canescens* (Grav.), Ulyett 1949a, 1949b on *Chelonus texanus* Cress. and *Cryptus mornatus* Pratt., respectively) (see also Hassell 1969).

Hassell (1969) proposed a statistical test to confirm the occurrence of interference between searching parasitoids by plotting the log k-value for parasitism against the log density of searching parasitoids as either an independent or a dependent variable. Each k-values was obtained by substracting the log of the host density after parasitism in the last column of Table 18 from the log of host density before parasitism (=240)(Hassell 1966). The slopes of the two regression lines are then compared with a hypothetical slope that "b" = 1 ; they must show significantly lower of "b" = 1. The test (Figure 28; Table 19) confirms that interference between searching female *Trioxys* was clearly present [P(b-1)<.025)].

The numbers of hosts mummified at each *Trioxys* and SAA density are presented in Table 20, and the k-values for parasitism which were calculated from Table 20 are presented in Appendix Table 27. The behavioural response of *Trioxys* to host density at each parasitoid density is illustrated in Figure 29.1, in which the k-values are plotted against the SAA densities as the independent variable (Hassell 1971). The responses of *Trioxys* at each parasitoid density were inversely density-dependent (or subproportional as called by Hassell,1966) with the slopes differing

Table 19. Test of significance of interference between searching *Trioxys* where log k-value for parasitism (Y) is plotted against log *Trioxys* density (X) as either an independent or a dependent variable (see Hassell 1969).

	Regression of:	
	Y on X	X on Y
n	15	15
b	0.1851	3.7320
SE(b)	0.0343	0.6924
d.f.	13	13
T*	2.38	3.95
P (b - 1)	<0.025	<0.025

* $T = (1.0 - b)/SE_{(b)}$

Table 20. The numbers of mummified SAA from Table 18 categorized by both different host density and parasitoid density. The total initial number of aphids at each density in each cage is given in the 2nd last column, and was used to calculate the % parasitism of the last column.

Number of *Trioxys* per cage	Initial host density per replicate	Number of host mummified Replicate				Total initial aphids	Parasitism (%)
		I	II	III	Total		
1	(10) x 4	34	32	37	103	120	85.8
	(20) x 2	31	35	35	101	120	84.2
	(40) x 2	45	56	58	159	240	66.3
	(80) x 1	24	47	45	116	240	48.3
2	(10) x 4	36	28	37	101	120	84.2
	(20) x 2	25	29	34	88	120	73.3
	(40) x 2	51	56	59	166	240	69.2
	(80) x 1	51	49	54	154	240	64.2
4	(10) x 4	34	33	36	103	120	85.8
	(20) x 2	32	30	37	99	120	82.5
	(40) x 2	54	65	60	179	240	74.6
	(80) x 1	56	58	56	170	240	70.8
8	(10) x 4	36	29	38	103	120	85.8
	(20) x 2	29	35	36	100	120	83.8
	(40) x 2	67	61	67	195	240	81.3
	(80) x 1	61	59	59	179	240	74.6
16	(10) x 4	37	31	38	106	120	88.3
	(20) x 2	32	34	35	101	120	84.2
	(40) x 2	68	71	70	209	240	87.1
	(80) x 1	59	68	58	185	240	77.1

Figure 29.

Responses of *Trioxys* to uneven host distribution. The k-values for parasitism are regressed on the SAA densities. Each graph shows the result obtained using a different parasitoid density.

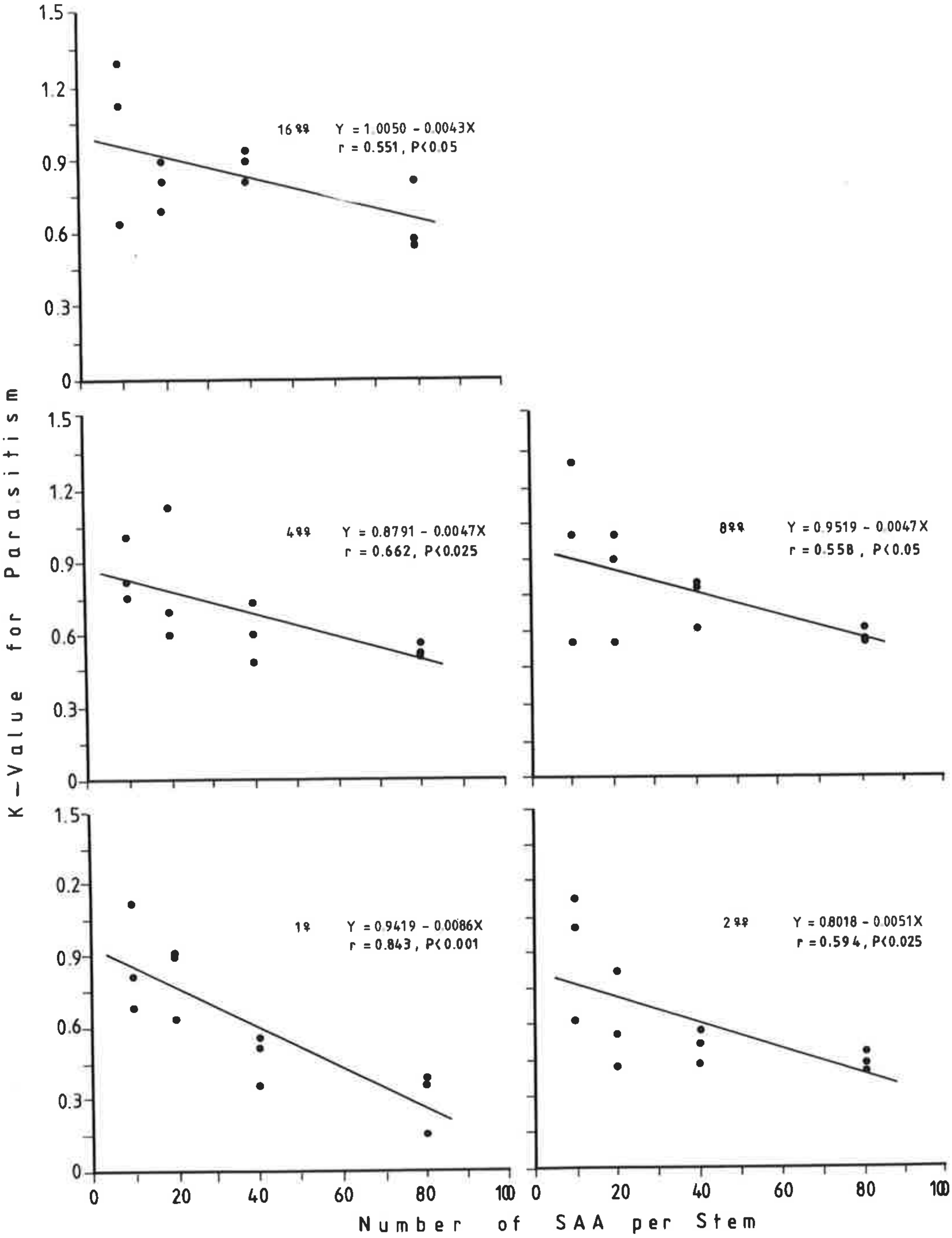

K—Value for Parasitism
Number of SAA per Stem
1.5
1.2
0.9
0.6
0.3
0
0.2
0
20
40
60
80
100
16♀♀ Y = 1.0050 - 0.0043X
r = 0.551, P<0.05
4♀♀ Y = 0.8791 - 0.0047X
r = 0.662, P<0.025
8♀♀ Y = 0.9519 - 0.0047X
r = 0.558, P<0.05
1♀ Y = 0.9419 - 0.0086X
r = 0.843, P<0.001
2♀♀ Y = 0.8018 - 0.0051X
r = 0.594, P<0.025

Fig. 29

significantly from b = 0; and the values of the slopes were plotted against *Trioxys* densities in Figure 29.2. The trend of the slopes increased sharply from 1 to 2 *Trioxys* but flattened out then. The flattening out of the slope after 2 *Trioxys* density was probably due to the interference between searching *Trioxys* increases as parasitoid density increases.

The inverse response of *Trioxys* to host density could have resulted from each female of *Trioxys* parasitizing a few~~er~~ of the SAA population when the density of the aphids was high then when it was low. This finding is not consistent with the behavioural responses of many insect parasitoids as discussed by Hassell (1969). However, the underlying cause of this phenomenon cannot be explained by the data available.

There are at least two possible hypotheses to explain why *Trioxys* showed an inversely density-dependent response behaviour: (i) *Trioxys* may aggregate in areas of higher host density but the total searching time spent by each parasitoid is proportionately less in higher host density due to a strong interference between searching *Trioxys* as described above (Figure 28; Table 19), and (ii) *Trioxys* may search at random but handling time of each parasitoid is proportionately longer in areas of higher host density.

6.2.2 Experiment VI

(1) Materials and Methods

Is was assumed that the inverse density-dependent response of *Trioxys* described in experiment V above could be due to both or either the following hypotyeses: (i) handling time per female *Trioxys* is proportionately longer in area of higher host density, (ii) interference between searching parasitoids is stronger in higher parasitoid density. In this experiment low parasitoid density (2 females of *Trioxys* per cage) was used to reduce as far as possible the in~~s~~cidence of interference between searching parasitoids and therefore the "handling time" could be tested seperately.

The materials used were basically similar to those of experiment V described in Section 6.2.1. The difference was only on the method. In each cage there were again 9 excised lucerne stems but only the middle one (in 3x3 grids) infested with a particular number of aphids. The other 8 stems had no aphids; so only the centre stem was enclosed with a plastic cup plus fluon as before to keep the aphids from escaping from it.

The treatments were different host density varying from 10 to 320 aphids (1st and 2nd instar nymphs) per cage. Each treatment was replicated 8 times. The aphid was allowed to settle down for 24 h before two mated, one day old females of *Trioxys* were introduced into the cage. The parasitoids were removed after 24 hours and the aphids were reared on freshly cut lucerne stems and held for several days until the parasitized aphids were mummified and could be counted.

The experiment was conducted in the insectary cubicle at 22-26 °C with 14-10 h L-D photoperiod and 50-60% RH.

(2) Results and Discussion

For this experiment the number of host parasitized at each host density is again expressed as number of host mummified. The numbers are presented in Table 21 and the calculated k-values for parasitism over all replicates for each host density are given in the last row of the table.

The relationship between k-value and host density as independent variable is illustrated in Figure 30 and shows a similar result to that of experiment V above. The data in Table 21 also show that the proportion of host parasitized decreases as host density increases. Since the parasitoid in each cage were exposed to only one particular host density and because there should have been minimal physical interference between two searching parasitoids especially at the higher host densities, the subproportional response of *Trioxys* to host density is likely to be due to the handling time of females of *Trioxys* getting proportionately longer as host density

Table 21. Numbers of hosts mummified in each of 8 replicates at different host densities. Two females of *Trioxys* were confined with the aphids in each replicate for 48 hours at 22-26°C, 14h L-D photoperiod and 50-60% RH.

Replicates	Initial host density (per replicate)					
	10	20	40	80	160	320
I	10	20	35	59	125	69
II	10	20	24	60	104	94
III	10	13	29	41	109	198
IV	10	18	40	57	97	131
V	9	17	40	67	132	111
VI	7	18	30	70	119	217
VII	10	14	32	72	134	168
VIII	7	18	34	67	103	193
Total parasitized:	73	138	264	493	923	1181
Mean hosts parasitized:	9.125	17.250	33.000	61.625	115.375	147.625
Mean hosts not parasitized:	0.875	2.750	7.000	18.375	44.625	172.375
% Parasitized:	91.3	86.3	82.5	77.0	72.1	46.1
k-value*:	1.0580	0.8617	0.7570	0.6389	0.5546	0.2687

* k-value = log (initial mean host density - mean number of host not parasitized) = - log (proportion of host not parasitized).

Figure 30.

Relationship between mean parasitism (expressed as the k-value) of *Trioxys* and initial SAA density as an independent variable; the relationship can be expressed as the linear function :

$Y = 0.9147 - 0.00214\ X\ (r = 0.940;\ P<0.05)$.

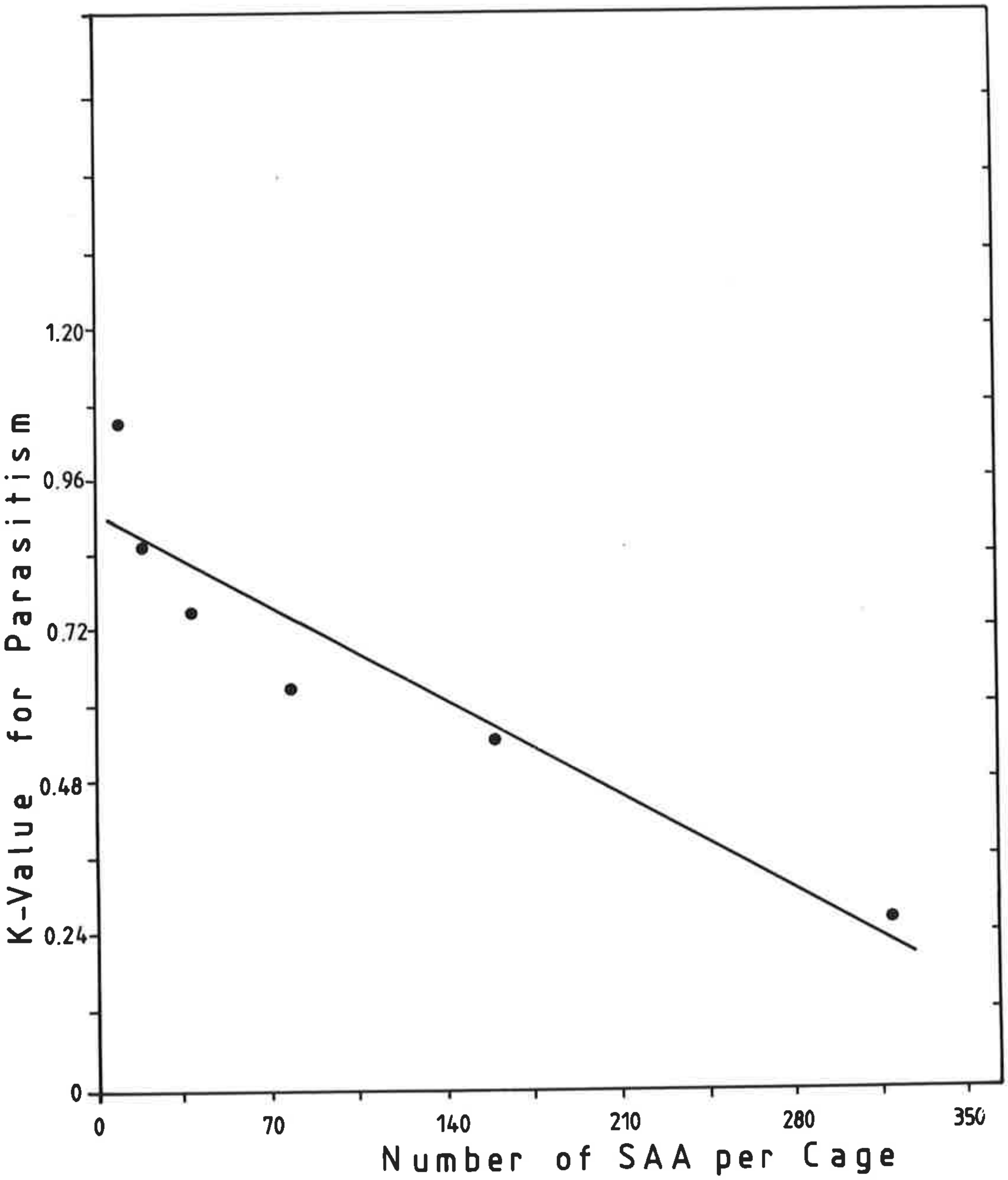

1.20
0.96
0.72
0.48
0.24
0
K-Value for Parasitism
0
70
140
210
280
350
Number of SAA per Cage

Fig. 30

increases.

The proportion of hosts mummified dropped markedly at the highest host density (320 aphids per cage) from 0.721 to 0.461 (Table 21) suggesting that the *Trioxys* then may have sufferred from egg limitation.

6.2.3 Experiment VII

(1) Materials and Methods

The only variable in experiment VI was host density; in particular, each female *Trioxys* was allowed to search for hosts for only 24 hours after mating. However, as is true of many insects, *Trioxys* has its highest oviposition rate immediately after eclosion, and the rate then decreases approximately exponentially to zero after the earlier peak (Force and Messenger 1964a). It was of interest, therefore, to determine the response of *Trioxys* to host density when *Trioxys* was allowed to search for different periods of time after eclosion.

In this experiment a female *Trioxys* was confined at each of 3 different initial host densities, namely 2, 4, and 8 newly adult aphids per cage, and at each host density she was allowed to search for one of 5 durations of time (=period of exposure) varying from 1 to 13 days.

The initial oviposition rate of *Trioxys* and the subsequent trend of the rate with time are influenced by temperature (Force and Messenger 1964a). In previous temperature studies, the daily fecundity rate of *Trioxys* decreased rapidly to zero; and the higher the temperature, the more rapid the decrease to zero. Temperature is likely therefore to give a realistic pattern of response of *Trioxys* to SAA only if it is comparable to the mean temperature in the field.

So in fact, the experiment was conducted in the field; and it was done 3 times - in early autumn, late autumn and summer- to determine the effect, on the interaction of *Trioxys* and SAA, of the mean temperature then prevailing in the field. The 3 experiments are labelled VIIA, VIIB, and VIIC. Their details are summarized in Table 22. A treatment of "aphid alone" (i.e. no *Trioxys* in the cage) was included in experiments VIIB and VIIC (see Table 22) to compare the growth rate of the SAA in the presence and absence of *Trioxys*.

All the lucerne stems used in this experiment were initially sprayed with the insecticide "Pyrethrum" to ensure that they were free from aphids. The adult SAA were obtained from the laboratory culture described in Section 2.2. The aphids for any one aphid density were artificially introduced onto a stem of "Hunter River" lucerne in a cage. Each stem was then covered with a cage as shown in Figures 31.1 and 31.2. The cage was a modification of a "spaghetti" container and had a 7.5 cm diameter and 30 cm length; the top and sides were covered with fine voile (242holes/cm^2) for ventilation. The aphids were allowed to produce progeny for 48 hours before a mated one day old female *Trioxys* was introduced into the cage.

A destructive sampling technique was employed to obtain the data for each replicate of the 15 combinations of 3 aphid densities x 5 searching times. On each sampling day, the lucerne stem was cut at the base and returned immediately to the laboratory where the parasitoid was removed and the number of live as well as mummified

Table 22. Details of the 3 field experiments on the interaction of host density and *Trioxys* searching time (=time of exposure).

Expts	Calender time of experiments	Initial host density*	*Trioxys* density per cage		Period of exposure (days)	Replicates
VIIA	24/3-8/4,1981	2, 4, 8	-	1	1,4,7,10,13	3
VIIB	5/5-22/5,1981	2, 4, 8	0	1	1,4,7,10,13	3
VIIC	19/2-25/2,1983	2, 4, 8	0	1	1,4,7,10,13	3

* Initial host density = number of reproductive adult aphids per cage.

Figure 31.

Type of the cage used in experiments VIIA, VIIB and VIIC.

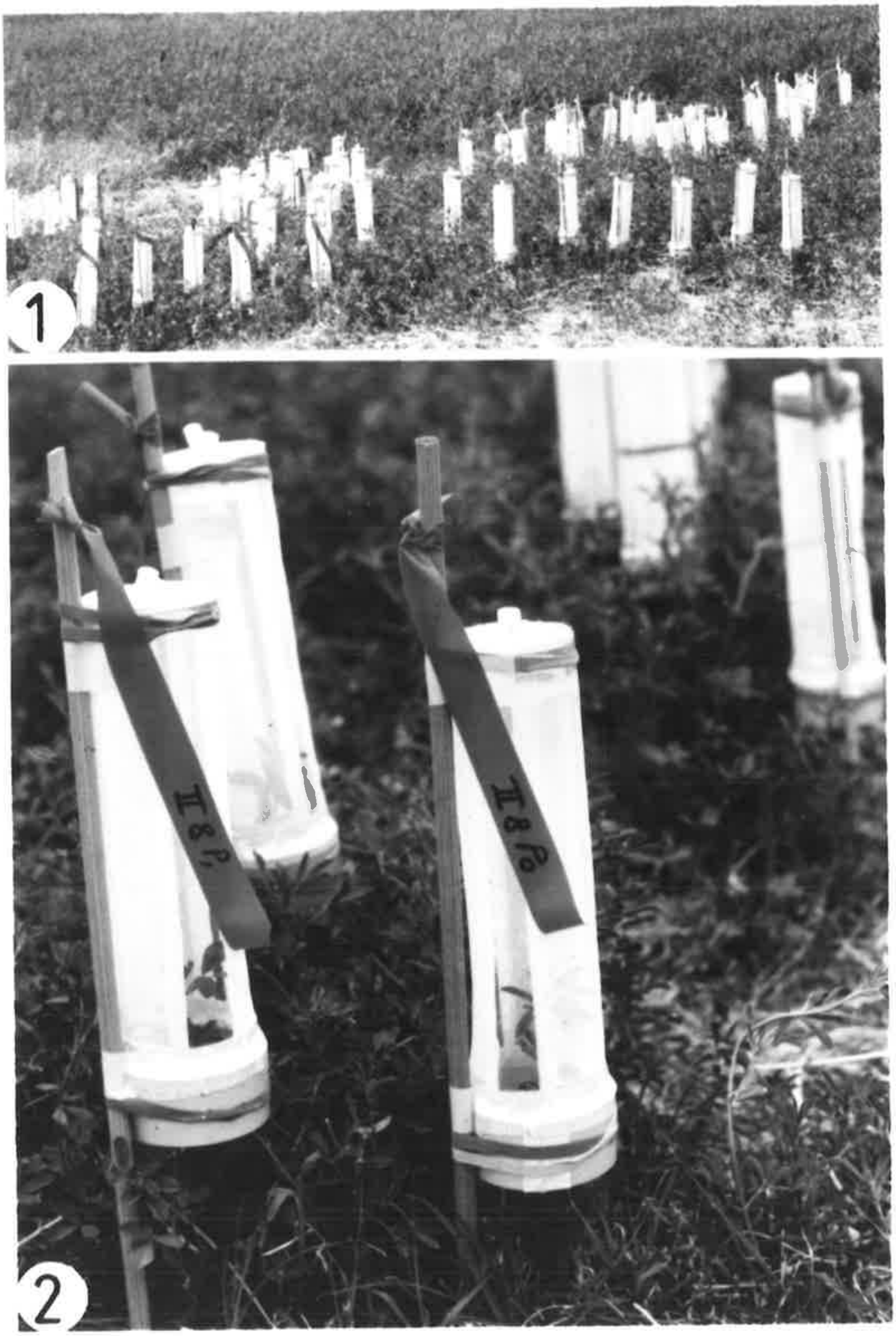


Fig. 31

aphids was recorded. The live aphids from each stem of each treatment "with *Trioxys*" were then reared on a fresh excised lucerne stem for several days until mummies were formed and could be counted.

(2) Experiment VIIA, (early autumn 1981)

(2.1) Results

Numbers of live and mummified aphids at each period of exposure are given in Table 23 and the k-values for parasitism were calculated after Hassell (1969) as described before [Section 6.2.1 (3)].

(2.1.1) Missing value

There is one missing value in Table 23 because in that replicate the lucerne stem wilted and many aphids died. So a missing value was estimated as a k-value and inserted in Appendix Table 28.1. The value was estimated from the other values in Appendix Table 28.1, using Pearce's (1965) method as follow:

Total of k-values of replicate II plus the missing value m=6.4707+m

Total of k-values of row plus the missing value m = 0.4228 + m

Grand total of the k-values plus the missing value m = 18.3705 + m

So, to make the residuals equal to zero:

$$m - (6.4707 + m)/15 - (0.4228 + m)/3 + (18.3705 + m)/45 = 0$$

$$45m - 19.4121 - 3m - 6.3420 - 15m + 18.3705 + m = 0$$

$$28m = 7.3826$$

$$m = 0.2637$$

This value of m is inserted in Appendix Table 28.1, and one degree

Table 23. Numbers of live (not parasitized) aphids and mummies per lucerne stem at difference host densities and with different exposure periods; experiment VIA , 24 March-8 April (early autumn) 1981. The symbols E and H denoted for exposure periods and host densities respectively.

		Replicates								
		I		II		III		Total		
(E)	(H)	Live aphids	Mummies	Live aphids	Mummies	Live aphids	Mummies	Live aphids	Mummies	% prstm
1	2	9	12	15	29	10	17	34	58	63.0
	4	11	22	19	32	20	25	50	79	61.2
	8	23	41	22	53	55	36	100	130	56.5
4	2	4	37	16	43	12	36	32	116	78.4
	4	48	45	29	52	11	57	88	154	63.6
	8	39	56	69	51	13	68	121	175	59.1
7	2	35	57	20	63	12	48	67	168	71.5
	4	48	98	30	77	67	64	145	239	62.2
	8	81	117	38	120	108	65	227	302	57.1
10	2	71	109	52	81	76	69	199	259	56.6
	4	80	89	103	83	81	76	264	248	48.4
	8	131	77	169	69	94	125	394	271	40.8
13	2	95	68	47	93	86	97	228	258	53.1
	4	154	72	96	92	145	102	395	266	40.2
	8	187	132	n.a	n.a	136	75	323	207	39.1
Total		1016	1032	725	938	926	960	2667	2930	52.3*

a) days after *Trioxys* introduction,

n.a = data were missing because the lucerne stem wilted and many aphids died.

* based on total.

of freedom was substracted from the total d.f. in subsequent analyses.

(2.1.2) Analysis of data

Initially I thought that the data might be usefullly analysed by comparing the slopes of regressions, so the k-values for parasitism in each replicate were plotted against the total number of aphids that had been produced in that replicate - for each duration of exposure separately (see Figure 32). The data were then analysed to determine if each regression was significantly linear. Unfortunately, the only significant linear regression was that for 4 days (Appendix Table 29), so recourse was then made to the analysis of variance to test the influence, on parasitism, of the two variables : (a) exposure period of *Trioxys* and (b) host density. The effect of the latter variable was desired to be examined more precisely than the former so a split plot analysis of variance was used. Of this design, Snedecor and Cochran (1967) say "Relative to randomized blocks, the split-plot design gives reduced accuracy on the main plot treatments and increased accuracy on sub-plot treatments and interactions". In addition, however, an ANOVA was also done with a randomized block design to compare with the split-plot.

Before the ANOVA was done, however, a Bartlett's test of homogeneity of variance was conducted, and then a Tukey's test of additivity was done because of the possibility that some of the k-values were proportional to each other rather than being additive.

Figure 32.

Relationship between parasitism (expressed as the k-value) by *Trioxys* and SAA density. Each graph shows the result obtained from different exposure periods:

(1) 1 day,
(2) 4 days,
(3) 7 days,
(4) 10 days,
(5) 13 days.

