MIGRANT PRODUCTION AND DISPERSAL IN THE COWPEA APHID, *APHIS CRACCIVORA* KOCH (HOMOPTERA : APHIDIDAE)

by

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SUMMARY

The cowpea aphid, *Aphis craccivora* Koch is an anholocyclic species and the principal vector of subterranean clover stunt virus, in temperate legume pastures in South Eastern Australia. It occurs in small numbers in late autumn and spring and so is not a pest in South Australia. The work described in this thesis was undertaken to investigate the possible causes of its non-pest status, to measure its emigration potential, and also to study the effects of growing broad beans on its population levels in the South Australian environment.

Three phases of field biology of *A. craccivora* were studied: migrant production, flight behaviour and colonization.

Field cage experiments on the growth of *A. craccivora* colonies on broad beans indicated apterous dispersal as a consistent and facultative behavioural mechanism. There is no evidence of reduced fecundity of apterae with increasing population density of a colony, prior to the start of dispersal. Reduced production of young nymphs was associated with apterous dispersal.

The rate of production of migrant alatae varied between 75 and 97% in colonies with 550 to over 4,000 aphids. The total number of alatae which dispersed from a broad bean plant varied between 3,300 and 7,700. The proportion of apterae among the adult emigrants varied from 5 to 15%. Parasitization soon after colonization frequently prevented the establishment of a colony.

The capacity to produce emigrants differs in host plant species. More alatae dispersed from broad beans than from common burr medic and subterranean clover plants of the same age. Apterae began to disperse earlier from common burr medic and subterranean clover than from broad beans; the time lag was approximately one generation time. Initial numbers of colonizing alatae influenced the rates and patterns of alata dispersal, without influencing the alata output from a colony. Host plants on which colonies had been initiated with 4 and 8 alatae, collapsed earlier than those with 1 and 2 alatae. The results defined the concept of finite carrying capacity of host plants which are transient resources for *A. craccivora*.

There is no evidence of behavioural polymorphism among *A. craccivora* alatae and it is probable that they are pre-reproductive obligatory migrants. However, temperatures below 16^{o}C do inhibit take-off in the field. Rains, dew, and excess honey dew, may also reduce the extent of alata dispersal in the field because of their wing distortion effects. The influence of prevailing environmental factors appears to determine the extent of long distance alata dispersal despite their innate migratoriness.

Field experiments and observations indicate that broad bean is a suitable crop for colonization by *A. craccivora* in South Australia. Two peaks of colonizing alatae were recorded, one small peak in late May and a major peak in mid-October or early November. The rate of primary infestation of a 4 week old broad bean crop was very low i.e., 0.04 alata per stem. Two features of colonization were observed;

interplant movement and aggregative behaviour of colonizing alatae. The significance of these aspects is discussed in relation to the success of colonization and establishment of the aphid in a new area.

The results have been discussed with reference to the deterministic population model (Gutierrez *et al.* 1974a) of *A. craccivora*, and the role of migration in its entirety is defined in relation to the survival and the abundance of this aphid. It is concluded that *A. craccivora* is not adapted to reach pest proportions in temperate legume pastures and it is predicted that it has a potential of attaining pest status if broad beans are grown on a large scale in South Australia.

DECLARATION

The work presented in this thesis is my own unless otherwise acknowledged, and has not been published previously or submitted to any university for the award of any degree.

Ahmad bin Mohammad

June, 1979.

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SECTION 1

INTRODUCTION

The cowpea aphid, *Aphis craccivora* Koch, 1854 (Aphididae: Homoptera) is an important pest of plants of the family Leguminosae, but infests other dicotyledons as well. It is a cosmopolitan and polyphagous insect and as such is the subject of considerable economic literature (Bodenheimer and Swirski 1957; Eastop 1966).

1.1: Synonomy of *Aphis craccivora*

A. craccivora Koch, has often been confused with other black aphids and various names have been applied to it. *A. robiniae* Macchiati, *A. leguminosae* Theobald, 1915 (Hille Ris Lambers 1948) and *A. loti* Kaltenbach (Gair and Taylor 1957) are synonyms of *A. craccivora* Koch. *A. laburni* Kaltenbach, 1843, and *A. medicaginis* Koch, 1854, are distinct European species whose names have been applied to *A. craccivora* in Australia (Hille Ris Lambers 1948; Dyce 1951; Eastop 1966; Carver 1974, personal communication). This aphid has also been described as *A. medicaginis* in New Zealand (Cottier 1953), Hawaii (Zimmerman 1948) and the U.S.A. (Anon 1962).

Various common names have also been applied to this aphid in different parts of the world, i.e. the cowpea aphid in the U.S.A. (Huffaker and Messenger 1976) and Australia (Gutierrez *et al.* 1971, 1974a, 1974b; Behncken and Maleevsky 1977), the groundnut aphid in India (Patel and Patel 1971; Patel *et al.* 1976) and Africa (Jones 1967), the black bean aphid in the Philippines (Bernado 1969) and the oriental pea aphid in Japan (Kawada 1973).

1.2: Distribution and host plants of *A. craccivora*

The origin of this species is uncertain and probably somewhere in the steppe areas of the Palearctics (Stary 1968). This aphid is truely cosmopolitan in its distribution and occurs predominantly in the mediterranean, subtropical and tropical regions.

In the Middle East, it occurs in Egypt (Hassanein *et al.* 1971; Saleh *et al.* 1972), Israel, Jordan, Lebanon, Iraq, Turkey and Iran (Bodenheimer and Swirski 1957; Schalk 1973; Kaiser 1972, 1973). In the African continent it has been recorded in North Africa (Real 1955), Congo (Jepson 1948), Kenya (Eastop 1953; Jones 1967), Sudan (Clinton 1962), Nigeria (A'Brook 1964, 1968; Booker 1963), Ethiopia (Eastop 1966), Tanzania (Evans 1954), Uganda (Davies 1972), Malawi (Adams 1967; Farrell 1976) and South Africa (van der Merwe 1931; Müller and Scholl 1958). In Europe, it occurs in Germany (Falk 1957, 1958), Bulgaria (Grigorov 1960), Czechslovakia (Stary 1968a), the U.S.S.R. (Stary 1968) and southern England (Eastop 1966). In Asia, it occurs in Afghanistan (Stolyarov *et al.* 1974), Pakistan (Ghani 1971), China (Eastop 1966), India (Patel and Patel 1971), Japan (Kawada 1973), and Ceylon (Eastop 1966). In South East Asia, *A. craccivora* has been recorded in the Philippines (Bernabe 1972; Bernado 1969), Java, Borneo (Eastop 1966), Malaysia (Poh and Lim 1972) and New Guinea (Eastop 1966). In the South Pacific, it has been found in New Zealand (Cottier 1953; Lowe 1966), Fiji, Samoa, Tahiti (Eastop 1966) and also in Hawaii (Zimmerman 1948; Higa and Namb 1970). In the Americas, it occurs in Canada (Evans 1973), the U.S.A. (Leonard 1973; Radke *et al.* 1973; Huffaker and Messenger 1976), Mexico, Argentina, Guyana, Chile, Colombia, Surinam (Eastop 1966) and Bolivia (Squire 1972). In the Caribbean, it occurs

in Jamaica and Trinidad (Eastop 1966; Hague and Chenulu 1972; see also Commonwealth Institute of Entomology map A99, 1959).

A. craccivora is an introduced species in Australia (Eastop 1966; Carver and Stary 1974) and occurs in Queensland (Passlow 1969), New South Wales (Dyce 1951; Johnson 1951, 1957; Grylls 1972), Victoria (O'Loughlin 1963; Nancarrow 1976), Tasmania (Martyn and Miller 1963), South Australia (Edwards 1953), Central Australia (White 1967) and Western Australia (Carver 1974 - personal communication).

Legumes are principal hosts of this species in many regions. Besides legumes, it has been found to attack cotton in Egypt (Hassanein *et al.* 1971), Afghanistan (Stolyarov *et al.* 1974) and the U.S.A. (Smith and Falcon 1973); citrus in Israel (Bodenheimer and Swirski 1957; Stroyan 1961); grain crops in Bolivia (Squire 1972) and forest trees in Turkey (Canakcioglu 1972).

In Australia it has been recorded on 67 plants belonging to 19 different families (Dyce 1951). Pasture legumes (Gutierrez *et al.* 1971), field beans and peas (Anon 1955, 1971; Edwards 1953; Martyn and Miller 1963; Saunders 1968; Martyn *et al.* 1969; Passlow 1969; Grylls 1972) are mainly attacked. The aphid has also been found on many endemic plants in Central Australia (White 1967) and North West New South Wales (Johnson 1951, 1957).

1.3: Economic importance of *A. craccivora*

A. craccivora is economically important for two reasons. Firstly it is a pest on crops like broad beans (Saleh *et al.* 1972;

Grylls 1972), french beans, cowpeas, pulses (Bernabe 1972; Waghmare and Pokharkar 1974) and groundnuts (Passlow 1969; Patel and Patel 1971; Farrell 1976) in different parts of the world.

Secondly, and more importantly, it is a mobile species and an efficient vector of many viral pathogens such as rosette virus of groundnuts in the African continent (Evans 1954; Müller and Scholl 1958; Booker 1963; A'Brook 1964) and India (Kousalya *et al.* 1971); peanut mottle virus in East Africa (Bock 1973) and the U.S.A. (Kuhn and Demski 1975); groundnut mosaic virus in Malaysia (Poh and Lim 1972); cowpea mosaic virus in Trinidad (Haque and Chenulu 1972), Iran (Kaiser *et al.* 1971) and Australia (Bencken and Maleevsky 1977); broad bean yellow mosaic virus in Iran (Kaiser *et al.* 1971), Egypt (Abu Salih *et al.* 1973; El-Kady and Salem 1974), India (Nagaich and Vashisth 1965) and Canada (Evans 1973); pea leaf roll virus in Iran (Kaiser and Schalk 1973); subterranean clover stunt virus (Grylls and Butler 1956; Smith 1966; Gutierrez *et al.* 1971; Grylls 1972; Nancarrow 1976) and sugarcane mosaic virus in Australia (Teakle and Grylls 1973); papaya mosaic virus in Hawaii (Higa and Namb 1970) and India (Khurana and Bhargava 1971); watermelon mosaic virus in Florida (Adlerz 1972, 1974); cucumber mosaic virus in India (Singh 1969) and Iran (Kaiser *et al.* 1971); and Tristeza virus of citrus in India (Verma *et al.* 1965).

1.4: Life cycle of *A. craccivora*

As an aphid of worldwide distribution, *A. craccivora* has successfully adapted itself to different climates. In northern and temperate zones where winters are severe, its life cycle is holocyclic

i.e., it overwinters in the egg stage in Southern Germany (Falk 1957; Müller 1966, 1971) and Bulgaria (Grigorov 1960) on lucerne (*Medicago sativa*) and on common vetch (*Coronilla varia*) in the North Eastern United States of America (Radke *et al.* 1973). Alatae from these primary hosts migrate to beans. However, in the sub-tropics and tropics, this aphid is exclusively anholocyclic, i.e., it reproduces parthenogenetically and viviparously throughout the year on a wide range of host plants. Detailed studies on its biology in North Africa (Real 1955), East Africa (Evans 1954), South Africa (van der Merwe, 1931), the Middle East (Bodenheimer and Swirski 1957), India (Patel and Patel 1971) and Australia (Dyce 1951; Johnson 1951; Gutierrez *et al.* 1971; Carver 1974, personal communication) revealed its anholocyclic life-cycle. Basu *et al.* (1968) recorded sexuales of *A. craccivora* in India. Their finding may, however, be regarded as an exception.

The fact, that *A. craccivora* survives in different climatic zones by a change of its life cycle, has led aphid biologists to speculate about the probable evolutionary pathways leading to such an adaptation. Müller and Scholl (1958) maintain that this species consists of several biological races throughout its range. Müller (1966) regards *A. craccivora* (in the sub-tropics and tropics) as an anholocyclic population of the holocyclic European species. Further experiments by Müller (1971), revealed that, after five years of exclusive parthenogenetic reproduction, *A. craccivora* had not lost the ability to produce sexuales in East Germany and this led the author to conclude that anholocyclic populations of this aphid evolved by mutation rather than by gradual physiological changes.

1.5: Past work on the ecology of *A. craccivora* in Africa and India

Despite numerous observations on the occurrence of *A. craccivora* in different parts of the world, it is surprising that a few detailed studies have been made on its ecology. Comprehensive studies on the ecology of *A. craccivora* in Africa include those of van der Merwe (1931), Real (1955), Evans (1954), Davies (1972) and Farrell (1976). These studies do provide a wealth of basic field data on the infestation of groundnuts in relation to spacing and plant density, mean aphid numbers per plant or unit area, morph composition and size of aphid colonies, incidence of natural enemies and off-season hosts for the aphid. The main interest evoking these studies has been the relationship between *A. craccivora* and the spread of rosette disease in groundnuts. With the exception of the study by Farrell (1976), none of these studies has attempted to explore - why does this aphid attain low populations per unit area, and what are the causes which determine changes in its populations in groundnut monocultures within the perspective of a subtropical or tropical climate. In other words, in the tropics, the ecology of *A. craccivora* has not been studied in its own right within the framework of any conventional model of insect population dynamics (e.g. Andrewartha and Birch 1954; Clark *et al.* 1967; Varley and Gradwell 1960, 1970), as is the case with many aphid species in temperate climates such as, the cabbage aphid (Hafez 1961; Hughes 1963; Lamb and Lowe 1961, 1967), the green peach aphid (Blackman 1974; Tamaki 1974; Barbagallo *et al.* 1972), the black bean aphid (Way 1967; Way and Banks 1967), the walnut aphid (Sluss 1967) and the rose aphid (Maelzer 1977).

Farrell (1976) concludes that emigration regulates *A. craccivora* populations at a low density on groundnuts. He concluded also that closer spacing or high densities of groundnut plants, adversely affected the rate of increase of the aphid. His study demonstrated density dependent build-up of syrphid and coccinellid predators of *A. craccivora* on groundnuts in a tropical climate, as did Hughes (1963) demonstrate the build-up of predators of the cabbage aphid in Canberra, Australia.

However, Farrell (1976) could not demonstrate conclusively that emigration was the main cause of low population densities (150 aphids/m^2) of *A. craccivora* on groundnuts in Malawi. The percentage of fourth instar alatiform nymphs in his samples varied mostly between 5 and 55. Nor did he present any empirical evidence regarding the lower levels of nutrition in dense groundnut plants, which he thought, had adversely affected the rate of increase of the aphid in his experiments. His study, nevertheless, has the distinction of elucidating the causes of changes in the numbers of *A. craccivora* on groundnuts in a tropical climate.

Studies by Patel and Patel (1971) provide useful information on the flight periodicity, build-up of *A. craccivora* populations on groundnuts and the off-season survival of this aphid in Gujrat State of India. The authors failed to interpret their data and could not draw any meaningful conclusion about the population dynamics of the aphid. The same criticism holds true for the studies by Saleh *et al.* (1972) in Egypt.

1.6: Past work on the ecology of *A. craccivora* in Australia

Detailed studies on the morphology, biology and host range of *A. craccivora* were made by Dyce (1951), following the swarms of black aphids observed in Sydney in 1948 and 1950. Johnson (1951) also studied the biology and host relations of *A. craccivora* in New South Wales, with emphasis on the origin of aphid swarms and the distribution of aphid infestations over an area of 26,000 sq.km in North West New South Wales. His observations (Johnson 1957) are worth mentioning here. *A. craccivora* was breeding on burr medic (*Medicago hispida* var. *denticulata*), a common legume in pastures, and Shepherd's purse (*Capsella bursapastoris*, a widespread weed in New South Wales. The aphids were numerous on spindly plants growing under moisture stress and plants with luxurious growth had relatively few or no aphids. The natural enemies of the aphid were absent. Johnson (1951) reported also that an experimental plot of broad beans at Sydney University was infested by *A. craccivora*. The aphid populations grew for 3 weeks and thereafter natural enemies, i.e., the Aphidiid parasites, coccinellids, syrphids and chamaemyiids exterminated the aphids within 2 weeks in late spring.

O'Loughlin (1963) and Hughes *et al.* (1964, 1965) provide data on the flight periodicity of *A. craccivora* in different states. Carver and Randles (1961 - personal communication) also recorded *A. craccivora* flights by yellow tray traps at Waite Institute and Adelaide Hills. They observed two peaks of alatae; a major peak in September to October and a minor peak in May.

Grylls (1972) studied the infestation of beans and peas by *A. craccivora* on the Central Tablelands of New South Wales. Experimental plots were planted in late October, late November and mid January. The numbers of aphids and natural enemies were recorded every two weeks. The average number of aphids per plant for the first two plantings were 10 to 270 on peas, 90 to 150 on *Phaseolus* beans and 50 to 250 on broad beans. Negligible aphid populations developed on peas and *Phaseolus* beans on the third planting, but heavy populations of up to 11,000 aphids per plant were observed on broad beans in early April. Thereafter, natural enemies of the aphid, especially coccinellids increased in numbers and exterminated the aphids by the end of May. The build-up of *A. craccivora* populations was observed on broad beans despite frequent low temperatures of $< 1.8^{o}C$ during April and May. In the discussion of his results, Grylls (1972) commented that, the presence of suitable host plants was as much a limiting factor as climate, for the build-up of *A. craccivora* populations.

Gutierrez *et al.* (1971, 1974a, 1974b) prepared a deterministic model of *A. craccivora* populations in the temperate legume pastures of New South Wales. Their objectives were to understand the ecology of this insect and to use that understanding in investigating the epidemiology of subterranean clover stunt virus (SCSV), which is transmitted by *A. craccivora*. *A. craccivora* is a pest in temperate legume pastures because it is an efficient vector of SCSV, not because it can attain damaging population levels (Gutierrez *et al.* 1971). The cowpea aphid model (Gutierrez *et al.* 1974a) is an improvement over other aphid models (Hughes and Gilbert 1968; Gilbert and Gutierrez 1973) as it incorporates effects of temperature, rainfall and soil moisture on the growth of host plants of the aphid also on a regional basis.

Various components of the biology of the aphid, i.e. rates of development and age-specific fecundity on principal host plants on a physiological time scale, relationship between population density and alata production, effects of crowding on potential rate of increase and effects of abiotic and biotic mortality factors on aphid populations, make the model more realistic. The authors used the model to examine the aphid-host plant relationship (on burr medic and subterranean clover) in the temperate environment of South Eastern Australia and concluded that *A. craccivora* was not adapted to the temperate climate of the region, as they believed that this aphid was primarily a warm weather species.

Gutierrez *et al.* (1971, 1974a) put forward also the hypothesis that *A. craccivora* survives in the vast and ephemeral habitat of South Eastern Australia because of its migratory ability. Based on their records of yellow tray trap catches (1974b) of this aphid and its biology, especially its ability to produce migrant alatae at low population densities in a short time (1974a), the authors regarded *A. craccivora* as a super-migrant species as well.

The authors also used the model to examine the potential of various biotic mortality factors to control *A. craccivora* numbers (1974a) and concluded that a suitable Aphidiid parasite from the Middle East might be a potential agent for this aphid in South Eastern Australia.

The work of Gutierrez *et al.* (1971, 1974a, 1974b) is the first systematic attempt to understand the ecology of *A. craccivora* in a temperate environment. Despite the apparent realism of the model,

a thorough study of their work indicates that the conclusions drawn from it may be regarded as either misleading or an over-simplification. This criticism is based on three reasons: 1) the model is based on the field data of one year only; 2) some of the important parameters regarding the biology and behaviour of the aphid are either lacking or poorly worked out and that too in laboratory without supporting evidence from the field; and 3) the authors did not compare their results with those of other workers, both in Australia and abroad.

1.7: Preliminary observations on the field biology of *A. craccivora* in Adelaide in summer 1974-75

Initial observations in Brownhill Creek National Park in late October 1974 revealed natural infestations of *A. craccivora* on vetch plants (*Vicia sativa* L.) which were growing in small patches (1-3 m^2) mixed with sweet peas (*Pisum* sp.) along 1½ Km. roadside. Of the 4 patches 3 had aphids. Each infested patch had one or two heavily infested plants surrounded by many lightly infested ones. The aphids were aggregated on growing tips. Syrphid and coccinellid larvae were also present. Black ants were also attending the infested plants. The pea plants were free of aphids.

These observations prompted two questions, i.e. 1) how do the infestations of this aphid grow and spread, and 2) how do they decline? The answers to these questions were sought by a pilot study. The following field study was, therefore, undertaken in Alverstoke Orchard of Waite Institute in November - December 1974.

Broad beans (*Vicia faba* cultivar Seville Long Pod) and green peas (*Pisum sativum* cultivar Green Feast) were sown at intervals of 2 weeks in two small adjacent plots (5 x 4.5 m). A spacing of 60 cm between and 10 cm within a row was followed. These plots are referred to as Plot I and II in the text. Due to poor germination plots I and II had 33 and 35 broad bean plants. The plants were watered by furrow irrigation whenever necessary. No fertilizer applications were made and weeds were removed as necessary.

North of the plots, a Kale crop was heavily infested with the cabbage aphid and the green peach aphid. Fifty potted citrus plants were also present near the plots.

All the plants in both the plots were observed for *A. craccivora* at irregular intervals (1-5 days) for 6 weeks. The initiation of *A. craccivora* infestations, their progress and the incidence and impact of natural enemies on infested plants were recorded. The visual observations may have underestimated the actual aphid numbers on plants, nevertheless, they represented a nearly accurate picture of changes associated with the development of infestations.

Newly germinated seedlings were exposed to colonization in plots I and II from 13th November and 5th December. The pea plants were not infested to any great extent. Colonizing *A. craccivora* alatae settled invariably on the growing tips or crowns of broad bean seedlings. All aphids on an infested crown were regarded as a colony. Individual colonies had either alatae with nymphs or one or more nymphs only. The colonies with isolated nymphs were indicative of the loss or

movement of colonizing alatae. Not all alatae were seen reproducing on the same plants for the rest of their reproductive lives (Table 1.1). Initiation of a colony did not necessarily ensure its establishment (Table 1.2) because of predation of isolated nymphs and also their probable movement off the colonized crowns. The colonization by incoming alatae was regarded as primary infestation.

Following primary infestation, the first maturing nymphs became apterae. These apterae settled and reproduced on upper internodes, leaves and crowns of broad bean stems. As the number of apterae increased subsequently, many settled on middle and lower internodes and leaves. A few apterae initiated new colonies by settling on young crowns of basal axillary stems. As apterae reached a certain number in a colony (70-90), a few walked off the plants and initiated new colonies in the vicinity of parent colonies. An increase in the total colonized stems in Plot I from 19th to 23rd December (Table 1.1) indicated dispersal and recolonization by apterae. This colonization by apterae was regarded as secondary infestation.

No *A. craccivora* alatae were recorded in Plot I from 14th to 23rd December (Table 1.1). Alata production in Plot I was observed on 29th December and 18 teneral alatae were recorded in a colony. Simultaneously, *A. craccivora* alatae were recorded on 5 other plants also in Plot I. It is probable that the alatae on these 5 plants had moved from the only colony which was producing alatae in Plot I. This recolonization by alatae which were produced within the plot, was also regarded as secondary infestation.

Table 1.1. Observations on the arrival of *A. craccivora* alatae on broad bean plants in the plots - 1974.

Date of observation	Plot I		Plot II	
	No. of plants with alatae	No. of alatae per plant	No. of plants with alatae	No. of alatae per plant
Nov 19 1974	2	1,1	-	-
30	2	1,1	-	-
Dec 3	3	1,1,3	-	-
9	-	-	1	2
10	2	1,1*	0	0
11	2	1,1*	0	0
12	2	1,1*	0	0
14	0	0	2	2,1
17	0	0	1	1
18	0	0	2	1,1*
19	0	0	2	1,1*
21	0	0	0	0
23	0	0	2	1,1
29	6	18/,1,1,3,2,2	0	0
Jan 6 1975	-	-	1	1

\- No observations made.

* Alatae recorded on the same plants.

/ Plant with teneral alatae.

Table 1.2. Pattern of infestation of broad bean plants by *Aphis craccivora* in the plots - 1974.

Date	Plot I**		Plot II**	
	No. of infested plants	Total colonized stems	No. of infested plants	Total colonized stems
Nov 23 1974	1	1	-	-
Dec 3	5	7	-	-
4	5	7	-	-
9	-	-	7	8
10	5	6	7	8
11	5	7	6	8
12	4	7	6	8
14	2	4*	3	5
17	2	4*	4	6
18	2	4*	5	6
19	8	12/*	-	-
21	8	13/*	7	7
23	8	15/*	6	6
29	12/	26/	5	7
30	14/	30/	-	-
Jan 6 1975	-	-	9/	16/

\- No observations made.

* No alatae recorded.

** Total plants in Plots I and II = 33 and 35.

/ Secondary infestations by apterae and alatae, which were produced in Plots I and II.

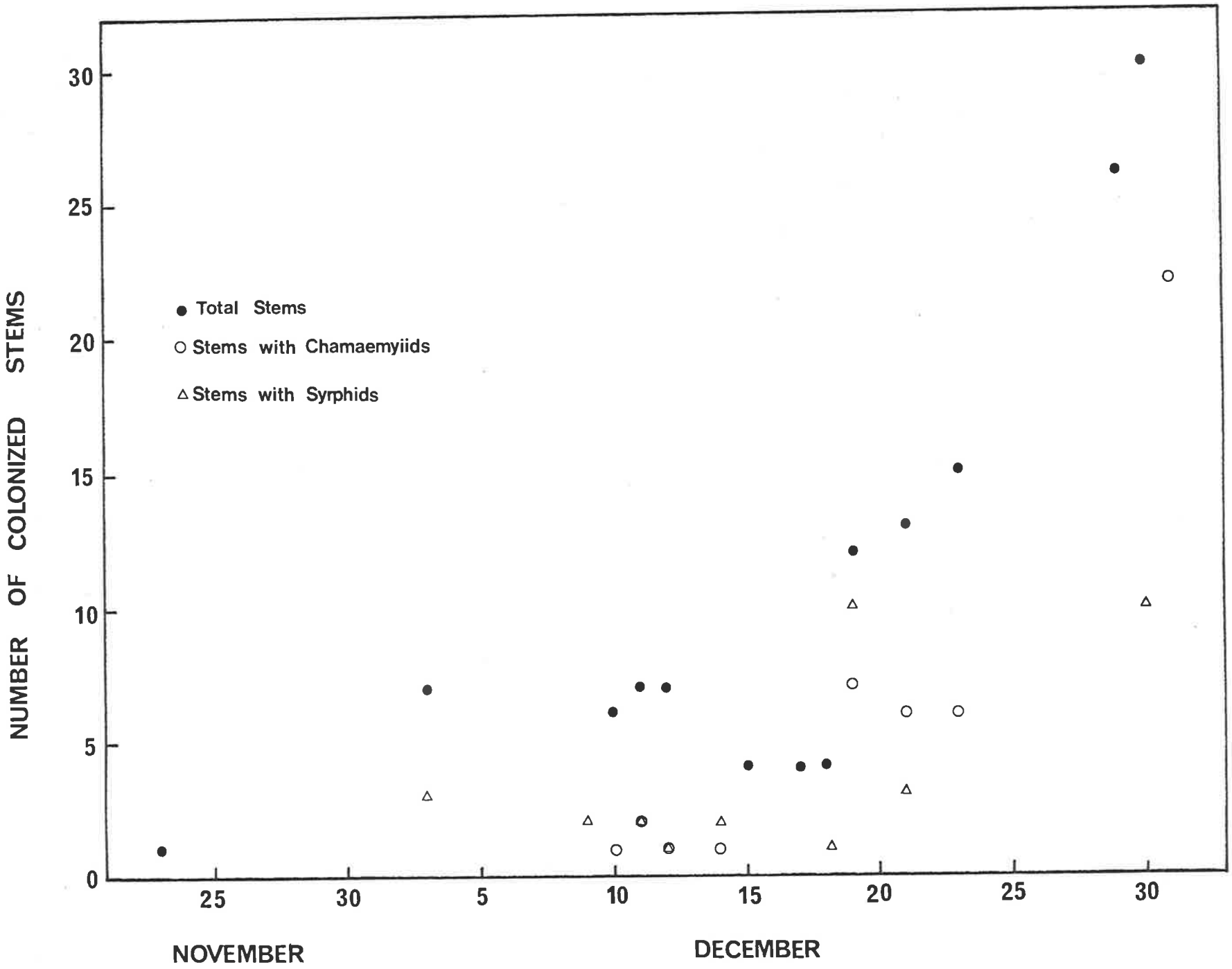
A. craccivora infestations were attacked by the following species of natural enemies which are polyphagous in South Australia.

1) *Aphidius colemani* Viereck (Aphidiidae : Hymenoptera)
2) *Leucopis* sp. (Chamaemyiidae : Diptera)
3) *Simosyrphus grandicornis* (Syrphidae : Diptera)
4) *Stethorus (scymnus) notescens* (Coccinellidae : Coleoptera)
5) *Coccinella repanda* (Coccinellidae : Coleoptera)
6) *Chrysopa* sp. (Chrysopidae : Neuroptera)

The Aphidiid parasites were not active and only 3 aphids were parasitized. No hyper-parasites were recorded from aphid mummies. Chamaemyiid and syrphid larvae were observed in colonies two weeks after primary infestation whereas *Stethorus* grubs appeared later. *Coccinella repanda* and *Chrysopa* sp. were recorded occasionally. 60-80% of colonies had chamaemyiid eggs (Figure 1.1). Predation by larvae of both syrphids and chamaemyiids not only exterminated small colonies (up to 50-60 aphids/colony) but also delayed the development of the established colonies.

Decline or collapse of a colony was dependent on the age of the seedling at colonization. Colonization of 2-3 week old seedlings unchecked by predators resulted in 1,000-1,200 aphids/plant in 4-5 weeks. Consequently, the plants wilted. Many aphids walked off a wilting plant prior to its death and probably settled on adjacent plants. Older seedlings sustained 1,000-3,000 aphids without wilting. Emigration by alatae and apterae and predation caused decline of colonies with 1,000-3,000 aphids.

Figure 1.1: Incidence of aphids (*Aphis craccivora*) syrphids (eggs/larvae) and chamaemyiids (eggs/larvae) in Plot I in Alverstoke Orchard - December 1974.


NUMBER OF COLONIZED STEMS
30
25
20
15
10
5
0
● Total Stems
○ Stems with Chamaemyiids
△ Stems with Syrphids
25
30
5
10
15
20
25
30
NOVEMBER
DECEMBER

The following conclusions were made from the above observations.

1) Three types of behaviour, i.e. the behaviour of colonizing *A. craccivora* alatae and recolonization by both the apterae and alatae, determined the number of infested broad bean stems.

2) The predators (syrphids and chamaemyiids) successfully exterminated newly established small colonies (up to 50 aphids).

3) Population levels of 1,000-3,000 aphids developed on a broad bean plant in summer.

4) Emigration by alatae and apterae was the most important cause of decline of *A. craccivora* population on a broad bean plant.

5) The build-up of predators followed the aphid population build-up and the impact of predation in reducing aphid numbers on a broad bean plant was complementary to emigration.

1.8: The present study

After going through the above review of the past work on the ecology of *A. craccivora* (Sections 1.5 and 1.6) one might wonder what initiated another study on this subject. There are two aspects to an answer of this question; the first would be a practical utility of such a project in South Australia; and the second, an academic exercise for testing a new idea to understand and explain the abundance of this aphid in general.

Nothing was known about the status of *A. craccivora* in this state except the flight periodicity records (Carver and Randles 1961 - personal communication) and a few records of infestations on different host plants (Carver 1974 - personal communication). The practical questions which gave rise to the present study were: why is this aphid not a pest in South Australia; if it is not a pest, how does it survive; and, could this insect become a threat to the cultivation of broad beans in this state, etc., etc?

A critical review of the literature revealed a few analogies and controversies about the ecology of this insect. This aphid attains low densities (150-500/m^2 or per plant) on closely spaced groundnuts in Africa (Farrell 1976) and India (Patel and Patel 1971), as is also the case in dense legume pastures (1,000/45 stems) in South Eastern Australia (Gutierrez *et al.* 1971). This aphid attains high numbers on broad beans in Egypt (Saleh *et al.* 1972) and Australia (Grylls 1972) and on other broad leaved grain legumes in India (Waghmare and Pokharkar 1974). If this species is adapted to only warmer climates (Gutierrez *et al.* 1974a), one might expect its high populations per unit area on groundnuts in Africa and India. Conversely, its high populations cannot be expected in a temperate environment as Grylls (1972) and the preliminary observations (Section 1.7) have demonstrated. What becomes obvious from the preceding lines is that the type of host plant is also important in determining the regional abundance of this aphid. The size and structure of a host plant ultimately determine the upper size of a colony of aphids (see Section 2). There are many examples in the literature to support this argument, for example; the cabbage aphid numbers can reach up to 10,000 on a Kale plant (Hughes

1963); *Aphis fabae* can develop its numbers up to 15,000 on a broad bean stem (Way 1967); and a rose bud can support < 500 *Macrosiphum rosae* (Maelzer 1977).

The concept of a colony of aphids on a plant as an independent and biologically functional unit, coined by Way (1968, 1973) is, therefore, fundamental to the present study. According to Way (1973), the rate of emigration of a colony would be dependent upon its size and age-structure. As the structure, surface area and size of a host plant influence the interaction among the aphids in a colony (Johnson 1965; Shaw 1970), the time and rates of emigration can be expected to vary according to the host plant characteristics; i.e., plants with a smaller surface area would stimulate migrant production and dispersal at an earlier time after colony inception and at smaller population densities (per plant), than plants with a larger surface area. On the other hand, the total number of emigrants dispersed from plants with a smaller carrying capacity would be fewer than from the plants which can sustain a higher population of aphids. And, since the recolonization of suitable crops in an area by emigrants of an aphid species is an important factor for the build-up of its populations (Hughes 1963), the level of production of emigrants from a crop might be a crucial factor in the regional abundance of an aphid.

According to Gutierrez *et al.* (1974a), *A. craccivora* is a super-migrant species. The relationship between population density per stem and the alata production on subterranean clover, as given by the authors (Figure 3), does not support their thesis. If this aphid

is a super-migrant, it ought to be able to produce a higher, not a smaller proportion of emigrant alatae at a higher population level. It is probable that the authors did not work out this important relationship properly, and if this is so, the outputs of their model and the conclusions arrived at from it, are questionable.

The ideas outlined in the preceding paragraphs gave rise to a new hypothesis to be tested in the present study. This was that, the abundance of *A. craccivora* in a crop can be explained by the regulating influence of emigration at an upper size of its colonies, as determined by the structure and surface area of the host plants. This hypothesis is testable and broad enough to explain the abundance of this cosmopolitan aphid in general, provided that the weather and natural enemies do not act as limiting factors to the aphid population increase.

The present study is an attempt to test the principal components of this hypothesis. A systematic study to quantify the emigration potential of this aphid in relation to size of its colonies on different host plant species, was the principal component of this project. This information is lacking in the literature and it can be useful in understanding the abundance and population dynamics of this aphid, because the previous studies by Farrell (1976) and Gutierrez *et al.* (1971, 1974a) and the pilot study (Section 1.7) have revealed emigration as the most important cause of decline in *A. craccivora* colonies. Complementary studies on the flight and colonization behaviour of migrant alatae could complete the picture of emigration and recolonization, the two inter-dependent aspects of the biology of *A. craccivora*.

This thesis consists of three main sections. Section 2 describes field experiments on the growth of colonies of *A. craccivora* and rates of migrant production in relation to different host plant species and initial colonization densities. Section 3 consists of experiments and observations on the flight behaviour of alatae. Section 4 describes experiments and observations on the colonization of broad beans by *A. craccivora* in the South Australian environment. A discussion of the results in relation to the ecology of this aphid is presented in Section 5.

SECTION 2

COLONY GROWTH AND MIGRANT PRODUCTION

2.1: Introduction

Aphid species feeding on herbaceous plants are regarded as highly efficient in converting plant energy into insect biomass through their highly evolved parasitic mode of living (Kennedy and Fosbrooke 1973). This is so because they are free from the constraints of mating and fertilization due to parthenogenesis and viviparity, and also because of their high fecundity, short developmental period, small size, larviposition on food substrate, and their ability to produce dimorphic or polymorphic adults, capable of exploiting local as well as distant habitats. As a consequence of this parasitic mode of feeding and reproduction, aphids form aggregates on their host plants and because of their aggregative feeding, they cause economic damage to cultivated crop plants.

The advantages of the highly evolved adaptations of feeding and reproduction in the herbaceous aphids are, however, limited by the discontinuity of their habitats in time and space. The temporary nature of habitat suitability demands constraints on the realization of reproductive potential to a fuller extent on one hand, and also the necessity of evolving mechanisms for short and long range mobility on the other; thus efficient use of the available and patchily distributed habitats can be made and the continuity of regional survival of a species can be ensured (Way 1973). Aphids achieve these goals through their aggregative behaviour.

In field, aphids live in aggregates of varying sizes and differing age-structures. Variations in the rates of deposition of colonizing alatae or apterae, in the time of colonization, in the extent of movement of colonizers and their progeny during the initial phases of colonisation and intensity of natural enemy activity, may all contribute to the size of an aggregate on a plant. Little attention has so far been paid to the study of biological properties of aphids in relation to size of their aggregates, and the concept of aggregate or colony of aphids on a plant as an independent and biologically functional unit, as distinct from another such aggregate or a colony on a different plant, is a fairly recent one (Way 1968, 1973). The intraspecific mechanisms operative in an aggregate may control the extent of food utilization (Way 1968; Way and Cammell 1970), size and fecundity of adults (Dixon and Wratten 1971; Taylor 1975) and morph determination (Johnson 1965; Shaw 1970), and therefore, signify the selective and survival value of colony as a biologically functional unit. In this context, it is reasonable to expect varying rates of emigration from colonies of differing ages and sizes.

In Australia *Aphis craccivora* is an anholocyclic and dimorphic aphid (Gutierrez *et al*. 1971, 1974a). Its winged and wingless morphs differ not only morphologically, but also in their developmental biology (Johnson and Birks 1960; Gutierrez *et al*. 1971, 1974a), behaviour, maturation of embryos, reproductive age and fecundity (Elliot and McDonald 1976). The differences in the developmental and reproductive biology of the two morphs probably suggest their distinct functions in this aphid. It is, therefore, reasonable to expect that the 'primitive' winged adults (alatae) are produced for migration and colonisation elsewhere and the 'advanced' wingless adults (apterae) for maintenance of the local populations

and efficient use of the existing food resources. In this context any degree of facultative migratory behaviour among the winged adults of this aphid may be degenerative, as it would greatly reduce the evolutionary and functional value of dimorphism. My experiments on migratory urge of alatae of this species have shown that this is not the case, as the results strongly support the idea that the alatae are indeed obligatory migrants (see Section 3.5.2).

Once the functional value of dimorphism is considered, it would be reasonable to expect that anholocyclic and dimorphic aphid species, such as *A. craccivora* would respond to changing environmental factors in the field by producing varying proportions of winged and wingless progenies. A quantitative measure of these proportions should, therefore, provide the potential rate of emigration of a colony in relation to its age and size.

The potential rate of emigration of a colony would, therefore, represent the species' physiological response to the environment. However, the actual or realised capacity for emigration in a colony and the range of dispersal of alatae are largely determined by the prevailing environmental factors, especially temperature, light intensity and wind velocity (Johnson *et al.*, 1957; Taylor 1958, 1963; Lewis and Taylor 1965. The winged adults, therefore, may appear to behave as if they were facultative migrants in the field. The environment thus influences the extent of emigration potential as well as its realisation in an aphid colony.

Detailed laboratory studies concerning the mechanism (Johnson and Birks 1960) and the effects of various environmental factors on morph determination in *A. craccivora* have been made (Johnson 1965, 1966a, 1966b). Laboratory studies on morph determination in aphids do provide a basic understanding of the underlying physiological mechanisms, but are of

limited value in the field because aphids live in aggregates of differing sizes on physiologically differing plant parts, and interact with a multitude of changing climatic factors. Nevertheless, from an ecological point of view, it would be valuable to assess to what extent the findings of these laboratory studies are traceable in aphid populations in the field. Despite many researches on the ecology of anholocyclic *A. craccivora* in different parts of the world (see Sections 1.5 and 1.6) this aphid remains an efficient vector of many viral pathogens in cultivated crops and pastures (see Section 1.3). This fact justifies a systematic study aimed at understanding its emigration potential and dispersive behaviour. Further, none of the studies mentioned above provides any empirical data on the production of the two morphs of this insect in relation to the size and ageing of its colonies in the field with reference to different host plant species and seasons. I, therefore, decided to fill this important gap in our knowledge of this anholocyclic aphid in the South Australian environment. I designed an experiment to quantify the potential and realised capacities for emigration in this aphid, in relation to the growth and size of its colonies on broad bean plants in field cages. Also, I studied the influence of initial colonization density (alatae per plant) on the size of its colonies and their realised capacities for emigration in field cages, on common burr medic, subterranean clover and lucerne, which are the common plant species in the South Australian legume pastures.

2.2: Experiment I: Growth and alata production in colonies of *A. craccivora*, initiated by one alata on broad beans in field cages

2.2.1: Introduction

The objectives of this experiment were:

1. to understand the population growth in colonies of *A. craccivora* and especially, to identify factors that limit ultimately the population growth and determine the upper size of its colonies in the absence of natural enemies; and

2. to quantify the emigration potential and realised capacities for emigration in relation to the growth of its colonies on broad beans.

The broad bean - *A. craccivora* system was selected for this experiment because of the reasons mentioned in Section 1.8. The experimental colonies were started on 2 week old potted broad beans with one (pre-reproductive) *A. craccivora* alata on each plant. This was in the light of the observations on the colonization behaviour of this aphid (see Section 4.2.2-C), as colonisation densities of 1 alata per broad bean stem were frequent in the field. The experimental colonies were kept in field cages in late April 1977 and the observations continued until mid-July.

The selection of late autumn-winter for this experiment was in accordance with the autumn infestation flights of *A. craccivora* and the colonisation of newly germinated pasture legumes in South Eastern Australia (Gutierrez *et al.* 1971, 1974a).

2.2.11: Methods

Cultures of *A. craccivora* were maintained on 2-3 week old potted broad bean seedlings in an insectary room with natural daylight, where temperature fluctuated between 18 and 25°C. Flight mature alatae were collected in a glass tube (5 cm x 2.5 cm) after their first flight from the seedlings to the glass wall of the insectary room. They were anaesthesized with CO_2 for releasing their settling response (Johnson 1958),

before they were used to initiate experimental colonies.

Broad beans (cultivar Crete 136) were sown singly in the University of California potting mixture (50% sand + 50% peat) in 15 cm diameter plastic pots. The pots were kept in a well-ventilated glasshouse until the plants were 18-20 cm tall with 6-8 opened leaves. The plants were 18 days old at colonization.

Wooden field cages were used to protect the colonies from immigrating aphids and natural enemies and to confine emigrating aphids also, so that they could be counted and removed frequently. The cages measured 45 x 45 x 65 cm high. The sides and roofs were of fine terylene net. The cages stood on flat sheets of galvanized iron (50 x 50 cm) and were held down by 30 cm elastic luggage straps between two pegs in the ground. A plastic foam strip on the base of the cages ensured a close fit onto the metal bases.

The cages were set up 1 to 1.5 m apart in the Alverstoke Orchard of Waite Institute. A total of 62 plants was colonized by placing one alata on each plant in one of the top half opened (whorled) leaflets. The colonized plants were kept in the cages. Of the 20 cages, 14 contained four plants each and the rest (6) one plant each. The caged plants were watered whenever necessary.

A thermohygrograph was kept 30 cm above ground in the shade to record the air temperature and relative humidity near the cages. The temperatures inside the cages were not recorded.

The cages with single plants were left undisturbed until the start of dispersal by apterae or alatae. Emigrating apterae and alatae which

walked away or flew from the plants in these 6 cages were counted and removed with a battery operated pooter at frequent intervals, until the colonies perished or they were 72 days old. These figures provided a measure of actual capacity for emigration which a colony founded by one alata on a bean plant could realise during its life.

Growth of the colonies and their potential rates of emigration were studied by frequent sampling of the colonies without replacement. Samples of the colonized plants were drawn from the cages that contained 4 plants. Initially it was planned to take samples of 4 colonies each, selected at random from different cages. However, as the experiment progressed, 16 colonies in four cages were parasitized by the Aphidiid parasite, *Aphidius colemani* Viereck, within a week of their initiation, and were rendered unfit for sampling. Samples of 2-3 colonies were, therefore, taken at intervals of 3 days until the colonies were 33 days old, and thereafter at 39, 45, 52 and 60 days. Apterae and alatae which walked away or flew from the plants inside these cages were removed periodically, so that they could not contribute to population of the colonies.

For each sampled colony, the pattern and extent of aphid infestation in relation to size and growth of the host plant were recorded. The plants were then washed in luke-warm water containing a little detergent and the aphids were removed with a brush. The aphids were stored in 80% alcohol and counted later, to determine total population and age-structure of the sampled colonies. The aphid instars were distinguished on the basis of the number of antennal segments and their relative lengths, cornicle length and the shape and length of cauda (see Appendix I). The number of aphids in each instar including alatiform and apteriform morphs in the third and fourth instars were recorded.

For samples with approximately 2,000 or more aphids, the total population and its age-structure was determined by a sub-sample of 50% aphids. The aphids with alcohol were transferred to a 9 cm diameter Petri dish marked into 8 radials and stirred with a brush to spread them evenly. After the aphids settled in the Petri dish, excess alcohol was removed with a pipette and the aphids in four alternate radials transferred to another Petri dish for counting. The alatae and apterae in all the samples were counted without sub-sampling. The percentage of alatiform nymphs in the third instar in a sampled colony provided a measure of its potential rate of emigration.

2.2.2: Temperature, relative humidity and photoperiod

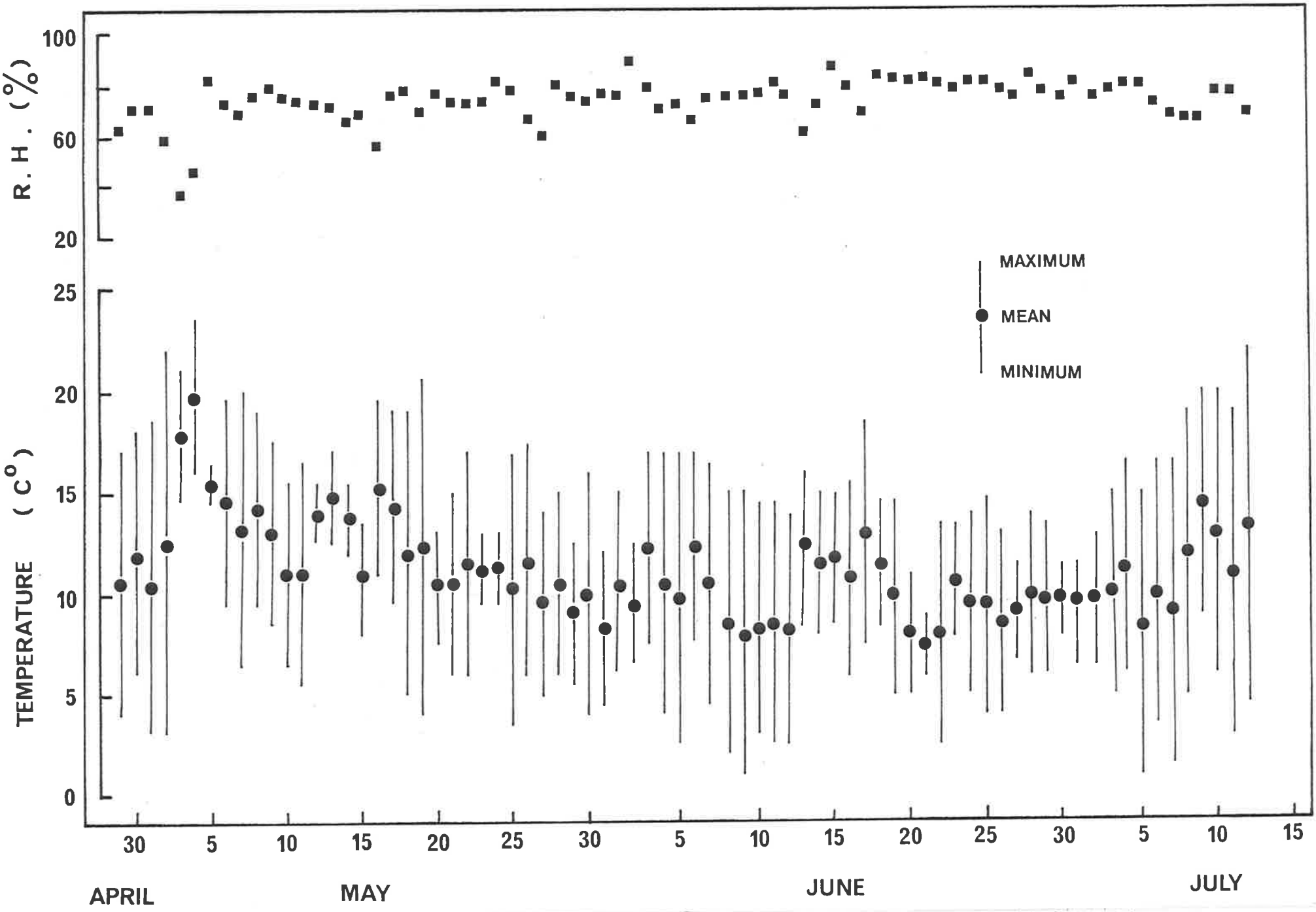
Figure 2.10 shows temperature and relative humidity at 30 cm above ground near the experimental cages. The mean daily temperatures $(\frac{\text{minimum} + \text{maximum}}{2})$ ranged from 8.3 to 19.8^{o}C in May and from 8 to 13^{o}C in June and July 1977. The mean daily relative humidity during the same period varied between 60 and 80%. Day-lengths during the experiment decreased from 11 to 10 hours.

2.2.3: Results

2.2.31: Growth of the experimental colonies

The term 'colony' in the context of this experiment applies to all aphids on a potted broad bean plant on which one alata of *A. craccivora* was placed to initiate an infestation at the beginning of the experiment.

Figure 2.10: Daily temperature and mean relative humidity 30 cm above ground near the experimental cages in Alverstoke Orchard - April-July 1977.


R. H. (%)
100
60
20
TEMPERATURE (C°)
25
20
15
10
5
0
MAXIMUM
MEAN
MINIMUM
30
5
10
15
20
25
30
5
10
15
20
25
30
5
10
15
APRIL
MAY
JUNE
JULY

This section describes the progress of infestations, their size and age-structure during course of the experiment.

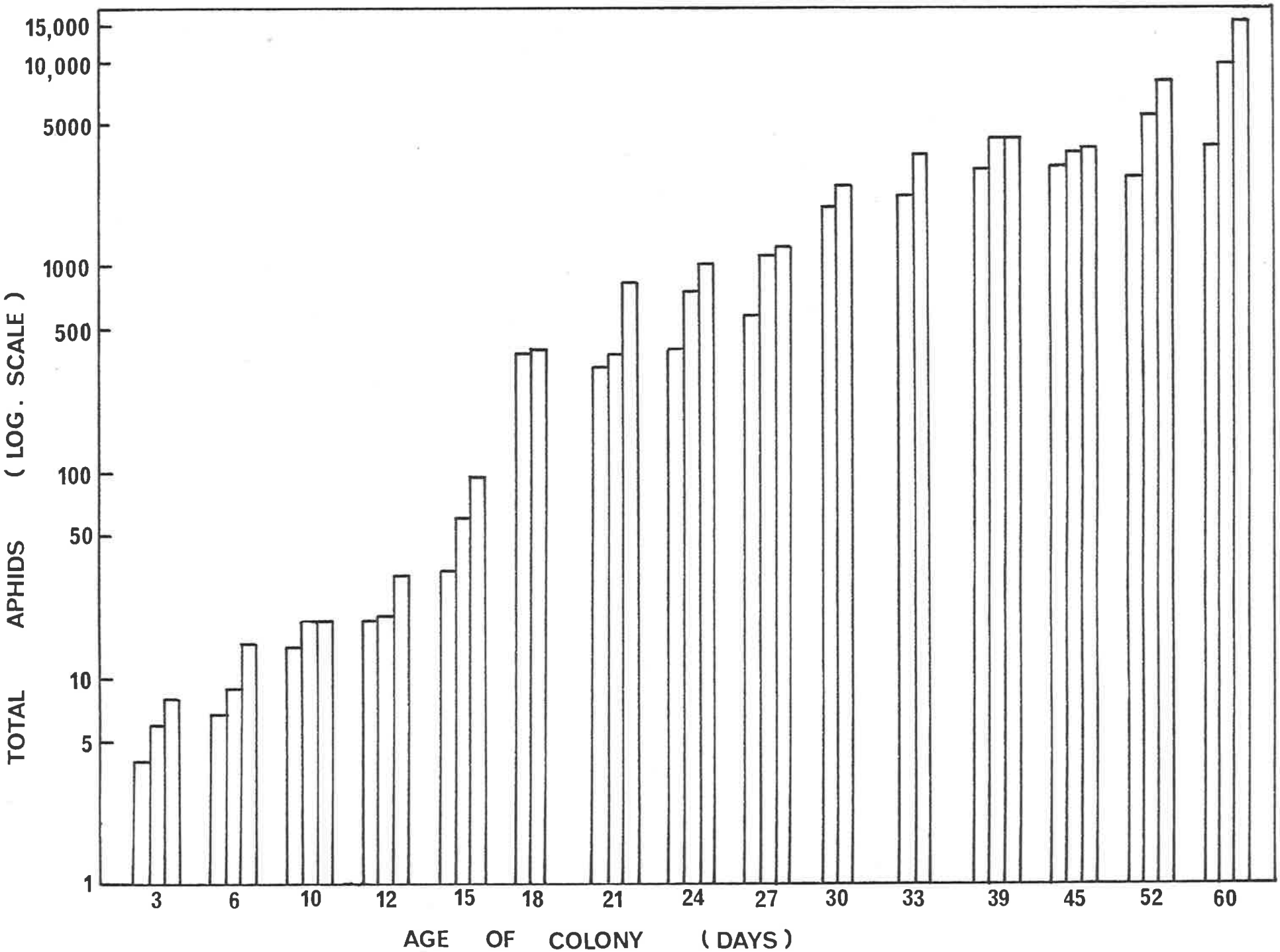
2.2.31-A: Progress of infestations of *A. craccivora* on broad bean plants

A detailed description of the growth of broad bean plants and the progress of infestations of *A. craccivora* during the experimental period are presented in Appendix II. The colonizing alatae were put on the crowns of main shoots; as they larviposited, their nymphs stayed on top leaves of the main shoot, until the colonies were 21 days old and the total population in the colonies reached between 300 and 800 aphids. The plants were producing floral primordia during this period and the aphids usually congregated on pedicels and calices of the unopened flower buds. Petioles of fully opened leaves on upper one-third of the main shoot and undersurfaces of stipules were then colonized by the first generation apterae and their nymphs. Meanwhile, each plant had produced 3-4 axillary basal shoots also. Crowns of these axillary basal shoots with their young and folded leaves were also colonized by the apterae and their nymphs. The middle and lower internodes of the main shoot and the leaves on it were the last to be colonized, probably because they were full of honey dew, excreted by the aphids above. At the last sampling when the colonies were 60 days old, all the shoots of a plant were fully colonized and the maximum number of aphids a shoot contained was 7,200.

2.2.31-B: Size of the sampled colonies in relation to age

Figure 2.11 shows total aphid population in the sampled colonies in relation to age of infestations. It took 15 to 17 days for the colonies to reach a population of 100 aphids and 24 to 27 days to reach a population of 1,000. The population in the sampled colonies

Figure 2.11: Total aphid population in the sampled colonies in relation to age. (Each bar represents a colony.)


15,000
10,000
5000
1000
500
100
50
10
5
1
TOTAL APHIDS (LOG. SCALE)
3
6
10
12
15
18
21
24
27
30
33
39
45
52
60
AGE OF COLONY (DAYS)

increased until the colonies were 39 days old. However, in two colonies sampled at 45 days, aphid populations were declining (see Section 2.2.31-C). Not all the colonies sampled at 52 and 60 days had declining aphid populations. Instead, the populations of these colonies varied between 3,000 and 15,000 aphids. The variation in respect of total aphid population among these colonies was 2 to 5-fold.

2.2.31-C: Age-structure in the sampled colonies

A detailed description of age-structure in aphid populations of the sampled colonies is presented in Appendix III.

The first generation apterae appeared in 12 to 15 day old colonies. The number of apterae increased with the total aphid population in the colonies and Figure 2.12 shows a positive correlation regarding this aspect. The 3 low points on the correlation represent the declining populations. Figure 2.13 shows the number of apterae in relation to the age of the colonies. Reduced number of apterae in a few colonies sampled at 45, 52 and 60 days was characteristic of their declining aphid populations.

Alatae first appeared when the colonies were 24 to 27 days old. Their numbers also increased subsequently with the age of the colonies.

First and second instar nymphs accounted for 40 to 85% of total aphid population in the sampled colonies. However, colonies sampled at 45 and 52 days with declining aphid populations had 15 to 37% nymphs in first and second instars. Another feature of these declining aphid populations was their increased proportion of fourth instar alatiform nymphs which varied between 26 and 50% (Figure 2.14).

Figure 2.12: Relationship between total aphid population and number of apterae in the sampled colonies.
R = 0.9205, P = 0.01.

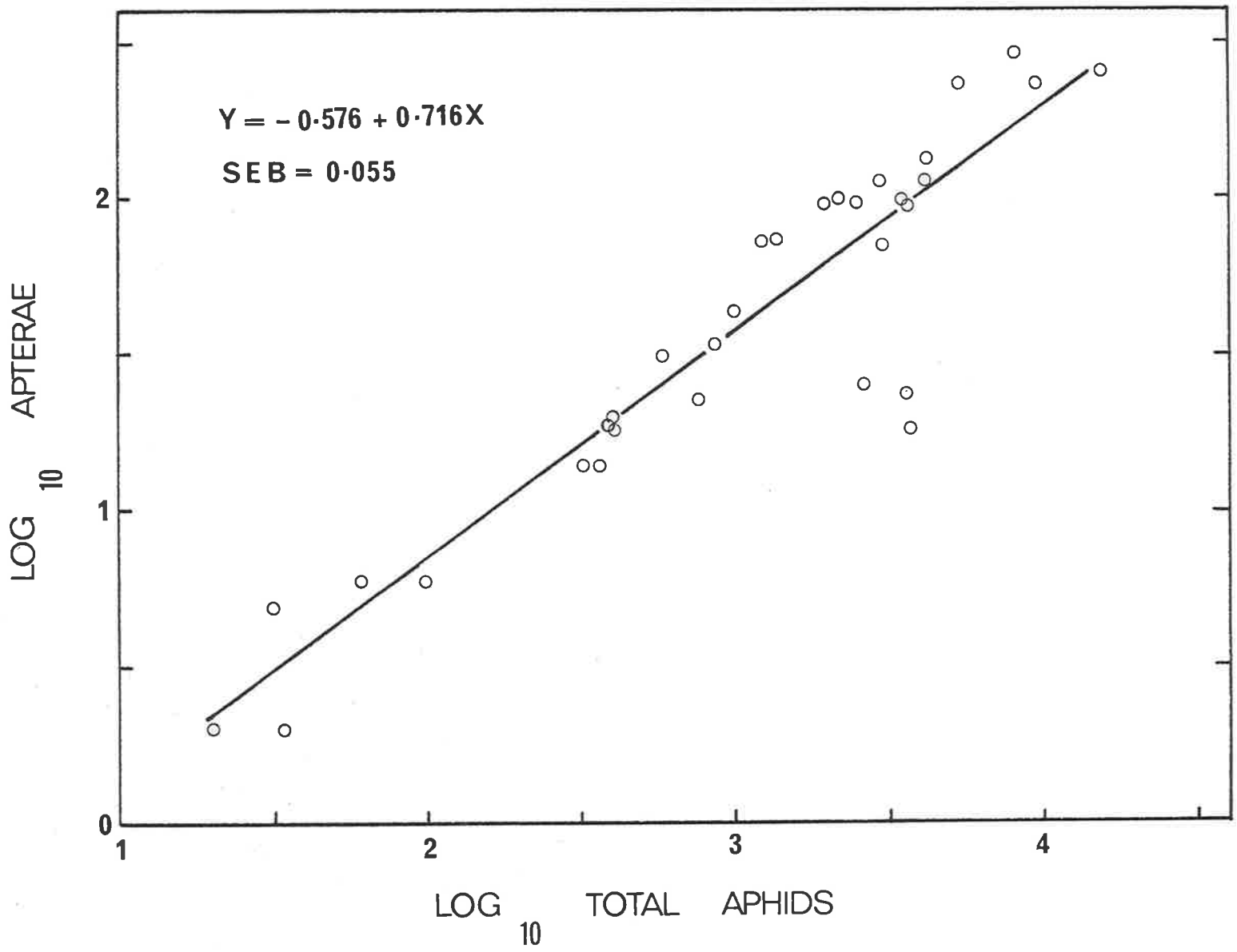

Y = - 0·576 + 0·716X
SEB = 0·055
LOG 10 APTERAE
LOG 10 TOTAL APHIDS
0
1
2
1
2
3
4

Figure 2.13: Number of apterae in relation to age of the sampled colonies. (Each bar represents a colony.)

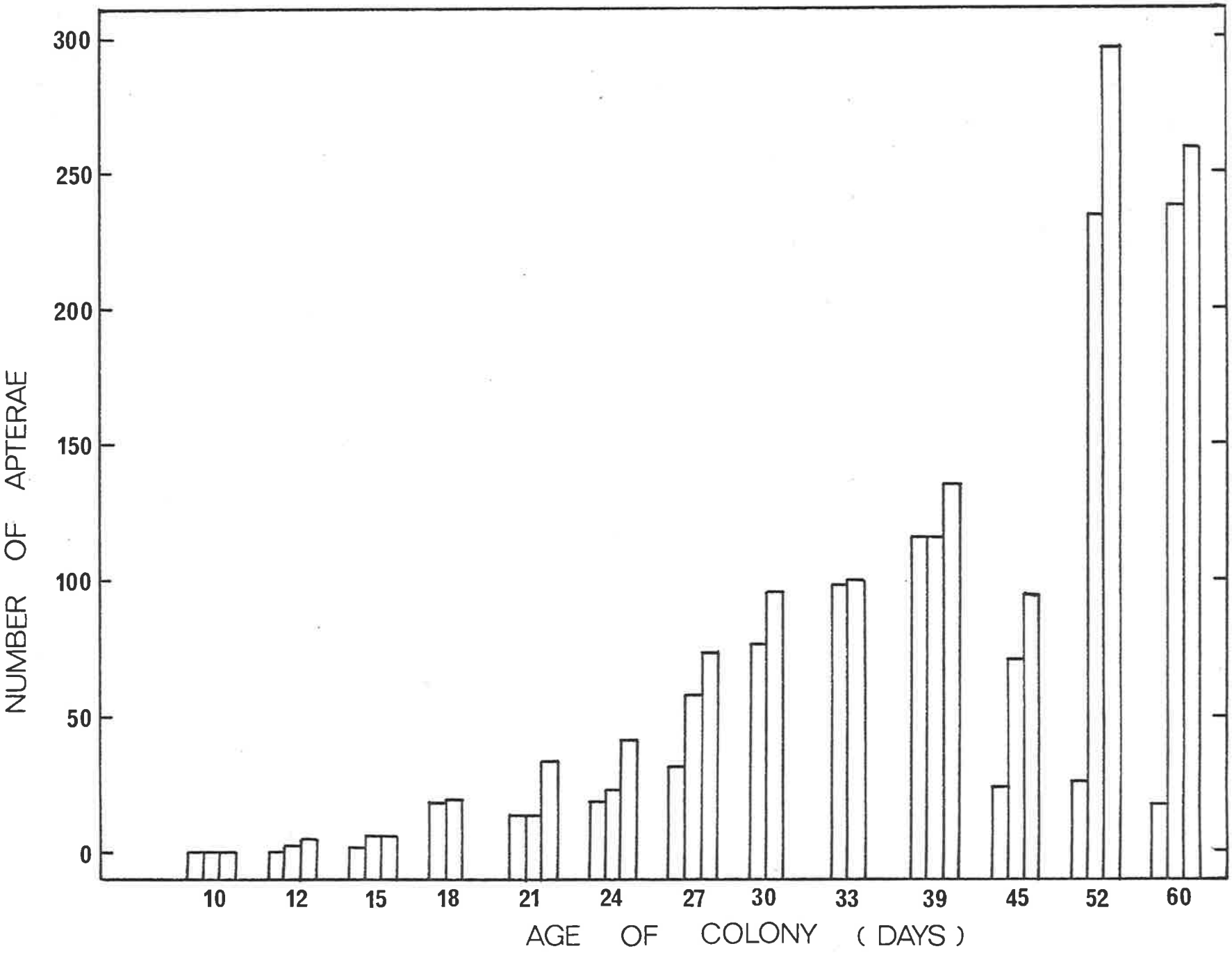
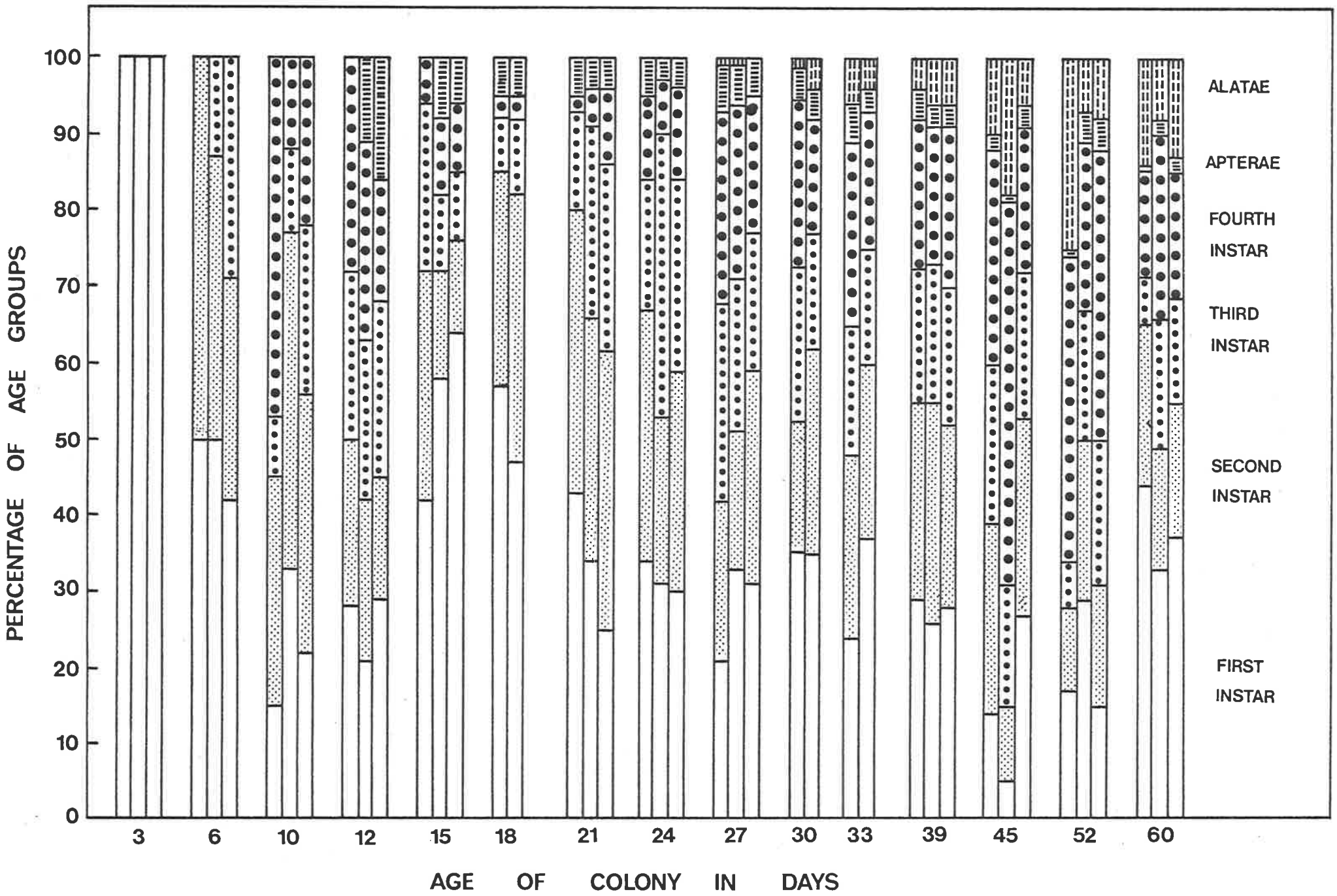

NUMBER OF APTERAE
300
250
200
150
100
50
0
10
12
15
18
21
24
27
30
33
39
45
52
60
AGE OF COLONY (DAYS)

Figure 2.14: Age-structure in the sampled colonies.
(Each bar represents a colony.)


PERCENTAGE OF AGE GROUPS
100
90
80
70
60
50
40
30
20
10
0
3
6
10
12
15
18
21
24
27
30
33
39
45
52
60
AGE OF COLONY IN DAYS
ALATAE
APTERAE
FOURTH INSTAR
THIRD INSTAR
SECOND INSTAR
FIRST INSTAR

2.2.31-D: Effect of parasitization on colony establishment

Two parasitized colonies, sampled at 18 and 30 days respectively, show how the timing of parasitization can be crucial for the fate of a population (see Appendix III). The former colony had a total of 9 aphids, of which 6 were mummified including the colonizing alatae. It had only 2 apterous adults and one-fourth instar apteriform nymph alive. Absence of first and second-instar nymphs suggested that the colony had been parasitized just after the colonizing alata had started to larviposit. It is probable that the live apterae were parasitized at a later stage or that they had escaped parasitization and were still pre-reproductive aphids. In either case, the probability of establishment of this colony was low. It is important to note that two parasite-free colonies sampled simultaneously at 18 days had 388 and 394 aphids.

The other colony, sampled at 30 days, had a population of 541 aphids, of which 18 were mummified. Aphids of all ages and morphs were present. The small numbers of mummified aphids pointed out that the colony had been parasitized approximately two weeks ago. The probability of death of this colony was fairly low, as it could survive parasitization because of its size and age-structure.

All the caged colonies were checked for parasite incidence following the sampling of the parasitized colony at 18 days and 8 other colonies in 2 cages had been destroyed by parasites.

2.2.32: Potential rate of increase ($e\lambda$) in relation to size of the sampled colonies

A measure of the potential rate of increase of aphid populations in the field can be worked out by Hughes' method (1962), provided the durations of first three instars are equal and the ratio between the numbers

of aphids in these instars, approximates to a geometric series. The durations of first, second and third instars in *A. craccivora* are equal on broad beans (Johnson 1959), on medics and subterranean clover (Gutierrez *et al.* 1971, 1974a) and on groundnuts (Farrell 1976) in the laboratory at constant temperatures. Expected instar frequencies were calculated by the method of Williams (1961). His parameter μ was calculated as follows:

$$\mu = \frac{\textit{No. of nymphs in second and third instar}}{\textit{No. of nymphs in first and second instar}}$$

According to Farrell (1976), the calculation of μ by this method, i.e., as reciprocal of eλ, gave a close approximation to the value obtained by the iterative method of Williams (1961) for samples of *A. craccivora* on groundnuts. The expected frequencies of nymphs in first, second and third instars were then calculated by multiplying the total nymphs (I + II + III) by $\frac{1}{1+\mu+\mu^2}$, $\frac{\mu}{1+\mu+\mu^2}$ and $\frac{\mu^2}{1+\mu+\mu^2}$ respectively.

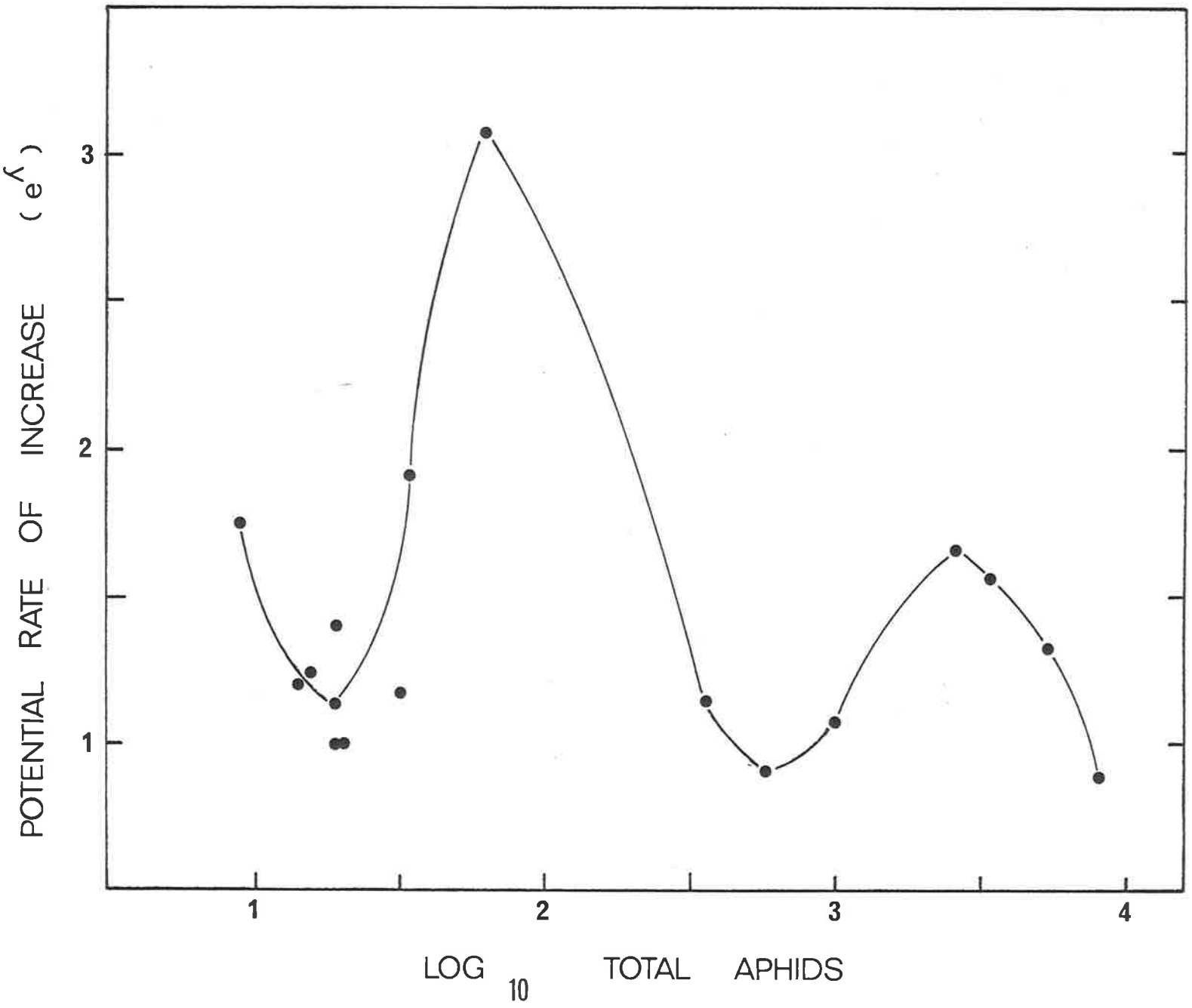
Of 39 colonies, 17 had stable instar distributions (see Appendix IV) and their potential rate of increase was calculated by Hughes' (1962) method as follows:

$$e\lambda = \frac{\textit{No. of nymphs in first and second instar}}{\textit{No. of nymphs in second and third instar}}$$

Figure 2.15 shows values of eλ in relation to the total aphid population of the sampled colonies. The highest value of 3.07 was recorded in a colony with a total population of 60 aphids. In colonies with higher aphid populations the values of eλ ranged from 0.9 to 1.6.

Figure 2.15: Potential rate of increase (e^{λ}) in relation to size of the sampled colonies (with stable instar distributions.)

Curve fitted by eye.


POTENTIAL RATE OF INCREASE (e^y)
3
2
1
1
2
3
4
LOG 10 TOTAL APHIDS

The highest value of 3.07 appears to be due to maturation of apterae in a short period in a colony wherein previously only one alata was reproducing. However, variations among the colonies in respect of potential rate of increase are so great that it is not possible to establish any meaningful relationship between these values and the aphid populations of the colonies. The differences in the values of e^{λ} are probably a result of variations in their rates of larviposition as affected by their numbers in a colony. It is, however, interesting to note that the potential rate of increase varied widely even in colonies which were initiated simultaneously with one alata and which grew under identical conditions in the absence of natural enemies.

2.2.33: Population growth in the colonies up to 30 days

Population growth of aphid colonies in the field is influenced by many factors, notably temperature, condition of host plant, number of reproducing adults, intraspecific competition and natural enemy activity.

Since natural enemies were excluded and the host plants were in good condition at least until the alatae and apterae started to disperse from the colonies, these two factors can be regarded as having had minimal influence on the growth of the experimental colonies. The colonies were protected from immigrating aphids and few aphids left the colonies before the thirtieth day. It is, therefore, reasonable to attempt to interpret the population growth of the colonies in relation to two other factors, namely temperature and the number of reproducing apterae.

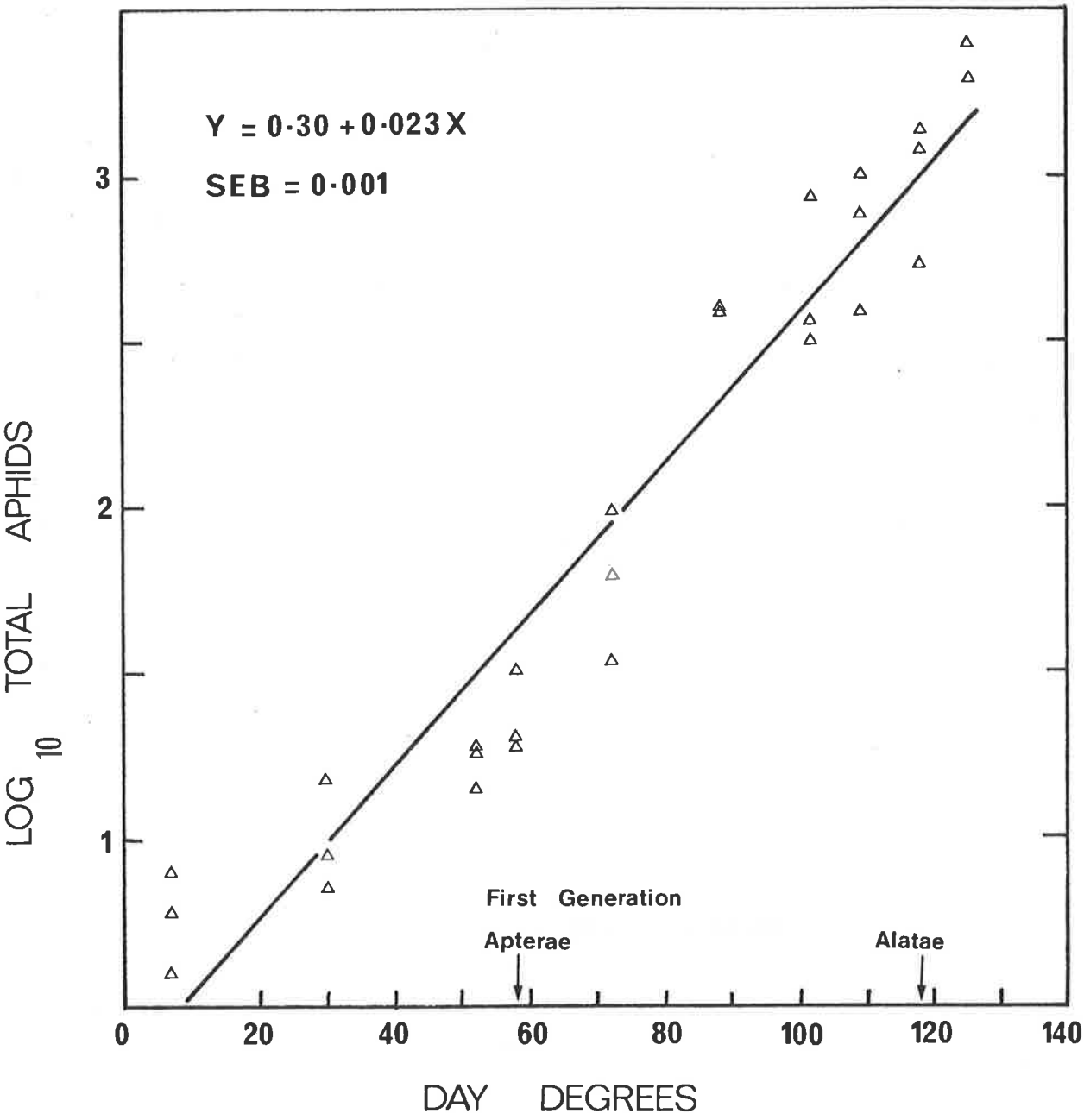
2.2.33-A: Relationship between temperature and population growth

Numerical changes in aphid populations in the field can best be interpreted in relation to fluctuating field temperatures by using a physiological time scale of day-degrees (Hughes 1973) and many workers have used this physiological time in the development of deterministic models of aphid populations (Hughes 1963; Hughes and Gilbert 1968; Gilbert and Gutierrez 1973; Gutierrez *et al.* 1974a; Maelzer 1977). The threshold temperature for development of the South East Australian biotype of *A. craccivora* is 8.3^{o}C (Gutierrez *et al.* 1971, 1974a). Day-degrees above this temperature were accumulated from 2-hourly mean temperatures recorded by a thermohygrograph which was kept in shade near the cages.