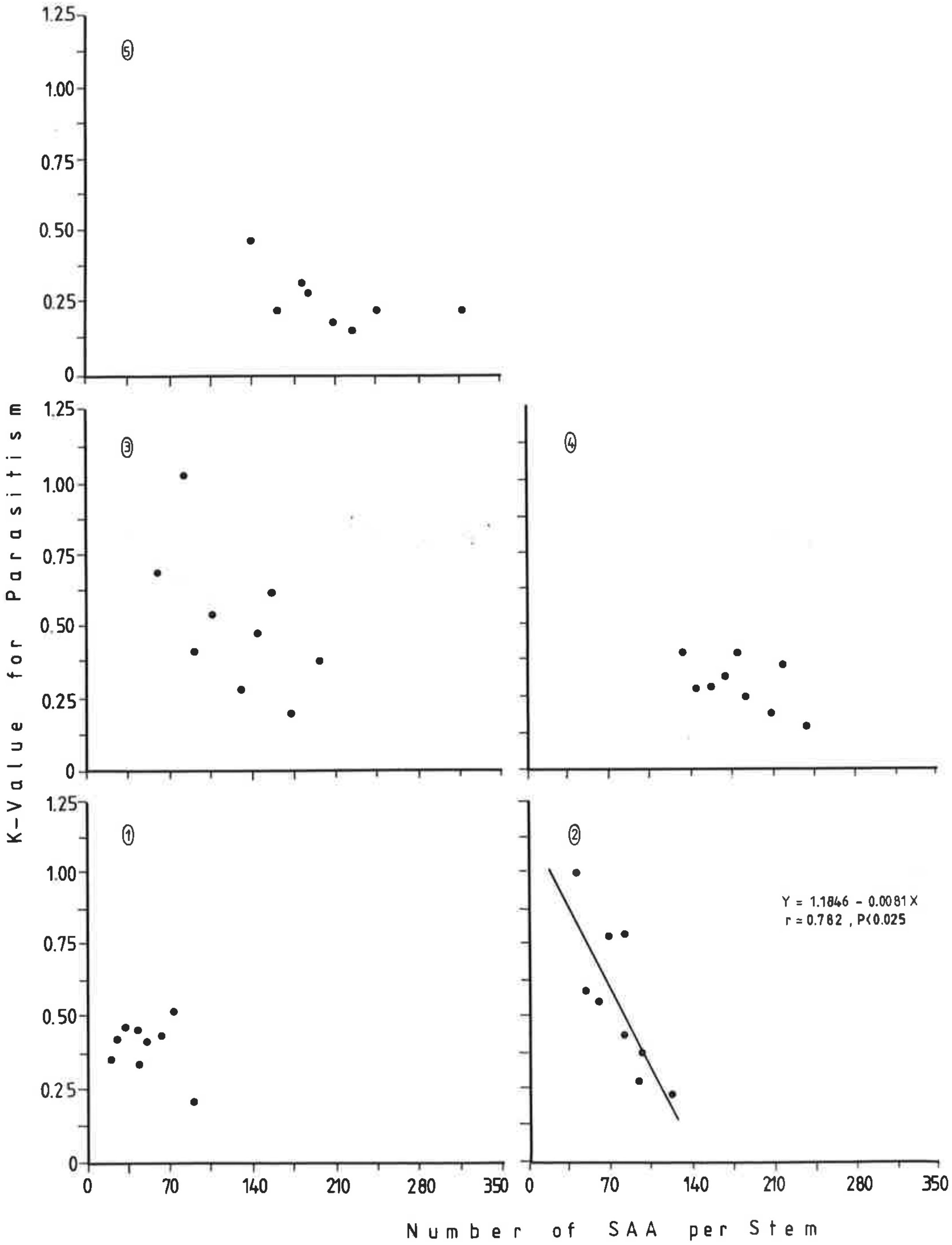

1.25
1.00
0.75
0.50
0.25
0
⑤
③
④
①
②
Y = 1.1846 - 0.0081 X
r = 0.782 , P<0.025
K-Value for Parasitism
0
70
140
210
280
350
Number of SAA per Stem

Fig. 32

2.1.3 Bartlett's test of homogeneity of variance

The test was adopted from Snedecor and Cochran (1967; p 296-298) to test the null hypothesis that all variance were homogeneous; the computation of the test is given in Appendix Table 30. The test shows that variances were homogeneous.

2.1.4 Tukey's test of additivity

The test was taken from Snedecor and Cochran (1967; p 331-337). The application of Tukey's additivity test and the analysis of variance for the test of additivity of the mean of the k-values for parasitism is given in Appendix Tables 31.1 and 31.2. The mean square of "non additivity" is compared with the residual mean square: 0.0155/0.0027 = 5.47 with 1,7 d.f. and gave $0.01<P<0.05$. A *prima facie* case can then be made for transforming the data before using ANOVA. However, a transformation of a k-value may be biologically unreal, and since the F ratio of 5.74 was only slightly larger than the value of 5.59 at $P = 0.05$ the acceptance of the hypothesis of additivity at a slightly lower probability than $P = 0.05$ was considered a better compromise. The k-values were then tested by ANOVA.

2.1.5 The null hypotheses

To illustrate the null hypotheses to be tested by ANOVA, the treatment means to be tested are given in Table 24 and convenient symbols for them are also given in the table. The analysis tested the null hypotheses that:

(i) the mean k-values of the exposure periods are equal,

i.e. E1 = E2 + ... = E5,

(ii) the mean k-values of the host densities are equal,

i.e. H1 = H2 = H3,

(iii) the mean k-values for the 15 combinations of host density and exposure period are equal,

i.e. EH1 = EH2 = ... = EH15.

2.1.6 ANOVA with the split-plot design

The ANOVA for the split plot design is calculated from Appendix Tables 28.1 and 28.2 and is given in Table 25. The mean square for exposure periods (E) is tested against the error (a) mean square, and the mean square for host densities (H) and interaction between exposure period-host density (EH) are tested against the error (b) mean square. The variance ratios then give the following F tests:

(i) Exposure periods: F = 0.1726/0.0416 = 4.1490;

d.f. = 4,8 ; P<.05

(ii) Host densities : F = 0.1189/0.0271 = 4.3874;

d.f. = 2,19 ; P<.01

(iii) Interactions : F = 0.0062/0.0271 = 0.2288;

d.f. = 8,19 ; P>.25 ; N.S.

Although the F test for "Exposure periods" and "Host densities" are significant, they give no information about which of the means are causing the significance. To examine more closely all possible differences between the means of the k-values of both treatments, a least significant different (l.s.d.) was estimated as follows:

Table 24. The means of parasitism,expressed as the mean k-value, per replicate for each treatment; experiment VIIA, early autumn 1981. The symbols E1 to E5, H1 to H3 and EH1 to EH15 are also given to enable the hypotheses to be clearly stated in the text.

Exposure periods (days)	Host Densities (adults/stem)			Means for exposure periods
	2	4	8	
1	0.4223(EH1)	0.4194(EH2)	0.3986(EH3)	0.4134(E1)
4	0.7266(EH4)	0.5084(EH5)	0.4739(EH6)	0.5696(E2)
7	0.7189(EH7)	0.4422(EH8)	0.4039(EH9)	0.5217(E3)
10	0.3642(EH10)	0.2897(EH11)	0.2390(EH12)	0.2976(E4)
13	0.3455(EH13)	0.2300(EH14)	0.2198(EH15)	0.2651(E5)
Means for host densities	0.5155 (H1)	0.3779 (H2)	0.3470 (H3)	

Table 25. Analysis of variance with the split-plot design of the k-values for parasitism when 1 *Trioxys* female was exposed to different host densities and exposure periods; experiment VIIA, 24 March - 8 April (early autumn) 1981.

Source of variation	d.f.	SS	MS	F	P
Main-plots	14	1.0529			
Blocks (replicates)	2	0.0293			
Exposure periods (E)	4	0.6905	0.1726	4.1490	<.05
Error (a)	8	0.3331	0.0416		
Sub-plots	30	0.8023			
Host densities (H)	2	0.2377	0.1189	4.3874	<.05
Interaction (EH)	8	0.0429	0.0062	0.2288	>.25 N.S.
Error (b)*	19	0.5154	0.0271		
Total	43	1.0529			

* d.f. error was reduced by 1 for the missing value.

Table 26. Comparison between treatment means; split-plot design.

Treatments	Mean of the k-values		
(A) Exposure Periode			
E2 (4days)	0.5696	a	
E3 (7days)	0.5217	a	
E1 (1day)	0.4134	a	b
E4 (10days)	0.2976		b
E5 (13 days)	0.2681		b
l.s.d. (5%)	0.2216		
(B) Host Density			
H1, 2 adults/stem	0.5155	a	
H2, 4 adults/stem	0.3779	b	
H3, 8 adults/stem	0.3489	b	
l.s.d. (5%)	0.1258		

A t-test to determine the difference between two means gives a value of t as: t = difference between means/S.E.of difference. So a least significant difference can be calculated as:

l.s.d. = t x S.E. of difference. Then

(a) l.s.d. of exposure periods = t (8 d.f.) x S.E. of difference

$= 2.306 \times (\sqrt{2} \times \sqrt{0.0416})/\sqrt{9} = 0.2216$, and

(b) l.s.d. of host densities = t (20 d.f.) x S.E. of difference

$= 2.086 \times (\sqrt{2} \times \sqrt{0.0271})/\sqrt{15} = 0.1258$

These values of l.s.d^{s} are given in Table 26 to compare the respective means. Those means which are not significantly different are grouped by a common letter.

2.1.7 ANOVA with the randomized block design

The ANOVA for a randomized block design is given in Table 27. The mean squares of the main effects (exposure periods and host densities) and those of the interactions are all tested against the mean square of error as follows:

(i)exposure periods: F = 0.1726/0.0314 = 5.4968; d.f. = 4,27; $P<.005$

(ii) host densities: F = 0.1189/0/0314 = 3.7866; d.f. = 2,27; $P<.05$

(iii) interactions: F = 0.0062/0.0314 = 0.1975; d.f. = 8,27; $P>0.25$

To examine more closely all possible differences between the means of k-values of the exposure periods and host densities, an l.s.d. was again estimated for each group of means as follows:

l.s.d. of exposure periods = t (27 d.f.) x S.E. of difference

$= 2.052 \times (\sqrt{2} \times \sqrt{0.0314})/\sqrt{9} = 0.1714$

Table 27. Analysis of variance with the randomized block design of the k-values for parasitism when 1 *Trioxys* female was exposed to different host densities and exposure periods; experiment VIIA, 24 March - 8 April (early autumn) 1981.

Source of variation	d.f.	SS	MS	F	P
Total	43	1.8552			
Blocks (replicates)(B)	2	0.0293			
Exposure periods (E)	4	0.6905	0.1726	5.4968	<.005
Host densities (H)	2	0.2377	0.1189	3.7866	<.05
Interactions: (EH)	8	0.0492	0.0062	0.1975	N.S.
Error *	27	0.8485	0.0314		

* d.f. error was redued by 1 for the missing value.

Table 28. Comparison between treatment means; randomized block design.

Treatments	Mean of the k-value		
(A) Exposure Periode			
E2 (4days)	0.5696	a	
E3 (7days)	0.5217	a	
E1 (1day)	0.4134	a	b
E4 (10days)	0.2976		b
E5 (13 days)	0.2681		b
l.s.d. (5%)	0.1714		
(B) Host Density			
H1, 2 adults/stem	0.5155	a	
H2, 4 adults/stem	0.3779	b	
H3, 8 adults/stem	0.3489	b	
l.s.d. (5%)	0.1328		

l.s.d. of host densities = t (27 d.f.) x S.E. of difference

$= 2.052 \times (\sqrt{2} \times \sqrt{0.0314})/\sqrt{15} = 0.1328$

The multiple comparisons for significance between the mean k-values of exposure periods and those of host densities are summarized in Table 28.

2.1.8 Comparison of the split-plot and randomized block designs

(i) The variance ratios (VR)

The variance ratios of the split plot design are compared with those of the randomized block design (each was taken from Tables 25 and 27 respectively) in Table 29 below. They show that the randomized block design gave a higher precision for "exposure periods" and both designs gave the same precision for "host densities".

(ii) The l.s.d. (Table 26 versus Table 28)

The l.s.d. value for comparison of the means of k-values of host densities in the split plot design is marginally better than that of the randomized block design but the value of l.s.d. for comparison of the means of k-values of exposure periods in the split-plot is higher than that of the randomized block. Both designs, however, gave the same consequences of applying the l.s.d.'s to the means k-values for either exposure periods or host densities.

(2.2) Discussion

The results (Tables 26 and 28) clearly show the mean k-value for parasitism for the initial host density of 2 aphids per

Table 29. Comparison of level of precision of F test for the split-plot and randomized block design; experiment VIIA, 24 March-8 April (early autumn) 1981.

Treatments	Split-plot	Randomized block
Exposure periods	VR = 4.1490 d.f. = 4,8 0.05>P>0.01	VR = 5.4968 d.f. = 4,27 P<0.005
Host densities	VR = 4.3874 d.f. = 2,19 0.05>P>0.01	VR = 3.7866 d.f. = 2,27 0.05>P>0.01

stem is significantly higher than those for 4 aphids and 8 aphids per stem, but the difference between the mean k-values for initial host densities of 4 and 8 aphids per stem was not significant. It is concluded that *Trioxys* responded better in the lower host density i.e. the number of host that escaped parasitism was proportionately higher as the host density increased. This result supports the previous results obtained from both field census (Section 4.2) and from experiments V and VI (Sections 6.2.1 and 6.2.2) and suggests that this inverse density-dependent response of *Trioxys* could have resulted from differential handling time of the parasitoid which increases with host density.

The l.s.d. test shows that the there was no significant difference of the mean k-values between exposure periods of 1, 4, and 7 days. Similarly the exposure periods of 1, 10 and 13 days are not different. However, the the test shows that the mean k-value for parasitism of day 4 and 7 are significantly higher than those of day 10 and 13. These differences are likely to be due to the following factors:

(i) The oviposition rate of *Trioxys* could have been much reduced by day 7 after the introduction of the parasitoid because it usually oviposits at a higher rate for the first few days after eclosion (Force and Messenger 1964a),

(ii) at 21.1 ^{o}C (the mean temperature during this experiment was 20.6 ^{o}C) the developmental period of SAA was about 7.2-8.3 days (Messenger 1964), and so those SAA that escaped parasitism could have started to reproduce at day 8 from the start of the experiment (= 6 days after *Trioxys* introduction).

A combination of these two factors probably increased the proportion of aphids that escaped parasitism at and after day 8 from the start of the experiment. This proportion that escaped parasitism then is reflected by the proportions of parasitized hosts on days 10 and 13 being much lower than those on days 4 and 7.

(3) **Experiment VIIB, (late autumn 1981)**

(3.1) **Results**

Numbers of live (not parasitized) and mummified aphids at each period of exposure are given in Tables 30. In this table is also shown the numbers of aphid produced in each treatment of "aphids alone", i.e. no *Trioxys* in the cage.

The effect of *Trioxys* on the reduction of aphid numbers can be estimated by comparing the numbers of live aphids in treatments with *Trioxys* against treatments with no *Trioxys* (see Table 30 last line of columns 12 and 13). The estimate of total reduction on aphid numbers by *Trioxys* = (3916 - 1336)/3916 = 65.9% . The mean parasitism over all treatments with *Trioxys* can be estimated from data in columns 13 and 14 as 2338/(1336 + 2338) x 100 = 63.6%

(3.2) **Analysis of data**

The k-values for parasitism are calculated as described in Section 6.2.1. (3) after Hassell (1969); they are presented in Appendix Tables 32.1 and 32.2.

Table 30. Numbers of live (not parasitized) aphids (A) in treatments with no *Trioxys* (i.e."control" = -Tr.) and the mumbers of live (not parasitized) aphids and the mummies (M) of *Trioxys* in treatment with *Trioxys* (+Tr.) -at each of 3 host densities (H; =2, 4 and 8) and at each of 5 different exposure periods (E; = 1, 4, 7, 10, and 13 days). Experiment VIIB; 5-22 May (late autumn) 1981.

		Replicate I			Replicate II			Replicate III			TOTAL			
Treats.		-Tr.	+Tr.		-Tr.	+Tr.		-Tr.	+Tr.		-Tr.	+Tr.		%
(E)	(H)	A	A	M	A	A	M	A	A	M	A	A	M	Prstm.
1	2	20	7	9	19	4	6	11	14	11	50	25	26	51.0
	4	36	14	20	19	21	17	31	17	11	86	52	48	48.0
	8	71	18	16	43	37	22	73	54	27	187	109	65	37.4
4	2	36	12	22	20	9	17	39	19	14	95	40	53	57.0
	4	45	35	26	71	10	17	61	58	39	177	103	82	44.3
	8	98	47	34	119	35	50	89	75	29	306	157	113	41.9
7	2	35	7	35	46	9	27	41	35	23	122	51	85	62.5
	4	83	24	54	88	33	40	56	65	46	227	122	140	53.4
	8	109	68	52	140	57	96	116	108	73	365	233	221	48.7
10	2	62	10	43	33	5	35	49	32	24	144	47	102	68.5
	4	133	40	101	104	52	68	121	96	75	358	188	244	56.5
	8	162	63	93	180	87	112	153	175	120	495	325	325	50.0
13	2	60	8	49	53	8	58	76	71	53	189	87	160	64.8
	4	154	39	123	171	43	104	124	119	76	449	201	302	60.1
	8	216	69	125	258	104	109	192	181	137	666	354	371	51.2
TOTAL		1320	461	802	1364	514	778	1232	1119	758	3916	2094	2338	52.8*

* Based on totals.

I first explored the possibility of using ANOVA, as for experiment VIIA, to test the influence of the response of *Trioxys* on different host densities with different periods of exposure. So a Tukey's test of additivity was applied to the data; the results (Appendix Tables 33.1 and 33.2) indicated that the effects of host density and exposure period of *Trioxys* were significantly non-additive, with P<0.01. The data were so significantly non-additive that a transformation- probably to square or cubic roots- would be required for the assumption about additivity to be satisfied for the ANOVA. However, as mentioned in the disscussion of the analysis of the data for experiment VIIA, a transformation of the k-value is likely to be biologically unreal. So the attempt to use an ANOVA was discarded, and regression analysis was explored instead. For regression analysis, the behaviour responses of *Trioxys* at each exposure period were initially illustrated by plotting the k-values against host densities (Figure 33). The plots looked promising, so the linearity of the k-values on host densities was analyzed for each duration of exposure independently (Appendix Table 34). The results indicated that the regression were significant at P = 0.05 for day 1, 10 days and 13 days; and at 4 days and 7 days the F ratios had probabilities of 0.057 and 0.10 respectively. Since experiments with aphids are notoriously variable (Maelzer, pers. comm.) and since the regression model should really be a complex one with both X and Y measured with different errors (rather than with X measured with no error- see Acton 1966), it seemed that the best compromise was to accept the regressions at 4 and 7 days at P = 0.10 rather than the usually accepted P = 0.05 and then to examine the trend in the value

Figure 33.

Relationship between parasitism (expressed as the k-value) by *Trioxys* and SAA density. Each graph shows the result obtained from different exposure periods:

(1) 1 day,
(2) 4 days,
(3) 7 days,
(4) 10 days,
(5) 13 days.

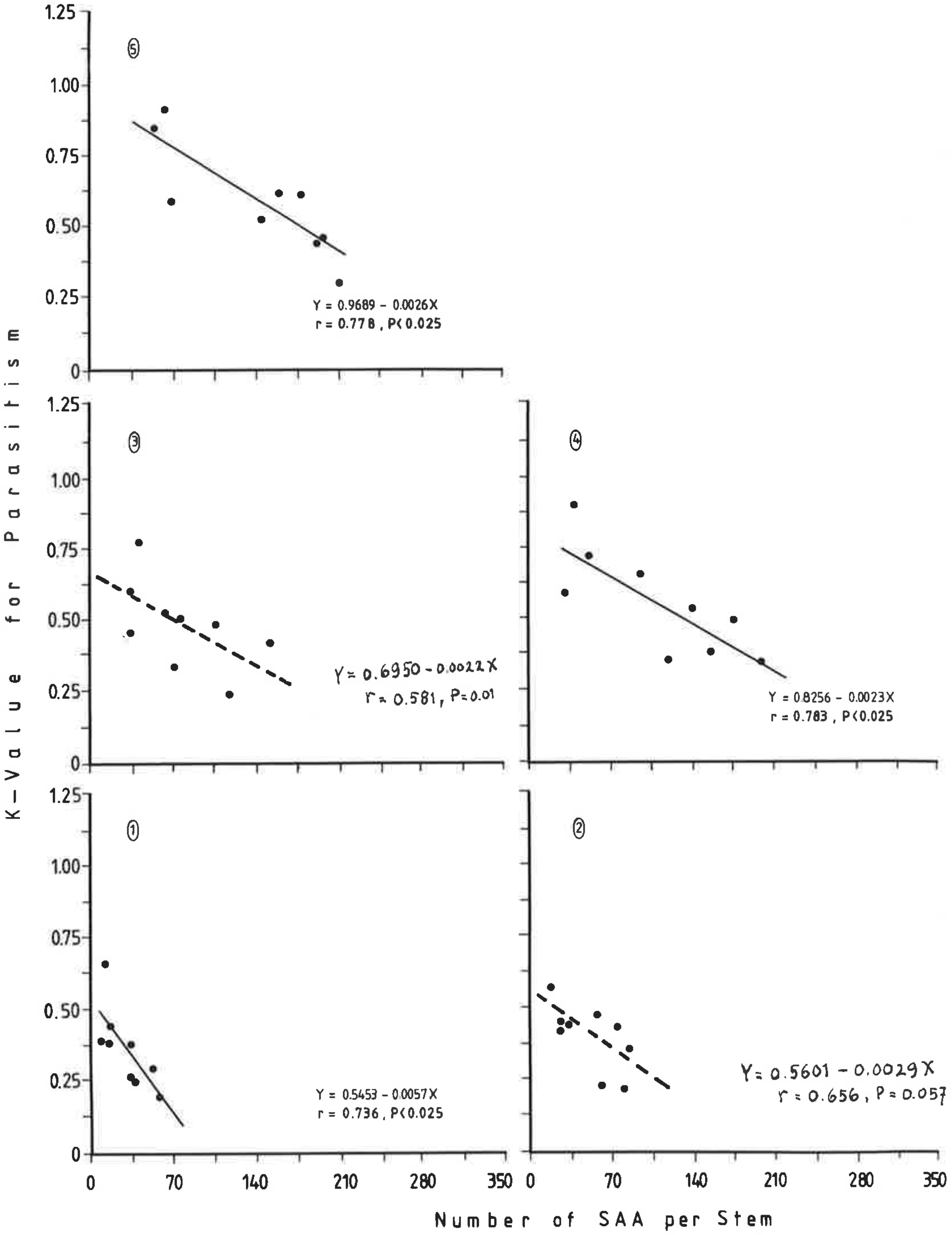

K – Value for Parasitism
Number of SAA per Stem
⑤
Y = 0.9689 – 0.0026X
r = 0.778 , P<0.025
③
Y = 0.6950 – 0.0022X
r = 0.581, P=0.01
④
Y = 0.8256 – 0.0023X
r = 0.783 , P<0.025
①
Y = 0.5453 – 0.0057X
r = 0.736 , P<0.025
②
Y = 0.5601 – 0.0029X
r = 0.656 , P = 0.057
1.25
1.00
0.75
0.50
0.25
0
0
70
140
210
280
350

Fig. 33

of the slopes. Consequently regression lines were also calculated for 4 days and 7 days and are drawn in Figure 33 as dotted lines; and the values of the slopes were plotted against exposure periods (Figure34).

(3.3) Discussion

The trend of the slopes in Figure 34 increased sharply from day 1 to day 4 but then flattened out. This result was expected (see information below) because of the direct influence of the relatively low temperature on the biology of *Trioxys* and SAA. At low temperatures the mean daily realized fecundity of *Trioxys* is relatively more constant than in warm temperature and only decreases gradually after about day 8 after eclosion (Force and Messenger 1964a, Roberts 1978). By contrast, the SAA develops slower and produces fewer progeny per day at low temperatures (Messenger 1964, Hughes and Roberts 1978). So at relatively low temperature, *Trioxys* needs distribute its progeny among relatively fewer hosts (compare the total numbers of aphids produced in each treatment "with *Trioxys*" in Table 23 with those in Table 30). The flattening out of the slope in Figure 34 after day 4 was probably due to the fecundity of *Trioxys* was declining then.

The responses of *Trioxys* at each host density are illustrated in Figure 35 in which the k-values for parasitism are plotted against the exposure periods of *Trioxys* ; all the regression lines were obviously linear. The difference in the response of

Figure 34.

Relationship of the slopes of regression lines in Figure 33 and exposure periods of *Trioxys* to the SAA. The slopes represent the response of the parasitoid (expressed as the k-value for parasitism) to different host density.

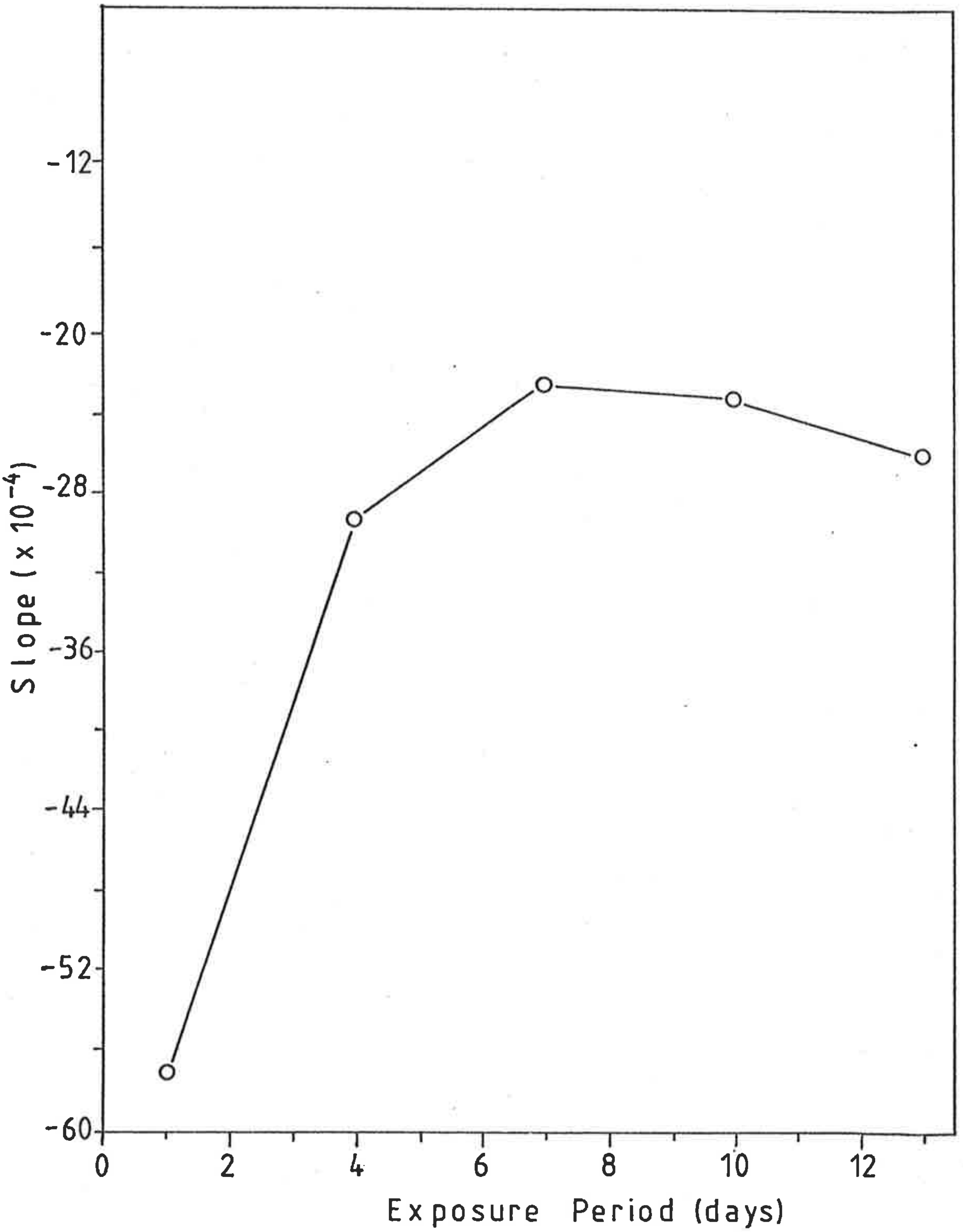

-12
-20
-28
-36
-44
-52
-60
Slope (x 10^{-4})
0
2
4
6
8
10
12
Exposure Period (days)

Fig. 34

Figure 35.