Figure 2.16 shows a significant relationship between the cumulative day-degrees above 8.3^{o}C and the total aphid population in the colonies sampled up to 30 days. It is evident from this relationship that 44 day-degrees were needed for a 10-fold increase in the aphid populations of the colonies and 58 to 60 day-degrees were needed for the development of each generation.

It is essential to point out here that the temperatures inside the cages were not recorded during this experiment. The temperature records of Experiment II (see Section 2.3.3) indicate higher temperatures inside the cages during sunny periods (an increase of 2 to 4^{o}C). Results of Experiment II also suggest that 72 day-degrees (above 8.3^{o}C) were needed for the development of one generation. A difference of 12-14 day-degrees may, therefore, be due to under-estimation of temperatures inside the cages during this experiment.

Figure 2.16: Regression of log. total aphid population of the sampled colonies on the cumulative day degrees above 8.3°C, until the start of apterous and alata dispersal.
R = 0.9639, P = 0.001.


Y = 0·30 + 0·023X
SEB = 0·001
LOG 10 TOTAL APHIDS
3
2
1
First Generation
Apterae
Alatae
0
20
40
60
80
100
120
140
DAY DEGREES

2.2.33-B: Relationship between the number of apterae and total aphid population

Figure 2.17 shows a significant relationship between the number of apterae and total aphid population in the colonies (with apterous adults), sampled up to 30 days. The total aphid population in the colonies increased 17.47 times for each 10-fold increase in the number of apterae. The number of apterae in a colony may, therefore, be a useful index of the size of field colonies where reproducing alatae are absent and no aphids are dispersing.

2.2.33-C: Relationship between the number of apterae and first and second instar nymphs

Figure 2.18 shows a significant relationship between the number of apterae and first and second instar nymphs in the colonies with apterous adults, sampled up to 30 days. The number of first and second instar nymphs in the colonies increased 10.7 times for each 10-fold increase in the number of apterae. This relationship, however, does not give any information regarding the intraspecific competition, if any, among the apterae and its adverse effect on their reproductive rate.

2.2.33-D: Ratios of first instar nymphs and apterae in the colonies, sampled until 33 days

Figure 2.19 shows ratios of first instar nymphs and apterae in the colonies until the start of apterous dispersal. There is no evidence of reduction of fecundity of apterae with increasing population of colonies, and the number of first instar nymphs per aptera remained more or less constant (8) (see also Table 2.1).

Figure 2.17: Log. total populations of the sampled colonies as function of log. apterae, until the start of apterous and alata dispersal.
R = 0.9785, P = 0.001.

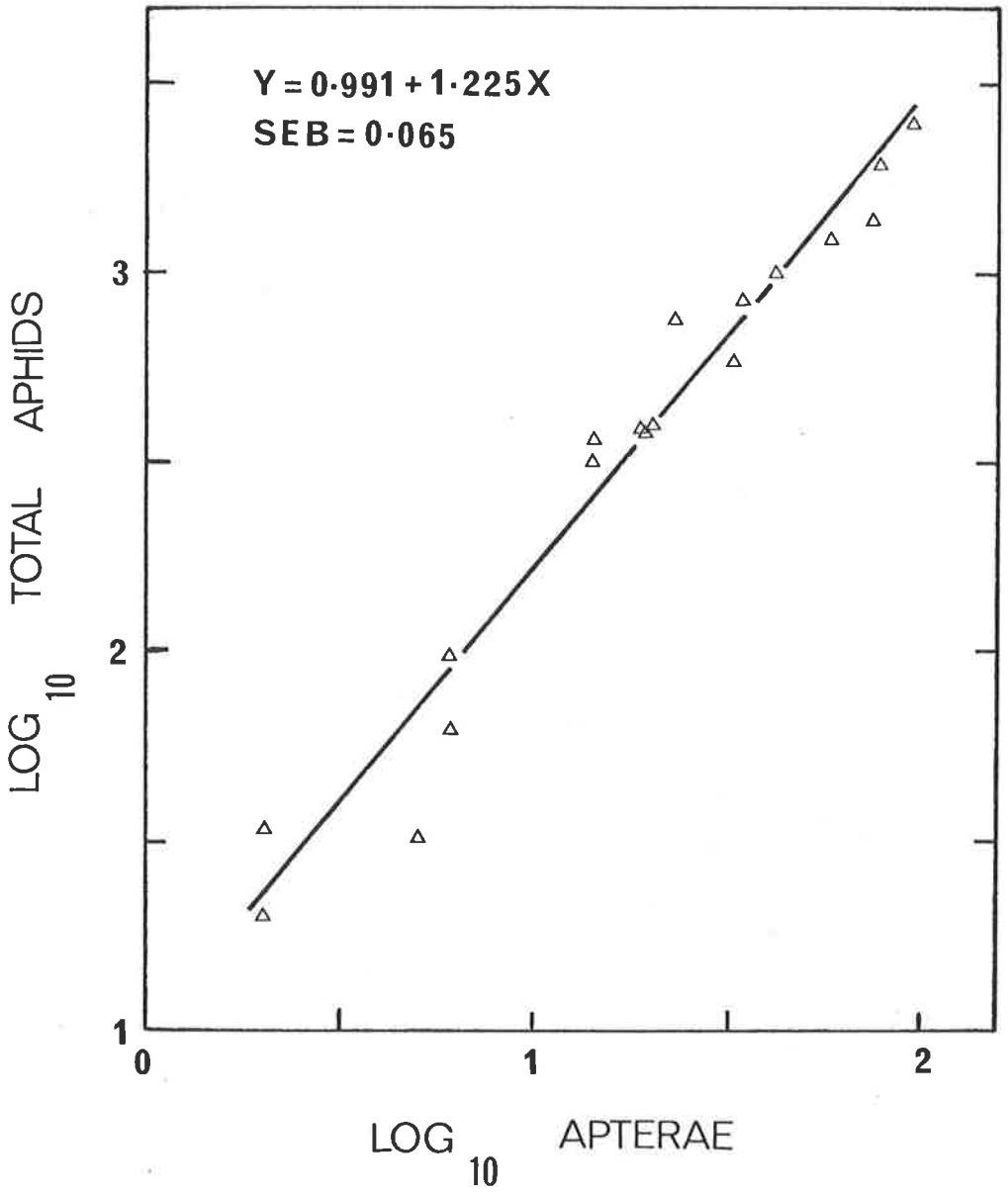

Y = 0·991 + 1·225X
SEB = 0·065
LOG 10 TOTAL APHIDS
LOG 10 APTERAE
1
2
3
0
1
2

Figure 2.18: Log. first and second instar nymphs in the sampled colonies as function of log. apterae, until the start of apterous and alata dispersal. R = 0.9507, P = 0.001.

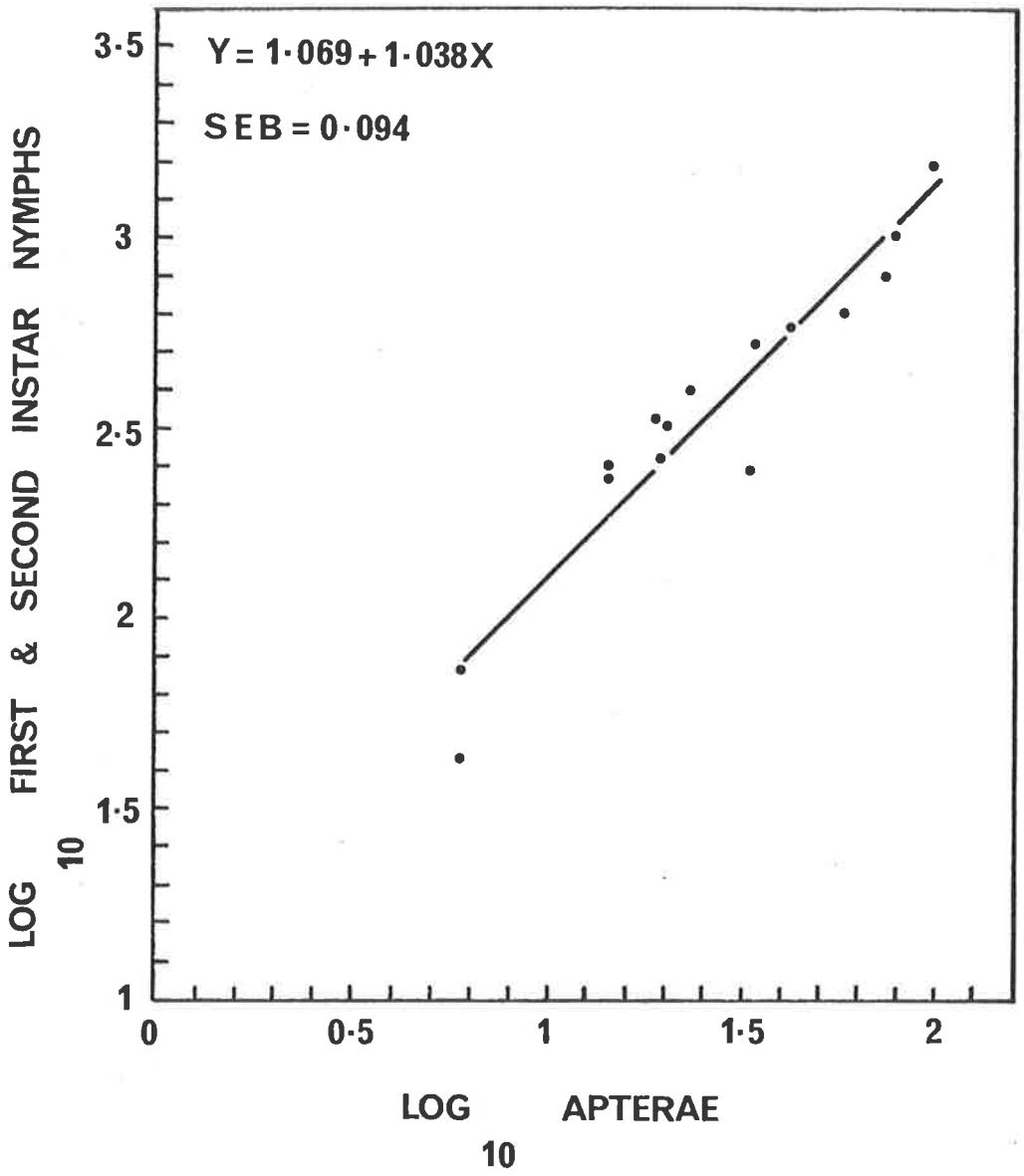

Y = 1·069 + 1·038X
SEB = 0·094
LOG 10 FIRST & SECOND INSTAR NYMPHS
3·5
3
2·5
2
1·5
1
0
0·5
1
1·5
2
LOG 10 APTERAE

Figure 2.19: Ratios of total first instar nymphs/total apterae in relation to total aphid population of the sampled colonies (until 33 days). R = 0.108615, P = N.S.

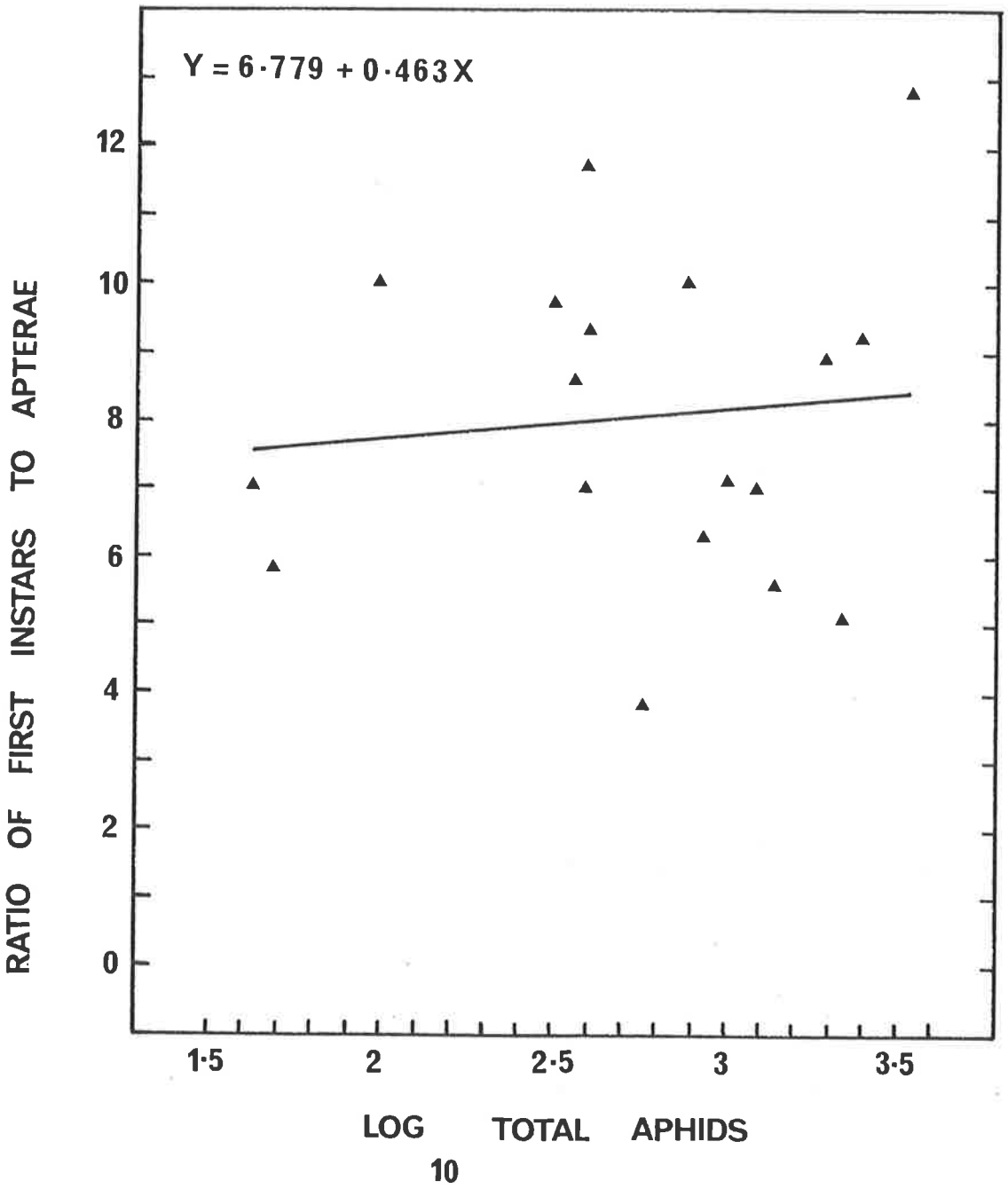

Y = 6·779 + 0·463X
RATIO OF FIRST INSTARS TO APTERAE
0
2
4
6
8
10
12
1·5
2
2·5
3
3·5
LOG 10 TOTAL APHIDS

Table 2.1. A comparison of the numbers of first instar nymphs and apterae of *Aphis craccivora* in the experimental colonies (sampled up to 33 days) on broad beans - 1977.

Age of colony in days	Plant No.	No. of first instar nymphs	No. of apterous adults	Total aphids
12	2	9	5	32
	3	4	2	20
15	1	35	6	61
	2	14	2	34
	3	60	6	97
18	1	222	19	388
	2	185	20	394
21	1	136	14	314
	2	215	34	848
	3	121	14	361
24	1	297	42	1005
	2	230	23	764
	3	133	19	393
27	1	413	74	1375
	2	121	32	573
	3	406	58	1225
30	1	687	77	1936
	2	885	96	2503
	3	169	48	542
33	1	1269	99	3470
	2	514	100	2171

2.2.34: Potential rate of emigration in the sampled colonies

Both alatae and apterae disperse from colonies in the field. Recent ideas on insect migration (Johnson 1960, Kennedy 1961, 1975) class alatae as migrants; alatae are obligatory fliers (see Section 3); they leave the host plant in a pre-reproductive phase of their biology, irrespective of the host's suitability for further feeding and reproduction and, most importantly, they go beyond their habitats and may reach distant patches of suitable habitats (Gutierrez *et al.* 1974a; Johnson 1957), so that continuity in the survival of the species may be ensured on a regional basis (Way 1973).

A. craccivora apterae, though, disperse from colonies, sometimes in large numbers over a long period (see Appendix VI); nevertheless, they do not move beyond local plant patches. They certainly do not ensure the continuity in the survival of the species on a regional basis as alatae do. It is also important to note that the first maturing apterae in a colony never move out of the colony (see Appendix III), whereas those maturing at a later time disperse. Whether the movement of the dispersing apterae is in response to crowding among themselves or is a response to the quality of host plant, or is an adaptation, is not known at the present and experiments in this direction will clarify this aspect.

It is also important to note that survival of the anholocyclic *A. craccivora* in the ephemeral Australian environment is probably accomplished by the existence of many individual colonies, spread over a vast area (Johnson 1957; White 1967). Each of these colonies may be contributing to regional survival of this species by producing varying number of alatae for varying periods, so that a continuous aerial population of flying alatae is maintained. Because of this important role

played by alatae, I would regard them as true migrants. As pointed out earlier (see Section 2.1), colonies respond to changing environment by producing varying proportions of alata progeny and a measure of these proportions could, therefore, represent the potential rate of emigration of a colony in relation to its age and size.

2.2.34-A: Rationale for using the proportion of alatiform nymphs in the third instar as a measure of potential rate of emigration of a colony

It is a convention to use the proportion of fourth instar alatiform nymphs as a measure of rate of emigration (Hughes 1963; Gutierrez *et al*. 1971, 1974a; Farrell 1976; Maelzer 1977). One reason for this is probably the ease with which fourth instar alatiform nymphs can be differentiated in aphid samples because of their well-developed wing pads. Another reason is that the number of emigrating alatae in an instar period in a population can be determined indirectly from the number of fourth instar alatiform nymphs in a sample by Hughes' method (1963). However, in doing so the parameter (κ) has to be determined in laboratory beforehand, since 'κ' represents the extra developmental time taken by alatiform fourth instar nymphs in relation to standard duration of preceding three instars in *Brevicoryne brassicae* (Hughes 1963), and *A. craccivora* (Johnson 1959; Gutierrez *et al*. 1971, 1974a).

The developmental period of fourth instar alatiform nymphs in *A. craccivora* in laboratory is 1.3 (Gutierrez *et al*. 1971) to 1.5 (Johnson 1959) times longer than the developmental period of fourth instar apteriform nymphs on medics and broad beans respectively. Because of this difference in developmental period of the two morphs, counts based on alatiform nymphs in the fourth instar would over-estimate the

percentage of alatiform progeny and under-estimate the percentage of apteriforms. To avoid this error in determination of potential rate of emigration, it is necessary to determine the proportion of alatiform progeny within a cohort of aphids with equal developmental period. I have used third instar nymphs for this purpose, as the developmental period of both the morphs in this instar is equal on broad beans (Johnson 1959) as well as on medics and subterranean clover (Gutierrez *et al.* 1971).

In *A. craccivora*, post-natal morph determination takes place in the first instar (Johnson and Birks 1960). But it is not possible to separate alatiform and apteriform nymphs in the second instar, and they can be distinguished at the earliest in the third instar (after their second moult). Hence, another advantage of using third instar for the present purpose is that the effects of changing aphid population on the potential rate of emigration of a colony, as reflected in the proportion of third instar alatiform nymphs, can be detected at the earliest possible stage.

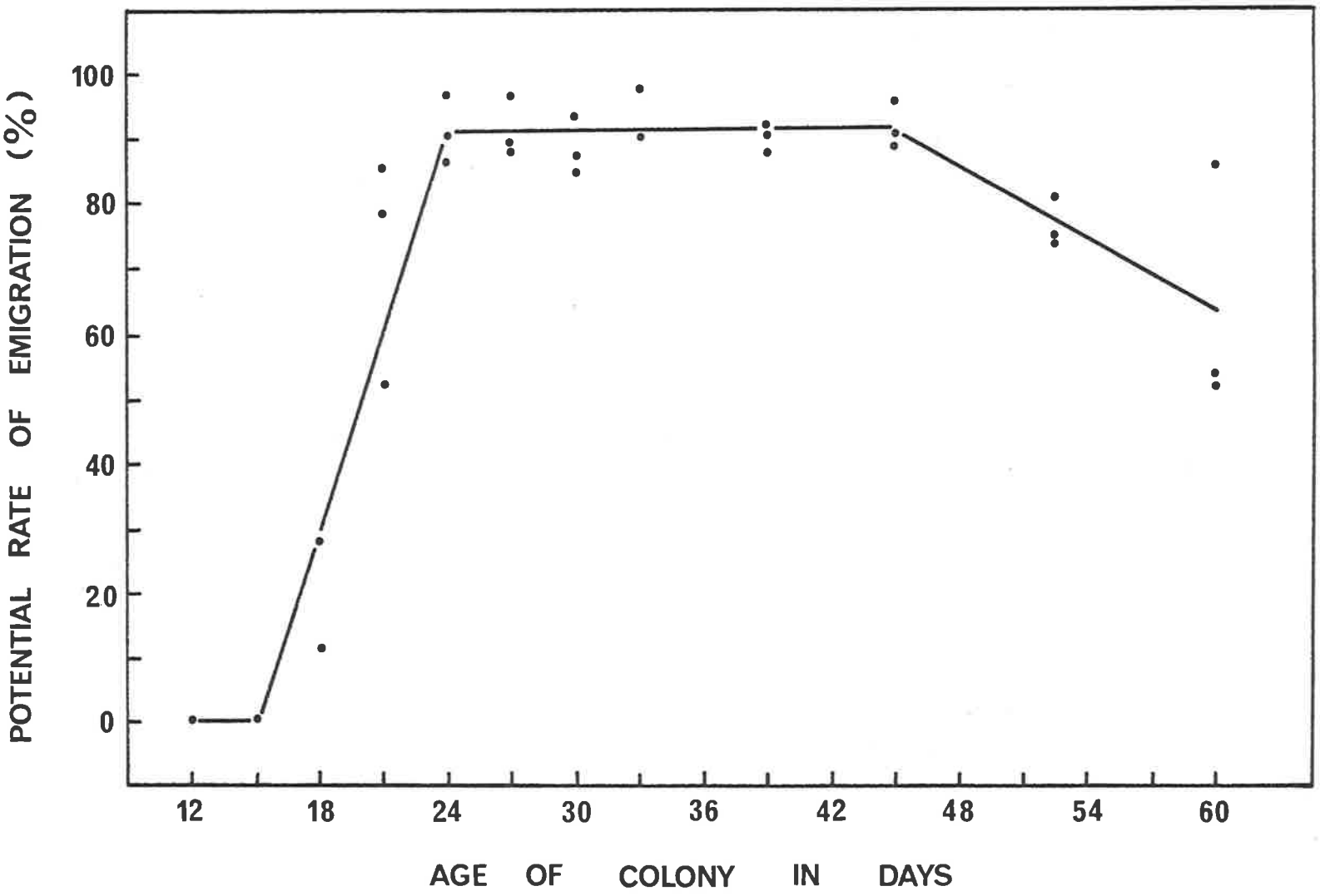
2.2.34-B: Potential rate of emigration in relation to age of the sampled colonies

Figure 2.20 shows the potential rate of emigration in relation to the age of sampled colonies; it was calculated as follows:

$$\textit{Potential rate of emigration \%} = \frac{\textit{No. of III alatiform nymphs in a colony} \times 100}{\textit{No. of III alatiform} + \textit{III apteriform nymphs}}$$

No alatiform third instar nymphs were recorded in the colonies sampled at 12 and 15 days. This meant that the first nymphs to mature in the colonies became apterae. Alatiform third instar nymphs were first seen in 18 day old colonies; in the colonies which were sampled

Figure 2.20: Potential rate of emigration (expressed as percentage of alatiforms among third instar nymphs) in relation to age of the sampled colonies.
Lines fitted by eye.


POTENTIAL RATE OF EMIGRATION (%)
100
80
60
40
20
0
12
18
24
30
36
42
48
54
60
AGE OF COLONY IN DAYS

subsequently at 21 and 24 days, the proportion of third instar alatiforms varied between 78 and 96%. It is interesting to note that this high proportion of alatiforms (85 to 97%) was maintained by the colonies until 45 days. The decline in this percentage in the colonies which were sampled at 52 and 60 days can be attributed to reproduction by alatae on the under-surfaces of leaves, and it is probable that the nymphs laid by these alatae were increasing the proportions of apteriform nymphs.

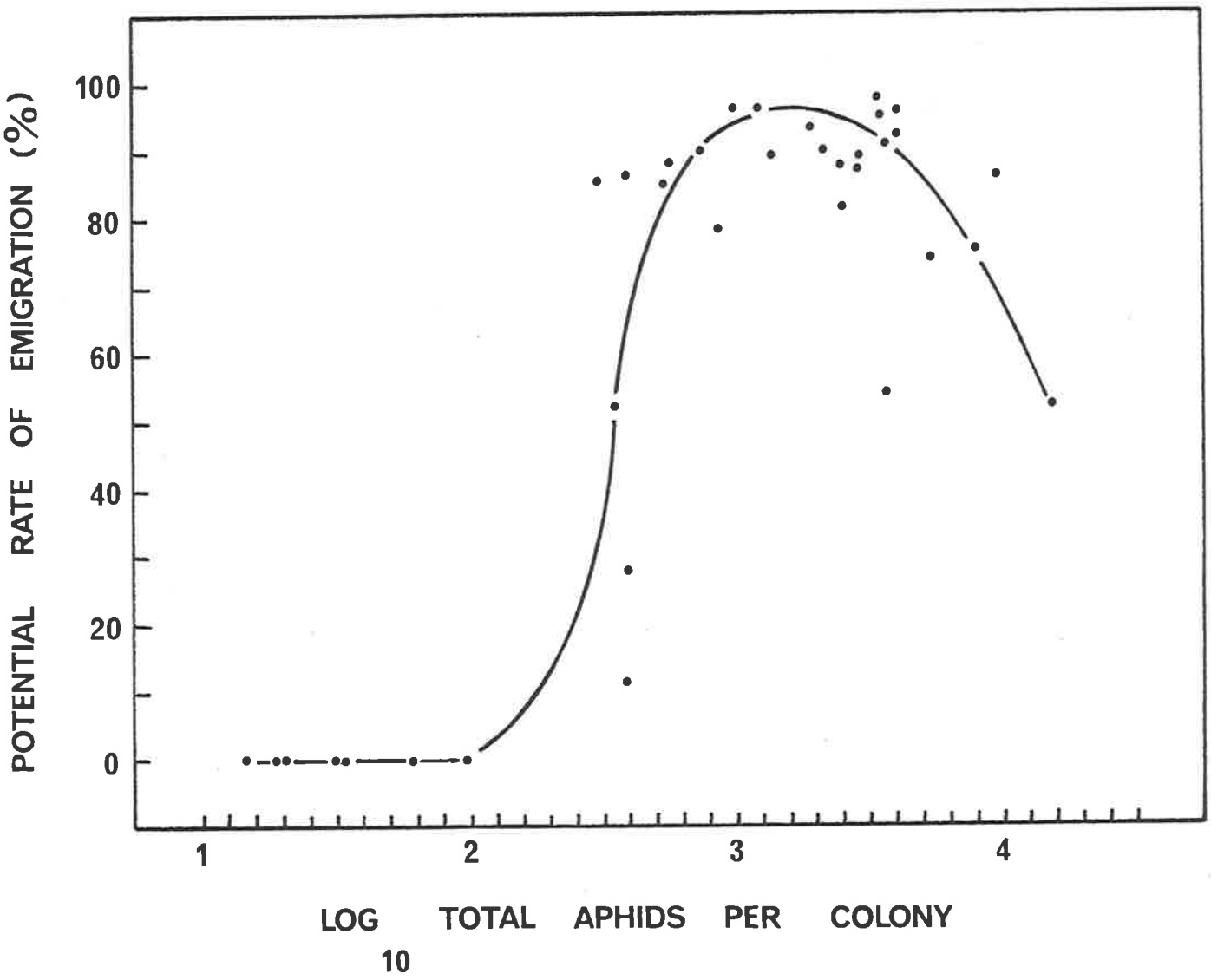
2.2.34-C: Potential rate of emigration in relation to size of the sampled colonies

Figure 2.21 shows the potential rate of emigration in relation to total aphid population in the sampled colonies. No alatiform progeny was observed in colonies with up to 100 aphids. Alatiform third instar nymphs were first seen in the colonies with more than 300 aphids and their proportion varied between 78 and 97% in the colonies with 550 to 4,000 aphids. In colonies with 5,000 to 15,500 aphids, the percentage of third instar alatiforms declined from 75 to 52%. The high potential for alata production by *A. craccivora* at high population densities on broad bean plants is evident from these results.

2.2.34-D: Relationship between state of crowding and alata determination in colonies, sampled prior to dispersal by alatae and apterae

The relationship between state of crowding (i.e., total population of a colony at the birth of a cohort of nymphs) and alata determination (i.e., the extent of alateness in that cohort) in colonies sampled prior to dispersal by alatae and apterae, was worked out by

Figure 2.21: Potential rate of emigration (expressed as percentage of alatiforms among third instar nymphs) in relation to size of the sampled colonies.
Curve fitted by eye.


POTENTIAL RATE OF EMIGRATION (%)
100
80
60
40
20
0
1
2
3
4
LOG TOTAL APHIDS PER COLONY
10

two methods. In each case, the numbers of first and second instar nymphs were excluded from the total aphid population of sampled colonies, because most of these nymphs were probably added to the aphid population after the third instar nymphs were born, i.e., they were absent until the last of the third instar nymphs was born. The percentage of alatiform nymphs in the third instar was then plotted against the remaining aphid population (III + IV + adults) of the colonies and Figure 2.22 shows this relationship. The threshold density per colony for 50% alata determination, as read off this graph is 92 aphids i.e., in a colony of 92 aphids, it is probable that 50% of its first instar nymphs would become alatiform.

The same relationship was worked out by linear regression of percentage of third instar alatiform nymphs over log-aphid population of sampled colonies also, after excluding the first and second instar nymphs, and Figure 2.23 shows this relationship. From this regression, the threshold density per colony for 50% alata determination is 108 aphids, which is not very different from 92 aphids per colony as determined by the graphic method.

It is interesting to note that threshold densities of 92 to 108 aphids per colony for alata determination correspond well with the observations that no alatiform nymphs in third instar were observed in colonies with up to 100 aphids, and that they were first recorded in colonies with more than 300 aphids (see Section 2.2.34-C and Appendix III). It is apparent that by the time the first instar nymphs in the colonies with 100 aphids became third instars, an additional 200 nymphs (I + II) were added to the population of these colonies during the two instar periods.

Figure 2.22: Relationship between colony size (at the birth of last third instar nymph) and percentage of alatiforms among third instar nymphs in the sampled colonies, prior to the start of apterous and alata dispersal (until 27 days). Threshold density per colony for 50% alateness = 92 aphids. Curve fitted by eye.

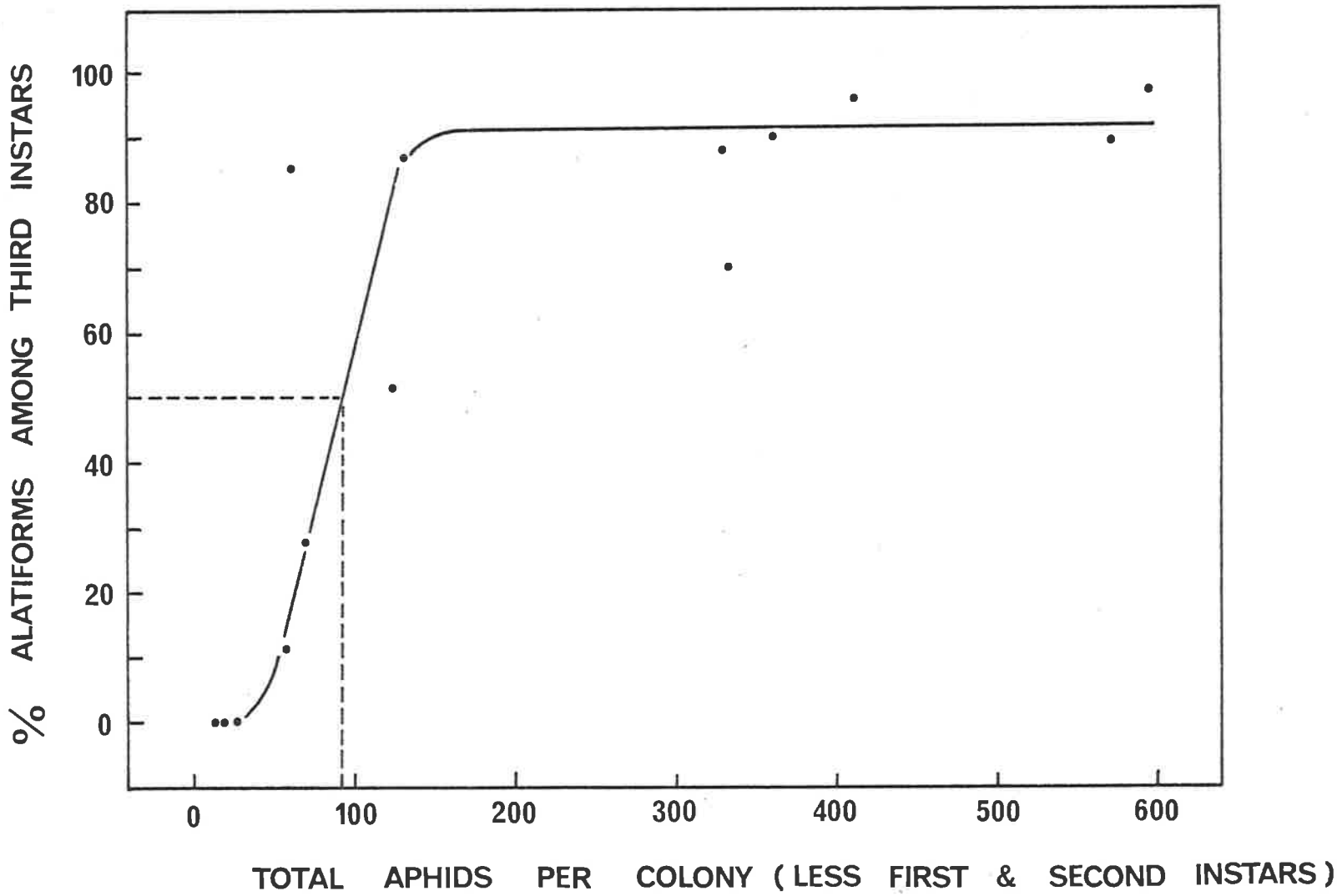
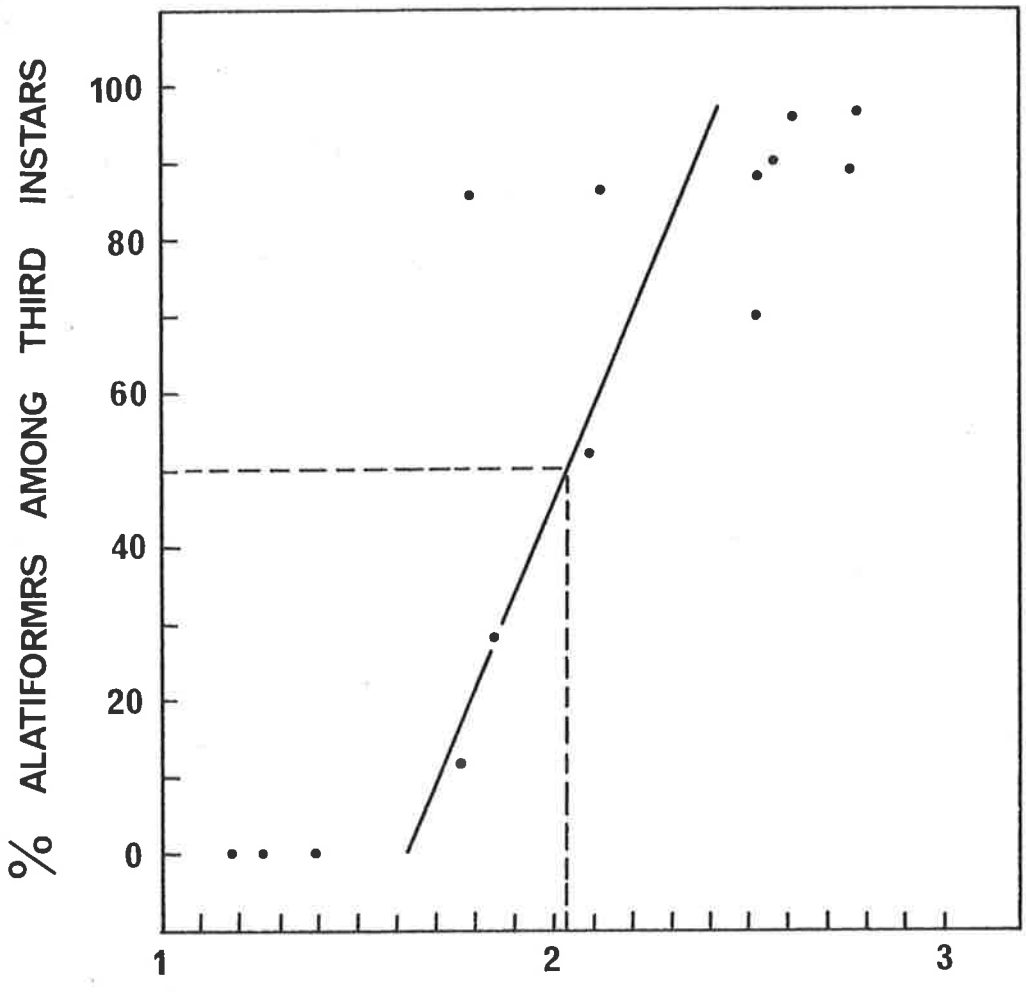

% ALATIFORMS AMONG THIRD INSTARS
100
80
60
40
20
0
0
100
200
300
400
500
600
TOTAL APHIDS PER COLONY (LESS FIRST & SECOND INSTARS)

Figure 2.23: Relationship between log. colony size (at the birth of last third instar nymph) and percentage of alatiforms among third instar nymphs in the sampled colonies prior to the start of apterous and alata dispersal (until 27 days). Threshold density per colony for 50% alateness = Log. 2.03 = 108 aphids. R = 0.8617, P = 0.01.

$Y = -75{\cdot}647 + 63{\cdot}51X$

$SEB = 9{\cdot}55$



2.2.35: Realised capacities for emigration

2.2.35-A: Cumulative number of dispersed alatae from a colony as a measure of its realised capacity for emigration

It is reasonable to regard the cumulative number of dispersed alatae from a colony as a measure of its realised capacity for emigration. Table 2.2 and Appendix V present these data from six single-caged colonies kept for this purpose. It is evident from Table 2.2 that individual colonies differed in their capacities to produce emigrant alatae.

The cumulative curves for dispersed alatae and apterae for six colonies have been presented in Figures 2.24 to 2.29. It is interesting to note that alatae started to disperse in these colonies at 27 to 30 days, whereas the alatiform third instar nymphs were first found in the colonies sampled at 18 days (Section 2.2.34-B). This meant that there was a time lag of 9-12 days for the realisation of potential for emigration in the colonies.

Of six plants studied for realised capacity for emigration, 2 died at 67 and 75 days following their colonisation; the rest were still producing alatae when the observations were stopped. The total output of alatae from these 4 plants would certainly be higher than their recorded numbers. It appears from these results (Table 2.2) that the total number of alatae which a colony can produce may be related to the peak aphid population reached in that colony.