Relationship between parasitism (expressed as the k-value) by *Trioxys* and the exposure period. Each line represents the plotted response of the parasitoids on different (initial) host densities, i.e.:

2 newly reproductive adult SAA per stem (○),
4 newly reproductive adult SAA per syem (□), and
8 newly reproductive adult SAA per stem (●).

Each of the relationship can be expressed as the linear function;

(○): $Y = 0.4281 + 0.0283\ X$ ($r = 0.9738$, $P<0.01$),
(□): $Y = 0.3425 + 0.0161\ X$ ($r = 0.9760$, $P<0.005$),
(●): $Y = 0.2639 + 0.0157\ X$ ($r = 0.9784$, $P<0.005$).

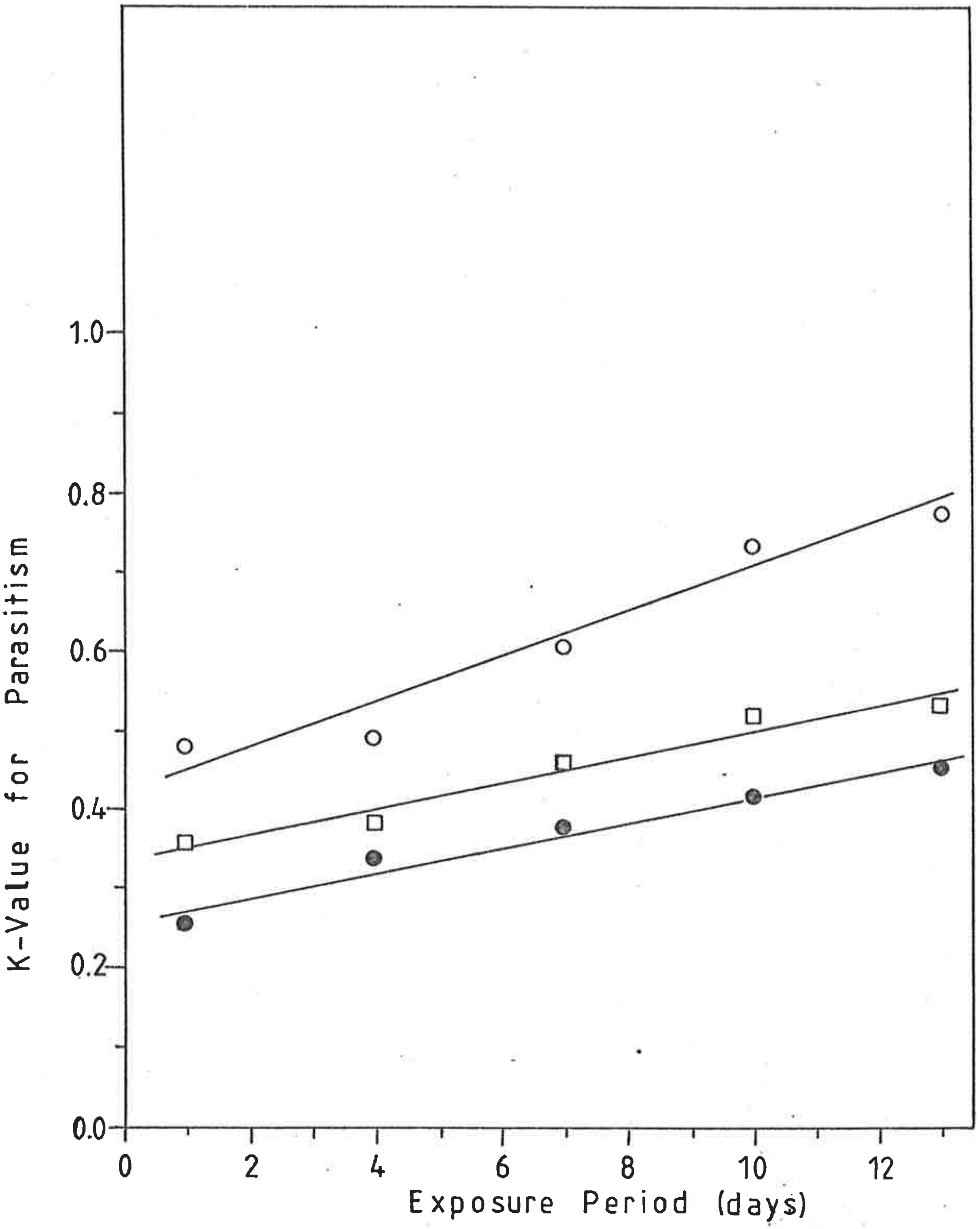

K-Value for Parasitism
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
Exposure Period (days)

Fig. 35

Trioxys at the different host densities can be inferred by comparing the slopes of the regression lines. The analysis (Appendix Table 35) indicated that the slope for 2 (initial) SAA per stem was significantly bigger than the slopes for 4 (and so 8) SAA per stem. However, there was no obvious difference between the slopes for 4 and 8 SAA per stem. Thus this result corroborates the previous results described in experiment VIIA and in Sections 6.2.1, 6.2.2 and suggests that the inverse density-dependent response of *Trioxys* could have resulted from differential handling time of the parasitoid which increases as host density increases.

(4) Experiment VIIC (summer 1983)

The summer experiment (experiment VIIC) was abandoned because most of the adult *Trioxys* died before day 4, probably due to the effect of high temperature inside the cage. During a 7 day period from the start of this experiment, the mean daily maximum temperature was 32.2 ^{o}C and it fluctuated from 25.6-36.8 ^{o}C. By comparison, the mean daily maximum temperatures during a 15 day period after the start of the experiments of early and late autumn 1981 were 20.6 ^{o}C and 14.4 ^{o}C, respectively.

6.3 The Effect of Host and Parasitoid Density on Sex Ratio of *Trioxys* progeny

6.3.1 Introduction

The proportion of female progeny produced by a parasitoid determines the number of hosts that will be parasitized in the next generation. Stary (1970) noted that the mean fecundity represents one of the important phenomena for understanding the effectiveness of the Aphidiid parasitoids under various conditions; and he believes, like Flanders (1939,1942,1946) that the proportion of male-female progeny of a parasitoid can vary as a result of various extrinsic and intrinsic factors acting on the female parasitoid. One of the most important of these factors is the host-parasitoid density ratio. Thus Lawrence (1981) found that the proportion of female progeny of *Biosteres longicaudatus* Ashmead in the larva of *Anastrepha suspensa* Loew. decreased as female parasitoid density increased. A similar result was observed by Wylie (1966) for *Nasonia vitripennis* (Walk.) parasitizing *Musca domestica* L. puparia. However, Wylie (1966) could not determine the reasons for the changing of the sex ratio of the parasitoid, and assumed that some mechanism associated with superparasitism could have been responsible.

Superparasitism in *Trioxys* populations has been commonly found because the females apparently are unable to distinguish previously parasitized hosts (Schlinger and Hall 1961). So one might expect, for *Trioxys*, that the incidence of superparasitism increases as the ratio of female *Trioxys* to SAA density increases.

Evidence obtained from field census (Section 3.3.1.3c) indicated that the sex ratio of *Trioxys* progeny was, indeed, influenced either by host or parasitoid densities. The following experiments VIII and IX were conducted in a controlled environment to quantify these influences on the sex ratio.

6.3.2 Experiment VIII; The Effect of *Trioxys* Density on the sex-ratio of the progeny

(1) Materials and Methods

The treatments were different densities of *Trioxys* females varying from 1 to 16 pairs per cage with 3 replicates of each treatment. Also in each cage were 160 SAA consisting of 1st, 2nd and 3rd instar nymphs. The aphids were obtained from laboratory culture and were transferred onto an excised "Hunter River" lucerne stem which was then caged with a "chimney glass" as shown in Figures 2.3 and 2.4. The cage had a diameter of 8cm and the top was covered with fine voile for ventilation. The aphids were allowed to settle down for 24 hours before the parasitoids were introduced into the cage.

Virgin females and males of *Trioxys* were obtained by rearing individual mummies. They were kept in separate cages after emergence and allowed to feed on honey solution for 24 hours before being introduced into the cage. Only those adult *Trioxys* which were of an average size were chosen for use in the experiment.

The male *Trioxys* were introduced one hour earlier than were the females. This method was adopted because the parasitoids tend to aggregate at the top of the cage for some time after introduction and mate rather than search for hosts. So the males were introduced earlier in the hope that they would disperse amongst the host within the cage before the females were introduced.

The experiment was conducted in the insectary cubicle at 20-24 °C, 50-60% RH and 14 h L-D photoperiod. Artificial illumination was provided from a bank of 10 flourescent tubes set about 50 cm obove the cages.

The parasitoids were removed after being confined with the host for 24 hours. The aphids were then reared for several days until mummies were formed. A freshly cut lucerne stem was provided for the aphids every two days. The number of mummies formed was then recorded and the mummies were removed carefully with a fine brush. Each mummy was placed in clear gelatine capsule until emergence and then sexed. A mummy which did not yield a parasitoid was dissected to determine the sex of the adult *Trioxys* but if a dead larva was found, it was recorded as such (see last column of Table 31.1).

(2) Results and Discussion

The number of hosts mummified at each parasitoid density and the corresponding number of female and male progeny that emerged are given in Table 31.1; the means of the data are shown

Table 31.1. Numbers of female and male progeny of *Trioxys* at each different its own density, each confined with 160 hosts, each group of which had been confined with a different number of parasitoids; experiment VIII.

Reps.	*Trioxys* density (pairs/cage)	Numbers of mummy	Males	Females	% males *	Numbers of dead larvae
I	1	114	67	46	59.3	1
	2	129	57	70	44.9	2
	4	140	92	45	67.2	3
	8	131	82	49	62.6	0
	16	152	102	49	67.6	1
II	1	104	69	32	68.3	3
	2	76	49	19	72.0	8
	4	160	107	49	68.6	4
	8	118	73	44	64.2	1
	16	120	58	54	51.8	8
III	1	120	61	54	53.0	5
	2	126	65	61	51.6	0
	4	146	69	75	47.9	2
	8	109	60	49	55.1	0
	16	114	62	52	54.4	0

* % male = number of male/(total number of male + female) x 100

Table 31.2. Means of data in Table 31.1.

Trioxys Densities	Numbers of *Trioxys* *	Females	Males	% Male**	SE (N = 3)
1	110	44	66	60.2	4.4
2	107	50	57	56.2	8.1
4	145	56	89	61.2	6.7
8	119	47	72	60.0	2.5
16	126	52	74	57.9	4.9

*Number of *Trioxys* = number of mummy minus number of dead larva.

**% male = mean % male of data in Table 30.1

in Table 31.2. The data show that the mean percentage of male progeny at different *Trioxys* densities did not vary much and ranged from 56 to 61%.

The means percentage male progeny were plotted against the parasitoid densities in Figure 36; and suggests that there was no relationship between the variables. This result is not in agreement with La~~r~~wrence (198~~2~~1) and Wylie (1966) both of whom demonstrated, for other parasites, a positive association between parasitoid density and sex ratio of the progeny. Figure 36 shows that the males predominated at any level of parasitoid density. This preponderance of males is unlikely to be the result of differential sex mortality during the rearing; it is much more likely to be a real effect and to be due to the availablity and density of the host (160 aphids per stem). When hosts are abundant, females *Trioxys* may begin to oviposit before mating; such oviposition will produce only male progeny (Schlinger and Hall 1961). When mating then takes place later, the females may produce female progeny but the premating interval after introduction may determine the proportion of eggs deposited before mating and thus influence the sex ratio of the progeny.

Another possible explanation of the preponderance of males is that the female *Trioxys* did mate before ovipositing but because hosts were abundant, they oviposited rapidly so that a greater proportion of their eggs escaped fertilization (Flanders 1956).

Figure 36.

Relationship between sex-ratio (% male) of *Trioxys* and the parasitoid density. The virgin parasitoids were confined to an initially constant number of aphids (= 160 SAA per cage) and allowed to search for hosts for 24 hours.

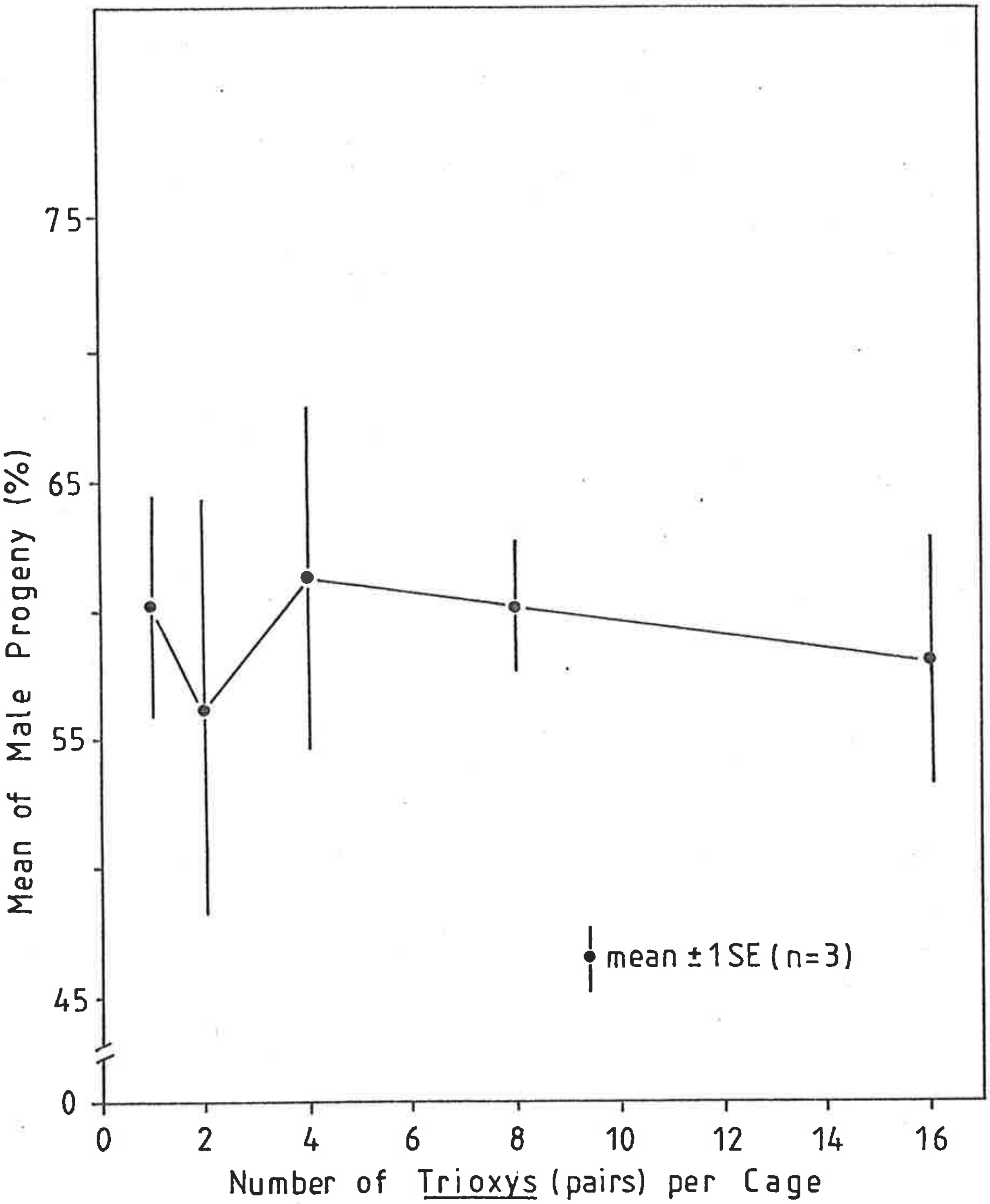

Mean of Male Progeny (%)
75
65
55
45
0
0
2
4
6
8
10
12
14
16
Number of Trioxys (pairs) per Cage
mean ± 1 SE (n=3)

Fig. 36

6.3.3 Experiment IX; The Effect of Host Density on the sex-ratio of the progeny of *Tryoxys*

(1) Materials and Methods

The materials and methods used in this experiment were virtually the same as those described in Section 5.3.2.1. But the treatments were different host densities varying from 10 to 320 SAA per stem per cage with a single pair of *Trioxys* (o + o) being introduced into each cage one day after the aphids were introduced. The parasitoids were allowed to parasitize the aphids for 48 hours. Each treatment was replicated 5 times.

The experiment was conducted at 22-26 °C, 14-10 h L-D photoperiod and 50-60% RH.

(2) Results and Discussion

The numbers of host mummified at different host densities and the corresponding numbers of male and female *Trioxys* that emerged are given in Table 32.1 and the means of the data are shown in Table 32.2. The relationship between percentage of male progeny and host density was better illustrated as a curvilinear (see Appendix Table 36) and the line $Y = 31.1417 + 0.1172X - 0.00018X^2$ ($r = 0.993$, $P<0.05$) was fitted to the data (Figure 37). The trend clearly indicates that the proportion of male progeny increased with host density.

Table 32.1. Numbers and the sexes of *Trioxys* progeny when one female *Trioxys* was presented with different host densities; experiment IX.

Reps.	Initial host density	Numbers host mummified	Numbers of males	% males *	Numbers of females	Numbers of dead larvae
I	10	7	2	28.6	5	0
	20	15	6	40.0	9	0
	40	32	6	19.4	25	1
	80	68	15	22.7	51	2
	160	114	47	42.0	65	2
	320	158	68	45.0	83	7
II	10	8	2	25.0	6	0
	20	19	6	31.6	13	0
	40	24	7	31.8	15	2
	80	70	26	37.7	43	1
	160	80	35	44.9	43	2
	320	199	101	51.8	94	4
III	10	7	3	42.9	4	0
	20	11	3	27.3	8	0
	40	30	13	43.3	17	0
	80	58	28	48.3	30	0
	160	96	43	44.8	53	0
	320	141	65	46.4	55	1
IV	10	7	3	42.9	4	0
	20	18	6	33.3	12	0
	40	26	10	38.5	16	0
	80	64	25	39.7	38	1
	160	84	39	48.1	42	3
	320	127	65	52.0	60	2
V	10	7	2	28.6	5	0
	20	12	4	33.3	8	0
	40	33	12	38.7	19	2
	80	68	32	47.1	36	0
	160	110	54	50.9	52	4
	320	127	71	56.3	55	1

Table 32.2. Means of data in Table 32.1

Initial Host Density	Numbers of *Trioxys* *	Female	Male	% Male**	SE (n = 5)
10	7.2	4.8	2.4	33.6	3.9
20	15.0	10.0	5.0	33.1	2.0
40	28.0	18.4	9.6	34.3	4.2
80	64.8	39.6	25.2	39.1	4.6
160	94.6	51.0	43.6	46.1	1.5
320	143.4	69.4	74.0	50.3	2.1

* Number of *Trioxys* = number of mummy minus number of dead larva.

** % male = mean % male of data in Table 32.1

Figure 37.

Relationship between sex-ratio (% male) of *Trioxys* and the SAA density. A male and virgin female of *Trioxys* was confined with the aphids and the female allowed to search for hosts for 48 hours. The relationship can be expressed as the curvi-linear function:

$$Y = 31.1417 + 0.1172\ X - 0.00018\ X^2\ (r = 0.99,\ \ P<0.05).$$

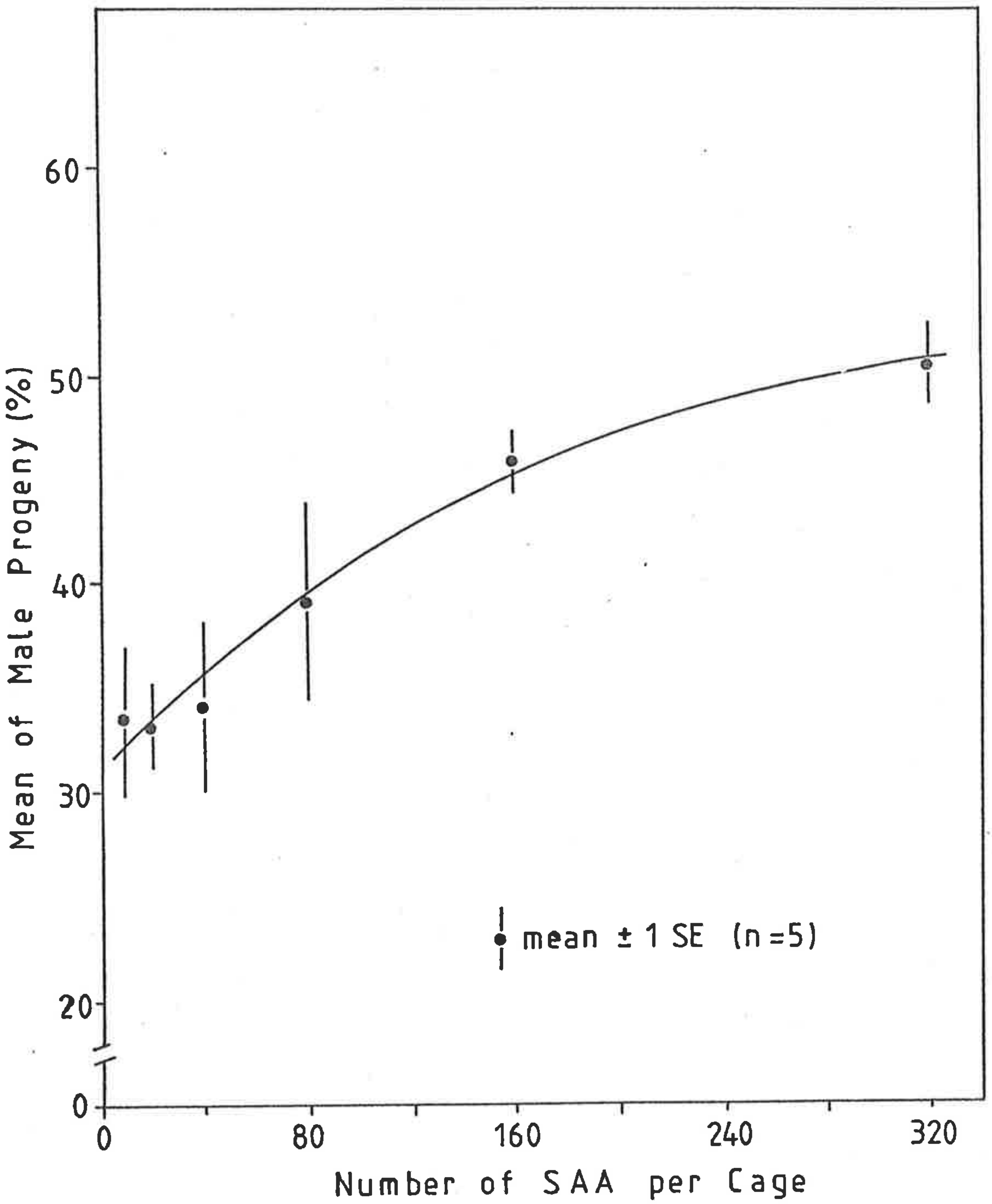

Mean of Male Progeny (%)
60
50
40
30
20
0
0
80
160
240
320
Number of SAA per Cage
mean ± 1 SE (n =5)

Fig. 37

An association between host density and sex ratio of *Trioxys* progeny has also been demonstrated in a wide range of insect parasitoids by Flanders (1956) who provides several possible explanations of the effect of host density in determining the sex ratio of parasitic hymenopterous insects.

6.4 The Impact of Competitors on *Trioxys* Abundance

6.4.1 Introduction

Like every group of animals, the parasitoids of aphids can be attacked by various natural enemies (competitors) such as secondary parasitoids, entomophagous fungi, and some species of predators. Stary (1970) divides these competitors into two groups: obligatory and facultative natural enemies. Secondary parasitoid species belong to the first group whereas entomophagous fungi and predators belong to the second. The impact of entomophagous fungi will not be discussed here because it is considered to be unimportant for SAA (Milner 1978).

The economic significance of secondary parasitoids on primary parasitoid abundance has been widely discussed by several people (DeBach 1949, Fiske 1970, George 1957, Evenhuis 1964, Hassell 1978, Paetzold and Vater 1966, Schlinger and Hall 1961, Stary 1966, 1970). The action of secondary parasitoids is generally believed to be economically harmful because they may reduce the numbers of primary parasitoids considerably. Berg *et al.* (1978), Schlinger and Hall (1961), and Wilson *et al.* (1978) have reported the occurrence of secondary parasitism on *Trioxys complanatus*. And I have found at least four genera of secondary parasitoids attacking the aphidiid parasitoids on lucerne in South Australia (Section 3.3.1.4a). They had been established in this state long before the introduction of SAA and its parasitoids in 1977. However, no information on their biology or quantitative impact has been published. And even overseas, most of the reports dealing with secondary parasitism on Aphidiidae describe only the biology and ecology of the parasitoids (Walker and Cameron 1981, Spencer 1926, Haviland 1921, Bennett and Sullivan 1978, Bocchino and Sullivan 1981, Gutierrez 1970a, 1970b, 1970e, 1970f, Gutierrez and van den Bosch 1970c, 1970d, Keller and Sullivan 1976, Matejko and Sullivan 1980, Shekar 1958, Stary 1977, Sullivan 1972, Sullivan and van den Bosch 1971, and Valentine 1975).

It is generally considered that the influence of secondary parasitism on the effectiveness of primary parasitoids used in biological control is difficult, if not impossible, to evaluate because of the complexity of studying processes involving at least three trophic levels of insects. Flanders (1943) believes that the influence of a secondary parasitoid can be tested only by establishing it in a region where primary parasitoids are responsible for keeping a pest under control. However, DeBach (1949) who studied the impact of natural enemies of the long-tailed mealybug on citrus, has suggested that selective pesticides may sometimes be used to show the influence of secondary parasitoids on primary parasitoid and pest populations. In this present study, a cage exclusion technique was used to demonstrate the impact of both secondary parasitoids and other competitors (especially predators) on *Trioxys complanatus* abundance.