What these results indicate is that *A. craccivora* has a potential for producing at least 3,200 to 7,500 emigrant alatae from one alata, if that alata happens to colonize a 2 week old broad bean plant, and if the colony grows in the absence of natural enemies.

Table 2.2. Cumulative numbers of alatae and apterae of *Aphis craccivora* which dispersed from single-caged colonies on broad beans - 1977.

Cage No.	Period of alata dispersal in days	Number of alatae	Period of apterous disperal in days	Number of apterae
2*	45	5754	42	139
3	41-D	4859	37-D	213
5	48-D	3842	42-D	188
7	45	3245	42	129
16*	46	3636	45	77
20*	49	7536	46	777

D = Death of host plant.

* = Parasitized colonies.

Figure 2.24: Cumulative numbers of dispersed alatae and apterae from a parasite-free colony in relation to age of the colony (cage 7). Arrows indicate the start of dispersal.

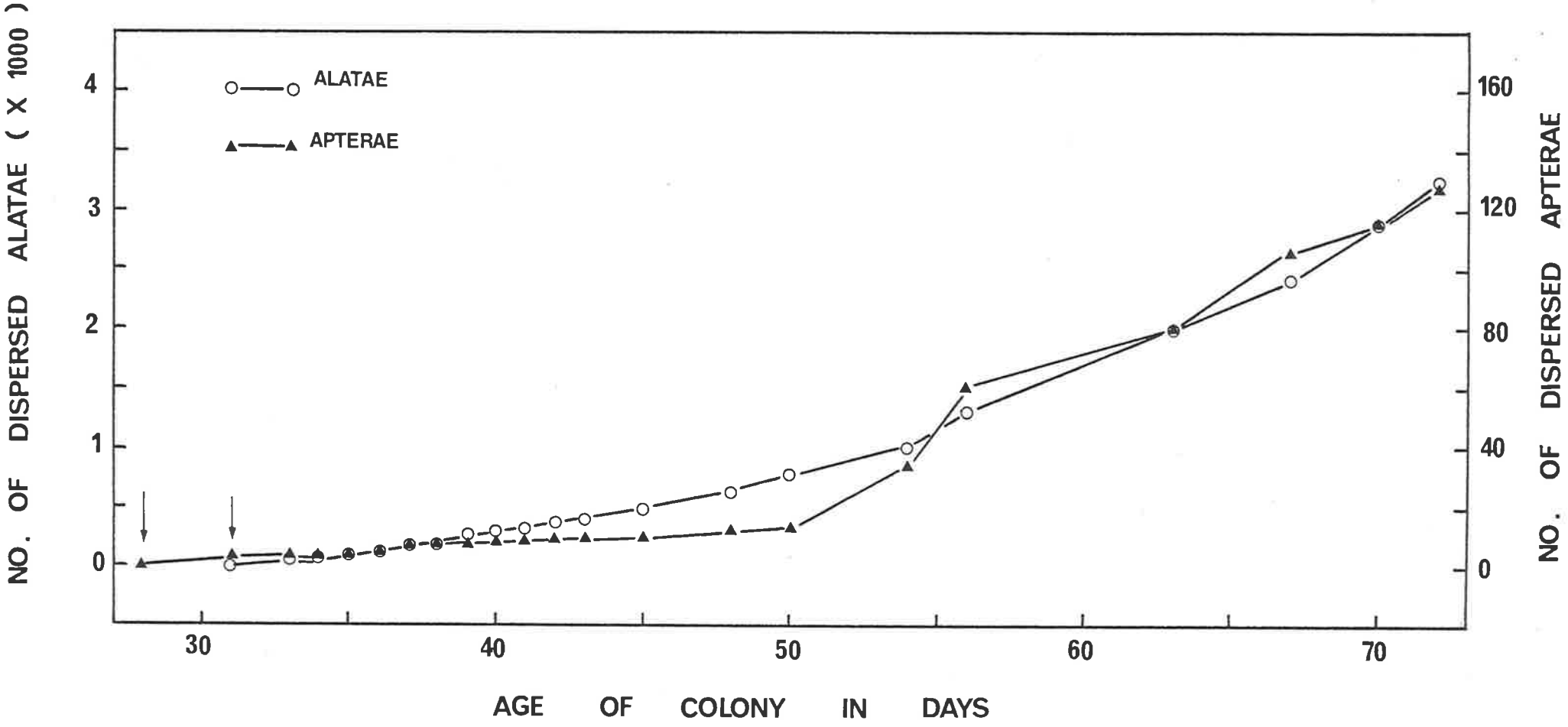

NO. OF DISPERSED ALATAE (X 1000)
NO. OF DISPERSED APTERAE
ALATAE
APTERAE
0
1
2
3
4
0
40
80
120
160
30
40
50
60
70
AGE OF COLONY IN DAYS

Figure 2.25: Cumulative numbers of dispersed alatae and apterae from a parasitized colony in relation to the age of the colony (cage 16).
P = Parasitized aphids seen.
Arrows indicate the start of dispersal.

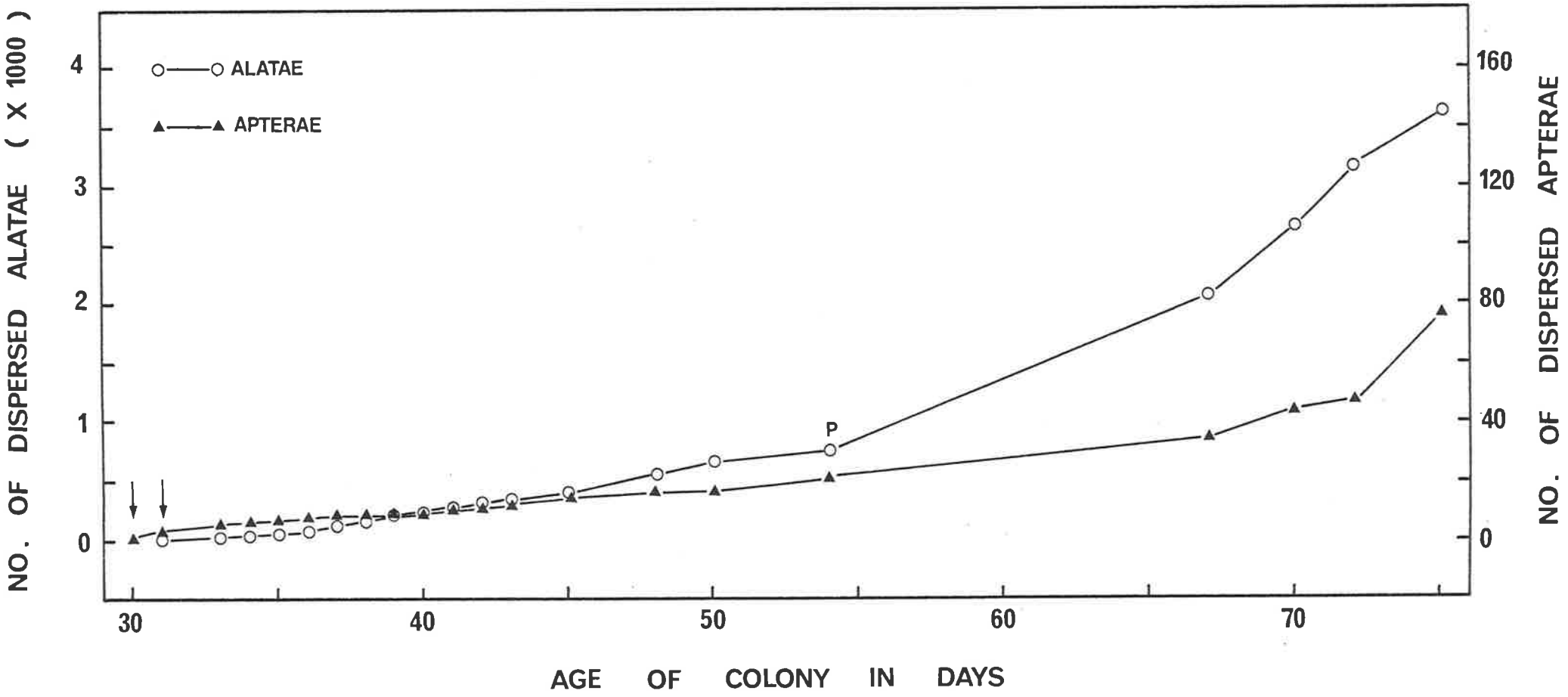

NO. OF DISPERSED ALATAE (X 1000)
NO. OF DISPERSED APTERAE
ALATAE
APTERAE
P
0
1
2
3
4
40
80
120
160
30
40
50
60
70
AGE OF COLONY IN DAYS

Figure 2.26: Cumulative numbers of dispersed alatae and apterae from a parasite-free colony in relation to age of colony (cage 5).
Arrows indicate the start of dispersal.
D = Death of host plant.

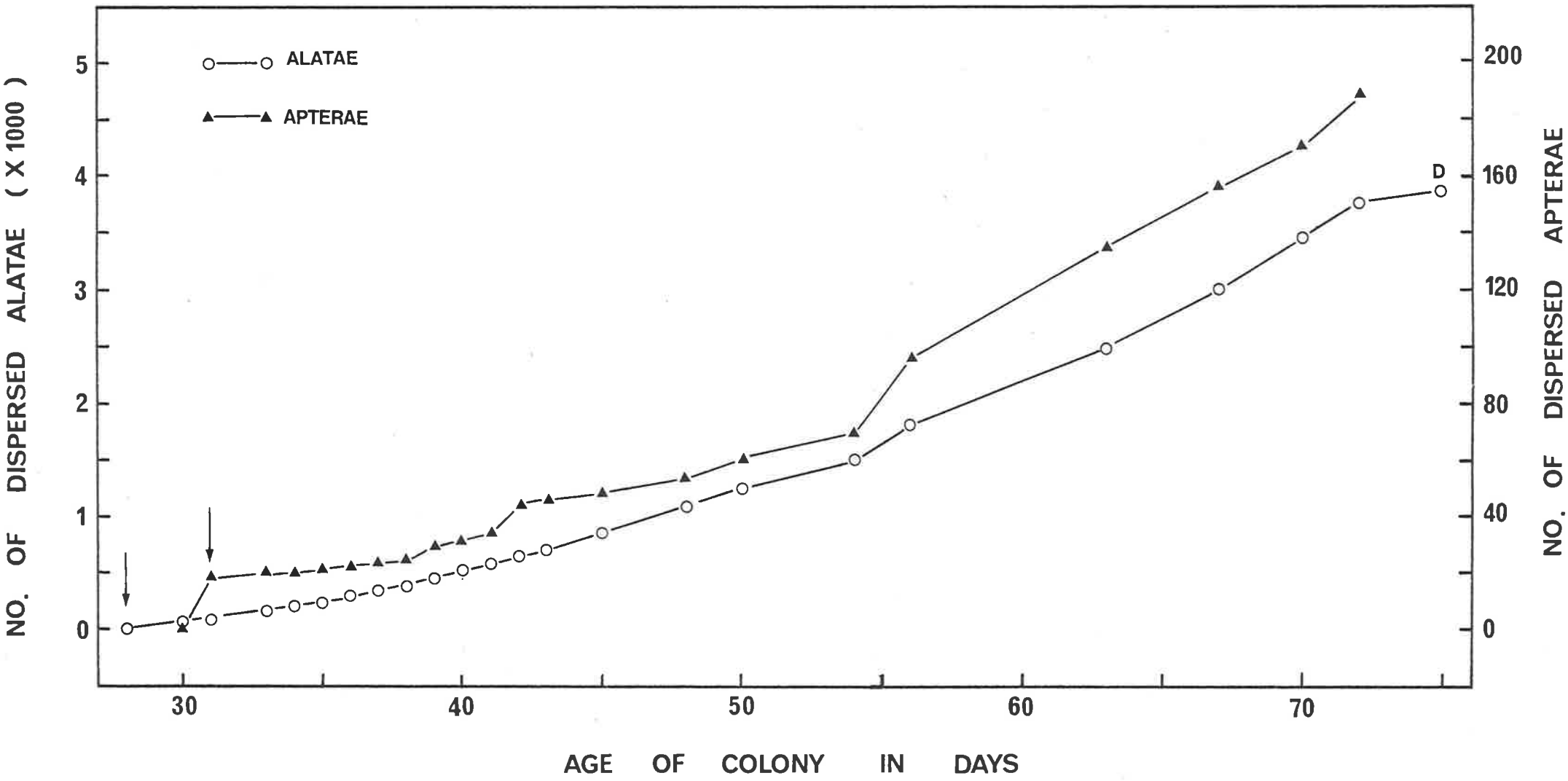
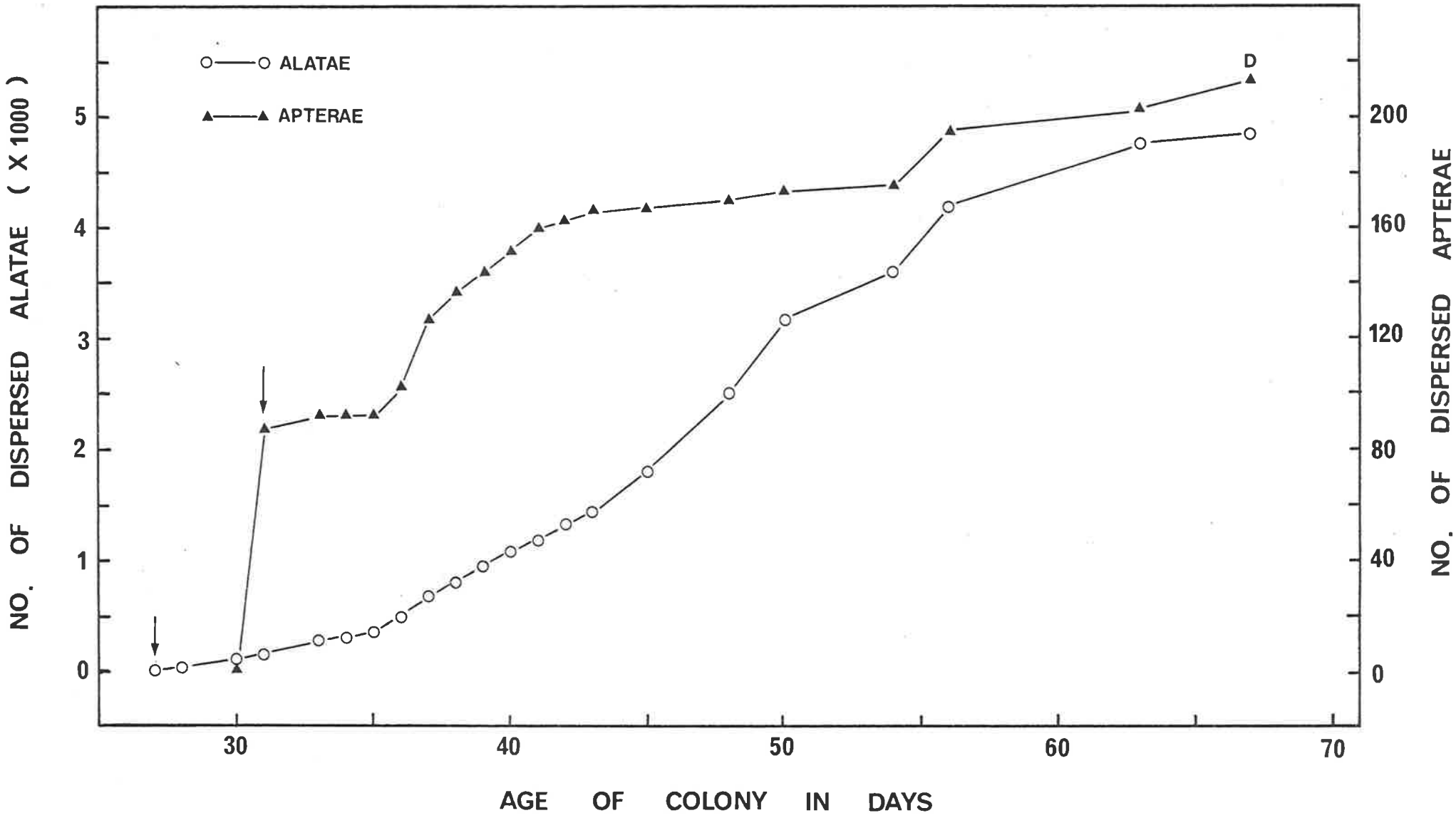

ALATAE
APTERAE
NO. OF DISPERSED ALATAE (X 1000)
NO. OF DISPERSED APTERAE
0
1
2
3
4
5
0
40
80
120
160
200
30
40
50
60
70
D
AGE OF COLONY IN DAYS

Figure 2.27: Cumulative numbers of dispersed alatae and apterae from a parasite-free colony in relation to age of the colony (cage 3).
Arrows indicate the start of dispersal.
D = Death of host plant.


ALATAE
APTERAE
D
NO. OF DISPERSED ALATAE (X 1000)
NO. OF DISPERSED APTERAE
0
1
2
3
4
5
0
40
80
120
160
200
30
40
50
60
70
AGE OF COLONY IN DAYS

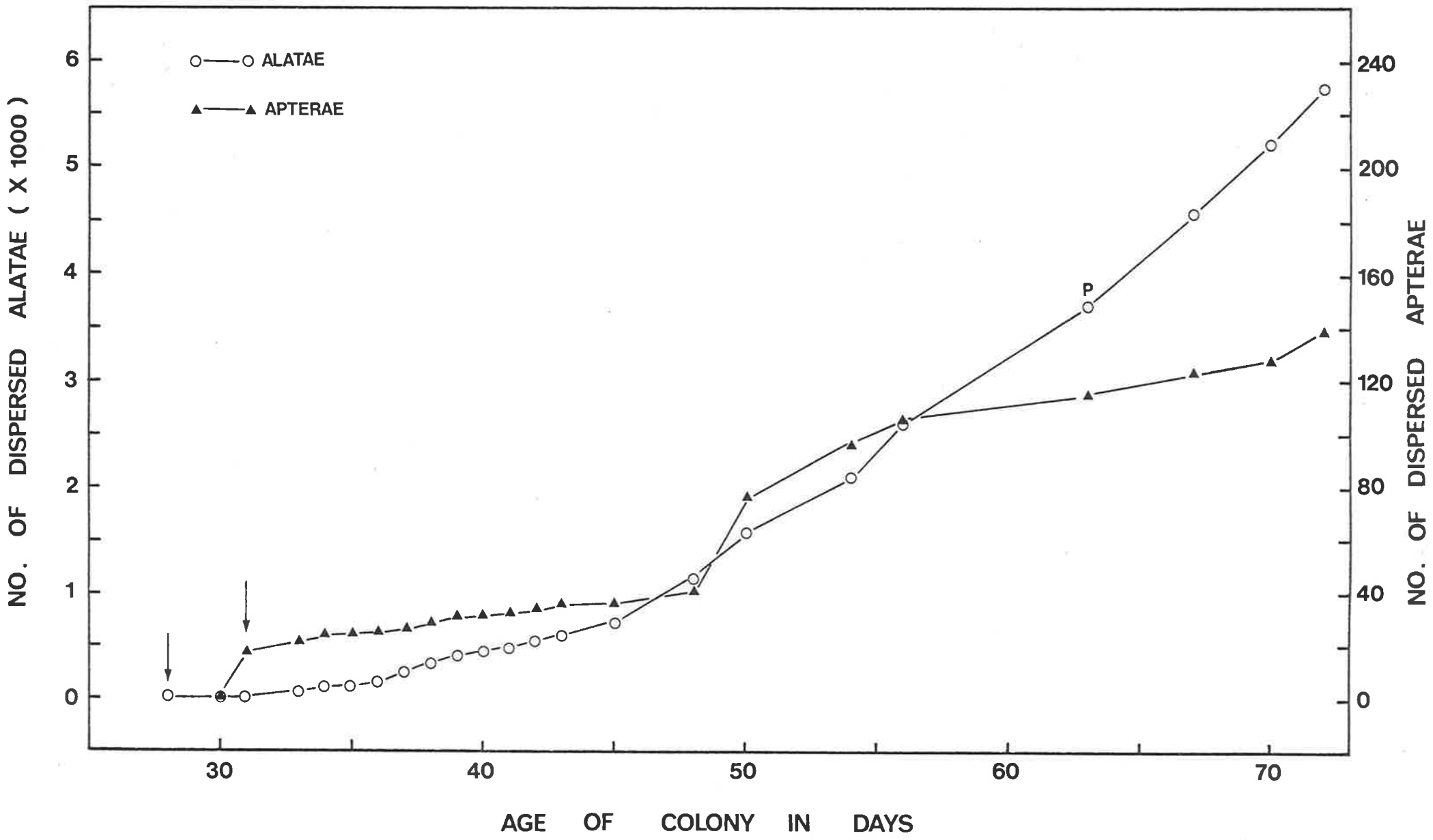
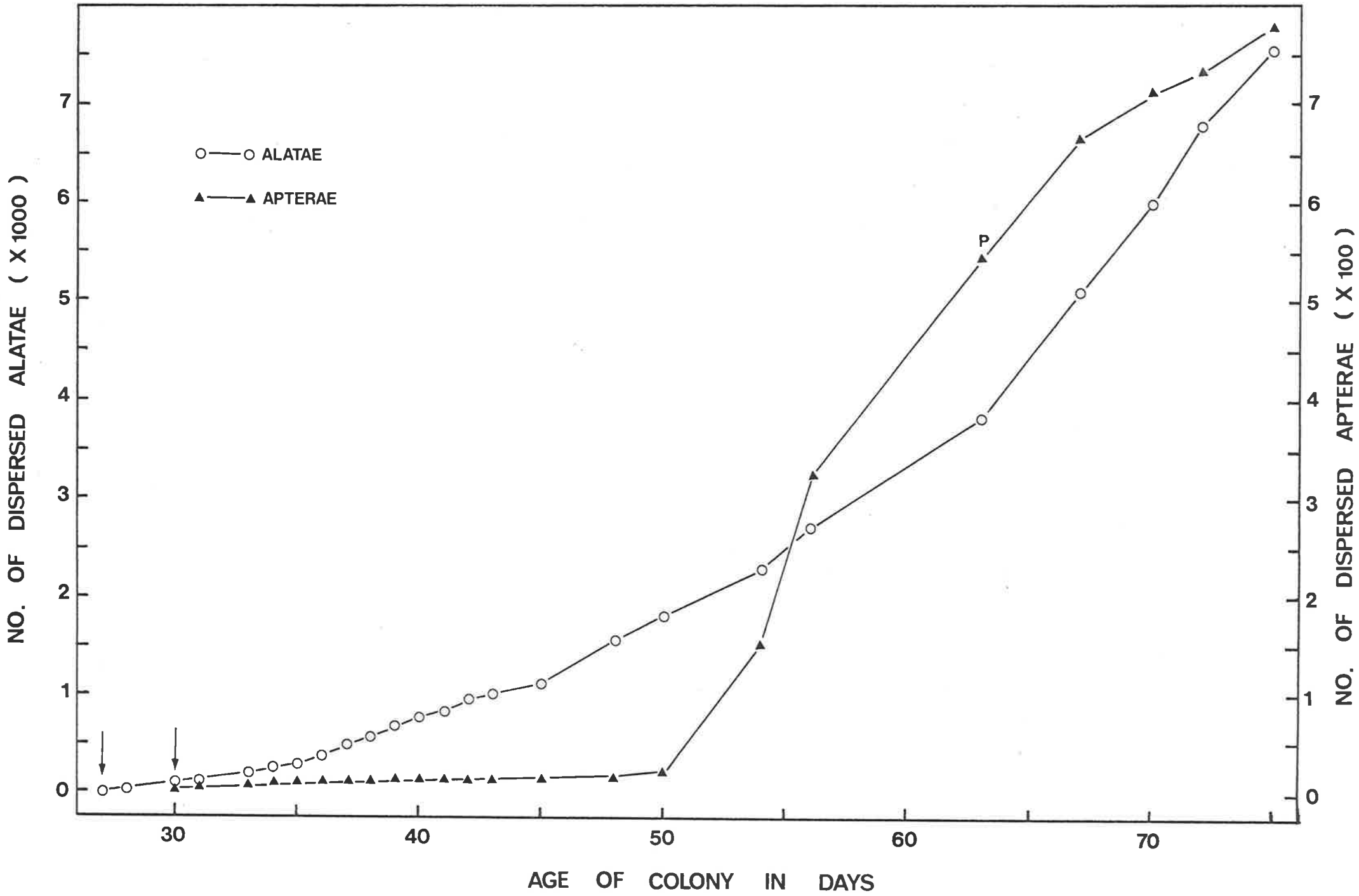

ALATAE
APTERAE
P
NO. OF DISPERSED ALATAE (X 1000)
NO. OF DISPERSED APTERAE
0
1
2
3
4
5
6
0
40
80
120
160
200
240
30
40
50
60
70
AGE OF COLONY IN DAYS

Figure 2.28: Cumulative numbers of dispersed alatae and apterae from a parasitized colony in relation to age of the colony (cage 2).
P = Parasitized aphids seen.
Arrows indicate the start of dispersal.

Figure 2.29: Cumulative numbers of dispersed alatae and apterae from a parasitized colony in relation to age of the colony (cage 20).
P = Parasitized aphids seen.
Arrows indicate the start of dispersal.


ALATAE
APTERAE
P
NO. OF DISPERSED ALATAE (X 1000)
NO. OF DISPERSED APTERAE (X 100)
0
1
2
3
4
5
6
7
30
40
50
60
70
AGE OF COLONY IN DAYS

The importance of the production of migrant alatae as realised through the framework of colony, is evident from these results.

2.2.35-B: Range of variation in the rates of dispersal of alatae among six colonies

To get an idea of the range of variation in the rates of dispersal of alatae among the six colonies, cumulative numbers of dispersed alatae were plotted separately for all the colonies in relation to their dispersal periods, regarding day 1 as the day on which alatae started to disperse from a colony. From these graphs the maximum and minimum cumulative numbers of dispersed alatae were read off at 10, 20, 30, 40 and 48 days. The rates of dispersal during the preceding 10 or 8 day periods were calculated on a per day basis by dividing the net increase in the cumulative values by the number of days (10 or 8).

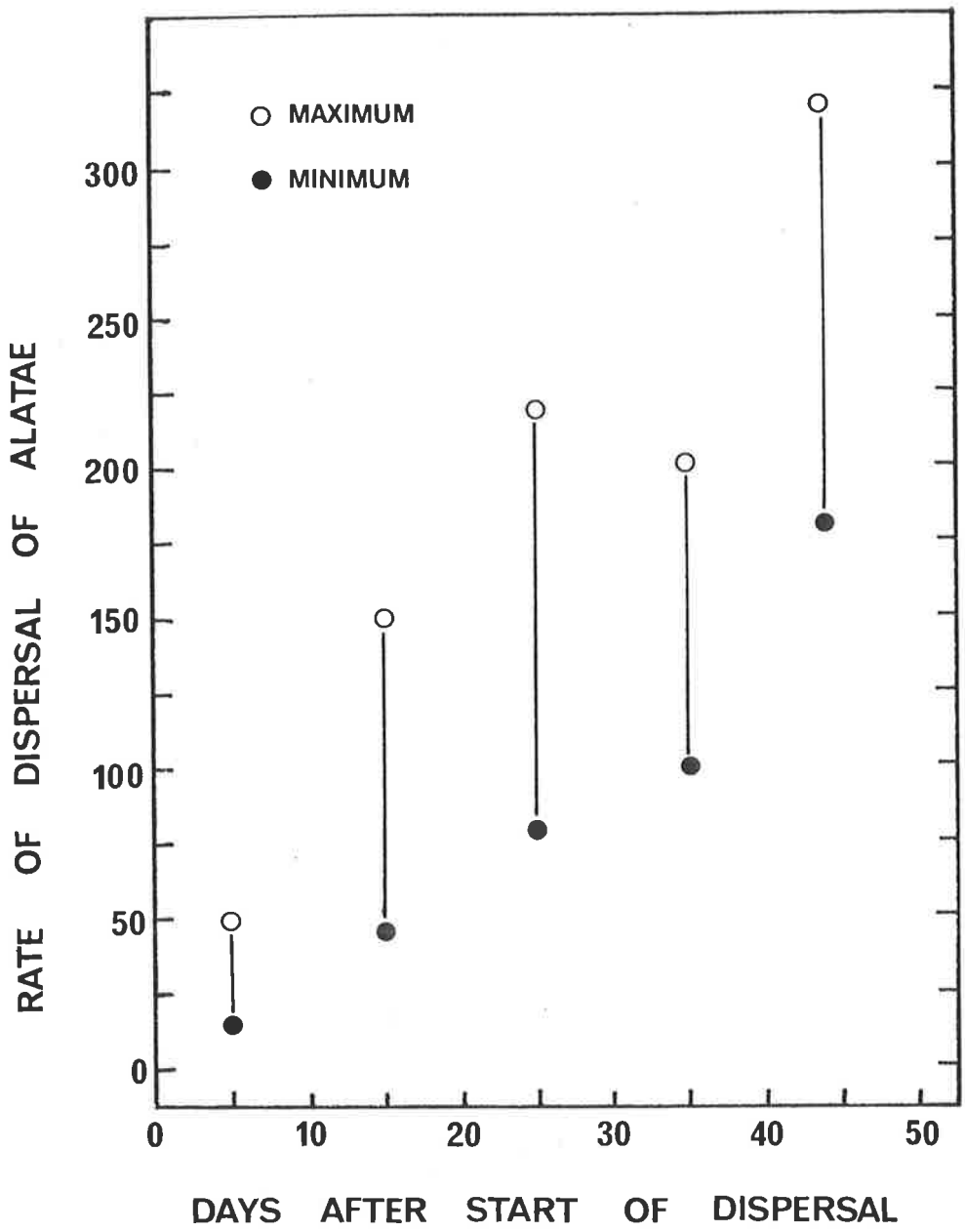
Figure 2.30 shows the range of variation in the rates of dispersal of alatae among the six colonies for 48 days, following the start of dispersal. Two aspects are evident. Firstly, variations in the rates of dispersal were 2 to 4-fold. Secondly, the rates of dispersal were positively related to the age of the colonies. The differences between the maximum and minimum rates of dispersal imply that the alata production and alata dispersal in *A. craccivora* is related to the population level of a colony; colonies with higher populations will produce alatae at a faster rate than those with lower populations.

2.2.36: Dispersal by apterae

2.2.36-A: Cumulative number of apterae, dispersed from six colonies

Table 2.2 shows the cumulative number of apterae which dispersed from six colonies. No apterae dispersed until the colonies

Figure 2.30: Range of variation in the rates of dispersal of alatae (per colony per day) among six colonies in relation to dispersal period. (Rates calculated for every 10 days.)


MAXIMUM
MINIMUM
RATE OF DISPERSAL OF ALATAE
300
250
200
150
100
50
0
0
10
20
30
40
50
DAYS AFTER START OF DISPERSAL

were 30 to 31 days old. Except one colony wherein 777 apterae dispersed, the number which dispersed varied between 77 and 213. There seems to be no relationship between the cumulative number of alatae and the cumulative number of apterae which dispersed from a colony.

2.2.36-B: Variation in the pattern of apterous dispersal in relation to dispersal period

Figures 2.24 to 2.29 show the pattern of apterous dispersal in the six colonies. Individual colonies differed in the pattern of apterous dispersal (see also Appendix VI). In one pattern, many apterae dispersed at the beginning of dispersal period; whereas in the other, only a few apterae dispersed at the beginning but many dispersed during the later half of dispersal period. Due to lack of a uniformity, apterous dispersal may be regarded as irregular. The irregularities, nevertheless, point towards the probable facultative nature of apterous dispersal as influenced by the specific conditions within a colony.

2.2.37: Ratios of total alatae to total apterae which dispersed from six colonies

Table 2.2 shows the total numbers of alatae and apterae which dispersed from six single-caged colonies. The ratios of total dispersed alatae to total dispersed apterae in parasite-free colonies varied from 20:1 to 25:1 and in the parasitized colonies these ratios varied from 10:1 to 45:1. It appears from these ratios that parasitization probably reduced the numbers of dispersing apterae.

2.2.4: Summary

The results of Experiment I can be summarised as follows:

Observations on the pattern of infestation of broad beans by *A. craccivora* indicate that this aphid is well adapted to the growth habits of its leguminous host plants. Parasitization by the Aphidiid parasite (*Aphidius colemani*) soon after colonization was detrimental to the establishment of a colony. Populations ranging from 3,000 to 15,500 aphids, developed on a broad bean plant during 5 to 8 weeks in early winter in field cages.

First and second instar nymphs accounted for 40 to 85% of total populations and stable distributions among first, second and third instar nymphs, approximating to a geometric progression, were a common occurrence in growing colonies. The values of e^{λ} varied between 0.9 and 3.1. Reduced proportions of young nymphs (15 to 37%) and increased proportions of fourth instar alatiform nymphs (26 to 50%) were characteristic of declining populations, following the dispersal by apterae and alatae.

Population growth in *A. craccivora* colonies is dependent upon the number of reproducing apterae and the prevailing temperatures. The ratios of first instar nymphs to apterae remained unaffected in relation to increasing populations of the colonies until the start of apterous dispersal.

The proportion of alatiforms among third instar nymphs was regarded as the best measure of potential rate of emigration of a colony. These rates varied from 75 to 97% in colonies with 550 to 4,000 aphids

and decreased from 75 to 52% in colonies with 5,000 to 15,500 aphids. The threshold density per colony for 50% alata determination was 92-108 aphids.

Alatae appeared among the second generation aphids. The total number of alatae which dispersed from a colonized broad bean plant ranged from 3,200 to 7,500 and the total dispersed apterae varied from 77 to 777.

Apterous dispersal is a consistent but irregular and facultative behavioural mechanism in *A. craccivora*. Parasitization apparently reduced the numbers of dispersing apterae, in old colonies.

2.3: Experiment II: Alata production in *A. craccivora* colonies, initiated by 1, 2, 4 and 8 alatae, on common burr medic, subterranean clover, lucerne and broad beans in field cages

2.3.1: Introduction

Common burr medic (*Medicago polymorpha* var. *vulgaris*), subterranean clover (*Trifolium subterraneum*) and lucerne (*Medicago sativa*) are common plant species in the South Australian legume pastures. Life table studies in *A. craccivora* (Gutierrez *et al.* 1971) established common burr medic as highly suitable, subterranean clover as moderately suitable and lucerne as an unsuitable host for the population growth of this aphid. Further, Gutierrez *et al.* (1971) commented on the host selection of *A. craccivora* alatae in the field. They reported common burr medic as a preferred species when it grew with other *Medicago* species. They also reported the development of large populations of this aphid on subterranean clover, but observed that lucerne was not

infested to any great extent in their study pastures in New South Wales. On the basis of these studies, Gutierrez *et al.* (1974a) developed a deterministic model of *A. craccivora* populations in the temperate pastures of South Eastern Australia. Their model, however, lacks empirical data on the rate of infestation of plants per unit area and the initial colonization density of the alatae per plant on common burr medic and subterranean clover in the field; an arbitary rate of infestation of 0.03 alata per stem was used to simulate the population build-up. The model also fails to consider effects of variations in the initial colonization density (per plant), on the size, age-structure, the time of production of first alata progeny and the extent and duration of alata production in individual colonies.

Results on colonization of broad bean seedlings by *A. craccivora* in the field indicated that the densities of 1 to 4 alatae per stem were frequent and up to 12 alatae colonized a single stem (see Section 4.2.2-C). The range of variation in the colonization density of alatae per stem is such that any systematic study aimed at understanding the emigration potential of *A. craccivora*, ought to take into account the influence of colonization density on the alata production capacity of the resultant colonies on different host plant species. I, therefore, designed an experiment to determine alata production and dispersal in the colonies initiated by 1, 2, 4 and 8 alatae, on common burr medic, subterranean clover, lucerne and broad bean plants in the field. I initiated the experimental colonies by confining the required number of alatae in leaf cages on 5 week old potted plants and kept them outdoors in field cages in mid-May 1978. The observations continued until the end of August. The objectives underlying this experiment

were: (1) to get an idea of the emigration potential and rates of dispersal of alatae and apterae in the experimental colonies; (2) to determine the generation status and the time of appearance of first alata progeny; and (3) to get an estimate of population levels of the experimental colonies soon after the start of alata dispersal.

2.3.2: Methods

2.3.2-A: Aphid supply

This experiment needed a large number of alatae for simultaneous initiation of the experimental colonies. For this purpose, *A. craccivora* apterae were collected from an infested broad bean plot. Fifty apterae were placed on each of 8-10 week old potted broad bean plants for 3 days for larviposition. A total of 8 plants was used. After infestation with apterae, the plants were kept in an insectary room, where temperature ranged between 19 and 21^{o}C and a bank of 8 fluorescent daylight tubes provided a 12 hour photoperiod. The light intensity on the plants varied between 520 and 560 lux. The apterae were removed on the fourth day with a fine brush without disturbing the nymphs on the plants. The plants were then kept in wooden cages (45 x 45 x 65 cm) with 3 sides and roof of fine terylene net, plywood base and a plywood side-door. Each cage had 4 plants. A large proportion of these nymphs developed as alatae. Alatae which flew to the sides and roofs of the cages were collected in the morning and evening, anaesthesized with CO_2 and kept on detached broad bean leaves. The leaves with the alatae were kept on moist filter papers in 9 cm diameter Petri dishes. Each Petri dish had 30 to 40 alatae.

The Petri dishes were kept at 15°C and a 12 hour photoperiod in a growth cabinet. The use of broad bean leaves was necessary to keep the alatae alive because of their high mortality in ventilated glass tubes and also in Petri dishes with only moist filter papers. The required number of alatae was collected in 2 days. However, many alatae (50-60%) had started larviposition (1-5 nymphs/alata) before they were used for initiation of the experimental colonies. The alatae were pooled together, before they were used for the experiment, to minimise the differences due to reproduction.

2.3.2-B: Host plants

Five or six seeds of common burr medic, subterranean clover (cultivar Clare) and lucerne (cultivar Hunter River) were sown in the recycled potting mixture (second soil) in 15 cm diameter plastic pots. Broad beans (cultivar 127) were sown singly. The pots were watered and kept in a well ventilated glasshouse. One week old seedlings of common burr medic, subterranean clover and lucerne were thinned, leaving one seedling per pot. The plants were 34-36 days old at colonization.

2.3.2-C: Leaf cages

Leaf cages were used to confine the alatae on the host plants for 4-5 days. The leaf cages were made from 2 mm thick transparent perspex tubes of 1.5 and 3.5 cm diameter. One cm wide rings were cut from the perspex tubes. A fine terylene net was glued at one end of the perspex ring, while the other end had a plastic foam ring glued to it. Clear perspex discs of 2 and 4 cm diameter and 1 mm thickness were glued with the same sized plastic foam discs to support

the leaf cages on the other side of a leaf or shoot. The cages and their supporting discs were held together by light weight aluminum hair clips. 1.5 cm diameter cages were used to confine one and two alatae and 3.5 cm diameter cages were used to confine 4 and 8 alatae.

2.3.2-D: Field cages

Wooden cages of two sizes were used to protect the colonies from immigrating aphids and natural enemies. The small cages used for the first experiment (see Section 2.2.11) were used to confine emigrating aphids from four colonized plants. The big cages were 85 x 85 x 75 cm high. These were similar to the small cages in the material and construction. The big cages were used to protect 16 colonized plants from natural enemies for 4 weeks. The plants in the big cages were kept in galvanised iron water trays (80 x 80 x 5 cm deep) to facilitate uniform watering. All the field cages had their tops covered with a thin transparent plastic sheet to prevent rainwater dripping on the colonized plants. All the cages were set up 1 to 2 m apart in the Alverstoke Orchard of Waite Institute. They were held down by a rope and a 30 cm luggage strap between two pegs in the ground.

2.3.2-E: Temperature records

The temperatures outside and inside two of each small and big cages were recorded with a Grant thermistor temperature recorder. The thermistors were shaded with an aluminum foil cone to protect them from direct sunlight and rain.

2.3.2-F: Design of the experiment

The design of this experiment was a 'complete randomized factorial design' (C.R.F.D.), comprising two factors, namely, host plant species and initial colonization density per plant. Four host plant species i.e., common burr medic, subterranean clover, lucerne and broad beans were used for initiating colonies with four densities of *A. craccivora* alatae i.e., 1, 2, 4 and 8 alatae per colony. The sixteen treatments were replicated four times to quantify alata production and dispersal, and eight times to detect the appearance of first alata progeny and to estimate population densities of the colonies soon after the start of alata dispersal.

2.3.2-G: Procedure

The required number of alatae was placed on the undersurfaces of leaves and the leaf cages were set to confine the alatae on the host plants. Sixty-four plants were colonized for alata production studies and 128 plants for the estimation of population densities. Plant labels were used to mark the treatments. The treatments were marked as L4, M1, SC2, B8, etc. The colonized plants were kept in the cages. Each of the 16 small cages had 4 replicates of one colonisation density on one host plant species. Each of the 8 big cages had 16 plants representing all the treatments with all the colonization densities and the host plant species. The arrangement of the colonized plants in the big cages was at random. All the leaf cages were removed 4-5 days after colonization. The caged plants were watered whenever necessary. The experiment was regarded as starting on the day of colonization.

When first generation apterae started appearing in the colonies, all the colonized plants were checked for the presence of third and fourth instar alatiform nymphs. The presence of alatiform nymphs at that time provided the generation status and the time of appearance of first alata progeny in the colonies, especially with reference to the winter of Adelaide.

Many of the colonized plants in 4 big cages were attacked by the Aphidiid parasite (*Aphidius colemani* Viereck) within 2 weeks of colonization and had to be discarded. At 46 days after colonization, all the remaining plants in the big cages (with the aphids) were harvested. They were cut at the base without disturbing the aphids and kept in polythene bags, labelled and stored at $2^{o}C$. The contents of each polythene bag were washed later in luke-warm water containing a little detergent, and all the aphids were removed with a brush. The aphids were stored in 80% alcohol and counted later to determine the total population of the sampled colonies. These figures provided a measure of the sizes of 46 day old colonies with reference to various initial colonization densities on the four host plant species.

Emigrating apterae and alatae which walked away or flew from the plants in the small cages were counted and removed with a vacuum cleaner at frequent intervals until the plants collapsed or the colonies were 106 days old. These figures provided an estimate of the actual numbers of alatae and apterae which emigrated from different sized colonies on the four host plant species.

2.3.3: Temperature, relative humidity and photoperiod

Table 2.3 shows ambient temperatures recorded at the Waite during the experiment. The relative humidity during this period varied between 60 and 85%. Day-lengths during the experimental period decreased from 10½ hours in May to 10 hours in June and thereafter increased to 11 hours by the end of August.

Temperatures inside the cages were 2 to 4°C higher than the outside temperatures during sunny periods. These temperature records are presented in Appendix XX.

2.3.4: Results

2.3.41: Suitability of host plant species for colonization by *A. craccivora* alatae

One interesting outcome of this experiment was that colonies of *A. craccivora* failed to develop on lucerne. Visible colonies developed on common burr medic, subterranean clover and broad beans. As the alatae were confined in the leaf cages for 4 to 5 days, they produced a few nymphs on lucerne plants during this period. The colonizing alatae walked off the lucerne plants after the leaf cages were removed. The progeny laid by the colonizing alatae, developed into adults, but the aphids were hardly visible on these plants. The number of alatae and apterae which dispersed from four lucerne plants are presented in Appendices VII and VIII respectively.

Table 2.3: Air temperatures during the experimental period - 1978.

Month	Temperatures in °C		
	Mean Maximum	Mean Minimum	Average = $\left(\frac{\text{Max.} + \text{Min.}}{2}\right)$
May	18.3	11.6	14.9
June	14.8	8.9	11.9
July	13.5	8.1	10.8
August	14.1	7.5	10.8

The results indicate two aspects of insect-plant relationship between *A. craccivora* and lucerne. Firstly, the colonizing alatae walked off the plants but their progeny stayed and completed development on lucerne. Secondly, the persistence of aphids until 74 days after colonization indicates that not all the apterae left lucerne plants. The acceptance of lucerne by the apterae suggests that lucerne can serve as an important resource for the survival of isolated colonies of *A. craccivora* at times when other favourable host plants are scarce or absent and especially in summers in South Australia. This might also lead to evolution of a new biotype of this aphid which could colonize and breed successfully on lucerne in the long term.

The results, nevertheless, indicate that lucerne is not a suitable host for colonization and population development of the South East Australian biotype of *A. craccivora*. Since the colonization on lucerne in the experimental colonies appeared more of an artefact due to the leaf cages, the data in Appendices VII and VIII were not included in the analysis of variance, carried out on the total numbers of alatae and apterae which dispersed from the experimental colonies.

2.3.42: Time of appearance and generation status of the first alata progeny in the experimental colonies

A. craccivora has been reported to produce alata progeny within a short period after colonization of its host plants (Gutierrez *et al.* 1971, 1974a; Farrell 1976). Johnson and Birks (1960) observed that the progeny of alatae viviparae of *A. craccivora* which were laid during the later half of their reproductive lives, developed into alatae on mature broad bean leaf discs. Further experiments

(Johnson 1966a, 1966b) revealed that rearing conditions with 10-12 hour photoperiod and 15-19°C were favourable for alata development in this aphid. These results implied that colonies of *A. craccivora*, initiated during late autumn and early winter, could produce alata progeny in the first generation on subterranean clover and medic plants in the temperate legume pastures of South Eastern Australia. This hypothesis, however, has not been tested empirically in the field and this experiment provided an excellent opportunity to test it. It was interesting to do so, because a positive evidence in this direction would not only confirm the findings of Johnson and Birks (1960) and Johnson (1965, 1966a, 1966b) regarding the mechanism of dimorphism in this anholocyclic aphid, but would also reveal the extent of plasticity and physiological sensitivity of this insect, to produce winged forms in its natural populations in response to certain environmental factors. Further, from an ecological point of view, the production of winged progeny in the first generation in the colonies would also signify the extent of adaptation of this aphid to the ephemeral and discontinuous patches of its habitats, and in this context *A. craccivora* might be regarded justifiably as a super-migrant species.

The experimental colonies were observed for the presence of first generation apterae at 2-3 day intervals, during the second week after colonization. Adult apterae were first observed at 14 days in a few colonies. All colonies in the big cages were observed at 18 days and those in the small cages at 19 days, for the presence or absence of adult apterae and third and fourth instar alatiform nymphs. The results are presented in Tables 2.31 and 2.32.

Table 2.31. Observations on the appearance of first generation apterae and alatiform nymphs in the colonies in the big cages 18 days after start of the experiment - 1978.

Host plant species	Colonisation density (alatae/plant)	Total plants	Plants with apterae	Plants with alatiform nymphs
Common burr medic	1	8	7	0
	2	7	4	3
	4	5	5	5
	8	8	8	8
Lucerne	1	8	3	0
	2	6	3	0
	4	3	0	0
Subterranean clover	1	7	1	0
	2	7	5	0
	4	8	7	1
	8	7	7	5
Broad bean	1	8	6	2
	2	5	4	3
	4	8	8	4
	8	6	4	5

Table 2.32. Observations on the appearance of first generation apterae and alatiform nymphs in the colonies in the small cages 19 days after start of the experiment - 1978.

Host plant species	Colonisation density (alatae/plant)	Total plants	Plants with apterae	Plants with alatiform nymphs
Common burr medic	1	4	4	3
	2	4	4	1*
	4	4	4	2
	8	4	4	4*
Lucerne	1	4	2	0
	2	4	4	0
	4	4	4	1
Subterranean clover	1	4	1	0
	2	4	3	0
	4	4	4	1
	8	2	2	2
Broad bean	1	4	4	1
	2	4	4	4
	4	4	4	4
	8	4	4	4

* Plants with teneral alatae also.

Alatiform nymphs among the first generation aphids were observed in most of the colonies except those initiated by 1 and 2 alatae on lucerne and subterranean clover. First generation alatae (tenerals) were also observed in the colonies initiated by 2 and 8 alatae on common burr medic. It appears from the results that the influence of the prevailing low temperatures (mean = 15°C) and short photoperiod (10 hrs 15 mins) and the age of common burr medic and broad bean plants (5 weeks), over-rode the influence of initial colonization density (per plant) on alata determination in the experimental colonies. The absence of alatiform nymphs in the colonies initiated by 1 and 2 alatae on lucerne and subterranean clover, however, suggests that the prevailing low temperatures, short photoperiod and the age of the host plants, did not provide enough stimuli necessary for alata determination up to 20 days after colonization. The influence of initial colonization densities of 4 and 8 alatae per plant, however, appears to have complemented the alata determining influences of the prevailing weather and the host plant age on lucerne and subterranean clover.

The absence of third and fourth instar alatiform nymphs in the colonies initiated by 1 and 2 alatae on lucerne and subterranean clover does not rule out the possibility that first generation alatiform nymphs appeared later than the 19th day. However, it would be difficult to ascertain the generation status of these nymphs because of the same aged second generation nymphs produced by the first generation apterae.

The results presented in this section, nevertheless, indicate an interaction between the initial colonization densities and the host plant species with reference to their influence on alata determination

in colonies of *A. craccivora* at a given age of host plants (5 weeks) and the same weather conditions (early winter), as prevailed during this experiment.

2.3.43: Dispersal by alatae

2.3.43-A: Time interval between colonization and the start of alata dispersal

As mentioned earlier, third and fourth instar alatiform nymphs were recorded in the colonies at 16 to 20 days after colonization, but dispersal by the alatae was not observed until after 35 days. Many alatae dispersed within the cages at 42 days. Since the cages were not observed between 35 and 42 days, it is not known when dispersal started in the individual cages. However, the start of dispersal in each cage can be estimated by extrapolating the curves of Figures 2.34, 2.35 and 2.36 back to the abcissa. The results (Table 2.33) show that neither the colonization densities nor the host plant species influenced the time of alata dispersal in the experimental colonies on common burr medic, subterranean clover and broad beans. However, the colonies initiated with 8 alatae on these host plants were first in this respect. The more or less simultaneous start of alata dispersal in the experimental colonies suggests the synchronising influence of the prevailing weather on alata production and dispersal in this aphid.

2.3.43-B: Rate of dispersal of alatae

One of the objectives of this experiment was to quantify the rate of dispersal of alatae in the experimental colonies. As the population growth in colonies of *A. craccivora* is exponential (see Section 2.2.31-B), the rate of dispersal of alatae might be expected

Table 2.33. The start of alata dispersal in the experimental colonies - 1978.

Host plant species	Colonisation density (alatae/plant)	Days to alata dispersal
Common burr medic	1	42
	2	42
	4	40
	8	39
Lucerne	1	48
	2	42
	4	52
Subterranean clover	1	42
	2	42
	4	42
	8	39
Broad bean	1	42
	2	41
	4	40
	8	41

to vary with the initial colonization density of its colonies, at least for a short period. The results of this experiment provided an opportunity to test this hypothesis. Mean rates of dispersal of alatae per day per colony, for the experimental colonies on common burr medic, subterranean clover and broad bean are presented in Figures 2.31, 2.32 and 2.33. The rates were calculated for every six days from the respective cumulative curves of total alatae which dispersed from a colony, starting from the first day of dispersal (Figures 2.34, 2.35 and 2.36).

Two features of alata dispersal are evident from these Figures (2.31, 2.32 and 2.33). Firstly the rate of alata dispersal in the colonies initiated by 4 and 8 alatae on common burr medic and subterranean clover was approximately 2 to 3 times higher than the rate in the colonies initiated by 1 and 2 alatae on these host plants for the first 18 days. Similarly on broad bean the rate of dispersal in the colonies initiated with 2, 4 and 8 alatae was 2 to 4 times higher than the rate in the colonies, started with one alata for 54 days. Secondly, many colonies with 4 and 8 alatae sustained alata output for a shorter period than the colonies with 1 and 2 alatae, because the host plants with 4 and 8 alatae collapsed earlier.

The combination of higher rates of dispersal and a shorter period of dispersal in the colonies initiated by more than one alata, compared with lower rates of dispersal over a long period in the colonies initiated with one alata, appears to have no significant effect on the total number of alatae which dispersed from a host plant. These results thus suggest the transient nature of these host plant species and define the concept of a finite carrying capacity of a host plant;

Figure 2.31: *Mean rates of dispersal of alatae (per colony per day) in relation to dispersal period, in the experimental colonies on common burr medic (*Medicago polymorpha* var. *vulgaris*).
M1, M2, M4 and M8 represent colonies initiated with 1, 2, 4 and 8 alatae.
*Mean of 4 colonies (rates calculated for every 6 days).

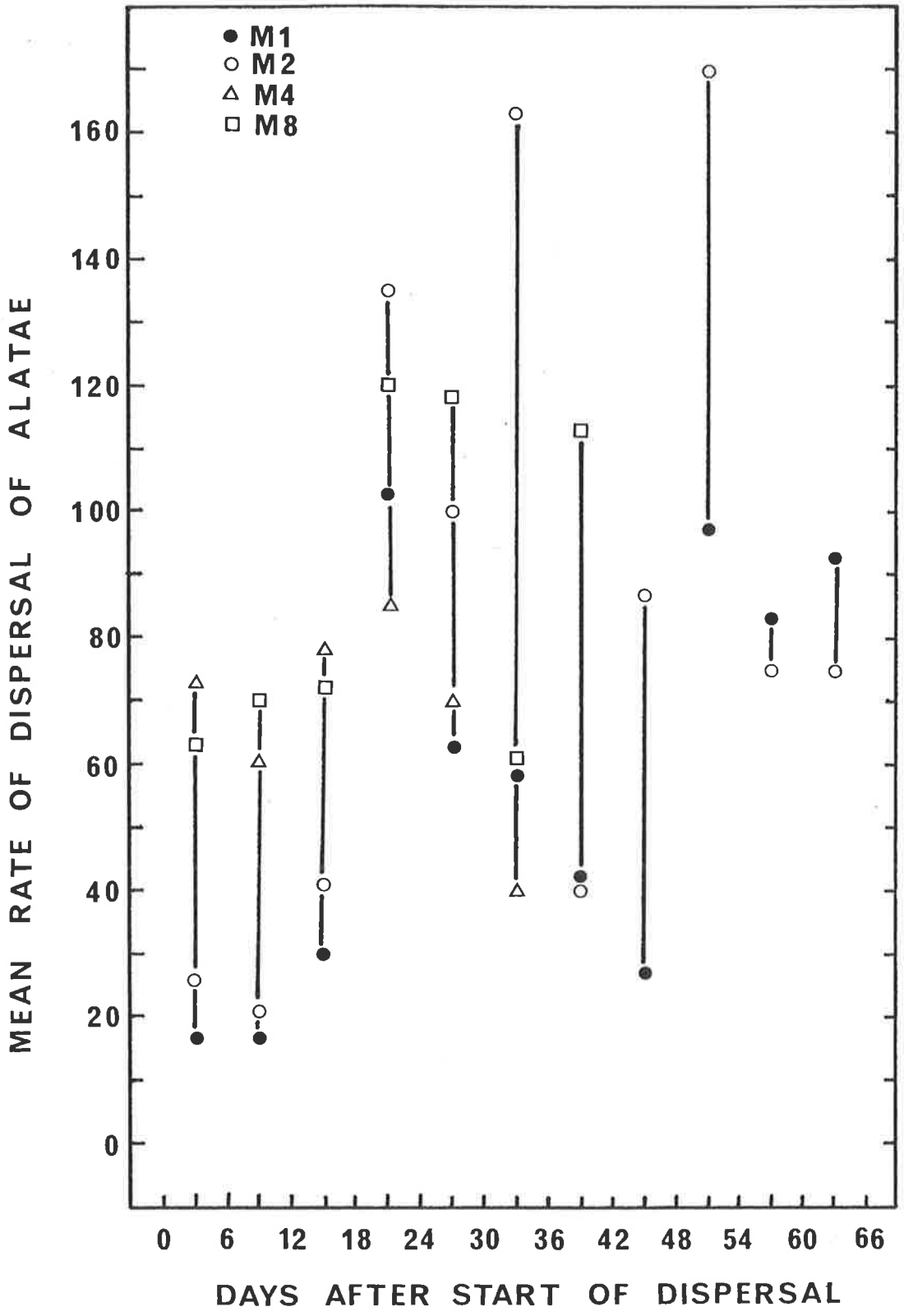

M1
M2
M4
M8
MEAN RATE OF DISPERSAL OF ALATAE
0
20
40
60
80
100
120
140
160
0
6
12
18
24
30
36
42
48
54
60
66
DAYS AFTER START OF DISPERSAL

Figure 2.32: *Mean rates of dispersal of alatae (per colony per day) in relation to dispersal period in the experimental colonies on subterranean clover (*Trifolium subterraneum*).
SC1, SC2, SC4 and SC8 represent colonies initiated with 1, 2, 4 and 8 alatae.
*Mean of 4 colonies; Mean of 2 colonies for SC8 (rates calculated for every 6 days).

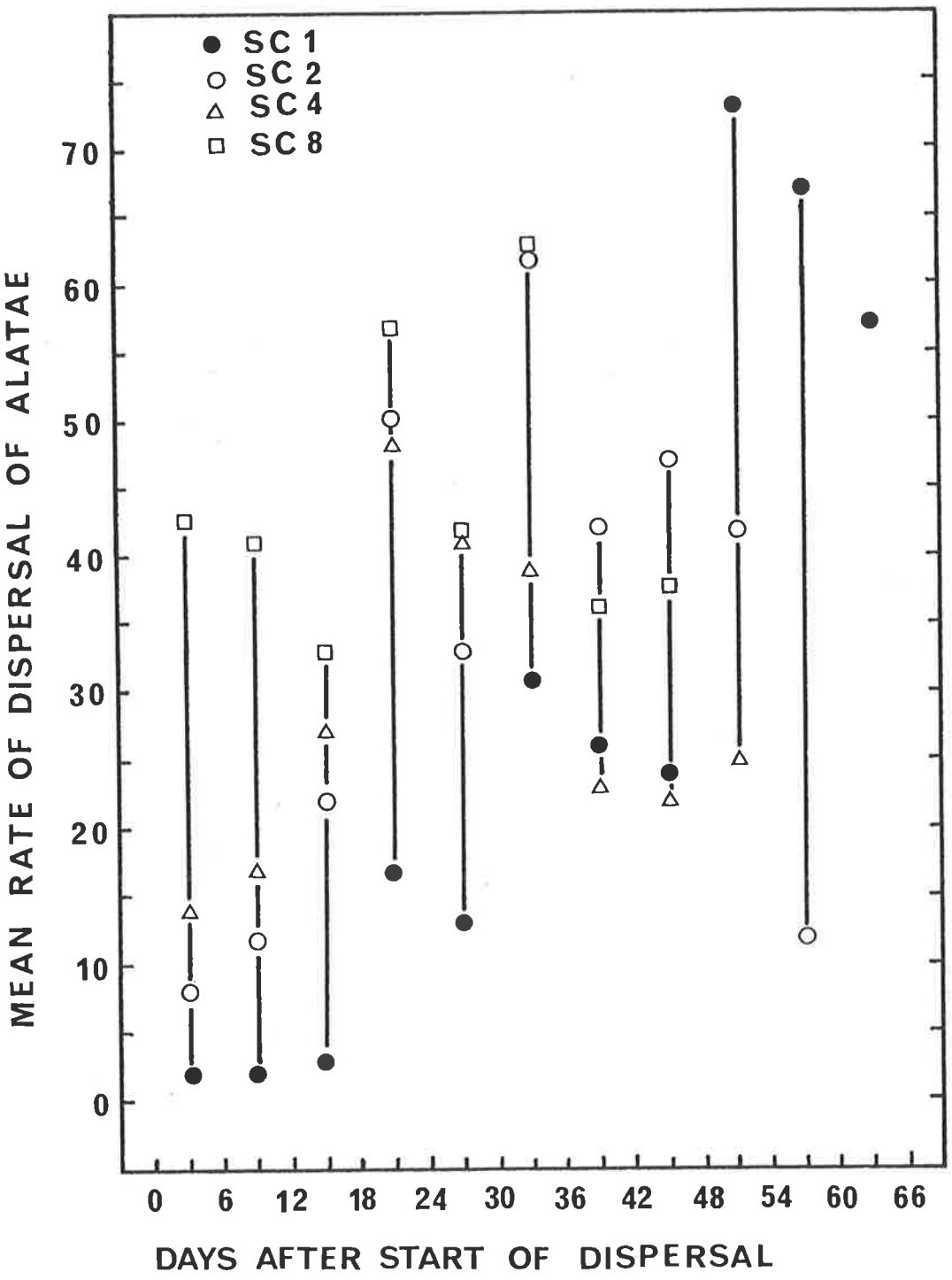

SC 1
SC 2
SC 4
SC 8
MEAN RATE OF DISPERSAL OF ALATAE
0
10
20
30
40
50
60
70
0
6
12
18
24
30
36
42
48
54
60
66
DAYS AFTER START OF DISPERSAL

Figure 2.33: *Mean rates of dispersal of alatae (per colony per day) in relation to dispersal period in the experimental colonies on broad beans (*Vicia faba* L.).
B1, B2, B4 and B8 represent colonies initiated with 1, 2, 4 and 8 alatae.
*Mean of 4 colonies (rates calculated for every 6 days).

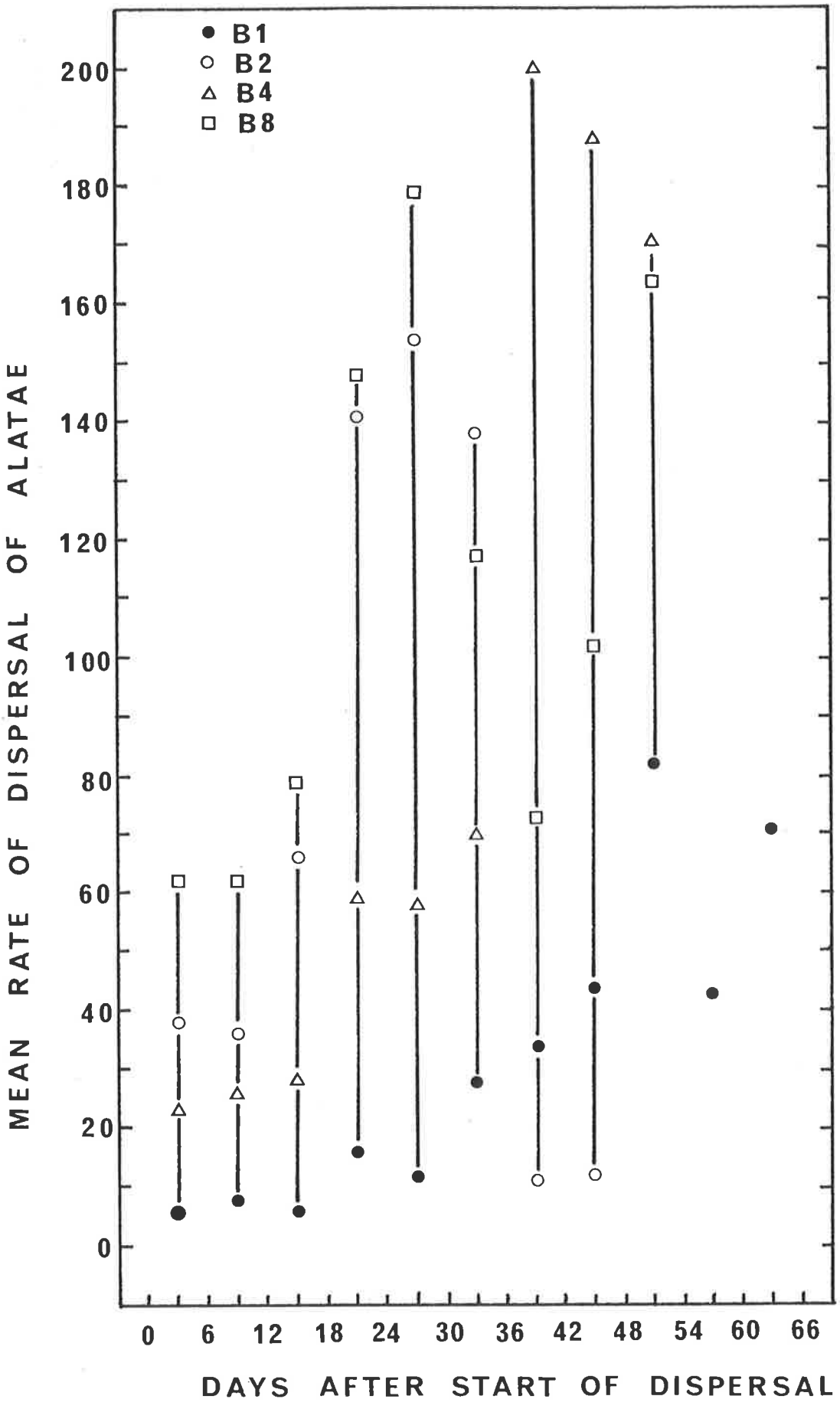

B1
B2
B4
B8
MEAN RATE OF DISPERSAL OF ALATAE
0
20
40
60
80
100
120
140
160
180
200
0
6
12
18
24
30
36
42
48
54
60
66
DAYS AFTER START OF DISPERSAL

Figure 2.34: *Mean cumulative numbers of alatae which dispersed from the experimental colonies on common burr medic (*Medicago polymorpha* var. *vulgaris*) in relation to dispersal period.

M1, M2, M4 and M8 represent colonies initiated with 1, 2, 4 and 8 alatae.

*Mean of 4 colonies. 1D, 2D, 3D and 4D indicate death of 1, 2, 3 and 4 host plants.

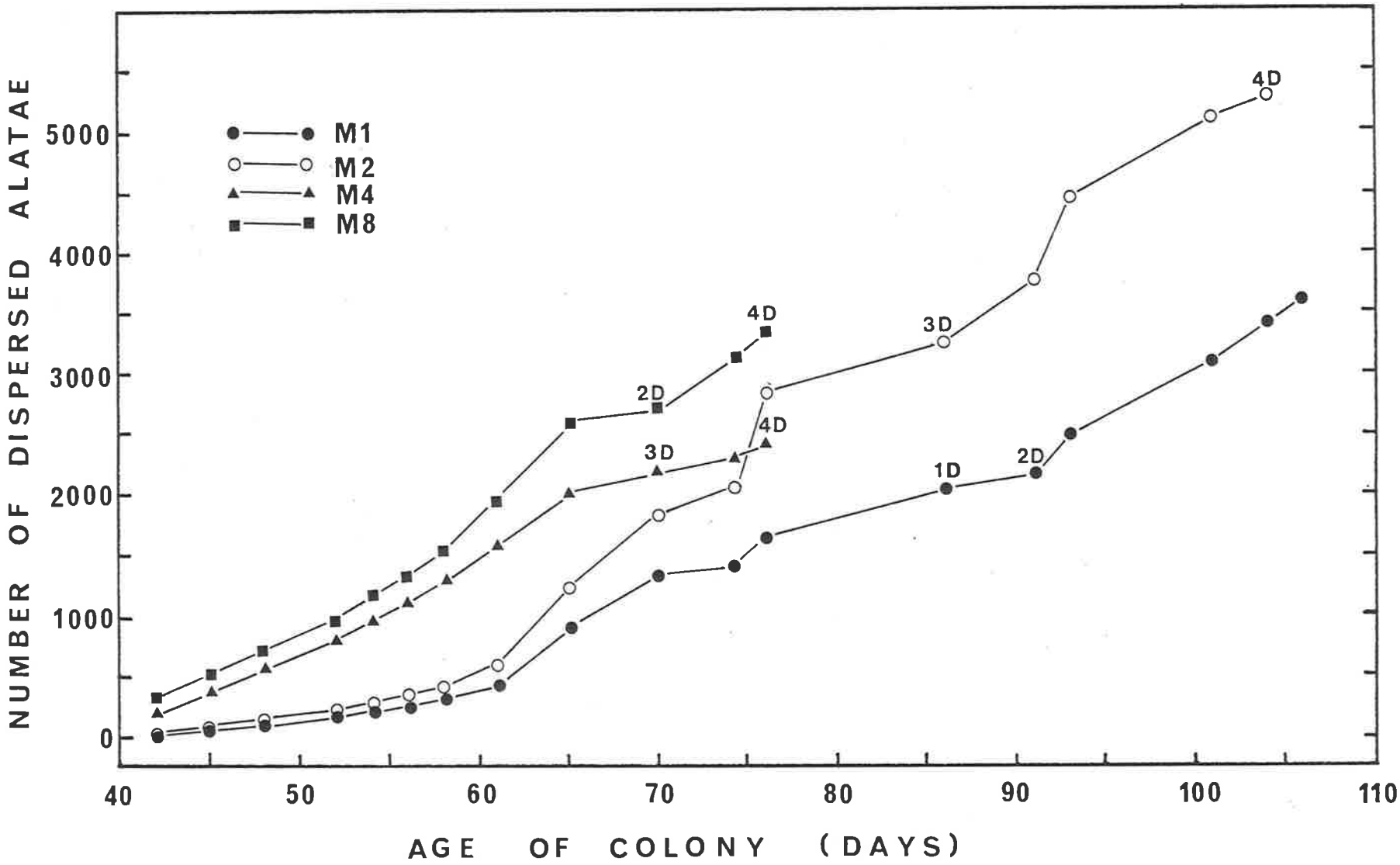

NUMBER OF DISPERSED ALATAE
5000
4000
3000
2000
1000
0
M1
M2
M4
M8
4D
3D
2D
4D
3D
4D
2D
1D
40
50
60
70
80
90
100
110
AGE OF COLONY (DAYS)

Figure 2.35: *Mean cumulative numbers of alatae which dispersed from the experimental colonies on subterranean clover (*Trifolium subterraneum*) in relation to dispersal period. SC1, SC2, SC4 and SC8 represent colonies initiated with 1, 2, 4 and 8 alatae.
*Mean of 4 colonies; mean of 2 colonies for SC8.
P = Parasitized aphids seen.
1D, 2D, 3D and 4D indicate death of 1, 2, 3 and 4 host plants.

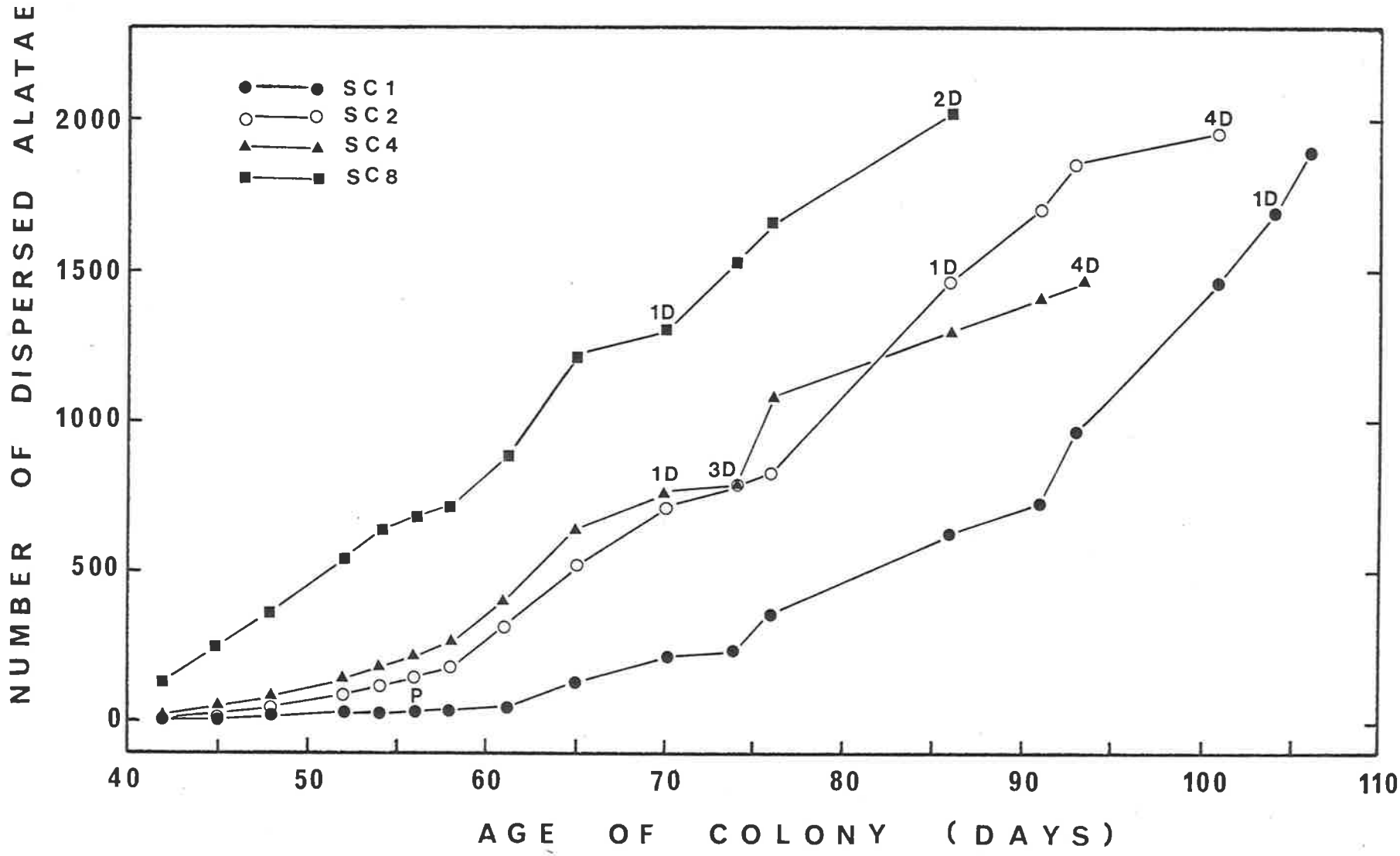
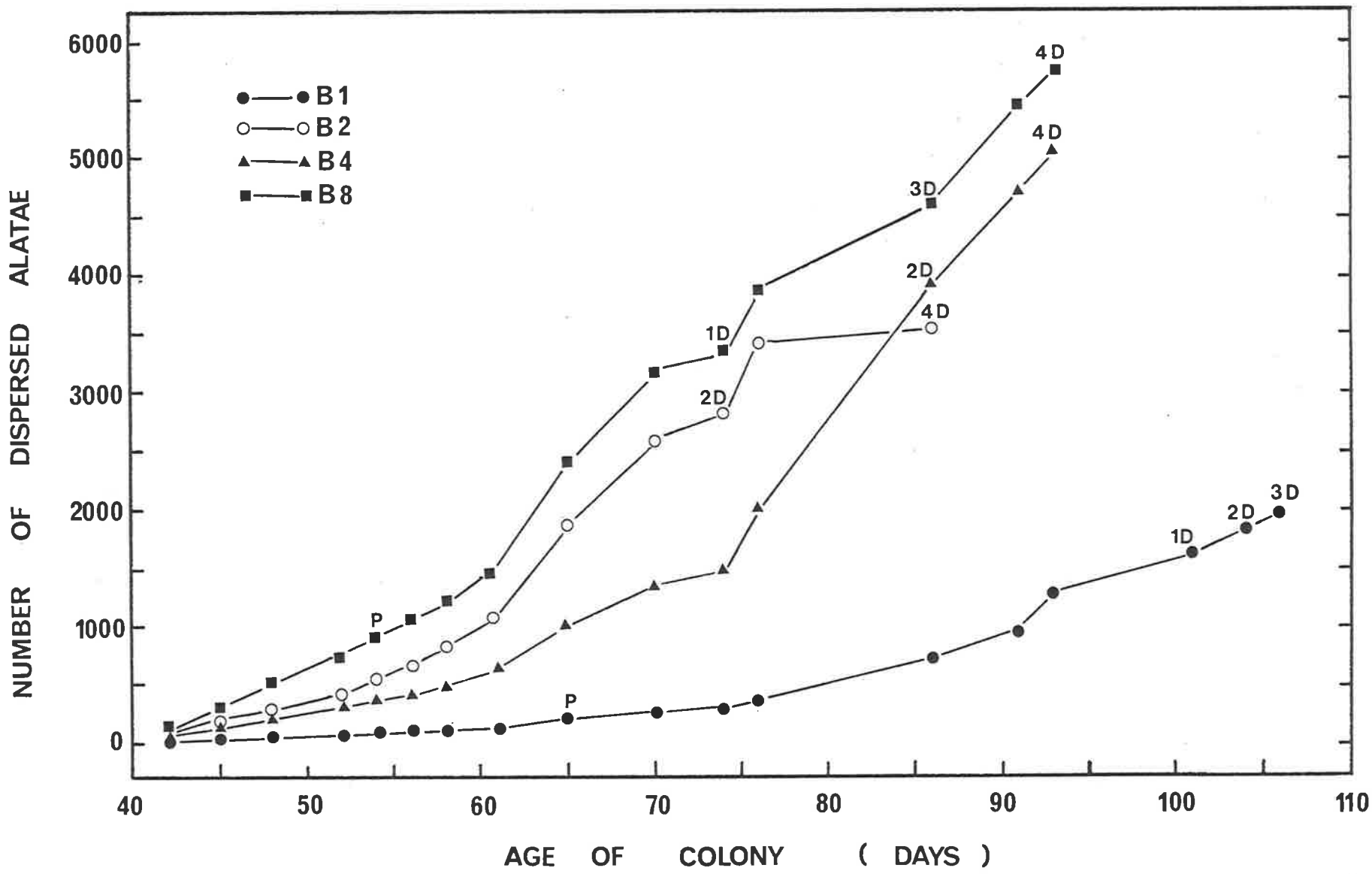

NUMBER OF DISPERSED ALATAE
2000
1500
1000
500
0
40
50
60
70
80
90
100
110
AGE OF COLONY (DAYS)
SC1
SC2
SC4
SC8
2D
4D
1D
1D
4D
1D
1D
3D
P

Figure 2.36: *Mean cumulative numbers of alatae which dispersed from the experimental colonies on broad beans (*Vicia faba* L.) in relation to dispersal period. B1, B2, B4 and B8 represent colonies initiated with 1, 2, 4 and 8 alatae.
*Mean of 4 colonies.
P = Parasitized aphids seen.
1D, 2D, 3D and 4D indicate death of 1, 2, 3 and 4 host plants.


B1
B2
B4
B8
NUMBER OF DISPERSED ALATAE
AGE OF COLONY (DAYS)
6000
5000
4000
3000
2000
1000
0
40
50
60
70
80
90
100
110
P
1D
2D
3D
4D

they also exclude the possibility of the existence of an intraspecific competition or stabilising mechanism solely due to population density, in the colonies of *A. craccivora*. These conclusions get support from the results of the following sections also, which describe the analysis of variance of the total numbers of alatae, apterae and adults which dispersed from the experimental colonies.

2.3.43-C: Analysis of variance of the total dispersed alatae

As mentioned in the 'Methods' (Section 2.3.2-G), each of the 16 small cages had 4 replicates of one colonization density on one host plant species. There were only two subterranean clover plants with 8 alatae each. The alatae which dispersed from the plants within a cage were counted and removed at frequent intervals, starting from 42 days until all the plants in a cage perished or the colonies were 106 days old. Not all the plants in a cage collapsed simultaneously. Of the 4 colonies initiated with one alata, two on common burr medic, three on subterranean clover and one on broad bean were still maintaining an output of alatae and apterae when the observations were stopped. Obviously, these colonies must have produced many alatae and apterae than their recorded numbers. However, as these plants were also collapsing, their additional output of aphids was probably small.

Since either four or two plants representing a colonization density on a host plant speices were placed in one cage, there was no way of ascertaining how many alatae actually dispersed from each of the plants within a cage. The number of alatae which dispersed from a plant could be calculated only by taking a mean of the total alatae which had dispersed in a cage. In other words, it was not possible to detect any variation between the number of alatae which had dispersed

from each plant as long as all the plants in a cage survived. The only variation in this respect was possible due to the death of the plants at different times. Those collapsed later, apparently produced many alatae (Figures 2.34, 2.35 and 2.36). The spatial arrangement of host plants, thus imposed a major constraint on the analysis of variance of the total alatae which dispersed from a colony, in that, an individual plant within a cage could not be regarded as an independent replicate for this purpose. Had the plants been placed singly in the cages, it would have been possible and appropriate to regard them as independent replicates. The only two subterranean clover plants with 8 alatae each, also constituted a minor constraint in this respect.

The analysis of variance could therefore be carried out upon, either the total number of alatae which dispersed from a cage or the mean cumulative number of alatae, calculated to have dispersed from a plant within a cage. The latter statistic was used for the analysis. The mean number of alatae which dispersed from a plant in each cage are presented in Appendices IX, X and XI respectively, for common burr medic, subterranean clover and broad beans.