6.4.2 Field Experiments

(1) Materials and Methods

Three identical experiments described here as experiment X, XI, XII were conducted in the study field at the Waite Institute in spring 1982, summer 1982/83, and autumn 1983, when both the primary parasitoid (*Trioxys*)and competitors were usually common in the field.

The treatments were 3 different sorts of cages of a potted lucerne plant seeded with aphids; each treatment was replicated 5 times. Two mated females of *Trioxys* were then allowed to parasitize the aphids for 3 days in the laboratory (see detail below), and the plants were then caged with either:

(A) fine nylon gauze (242 holes/cm^2) to exclude both secondary parasitoids and predators; or

(B) coarse nylon gauze (16 holes/cm^2) to exclude predators but not secondary parasitoids; or

(C) bird mesh (335 holes/m^2) to allow both secondary parasitoids and predators to reach the parasitized aphids on the plants.

The details of the experiments are summarized in Table 33.

The cage used in this experiment is illustrated in Figure 38; it was a cylinder with a 20cm diameter and 40cm height. The potted plants used were the same as those described in section 2.3. However, for easier observation, the number of stems was thinned to 10 per pot and some of the lower leaves were removed.

Table 33. Details of experiments X, XI and XII.

Treatments	Types of cages for treatments	Expected effects: Secondary parasitism	Expected effects: Predation
A	fine nylon gauze	-	-
B	coarse nylon gauze	+	-
C	partly open cage	+	+

Experiments	Time done	Treatments
X	11 - 24 October 1982	A, B, C
XI	23 Dec. 1982 - 6 Jan. 1983	A, B, C
XII	13 - 26 March 1983	A, B, C

Figure 38.

Types of cages used in experiment X, XI and XII:

A: treatment arrangement in the field,
B: fine gauze cage,
C: coarse gauze cage,
D: bird mesh cage.

The wall of the outer pot was smeared with "fluon" to prevent ants from reaching the aphids on the plant.

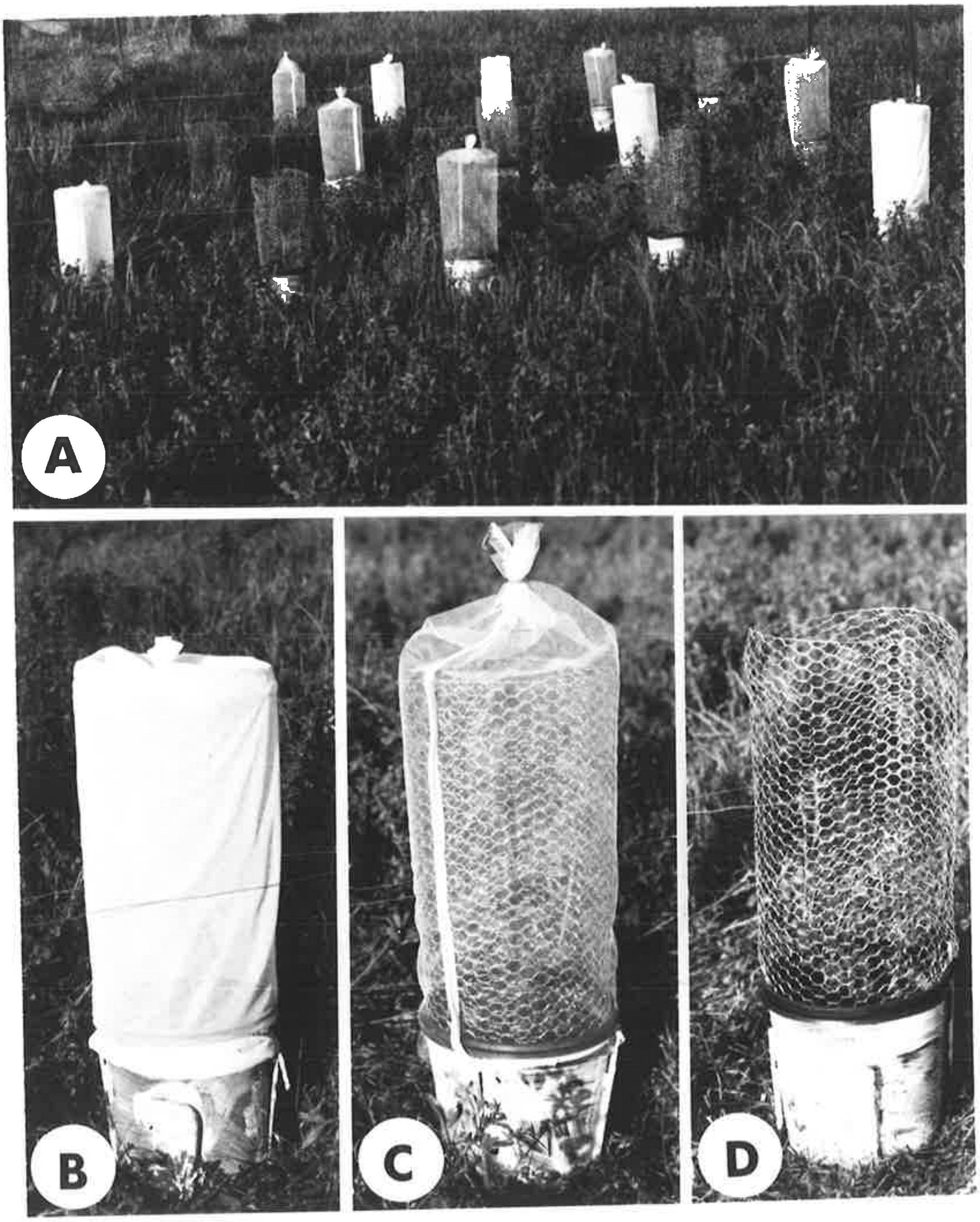


Fig. 38

Each experiment needed a 6 day preparation for parasitizing the aphids in the laboratory as follows:

Day 0: the plant was seeded with 100 of 1st and 2nd instar nymphs of SAA, then caged with a fine nylon gauze (242 holes/cm^2). The aphids were allowed to settle down for 24 hours.

Day 1: 2 mated one-day-old females of *Trioxys* were introduced into the cage. They were allowed to parasitize the aphids for 3 days. Honey solution on a dental roll was supplied as food for the adult parasitoids.

Day 4: the adult parasitoids were removed and the aphids were reared for a further 2 days.

Day 6: by day 6 from the start of the experiment the aphids were expected to consist of different stages of parasitoids e.g. young and old larvae and prepupa. These different stages of *Trioxys* in each unit of the experiment were expected to provide each stage the chance to be attacked by both endo- and ecto-secondary parasitoids as well as by predators. The 15 units of the experiment were then divided into 3 groups of 5 potted plants each. Each group, which represented a treatment, was then caged with a particular type of cage as described above. All the units were transferred to the study field and left there for 7 subsequent days during which the competitors were allowed to attack the aphids and the aphids that had been parasitized by *Trioxys*.

Day 13: all of the units of the experiment were removed and returned to the laboratory where the number of mummified aphids in each unit was recorded. Each mummy was removed carefully with a fine brush and placed individually in a gelatin capsule for emergence. The numbers of adult *T. complanatus* and secondary parasitoids were recorded as they emerged. A mummy which did not yield a parasitoid whithin 35 days from the beginning of the experiment was dissected to see whether it contained an adult primary or secondary parasitoid; but if a dead larval parasitoid was found, it was not included in the record.

(2) Results and Discussion

C.repanda was common in the study field during the periods of experiment X, XI, and XII. *M. tasmaniae* was also common during the course of experiment X (spring).

(2.1) Experiment X (11-24 October, spring 1982)

(a) The impact of predators

The numbers of *Trioxys* mummies that were found in each replicate of the fine gauze, coarse gauze, and bird mesh cages are presented in Table 34; and the means at each treatment are given in the 2nd last row of the table.

Comparisons between any two means were made with a t-test. The results are summarized in the last row of Table 34. Those means

Table 34. Numbers of mummies found in each replicate in each treatment (A,B, and C) comprising different cages; experiment X, 11 - 24 October (spring) 1982.

	Treatments; cages with		
Replicates	(A)fine gauze	(B)Coarse gauze	(C) bird mesh cages
1	83	64	41
2	74	67	56
3	56	64	19
4	83	82	64
5	91	88	78
Means	77.4	73.0	51.6
Significance of difference between means*	a	a	b

* Means with similar letters are not significantly different.

that are not significantly different are grouped by a common letter. The tests show that the mean number of mummies in the bird mesh cages was significantly less than those found in cages with either coarse gauze or fine gauze. However, there was no difference between the coarse and fine gauzes.

Furthermore, the mean numbers of mummies that yielded adult secondary parasitoids in the coarse gauze and bird mesh cages (Table 35) were obviously not different, and neither were the proportions of the total numbers of mummies that yielded secondary parasitoids (i.e. 60/365 versus 57/258); $\text{Chi}^2 = 3.33$; $P>0.05$. So it can be concluded that the secondary parasitoids found their ways into the coarse gauze and the bird mesh cages with equal facility, and the significant difference in the mean numbers of total mummies (Table 34) in the two can be attributed entirely to predators. The depressing effect of predators on the rate of parasitism of *Trioxys* can then be estimated as : (73.0 -51.6)/73.0 (see Table 33) = 29.3% . The predator mainly responsible for this reduction in the rate of parasitism by *Trioxys* was probably *Coccinella repanda*. Coccinelids have also been reported to destroy a large number of mummified aphids on lucerne in California by Hagen and van den Bosch (1968) and by Wilson *et al.* (1982) in South Australia.

(b) Impact of secondary parasitoids

Since the secondary parasitoids seemed not to differentiate between the coarse gauze and the bird mesh cages, the numbers of

Table 35. Numbers of mummies in each replicate of coarse gauze and bird mesh cages that yielded secondary parasitoids; experiment X, 11 - 24 October (spring) 1982.

	Treatments; cages with:	
Replicates	Coarse gauze	Bird mesh
1	6	11
2	9	8
3	18	12
4	13	16
5	14	10
Means	12.0	11.4

mummies in both these cages that gave rise to secondary parasitoids can be pooled and their mean (11.7) compared to the mean total number of mummies due to *Trioxys* in the fine gauze cages (77.4). The percentage of reduction in numbers of *Trioxys* due to secondary parasitoids in both the coarse gauze and the bird mesh cages can then be estimated as : (11.7/77.4) x 100 = 15.1% (see Tables 34 and 35).

Pachyneuron, an ecto-secondary parasitoid, constituted 95% of the total number of secondary parasitoids that emerged from the sample and so could have been responsible for the reduction of *Trioxys* number during this experiment. The only other species of secondary parasitoid that emerged was *Dendrocerus*, another ecto-secondary parasitoid; no endo-secondary parasitoids emerged from the mummies.

(2.2) Experiment XI (23 Dec. - 6 Jan., summer 1982/1983)

(a) The impact of predators

The numbers of *Trioxys* mummies that were found in each replicate of the fine gauze, coarse gauze, and bird mesh cages are given in Table 36; and the means at each treatment are presented in the 2nd last row of the table.

Comparisons between any two means were again made with a t-test. The results are summarized in the last row of Table 36. Those means that are not significantly different are grouped by a

Table 36. Numbers of mummies found in each replicate in each treatment (A,B, and C) comprising different cages; experiment XI, 23 December - 6 January (summer) 1982/1983.

	Treatments; cages with:		
Replicates	(A)fine gauze	(B)Coarse gauze	(C) bird mesh
1	75	71	38
2	76	54	59
3	63	81	35
4	93	59	77
5	90	78	25
Means	79.4	68.6	46.8
Significance of difference between means*	a	a	b

* Means with similar letters are not significantly different.

common letter. The tests show the same result as that of experiment X (spring), i.e. the mean number of mummies in the bird mesh cages was significantly less than that found in either coarse gauze cages or in fine gauze cages. However, there was no difference between the coarse and fine gauze.

The difference in numbers of mummies that yielded adult secondary parasitoids in the coarse gauze and bird mesh cages in each replicate (Table 37) were tested by a "trend test; 5 x 2 contingency table"; the test showed no significant difference ($\text{Chi}^2 = 3.19$; $P>0.05$). So it can be concluded again that the secondary parasitoids found their ways into the coarse gauze cages and the bird mesh cages with equal facility, and the significant difference in the mean numbers of total mummies (Table 36) in the two cages can again be attributed entirely to predators. The depressing effect of predators on the rate of parasitism of *Trioxys* can then be estimated as : (79.4 - 46.8)/79.4 (see Table 36) = 41.1% . The predator mainly responsible for this reduction in the rate of parasitism by *Trioxys* was again probably *Coccinella repanda*.

(b) Impact of secondary parasitoids

Since the secondary parasitoids seemed not to differentiate between the coarse gauze and the bird mesh cages, the numbers of mummies in both these cages that gave rise to secondary parasitoids can be pooled and their mean (10.8) compared to the mean total number of mummies in the fine gauze cages (79.4). The percentage of

Table 37. Numbers of mummies in each replicate of coarse gauze and bird mesh cages that yielded secondary parasitoids; experiment XI, 23 December - 6 January (summer) 1982/1983.

	Treatments; cages with:	
Replicates	Coarse gauze	Bird mesh
1	11	9
2	9	6
3	14	11
4	11	13
5	17	7
Means	12.4	9.2

reduction in numbers of *Trioxys* due to secondary parasitoids in both the former cages can be estimated as : (10.8/79.4) x 100 = 13.6% (see Tables 36 and 37)

The species of secondary parasitoids that emerged from *Trioxys* mummies in this experiment were *Pachyneuron* and *Dendrocerus*. *Pachyneuron*, as in spring 1982 (experiment IX), was again a dominant species; and again no endo-secondary parasitoids emerged from the *Trioxys* mummies in both coarse gauze and bird mesh cages.

(2.3) Experiment XII (13-26 March, autumn, 1983)

(a) The impact of predators

The numbers of *Trioxys* mummies that were found in each replicate of the fine gauze, coarse gauze, and bird mesh cages are given in Table 38; and the means at each treatment are presented in the 2nd last row of the table.

Comparisons between any two means were again made with a t-test. The results are summarized in the last row of Table 38. Those means that are not significantly different are grouped by a common letter. The tests show the same result as that of experiments X and XI, i.e. the mean number of mummies in the bird mesh cages was significantly less than that found in either coarse gauze or in fine gauze cages. However, there was no difference between the coarse and fine gauze.

Table 38. Numbers of mummies found in each replicate in each treatment (A,B, and C) comprising different cages; experiment XII, 13 - 26 March (autumn) 1983.

	Treatments; cages with:		
Replicates	(A)fine gauze	(B)Coarse gauze	(C) bird mesh
1	67	51	43
2	84	55	61
3	60	72	48
4	75	79	52
5	81	66	39
Means	73.4	64.6	48.6
Significance of difference between means*	a	a	b

* Means with similar letters are not significantly different.

The difference in numbers of mummies that yielded adult secondary parasitoids in the coarse gauze and bird mesh cages in each replicate (Table 39) were tested by "trend test; 5 x 2 contingency table"; the test showed no significant difference ($Chi^2 = 1.58$; $P>0.05$. So it can be concluded again that the secondary parasitoids found their ways into the coarse gauze and the bird mesh cages with equal facility, and the significant difference in the mean numbers of total mummies (Table 38) in the two cages can again be attributed entirely to predators. The depressing effect of predators on the rate of parasitism of *Trioxys* can then be estimated as : (73.4 - 48.6)/73.4 (see Table 38) = 33.8% . The predator mainly responsible for this reduction in the rate of parasitism by *Trioxys* was again probably *Coccinella repanda*.

(b) Impact of secondary parasitoids

Since the secondary parasitoids seemed not to differentiate between the coarse gauze and the bird mesh cages, the numbers of mummies in both these cages that gave rise to secondary parasitoids can be pooled and their mean (10.7) compared to the mean total number of mummies in the fine gauze cages (73.4). The percentage of reduction in numbers of *Trioxys* due to secondary parasitoids in both the former cages can be estimated as : (10.7/73.4) x 100 = 14.6% (see Tables 38 and 39)

The species of secondary parasitoids that emerged from *Trioxys* mummies in this experiment were *Pachyneuron* and *Dendrocerus*.

Table 39. Numbers of mummies in each replicate of coarse gauze and bird mesh cages that yielded secondary parasitoids; experiment XII, 13 - 26 March (autumn),1983.

	Treatments; cages with:	
Replicates	Coarse gauze	Bird mesh
1	7	8
2	13	8
3	10	9
4	15	11
5	12	14
Means	11.4	10.0

Pachyneuron, as in experiments X and XI, was again a dominant species; and again was no endo-secondary parasitoids emerged from the *Trioxys* mummies in both coarse gauze and bird mesh cages.

The fact that there was no difference in the numbers of ecto-secondary parasitoids that emerged from the mummies in the bird mesh and in the coarse gauze cages in these experiments suggests that predators may not destroy the mummy containing an ecto-secondary parasitoid. This result may be due to a different preferential ovipositing behaviour between the ecto- and endo- secondary parasitoids. An endo-secondary parasitoid usually oviposits in the primary parasitoid while the aphid is still alive whereas an ecto-secondary parasitoid usually oviposits on the primary parasitoid when the aphid is already dead (Sekhar 1958, Sullivan 1972). In the latter case, the skin of the mummified aphids may have hardened before the ecto-secondary perasitoid laid its egg and so may have been more difficult for predators to destroy. In the laboratory I have observed that an adult *C. repanda* attacked and failed to destroy a *Trioxys* mummy having a hardened skin (see Figure 23D); a normal adult *Trioxys* emerged from this scarred mummy a few days later.

6.4.3 Laboratory Experiment
(experiment XIII)

Introduction

It has been demonstrated in experiments X, XI, and XII (Section 6.4.2) that predation on SAA, by *C. repanda* in particular, may cause a significant reduction in the population of primary parasitoids but seems not to affect the population of secondary parasitoids.

The SAA population usually starts to become apparent in October (late spring) and its increase then coincides with the decrease of BGA+PA populations (Appendix Table 2.3). At the same time, the predator population is high because of an early build up on the abundant BGA+PA population in early spring (Figure 7). The *Trioxys* population may also start to increase at this time of the year and its adults are frequently caught in sweep net samples then. With these relative abundances of different species, one would expect that SAA and *Trioxys* could suffer from heavy predation which could disturb the host-parasitoid relationship.

The degree of reduction in the *Trioxys* population caused by predation may be determined by a number of factors e.g. the ratio of the density of parasitoid to predator at the beginning of the "aphid season", temperature etc. A high predator-parasitoid ratio, especially at the beginning of aphid season, may cause a significant reduction of parasitoid populations, e.g. Wilson et al. (1982). Hagen and van den Bosch (1968) found a similar reduction in the numbers of *Aphidius smithi* parasitizing the pea aphid in lucerne fields in California; if coccinellids invaded the field and started to reproduce before the aphids were mummified, numbers of parasitized aphids were eaten by the predators.

I therefore tested the hypothesis that predation on SAA, especially by Coccinelids, may affect the size of the primary parasitoid population. The hypothesis was tested in the laboratory (described here as experiment XIII) by exposing an initially constant number of aphids on a potted plant to six combinations of numbers of *Trioxys* and *Coccinella repanda*.

(1) Materials and Methods

There were 7 treatments comprising:

(i) aphids plus either one of 3 *Trioxys* densities (i.e. 2, 4, and 8 females);

(ii) aphids plus either one of the same 3 *Trioxys* densities plus one pair of *Coccinella repanda* adults;

(iii) aphids alone.

Each treatment was replicated 2 times.

The aphids and parasitoids were obtained from the laboratory culture described in Sections 2.2 and 2.3. The predators were collected from the lucerne field as pupae.

The initial SAA density per potted plant was 100 aphids of different developmental stages: 50 1st and 2nd instar nymphs, plus 30 3rd and 4th instar nymphs, plus 20 reproductive adults. The aphids were artificially introduced to each potted plant, then the plant was caged with a clear cylindrical plastic container provided with top and side ventilations through fine nylon gauze (242 holes/cm^2). In all but the "control" treatment, the aphids were allowed to settle down for 24 hours before one-day-old mated *Trioxys* females (either 2, 4, or 8) were introduced into the cage. Two days after, a pair of *Coccinella repanda* was introduced into each cage of the required 3 treatments. Honey solution on a dental roll was provided as food for *Trioxys*.

Numbers of live and mummified aphids were estimated by sampling 9 leaves, 3 each taken randomly from the top, middle, and bottom parts of the plants. The samples were taken at 3 day intervals starting from day 4 after SAA introduction. On each of the sampling dates, each caged plant was taken into the laboratory where the cage was opened inside a larger cage which had a clear perspex front and two sleeves for collecting the samples of leaves. After recording the numbers of aphids and mummies on each leaf, the leaves were placed amongst the folliage of the plant, the natural enemies were collected, and the plant plus natural enemies were returned to the experimental cage. The experiment was terminated when further sampling was considered to be inaccurate because the number of aphids was either too high or too low.

(2) Data analysis

The mean numbers of live aphids of each treatment at each time of sampling were compared in a randomized block analysis of variance with 7 treatments and 2 replicates.

The mean numbers of mummified aphids in each treatment at each time of sampling were similarly compared in an ANOVA with 6 treatments rather than 7 because the control (i.e. aphids alone) was omitted. For this analysis, the effects of the treatments can be divided into two main effects : (i) that of *Trioxys* densities, and (ii) that of *Coccinella* densities (i.e. with *Coccinella* versus with no *Coccinella*). Since the latter effect was desired to be estimated more precisely than of the former, a split-plot analysis of variance was used with 3 main plots of parasitoid densities each consisted of 2 sub-plots of predator and no predator. This type of analysis of variance was also able to test if there was interaction between the two main effects.

(3) Results and Discussion

(i) numbers of live aphids

The estimated numbers of live aphids per sample in each treatment at 4, 7, 10, and 13 days after the aphid introduction are shown in Tables 40.1 and 40.2.

A square root transformation was applied to the data to obtain homogeneous variances. The analyses of variance are given in Appendix Table 37. The F tests show that the treatment means did not differ significantly at day 4 after the aphid introduction but did differ significantly at days 7, 10, and 13. L.s.d's were then calculated for the comparison of the treatment means for each of the 3 latter days to determine differences among the means. The means,

Table 40.1. Numbers of live aphids per 9 trifoliate leaves of lucerne when aphids were exposed to "treatments" of *Trioxys* with or without *Coccinella* for time of sampling of 4 and 7 days; experiment XIII.

Time of sampling (days)*	Treatments		Replicates		
	Number of *Trioxys*	Number of *Coccinella*	I	II	mean
4	0	0	83	102	
		Total for "control"	83	102	92.50
	2	0	75	45	
	4	0	63	39	
	8	0	24	83	
	Total for treatments with no *Coccinella*		162	167	54.83
	2	2	29	63	
	4	2	23	58	
	8	2	49	38	
	Total for treatments with *Coccinella*		101	159	43.33
		Total for replicates	346	427	
7	0	0	321	274	
		Total for "control"	321	274	297.50
	2	0	43	65	
	4	0	10	74	
	8	0	34	34	
	Total for treatments with no *Coccinella*		87	173	43.33
	2	2	14	51	
	4	2	46	15	
	8	2	20	3	
	Total for treatments with *Coccinella*		80	69	24.83
		Total for replicates	488	516	

* time of sampling = number of days after aphid introduction.

Table 40.2. Continuation of Table 40.1. Numbers of live aphids per 9 trifoliate leaves of lucerne when aphids were exposed to "treatments" of *Trioxys* with or or without *Coccinella* for time of sampling of 10 and 13 days; experiment XIII.

Time of sampling (days)*	Treatments Number of *Trioxys*	 Number of *Coccinella*	Replicates I	 II	mean
10	0	0	695	853	
Total for "control"			695	853	639.00
	2	0	27	94	
	4	0	14	71	
	8	0	17	18	
Total for treatments with no *Coccinella*			58	183	40.17
	2	2	42	47	
	4	2	10	12	
	8	2	2	3	
Total for treaments with *Coccinella*			54	62	19.33
Total for replicates			807	1098	
13	0	0	1209	932	
Total for "control"			1209	932	1070.50
	2	0	11	33	
	4	0	11	20	
	8	0	16	12	
Total for treatments with no *Coccinella*			38	65	17.17
	2	2	13	28	
	4	2	18	18	
	8	2	4	10	
Total for treatments with *Coccinella*			35	56	15.17
Total for replicates			1282	1053	

* Time of sampling = number of days after aphid introduction.

Table 41. The results of analysis of the data in Tables 40.1,40.2. The means numbers of live aphids (expressed as square roots) per sample of 9 trifoliate leaves of lucerne in each of 7 treatments at 7, 10 and 13 days after the introduction of aphids; the l.s.ds. for differences between means and the results of applying these l.s.ds. are also given in the table. The treatments are represented as T.C., where T is the number of *Trioxys* per treatment and C is the number of *Coccinella repanda*.

Sampling dates					
7 days		10 days		13 days	
Treats. (T.C.)	Mean number of aphids	Treats. (T.C.)	Mean number of aphids	Treats. (T.C.)	Mean number of aphids
(0.0)	17.2347 a	(0.0)	27.7845 a	(0.0)	32.6497 a
(2.0)	7.3098 b	(2.0)	7.4458 b	(2.0)	4.5306 b
(4.0)	5.8823 b	(2.2)	6.6682 b	(2.2)	4.4485 b
(8.0)	5.8310 b	(4.0)	6.0839 bc	(4.2)	4.2426 b
(2.2)	5.4415 b	(8.0)	4.1829 bcd	(4.0)	3.8944 b
(4.2)	5.3277 b	(4.2)	3.3132 cd	(8.0)	3.7321 b
(8.2)	3.1021 b	(8.2)	1.5731 d	(8.2)	2.5811 b
LSD 5%	5.4561		3.5983		2.8240

Note that the mean which are not significantly different are grouped by a common letter.

the l.s.d. and differences denoted by non-alike letters are given in Table 41. The results indicate that the mean numbers of live aphids in all treatments differ significantly from those of "control" (i.e. aphids alone; T.C = 0.0) at day 7, 10, and 13 after aphid introduction. However there was no difference between any pair of contrasting treatments with and witout *Coccinella* i.e. between (2.0) and (2.2) or between (4.0) and (4.2) or between (8.0) and (8.2). It can be concluded therefore that both *Trioxys* alone and *Trioxys* plus *Coccinella* significantly reduced the numbers of aphids, but the addition of *Coccinella* seemed not to reduce the number of aphids any lower.

(ii) Numbers of mummified aphids

The estimated numbers of mummified aphids per treatment in each replicate and at each time of sampling are shown in Tables 42.1A, 42.2A and 42.3A; the treatment combination totals are given in Table 42.1B, 42.2B and 42.3B.

A square root transformation was again applied to the data to get honogeneous variances. The analyses of variance are presented in Appendix Table 38. The F tests show that neither the "*Trioxys* effect" nor the "Interaction effect" at any sampling date was significant. The F tests also show that the "*Coccinella* effect" (i.e. *Coocinella* densities (C)) in Appendix Table 38 was not significant at day 7 but it was significant at days 10 and 13. L.s.ds were consequently calculated and applied to the means of only those two latter data (Table 43). The results indicate that

Tabel 42.1A. Numbers of mummies per 9 trifoliate leaves of lucerne when aphids were exposed to "treatments" of *Trioxys* and or *Coccinella*; experiment XIII.