One of the conditions necessary for the analysis of variance is the independence of the variance from the mean. The relationship between the mean and the variance in the highly aggregated distributions in insects has been shown to obey a power law (Taylor 1961, 1965a) and this relationship has been demonstrated for the counts of the cabbage aphid *Brevicoryne brassicae* also (Hayman and Lowe 1961). The total number of alatae which dispersed from the experimental colonies were transformed by using logarithms, to minimise the dependence of variance on the mean,

if any. The analysis of variance was carried out on the means of the transformed data (Table 2.35).

Two-way analysis of variance was carried out to answer the following questions: (1) were there any significant differences among the host plant species; and (2) were there any significant differences among the initial colonisation densities, in respect of the total alatae, which dispersed from the experimental colonies?

The analysis of variance (Table 2.34) indicated significant differences ($P = 0.05$) between host plant species. Calculation of the least significant difference (L.S.D.) for the differences between host plants (Table 2.35) shows that significantly more alatae were produced on broad bean and common burr medic than on subterranean clover. There was no significant difference between broad bean and common burr medic.

These results suggest that the aerial abundance of *A. craccivora* alatae in a region may be dependent upon the alata producing capacities of its host plants. These results do not provide any evidence for intraspecific competition in the experimental colonies of *A. craccivora* which were initiated with 2, 4 and 8 alatae. This means that *A. craccivora* has evolved to utilize the available transient food resources most efficiently to its advantage, as far as alata production and alata dispersal are concerned.

2.3.44: Dispersal by apterae

2.3.44-A: Analysis of variance of the total dispersed apterae

The total *A. craccivora* apterae which dispersed from the experimental colonies are presented in Table 2.36. These figures

Table 2.34. Analysis of variance (on transformed data) for comparison of the effects of host plant species and initial colonisation densities on the cumulative numbers of alatae of *Aphis craccivora*, produced by and dispersed from the experimental colonies - 1978.

Source of variation	DF	SS	MS	F	P
Host plant species	2	0.26801	0.13401	5.7051	0.05
Colonisation density	3	0.04583	0.01528	0.6505	N.S.
Error	6	0.14094	0.02349		
Total	11	0.45478			

Table 2.35. Mean cumulative numbers of alatae of *Aphis craccivora*, produced by and dispersed per plant, on three host plant species at four initial colonisation densities - 1978.

Host plant species		Initial colonisation density (alatae per plant) 1	2	4	8
Common burr medic	(a)	2851	3765	2256	3040
	(b)	3.440	3.565	3.353	3.480
Subterranean clover	(a)	1840	1833	952	1660
	(b)	3.264	3.260	2.961	3.215
Broad bean	(a)	1837	3187	4506	4569
	(b)	3.263	3.501	3.651	3.652

(a) = Untransformed data

(b) = Transformed data

L.S.D. (host plant species) at 5% = 0.265

	Broad bean	Common burr medic	Subterranean clover
Log. mean for host plant species	3.517	3.460	3.175

confirm the results of the first experiment (see Section 2.2.36) and both the experiments have established apterous dispersal as an integral component of dispersal behaviour in this aphid.

Two-way analysis of variance on the transformed data (Table 2.37) showed that neither the host plant species nor the initial colonization densities had any significant influence on the total apterae which dispersed from the experimental colonies. Apterous dispersal in the colonies of *A. craccivora*, therefore, can be regarded as an essential but random behaviour, and might be a facultative response of the apterae to the specific conditions within a colony on a host plant. The results of the following sections qualify these conclusions.

2.3.44-B: Apterous dispersal in relation to initial colonization density

Figures 2.37, 2.38 and 2.39 present the cumulative curves for the mean numbers of *A. craccivora* apterae which dispersed from each of the experimental colonies on common burr medic, subterranean clover and broad bean. It is apparent from these curves that the number of dispersed apterae from the colonies initiated by 2, 4 and 8 alatae, were higher than the apterae which dispersed from the colonies initiated with one alata. This means that the rate of dispersal of apterae of *A. craccivora* was positively influenced by the initial colonization density in the experimental colonies. The colonies on subterranean clover demonstrate a clearcut positive relationship in this respect. This influence might be because of the high numbers of apterae in the colonies initiated with many alatae. The positive effect of initial

Table 2.36. Mean cumulative numbers of apterae of *Aphis craccivora*, produced by and dispersed per plant, on three host plant species at four initial colonisation densities - 1978.

Host plant species		Initial colonisation density (alatae per plant) 1	2	4	8
Common burr medic	(a)	287	308	141	325
	(b)	2.396	2.442	2.131	2.485
Subterranean clover	(a)	180	272	195	363
	(b)	2.245	2.426	2.223	2.557
Broad bean	(a)	183	416	565	503
	(b)	2.263	2.613	2.752	2.689

(a) = Untransformed data

(b) = Transformed data

Table 2.37. Analysis of variance (on transformed data) for comparison of the effects of host plant species and initial colonisation densities on the cumulative numbers of apterae of *Aphis craccivora*, produced by and dispersed from the experimental colonies - 1978.

Source of variation	DF	SS	MS	F	P
Host plant species	2	0.12456	0.06228	2.3864	N.S.
Colonisation density	3	0.13762	0.04587	1.7576	N.S.
Error	6	0.15659	0.02610		
Total	11	0.41877			

Figure 2.37: *Mean cumulative numbers of apterae which dispersed from the experimental colonies on common burr medic (*Medicago polymorpha* var. *vulgaris* in relation to dispersal period.

M1, M2, M4 and M8 represent colonies initiated with 1, 2, 4 and 8 alatae.

*Mean of 4 colonies.

1D, 2D, 3D and 4D indicate death of 1, 2, 3 and 4 host plants.

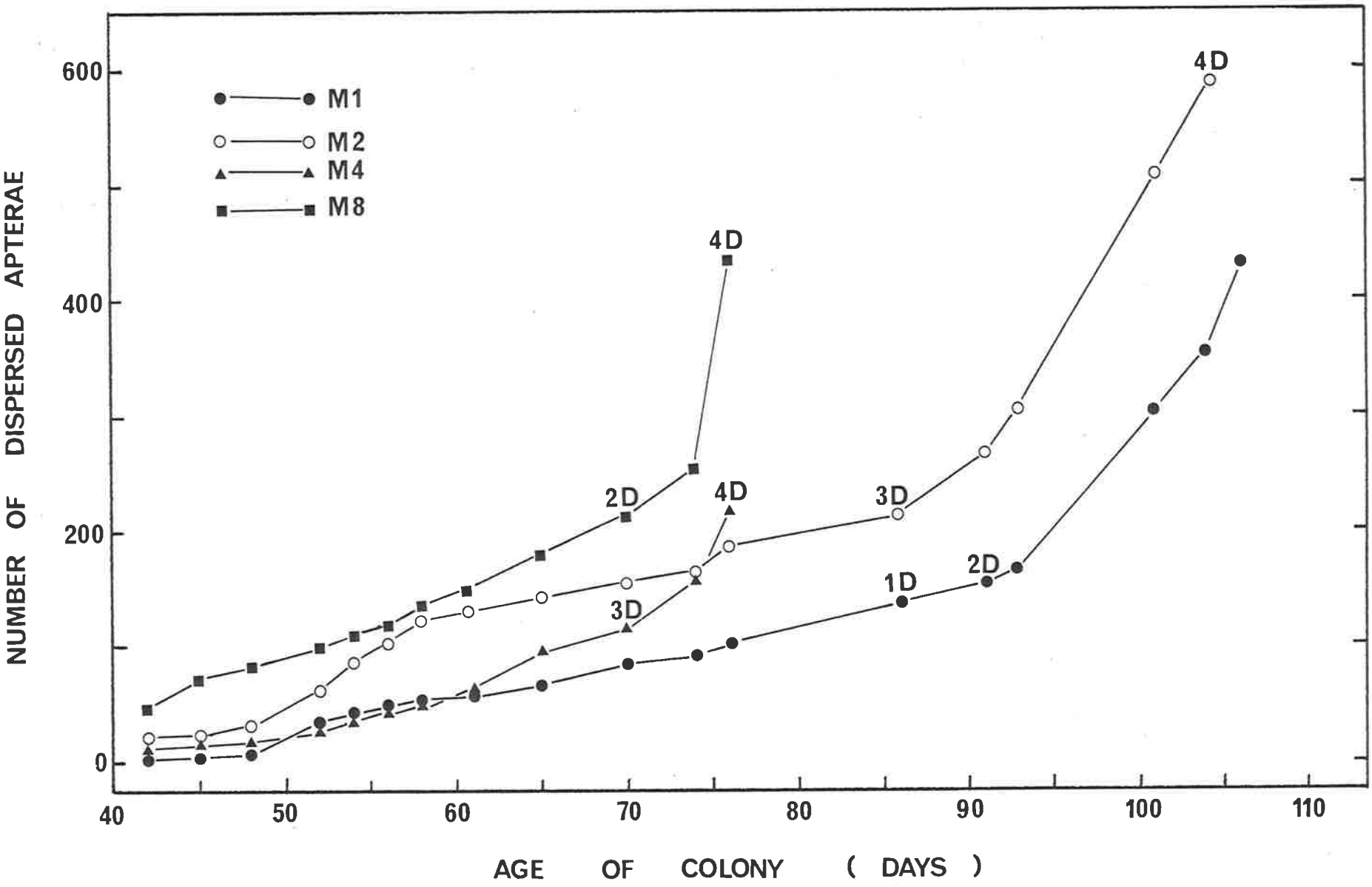

NUMBER OF DISPERSED APTERAE
600
400
200
0
40
50
60
70
80
90
100
110
AGE OF COLONY (DAYS)
M1
M2
M4
M8
4D
2D
4D
3D
4D
3D
1D
2D

Figure 2.38: *Mean cumulative numbers of apterae which dispersed from the experimental colonies on subterranean clover (*Trifolium subterraneum*) in relation to dispersal period.

SC1, SC2, SC4 and SC8 represent colonies initiated with 1, 2, 4 and 8 alatae.

*Mean of 4 colonies; mean of 2 colonies for SC8.

1D, 2D, 3D and 4D indicate death of 1, 2, 3 and 4 host plants.

P = Parasitized aphids seen.

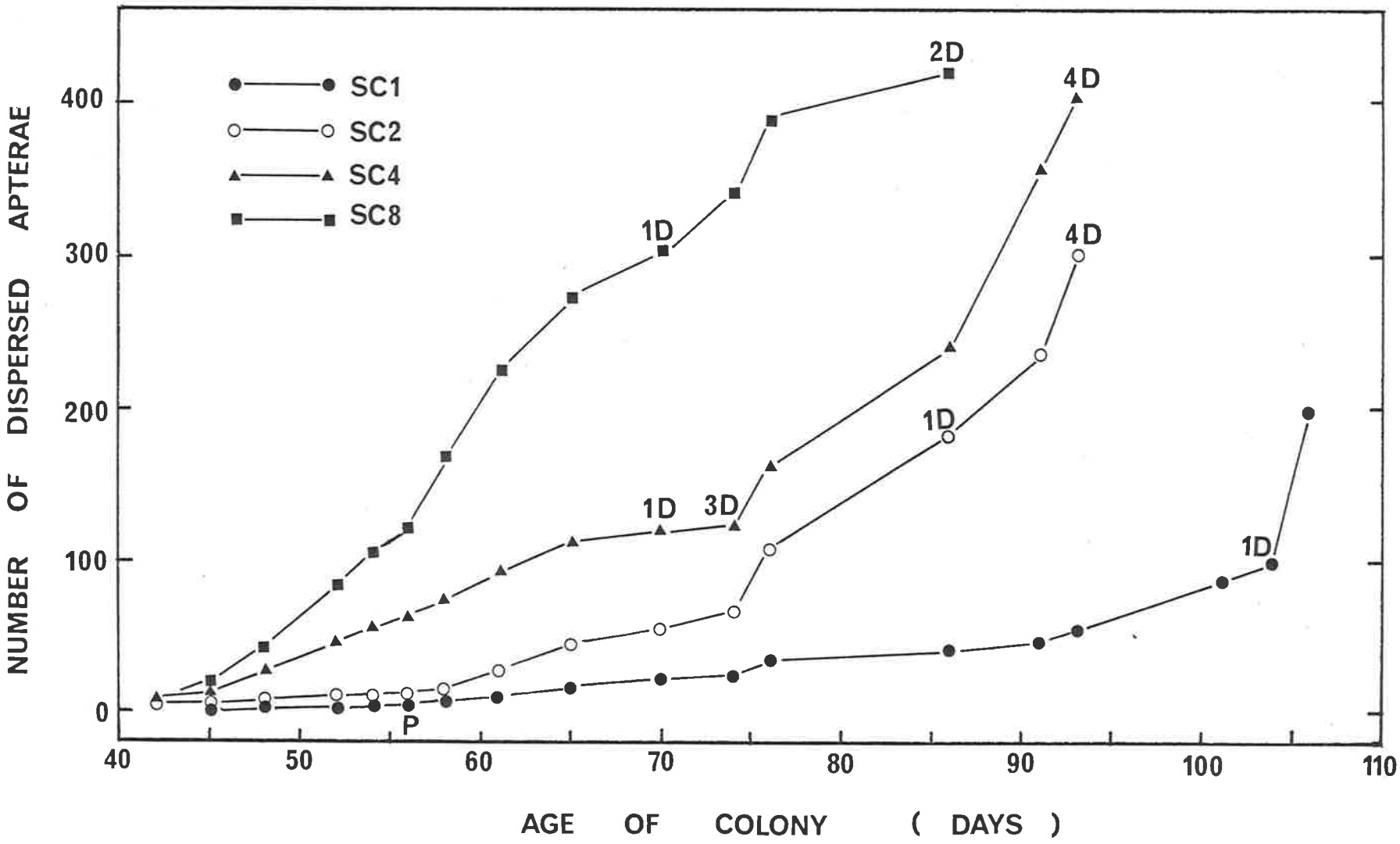
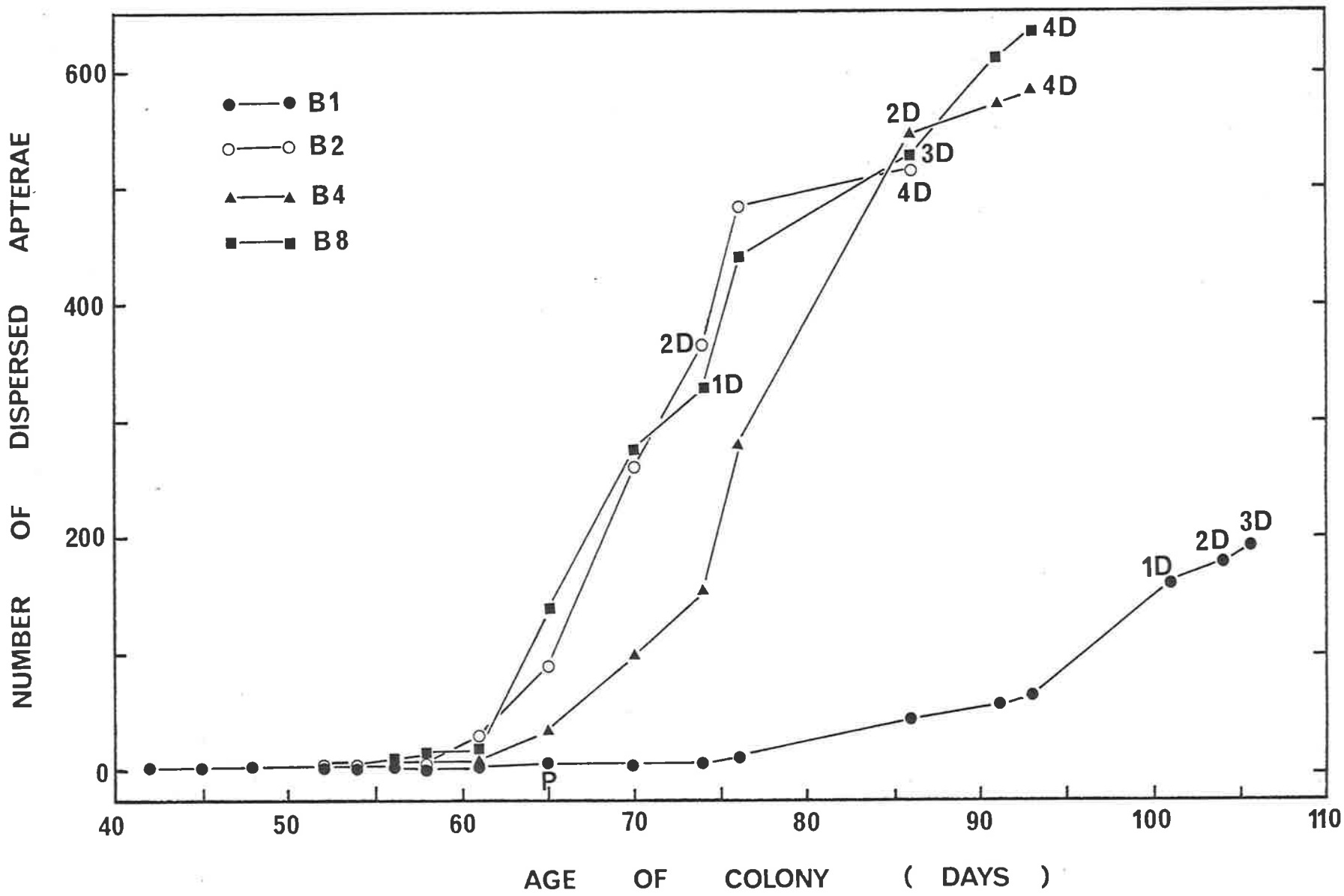

NUMBER OF DISPERSED APTERAE
AGE OF COLONY (DAYS)
SC1
SC2
SC4
SC8
2D
4D
1D
4D
1D
1D
3D
1D
P
0
100
200
300
400
40
50
60
70
80
90
100
110

Figure 2.39: *Mean cumulative numbers of apterae which dispersed from the experimental colonies on broad beans (*Vicia faba* L.) in relation to dispersal period.
B1, B2, B4 and B8 represent colonies initiated with 1, 2, 4 and 8 alatae.
*Mean of 4 colonies.
1D, 2D, 3D and 4D inidicate death of 1, 2, 3 and 4 host plants.
P = Parasitized aphids seen.


NUMBER OF DISPERSED APTERAE
600
400
200
0
B1
B2
B4
B8
4D
4D
2D
3D
4D
2D
1D
1D
2D
3D
P
40
50
60
70
80
90
100
110
AGE OF COLONY (DAYS)

colonization density on the rate of apterous dispersal, however, does not explain satisfactorily the facultative nature of apterous dispersal.

2.3.44-C: Apterous dispersal in relation to host plant species

A meaningful understanding of the facultative nature of apterous dispersal can be gained by a comparison of the cumulative curves of dispersed apterae among the three host plant species (Figures 2.37, 2.38 and 2.39). The most striking feature in such a comparison is the time of start and the pattern of apterous dispersal. Between 60 and 150 apterae dispersed until 61 days from the colonies initiated with 2, 4 and 8 alatae on common burr medic, and between 25 and 220 apterae dispersed from the colonies on subterranean clover. However, the number of apterae which dispersed from the colonies on broad beans until 61 days ranged between 5 and 30 only; thereafter, the rate of dispersal increased considerably. The delayed apterous dispersal in the colonies initiated with 2, 4 and 8 alatae on broad beans cannot be due to less number of apterae in these colonies. There is no reason to presume that the aphid populations in the colonies on broad beans were any lower than the corresponding populations in the colonies on common burr medic and subterranean clover. The results of the following section (Section 2.3.45) do not support any such assumption.

As the broad bean plants provided a larger surface area for the apterae to settle and larviposit than the same aged common burr medic and subterranean clover plants, it is likely that this feature of broad beans probably delayed the apterous dispersal. It appears from the cumulative curves (Figures 2.37, 2.38 and 2.39) that a large number of

the second generation apterae started to disperse from common burr medic and subterranean clover, whereas a majority of the third generation apterae started dispersal from broad beans. This means that conditions in the colonies on broad beans did not trigger apterous dispersal until the third generation apterae began to mature. The delayed apterous dispersal on broad bean compared with the early dispersal on common burr medic and subterranean clover, thus explains satisfactorily the facultative nature of apterous dispersal in the colonies of *A. craccivora* with reference to the size and surface area of the host plant species.

2.3.45: Analysis of variance of the total dispersed adult aphids

The mean cumulative number of adults (apterae + alatae) of *A. craccivora*, which dispersed from the experimental colonies are presented in Table 2.39. Two-way analysis of variance on the transformed data (Table 2.38) indicated that host plant species differed significantly ($P = 0.05$) in their capacities to produce *A. craccivora* adults, whereas the initial colonisation densities had no significant effects in this respect. Comparison between the host plant species by the method of the least significant difference (Table 2.39) indicated that significantly many adults were produced on broad bean than on subterranean clover. However, there were no significant differences between broad bean and common burr medic as well as between common burr medic and subterranean clover in this respect.

These results provide solid evidence in support of the original hypothesis of this research project that the abundance of

Table 2.38. Analysis of variance (on transformed data) for comparison of the effects of host plant species and initial colonisation densities on the cumulative numbers of adults (apterae + alatae) of *Aphis craccivora*, produced by and dispersed from the experimental colonies - 1978.

Source of variation	DF	SS	MS	F	P
Host plant species	2	0.23251	0.11625	5.2324	0.05
Colonisation density	3	0.05206	0.01735	0.7809	N.S.
Error	6	0.13330	0.02222		
Total	11	0.41787			

Table 2.39. Mean cumulative numbers of adults of *Aphis craccivora*, produced by and dispersed per plant, on three host plant species at four initial colonisation densities - 1978.

Host plant species		Initial colonisation density (alatae per plant) 1	2	4	8
Common burr medic	(a)	3138	4073	2397	3365
	(b)	3.479	3.598	3.379	3.523
Subterranean clover	(a)	2020	2105	1147	2023
	(b)	3.305	3.319	3.036	3.301
Broad bean	(a)	2020	3603	5071	5072
	(b)	3.304	3.553	3.702	3.697

(a) = Untransformed data

(b) = Transformed data

L.S.D. (host plant species) at 5% = 0.258

	Broad bean	Common burr medic	Subterranean clover
Log. mean for host plant species	3.564	3.495	3.240

anholocyclic *A. craccivora* in a region can be explained by the upper size of its colonies, prior to dispersal by the alatae and apterae, which in turn is determined by the carrying capacities of its host plant species. As mentioned earlier (Section 2.3.43-B), there is no evidence whatsoever in favour of the existence of any intraspecific competition or stabilising mechanism due to high population densities in the experimental colonies, as there were no significant differences in the total numbers of adults, which matured and dispersed from the colonies initiated with 1, 2, 4 and 8 alatae on the three host plant species (Table 2.38). Significant differences in this respect did exist between the host plant species (Table 2.38) and this evidence defines the concept of limited or finite carrying capacity of a host plant species in the context of the number of adult aphids which can be supported and produced on it. The early death of plants (in the experimental colonies with 4 and 8 alatae) suggests the transient nature of these host plant species for *A. craccivora*.

2.3.46: Ratios of total dispersed alatae to apterae

A ratio of total alatae to total apterae is a crude indicator of the proportion of alatae produced in an aphid colony with reference to the numbers of apterae. The ratios were calculated from the total number of alatae (Table 2.35) and apterae (Table 2.36) which dispersed from the experimental colonies. Table 2.4 shows that host plant species differed in this respect. The colonies on common burr medic produced a higher proportion of alatae than the colonies on broad beans and subterranean clover.

Table 2.40. Ratios of mean cumulative alatae/mean cumulative apterae of *Aphis craccivora*, produced by and dispersed per plant in the experimental colonies - 1978.

Host plant species	Initial colonisation density (alatae/plant)			
	1	2	4	8
Common burr medic	9.93	12.22	16.00	9.35
Subterranean clover	10.22 P	6.74	4.88	4.57
Broad bean	10.04 P	7.66	7.98	9.08 P

P = Parasitized colonies.

It is interesting to note from Table 2.4 that parasitization apparently increased the proportion of alatae which dispersed from the attacked colonies on both broad beans and subterranean clover. This is contrary to what might be expected of parasitization - a drastic reduction in the proportion of the alatae which can disperse from a colony (Gutierrez *et al*. 1974a). It is likely that the parasitization had a relatively adverse effect on the numbers of dispersing apterae than the dispersing alatae. In this way the reduced numbers of apterae which dispersed from the parasitized colonies might apparently inflate the proportion of dispersed alatae.

These results, nevertheless, suggest that female parasites may discriminate between apterous and alatiform morphs in the colonies of *A. craccivora* and appear to prefer apterous adults and advanced apteriform numphs for oviposition. Similar observations were also made during Experiment I (see Section 2.2.37).

2.3.47: Proportions of dispersed apterae

The proportions of apterae among the adult aphids which dispersed from the experimental colonies are presented in Table 2.41. It appears from Table 2.41 that higher proportions of apterae dispersed from the colonies on subterranean clover than from the colonies on common burr medic and broad beans. The analysis of variance, however, does not indicate significant differences in this respect (Table 2.42). It is also evident from the results (Table 2.41) that the proportions of dispersed apterae from the parasitized colonies were not any different from those which dispersed from the parasite-free colonies. What do

Table 2.41: Percentages of *A. craccivora* apterae which dispersed from the experimental colonies - 1978.

Host plant species		Initial colonization density (alatae per plant) 1	2	4	8
Common burr medic	(a)	9.15	7.57	5.88	9.66
	(b)	3.025	2.751	2.425	3.108
Subterranean clover	(a)	8.91 P	12.92	17.00	17.94
	(b)	2.985	3.594	4.123	4.235
Broad bean	(a)	9.06 P	11.55	11.14	9.92 P
	(b)	3.010	3.399	3.338	3.150

(a) Untransformed percentages.

(b) Square root transformations.

P = Parasitized colonies.

Table 2.42: Analysis of variance (on transformed data) for comparison of the effects of host plant species and initial colonization densities on the percentages of *A. craccivora* apterae which dispersed from the experimental colonies - 1978.

Source of Variation	DF	SS	MS	F	P
Host plant species	2	1.65476	0.82738	4.9754	N.S.
Colonization densities	3	0.36659	0.12220	0.7348	N.S.
Error	6	0.99777	0.16629		
Total	11	3.01912			

these results indicate is that assessments of alata producing capacities of *A. craccivora* colonies, based on ratios of dispersed alatae to apterae, can be misleading (Section 2.3.46).

2.3.48: Relationship between temperature and population growth

Day-degrees above the threshold temperature (8.3°C) were accumulated from the maximum and minimum temperatures, recorded inside the field cages (see Appendix XX), by using a computer program (Frazer and Gilbert 1976). This program draws a sine curve from minimum to maximum temperatures and integrates the areas of the curve above the threshold temperature.

It is evident from Appendix XX that 72 day-degrees were needed for completion of one generation (apterae) and 83 to 92 day-degrees were needed for maturation of the first alatae in the experimental colonies. These results (in the field cages) correspond well with the results on the rate of development of this aphid at constant temperatures (Gutierrez *et al.* 1971, 1974a).

Alata dispersal in the cages was observed at 163 day-degrees after the inception of the colonies and the plants in the big cages were harvested at 192 day-degrees for population counts (Appendix XX).

2.3.49: Populations of the colonies sampled at 46 days

As mentioned earlier (see Section 2.3.2-G), there were 8 replicates of each colonization density on the four host plant species, in the big cages, to determine the size of colonies soon after the start of dispersal. The colonies were observed 4 days after their inception

and considerable mortality among the colonizing alatae was recorded. Further, the colonies in three cages were attacked by the parasites and the aphid populations did not develop on lucerne. The remaining colonies were sampled at 46 days; their total populations and the numbers of apterae were counted later. These data are presented in Appendix XXI. It was not possible to apply the analysis of variance to the population data of the sampled colonies because of the missing treatments as well as unequal numbers of replications due to mortalities of the colonizing alatae (within 4 days) and the parasitization. However, a meaningful understanding of the data could be made by regression analysis. The following sections describe relationships between the initial numbers of alatae and the total populations on one hand and between the numbers of apterae and the total populations of the sampled colonies on the other, on subterranean clover, common burr medic and broad beans.

2.3.49-A: Relationships between initial numbers of colonizing alatae and total populations

Figure 2.40 shows relationships between initial numbers of colonizing alatae and log. total populations of the sampled colonies. The populations of the colonies on common burr medic and broad beans were not significantly related to the initial numbers of colonizing alatae. The populations of the colonies on subterranean clover were, however, significantly related ($R = 0.8015$, $P = 0.001$) to the initial numbers of colonizing alatae.

2.3.49-B: Relationships between numbers of apterae and total populations

Figure 2.41 shows significant relationships between log. numbers of apterae and log. total populations of the sampled colonies on subterranean clover ($P = 0.001$), common burr medic ($P = 0.05$) and broad

Figure 2.40: Relationships between initial colonization densities (alatae per plant) and log. total populations of the experimental colonies (sampled at 46 days) on common burr medic, subterranean clover and broad beans.

M = common burr medic
(Y = 3.1218+0.0112X; R=0.1069; P=N.S.)

SC = subterranean clover
(Y = 2.2934+0.1616X; R=0.8015; P=0.001)

B = broad bean
(Y = 3.1531+0.033X; R=0.23; P=N.S.)

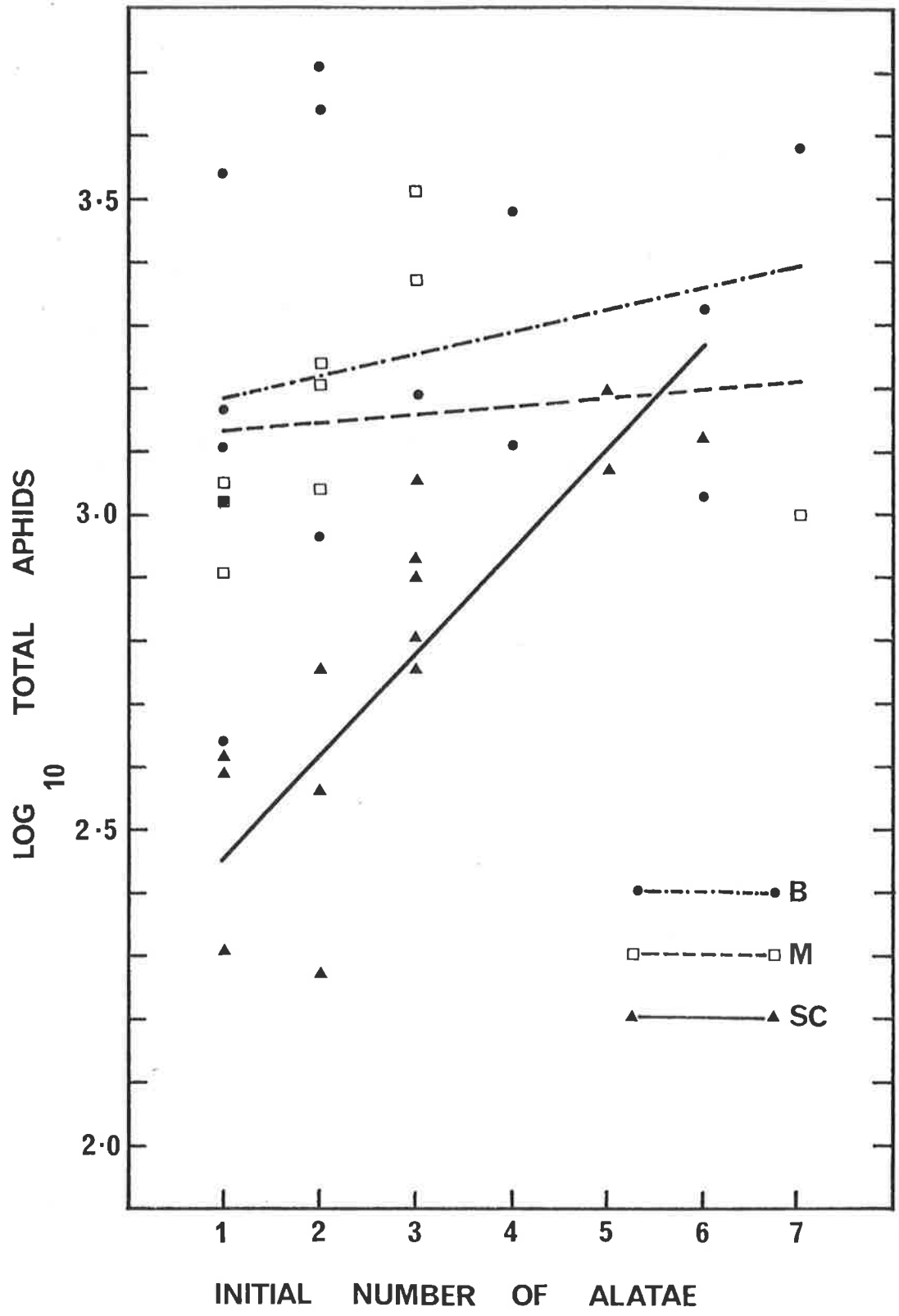
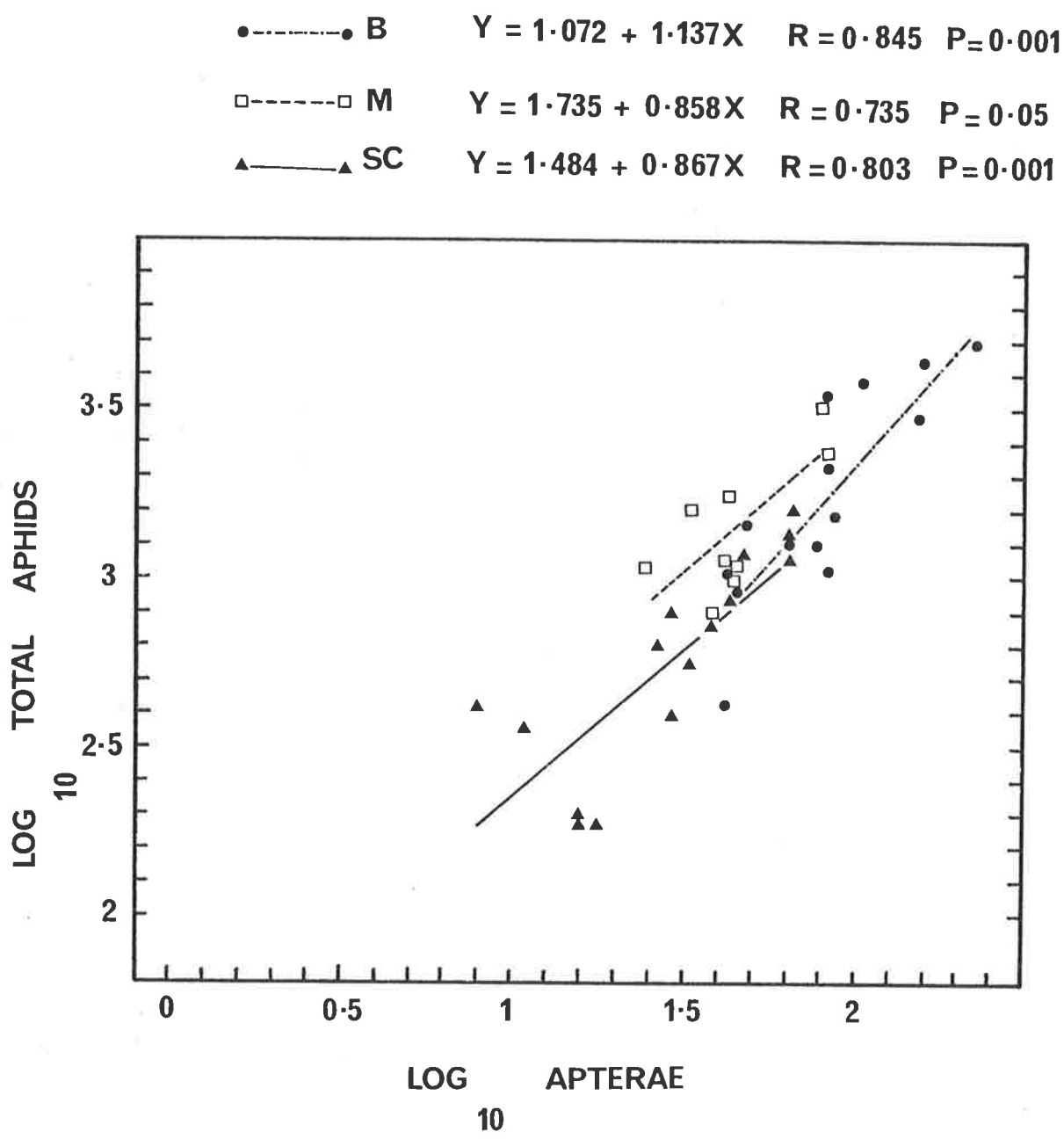

LOG 10 TOTAL APHIDS
3·5
3·0
2·5
2·0
1
2
3
4
5
6
7
INITIAL NUMBER OF ALATAE
B
M
SC

Figure 2.41: Log. total populations of the experimental colonies as function of log. apterae (sampled at 46 days) on common burr medic, subterranean clover and broad beans.

M = common burr medic.

SC = subterranean clover.

B = broad bean.


B Y = 1·072 + 1·137X R = 0·845 P = 0·001
M Y = 1·735 + 0·858X R = 0·735 P = 0·05
SC Y = 1·484 + 0·867X R = 0·803 P = 0·001
LOG 10 TOTAL APHIDS
3·5
3
2·5
2
0
0·5
1
1·5
2
LOG 10 APTERAE

beans (P = 0.001). Analysis of variance (Table 2.43) shows significant differences among the slopes of these relationships. The slopes for subterranean clover and common burr medic differed significantly (P = 0.05 and 0.005) from the slope for broad beans. However, differences between the slopes for subterranean clover and common burr medic were not significant.

It is important to mention here that the dispersing alatae and apterae became smaller in the experimental colonies as the host plants deteriorated. The reduced size was approximately one-third to one-fourth of the size of adults which dispersed at 40-42 days. No measurements on the size of the dispersed aphids were made.

Nymphal dispersal was negligible from the experimental colonies except when the host plants wilted.

2.3.5: Discussion

The results of Experiment II are important in two respects. Firstly, these results confirm the results of Experiment I. For example, the relationship between the numbers of apterae and total populations, the facultative nature of apterous dispersal and the production of alatae on broad bean plants are confirmed by both the experiments. Secondly, and more importantly, the results of Experiment II provide direct evidence in support of the hypothesis of this research project in two ways. Significant differences in the total numbers of alatae which dispersed from different host plant species (Tables 2.34 and 2.35) and significant differences among the relationships between the numbers of apterae and total populations of the sampled colonies (Figure 2.41 and Table 2.43)

Table 2.43: Analysis of variance for comparison of regression coefficients for relationships between the numbers of apterae and total populations of the sampled colonies on three host plant species.

Source	DF	Deviations from regression SS	MS	F	P
Within	32	2.32248	0.07258		
Pooled	34	3.29736			
Difference	2	0.97488	0.48874	6.7341 (df = 2,32)	0.005
Comparison of slopes for subterranean clover and broad bean					
Within	25	2.1546	0.08618		
Pooled	26	2.71504			
Difference	1	0.56044	0.56044	6.5028 (df = 1,25)	0.05
Comparison of slopes for common burr medic and broad bean					
Within	19	0.72139	0.03796		
Pooled	20	1.47187			
Difference	1	0.75048	0.75048	19.7661 (df = 1,19)	0.005
Comparison of slopes for common burr medic and subterranean clover					
Within	20	1.76897	0.08845		
Pooled	21	1.79715			
Difference	1	0.02818	0.02818	0.3186 (df = 1,20)	N.S.

indicate the importance of host plant species on the abundance of *A. craccivora* populations and the extent of dispersal by alatae from its colonies. Dispersal by alatae and apterae was observed in the colonies (in small cages) at 39-42 days (Table 2.33 and Figures 2.34 to 2.39) and the colonies (in big cages) were sampled at 46 days for population counts. It is, therefore, likely that a few alatae and apterae may have dispersed from the sampled colonies on common burr medic and subterranean clover before sampling. However, no apterae dispersed from the colonies on broad beans in small cages until 59-60 days (Figure 2.39) and a small number of alatae (< 250) dispersed until 46 days. Since the total populations of the sampled colonies were dependent upon the number of apterae (Figure 2.41), the latter can be regarded as a valid measure of upper size of colonies on each of the three host plant species. It is evident from Appendix XXI that the numbers of apterae in the sampled colonies varied from 8 to 65 on subterranean clover, 24 to 81 on common burr medic and 44 to 236 on broad beans. The higher numbers of apterae in the colonies on broad beans together with the absence of apterous dispersal in the colonies in small cages until 60 days (Figure 2.39), suggest delayed apterous dispersal and apterous settling and larviposition and the consequent upper sizes of colonies on broad beans.

Further, the significant and higher regression coefficient ($Y = 1.072 + 1.1369X$) between log. apterae and log. total populations on broad bean plants is also biologically meaningful in that it suggests a higher rate of increase in total populations of the colonies with the increasing numbers of apterae. What this means is, the realised fecundities of *A. craccivora* apterae are higher on broad beans than on either common burr medic or subterranean clover plants. The significant relationship ($R = 0.8015$, $P = 0.001$) between initial numbers of colonizing alatae and total populations of the sampled colonies on subterranean clover

(Figure 2.40) is probably due to slow population growth of colonies on that host plant.

Gutierrez *et al.* (1974a) used the ratios of total alatae to total apterae as criteria for optimum alata production in *A. craccivora* colonies. The maximum ratios, as simulated by their model, varied from 3.59 to 3.64 on common burr medic and subterranean clover. The ratios of total alatae to total apterae, as calculated from the present results (Table 2.40), are far higher than the outputs of the simulation model. These differences between the empirical and simulated ratios suggest that the inputs of the model need improvement. Further, it is also noteworthy that this statistic (ratio of total alatae/total apterae) can be a misleading criterion (see Section 2.3.47).

2.3.6: Summary

The results of Experiment II can be summarised as follows.

Colonizing *A. craccivora* alatae walked off 5 week old lucerne plants and the experimental colonies failed to develop on this host. Alatiform progeny among the first generation aphids was recorded in the experimental colonies except those initiated by 1 and 2 alatae on subterranean clover and lucerne.

The rates of dispersal of alatae were positively related to the initial numbers of colonizing alatae. The outputs of alatae differed significantly ($P = 0.05$) on different host plant species and were unaffected by initial numbers of colonizing alatae. More alatae dispersed from broad beans than from common burr medic and subterranean clover. Host

plants with 4 and 8 initial colonizing alatae collapsed earlier than those with 1 and 2 alatae. The rates of dispersal of apterae on common burr medic and subterranean clover plants were related to the initial numbers of colonizing alatae. Delayed apterous dispersal was characteristic of the colonies on broad beans. Neither the initial numbers of colonizing alatae nor the host plant species had any significant effect on the outputs of apterae. Apparently higher proportions of apterae among the dispersed adults were recorded in the colonies on subterranean clover but these differences were not significant. The ratio of total dispersed alatae to total dispersed apterae can be a misleading statistic.

Population counts of the colonies sampled at 46 days after the start of experiment revealed a significant relationship between initial numbers of alatae and total populations on subterranean clover. No such relationships were recorded among the colonies on common burr medic and broad beans. The relationships between numbers of apterae and total populations of the sampled colonies were significantly different on common burr medic, subterranean clover and broad beans. These relationships indicated a higher number of apterae and higher rates of their realised fecundities on broad bean plants.

SECTION 3

FLIGHT BEHAVIOUR

3.1: Introduction

Flight is a vital aspect of dispersal behaviour in insects. A lot of interesting and novel research has been done on aphid flight behaviour and aphid migration (Broadbent 1949; Berry 1969; Berry and Taylor 1968; Burns 1972; Cockbain 1961a, 1961b; Cockbain *et al.* 1963; Dixon 1969, 1971; Dry and Taylor 1970; Haine 1955; Halgren and Taylor 1968; Johnson 1954; Johnson *et al.* 1957; Johnson 1958; Johnson 1960, 1963, 1969; Kennedy 1961; Kennedy and Booth 1963, 1964; Lewis and Taylor 1965; Shaw 1970, 1970a; Taylor, 1957, 1958, 1963, 1965; Woodford 1969). This necessarily incomplete bibliography indicates the degree of interest in aphid flight and dispersal over the past three decades and this interest is essentially due to the importance of aphids as vectors of viral pathogens in cultivated crops (Swenson 1968).

As this project was concerned with a detailed understanding of migration and dispersive behaviour of *Aphis craccivora*, some fundamental aspects of its flight behaviour were worth investigating, as this information is lacking in the literature. The main objective underlying the observations and experiments described in this section, was to determine whether the flight behaviour of *A. craccivora* conformed to the oogenesis-flight syndrome hypothesis (Johnson 1960; Kennedy 1961, 1975), characteristic of evolved adaptation in so many migrant insect species (Dingle 1972). Colonies of *A. craccivora* on broad beans, produced a high proportion (> 85%) of alatae at low population densities and maintained this proportion until the aphids

declined (see Section 2.2.34-C). Although the production of high proportion of alatae, which is an adaptation of the species to a set of environmental factors, determines its emigration potential, the flight behaviour of alatae, is also equally important for the realisation of this potential. For example, if all the alatae are pre-reproductive and compulsive fliers, then the actual emigration would be approximately equal to the emigration potential of a colony. On the other hand, if 50% of the alatae do not fly in pre-reproductive stage but reproduce in a colony instead, then the actual emigration would be half of the emigration potential and the flight behaviour of the alatae can be regarded as post-reproductive and facultative.

This post-reproductive and facultative flight behaviour had to be distinguished and separated from the apparent facultative flight behaviour of the alatae in the field. Low temperatures and low light intensities (Taylor 1963, 1965; Halgren and Taylor 1968), damaged wings and parasitization (Johnson 1959) may inhibit aphid take-off and flight in the field.

The experiments described in this section were, therefore, designed to increase the knowledge of the flight behaviour of *A. craccivora*. These comprised temperature relations of take-off in the laboratory; assessment of the strength of the migratory urge among alatae in the laboratory; observations on teneral period and take-off behaviour in the laboratory; observations on take-off behaviour in the field; a description of free flight capability of the alatae in a flight chamber; observations on the occurrence of wing muscle autolysis in the laboratory; and observations on the reproductive and flight capabilities of the alatae collected from a parasitized infestation.

The results of these experiments not only exemplify *A. craccivora* as a migrant insect, but more importantly, reveal also that the extent of migration and dispersal of this aphid in a region, is primarily dependent on the prevailing environmental factors.

3.2: Temperature relations of take-off in laboratory

Low temperature and low light intensity inhibit aphid take-off in nature (Johnson and Taylor 1957; Taylor 1963). The following experiment was designed to observe take-off by *A. craccivora* alatae in laboratory over the range of temperatures prevalent in Adelaide.

3.2.1 Methods

The alatae were reared in the laboratory by the method described by Shaw (1970) for rearing *Aphis fabae* alatae. The aphids were maintained on 2-4 week old potted broad bean seedlings in an insectary room with natural daylight where temperature fluctuated between 14 and 25°C. Approximately 100 newly moulted apterae were collected in a plastic tube (4 x 1.5 cm diameter) and left for 3 hours to induce stimuli for the production of alatiform progeny (Johnson 1965). Two one-week old potted broad bean seedlings were cut off just above their lowest modified stipule and the growth primordia were carefully removed with fine forceps. Approximately 50 crowded apterae were transferred to each of the cut seedling's stipules and the seedlings were then covered by transparent perspex cages (3.5 x 3.5 cm) with a fine mesh at one end. The seedlings with apterae were kept in an insectary room where temperature ranged between 15 and 25°C and a 12 hour photoperiod was provided by a bank of 8 daylight fluorescent tubes. The light intensity on the plant level varied between 665 and 690 lux. The cages and apterae were removed after 24 hours, leaving the nymphs. The seedlings were then covered by perspex

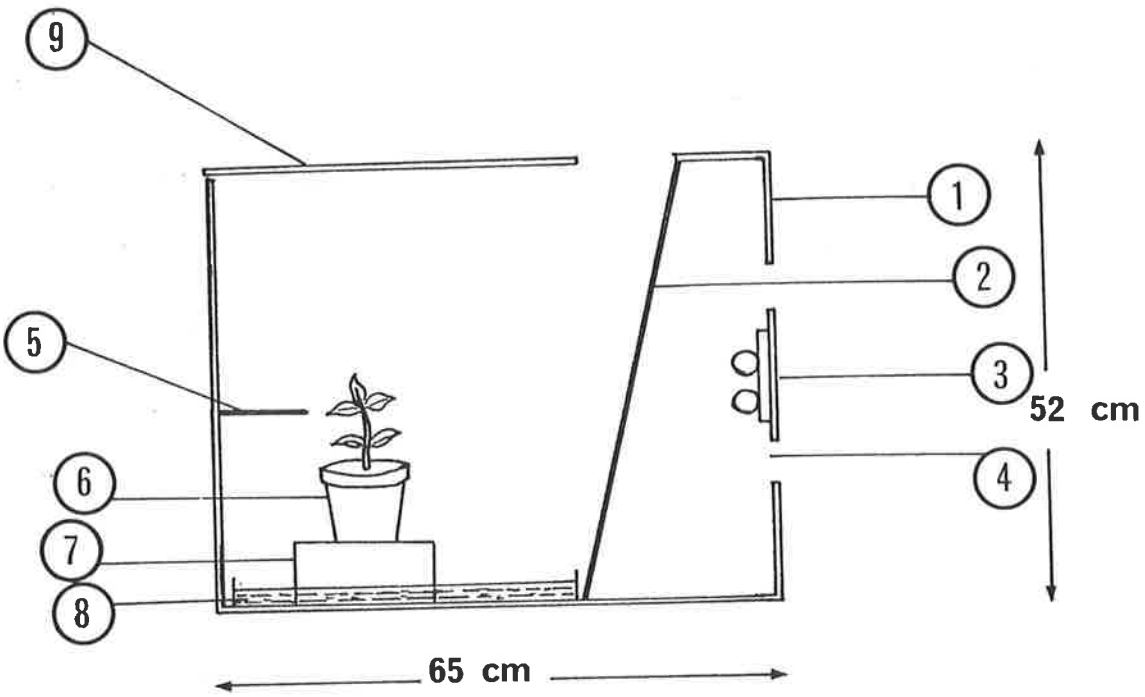
cages (20 x 8.5 cm). They were watered whenever necessary. Most of these nymphs became alatae in 6-7 days. 40-50 teneral alatae were transferred to each of 6 one-week old potted broad bean seedlings. The seedlings with the alatae were kept in the dark at 25-27^{o}C for 15-22 hours to make the alatae flight mature.

Take-off was tested in a masonite flight testing box (63 x 65 x 52 cm) (Figure 3.1). Two 40 watt fluorescent lamps were fixed to one wall inside the box. Aeration was provided by open spaces in the wall above and below the lamps. A rectangular glass sheet was set in a slanting position in front of the lamps inside the box. The portion between the lamps and the slanting glass was painted white. The rest of the interior of the box was painted black. Trays containing water with detergent were kept close to the base of the glass wall inside the box. The potted seedlings with the alatae were to be kept on a raised platform in the water moat 25 cm away from the glass wall. A thermistor probe was placed near the seedlings to record the temperature in the vicinity of the alatae. The top of the box above the seedlings was closed, leaving a 15 cm wide opening from the top edge of the glass wall.

The seedlings with the alatae were transferred from 25-27^{o}C to the testing box in early morning. The temperature inside the box at that time was 12^{o}C. The alatae were left undisturbed for one and a half hours in the box, during which the temperature increased to 13^{o}C. The lamps of the flight testing box were then put on and the room temperature was gradually increased. When the temperature became suitable for take-off the alatae flew from the seedlings to the glass wall. As soon as an alata landed, it was dropped by a brush into the water. This water moat

Figure 3.1: A vertical section of the flight testing box.

1. Masonite walls
2. Glass sheet
3. Fluorescent lamps
4. Open spaces for aeration
5. Thermistor probe
6. Potted seedling with alatae
7 Raised wooden platform
8. Water moat
9. Removable upper masonite cover.


9
1
2
5
3
52 cm
6
4
7
8
65 cm

also prevented the alatae walking from the seedlings to the base of the glass wall. The alatae which took off were recorded over a period of 4 hours, during which the temperature inside the box was slowly increased from 13 to 35°C. It was not possible to increase the temperature beyond 35°C and the observations were stopped. All the seedlings were checked for the remaining alatae and their nymphs.

3.2.2: Results

No alatae took off below 17°C and above 32°C (Table 3.1). However, a large number of the alatae took off between 20 and 23°C. A meaningful understanding of the distributions of take-offs over the test temperatures can be gained from Figure 3.2. It is evident that 70% of the fliers took off when the temperature increased to 23°C and another 20% took off up to 29°C. The upper temperature limit of 32°C is unreliable because it is highly probable that no more fliers were left on the seedlings when the temperature increased beyond 32°C.

Similar unimodal frequency distributions of take-offs, skewed to the right, have also been observed for other species of herbaceous aphids (Dry and Taylor 1970). The range of temperatures over which the take-offs were distributed was very wide in this experiment and it is likely that this range would be much shorter in the field as has been shown in *Aphis fabae* (Taylor 1957, 1963). It is also probable that the specific conditions of this experiment might have influenced the alata behaviour considerably. This seems more likely from the results in Table 3.2.

Not all the alatae took off in this experiment (Table 3.2). Approximately 38% walked off the plants and 22% did not fly at all. Later

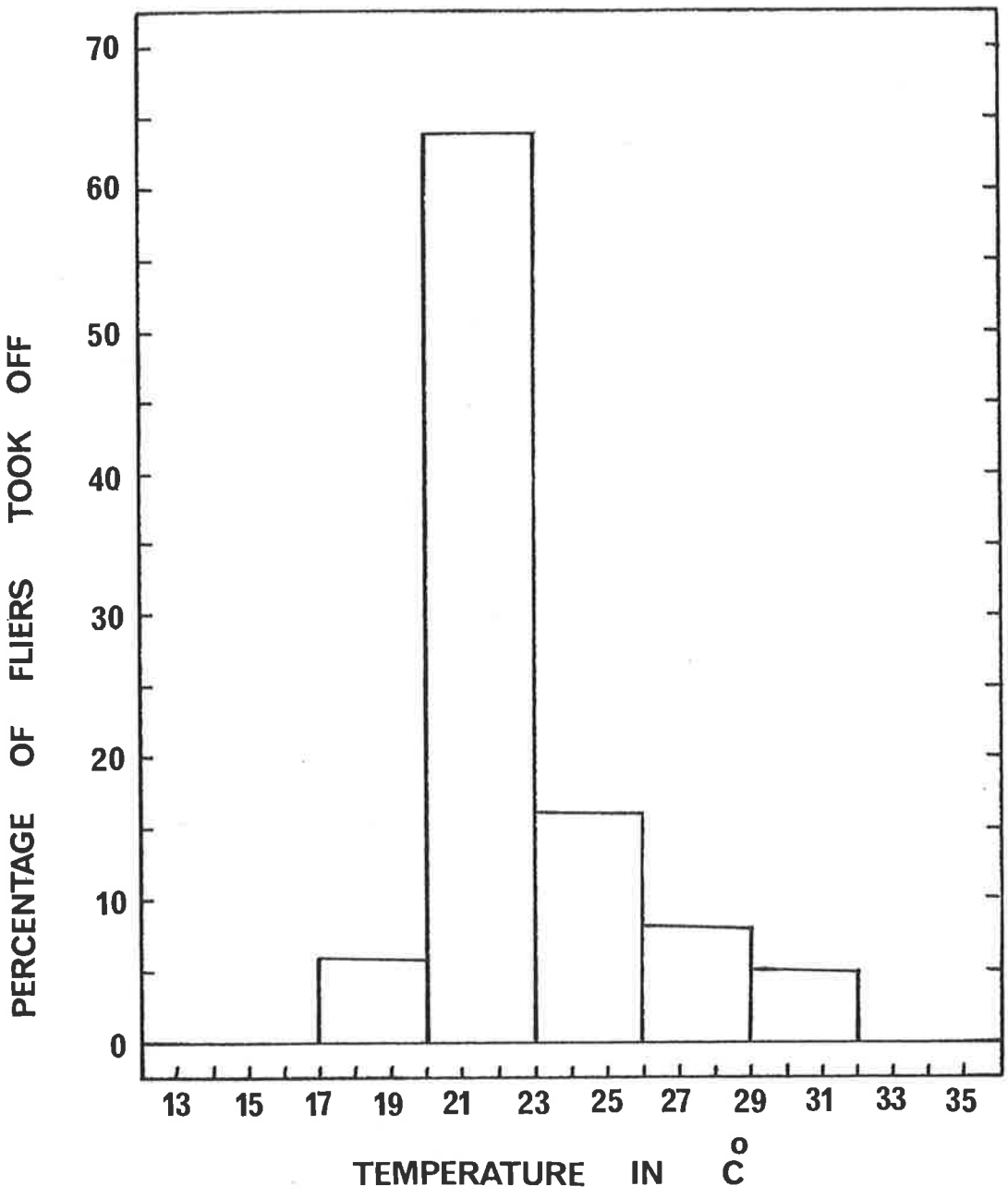
Table 3.1. Take-off by *Aphis craccivora* alatae in relation to increasing temperatures in the laboratory.

Temperature (°C)	Length of exposure (minutes)	No. of alatae took off	Temperature (°C)	Length of exposure (minutes)	No. of alatae took off
13-14	10	0	24-25	5	7
14-15	13	0	25-26	7	8
15-16	11	0	26-27	3	3
16-17	18	0	27-28	20	3
17-18	16	1	28-29	2	2
18-19	7	1	29-30	2	3
19-20	10	5	30-31	5	1
20-21	16	29	31-32	10	1
21-22	14	18	32-33	10	0
22-23	10	18	33-34	14	0
23-24	15	3	34-35	16	0

Table 3.2. Behaviour of flight mature *Aphis craccivora* alatae kept on broad bean seedlings in the laboratory.

Behaviour of alatae	Number of alatae	%
Flew from the plants	103	40.4
Walked off the plants	96	37.6
Stayed and reproduced on the plants	56	22.0
Total	255	100

Figure 3.2: Take-off by *A. craccivora* alatae in the laboratory over a range of increasing temperatures.


PERCENTAGE OF FLIERS TOOK OFF
70
60
50
40
30
20
10
0
13
15
17
19
21
23
25
27
29
31
33
35
TEMPERATURE IN °C

experiments on teneral period (Section 3.4) indicated that alatae of this species took 11-12 hours to become flight mature at 21-22°C. Since the alatae in this experiment were held in dark for 15-22 hours at 25-27°C prior to flight tests, far longer than they would require to become flight mature; they were certainly prevented from taking off when they became flight mature. This interference with their first take-off behaviour due to dark, might have released settling response in the alatae which did not fly (22%), while the others (38%) became restless and walked off the plants. The take-offs beyond 26°C may be due to restlessness caused by the high temperatures.

Much more work is needed for a fuller understanding of temperature relations of take-off in *A. craccivora*. The results of this experiment, nevertheless, indicate two points of ecological interest. Firstly they indicate that dispersal of *A. craccivora* alatae can occur only when the ambient temperatures are above 17°C. This means that, for most of the time, temperatures would be a limiting factor for the dispersal of this species in winter months in South Eastern Australia, when this aphid produces a high proportion of alatae in its colonies (see Section 2). The occurrences of flights of the alatae in late autumn and early spring in South Eastern Australia (Gutierrez *et al.* 1971, 1974b) and in South Australia (Carver and Randles 1961 - personal communication) are well explained by the results of this experiment. Secondly, the results of this experiment also indicate that an interference with the first take-off by the alatae when they become flight mature results in settling and parturition, at least in a proportion of flight mature alatae (see Table 3.2). This implies that during winter months a high proportion of *A. craccivora* alatae which would be prevented from take-off by low temperatures, could

settle on their host plants without flight and might contribute to the growth of the existing colonies, in a similar way as apterae.

3.3: Take-off behaviour in the field at 14 to 17°C

3.3.1: Methods

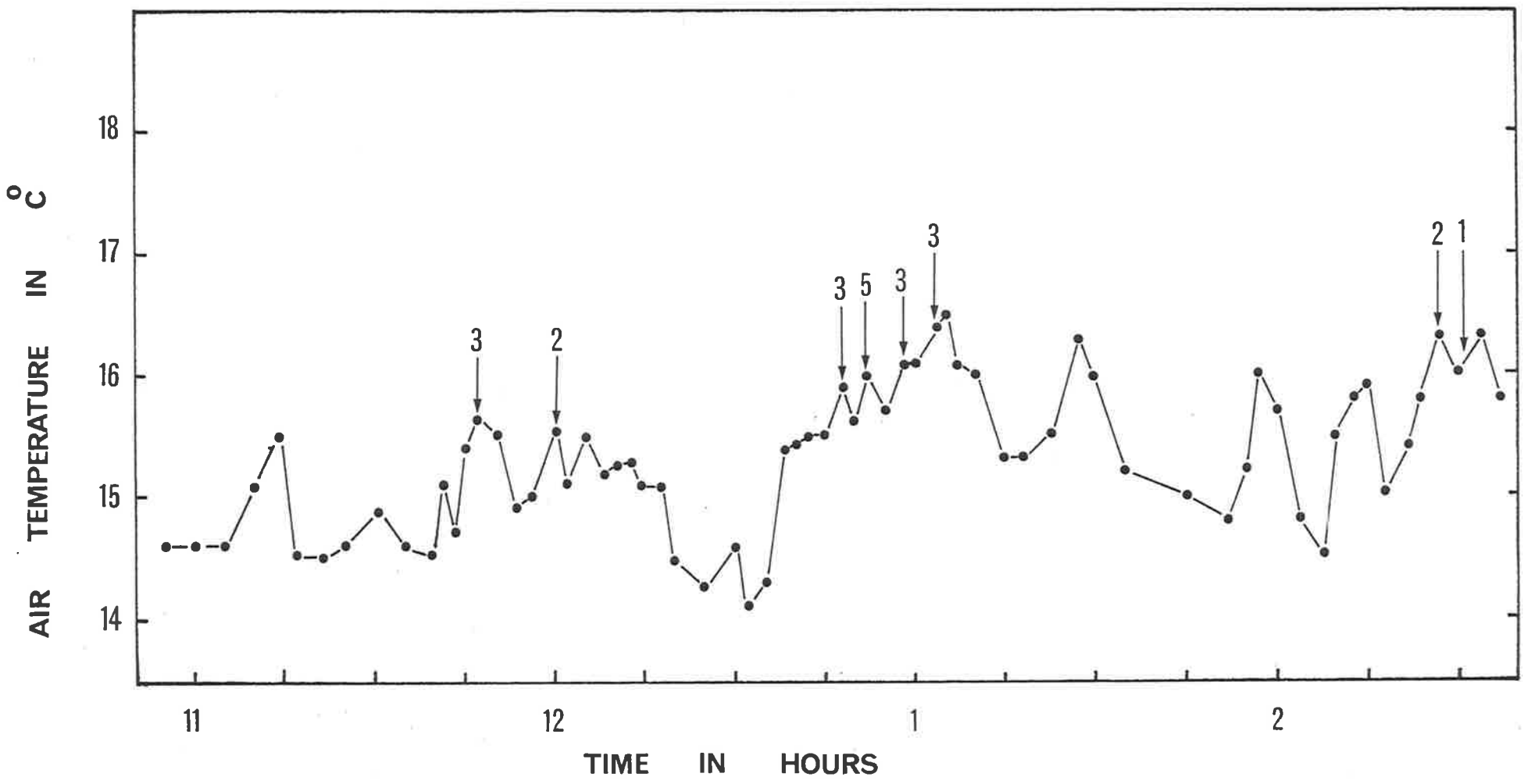
Observations were made in a naturally infested plot (3 x 3 m) of broad beans (approximately 10 weeks old) at the Waite Institute, on a cool, dry and partially cloudy day, in the last week of May 1976. Two infested plants approximately 30-35 cm high, which had many alatae were selected. A thermistor probe was placed approximately 30 cm above the soil surface to record the air temperature in the vicinity of the alatae. The distal metallic end of the probe was shaded by an aluminum foil cone from direct sunlight. The temperature was recorded at intervals of 2 to 5 minutes with an Edale thermistor-thermometer. Take-offs by the alatae were recorded by continuous observations over three and a half hours, during which the temperature fluctuated between 14 and 16.5°C.

3.3.2: Results

None of the alatae took off below 15.5°C (Figure 3.3). Of 22 alatae, 17 took off between 16 and 16.5°C.

The temperature at the beginning of the observations was 14.5°C and the alatae were walking and aggregating along the edges of the leaves near the leaf tips in groups of 2 to 5. A few alatae, which had probably dropped off the broad bean plants, were seen walking onto the erect leaf blades of graminaceous weeds and stopping near the tips. When the

Figure 3.3: Take-off by *A. craccivora* alatae in the field at low temperatures.
Numbers on tops of arrows indicate take-offs by alatae.
Air temperature recorded at 30 cm above soil surface.


AIR TEMPERATURE IN °C
18
17
16
15
14
3
2
3
5
3
3
2
1
11
12
1
2
TIME IN HOURS

temperature rose to 15.5°C at 11.15 am, the alatae on broad bean, as well as those on grass leaf tips, started opening and folding their wings but none took off. As the temperature dropped to 14.5°C within a short time, the alatae were walking along the leaf edges without activation of wings. They started opening and folding of wings at 11.45 am, as the temperature had reached 15.5°C. Three alatae took off after two minutes when the temperature was 15.6-15.7°C.

Sequences of walking and aggregating along the edges near leaf tips followed by opening and folding of wings by the alatae, formed a common pattern of pre-take-off activity.

Figure 3.3 shows no take-offs between 12.05 and 12.45 pm, but 14 alatae took off shortly after 12.45 pm. This could be explained in two ways. Firstly, it is reasonable to assume that no take-offs were observed because the temperature was not suitable. Secondly, it is equally reasonable to presume that there were no flight mature alatae during this period. If the second possibility is true, then no pre-take-off activity by the alatae could be expected during this period, because the alatae stay on plants without any movement until they become flight mature (see Section 3.4). The observations, however, do not support the second possibility because the alatae were walking and opening their wings until 12.08 pm. They again started opening and folding their wings at 12.42 pm when the temperature rose to 15.5°C. This activity indicated that flight mature alatae were there on the plants but could not take off, because the temperature had dropped well below 15.5°C, soon after 12.05 pm.

Similarly, no take-offs were observed between 1.05 and 2.25 pm, despite the rise of temperature thrice to nearly 16°C during this period. The alatae were not active at 1.27 pm when the temperature rose to 16.3°C.

This indicates that probably they were not flight mature.

The temperature dropped subsequently and again rose to 16°C at 1.57 pm and the alatae started opening and folding wings, but none took off. The temperature again dropped and then rose to 16°C at 2.15 pm and the alatae were again active, but none took off. However 3 alatae took off between 2.27 and 2.31 pm, when the temperature rose to 16.2°C. These observations indicate that flight mature alatae could not take off between 1.57 and 2.27 pm because the temperature of 16°C had not lasted long enough at 1.57 and 2.15 pm, and had quickly dropped to 14.5 and 15°C respectively. The sudden drop in the temperature was due to interruption of sunlight by the frequent movements of clouds. It is probable that alatae in the sunlight may experience higher temperatures than those in the shade, and would take off earlier.

The field observations described in this section not only supported the conclusions derived from the laboratory experiment on temperature relations of take-off (Section 3.2), but also provided an insight into the pre-take-off behaviour of *A. craccivora* alatae. The following section describes two experiments designed to ascertain the occurrence and variation in the pre-take-off activity among the alatae in laboratory.

3.4: Teneral period and take-off behaviour in the laboratory at 21-22°C

The interval between the final ecdysis of alatae and their first take-off, known as the teneral period, has been shown to be a developmental period from its temperature response curve in *Aphis fabae* (Taylor 1957) and *Myzus persicae* (Woodford 1969). The word 'teneral' in aphids aptly

describes the stage up to flight maturity. Owing to lack of a reliable and clearcut morphological criterion for defining flight maturity in *Aphis fabae*, Taylor (1957) regarded first flight as a good criterion for the termination of teneral period, if the prevailing temperature and light intensity were flight-permitting. Woodford (1969), however, disagrees with Taylor's definition of teneral period as a purely developmental period. He argues that since the termination of an essentially developmental period, i.e., the teneral stage, is characterised by a behavioural process, i.e., the flight, the definition of the teneral stage should, therefore, include the developmental as well as behavioural components. This argument draws support from the experiments wherein Woodford (1969) demonstrated significant influence of host plant and other surfaces on the teneral period in *Myzus persicae*.

The above concepts and field observations on take-off (Section 3.3) formed a basis for closer laboratory observations on teneral period and take-off behaviour in *A. craccivora* alatae. The objectives underlying these experiments were two-fold; firstly to estimate the thermal unit requirements of the teneral stage in this aphid; and secondly to ascertain the occurrence of pre-take-off activity and its variation among the alatae, so that it could be used as a reliable behavioural criterion other than flight, to distinguish flight mature alatae from the flight immature ones in both laboratory as well as in the field.

3.4.1: Methods

Aphids were cultured in laboratory at 25±1°C and 12:12 L.D. cycle on 2-4 week old broad bean seedlings (cultivar Seville Long Pod) grown in 15 cm diameter pots.

3.4.1-A: Experiment I

The first experiment involved the sticky canister method (see Section 3.5). Detached broad bean leaves, kept in perspex tubes (5 x 3.5 cm) filled with water, were used instead of decapitated potted seedlings. 2-10 newly moulted alatae were transferred to 3 bean leaves set up this way. Each leaf was then placed in the centre of a 15 cm diameter Petri dish containing water and was covered by a sticky canister. The temperature near the canisters varied between 21-22^{o}C. Temperature measurements inside the canisters, made with an Edale thermistor thermometer, did not show any variation in this respect. The canisters were placed 90 cm beneath a bank of 8 fluorescent lights, which were put on throughout the experiments. The light intensity inside the canister varied between 560 and 600 lux. The canisters were observed at intervals of 15 minutes until all the alatae were either stuck or trapped in water. The temperature and light intensity were thus flight permitting throughout the experiment. This experiment gave an approximate length of teneral stage at 21-22^{o}C and formed the basis of another experiment. The following experiment describes closer observations made individually on the teneral period and pre-take-off activities of 15 alatae under similar temperature and light intensity.

3.4.1-B: Experiment II

Teneral alatae moulted within half an hour, were transferred singly to the bean leaves kept in the perspex tubes filled with water. Each leaf was then kept in the centre of a 15 cm diameter Petri dish (without water) and covered by a clean non-sticky canister. A total of 15 alatae were set up this way beneath the bank of fluorescent lights. The temperature near the canisters varied between 21 and 22^{o}C.

Observations which started 9 hours later on the behaviour of the alatae, continued until all the alatae took off.

3.4.2: Results

Table 3.3 shows results of the first experiment on the duration between ecdysis and first take-off by the alatae at 21-22°C. All the alatae were trapped by the sticky canisters and all flew without reproduction.

The observations of the second experiment (Table 3.4) show that teneral development in *A. craccivora* alatae comprised two distinct phases; a prolonged phase of inactivity, followed by a short phase of activity prior to first take-off. Although the number of alatae observed in this experiment was small, yet the phase of pre-take-off activity was remarkably consistent. It is this behaviour which probably escaped the attention of Taylor (1957) and Woodford (1969), because their experiments on take-off behaviour lacked close and continuous observations. All the 15 alatae flew without reproduction.

On the basis of the results (Table 3.4), the period of inactivity can be regarded as teneral period which represents a developmental period. Once the alatae take out their stylets from the plant tissue and start waving antennae and walk along the leaf edges, this activity marks the end of developmental period and, therefore, is a good criterion for flight maturity. During this brief and active phase, the alatae alternated walking with brief stops; opened and closed wings 6-9 times, and contacted fore-tarsi with the take-off point on the leaf, before they took off. Some alatae had difficulty in coupling their hind-wings with the forewings, and opened and closed wings more than the other alatae, and this resulted in prolonged pre-take-off activity.

Table 3.3. Duration between ecdysis and first take-off in *Aphis craccivora* at 21-22°C in the laboratory.

Canister	No. of alatae	Duration in hours and minutes
1	2	Mean = 11-00 Range = 10-45 to 11-15
2	10	Mean = 11-30 Range = 11-00 to 12-00
3	5	Mean = 11-06 Range = 11-00 to 11-30

Table 3.4. Teneral period and pre-take-off activity in *Aphis craccivora* alatae at 21-22°C in the laboratory.

Batch	Aphid	Duration of inactivity in hours and minutes	Duration of pre-take off activity in minutes
1	1	10-35	10
	2	11-00	5
	3	11-17	5
	4	11-19	5
	5	11-21	9
	6	11-23	7
	7	11-23	2
2	8	11-02	1
	9	11-06	4
	10	11-09	4
	11	11-16	7
	12	12-20	8
3	13	11-25	5
	14	11-45	4
	15	11-45	9
	Mean ($\bar{x}$)	11-34	5.7
	Range	10-35 to 12-20	1 to 10

The length of pre-take-off activity is probably dependent on the prevailing temperature as well as on the individual variation due to behaviour. In the field, flight mature *A. craccivora* alatae did not take off when the temperature was below 15.5°C. The alatae were engaged in pre-take-off activity until the temperature rose to 16-16.5°C (Section 3.3). The results in Table 3.4 show individual variations in both the developmental and behavioural components of the teneral stage at 21-22°C. The results of this experiment thus confirm and segregate the developmental and behavioural components of the teneral stage in *A. craccivora*. The pre-take-off activity of the alatae provides a reliable criterion for defining flight maturity, as, unlike the take-off, it remained unaffected by the prevailing temperatures of 14-16°C.

3.5: Assessment of migratoriness among the alatae in the laboratory

It is well known that alatae take off from their host plants as soon as they become flight mature, following completion of teneral period if the prevailing temperature and light intensity are take-off permitting (Johnson *et al*. 1957; Taylor 1957, 1958, 1963, 1965; Woodford 1969). This act of first and pre-reproductive take-off by alatae has been regarded as migratory, because they leave the host plants on which they matured, irrespective of plants' physiological suitability for feeding and reproduction (Johnson 1960; Kennedy 1961, 1975). However, if a proportion of flight mature alatae stays on their host plants and reproduces before take-off, under flight permitting conditions, then such act of first take-off might be regarded as post-reproductive and facultative. This would mean that the adaptive significance of first take-off as a migratory act would diminish, because migration in aphids involves not only the production of migrant morphs, but also an active and

pre-reproductive migratory urge in association with a temporary depression of responses to vegetative stimuli (Kennedy 1961). One of the objectives of this research was to assess the strength of migratory urge among alatae of *A. craccivora*. The following experiment was set up in the laboratory for this purpose.

A valid and true assessment of migratory urge in alatae is possible only in the absence of flight inhibiting internal as well as external factors. This would require that the test insects should have normal wings (without any deformities) and be free from parasitization; and that they must be tested for their migration ability under flight-permitting temperature and light intensity when they become flight mature, because any interference with their first take-off may result in the release of settling response and parturition (see Section 3.2). All these flight inhibiting constraints were avoided in this experiment. The alatae came from parasite and disease-free cultures and their wings were checked later for any deformity. The temperature in the insectary room was either 21-22^{o}C or 23-25^{o}C; and the lights were put on continuously until the conclusion of the experiment. Thus the temperature and light intensity were flight-permitting throughout the experiment.

3.5.1: Methods

Clear plastic canisters (1 mm thick, 13.5 cm diameter and 13.5 cm high) were coated with a thin layer of tanglefoot (1:1 castor oil and resin w/w) on the inner sides after the removal of the lids. These canisters had two 4 cm diameter holes near the open end covered with muslin for ventilation. After coating with tanglefoot, the canisters were left inverted on a paper surface overnight, during which time any excess

tanglefoot dripped off, leaving a uniform thin coating.

Broad bean seedlings (cultivar Seville Long Pod) were grown singly in the University of California Potting Mixture in small plastic pots (5 cm^2 x 6 cm high) in a glasshouse. The seedlings with 2-3 fully opened leaves were decapitated and all the leaves were removed except the basal leaf.

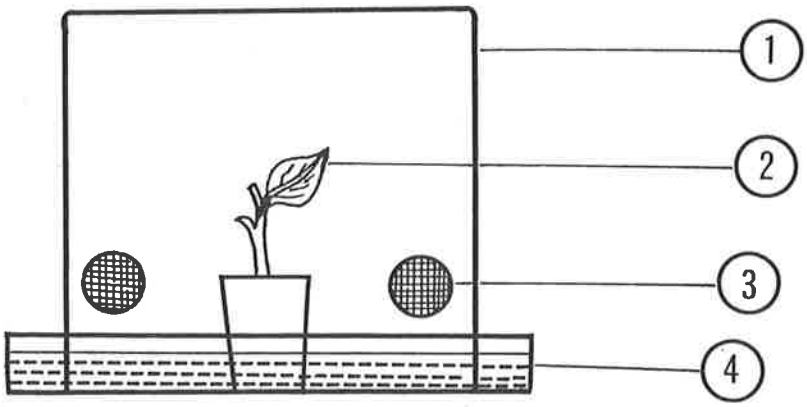
The aphids came from the cultures described in Section 3.4.1. Advanced fourth instar alatiform nymphs or teneral alatae with opaque wings were transferred to the basal leaf of a decapitated seedling. Initially one aphid was transferred to a seedling but in the later experiments as many as 50 aphids were transferred. One seedling was kept in the centre of a 15 cm diameter Petri dish containing water to 1 cm depth and a sticky canister was then inverted over the Petri dish (Figure 3.4). This water trapped any alatae that walked or dropped off the seedling. The inner walls of the sticky canister trapped those alatae which flew just more than 7 cm from the plant.

Six to ten canisters with this set-up were used at a time and they were kept in an insectary room approximately 90 cm beneath a bank of 8 fluorescent lights. The light intensity inside the canisters varied between 560-600 lux. Once a batch of aphids was set up this way, it was observed for two consecutive days. The positions of the alatae in each set-up were recorded and the seedlings were checked thoroughly for the nymphs, when all the alatae had moved off a seedling.

Trapping of the alatae by sticky walls of canisters, together with the absence of nymphs on the seedling, indicated pre-reproductive take-off, characteristic of migratoriness. Presence of nymphs on the seedling

Figure 3.4: Experimental set-up, used for assessment of migratoriness among *A. craccivora* alatae.

1. Transparent plastic canister with inner sticky coating (13.5 X 13.5 cm diameter).
2. Decapitated bean seedling in a small pot with test alata.
3. Muslin covered holes for aeration.
4. 15 cm Petri dish with water to trap dropping and walking off alatae.


1
2
3
4

indicated reproduction by the flight mature alatae before take-off or walking or dropping off the seedling. The set-up used in this experiment ensured that the alatae could not come back to the seedling after they had left it, either by flight or walking or dropping from it.

3.5.2: Results

Except the one alata with distorted forewings, none of the alatae reproduced before take-off or walking or dropping off the seedlings (Tables 3.5 and 3.6). The only alata with distorted forewings had settled on the seedling without any movement and produced 5 nymphs (Table 3.6). Nearly 18% of the test alatae were trapped in water (Table 3.6).

The dropping off behaviour of flight mature *A. craccivora* alatae may be more common in the field. Mechanical disturbances due to winds, might dislodge many alatae before they can fly. During rainy periods, wings of the dropped alatae might be distorted and this would result in their death or settling on a nearby plant without flight. The settling by these dropped alatae on nearby plants may result in patches of colonized plants in a field.

These results emphasise that *A. craccivora* alatae are pre-reproductive obligatory migrants. They also indicate that deformities of wings may adversely influence their flight behaviour. This is a point of ecological interest, because in dense colonies of *A. craccivora* in the field, wing distortion is more common than might be expected, because of an excess of honeydew excretion. Besides honeydew, dewdrops and rains also distort wings of alatae in natural populations (see Section 4). These results suggest that all these factors, i.e., wing distortion by honeydew and rains, the alatae's dropping behaviour off the plants and low

Table 3.5. Results of experiments on migratoriness among flight mature alatae of *Aphis craccivora* in the laboratory with one aphid per seedling at 24±1°C and 24:0 L:D.

Date	Type of aphid	Total aphids	Aphids trapped in water	Aphids stuck to top	Aphids stuck to sides	Number of seedlings with nymphs
19.3.76	Teneral alatae	10	3	0	7	0
20.3.76	Fourth instar alatiform	6	0	1	5	0
21.3.76	"	6	3	0	3	0
22.3.76	"	10	2	2	6	0
24.3.76	Teneral alatae	8	2	1	5	0
Total		40	10	4	26	0

Table 3.6. Results of experiments on migratoriness among flight mature alatae of *Aphis craccivora* in the laboratory with many aphids per seedling at 21.5±0.5°C and 24:0 L:D.