Time of sampling (days)*	Treatments		Replicates		
	Number of *Trioxys*	Number of *Coccinella*	I	II	Totals
7	2	0	38	14	52
	4	0	31	23	54
	8	0	22	46	68
Total for treatments with no *Coccinella*			91	83	174
	2	2	4	12	16
	4	2	20	3	23
	8	2	14	12	26
Total for treatments with *Coccinella*			38	27	65
Total for replicates			129	110	239

Table 42.1B. Treatment totals from Table 42.1A re-arranged for combinations of *Trioxys* densities X presence or absence of *Coccinella*.

Time of sampling	Number of *Trioxys* per cage	Number of *Coccinella* per cage		Totals
		0	2	
7	2	52	16	68
	4	54	23	77
	8	68	26	94
Totals		174	65	239

Tabel 42.2A. Numbers of mummies per 9 trifoliate leaves of lucerne when aphids were exposed to "treatments" of *Trioxys* and or *Coccinella*; experiment XIII.

Time of sampling (days)	Treatments		Replicates		
	Number of *Trioxys*	Number of *Coccinella*	I	II	Totals
10	2	0	39	37	76
	4	0	52	22	74
	8	0	32	37	69
Total for treatments with no *Coccinella*			123	96	219
	2	2	4	6	10
	4	2	2	13	15
	8	2	4	4	8
Total for treatments with *Coccinella*			10	23	33
Total for replicates			133	119	252

Table 42.2B. Treatment totals from Table 42.2A re-arranged for combinatios of *Trioxys* densities x presence of absence of *Coccinella*

Time of sampling	Number of *Trioxys* per cage	Number of *Coccinella* per cage		Totals
		0	2	
10	2	76	10	86
	4	74	15	89
	8	69	8	77
	Totals	219	33	252

Tabel 42.3A. Numbers of mummies per 9 trifoliate leaves of lucerne when aphids were exposed to "treatments"of *Trioxys* and or *Coccinella*; experiment XIII.

Time of sampling (days)*	Treatments		Replicates		
	Number of *Trioxys*	Number of *Coccinella*	I	II	Totals
13	2	0	24	13	37
	4	0	31	10	41
	8	0	25	10	35
Total for treatments with no *Coccinella*			80	33	113
	2	2	0	2	2
	4	2	5	4	9
	8	2	4	2	6
Total for treatments with *Coccinella*			9	8	17
Total for replicates			89	41	130

* Time of sampling = days after aphid introduction.

Table 42.3B. Treatment totals from Table 42.3A re-arrange for combinations of *Trioxys* densities x presence or absence of *Coccinella*.

Time of sampling	Number of *Trioxys* per cage	Number of *Coccinella* per cage		Totals
		0	2	
13	2	37	2	39
	4	41	9	50
	8	35	6	41
Totals		113	17	130

Table 43. The results of the analysis of data in Tables 42.1,42.2 and 42.3. Test of significant for mean numbers of mummified aphids (expressed as square roots) in the treatments " *Trioxys* alone" and "*Trioxys plus Coccinella*.

Treatments	Mean numbers of mummies at	
	10 days	13 days
Trioxys alone	6.0 a	4.2 a
Trioxys plus Coccinella	2.3 b	1.5 b
l.s.d. (5% ; d.f. = 3)	1.8	2.0

the numbers of mummies of the treatments "*Trioxys plus Coccinella*" were significantly less than those of treatments "*Trioxys*" alone at day 10 and 13 after the aphid introduction. This result confirms the earlier finding from the field experiment [Section 6.4.2 (2)] that predation on SAA by *Coccinella* may reduce the population of the primary parasitoid, *Trioxys complanatus*, in the following generation.

Chapter 7

General Discussion

Trioxys complanatus has been known as a good agent for biological control of SAA in lucerne in California (van den Bosch *et al.* 1959). So this parasitoid was imported and then released in Australia for controlling the newly introduced SAA. *Trioxys* has now established well in all lucerne growing States. However, attempts to control the SAA population with this parasitoid in South Australia so far have been unsuccessful, or only partially successful. Even with the aid of native predators, *Trioxys* did not control the SAA during the early period of peak abundance of the aphid (Allen 1978) and mean densities of SAA greater than 400 per stem were common (Allen 1982). Could both biotic and abiotic factors have contributed, in some degree, to the reduction of *Trioxys* effectiveness?

The hypothesis that generated this study was derived from the above facts and question. However, because of the complexity of the hypothesis, its components were isolated into a logical sequence and then tested individually both in the field and the laboratory.

The earlier research and the analysis of local population data enabled me to obtain general trends of SAA-natural enemy interaction. This analysis also provided an indication of the follow-up research that could be done to further explore the relationship between the aphid and its natural enemies.

7.1 Aphid-natural enemy relationship and some factors affecting the relationship

For convenience of discussion, the term "parasitoid" is again replaced with *Trioxys* because *Trioxys* was the only parasitoid attacking the SAA in the study field; and the term "predator" is again used for any predator except <u>ants</u>.

The SAA population in Adelaide displayed two distinct periods of abundance in January (summer) and in March-April (autumn) each year (see Figure 5). It seemingly disappeared in winter (June-August) and was not of economic importance in spring. A similar seasonal trend in numbers of SAA was also observed in crops by Wilson *et al.* (1982) at Meningie, Netherton, and Virginia in 1978-1979, shortly after the introduction of the aphid into this State. Allen (1984) also reported a similar seasonal abundance of SAA in irrigated lucerne stands in the costal Langhorne Creek (near Meningie) region in 1980/1981.

The cool, wet winter in Adelaide probably exerts a strong and direct depressive influence on the development and reproduction of SAA so that it is very scarce then. The species is also scarce in spring when weather should be more favourable for its increase, and evidence is presented in chapter 5 that the low numbers then are more likely to be due to the action of natural enemies, especially *Trioxys* and the predators *Micromus* and *Coccinella,* and probably ants *Irridomyrmex* sp. to some extent.

In spring to early summer, with higher temperatures and an abundance of prey (BGA plus PA), *Micromus* and *Coccinella* increased in numbers very rapidly and reached a peak in November (late spring) (Figure 7). This high population of predators seemed not only to be related to the collapse of BGA plus PA populations but also to the scarcity of SAA during this period of the year (compare Figure 7 and Figure 5).

The seasonal fluctuation of *Trioxys* numbers appeared to follow the rise and fall of the SAA population (Figure 6). However, *Trioxys* numbers were very low in spring, and so were those of parasitized aphids; the latter could not be detected in stem samples until the end of December when the SAA population had reached a relatively high number (Appendix Table 2.4). Heavy predation on the developing SAA population in spring probably has a direct relation to the scarcity of *Trioxys* numbers during this period of the year. A direct reduction in numbers could occur because the predators consume some of the parasitoids as parasitized aphids.

The apparent numerical response of the numbers of natural enemies, especially *Trioxys* and *Coccinella*, to the rises and falls of the SAA numbers were plotted and then examined more closely by regression analysis as used by Wright and Laing (1982). Such analysis gave indications of a significant relationship of both *Coccinella* and *Trioxys* with the SAA numbers. Other workers have analyzed field census data and have suggested a significant impact on SAA populations in lucerne of *Trioxys* (Lehane 1982, van den Bosh *et al.* 1959, Wilson *et al.* 1982) and of *Coccinella* (Ridland and Berg 1978a). However, as mentioned before, this method of analysis cannot demonstrate that either *Trioxys* or *Coccinella* was responsible for regulating the SAA population.

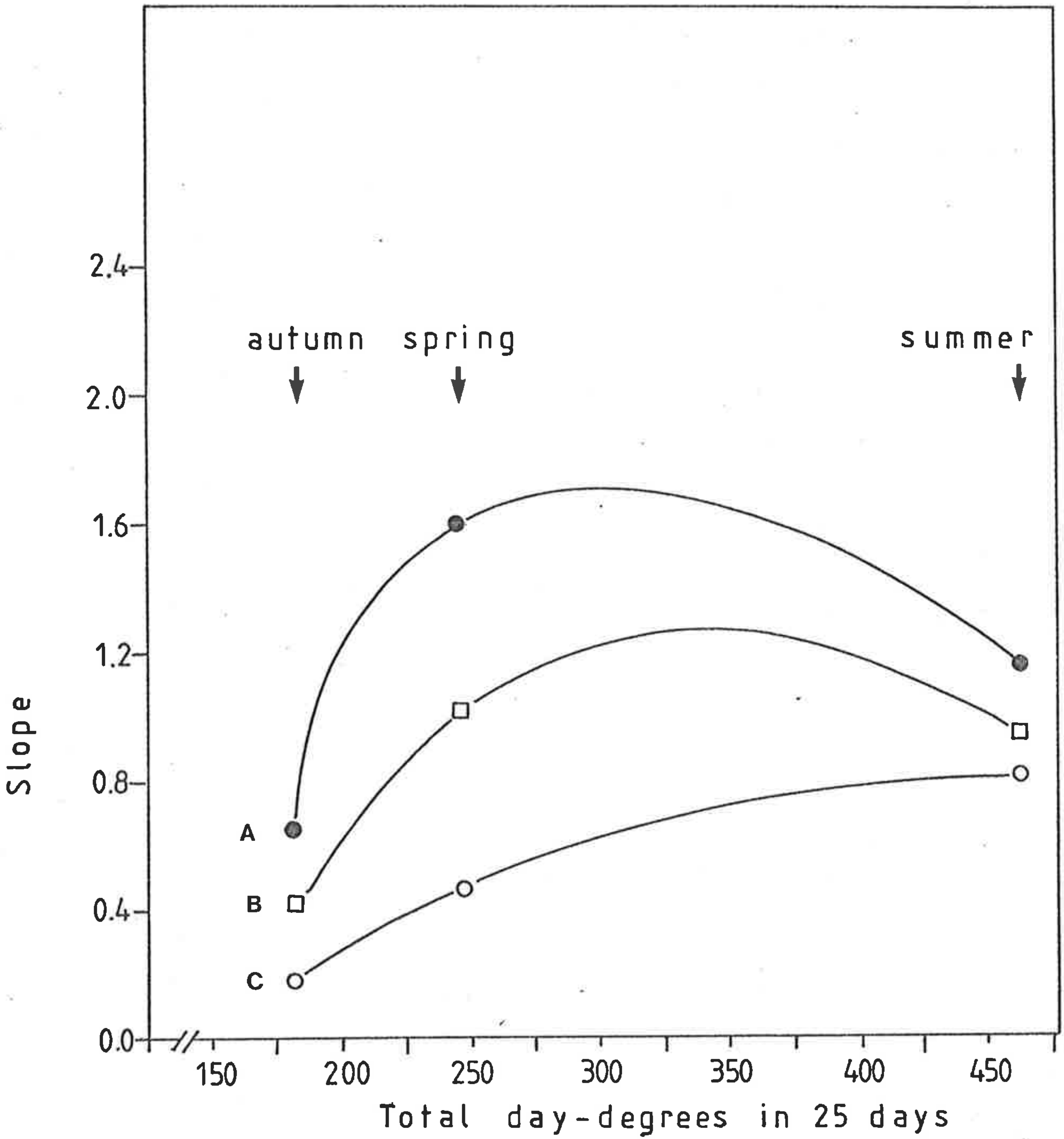
More convincing evidence of the regulatory power of natural enemies of SAA is presented in this thesis and was achieved by comparing experimental plots with natural enemies against similar plots with natural enemies excluded. Experiments were done in spring, summer and autumn to allow the measurement of the influence of seasonal temperatures on the performance of the natural enemies.

The growth rate of the population SAA in both the absence and presence of natural enemies in different seasons are illustrated in Figure 39 in which the slopes of the regression lines represent the growth rate of SAA in three different sorts of cages (see treatment A, B and C in Figure 22, 24 and 25) and are plotted against the total "day degrees" (^{o}D) during 25 days of each experiment. With only 3 points for each "curve", no curve fitting is possible and curves have been drawn by eye to illustrate the likely trends. Clearly, however, in the absence of natural enemies (line A), the SAA grew more rapidly in spring than in either summer or autumn. This difference in the growth rate of SAA in different seasons is likely to be mainly due to the direct influence of the higher summer and autumn temperatures on the rate of development and fecundity of the aphid. But an indirect influence through changes in the physiology of the plant should not be discounted. This latter effect, however, could not be tested.

Seasonal differences in temperature also influenced the performances of natural enemies during this study (Figure 39). In spring and autumn, both *Trioxys* alone and *Trioxys* plus predators exerted a greater reduction of the SAA growth rate than they did in summer. The higher mean daily temperature may have contributed to some degree to the poor performance of *Trioxys* during summer. But the

Figure 39.

Relationship between the growth rate (= slope) of SAA per day (expressed as square root of number of SAA) in different type of cages (A, B and C) in different seasons and the total day-degrees during the experiment (see Appendix Tables 18, 23 and 25). With only 3 points for each "curve", no curve fitting is possible and curves have been drawn by eye to illustrate the likely trends. The type of cages was as follow: (A) fine nylon gauze cage, (B) coarse nylon gauze cage and (C) partly open cage.



2.4
2.0
1.6
1.2
0.8
0.4
0.0
Slope
autumn
spring
summer
A
B
C
150
200
250
300
350
400
450
Total day-degrees in 25 days

Figure 39

high SAA-*Trioxys* density ratio in early summer could also have been responsible. This high SAA-*Trioxys* density ratio is probably due to heavy predation, mainly by *Coccinella* and *Micromus*, in late spring (see Section 3.3.1.5). The "critical period" of predation for the *Trioxys* population is likely to be during a few weeks in late spring when the number of predators is higher than either the number of prey or *Trioxys*. Heavy predation then may be more disadvantagous to *Trioxys* than to SAA and cause resultant increases in the SAA-*Trioxys* density ratio in early summer (see Section 3.3.1.1).

The direct impact of predation on the *Trioxys* population which may affect the effectiveness of *Trioxys* has been demonstrated in the laboratory and the field. The laboratory experiment data (Section 6.4.3) suggested that 1 female *Trioxys* was able to control SAA in a cage when the aphid population was started with 100 aphids; when 1 pair of *Coccinella* adults were added - in another treatment - the number of aphids was no lower but the numbers of *Trioxys* were reduced in the following generation. The field experiment data (Section 6.4.2) showed that predators alone (mainly *Coccinella*) were capable of destroying 29-41% of *Trioxys* numbers, depending on the season. Evidence of another disadvantagous of predation on SAA is also presented in this thesis i.e. it did not reduce the numbers of ecto-secondary parasitoids. With the additional action of these secondary parasitoids, the population of *Trioxys* was further decreased by 14-15%.

The poor performance of *Coccinella* during summer is not clear because summer weather and abundance of prey should be favourable for its intensive predation and reproduction (Frazer *et al.* 1981, Baumgaertner *et al.* 1981). However, parasitism by *Dinocampus coccinellae* and *Tetrastichus* sp., which are relatively high in this period of the year, could have been responsible.

7.2 Effect of temperature

The influence of temperature on aphids and natural enemies has been reported by many people (Burnett 1949, 1951, 1954,1956, Flanders 1947, Ives 1981, Jones 1979, Maelzer 1977,1981, Tamaki *et al.* 1980). Campbell *et al.* (1974) also suggested that the temperature requirements of some aphids and those of the parasitoids and secondary parasitoids associated with these aphids differed from place to place for the same species and from species to species. Thus as suggested by Maelzer (1981), the ecology of the citrus aphid, *Toxoptera citricidus*, and its parasitoids on the wet subtropical coastal plains on northern N.S.W. will be quite different from the ecology of the same species in the Mediterranean-type of climate of Adelaide, South Australia. But little information is available about the temperature requirements of the same aphid and parasitoid species in different places.

Temperature also influences the phenology of an aphid species by its influences on the phenology of the host plant and on the interaction of the aphids with its natural enemies. For aphids on perennial pasture plant species, such as lucerne, the influence of plant phenology may not be as important as it seems to be for other aphid species on other host plants in Australia (Maelzer 1981) - and the phenology of SAA in Australia, as in the U.S.A., seems to be determined largely by the relative influences of temperature on the rates of increase of SAA and those of its natural enemies. However, it is not clear exactly how temperature affects the interaction because much of available information is only for SAA and *Trioxys* and much of it was obtained in the laboratory and is not easily applied to the field. Thus Force and Messenger (1964a) measured the effect of constant temperature on the innate capacity of increase (r_m) of both *Trioxys* and SAA in the laboratory. They found (*ibid*) that the r_m for *Trioxys* was higher than that for SAA between 15.6 and 32.2°C; but below and above this range, the value of r_m for SAA was higher than for *Trioxys*. However high maximum temperatures in the field could cause high mortality and/or retard the rate of SAA development (Allen 1984, Dickson *et al.* 1955, Messenger 1964, Nielson and Barnes 1961).

The level of mortality that could be caused by high field maximum temperatures is discussed by Allen (1984) who concluded that daily maximum temperatures equal to, or greater than, 38°C for two or more consecutive days caused estimated mortalities up to 77%. A similar indication was reported by Nielson and Barnes (1961). No quantitative data are available for *Trioxys* but the various references above (Allen 1984, Force and Messenger 1964a, Nielson and Barnes 1961) generally indicate that high temperatures would be more disadvatagous to *Trioxys* than to SAA. So the lack of influence of *Trioxys* during January-February (summer) in South Australia was likely, indeed, to be due to high daily maximum temperatures.

Variations in temperature from year to year may also influence the relative abundance of aphids in any one year. Thus numerous workers on aphid biology believe that many aphid species are less abundant after relatively mild springs because the temperatures that prevail then are relatively more favourable to natural enemies and allow the natural enemies to build-up more rapidly in numbers and retard the growth of aphid populations (Suter and Keller 1977). For such an aphid species, an outbreak can sometimes be predicted by the weather in spring , e.g. Carter *et al.* (1982b) for cereal aphid, *Sitobion avenea* in England. However, the relationship between spring weather in South Australia and abundance of SAA in the following summer is unknown. Most of the available data, as well as those presented in this thesis, have not been gathered for a sufficiently large number of years for testing the hypothesis proposed by Suter and Keller (1977).

7.3 The impact of ants

It is well known that some populations of homopteran species appear to thrive when attended by ants. Numerous workers (Bank 1962, Bartlett 1961, Bradley 1973, Bradley and Hinks 1968, El-Ziady and Kennedy 1956, Flanders 1943,1945,1951, Johnson 1959, Tilles and Wood 1982, Way 1963, Williams 1954) have reported that ants exert beneficial effects on the growth of aphid colonies through the defence of the aphids against attack by natural enemies. For example, Bartlett (1961) reported that disturbance by ants resulted in from 27.4 - 98.4% reduction in parasitization, depending on the parasitoid species. By contrast, very few workers have reported the adverse effect of ants on pest populations. Lindquist (1942) reported the depressing effect of ants on the numbers of screwworm, *Cochliomyia americana* C. & P., that emerged from the body of animals that die from screwworm infestations; an emergence of 4.1% and 93.1% of screwworm flies was recorded from carcasses which were exposed and protected from the ants respectively. Some other workers have reported the predation by ants on insect pests of tropical tree crops, e.g. Brown (1959) and Phillips (1957) reported that good crops of coconut palm in the Solomon Islands were borne by palms inhabited by colonies of *Oecophylla smaragdina*, because this ant destroyed the pest, *Amblypelta cocophaga*; and Room (1975) suggested that in Papua New Guinea the most important cocoa pest, *Pantorhytes szentivanyi*, is controlled by the ant *Anoplolepis longipes*, and that in Ghana the ant *Oecophylla longinoda* similarly controls the cocoa capsid, *Distantiella theobroma*.

In this study, ants (*Irridomyrmex* sp.) exerted a great reduction in the number of SAA in summer when other natural enemies seemed to have little influence on the aphid population. The estimated reduction in the growth rate of aphid by ants during this season was 94%. These ants, however, were ineffective in the wet autumn, particularly when heavy rain fell. The heavy rain may have reduced the population of ants in the field either through drowning or causing the ground to be unsuitable for nesting.

The impact of the ants on the SAA population in spring could not be tested. However, the disturbance by ants of the treatments in the parasitoid-predator exclusion experiment (Expt.-I) indicated that the ants may had a suppressing effect on the aphid numbers in spring as well.

7.4 The future control of SAA

Since the " cost/potential-benefit" ratio for chemical control of SAA in non-irrigated lucerne farming is high, the use of aphid-resistant cultivars, grazing management (Allen 1984) and natural enemies will probably be the main control measures relied upon by livestock producers in South Australia. However the occurrence of new biotypes of SAA that can thrive on the present resistant cultivars are likely to evolve in the future, so that natural enemies should always be an important component of integrated control for SAA in South Australia.

Evidence is presented in this thesis that natural enemies were likely to be a major cause of the non-economic status of SAA in spring and that there is consequently no need of control measures for the SAA then. A similar conclusion was reached by Allen (1984) for SAA populations in dryland lucerne pastures in South Australia.

The natural enemies that were responsible for keeping SAA under control during spring were the parasitoid *Trioxys complanatus* and the predators *Coccinella repanda* and *Micromus tasmaniae* and probably ants *Irridomyrmex* sp., to some extent. *Micromus* numbers gradually decreased as air temperatures increased in summer but *Trioxys* , *Coccinella* and *Irridomyrmex* were still abundant then. *Trioxys* and *Coccinella*, however, exerted an insignificant influence on the SAA population in summer and it is then that additional control measures for SAA must be considered. By contrast, *Trioxys* is considered to be an effective parasitoid against SAA in eastern Australia (Lehane 1982). However, Lehane's conclusion (*ibid*) is derived from the inferred relationship between the incidence of parasitism by *Trioxys* and low numbers of SAA in the field, rather than on more definitive data. The uncertainty of this relationship has been criticized by a number of workers (Allen 1984, DeBach and Bartlett 1964, DeBach and Huffaker 1971, Huffaker and Kennet 1969) who believe that it is inadequate for the assesment of the regulatory or controlling power of natural enemies.

For the economic control of SAA , the only alternative to control by plant resistance may well be the augmentation of natural enemies, either native or exotic. The two major methods of augmenting natural enemies are (i) the manipulation of the composition of the natural enemy complex by the introduction of new species and (ii) the modification of the environment in favour of the existing established natural enemies (DeBach and Hagen 1964, Huffaker *et al.* 1977, Rabb *et al.* 1976, Tamaki *et al.* 1974, van den Bosch and Telford 1964). Before either method is attempted, the effectiveness of the existing natural enemies against the pest complex should be estimated.

Evidence is given that the ineffectiveness of *Trioxys* against SAA in summer was likely to be due to a high host-parasitoid density ratio (see Figures 5, 6 and Sections 6.2.1, 6.2.2, 6.2.3) in early summer and it is then that inoculative, rather than inundative, releases of *Trioxys* might effectively help to reduce the SAA number in summer. Inundative releases of natural enemies are less preferred for economic reasons rather than ecological ones. Stinner (1977) suggested that the major problem encountered in using inundative releases of natural enemies centers on their cost/benefit ratio as compared to alternatives, such as pesticides. However the cost/benefit ratio of either inoculative or inundative releases could not be tested for this thesis.

Coccinella repanda in dryland lucerne pastures is low in numbers and is not effective against SAA in summer (Allen 1984). This author beleives (*ibid*) that part of the reason for the low abundance of *Coccinella* is periodic severe grazing; however, his efforts to augment predation by this predator through less-severe grazing were not successfull; its numbers were still too low to offer any reasonable control of SAA. By contrast, in this study I found that *Coccinella* was abundant in numbers during periods of late spring to mid summer and during mid autumn. An indication has been given that the poor performance of *Coccinella* during summer was probably due to parasitism by *Dinocampus* and *Tetrastichus* (see Section 5.2.4.2). The activity of these parasitoids may possibly be reduced by applying a selective insecticide at the right time.

Another alternative for augmentation of natural enemies is by importation of exotic species. Any species of natural enemy which is likely to exert control on SAA in summer should have the following characters: (i) have a wide host range to survive at times when the SAA is not abundant, (ii) most active in warm temperature, and (iii) be less preferred by *Dinocampus* and *Tetrastichus*.

In conjunction with the augmentation of natural enemies of SAA, the biology and ecology of *Irridomyrmex* sp. should be investigated before the augmentation of these ants can be attempted. A considerable amount of work has been done by Greenslade (1971a, 1971b,1972) on the ecology of some species of *Irridomirmex* in the Solomon Islands. However, to my knowledge, no work has been done in South Australia.

REFERENCES

Acton, F.S. (1966). The analysis of straight-line data. Dover Publications, Ney York, 267 pp.

Allen, P.G. (1978). Integrated control of aphids in dry-land Hunter River lucerne on sands in South Australia. *Proc. Lucerne Aphid Workshop, Tamworth, 1978*, Dept. Agric., N.S.W., 172-174.

Allen, P.G. (1982). The impact of spotted alfalfa aphid on dry land lucerne in South Australia. *Proc. 3rd Australasian Conf. Grassld. Invert. Ecol. Adelaide 1981* Ed. K.E. Lee, Dept. Agric. S.A., 17-23.

Allen, P.G. (1984). The management of spotted alfalfa aphid, *Therioaphis trifolii* (Monell) f. *maculata*, in dryland lucerne pasture in South Australia. PhD Thesis, University of Adelaide.

Bailey, P.T., P.E. Madge, D.A. Maelzer, and D.E. Pinnock (1982). Integrated control of twospotted mite, *Tetranychus urticae* Koch on irrigated seed lucerne at Keith, South Auatralia. *Proc. 3rd Australasian Conf. Grassl. Invertr. Ecol. Adelaide, 1981.* Ed. K.E. Lee. Dept. Agric. S.A., 371-375.

Banks, C.J. (1962). Effect of ant *Lasius niger* (L.) on insects preying on small populations of *Aphis fabae* Scop. on bean plants. *Ann. appl. Biol.*, 50, 669-679.

Bartlett, B.R. (1961). The influence of ants upon parasites, predators, and scale insects. *Ann. ent. Soc. Am.*, 50, 543-551.

Bartlett, B.R. (1964). Integration of chemical and biological control. *In* Biological Control of Insect Pest and Weeds. Ed. P. DeBach, Chapman and Hall, London, 489-511.

Batra, S.W.T. (1982). Biological control in agroecosystems. *Science*, 215, 134-139.

Baumgaetrtner, J.U., B.D. Frazer, N. Gilbert, B. Gill, A.P. Gutierrez, P.M. Ives, V. Nealis, D.A. Raworth, and C.G. Summers (1981). Coccinellids (Colleoptera) and aphids (Homoptera). The overall relationships. *Can. Ent.*, 113, 975-980.

Bennett, A.W. and D.J. Sullivan, S.J. (1978). Defensive behavior against tertiary parasitism by larva of *Dendrocerus carpenteri* an aphid hyperparasitoid. *N.Y. ent. Soc.*, 83, 153-160.

Berg, G.N. and P.Ridland (1978). Lucerne aphid trapping in Victoria. *Proc. Lucerne Aphid Workshop, Tamworth*, 1978, Dept. Agric. N.S.W., 17-18.

Berg,G.N. and P.M. Ridland (1981). Characterisation of the spotted alfalfa aphid population in Victoria. *J. Aust. ent. Soc.*, 20, 317-318.

Berg, G., P. Ridland, and J. Blackstock (1978). Field rearing of *Trioxys complanatus* in Victoria. *Proc. Lucerne Aphid Workshop, Tamworth, 1978* Dept. Agric. N.S.W., 75-76.

Bocchino, F.J. and D.J. Sullivan, S.J. (1981). Effect of venom from two aphid hyperparasitoids, *Ashapes lucens* and *Dendrocerus carpenteri* (Hymenoptera: Pteromalidae and Megaspilidae), on larva of *Aphidius smithi* (Hymenoptera: Aphidiidae). *Can. Ent.*, 113, 887-889.

Boller, E. (1972). Behavioural aspects of mass-rearing of insects. *Entomophaga*, 17, 9-25.

Bradley, G.A. (1973). Effect of *Formica obscuripes* (Hymenoptera: Formicidae) on the predator-prey relationship between *Hyperaspis congressis (Coleoptera: Coccinellidae) and* Toumeyella numismaticum *(Homoptera: Coccidae)*. Can. Ent., 105, 1113-1118.

Bradley, G.A. and J.D. Hinks (1968). Ants, aphids and jack pine in Manitoba. *Can. Ent.*, 100, 40-50.

Brown, E.S. (1959). Immature nutfall of coconuts in Solomon Islands. I. Distribution of nutfall in relation to that of *Amblypelta* and certain species of ants. *Bull ent. Res.*, 50, 97-133.

Brownlee, H., P. Walter, and R. Wetherall (1979) Insecticides and varieties to combat lucerene aphids. *Wool. Tech. Sheep Breeding*, 27, 1-14.

Burnett, T. (1949). The effect of temperature on an insect host parasite population. *Ecology*, 30, 113-134.

Burnett, T. (1951). Effects of temperature and host density on the rate of increase of an insect parasite. *American Naturalist*, 85, 337-352.

Burnett, T (1954). Influence of natural temperatures and controlled host density on oviposition of an insect parasite. *Physio. Zool.*, 27, 239-248.

Burnett, T. (1956). Effects of natural temperatures on oviposition of various numbers of an insect parasite (Hymenoptera, Chalcididae, Tenthredinidae). *Ann. ent. Soc. A.*, 49, 55-59.

Campbell, A., B.D. Frazer, N. Gilbert, and A.P. Gutierrez (1974). Temperature reguirements of some aphids and their parasites. *J. App. Ecol.*, 11, 431-438.

Carter, N., A.F.G. Dixon, and R. Rabbinge (1982a). Cereal aphid populations: biology, simulation and prediction. Centre for Agricultural Publishing and Documentation. Wageningen, 91pp.

Carter, N., S. Gardner, A.M. Frazer and T.H.L. Adams (1982b). The role of natural enemies in cereal aphid population dynamics. *Ann. Appl. Biol.*, 101, 190-195.

Cochran, W.G. (1963). Sampling techniques, 2nd ed. 413pp, Wiley, New York.

Davis, D.W., M.P. Nichols, and E.G. Armbrust (1974). The literature of arthropods associated with alfalfa. 1. A bibiliography of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton) (Homoptera; Aphididae). *Illinois Natural History Survey and Biological Notes*, 87,11pp.

DeBach, P. (1946). An insecticidal check method for measuring the efficacy of entomophagous insects. *J. econ. Entomol.*, 39, 695-697.

DeBach, P. (1949). Population studies of the long-tailed mealybug and its natural enemies on citrus trees in southern California. *Ecology*, 30, 14-25.

DeBach, P. (1955). Validity of the insecticidal check method as a measure of the effectiveness of natural enemies of Diaspinae scale insects. *J. econ. Entomol.*, 48, 584-588.

DeBach, P. (1971). Experimental techniques for evaluation of the effectiveness of natural enemies. *In* Biological Control. Ed, C.B. Huffaker, Plenum, New York, London, 113-140.

DeBach, P. and B.R. Bartlett (1964). Methods of colonization, recovery and evaluation. *In* Biological Control of Insect Pests and Weeds. Ed. P. DeBach, Chapman and Hall, London, 402-426.

DeBach, P., E.J. Dietrick, and C.A. Fleschner (1949). A new technique for evaluating the effeciency of entomophagous insects in the field. *J. econ. Entomol.*, 42, 546-547.

DeBach, P., C.A. Fleschner, and E.J. Dietrick (1951). A biological check method for evaluating the effectiveness of entomophagous insects. *J. econ. Entomol.*, 44, 763-766.

DeBach, P. and K.S. Hagen (1964). Manipulation of entomophagous species. *In* Biological Control of Insects Pests and Weeds. Ed. P. DeBach, Chapman and Hall, London, 429-458.

DeBach, P. and C.B. Huffaker (1971). Experimental technicques for evaluation of the effectiveness of natural enemies. *In* Biological Control. Ed. C.B. Huffaker, Plenum, New York and London, 113-149.

DeBach, P., C.B. Huffaker, and A.W. MacPhee (1976). Evaluation of the impact of natural enemies. *In* Theory and Practice of Biological Control. Eds. C.B. Huffaker and P.S. Messenger. Academic, New York, 255-298.

DeBach, P. and H.S. Smith (1941a). The effect of host density on the rate of reproduction of entomophagous parasites. *J. econ. Entomol.* 34, 741-745.

DeBach, P. and H.S. Smith (1941b) Are population oscillation inherent in the host-parasite relation ? *Ecology,* 22, 363-369.

Dickson, R.C., E.F. Laird, Jr., and G.R. Pesho (1955). The spotted alfalfa aphid (Yellow clover aphid on alfalfa). *Hilgardia,* 24, 93-118.

Diehl, S.G. and R.M. Chatters (1956). Studies on the mechanism of feeding of the spotted alfalfa aphid on alfalfa. *J. econ. Entomol.,* 49,589-591.

Dietrick, E.J. (1961). An improve backpack motor fan for suction sampling of insect population. Scientific Notes. *J. Econ. Entomol.,* 54, 394-395.

Doutt, R.L. (1964). Biological characteristics of entomophagous adults. *In* Biological Control of Insect Pests and Weeds. Ed. P. DeBach, Chapman and Hall, London, 145-167.

Doutt, R.L., D.P. Annecke, and E. Tremblay (1976). Biology and host relationships of parasitoids. *In* Theory and Practice of Biological Control. Eds. C.B. Huffaker and P.S. Messenger, Academic, New York, 143-167.

Dunbier, M.W., T.J. Ellis, and P.A. Burnett (1978). Production of aphid-resistant lucerne cultivars for New Zealand. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric. N.S.W., 204-209.

Ebeling, W. (1945). DDT and rotenone used in oil to control the california red scale. *J. econ. Entomol.,* 38, 556-563.

El-Ziady, S. and J.S. Kennedy (1956). Beneficial effect of the common garden ant, *Lasius niger* L. on the black bean aphid, *Aphis fabae* Scopoli. *Proc. R. ent. Soc. Lond.* (A), 31, 61-65.

Evenhuis, H.H. (1964). The interrelations between appel aphids and their parasites and hyperparasites. *Entomophaga,* 9, 227-231.

Finney, G.L., B Puttler, and L. Dawson (1960). Rearing of three spotted alfalfa aphid hymenopterous parasites for mass release. *J. econ. Entomol.* 53, 655-659.

Fiske, W.F. (1910). Superparasitism: an important factor in the natural control of insects. *J. econ. Entomol.* 3, 88-97.

Flanders, S,E. (1939). Environmental control of sex in hymenopterous insects. *Ann. ent. Soc. Am.,* 32, 11-26.

Flanders, S.E. (1942). The sex ratio in the Hymenoptera: a function of the environment. *Ecology,* 23, 120-121.

Flanders, S.E. (1943a). Indirect hyperparasitism and observations on three species of indirect hyperparasites. *J. econ. Entomol.,* 36, 921-926.

Flanders, S.E. (1943b). The argentine ant versus the parasites of the black scale. *Calif. Citograph,* 23, 117-137.

Flanders, S.E. (1945). Coincident infestations of *Aonidiella citrina* and *Coccus hesperidum*, a result of ant activity. *J. Econ. Ent.,* 38, 711-712.

Flanders, S.E. (1946). Control of sex and sex-limited polymorpism in the Hymenoptera. *Quart. Rev. Biol.,* 21, 135-143.

Flanders, S.E. (1947). Element of host discovery exemplified by parasitic Hymenoptera. *Ecology,* 28, 299-309.

Flanders, S.E. (1951). The role of ant in the biological control of homopterous insects. *Can. Ent.*, 83, 93-98.

Flanders, S.E. (1956). The mechanism of sex-ratio regulation in the (parasitic) Hymenoptera. *Ins. Sociaux,* 3, 325-334.

Force, D.C. and P.S. Messenger (1964a). Fecundity, reproductive rates, and innate capasity for increase of three parasites of *Therioaphis maculata* (Buckton). *Ecology,* 45, 706-715.

Force, D.C. and P.S. Messenger (1964b). Duration of development, generation time, and longevity of three hymenopterous parasites of *Therioaphis maculata,* reared at various contant temperatures. *Ann. ent. Soc. Am.,* 57, 405-413.

Force, D.C. and P.S. Messenger (1965). Laboratory studies on competition among three parasites of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton). *Ecology,* 46, 853-859.

Force, D.C. and P.S. Messenger (1968). The use of laboratory studies of three hymenopterous parasites to evaluate their field potential. *J. econ. Entomol.,* 61, 1374-1378.

Forrester, N.W. (1978a). Seasonal abundance of spotted alfalfa aphid, blue green aphid and their predators at Tamworth, N.S.W. *Proc. Lucerne Workshop Tamworth 1978,* Dept. Agric. N.S.W., 53-56.

Forrester N.W. (1978b). Parasitism and desease incidence in field populations of spotted alfalfa aphid and blue green aphid at Tamworth, N.S.W.*Proc. Lucerne Aphid Workshop, Tamworth, 1978, Dept. Agric.* 80-84.

Franzmann, B.A. and P.D. Rossiter (1981). Toxicity of insecticides to *Trioxys complanatus* Quilis (Hymenoptera: Braconidae) in lucerne. *J. Aust. ent. Soc.,* 20 : 313-315.

Frazer, B.D., N. Gilbert, P.M. Ives, and D.A. Raworth (1981). Predator reproduction and the overall predator-prey reletionship. *Can. Ent.*, 113, 1015-1024.

George, K.S. (1975). Preliminary investigation on the biology and ecology of the parasites and predators of *Brevicoryne brassicae* (L.). *Bull. ent. Res.,* 48, 619-629.

Greenslade, P.J.M. (1971a). Interspecific competition and frequency changes among ants in Solomon Islands coconut plantations. *J. appl. Ecol.,* 8, 323-352.

Greenslade, P.J.M. (1971b). Phenology of three ant species in the Solomon Islands. *Aust. ent. Soc.* 10, 241-252.

Greenslade, P.J.M. (1972). Comparative ecology of four tropical ant species. *Insectes Sociaux,* 19, 195-212.

Greenslade, P.J.M. (1979). A guide to Ants of South Australia. *Special Educational Bull.,* South Australian Museum, Adelaide, 44 pp

Griffiths, J.T., Jr. and W.L. Thompson (1947). The use of DDT on citrus trees in Florida. *J. econ. Entomol.,* 40, 386-388.

Gutierrez, A.P. (1970a). Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 3. Host suitability studies. *Ann. ent. Soc. Am.,* 63, 1485-1491.

Gutierrez, A.P. (1970b). Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 4. The effect of age of host on host selection. *Ann. ent. Soc. Am.,* 63, 1491-1494.

Gutierrez, A.P. (1970c). Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 5. Host selection. *Ann. ent. Soc. Am.,* 63, 1495-1498.

Gutierrez, A.P. (1970d). Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 6. Description of sensory structures and a synopsis of host selection and host specificity. *Ann. ent. Soc. Am.*, 63, 1707-1709.

Gutierrez, A.P. and R. van den Bosch (1970a). Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 1. Review of hyperparasitism and the field ecology of *Charips victrix*. *Ann. ent. Soc. Am.*, 63, 1345-1354.

Gutierrez, A.P. and R. van den Bosch (1970b). Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix* (Hymenoptera: Cynipidae). 2. The bionomics of *Charips victrix*. *Ann. ent. Soc. Am.*, 63, 1355-1360.

Hagen, K.S. and R. van den Bosch (1968). Impact of pathogen, parasites, and predators on aphids. *Ann. Rev. Ent.*, 13, 325-384.

Hagen, K.S., R. van den Bosh, and D.L. Dahlsten (1971). The importance of naturally-occurring biological control in the western United States. *In* Biological Control. Ed. C.B. Huffaker, Plenum, New York- London, pp 253-292.

Hanson, C.H. (1961). Moapa alfalfa pays off. *Crops and Soils*, 13, 11-13.

Hassell, M.P. (1966). Evaluation of parasite or predator responses. *J. Anim. Ecol.*, 36, 65-75.

Hassell, M.P. (1971). Mutual interference between searching insect parasites. *J. Anim. Ecol.*, 40, 473-486.

Hassell, M.P. (1978). The dynamics of arthropod predator-prey systems. Princeton Univ. Press, New Jersey, 237 pp.

Hassell, M.P. (1982). What is searching efficiency ? *Ann. Appl. Biol.*, 101, 170-175.

Hassell, M.P. and G.C. Varley (1969). New inductive population model for insect parasites and its bearing on biological control. *Nature*, 223, 1133-1137.

Heathcote, G.D. (1972). Evaluating aphid population on plants. *In* Aphid Technology. Ed. H.F. van Emden, Academic Press, London and New York, pp 105-145.

Hintz, S.D. (1964). Correlation between insect populations, damage, and yield for the spotted alfalfa aphid. *Proc. North Central Branch Entomol. Soc. Amer.*, 19, 35-37.

Hodek, I. (1973). Biology of Coccinellids. Academia, Prague, 260 pp.

Hodek, I., K.S. Hagen, and H.F. van Emden (1972). Methods for studying effectiveness of natural enemies. *In* Aphid Technology. Ed. H.F. van Enden, Academic, London and New York, pp 147-188.

Holling, C.S. (1959). The components of predation as revealed by study of small-mammal predation of the european pine sawfly. *Can. Ent.*, 91, 293-320.

Holling, C.S. (1961). Principles of insect predation. *Ann. Rev. Ent.*, 6, 163-182.

Huffaker, C.B. (1970). Summary of a pest management conference - a critique. *In* Concepts of Pest Management. Proc. North Carolina State Univ. Eds. R.L. Rabb and F.E. Guthrie, N.C. State Univ. Press, 151-188.

Huffaker, C.B. and C.E. Kennett (1969). Some aspects of assessing efficiency of natural enemies. *Can. Ent.*, 101, 425-447.

Huffaker, C.B., C.E. Kennett, and G.L. Finney (1962). Biological control of olive scale, *Parlatoria oleae* (Colvee), in California by imported *Aphytis maculicornis* (Masi) (Hymenoptera: Aphelinidae). *Hilgardia*, 32, 541-636.

Huffaker, C.B. and P.S. Messenger (1964). The ecological basis of biological control. *In* Biological Control of Insect Pests and Weeds. Ed. P. DeBach, Reinhold, New York, 45-73.

Huffaker. C.B., P.S. Messenger, and P. DeBach (1971). The natural enemy component in natural control and the theory of biological control. *In* Biological Control. Ed. C.B. Huffaker, Plenum, New York and London, pp 16-67.

Huffaker, C.B., R.L. Rabb, and J.A. Logen (1977). Some aspects of population dynamics relative to augmentation of natural enemy action. *In* Biological Control by Augmentation of Natural Enemies. Eds. R.L. Ridgway and S.B. Vinson, Plenum, New York and London, 3-38.

Huffaker, C.B., F.J. Simmonds, and J.E. Laing (1976). The theoretical and empirical basis of biological control. *In* Theory and Practice of Biological Control. Eds. C.B. Huffaker and P.S. Messenger, Academic, New York, 41-78.

Hughes, R.D., R. Morton, and J.A. Roberts (1982). Assessment of the parasitization of aphids. *Proc. 3rd Australian Conf. Grassl. Invert. Ecol.*, Ed. K.E. Lee, pp183-189.

Hughes, R.D. and J.A. Roberts (1978). Temperature relationships of spotted alfalfa aphid. *Proc. Lucerne Aphid Workshop, Tamworth, 1978*, Dept. Agric. N.S.W. 25-27.

Ives, P.M. (1981). Estimation of coccinellid numbers and movement in the field. *Can. Ent.*, 113, 981-997.

Johnson, B. (1959). Ants and form reversal in aphids. *Nature,* 184, 740-741.

Johnson, B. (1965). Wing polymorphism in aphids. II Interaction between aphids. *Ent. exp. et appl.* 8 : 49 - 64.

Jonhson, B. (1966). Wing polymorphism in aphids. IV The effect of temperature and photoperiod. *Ent. exp. et appl.* 9 : 301 - 313

Johnson, C.G. (1954). Aphid migration in relation to weather. *Bio. Rev.* 29 : 87 - 118.

Jones, M.G. (1979). Abundance of aphids on cereals from berore 1973 to 1977. *J. Appl. Ecol.,* 16, 1-22.

Keller, R.S.M., L.J. and D.J. Sullivan, S.J. (1976). Oviposition behavior and host feeding of *Ashphes lucens,* an aphid hyperparasitoid. *J.N.Y. ent. Soc.,* 84, 206-211.

Knipling, E.F. (1977). The theoretical basis for augmentation of natural enemies. *In* Biological Control by Augmentation of Natural enemies. Eds. R.L. Ridgway and S.B. Vinson, Plenum, New York and London, pp 151-182.

Laughlin, R., P. Allen, and J. Hardy (1978). *Culex annulirostris* Skuse on the river Murray in South Australia, 1975-1977. Report to S.A. Health Commission, 1978. Waite Agric. Res. Inst., 8pp.

Lawrence, P.O. (1981). Interference competition and optimal host selection in the parasitic wasp, *Biosteres longicaudatus. Ann ent. Soc. Am.,* 74, 540-544.

Lehane, L. (1982). Biological control of lucerne aphids. Rural Research, C.S.I.R.O., 114, 4-10.

Lindquist, A.W. (1942). Ants as predators of *Cochliomyia americana* C. & P. *J. Econ. Ent.,* 35, 850-852.

Lodge, G.M., B.A. Hamilton, and L.R. Greenup (1978). Persistance and production of lucerne varieties under dryland grazing and haycutting. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric., N.S.W., 133-135.

Lloyd, D.L., J.W. Turner and T.B. Hilder (1980). Effects of aphids on seedling growth of lucerne lines 2. spotted alfalfa aphid (*Therioaphis trifolii* f. *maculata* (Monell)) in field conditions. Aust. J. Agric. Anim. Husb. 20 : 452-456.

Mackauer, M. (1972). Genetic aspects of insect production. *Entomophaga* 17, 27-48.

Maelzer. D.A. (1977). The biology and main causes of changes in numbers of the rose aphid, *Macrosiphum rosae* (L.), on cultivated roses in South Australia. *Aust. J. Zool.,* 25, 269-284.

Maelzer, D.A. (1978). The growth and voracity of larvae of *Leis conformis* (Boisd.)(Coleoptera: Coccinellidae) fed on the rose aphid *Macrosiphum rosae* (L.)(Homoptera: Aphididae) in the laboratory. *Aust. J. Zool.,* 26, 293-304.

Maelzer, D.A. (1981). Aphids - introduced pest of man's crops. *In* the Ecology of Pest - Some Australians Case Histories. Eds. R.L. Kitching and R.E. Jones, C.S.I.R.O., Melbourne, Australia. pp 89-105.

Maelzer, D.A., D.E. Pinnock, P.E. Madge, and P.T. Bailey (1981). Intergrated pest management project. Summary of aims and conclusion, and some idea for the future. Unpublished report. Dept. Ent. Waite Inst.

Matejko, I. and D.J. Sullivan, S.J. (1981). Bionomics and behavior of *Alloxysta megourae,* an aphid hyperparasitoid (Hymenoptera: Alloxystidae). *J.N.Y. ent. Soc.,* 86, 275-282.

Messenger, P.S. (1964). The influence of rhythmitically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid, *Therioaphis maculata. J. econ. Ent.,* 57, 71-76.

Messenger, P.S. (1970). Bioclimatic inputs to biological control and pest management programs. *In* Concepts of Pest Management. *Proc. Conf. North Carolina State Univ.* Eds. R.L. Rabb and F.E. Guthrie, pp 84-102.

Messenger, P.S. and D.C. Force (1963). An experimental host-parasite system: *Therioaphis maculata* (Buckton) - *Praon palitans* Muesebeck (Homoptera: Aphididae-Hymenoptera: Braconidae). *Ecology,* 44, 532-539.

Milner, R.J. (1978). The effects of desease on population of lucerne aphids. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric. N.S.W., 105-108.

Mohr, G. (1978). On estimating the losses to agriculture from exotic lucerne aphid infestation in N.S.W. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric., N.S.W., 175-177.

Morris, R.F., W.F. Cheshire, C.A. Miller, and D.G. Mott (1958). The numerical response of avian and mammalian predators during a gradation of the spurce budworm. *Ecology,* 39, 487-494, Neuenschwander, P., K.S. Hagen, and R.F. Smith (1975). Predation on aphid in California fields. *Hilgardia,* 43, 63-78.

Nicholson, A.J. (1933). The balance of animal populations. *J. anim. Ecol.,* 2, 131-178.

Nielson, M.W. and O.L. Barnes (1961). Population studies of the spotted alfalfa aphid in Arizona in relationto temperature and rainfall. *Ann. ent. Soc. Am.,* 54, 441-448.

Nielson, M.W. and H. Don (1974a). A new virulent biotype of the spotted alfalfa aphid in Arizona. *J. econ. Entomol.,* 67, 64-66.

Nielson, M.W. and H. Don (1974b). Interaction between biotype of the spotted alfalfa aphid and resistance in alfalfa. *J. econ. Entomol.,* 67, 268-370.

Nielson, M.W., H. Don, M.H. Schonorst, W.F. Lehman, and V.L. Marbel (1970). Biotype of the spotted alfalfa aphid in western United States. *J. econ. Entomol.,* 63, 1822-1825.

Paetzold, D. and G. Vater (1966). Population dynamics of parasites and hyperparasites of *Brevicoryne brassicae (L.). In* Ecology of Aphidophagous Insects. Ed. I. Hodek, Academia, Prague, 279-281.

Passlow, T. (1977). The spotted alfalfa aphid, a new pest of lucerne. *J. Queensl. Agric.,* 103, 329-330.

Pearch, S.C. (1965). Biological Statistics: An Introduction. McGraw-Hill Book Company, N.Y. 212 pp.

Phillips, J.S. (1957). Immature nutfall of coconuts in British Solomon Islands Protectorate. *Bull. ent. Res.,*, 47, 575-595.

Rabb, R.L., R.E. Stinner, R. van den Bosch (1976). Consevation and and augmentation of natural enemies. *In* Theory and Practice of Biological Control. Eds. C.B. Huffaker and P.S. Messenger. Academic Press, Inc., N.Y., 233-254.

Randolph, N.M. (1957). Control of the spotted alfalfa aphid on alfalfa. *J. econ. Entomol.,* 50, 124-126.

Reilly, T.L.C. and D.L. Godyn (1979). Lucerne.... does aphid spaying pay? *N.S.W. Agric. Gazette,* 90, 3 pp.

Ridland, P. and G. Berg (1978a). Seasonal abundance of spotted alfalfa aphid and its natural enemies in Victoria. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric., N.S.W., 19-24.

Ridland, P. and G. Berg (1978b). Seedling screening of lucerne varieties for resistance to spotted alfalfa aphid. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric., N.S.W., 217-220.

Roberts, J.A. (1978). Studies on the biology of *Trioxys complanatus*. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric., N.S.W., 99-101.

Room, P.M. (1975). Relative distributions of ant species in cocoa plantations in Papua New Guinea. *J. appl. Ecol.,* 12, 47-61.

Schlinger, E.I. and J.C. Hall (1959). A synopsis of the biologies of three imported parasites of the spotted alfalfa aphid. *J. econ. Entomol.,* 52, 154-157.

Schlinger, E.I. and J.C. Hall (1961). The biology, behavior, and morphology of *Trioxys* (Trioxys) *utilis,* an internal parasite of the spotted alfalfa aphid, *Therioaphis maculata* (Hymenoptera: Broconidae, Aphidiinae). *Ann. ent. Soc. Am.,* 54, 34-45.

Sekhar, P.S. (1958). Studies on *Asaphes fletcheri* (Crawford), a hyperparasite of *Aphidius testaceipes* (Cresson) and *Praon aguti* (Smith), primary parasites of aphids. *Ann. ent. Soc. Am.,* 51, 1-7.

Smith, H.S. and P. DeBach (1942). The measurement of the effect of entomophagous insects on population density of their hosts. *J. econ. Entomol.,* 35, 845-849.

Smith, M.V. (1978). Existing hunter river dryland lucerne stands....should they be protected? *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric., N.S.W., 253-255.

Smith, R.F. and K.S. Hagen (1959). The integration of chemical and biological control of the spotted alfalfa aphid. Impact of commercial insecticide treatments. *Hilgardia,* 29, 131-154.

Snedecor, G.W. and W.G. Cochran (1972). Statistical Methods. The Iowa State Univ. Press, Ames, Iowa, USA, 593 pp.

Solomon, M.E. (1949). The natural control of animal population. *J. Anim. Ecol.,* 18, 1-35.

Spencer, H. (1926). Parasites and hyperparasites of aphids. *Ann. ent. Soc. Am.,* 19, 119-151.

Stary, P. (1966). The Aphidiidae of Italy. *Bullettino dell Instituto di Entomologia della Universita di Bologna,* 28, 65-139.

Stary, P. (1970) Biology of aphid parasites (Hymenoptera: Aphidiidae) with respect to integrated control. The Hague, 643 pp.

Stinner, R.E. (1977). Effeciency of innundative releases. *Ann. Rev. Entomol.* 22, *515-531.*

Sullivan S.J., D.J. (1972). Comparative behavior and competition between two aphid hyperparasites: *Alloxista victrix* and *Asaphes californicus* (Hymenoptera: Cynipidae; Pteromalidae). *Environ. Ent.,* 1, 234-244.

Sullivan S.J., D.J. and R. van den Bosch (1971). Field ecology of the primary parasites and hyperparasites of the potato aphid, *Macroshipum euphorbiae,* in the east San Francisco bay area. *Ann. ent. Soc. Am.,* 64, 389-394.

Suter, V.H. and S. Keller (1977). Okologische untersuchungen an feldaulich wichtingen blattlausarten als grundlage fur eine befallsprognose. *Z. ang. Ent.,* 83, 371-393.

Swincer, D.E., C.G. Wilson, and K.J. Walden (1978). Pest management approach. *Proc Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric., N.S.W., 256-258.

Tamaki, G., J.U. McGuire, and J.E. Turner (1974). Predator power and efficacy: A model to evaluate their impact. *Ent. Ent.,* 3, 625-630.

Tamaki, G., M.A. Weiss, and G.E. Long (1980). Impact of high temperatures on the population dynamics of the green peach aphid in field cages. *Environ. Entomol.,* 9, 331-337.

Tilles, D.A. and D.L. Wood (1982). The influence of carpenter ant (*Camponotus modoc*) (Hymenoptera: Formicidae) attendance on the development and survival of aphids (*Cinara* spp.) (Homoptera: Aphididae) in a giant sequoia forest. *Ca. Ent.*, 114, 1133-1142.

Trumble, H.C. (1948). Rainfall, evaporation and drought-frequency in South Australia. *J. Dept. Agric. S. Aust.* 52 : 55-64

Turnbull, A.L. and C.F. Nicholls (1966). A "quick trap" for area sampling of arthropods in gassland communities. *J. econ. Entomol.,* 59, 1100-1104.

Valentine, E.W. (1975). Additions and corrections to Hymenoptera hyperparasitic on aphids in New Zealand. *J.N.Z. Entomol.,* 6, 59-61.

van den Bosch, R., E.I. Schlinger, E.J. Dietrick, and I.M. Hall (1959). The role of imported parasites in biological control of the spotted alfalfa aphid in southern California. *J. econ. Entomol.,* 52, 141-153.

van den Bosch, R. and A.D. Telford (1964). Environmental modification and biological control. *In* Biological Control of Insect Pests and Weeds. Ed P. DeBach, Chapman and Hall, London, pp 459-488.

van den Bosch, R., Schlinger, E.C., Dietrick, E.J., Hall, I.M., and B. Puttler (1964). Studies on succession, distribution and phenology of imported parasites of *Therioaphis trifolii* (Monell) in southern California. *Ecology* 45, 602-621.

van Emden, H.F. (1963). A field technique for comparing the intensity of mortality factors acting on cabbage aphid, *Brevicoryne brassicae* (L.) (Hem.: Aphididae), in different ares of a crop. *Ent. exp. appl.,* 6, 53-62.

Varley, G.C. and G.R. Gradwell (1963). The interpretation of insect population changes. *Proc. Ceylon. Ass. Advmt. Sci., (1962),* 18, 142-156.

Varley G.C. and G.R. Gradwell (1971). The use of models and life table in assessing the role of natural enemies. *In* Biological Control. Ed C.B. Huffaker, Plenum, New York and London, pp 93-112.

Waage, J.K. (1982). Sex ratio and population dynamics of natural enemies- some possible interaction. *Ann. Appl. Biol.,* 101, 159-164.

Walden, K.J., D.E. Swincer, and C.G. Wilson (1978). Sampling techniques for the spotted alfalfa aphid. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric., N.S.W., 63-65.

Walker, A.J.K. (1959). Lucerne in South Australia. *Bull. Dept. Agric. S. Aust.* 454, 24pp

Walker, G.P. and P.J. Cameron (1981). The biology of *Dendrocerus carpentery* (Hymenoptera: Ceraphronidae), a parasite of *Aphidius* species, and field observations of *Dendrocerus* species as hyperparasites of *Acyrthosiphon* species. *N.Z.J. Zool.,* 8, 531-538.

Watt, J.W. (1978). Granular insecticide protection of seedling lucerne against aphids. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric. N.S.W., 158-160.

Way, M.J. (1963). Mutualism between ants and Honeydew-producing Hymenoptera. *Ann. Rev. Entomol.,* 8, 307-344.

Webber, G.D., P.S. Cocks and B.C. Jefferies (1976). Farming system in South Australia, dry land farming in a semi-arid climate. S.A. Dept. Agric. and Fisheries, 102pp.

Williams, G. (1954). Field observations on the cacao mirids, *Sahlbergella singularis* Hagl., and *Distantiella theobroma* (Dist.) in Gold Coast. III. Population fluctuation. *Bull. ent. Res.* 45, 723-744.

Wilson, C.G., D.E. Swincer, and K.J. Walden (1981). The origin, distribution and host range of the spotted alfalfa aphid, *Therioaphis trifolii* (Monell) f. *maculata,* with description of its spread in South Australia. *J. ent. Soc. sth. Afr.,* 44, 331-341.

Wilson. C.G., D.E. Swincer, and K.J. Walden (1982). The introduction of *Trioxys complanatus* Quilis (Hymenoptera: Aphidiidae), an internal parasite of the spotted alfalfa aphid, into South Australia. *J. Aust. ent. Soc.* 21, 13-17.

Woolcock, L.T. (1978). Introduction and rearing of SAA parasites. *Proc. Lucerne Aphid Workshop, Tamworth, 1978,* Dept. Agric., N.S.W., 72-74.

Wright, E.J. and J.E. Laing (1978). The effects of temperature on development, adult longevity and fecundity of *Coleomegilla maculata lengi* and its parasite, *Perilitus coccinellae. Proc. ent. Soc. Ont.,* 109, 33-47.

Wright, E.J. and J.E. Laing (1982). Numerical response of coccinellids to aphids in corn in southern Ontario. *Can. Ent.,* 112, 977-988.

Wylie, H.G. (1966) Some mechanisms that affect sex ratio of *Nasonia vitripennis* (Walk.) (Hymenoptera: Pteromalidae) reared from superparasitized housefly pupa. *Can. Ent.,* 98, 645-653.

APPENDICES

Appendix Table 1. The species of predators, parasitoids, and secondary parasitoids found associated with aphids on lucerne in the study field, January 1981 - October 1982.

Insecta	Relative abundance
HEMIPTERA	
Aphididae	
Therioaphis trifolii (Monell) f. *maculata*	very common in January to April
Acyrthosiphon kondoii Shinji)	very common in April-May and August-September
)	
Acyrthosiphon pisum (Harris))	
HYMENOPTERA	
Aphidiidae	
Trioxys complanatus (Quilis)	very common in January to April
Aphidius spp.	very common in April-May and August-September
Pteromalidae	
Pachyneuron spp.	common in April-May
Ceraphronidae	
Dendrocerus spp.	common in April-May
Alloxistinae	
Phaenoglyphis sp.	less common
Alloxista sp.	less common
Braconidae	
Dinocampus coccinellae (Schrank))	common in November-January
Eulopidae)	
Tetrastichus sp.)	
COLEOPTERA	
Coccinellidae	
Coccinella repanda Thunberg	very common in October-January and March-May
Leis conformis (Boisd.)	rare
NEUROPTERA	
Hemerobidae	
Micromus tasmaniae (Walker)	common in September-November
Chrysopidae	
Chrysopa signata Schnieder	common in December-January
DIPTERA	
Syrphidae	
Melangyna viriceps (Macquart)	common in October-January
Simosyrphus grandicornis (Macquart)	common in October-January
ARACHNIDAE	
Spiders	common throughout the year but in low numbers.

Appendix Table 2.1. The estimated numbers of aphids and natural enemies (L = larvae, A = adults) on lucerne plants in the study field at the Waite Agricultural Research Institute from January 1981 to October 1982.

Date of sampling	Numbers of aphids per 30 stems		Numbers of predators per 100 sweeps				Numbers of parasitoids per 30 stems	
	SAA	(BGA+PA)	*C. repanda*		*M. tasmaniae*		*Trioxys*	Second. p.toids
			L.	A.	L.	A.		
1	2	3	4	5	6	7	8	9
8/1	1027	26	12	16	0	3	42	1
15/1	1181	48	17	26	0	0	63	2
22/1	1741	19	29	47	0	0	68	2
30/1	2895	49	10	84	0	0	84	1
9/2	3636	1	2	133	0	0	86	3
17/2	3451	15	0	192	0	0	93	8
24/2	4396	31	0	108	0	0	119	15
3/3	4357	10	0	152	0	0	90	8
10/3	6402	54	0	181	0	0	101	6
17/3	5291	7	0	227	0	0	125	19

N.B. The lucerne plants were then mown and grazed but a plot of 30m X 30m was fenced. The numbers of aphids continued to be estimated in the plot for the next 10 sampling occasions but no sweeps for predators were taken because the plot was too small.

Appendix Table 2.2. The estimated numbers of aphids and natural enemies for the period 25 March to 28 May 1981 (L = Larvae, A = Adults).

Date of sampling	Numbers of aphids per 30 stems		Numbers of predators per 100 sweeps				Numbers of parasitoids per 30 stems	
	SAA	(BGA+PA)	*C. repanda* L.	*C. repanda* A.	*M. tasmaniae* L.	*M. tasmaniae* A.	*Trioxys*	Second. p.toids
1	2	3	4	5	6	7	8	9
25/3	4151	43					17	5
1/4	5150	102					56	11
8/4	5742	311					63	4
15/4	6941	178					114	15
23/4	12398	682					118	11
29/4	8235	1032					149	28
5/5	3515	2547					85	21
13/5	2262	3106					101	9
21/5	669	2705					57	14
28/5	543	2988					32	19

The lucerne plants were mown and then grazed and no samples were taken until July.

Appendix Table 2.3. The estimated numbers of aphids and natural enemies for the period of 10 July to 19 November 1981 (L=Larvae, A = Adults).

Date of sampling	Numbers of aphids per 30 stems		Numbers of predators per 100 sweeps				Numbers of parasitoids 30 stems	
	SAA	(BGA+PA)	*C. repanda*		*M. tasmaniae*		*Trioxys*	Second. p.toids
			L.	A.	L.	A.		
1	2	3	4	5	6	7	8	9
10/7	0	6	0	1	0	0		
16/7	0	59	0	0	0	1		
25/7	0	39	0	4	0	5		
31/7	0	20	0	8	0	8		
6/8	0	171	0	18	0	45		
15/8	0	444	0	7	0	60		
22/8	0	622	0	20	9	47		
3/9	0	2448	0	10	35	25		
10/9	0	10012	0	3	37	24		
17/9	0	13215	0	2	33	15		
25/9	0	11071	55	1	167	46		
1/10	0	7602	96	0	37	65		
The lucerne plants were then cut.								
13/10	0	3104	11	5	2	221		
21/10	3	4577	17	16	2	72		
29/10	16	2264	117	213	1	220		
5/11	4	72	447	480	121	219		
12/11	7	7	4	161	5	20		
19/11	2	10	3	137	1	23		

The lucerne plants were then cut. Many winged aphids were in the air.

Appendix Table 2.4. The estimated numbers of aphids and natural enemies for the period 10 December 1981 to 16 April 1982 (L = Larvae, A = Adults).

Date of sampling	Numbers of aphids per 30 stems		Numbers of predators per 100 sweeps				Numbers of parasitoids 30 stems	
	SAA	(BGA+PA)	*C.repanda*		*M.tasmaniae*		*Trioxys*	Second. p.toids
			L.	A.	L.	A.		
1	2	3	4	5	6	7	8	9
10/12	27	3	0	30	0	4	0	0
17/12	57	4	0	67	0	5	0	0
24/12	574	7	0	84	0	26	0	0
31/12	2850	8	1	99	0	19	1	0
7/1	3653	25	35	87	1	15	3	1
14/1	6026	3	95	89	1	26	9	4
21/1	2809	6	23	349	0	81	14	1
The lucerne plants were then mown. Many hot days in February and the plants grew very slowly even though they were watered for 6 hours for 7 nights after being mown.								
23/2	5	3	0	2	0	0	0	0
2/3	15	4	0	5	0	0	0	0
10/3	118	8	0	7	0	0	1	1
17/3	122	13	0	16	0	1	6	1
24/3	431	83	0	46	1	0	25	2
1/4	942	272	0	62	0	0	57	1
9/4	866	719	13	66	0	0	61	2
16/4	1599	1061	25	97	0	0	85	5
The lucerne plants were mown and then grazed.								

Appendix Table 2.5. The estimated numbers of aphids and natural enemies for the period 10 May to 17 October 1982 (L = Larvae, A = Adults).

Date of sampling	Numbers of aphids per 30 stems		Numbers of predators per 100 sweeps				Numbers of parasitoids 30 stems	
	SAA	(BGA+PA)	*C. repanda*		*M. tasmaniae*		*Trioxys*	Second. p.toids
			L.	A.	L.	A.		
1	2	3	4	5	6	7	8	9
10/5	22	218	0	3	0	0		
17/5	226	470	0	12	0	0		
24/5	153	1298	0	8	0	0		
31/5	20	4839	0	2	0	0		
7/6	17	3871	0	2	0	0		
17/6	3	9006	0	0	0	0		
24/6	0	8328	0	5	0	0		
1/7	0	14213	0	0	0	0		
8/7	0	19886	0	0	0	0		
15/7	0	10684	0	3	0	5		
The lucerne plants were then mown.								
2/9	0	238	0	15	0	29		
9/9	0	829	0	28	23	37		
16/9	0	2755	0	33	51	46		
24/9	0	7964	24	19	85	95		
1/10	8	4776	23	9	58	70		
8/10	9	3869	42	0	22	116		
17/10	33	2372	0	3	3	192		
The lucerne plants were then grazed.								

Appendix Table 3. Sex-ratios of *Trioxys complanatus* emerging from stem samples (Section 3.2.2.4.1) at each date of sampling from 8 January to 28 May 1981 and from 10 December 1981 to 16 April 1982.

Date of sampling	Numbers of *Trioxys* per 30 stems			Date of sampling	Numbers of *Trioxys* per 30 stems		
	Total	Males	(%)		Total	Males	(%)
8/1	42	22	52	10/12	0	0	0
15/1	63	46	73	17/12	0	0	0
22/1	68	46	68	24/12	0	0	0
30/1	84	60	71	31/12	0	0	0
9/2	86	59	69	7/1	3	1	33
17/2	93	62	67	14/1	9	4	44
24/2	119	74	62	21/1	14	6	43
3/3	90	54	60				
10/3	101	76	75				
17/3	125	87	70				
25/3	17	9	53	23/2	0	0	0
1/4	56	36	64	2/3	0	0	0
8/4	63	42	67	10/3	1	0	0
15/4	114	85	75	17/3	6	2	33
23/4	118	90	76	24/3	25	10	40
29/4	149	113	76	1/4	57	37	65
5/5	85	69	81	9/4	61	37	54
13/5	101	77	76	16/4	85	52	61
21/5	57	43	75				
28/5	32	24	75				

Appendix Table 4. Sex-ratios of *Trioxys complanatus* trapped by "suction" and "dark" traps from 23 February - 16 April 1982.

	Suction traps		Dark traps	
Date of sampling	Numbers of *Trioxys* per 3 traps	Males (%)	Numbers of *Trioxys* per 3 traps	Males (%)
23/2	4	50	0	0
2/3	8	38	1	100
10/3	26	54	2	50
17/3	125	56	5	40
24/3	171	57	13	46
1/4	360	73	30	63
9/4	494	86	33	85
16/4	1436	95	363	90

Appendix Table 5. Numbers of parasitoids* trapped in "suction" and "dark" traps from 13 October 1981 to 16 April 1982.

	"Suction traps"		"Dark traps"	
Date of sampling	*Trioxys*	Secondary parasitoids	*Trioxys*	Secondary parasitoids
Oct. 13	0	0	0	0
21	0	0	0	0
29	0	0	0	2
Nov. 5	0	0	0	0
12	0	0	0	3
19	0	2	0	2
Dec. 12	0	0	0	0
17	0	1	0	0
24	0	0	0	0
31	0	1	0	1
Jan. 7	0	1	1	0
14	0	0	1	0
21	0	0	0	0
Feb. 23	4	1	0	0
Mar. 2	8	4	1	1
10	26	2	2	0
17	125	1	5	0
24	171	8	13	1
Apr. 1	360	1	30	0
9	494	1	43	0
16	1436	15	363	4

* total number of parasitoids cought from 3 traps.

Appendix 6. Test of significance for a deviation of the first point of the "autumn data" (Table 4.2, 25 March 1981) that looks suspiciously large. (Snedecor and Cochran 1967; p 157-158).

Step 1. It has been mentioned in Section 4.2 that for the first point of "autumn data" with $X = 2.05$, $Y = 0.8937$, the deviation

$d_{yx} = - 0.5368$ is as large as twice any other deviation.

Step 2. Compute the regression with this point omitted.

With $n = 10 - 1 = 9$, the value of $\overline{X} = 1.97$; $S_x^2 = 2.1088$

$\hat{Y} = 1.4751 + 0.2286X$; $S_{yx}^2 = 0.0204$ with 7 d.f.

Step 3. For the point, $X = 2.05 - 1.97 = 0.08$,

$\hat{Y} = 1.4751 + (0.2286)(0.08) = 1.4934$

$Y = 0.8937$

Step 4. Since the point was not used in computing this line, it can be regarded as a new member of the population, and a test whether its deviation from the line is within sampling error:

$d_{yx}^2 = Y - \hat{Y} = 0.8937 - 1.4934 = - 0.5997$

the variance due to sampling error is:

$S_{y-\hat{y}}^2 = S_{yx}^2 \, [(1 + 1/(n-1) + (x^2/SS_x^2)]$

$= 0.0204 \, [(1 + 1/9 + (0.08)^2/2.1088)] = (0.0204)(1.1143) = 0.0227$

The value of t is

$t = (Y - \hat{Y})/S_{y-\hat{y}} = -0.5997/\sqrt{0.0227} = 3.979$, with 7 d.f.

The 1% level of t is 3.499 and the 0.5% level is 4.029.

By interpolation, P is about 0.00547.

This probability of t-test does not apply, because the test assumes that the new member is randomly drawn. Instead, the probability level is estimated as nP, and so should be $= (10)(0.00547) = 0.0547$, therefore the <u>null hypothesis is not rejected</u> at the usual 5% probability level.

Appendix Table 7. Comparison of regression lines the responses of *Trioxys* to the changing of SAA in 1981 (January-May) and in 1982 (February-April).

	Deviation from regression		
Within years	d.f.	SS	MS
1981	17	.3006	.0177
1982	6	.1107	.0185
	23	.4113	.0179
Pooled	24	1.1695	.0487
Difference between slopes	1	.7582	.7582

Tests of hypotheses:

(a) Residual variances are homogeneous:

$F = .0185/.0177 = 1.05$; d.f. = 6,17; $P>0.05$; N.S.

(b) Homogeneity of slopes:

$F=.7582/.0179 = 42.36$; d.f. = 1,23; $P<.001$

Appendix Table 8. Comparison of regression lines of responses *C. repanda* to SAA in summer (December1981-January 1982) and in autumn (March-April 1982).

	Deviation from regression		
Within seasons	d.f.	SS	MS
Summer	5	.3092	.0618
Autumn	5	.0792	.0158
	10	.3884	.0388
Pooled	11	.5174	.0470
Difference between slopes	1	.1290	.1290
Combined	12	.7025	
Difference between intercepts	1	.1851	.1851

Tests of hypotheses:

(a) Residual variances are homogeneous:

F = .0618/.0158 = 3.91 ; d.f. = 5,5; P>0.05; N.S.

(b) Homogeneity of slopes:

F= .1290/.388 = 3.32; d.f. = 1,10; P>0.05; N.S.

(c) Homogeneity of intercepts:

F = .1851/.0470 = 3.94 ; d.f. = 1,11 ; P>.05 ; N.S.

Appendix Table 9. Analyses of variance of linear regression of growth rate of SAA in "fine gauze", "coarse gauze", and "partly open" cages; parasitoid-predator exclusion experiment I, 28 Oct. - 25 Nov.(spring) 1982.

Source of variation	d.f.	SS	MS	F	P
(A)Fine cages					
Linear regression	1	1441.46	1441.46	98.33	<.005
Deviation from linearity	13	190.59	14.66		
Total	14	1625.17			
(B)Coarse cages					
Linear regression	1	586.06	586.06	22.21	<.005
Deviation from linearity	13	343.13	26.39		
Total	14	929.19			
(C)Partly open cages					
Linear regression	1	122.03	122.03	10.15	<0.025
Deviation from linearity	13	156.26	12.02		
Total	14	278.29			

Table Appendix 10. Test of significance of linear regression of the growth rate of SAA in "fine gauze", "coarse gauze", and "partly open" cages; parasitoid-predator exclusion experiment I, 26 October - 25 November (spring) 1982.

(A) Fine cages

Source of variation	d.f.	SS	MS
Deviation from linear regression	13	190.59	
Deviation from curvilinear regression	12	190.48	15.87
Reduction in SS	1	.11	0.11
F = 0.11/15.87 = 0.007 ; d.f. = 1,12; P>0.05; N.S.			

(B) Coarse cages

Source of variation	d.f.	SS	MS
Deviation from linear regression	13	343.13	
Deviation from curvilinear regression	12	363.54	21.96
Reduction in SS	1	79.59	79.59
F = 79.59/21.96 = 3.62; d.f. = 1,12; P>0.05; N.S.			

(C) Partly open cages

Source of variation	d.f.	SS	MS
Deviation from liner regression	13	156.26	
Deviation from curvilinear regression	12	156.25	13.02
Reduction in SS	1	0.01	
F = .006/13.021 = .001; d.f. = 1,12; P>0.05; N.S.			

Appendix Table 11. Comparison of regression lines of growth rate of SAA in "fine gauze" and "coarse gauze" cages; parasitoid - predator exclusion experiment I, 26 October-25 November (spring) 1982.

	Deviation from regression		
Within cages	d.f.	SS	MS
Fine cages	13	190.59	14.66
Coarse cages	13	343.1366	26.3951
	26	526.8442	20.2632
Pooled	27	621.4824	23.0179
Difference between slopes	1	94.6382	94.6382

Tests of hypotheses:

(a) Residual variances are homogeneous

F = 26.3951/14.1314 = 1.87; d.f. = 13,13; P>.05; N.S.

(b) Homogeneity of slopes;

F = 94.6382/20.2632 = 4.67; d.f. = 1,26; P<.05

Appendix Table 12. Comparison of regression lines of growth rate of SAA in "coarse gauze" and "partly open" cages; parasitoid-predator exclusion experiment I, 26 October-25 November (spring) 1982.

	Deviation from regression		
Within cages	d.f.	SS	MS
Coarse cages	13	343.1366	26.3951
Partly open cages	13	156.2551	12.0196
	26	499.3917	19.2074
Pooled	27	586.0066	21.7039
Difference between slopes	1	86.6149	86.6149

Tests of hypotheses;

(a) Residual variances are homogeneous:

F = 26.39/12.0196 = 2.20 ; d.f. = 13,13 ; P>.05 ; N.S.

(b) Homogeneity of slopes:

F = 86.6149/19.2074 = 4.51 ; d.f. = 1,26 P<.05

Appendix Table 13. The analyses of variance of linear regression of growth rate of SAA in different sorts of cages (treatments): (A)=fine cages + fluon; (B)=Coarse cages + fluon;(C)=Partly open cages + fluon; (D)=fine cages with no fluon; (E)=Fine cages plus fluon until day but 18 after the start of the experiment, then open to natural enemies; (F)=Fine cages plus fluon until day 18 after the start of the experiment, then open to natural enemies (except ants). Parasitoid- predator exclusion experiment II, 4 -29 January (summer) 1983.

Source of variation	d.f.	SS	MS	F	P
(A).					
Linear regression	1	752.25	752.25	73.75	<.005
Deviation from linearity	13	132.62			
Total	14	884.87			
(B).					
Linear regression	1	501.01	501.01	52.03	<.005
Deviation from linearity	13	125.20	9.63		
Total	14	626.22			
(C).					
Linear regression	1	370.39	370.39	21.81	<.005
Deviation from linearity	13	220.75	16.98		
Total	14	591.14			
(D).					
Linear regression	1	0.03	0.03	0.003	>.25 N.S.
Deviation from linearity	13	130.72	10.06		
Total	14	130.75			
(E).					
Linear regression	1	74.33	74.33	0.87	>.25 N.S.
Deviation from linearity	13	766.28	85.14		
Total	14	840.61			
(F).					
Linear regression	1	463.58	463.58	12.81	<.005
Deviation from linearity	13	470.32	36.18		
Total	14	933.90			

Appendix Table 14. Test of significance of the linear regression of the growth rate of the SAA in different sorts of cages (treatments): (A)=Fine cages plus fuon; (B)=Coarse cages plus fluon; (C)=Partly open cages plus fluon; (D)=Fine cages with no fluon; (E)= Fine cages plus fluon until day 18 from the start of the experiment, then open to natural enemies;(F)=Fine cages plus fluon until day 18 from the start of the experiment, then open to natural enemies (except ants). Parasitoid-predator exclusion experiment II, 4 - 29 January (summer) 1983.

Source of variation	d.f.	SS	MS
(A).			
Deviation from linear regression	13	132.62	
Deviation from curvilinear regression	12	131.03	10.92
Reduction in SS	1	1.59	1.59
F = 1.59/10.92 = 0.15 ; d.f. = 1,12 ; P>.05 ; N.S.			
(B).			
Deviation from linear regression	13	125.21	
Deviation from curvilinear regression	12	121.87	10.16
Reduction in SS	1	3.34	3.34
F = 3.34/10.16 = 0.33 ; d.f. = 1,12 ; P>.05 ; N.S.			
(C).			
Deviation from linear regression	13	220.75	
Deviation from curvilinear regression	12	215.10	17.93
Reduction in SS	1	5.65	5.65
F = 5.64/17.93 = 0.31 ; d.f. = 1,12 ; P>.05 ; N.S.			
(F).			
Deviation from linear regression	13	470.33	
Deviation from curvilinear regression	12	384.57	32.08
Reduction in SS	1	85.76	85.76
F= 85.76/32.08 = 2.68 ; d.f. = 1,12 ; P>.05 ; N.S.			

Appendix Table 15. Comparison of regression lines of SAA growth rate in "fine gauze" and "coarse gauze"cages;parasitoid-predator exclusion experiment II, 4 - 29 January (summer) 1983.

	Deviation from regression		
Within cages	d.f.	SS	MS
Fine cages	13	132.6204	10.2016
Coarse cages	13	125.2026	9.6310
	26	257.8230	9.9167
Pooled	27	270.5442	10.0202
Difference between slopes	1	12.7112	12.7112
Combined	28	308.6786	
Difference between intercepts	1	38.1344	38.1344

Test of hypotheses:

(a) Residual variances are homogeneous:

F = 10.2016/9.6310 = 1.03 ; d.f. = 13,13 ; P>.05 ; N.S.

(b) Homogeneity of slopes:

F = 12.7112/9.9167 = 1.28 ; d.f. = 1,26 ;P>.05 ; N.S.

(c) Homogeneity of intercepts:

F = 38.1344/ 10.0202 = 3.8058 ; d.f. = 1,27 ; P>.05 ; N.S.

Appendix Table 16. Comparison of regression lines of the SAA growth rate in "fine gauze" and "partly open" cages; parasitoid-predator exclusion experiment II, 4 - 29 January (summer) 1983.

	Deviation from regression		
Within cages	d.f	SS	MS
Fine cages	13	132.6204	10.2016
Partly open cages	13	220.7463	16.9805
	26	353.3667	13.5910
Pooled	27	386.8385	14.3273
Difference between slopes	1	33.4698	33.4698
Combined	28	582.7099	
Difference between intercepts	1	195.8714	195.8714

Test of hypotheses:

(a) Residual variances are homogeneous:

F = 16.9805/10.2016 = 1.67 ; d.f. = 13,13 ; P>.05 ; N.S.

(b) Homogeniety of slopes:

F = 33.4698/13.5910 = 2.46 ; d.f. = 1,26 ; P>.05 ; N.S.

(c) Homogeneity of intercepts:

F = 195.8714/ 14.3273 = 13.6712 ; d.f. = 1,27 ; P<.001

Appendix Table 17. Comparison of regression lines of growth rate of SAA in "fine cages" and "treatment F" (see Section 5.2.1 for detail of the treatments); parasitoid-predator exclusion experiment II, 4 - 29 January (summer) 1983.

	Deviation from regression		
Within cages	d.f.	SS	MS
Fine cages	13	132.6204	10.2016
Treatment F cages	13	470.3236	36.1787

Test of hypothesis:

(a) Residual variances are homogeneous:

F = 36.1787/10.2016 = 3.5464 ; d.f. 13,13 ; P<.05

Appendix Table 18. Air temperatures for the first 25 days during experiment I, spring 1982.

Day	Date	Maximum temperature (^{o}C)	Minimum temperature (^{o}C)	Day-degrees above 7.4^{o}C *
1	Oct. 26	31.6	26.2	18.8
2	27	28.0	12.4	12.8
3	28	20.3	10.8	8.2
4	29	22.1	10.3	8.8
5	30	24.7	9.9	9.9
6	31	22.9	10.8	9.5
7	Nov. 1	23.5	12.7	10.7
8	2	29.5	17.5	16.1
9	3	27.2	23.7	18.1
10	4	17.7	13.3	8.1
11	5	17.2	10.0	6.2
12	6	20.6	9.7	7.8
13	7	26.2	13.6	12.5
14	8	28.0	21.4	17.3
15	9	20.5	15.7	10.7
16	10	17.3	12.8	7.7
17	11	18.4	11.4	7.7
18	12	19.0	11.2	7.7
19	13	19.2	9.7	7.1
20	14	15.0	12.8	6.5
21	15	15.9	10.4	5.8
22	16	16.4	7.6	4.6
23	17	15.7	9.5	5.4
24	18	19.6	9.1	7.0
25	19	22.5	12.0	9.9
			Total day-degrees	244.9

* after Hughes and Roberts (1978).

Appendix Table 19. Analysis of variance for linear regression of growth rate of SAA in different sorts of cages (treatments): (A)=finecages + fluon; (B)=coarse cages + fluon; (C)=partly open cages + fluon; (D)=fine cages with no fluon; (E)=fine cages + fluon until day 18 and then opened to natural enemies; (F)=fine cages until day 18 and then opened to natural enemies other than ants; parasitoid-predator exclusion experiment III, 28 April - 23 May (autumn) 1983.

Source of variation	d.f.	SS	MS	F	P
(A)					
Linear regression	1	234.45	234.45	94.92	<.005
Deviation from linearity	13	32.15	2.47		
Total	14	266.60			
(B)					
Linear regression	1	94.16	94.16	20.74	<.005
Deviation from linearity	13	58.98	4.54		
Total	14	153.14			
(C)					
Linear regression	1	16.91	16.91	9.61	<.025
Deviation from linearity	13	22.85	1.76		
Total	14	39.76			
(D)					
Linear regression	1	157.36	157.36	48.42	<.005
Deviation from linearity	13	42.29	3.25		
Total	14	199.65			
(E)					
Linear regression	1	128.44	128.44	17.64	<.005
Deviation from linearity	13	94.69	7.28		
Total	14	223.13			
(F)					
Linear regression	1	126.90	126.90	21.84	<.005
Deviation from linearity	13	75.54	5.81		
Total	14	202.44			

Appendix Table 20. Test of significance for linear regression of the growth rate of SAA in different sorts of cages (Treatments): (A) = fine cages +fluon; (B)=coarse cages + fluon; (C) = partly open cages + fluon; (D)=fine cages with no fluon; (E) = fine cages until day 18 and then were opened to natural enemies; (F) = fine cages + fluon until day 18 and then were opened to natural enemies other than ants; parasitoid-predator exclusion experiment III, 28 April-23 May (autumn) 1983.

Source of variation	d.f.	SS	MS
(A)			
Deviation from linear regression	13	32.15	
Deviation from curvilinear regression	12	24.20	2.02
Reduction in SS	1	7.95	7.95
F= 7.95/2.02 = 3.94 ; d.f. =1,12 ; P>.05 ; N.S.			
(B)			
Deviation from linear regression	13	58.98	
Deviation from curvilinear regression	12	58.67	
Reduction in SS	1	0.31	0.31
F = 0.31/4.87 = 0.06 ; d.f. =1,12 ; P>.05 ; N.S.			
(C)			
Deviation from linear regression	13	22.85	
Deviation from curvilinear regression	12	17.00	1.42
Reduction in SS	1	5.85	5.85
F = 5.85/1.42 = 4.12 ; d.f. = 1,12; P>.05 ; N.S.			
(D)			
Deviation from linear regression	13	42.29	
Deviation from curvilinear regression	12	37.41	3.12
Reduction in SS	1	4.88	4.88
F = 4.88/3.12 + 1.56 ; d.f. = 1,12 ; P>.05 ; N.S.			
(E)			
Deviation from linear regression	13	94.69	
Deviation from curvilinear regression	12	94.67	7.89
Reduction in SS	1	0.02	0.02
F = 0.02/7.89 = 0.0025 ; d.f. = 1,12 ; P>.05 ; N.S.			
(F)			
Deviation from linear regression	13	75.53	
Deviation from curvilinear regression	12	74.72	6.23
Reduction in SS	1	0.81	0.81
F = 0.81/6.23 = 0.13 ; d.f. = 1,12 ; P>.05 ; N.S.			

Appendix Table 21. Comparison of regression lines of growth rate of SAA in "fine gauze" and "coarse gauze" cages; parasitoid-predator exclusion experiment III, 28 April-23 May (autumn) 1983.

	Deviation from regression		
Within cages	d.f.	SS	MS
Fine cages	13	32.1465	2.4728
Coarse cages	13	58.9807	4.5370
	26	91.1272	3.5049
Pooled	27	106.8543	3.9576
Difference between slopes	1	15.7271	15.7271

Test of hypothesis:

(a) Residual variances are homogeneous:

$F = 4.5370/2.4728 = 1.83$; d.f. = 13,13 ; $P>.05$; N.S.

(b) Homogeneity of slopes:

$F = 15.7271/3.5049 = 4.49$; d.f. = 1,26 ; $P<.05$

Appendix Table 22. Comparison of regreesion lines of growth rate of SAA in "fine gauze" and in "partly open" cages; parasitoid-predator exclusion experiment, 28 April - 23 May (autumn) 1983.

	Deviation from regression		
Within cages	d.f.	SS	MS
Fine cages	13	32.1465	2.4728
Partly open cages	13	22.8441	1.7572
	26	54.9906	2.1150
Pooled	27	117.7023	4.3593
Difference between slopes	1	62.7117	62.7117

Test of hypotheses:

(a) Residual variances are homogeneous:

F = 2.4728/1.7572 = 1.41 ; d.f. = 13,13 ; P>.05 ; N.S.

(b) Homegeneity of slopes:

F = 62.7117/2.1150 = 29.65 ; d.f. = 1,26 ; P<.001

Appendix Table 23. Air temperatures for the first 25 days during experiment II, summer 1982/1983.

Day	Date	Maximum temperature (^{o}C)	Minimum temperature (^{o}C)	Day-degrees above 7.4^{o}C *
1	Jan. 4	36.0	17.3	19.3
2	5	32.0	16.0	16.4
3	6	20.8	13.6	9.8
4	7	23.5	16.0	12.4
5	8	31.0	12.8	14.5
6	9	37.6	25.9	24.4
7	10	42.2	29.2	28.3
8	11	24.1	19.2	14.3
9	12	23.7	13.8	11.4
10	13	26.1	14.7	13.0
11	14	31.5	16.8	16.8
12	15	36.4	19.4	20.5
13	16	32.1	19.4	18.4
14	17	38.3	20.8	22.2
15	18	38.5	30.3	27.0
16	19	39.0	30.4	27.3
17	20	39.4	24.4	24.5
18	21	38.8	23.5	23.8
19	22	42.9	28.9	28.5
20	23	41.4	28.0	27.3
21	24	21.5	16.6	11.7
22	25	21.5	14.0	10.4
23	26	25.9	11.9	11.5
24	27	29.5	14.8	14.8
25	28	25.0	16.8	13.5
			Total day-degrees	462.0

* after Hughes and Roberts (1978).

Appendix Table 24. Comparison of regression lines of growth rate of SAA in "fine gauze" and in "treatment D" cages; parasitoid-predator exclusion experiment, 28 April - 23 May (autumn) 1983.

	Deviation from regression		
Within cages	d.f.	SS	MS
Fine cages	13	32.1465	2.4728
Treatment "D" cages	13	42.2838	3.2526
	26	74.4303	2.8627
Pooled	27	78.2596	2.8985
Difference between slopes	1	3.8293	3.8293
Combined	28	95.3623	
Difference between intercepts	1	17.1027	17.1027

Test of hypotheses:

(a) Residual variances are homogeneous:

F = 3.2526/2.4728 = 1.32 ; d.f. =13,13 ; P>.05

(b) Homogeneity of slopes:

F = 3.8293/2.8627 = 1.34 ; d.f. = 1,26 ; P>.05

(c) Homogeneity of intercepts:

F = 17.1027/2.8985 = 5.9005 ; d.f. = 1,27 ; P<.05

Appendix Table 25. Air temperatures for the first 25 days during experiment III, autumn 1983.

Day	Date	Maximum temperature (^oC)	Minimum temperature (^oC)	Day-degrees above 7.4^{o}C *
1	April 28	15.9	9.8	5.5
2	29	16.8	11.4	6.7
3	30	16.0	12.8	7.0
4	May 1	18.5	11.0	7.4
5	2	19.8	13.0	9.0
6	3	20.3	13.9	9.7
7	4	17.6	13.6	8.2
8	5	17.2	12.8	7.6
9	6	15.4	11.3	6.0
10	7	17.1	11.3	6.8
11	8	18.1	9.8	6.6
12	9	20.5	10.3	8.0
13	10	17.2	13.0	7.7
14	11	15.2	10.4	5.4
15	12	16.4	9.4	5.5
16	13	15.6	12.5	6.7
17	14	16.5	9.7	5.7
18	15	19.2	8.7	6.6
19	16	21.4	11.9	9.3
20	17	24.0	14.4	11.8
21	18	22.2	17.9	12.7
22	19	17.1	13.3	7.8
23	20	14.9	9.4	4.8
24	21	15.0	11.7	6.0
25	22	14.1	9.2	4.3
			Total day-degrees	182.8

* after Hughes and Roberts (1978).

Appendix Table 26. The area of discovery of *Trioxys* at each parasitoid density calculated from data in Table 18 by a formula described in Section 6.2.1 (2).

Trioxys density per cage	Area of discovery per *Trioxys* density		
Relicates:	I	II	III
1	0.8172	1.2322	1.3062
2	0.5685	0.5620	0.7277
4	0.3305	0.3730	0.3873
8	0.2093	0.1820	0.2240
16	0.1061	0.1186	0.1136

Appendix Table 27. K-values for parasitism of different densities of *Trioxys*. Each parasitoid density was confined with 240 hosts which were distributed unevenly on 9 lucerne stems in a cage. These data were calculated from data in Table 20.

Trioxys densities	Host densities	K-values for parasitism			
		Rep. I	Rep. II	Rep III	Means
1	10	0.8239	0.6990	1.1250	0.8826
	20	0.6479	0.9031	0.9031	0.8180
	40	0.3591	0.5229	0.5607	0.4809
	80	0.1549	0.3846	0.3591	0.2995
2	10	1.0000	0.5229	1.1250	0.8826
	20	0.4207	0.5607	0.8239	0.6035
	40	0.4407	0.5229	0.5809	0.5148
	80	0.4407	0.4118	0.4882	0.4469
4	10	0.8239	0.7570	1.0000	0.8603
	20	0.6990	0.6021	1.1250	0.8087
	40	0.4882	0.7270	0.6021	0.6057
	80	0.5229	0.5607	0.5229	0.5355
8	10	1.0000	0.5607	1.3011	0.9539
	20	0.5067	0.9031	1.0000	0.8213
	40	0.7892	0.6244	0.7892	0.7343
	80	0.6244	0.5809	0.5809	0.5954
16	10	1.1250	0.6479	1.3011	1.0247
	20	0.6990	0.8239	0.9031	0.8087
	40	0.8239	0.9489	0.9031	0.8920
	80	0.8239	0.9489	0.9031	0.6552

* Each k-values was obtained by subtracting the log of host density after parasitism from the log of host density before parasitism (see original data in Table 20).

Appendix Table 28.1. The k-values for parasitism of 1 female *Trioxys* confined with different host density. These data were calculated from Appendix Table 23.

Exposure periods (days) a)	Initial aphid density (adults)	Replicates		
		I	II	III
1	2	0.3680	0.4674	0.4314
	4	0.4772	0.4289	0.3522
	8	0.4445	0.5327	0.2187
	Total	1.2897	1.4290	1.0023
4	2	1.0108	0.5668	0.6021
	4	0.2878	0.4461	0.7912
	8	0.3867	0.2404	0.7946
	Total	1.6853	1.2533	2.1879
7	2	0.4198	1.0379	0.6990
	4	0.4832	0.5523	0.2912
	8	0.3882	0.6189	0.2047
	Total	1.2912	2.2091	1.1949
10	2	0.4041	0.4079	0.2806
	4	0.3248	0.2567	0.2875
	8	0.2008	0.1487	0.3674
	Total	0.9297	0.8133	0.9355
13	2	0.2345	0.4741	0.3280
	4	0.1666	0.2919	0.2314
	8	0.2320	0.2637*	0.1908
	Total	0.6331	1.0297	0.7502
Totals for replicate		5.8290	6.7344	6.0708

a) days after *Trioxys* introduction.

* value of missing value inserted from Section 6.2.3 (2.1.1)

Appendix Table 28.2. Treatment combination totals which were summed from Appendix Table 28.1

Exposure periods (days)	Initial host densities			Totals for exposure period
	2	4	8	
1	1.2668	1.2583	1.1959	3.7210
4	2.1797	1.5251	1.4217	5.1265
7	2.1567	1.3267	1.2118	4.6952
10	1.0926	0.8690	0.7169	2.6785
13	1.0366	0.6899	0.6899	2.4130
Totals for host densities	7.7324	5.6690	5.2328	18.6342

Appendix Table 29. The analyses of variance of linear regression of parasitism (expressed as the k-value) by *Trioxys* on different host densities; the parasitoid was allowed to search at various length of times (exposure periods); experiment VIIA, 24 March-8April (early autumn) 1981.

Exposure periods	Source of variation	d.f.	SS	MS	F	P
1 day	Linear regression	1	0.0053	0.0053	0.6092	>.25 NS
	Deviation fron linearity	7	0.0612	0.0087		
	Total	8	0.0665			
4 days	Linear regression	1	0.3253	0.3253	11.0271	<.025
	Deviation from linearity	7	0.2066	0.0295		
	Total	8	0.5319			
7 days	Linear regression	1	0.1785	0.1785	3.9933	<.10 NS
	Deviation from linearity	7	0.3131	0.0447		
	Total	8	0.4916			
10days	Linear regression	1	0.0187	0.0187	2.97	<.25 NS
	Deviation from linearity	7	0.0440	0.0063		
	Total	8	0.0627			
13days	Linear regression	1	0.0221	0.0221	2.99	<.25 NS
	Deviation from linearity	6	0.0445	0.0074		
	Total	7	0.0666			

Appendix Table 30. Bartlett's test of homogeneity of variance. All estimates having f = 2 degrees of freedom; experiment VIIA, early autumn 1981

Treatments		Variance	
Exposure periods	Host density	S_i^2	log S_i^2
1	2	0.002533	-2.5964
	4	0.003973	-2.4009
	8	0.026200	-1.5817
4	2	0.060900	-1.2154
	4	0.066300	-1.1785
	8	0.082500	-1.0835
7	2	0.095800	-1.0186
	4	0.018300	-1.7375
	8	0.043100	-1.3655
10	2	0.005245	-2.2803
	4	0.001163	-2.9344
	8	0.013000	-1.8861
13	2	0.014600	-1.8356
	4	0.003927	-2.4059
	8	0.001336	-2.8742
Total		0.438877	-28.3945
$\bar{S}_i$		0.029258	-1.5338

$M = 2.3026\ f\ (a \log \bar{S}_i^2 - \sum \log S_i^2)$

$= 2.3026 \times 2\ (\ 15 \times (-1.5338) - (-28.3945) = 24.8105$

$C = 1 + [(a + 1)/\ 3af = 1 + 16/60 = 1.2667$

$Chi^2 = M/C = 19.5867$;d.f.= 14 ; $P > 0.05$; N.S.

Eccept null hypothesis that all variance were homogeneous.

Appendix Table 31.1. The aplication of Tukey's additivity test to the means of k-values for parasitism when one *Trioxys* female was exposed to different host densities and allowed to serach for hosts for different exposure periods; experiment VIIA, 24 March - 8 April (early autumn) 1981 (after Snedecor and Cochran 1967; Table 11.19.1).

Exposure periods (days)	Initial host densities			Sum	Mean	$D_{i.}$	W_i
	2	4	8				
1	0.4223	0.4194	0.3986	1.2403	0.4134	-0.001	0.0017
3	0.7266	0.5084	0.4739	1.7083	0.5696	0.156	0.0243
7	0.7189	0.4422	0.4039	1.5650	0.5217	0.108	0.0304
10	0.3642	0.2897	0.2390	0.8929	0.2976	-0.117	0.0109
13	0.3455	0.2300	0.2288	0.8043	0.2681	-0.146	0.0117
Sum	2.5775	1.8897	1.7442	6.2114			
Mean	0.5155	0.3779	0.3488		0.4141		
$d_{.j}$	0.101	-0.036	-0.065				

X.. = 0.4141

N = 0.0041

D = 0.0011

SS for non-additivity = $(.0041)^2/D$ = 0.0155 (this value was given in ANOVA for test of additivity in Appendix Table 31.2).

Table Appendix 31.2. Analysis of variance for test of additivity of the means of the k-values for parasitism when 1 *Trioxys* female was exposed to different host densities and exposure periods; experiment VIIA, early autumn 1981 (see Appendix Table 31.1 for calculations).

Source of variation	d.f.	SS	MS	F	P
Period of exposures	4	0.2119			
Host densities	2	0.0792			
Error	8	0.0346			
Non-additivity	1	0.0155	0.0155	5.74	<0.5
Residual	7	0.0191	0.0027		

Appendix Table 32. The k-values for parasitism of 1 female *Trioxys* confined with different host densities. These data were calculated from Tables 30.1 and 30.2. Experiment VIIB, 5-22 May (late autumn) 1981.

Exposure periods (days)	Initial host densities	Replicates		
		I	II	III
1	2	0.3910	0.3980	0.6690
	4	0.3854	0.2576	0.4523
	8	0.2762	0.2027	0.3011
	Total	1.0526	0.8583	1.4224
4	2	0.4523	0.4608	0.5798
	4	0.2413	0.4314	0.4847
	8	0.2273	0.3613	0.4437
	Total	0.9209	1.2535	1.5082
7	2	0.7782	0.6049	0.4649
	4	0.5119	0.3448	0.5342
	8	0.2467	0.4289	0.4894
	Total	1.5368	1.3786	1.4885
10	2	0.7243	0.9031	0.6021
	4	0.5472	0.3632	0.6601
	8	0.3938	0.3594	0.5027
	Total	1.6653	1.6257	1.7649
13	2	0.8528	0.9165	0.5960
	4	0.6185	0.5339	0.4628
	8	0.4490	0.3114	0.6163
	Total	1.9203	1.7618	1.6731
Total for replicates		7.0959	6.8779	7.8571

Appendix Table 32.2. Treatment combination totals which were summed from Appendix Table 32.1

Exposure periods (days)	Initial host densities			Totals for exposure period
	2	4	8	
1	1.4580	1.0953	0.7800	3.3333
4	1.4929	1.1574	1.0323	3.6826
7	1.8480	1.3909	1.1650	4.4039
10	2.2295	1.5705	1.2559	5.0559
13	2.3653	1.6152	1.3747	1.3747
Totals for host densities	9.3937	6.8293	5.6079	21.8309

Appendix Table 33.1. The application of Tukey's additivity test to the means of k-values for parasitism when one *Trioxys* female was exposed to different host densities and allowed to search for hosts for different exposure periods; experiment VIIB, 5-22 May (late autumn) 1981 (after Snedecor and Cochran 1967; Table 11.19.1)

Exposure periods (days)	Initial host densities			Sum	Mean	$d_{i.}$	W_i
	2	4	8				
1	0.4860	0.3651	0.2600	1.1111	0.3704	-0.115	0.0287
4	0.4976	0.3858	0.3441	1.2275	0.4092	-0.076	0.0204
7	0.6160	0.4636	0.3883	1.4679	0.4893	0.004	0.0299
10	0.7432	0.5235	0.4186	1.6853	0.5618	0.077	0.0426
13	0.7884	0.5384	0.4582	1.7850	0.5950	0.110	0.0441
Sum	3.1312	2.2764	1.8692				0.1657
Mean	0.6262	0.4553	0.3738		0.4851		
$d_{.j}$	0.141	-0.030	-0.111				

Check = 0.1657

N = 0.0034

D = 0.0012

SS for non-additivity = N^2/D =0.0096

B = N/D = 0.0034/0.0012 = 2.8333

$\hat{p}$ = 1 - (BX) ; X = 0.4851

= 1 - (2.8333 x 0.4851) = -0.3744

Appendix Table 33.2. Analysis of variance and test of non-additivity for means of k-values for exposure periods and host densities; experiment VIIB, 5-22 May (late autumn) 1981.

Source of variation	d.f.	SS	MS	F	P
Exposure periods	4	0.1107			
Host densities	2	0.1659			
Error	8	0.0134			
Non-additivity	1	0.0096	0.0096	17.78	<0.01
Residual	7	0.0038	0.00054		

Appendix Table 34. The analyses of variance of linear regression of parasitism (expressed as the k-value) by *Trioxys* on host densities; the parasitoid was allowed to search at various length of times (exposure periods); experiment VIIB, 5-22 May (late autumn) 1981.

Exposure periods	Source of variation	d.f.	SS	MS	F	P
1 day	Linear regression	1	0.0823	0.0823	8.31	<0.025
	Deviation from linearity	7	0.0695	0.0099		
	Total	8	0.1518			
4 days	Linear regression	1	0.0450	0.0450	5.29	=0.057 N.S.
	Deviation from linearity	7	0.0596	0.0085		
	Total	8	0.1046			
7 days	Linear regression	1	0.0619	0.0619	3.58	=0.10 N.S.
	Deviation from linearity	7	0.1214	0.0173		
	Total	8	0.1833			
10days	Linear regression	1	0.1636	0.1636	11.13	<0.025
	Deviation from linearity	7	0.1029	0.0147		
	Total	8	0.2665			
13days	Linear regression	1	0.1775	0.1775	10.69	<0.025
	Deviation from linearity	7	0.1162	0.0166		
	Total	8	0.2937			

Appendix Table 35. Comparison of regression lines of *Trioxys* responses (expressed as the k-value for parasitism) on different exposure periods and host densities; experiment VIIB, 5-22 May (late autumn) 1981.

	Deviation from regression		
Within (initial) host densities	d.f.	SS	MS
2 SAA per stem	3	0.00390	0.00130
4 SAA per stem	3	0.00120	0.00040
	6	0.00510	0.00085
Pooled	7	0.01180	0.00170
Difference between slopes	1	0.00670	0.00670

Test of hypotheses:

(a) Variances are homogeneous:

F = 0.00130/0.00040 = 3.250; d.f. = 3,3; P>.05; N.S.

(b) Homogeneity of slopes :

F = 0.00670/0.00085 = 7.8824; d.f. = 1,6; P<.05

Appendix Table 36. The analysis of variance for regression of percentage of male progeny of a pair of *Trioxys* on different host densities (see Table 32.2); experiment IX.

Source of variation	d.f.	SS	MS	F	P
Total	5	262.3053			
Linear regression	1	243.3238	243.3238		
Deviation from linearity	4	18.9815	4.7454	51.2757	<.005
Quadratic regression	1	15.2445	15.2445	12.2380	<.05
Deviation from quadratics	3	3.7371	1.2457		

Appendix Table 37. Analyses of variance for numbers of live aphids at different times of sampling; experiment XIII. The original data are in Tables 40.1 and 40.2.

Source of variation	d.f.	SS	MS	F	P
Day 4					
Treatments	6	15.4036	2.5673	.874	>.05 N.S.
Replicates	1	2.6515	2.6515	.903	>.05 N.S.
Error	6	17.6247	2.9374		
Total	13	35.6797			
Day 7					
Treatments	6	255.3965	42.5661	8.561	<.01
Replicates	1	0.7929	0.7929	0.160	>.05 N.S.
Error	6	29.8314	4.9719		
Total	13	286.0209			
Day 10					
Treatments	6	949.7248	158.2875	73.200	<.005
Replicates	1	12.3349	12.3349	5.704	>.05 N.S.
Error	6	2.1624			
Total	13	975.0341			
Day 13					
Treatments	6	1421.6174	236.9362	96.991	<.005
Replicates	1	0.1954	0.1954	0.080	>.05 N.S.
Error	6	14.6572	2.4429		
Total	13	1436.4700			

Appendix Table 38. Analyses of variance (split-plot) of numbers of mummies per female *Trioxys* in the presence and in the absence of adult *Coccinella* at different times of sampling. The Original data are in Tables 42.1, 42.2 and 42.3.

Source of variation	d.f.	SS	MS	F	P
Day 7					
Main plots	5	5.54			
Replicates	1	0.59	0.59	0.33	>.05 N.S.
Trioxys densities (T)	2	1.41	0.71	0.40	>.05 N.S.
Error (a)	2	3.54	1.77		
Subplots	6	19.97			
Coccinella densities (C)	1	8.31	8.31	2.34	>.05 N.S.
Interaction (TC)	2	1.01	0.51	0.14	>.05 N.S.
Error (b)	3	10.65	3.55		
Total	11	25.51			
Day 10					
Main plots	5	0.30			
Replicates	1	0.02	0.02	0.57	>.05 N.S.
Trioxys densities (T)	2	0.21	0.11	2.75	>.05 N.S.
Error (a)	2	0.07	0.04		
Subplots	6	48.05			
Coccinella densities (C)	1	42.19	42.19	45.37	<.01
Interaction (TC)	2	3.08	1.54	1.66	>.05 N.S.
Error (b)	3	2.78	0.93		
Total	11	48.35			
Day 13					
Main-plots	5	4.40			
Replicates	1	2.05	2.05	3.42	>.05 N.S.
Trioxys densities (T)	2	1.16	0.58	0.97	>.05 N.S.
Error (a)	2	1.19	0.60		
Sub-plots	6	26.68			
Coccinella densities (C)	1	22.25	22.25	19.69	<.05
Interaction (TC)	2	1.04	0.52	0.46	>.05 N.S.
Error (b)	3	3.39	1.13		
Total	11	31.08			