Date	Canister	Type of aphid	Total aphids per seedling	Aphids trapped in water	Aphids stuck to top	Aphids stuck to sides	Number of reproducing aphids	Number of nymphs on seedling
1.10.76	1	Teneral alatae	25	3	2	20	0	0
	2	"	25	7	1	17	0	0
	3	Fourth alatiform	24	3	3	18	0	0
	4	"	25	4	3	18	0	0
	5	"	50	8	7	35	0	0
	6	"	48	3	2	43	0	0
2.10.76	7	Teneral alatae	50	10	2	38	0	0
	8	"	50	8	0	42	0	0
	9	"	42	10	0	32	0	0
	10	Fourth alatiform	50	11	0	38	1*	5
5.10.76	11	Teneral alatae	30	5	0	25	0	0
	12	"	25	7	0	18	0	0
7.10.76	13	"	18	3	0	15	0	0
	14	"	30	10	0	20	0	0
	15	"	2	0	0	2	0	0
	16	"	10	0	0	10	0	0
	17	"	5	0	0	5	0	0
	18	"	12	0	0	12	0	0
		Total	521	92	20	408	1	5

* Alata with distorted forewings.

temperatures, might seriously limit the flight and dispersal of *A. craccivora* in winter in South Eastern Australia.

3.6 Observations on free flight in a flight chamber

Flight in winged aphids is important for two reasons: firstly, from a physiological point of view it is a pre-requisite for their settling and subsequent reproduction (Johnson 1958; Johnson 1963), and secondly, it is a means for the fulfilment of migration (Johnson 1960; Kennedy 1961) in the sense that they leave their breeding host plants through active flight. In this ecological context, the question as to what proportions of alatae may reach varying distances from a source after the flight, is of paramount importance and indeed difficult to be answered because of the practical difficulties involved in following these small insects in flight (Johnson 1956). Laboratory studies on free flight, though may not necessarily simulate aphid flight in nature, nevertheless, quantitative information regarding the variation in flight duration between different individuals and what proportions in a population can fly for different times, can be obtained in laboratory only. These data, together with qualitative information regarding the influence of different ecological factors on the flight behaviour of alatae, may be useful for an assessment of the dispersive potential of an aphid population, under a given set of weather conditions. The novel technique of free flight chamber (Kennedy and Booth 1963) is a useful means to achieve the quantitative information on flight capabilities of alatae in a population. The following observations describe some aspects of free flight of *A. craccivora* alatae in a flight chamber.

3.6.1: Methods

3.6.1-A: Aphid supply

The aphids were cultured on 2-4 week old potted broad bean (cultivar Seville Long Pod) seedlings. The plants were kept in an insectary room with provision for natural daylight through a vertical glass wall. The plants which were producing alatae were kept 1.5 to 2 metres away from the glass wall. Approximately 90 cm above the plants, a bank of 8 fluorescent lights provided a 14 hour photoperiod. The flight mature alatae were not attracted to fluorescent lights; instead they were attracted to natural day light, and flew either horizontally or diagonally to land on the glass wall.

The alatae which were walking on the glass wall were collected in a glass tube (5 x 3 cm) for flight tests and these are referred to as 'alatae of unknown age and flight history' in the text. The alatae which had just taken off from the plants were also collected soon after their landing on the glass wall, and these are referred to as 'new alatae'. These were kept either in glass tubes (15 cm x 3 cm) in groups of 10 to 15 or singly on young detached broad bean leaves in glass tubes.

3.6.1-B: Flight chamber

A modified Kennedy flight chamber (Laughlin 1974) was used for free flight tests. It was a vertical wind tunnel (1 x 1 x 1 m) in which the air speed could be controlled and the direction of airflow could be reversed. It was, therefore, possible to fly alatae at a desired level beneath an overhead light source. The inside of the chamber was painted black. The top screen was of black fine nylon net except a 25 sq. cm. white nylon window in the centre, for illumination.

A 100 watt incandescent lamp illuminated the chamber. The temperature in the chamber was controlled by an air conditioner. A thermistor probe placed in one of the side walls recorded the temperature. The speed of airflow in both the directions was calibrated by a battery-operated hot-wire anemometer before flight tests. Variations in the airflow during the flight tests were recorded automatically on the temperature chart by a pencil marker, which was linked with airflow control lever. An instant event marker was installed to mark the time of take-offs and other flight incidents during flight tests. The uninterrupted flight durations of individual fliers were recorded by a stop watch.

The temperature in the chamber varied between 23 and 29^{o}C during the flight tests. The maximum speeds of upward and downward airflows were 89 and 108 cm/sec.

3.6.1-C: Procedure for flight tests

The airflow was stopped and the alatae were placed singly in the centre of the bottom screen and allowed to take off on their own. In case of the alatae kept singly on bean leaves before tests, the leaves with the alatae were placed on the bottom screen. When the alatae took off, a gentle upward airflow was applied until the fliers were 10-20 cm beneath the light window. The direction of the airflow was reversed at that stage to prevent the fliers from landing on the light window. If the fliers began to sink down, they were supported by an appropriate upward airflow.

Many alatae were lost during their free flights by either landing on the walls or coming out of the chamber; and the flight durations recorded must therefore be regarded as minimal.

The alatae which did not take off on their own until after 5 minutes of being placed on the bottom screen, were taken on the tip of a fine brush and dropped 10 times from a height of 50-60 cm. If flight was not induced by flicking, the alatae were regarded as incapable of flight.

3.6.2: Results

3.6.2-A: Pre-take-off behaviour

The alatae kept in glass tubes before flight tests wandered in 2-5 cm diameter circles and semi-circles from 5 seconds to 3-4 minutes, when placed on the bottom screen. During this time they opened and closed their wings several times and often kept the wings vertical. Those which took off on their own came to a standstill before taking off, waved their antennae continuously, opened wings and took off in 2-4 seconds.

Of the alatae kept singly on bean leaves, a few did not move for 7 to 10 minutes; others walked half-way along the leaf edges several times from 15 seconds to 10 minutes, before taking off. All these alatae had been collected soon after their first flights and were kept on bean leaves for one to one and a half hours prior to flight tests; and their reluctance for a second take-off was remarkable. The reluctance for a second take-off by the alatae from a host plant may shorten the range of dispersal of alatae of this species in the field, especially more so in cool weather.

3.6.2-B: Flight capability

The flight test procedure (Section 3.6.1-C) enabled classification of the alatae into two groups on the basis of their flight capability, i.e., flight capable and flight incapable. The flight capable alatae can be divided into two groups on the basis of their readiness for flight, i.e., the first group would consist of the alatae which took off on their own; the second group would comprise those which were reluctant to fly on their own and could only be induced to fly by flicking.

Of 250 alatae of unknown age and flight history, 31 were incapable of flight. These alatae could only open and hold their wings in a vertical position when dropped but could not fly. These were probably old and reproducing alatae which had dropped off or walked away from the plants to the glass wall of the insectary room. These flight incapable alatae led to an experiment on wing muscle autolysis (Section 3.7).

All the new alatae (66) flew for a second time in flight chamber, 1-2 hours after their first flight.

3.6.2-C: Pattern of free flight in relation to size of the alatae

After taking off, the alatae flew spirally upwards towards the light window. Large alatae flew steadily in spirals of approximately 20-30 cm diameter, with minimal vertical movements. They flew for longer periods also. Small alatae flew in narrow spirals of approximately 6-10 cm diameter and because of their frequent vertical

movements, they were difficult to handle. They flew for short durations.

3.6.2-D: Durations of free flight

Figure 3.5 shows frequency distributions of minimum recordable flight durations of the alatae. Among 'the alatae of unknown age and flight history', nearly 65% flew for more than one minute and 15% flew for more than 5 minutes (Figure 3.5-A). The corresponding percentages among 'new alatae' which were kept in glass tubes prior to flight tests, were 60 and 30 (Figure 3.5-B). Among 'new alatae' kept singly on young bean leaves for one to one and a half hours, 30% flew for more than one minute and 10% for more than 5 minutes (Figure 3.5-C). It is likely that a compulsive stay of one to one and a half hours by the alatae on a host leaf, after their first take off, had an adverse effect on the duration of their subsequent flights.

3.6.2-E: Rate of climb of the alatae during free flight

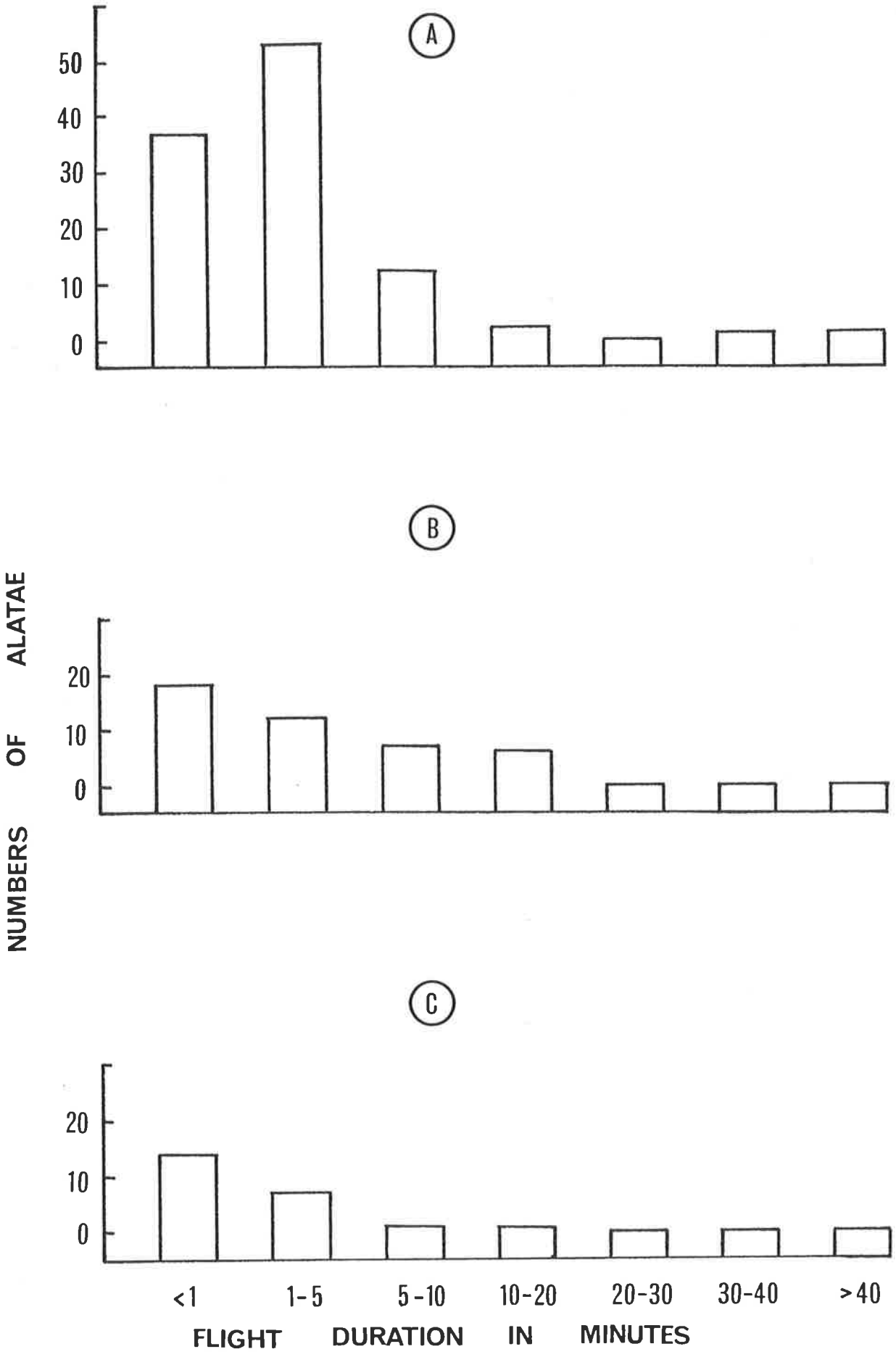
The alatae were balanced by an appropriate downward airflow during their free flights, so that they could not land on the light window of top screen. An estimate of this balancing airflow provided a measure of their rate of climb during free flight. Rate of climb in early phase of flight varied between 45 and 60 cm/second. Changes in the rate of climb were also variable for individual fliers. For the alatae with sustained flights of more than 10 minutes, a steady rate of climb of 10-20 cm/second was observed for a greater part of their flights.

Figure 3.5: Frequency distributions of flight durations of *A. craccivora* alatae in a flight chamber.

A = Alatae of unknown age and previous flight history (total alatae = 106).

B = Alatae collected soon after their first flight and kept in glass tubes (total alatae = 43).

C = Alatae collected soon after their first flight and kept on young bean leaves for ½ to 1½ hours (total alatae = 23).


A
50
40
30
20
10
0
B
NUMBERS OF ALATAE
20
10
0
C
20
10
0
<1
1-5
5-10
10-20
20-30
30-40
>40
FLIGHT DURATION IN MINUTES

The observations on pre-take-off behaviour and flight capability of alatae in *A. craccivora* are not unexpected. Similar results have been reported for *Aphis fabae* (Johnson 1958). The scanty information reported above, on distributions of flight durations together with the rate of climb of alatae in *A. craccivora*, is also in conformity with the findings of similar experiments in *Aphis fabae* (Kennedy and Booth 1963).

The data on duration of free flights and rate of climb of the alatae do not tell anything about how long the alatae do fly or can fly in nature; what these data provided is empirical evidence on the flight capabilities of the alatae. These capabilities, at least in part, suggest that the alatae may reach long distances on wind currents, i.e., a last link which completes a whole body of empirical evidence in support of the thesis that *A. craccivora* is a migrant species. Results on the high alata producing capacity (see Section 2), and the information on the pre-reproductive obligatory flight behaviour of the alatae of this species (see Section 3.5), are other components of empirical evidence in this respect.

3.7: Wing muscle autolysis in the laboratory

It is well known that wing muscles of herbaceous aphids undergo autolysis following their settling on a host plant (Johnson 1957a). A simple laboratory experiment was designed to study the occurrence of autolysis in *A. craccivora* alatae in relation to age.

3.7.1: Methods

A laboratory culture of *A. craccivora* was maintained on 2-4 week old potted broad bean seedlings (cultivar Seville Long Pod) at 20-25^{o}C and 12:12 LD cycle. About 80-90 teneral alatae within 2-3 hours

of their moulting were transferred to a 2 week old decapitated broad bean seedling. After transferring the alatae, the potted seedling was covered with a lantern lamp cage and kept at 25°C and 12:12 LD cycle. A sample of 5-7 alatae was taken daily, starting from 0 to 10 days for the study of the autolysis.

The alatae were killed and fixed in freshly prepared alcoholic Bouin's fixative for 24-48 hours. After fixation, they were cut in half longitudinally and left for 2-3 hours in 50% alcohol saturated with Lithium carbonate, to wash excess of picric acid. The cut alatae were then dehydrated in 70, 80, 90, 95% and absolute alcohol for at least 5 minutes at a concentration, cleared in clove oil for 3-6 hours and mounted in Canada balsam. This method proved quite satisfactory for detection of wing muscle autolysis, as the fibrillar bundles were distinctly seen under a microscope, because of a light greenish yellow tinge of picric acid. As no additional staining was involved, this method was simple and also less time consuming.

3.7.2: Results

Similar to the thoracic musculature of *Aphis fabae*, as described by Weber (1930), dorsal longitudinal muscles I and II, dorsoventral muscles I and II, and pleural muscles I and II are fibrillar muscles in *A. craccivora*. The dorsal oblique muscle is well developed in *A. craccivora*. All these muscles in *A. craccivora* undergo autolysis.

Intact muscles with closely packed fibrils were seen in the teneral, 1 and 2 day old alatae. Disintegration of fibrils in the muscles was observed in 3 day old alatae. Though the fibrils became loose and wavy with the ageing of the alatae, they did not disappear completely, even in 10 day old alatae.

These results imply that the flight capability of *A. craccivora* may decrease with ageing. At lower temperatures, the autolysis may be delayed and the alatae may remain flight capable for relatively longer periods.

3.8: Reproduction and flight capability among the alatae collected from a parasitized infestation

The observations reported in this section describe detrimental effects of parasitization on reproductive and flight capabilities of *A. craccivora* alatae, which were collected from an infestation on broad beans.

3.8.1: Methods

Teneral alatae with opaque wings were collected in April 1976 from a parasitized infestation on broad beans in the Alverstoke orchard. They were kept singly on the undersurfaces of basal leaves of 1-2 week old potted and decapitated broad bean seedlings. Small leaf cages (1 x 1.5 cm diameter) were used to confine the alatae on leaves. The seedlings were then kept in the dark for 42 hours at a temperature of 25^{o}C. The alatae were then tested for flight capability in the flight chamber in a similar way described in Section 3.6.1-C.

3.8.2: Results

On the basis of results (Table 3.7) these alatae can be classed into three groups as follows:

1) This group consisted of the alatae which had reproduced prior to flight tests and were still flight capable.

Table 3.7. Reproduction and flight capability in *Aphis craccivora* alatae, collected from a parasitized infestation.

Group	Aphid	No. of nymphs produced	Flight capability	Take-off initiative
I	2	1	+	-
	4	1	+	+
	6	4	+	+
II	3	0	+	-
	5	0	+	+
	9	0	+	-
III	1	0	-	-
	7	0	-	-
	8	0	-	-
	10	0	-	-
	11	0	-	-

2) This group included the alatae which had not reproduced prior to flight tests and were still flight capable.

3) This group comprised the alatae which had not reproduced prior to flight tests and lost their flight capability also. These alatae were parasitized. They could only open their wings, but could not support their swollen bodies in free flight. These alatae indicated detrimental effects of parasitization on their reproduction as well as flight capability.

3.9: Dispersal pattern of the flight mature alatae in a small broad bean plot in winter

The experiments and observations described above (Sections 3.2 to 3.8), provided an understanding of some basic ecological and physiological aspects of flight behaviour of *A. craccivora*. These results, however, do not throw any light on dispersal patterns of the alatae in the field. Heathcote and Cockbain (1966) observed short flights by *Myzus persicae* when the environmental temperature was not sufficiently above the flight threshold. Cockbain (1961b) also reported similar observations in *Aphis fabae*. Migratory and trivial flights have been well distinguished in the field in the sycamore aphid, *Drepanosiphum platanoides* (Dixon 1969). The results regarding the frequency distribution of take-offs in relation to increasing temperature (Section 3.2) and the durations of free flights of the alatae in the flight chamber (Section 3.6) also implied that not all flying *A. craccivora* alatae are long distance migrants. The following experiment was designed to observe the dispersive behaviour of the flight mature alatae from a plant and study their dispersal pattern in a small broad bean plot on 2 cool and dry days in mid-June 1978.

3.9.1: Methods

100 apterae were collected from a broad bean infestation and crowded in a small glass tube (5 x 1 cm) for 3 hours. 50 apterae were placed on each of two, 4-6 week old potted broad bean plants and left for larviposition in an insectary room with 20-21°C and a 12 hour photoperiod. 24 hours later, the apterae were removed with a fine brush, leaving nymphs. A high proportion of these nymphs developed into alatae.

Broad bean seeds (culture 127) were soaked in water overnight and sown singly in the University of California Potting Mixture in peat pots (5 x 5 x 5 cm, Jiffy strips No. 517). The peat pots were kept in a glasshouse and watered whenever necessary until the seedlings were 10-12 days old.

An open site, measuring 7 x 7 m and free from any shade, was selected in the Alverstoke Orchard of Waite Institute. All weeds were removed and the soil worked to a fine tilth prior to planting of the seedlings. 81 seedlings were planted with a spacing of 80 x 80 cm in 9 rows, each with 9 seedlings. The seedlings were irrigated with an overhead sprinkler whenever necessary.

On the evening of the 12th day after planting, all the plants in the experimental plot were cleaned of aphids and their progeny. Only three *A. craccivora* alatae had established colonies on 3 different plants during this period. The central plant (the 5th plant in the 5th row) was uprooted and the soil was levelled. The experiment began on the following day.

A potted broad bean seedling of the same age as those in the plot was decapitated, leaving a 15 cm stem with 4 basal leaves. 100 teneral alatae, moulted during one hour, were transferred onto the leaves of the

decapitated seedling between 9 and 10 pm. The seedling was then left in the dark (in a cage covered in black cloth) at 20-21°C for 14 hours, so that the alatae would become flight mature.

The cage with the alatae was taken to the plot the next day and was kept there for 2 hours. A metal tray (45 x 30 x 4 cm deep) containing water and detergent was placed in the centre of the plot. The seedling with the alatae was placed in the centre of the tray on a wooden platform (10 x 10 x 4 cm high). The purpose of this moat was to trap those alatae which walked or dropped off the seedling. A shaded thermohygrograph, placed at one edge of the plot recorded the temperature. The experiment was repeated on the following day with 51 flight mature alatae.

3.9.2: Results

100 flight mature alatae were exposed in the plot for dispersal on 15th June 1978 from 2.40 to 4.50 pm. It was a calm and completely cloudy day and the temperature during the exposure period ranged between 13 and 13.5°C. None of the alatae either took off or dropped off the seedling until 4.50 pm. The seedling was removed from the plot.

All the plants were checked for immigrant alatae in the morning on 16th June. There were no alatae. 51 flight mature alatae were then exposed for dispersal from 12.00 noon to 6.00 pm. It was a windy and completely cloudy day and the temperature during the exposure period varied between 12.5 and 15.5°C. The maximum temperature lasted for 10-15 minutes only. Of 51 alatae exposed, 25 were missing on the seedling at 6.00 pm. No alatae were trapped in the water tray. All the plants were checked,

but none had any alata.

These observations indicated two aspects of dispersal behaviour of *A. craccivora* alatae in the field; firstly the concept of operation of variable temperature thresholds for take-off within a population of fliers; and secondly the flight persistence of the fliers; the persistence which eventually carried them away from the plot.

The observations on the first day indicated that no dispersal can occur at 13-13.5^{O}C in the field. Take-off by 50% alatae on the second day indicated that not all the alatae in a population had the same take-off threshold of 15.5^{O}C.

It was interesting to find out that even at a temperature of 15.5^{O}C, which was not suitable for take-off by all the exposed alatae on 16th June, those which had flown did not make short or trivial flights, as expected, but were lost from the plot. This behaviour indicated their persistent flight away from their host plant, characteristic of adaptive migratory behaviour (Kennedy 1961, 1975), even at temperatures just below the take-off threshold. The implication of this pattern of flight, especially from isolated patches of infestations, would be the dispersal of this species away from the patches of its host plants, especially when the mean size of host plant patches is small in a locality.

Much more work is needed along these lines for a fuller understanding of the dispersal, as well as the post flight behaviour of the alatae in the field under varying weather components, i.e., temperature, relative humidity, cloudiness and windspeed. A suitable method for marking the flight mature alatae in the field populations, such as the use of a fluorescent dust, may perhaps greatly facilitate such studies.

3.10: Summary

Results of the experiment on temperature relations of take-off in *A. craccivora* indicated no take-offs below 16°C and approximately 70% fliers took off between 16 and 23°C. The frequency distribution curve for take-offs is unimodal and skewed to the right. The upper temperature limit for take-offs was 32°C. Of the alatae tested, 38% walked off the plants and 22% did not fly but stayed and reproduced on broad bean plants. It is probable that these alatae were prevented from taking off due to dark when they had become flight mature. In field, flight mature alatae did not take off below 15.5 - 16.5°C.

In laboratory, duration between ecdysis and first take-off at 21-22°C is 11 to 12 hours. Laboratory experiments and field observations indicated developmental and behavioural components of teneral stage in this aphid. The pre-take-off activity is a reliable criterion for defining flight maturity in both laboratory and field conditions.

Laboratory experiments on the assessment of migratoriness at 21-25°C, 24:0 L:D cycle and 560-600 lux indicated that *A. craccivora* alatae were obligatory pre-reproductive fliers. In field, rains, excess honey dew and parasitization cause wing distortion and may limit flight and dispersal of alatae.

In a free flight chamber 65% alatae flew for 1-5 minutes and 15% flew for more than 5 minutes. The rate of climb of fliers varied between 10 and 20 cm/sec.

Wing muscles of *A. craccivora* showed first signs of autolysis in 3 day old alatae which were kept at 25°C in the laboratory. The autolysis progressed with age; the disintegrated fibrils did not disappear completely even in 10 day old alatae.

In field, parasitization adversely affects reproduction as well as flight capability of alatae. A field plot experiment indicated two features of alata dispersal. Fifty percent flight mature alatae did not fly at 15.5°C and none of those which flew was found on the surrounding broad bean plants in a 7x7 m plot.

It can be concluded from results of this section that the extent of long distance migration in *A. craccivora* is determined by the prevailing environmental factors despite the innate migratoriness of the alatae.

SECTION 4

COLONIZATION

4.1: Introduction

Colonization of host plants is characteristic of insect pests in general and especially of migratory insects. It is only through migration and recolonization that insects like aphids, the inhabitants of ephemeral habitats, ensure the continuity of their survival (Southwood 1962; Way 1973; Taylor 1977).

Studies on colonization by herbaceous aphids have revealed several aspects of their behaviour and ecology in a region. These aspects are, flight periodicity (Fisken 1959); initial colonisation density per plant (Forsythe and Gyrisco 1963; Shiyomi and Nakamura 1964; Shiga 1965); effects of wind direction (Johnson 1950; Taylor and Johnson 1954) and windbreaks (Lewis 1966; Lewis and Stephenson 1966; Lewis 1969) on the pattern of infestation; effects of age and height of host plants (Dunn 1969), spacing (A'Brook 1964, 1968; Heathcote 1969) and crop density (Way and Heathcote 1966; Davies 1972; Farrell 1976a on the intensity of colonization; and effects of trap crops (Farrell 1976b)and weeds (van Emden 1965; Smith 1969) on the extent of aphid infestation and the abundance of natural enemies (Chandler 1968; Smith 1969). The knowledge of the pattern and extent of colonization by aphid species may be useful not only for the prediction of the probability of infestation of a suitable crop in an area, but more importantly for the prevention of the colonization itself (Swenson 1968).

The present study was aimed at understanding the migration ecology of *Aphis craccivora* in South Australia. Field observations on the probability of colonization of a host crop and the colonization behaviour of this species were desirable in this context; for, except the flight periodicity records from yellow tray traps (Hughes *et al.* 1965; Carver and Randles 1961 - personal communication) and some incidental observations in the far north of the state (White 1967), no other report is available in the literature, regarding the incidence of *A. craccivora* in South Australia.

The objectives underlying the observations on colonization by *A. craccivora* were to increase knowledge about the temporal population dynamics of migratory alatae and also to assess the probability of infestation of a suitable host crop such as broad bean in the South Australian environment. This section describes colonization of broad beans in small experimental plots at Mortlock Experiment Station and the Waite Institute during spring and autumn of 1975, 1976 and 1977; aphid incidence in mature broad beans at Mortlock and Port Clinton (Yorke Peninsula) in late Spring 1976; the pattern and extent of primary infestation of young broad beans at Mortlock in early spring 1977; and observations on the survival of this aphid in summers of 1976-77 and 1977-78 at various locations in South Australia.

The observations reported here support the conclusions of Hughes *et al.* (1965). Further it has been shown that broad bean is not only suitable for colonization by *A. craccivora* but that large aphid populations per unit area can develop on this crop under certain weather conditions in South Australia. In addition, the colonization

behaviour of the immigrant alatae has been inferred from their recorded numbers and the corresponding numbers of stems colonized in the experimental plots between two consecutive observations. The incidence and impact of natural enemies in the colonized stems has also been discussed in relation to the success of colonization.

4.2: Colonization in the experimental plots

Empirical studies on colonization by *A. craccivora* involved periodic planting of young and insect-free broad bean seedlings as trap plants at Mortlock and Waite. The number of incoming alatae and their progenies on the trap plants were counted at approximately weekly intervals.

4.2.1: Methods

Approximately one week old broad bean seedlings (cultivar Seville Long Pod or Crete 136) were used as trap plants. The seeds were soaked in water overnight and sown singly in the University of California potting mixture, in each of 5x5x5 cm peat pots (Jiffy Strips No. 517). The peat pots were kept in a glasshouse and watered regularly until the seedlings were of desired age and growth stage.

Only the seedlings with 2-4 fully opened leaves were selected for planting. The soil of the experimental plots at Mortlock and Waite, was red loam which becomes sticky after watering and cracks when dry. The area of planting was cultivated to a fine tilth with a hand-operated rotary hoe when the soil was moist. If hard and dry, the soil was manually dug and pulverised with forks and rakes and

weeds and stones were removed. The seedlings with their peat pots were planted singly in 8-12 cm deep holes 0.5 m apart. The seedlings were either sprinkle-irrigated or watered individually with a hose after planting. Thereafter the plants were watered by surface flooding as necessary. This method of planting of the seedlings was necessary because of poor germination of the seed stock.

There were two adjacent plots at each location. The distance between the adjacent plots varied from 1 to 4 m. The two plots at each location were expected to reveal the extent of variation in the rate of alightment and settling of *A. craccivora* alatae.

The area of the plots at the beginning was 9 m^2 (3x3 m/plot) with 49 seedlings planted 0.5x0.5 m apart in 7 rows of 7 seedlings each. The plot size was reduced later to 4 m^2 (2x2 m/plot) and each plot had 25 seedlings planted in 5 rows of 5 seedlings each, with the same spacing. The spacing was wide enough to trap many *A. craccivora* alatae (A'Brook 1964, 1968). The prime consideration regarding the size of the plots, was the practical feasibility for a thorough search for incoming alatae and their nymphs with a reasonable time and effort. The probable effect of the size of plot on the rate of alightment and settling of colonizing alatae has been discussed at the end of this section (see Section 4.2.2 - H).

All the plants in each plot were thoroughly searched individually for *A. craccivora* alatae and their nymphs at approximately weekly intervals. The infested plants were cleaned of aphids for recolonization in the following week. New seedlings were planted once in 4-6 weeks on adjacent land. The old seedlings were then uprooted

and destroyed. The sampling interval exceeded one week many times.

4.2.2: Results

4.2.2-A: Colonization of broad bean plants - a description

A. craccivora alatae colonized mostly the crowns of broad bean seedlings. If the plants were in bloom, the alatae colonized calyces of unopened and newly-opened flower buds also. Occasional colonization of the under-surfaces of stipules and upper 2-3 cm of stem was also observed, especially when the crown had many alatae. Alatae did not colonize fully opened leaves and the rest of the stem. Crowns of the axillary stems were also colonized frequently.

4.2.2-B: Rates of influx of alatae

One of the objectives in studying the colonization of broad bean seedlings by *A. craccivora* was to seek information on the flight periodicity and seasonal abundance of alatae at a location in South Australia. The flight periodicity records from yellow tray traps at Waite and Adelaide Hills (Hughes *et al.* 1965; Carver and Randles 1961 - personal communication) revealed a small peak in autumn followed by a larger peak in spring. Although the yellow tray traps may provide some measure of abundance of flying alatae of yellow-sensitive aphid species, however, from these records, it would be difficult to infer the rate of settlement and the probability of colonization of a host crop on an area basis (see Section 4.1), notwithstanding the colonization behaviour and the pattern of infestation in a crop. The rate of influx of colonizing alatae in a trap host crop, together with

concurrent population estimates might be a useful measure of abundance of an aphid species in a locality. For a migratory species such as *A. craccivora*, even the rate of influx of colonizing alatae by itself may be a useful index of the abundance and migratory activity of the aphid in an area.

The experimental plots at Mortlock and Waite provided data on the rates of influx of *A.craccivora* alatae during 1975, 1976 and 1977. The number of alatae recorded in both the plots at a sampling occasion was divided by the preceding interval, and the rate of influx has been expressed on a daily basis over the area of the plots.

The results at Mortlock (Tables 4.11 and 4.12) reveal a pattern of flight periodicity and abundance of *A. craccivora* alatae (see also Appendices XV A, B and C). Peaks of influx of alatae were recorded in early November during 1975 and 1976. In 1977, the peak of influx of alatae was observed in mid-October. The results also indicate abundant aphid populations in 1976 and 1977, in relation to the population level in 1975. Small numbers of alatae were consistent in autumn (March to May) also. No alatae were recorded in January 1976 (mid-summer).

The results at Waite (Table 4.13) also reveal a similar pattern except that the aphid populations were far smaller than those observed at Mortlock (see also Appendix XV-D). The above pattern of flight periodicity of *A. craccivora* alatae, supports the conclusions of Hughes *et al.* (1965).

4.2.2-C: Distribution patterns of colonizing alatae

The description of the pattern of distribution of insects in space is of considerable ecological significance, not only

Table 4.11. Rates of influx of *Aphis craccivora* alatae in the experimental plots at Mortlock 1975-76.

Date	Preceding interval in days	No. of alatae/day/area
Sept 19, 1975	10	0.3*
23	4	2.0
Oct 2	9	1.4
10	8	0.5
21	11	1.0
28	7	2.4
Nov 4	7	9.3 P
11	7	0
18	7	2.1
27	9	0.7
Dec 5	8	0.3
23	18	0.3
30	7	0
Jan 6, 1976	7	0
13	7	0
19	6	0
Feb 3	15	0
9	6	0.2
16	7	0.1
Mar 2	15	0
9	7	0.3
16	7	0.6
23	7	0.1
30	7	0.1
Apr 13	14	0.4
20	7	0.4
May 4	14	0.1
11	7	0.6
25	14	0
June 3	9	0

* Area of plots = 18 sq. m.
P = Peak of alatae.

Table 4.12. Rates of influx of *Aphis craccivora* alatae in the experimental plots at Mortlock 1976-78.

Date	Preceding interval in days	No. of alatae/day/area
Oct 13, 1976	7	5.1*
26	13	14.6
Nov 3	8	72.8 P
18	15	2.1
24	6	23.8**
Dec 13	19	0.1
23	10	0
May 5, 1977	7	0.1
14	9	0.3
21	7	0.6
30	9	0.1
Aug 27, 1977	8	1.0
Sept 3	7	8.0
13	10	4.1
Oct 7	24	4.8
13	6	34.5 P
27	14	4.6
Nov 2	6	3.2
24	22	0.6
Feb 13, 1978	11	0
20	7	0
Mar 2	10	0.1
9	7	0
31	22	< 0.1

* Area of plots = 18 sq m.
** Area of plots = 8 sq m.
P = Peak of alatae.

Table 4.13. Rates of influx of *Aphis craccivora* alatae in the experimental plots at Waite 1975-77.

Date	Preceding interval in days	No. of alatae/day/area
Sept 11, 1975	9	0.7*
18	7	0.1
25	7	1.4
Oct 6	11	0.3
20	14	0.2
27	10	1.7 P
Nov 6	10	0.4
Mar 17, 1976	2	0 **
18	1	3.0
19	1	3.0
20	1	0
22	2	0
July 6	42	0
Aug 24	49	0
Oct 12, 1976	7	2.6* P
20	8	1.3
Mar 3, 1977	17	0.2**
May 12	16	5.8 P
24	12	1.2

* Area of plots = 18 sq m.
** Area of plots = 8 sq m.
P = Peak of alatae.

for a basic understanding of the condition of an insect population, but also for devising efficient sampling schemes and analysis procedures in population dynamics studies (Southwood 1966). It is, therefore, not surprising that many ecologists have studied distributions of aphids in cultivated crops (Sylvester and Cox 1961; Forsythe and Cyrisco 1963; Shiyomi and Nakamura 1964; van Emden 1965; Lewis 1966; Shiga 1965; Bullock 1968; Dean 1973; Dean and Lurring 1970; Soong 1974; Sakuratani 1977) and trees of economic importance (Bryant 1976; Dixon 1976). The distributions of colonizing alatae in a field during the initial phases of an infestation have been described as random and as the aphids reproduce, these distributions tend to become contagious or aggregated (Sylvester and Cox 1961; Shiyomi and Nakamura 1964; Shiga 1965).

The present study provided an excellent opportunity to study the distribution patterns of colonizing *A. craccivora* alatae in the experimental plots. In this context, it was interesting to see whether the dispersion of colonizing alatae of this species departed from randomness; and if so, to measure the extent of departure, i.e., the degree of aggregation, by an appropriate mathematical model. As mentioned above in the Methods (see Section 4.2.1), all broad bean stems in both the plots were checked for colonizing alatae at approximately weekly intervals; each sampling occasion therefore provided the data on the distribution pattern of *A. craccivora* alatae. As the aphids in the plots were least affected by the activity of natural enemies between two consecutive observations, the natural enemies could be excluded easily as a possible or contributing cause of the observed pattern of distribution of alatae. A uniform spacing of the seedlings in the plots (0.5x0.5 m)

throughout the studies, provided a homogenous spatial pattern of the plants. Under these conditions any changes observed in the distribution patterns of colonizing *A. craccivora* alatae, could be attributed with a greater certainty to either the rate of influx of alatae or their colonization behaviour. When the rate of influx of invading alatae is minimal relative to the number of colonizable stems, the pattern of dispersion of alatae is random; and this randomness would be merely an artefact due to low density of colonizing alatae per stem (Southwood 1966) and would not explain their aggregative colonization behaviour. It should, therefore, be possible to explain the aggregative colonization behaviour of alatae, only when their rates of influx are substantial. The present study provided many sampling occasions when the rates of influx of *A. craccivora* alatae were substantially higher in the experimental plots (see Tables 4.3 and 4.4, and Appendices XVIII A and B) and the observed aggregated distributions may be attributed to the colonization behaviour of alatae.

All broad bean stems in both the plots were regarded as sampling units at an observation. As each stem had a 'colonizable crown', all the sampling units were regarded as homogenous in the sense of their suitability for colonization by *A. craccivora* alatae (see Section 4.2.2-A). For each observation, a frequency distribution table for the stems with varying numbers of alatae was prepared and mean numbers of alatae per stem ($\bar{x}$) and variance (s^2) calculated. The ratios of $s^2/\bar{x}$ were calculated for all the sampling occasions when *A. craccivora* alatae had been recorded. The observations were grouped into two classes: 1) those with two categories and 2) those with > two categories.

The observations with only two categories, i.e. number of stems each with 0 and 1 alata, were regarded as random, as the χ^2 test for the goodness of fit to any theoretical frequencies could not be applied to these distributions for want of minimum number of categories (see Appendices XVII A and B). The apparent random dispersion of alatae in these observations ($s^2/\bar{x}$ = nearly 1.0) appears to be an artefact due to low rates of influx of alatae in relation to the total colonizable stems in the plots. However, it is interesting to note that, of the 45 observations with colonizing alatae, 36 could be classed under this group. This means that the distributions of colonizing *A. craccivora* alatae are random at many occasions (P = 0.8) essentially due to their lower rates of influx. These results are similar to those reported for other herbaceous aphids (Forsythe and Gyrisco 1963; Shiyomi and Nakamura 1964; Shiga 1965).

For the observations with > two categories, i.e., number of stems each with 0, 1, 2, 3, ... x alatae, and $s^2/\bar{x}$ = nearly 1.0, expected frequencies for Poisson distribution were calculated (Snedecor and Cochran 1962) and χ^2 test was applied. Of the 8 observations, 6 fitted the Poisson distribution (Table 4.2). This means that the random distributions of colonizing *A. craccivora* alatae on these 6 occasions were real but not an artefact due to low rates of influx of alatae; i.e., the presence of an alata on a stem did not influence in any way the settling of other alatae in the experimental plots.

The observations with > 3 categories and $s^2/\bar{x}$ = > 1.0 were regarded as aggregated and fitted to the negative binomial distribution, which adequately describes contagious distributions of insects (Bliss 1958). The negative binomial parameter 'k' was calculated by the

Table 4.2. Results of fitting Poisson distribution to observed distributions of colonizing *Aphis craccivora* alatae in the experimental plots - 1975-77.

Location	Date	O/E	No. of stems with indicated number of alatae (x)			Mean alatae per stem ($\bar{x}$)	s^2	χ^2 l.d.f	P (0.05)
			0	1	>1				
Mortlock	4.11.75	O	237	53	4				
		E	235.7	52.1	6.2	0.2211	0.2615	0.9494	N.S.
	18.11.75	O	59	13	1				
		E	59.4	12.2	1.3	0.2055	0.1933	0.1426	N.S.
	16.3.76	O	35	2	1				
		E	34.2	3.6	0.2	0.1053	0.1508	4.9498	0.05*
	2.11.77	O	258	12	3				
		E	255.6	16.9	0.6	0.0659	0.0839	11.8389	0.01**
	24.11.77	O	298	11	1				
		E	297.3	12.5	0.3	0.0419	0.0468	2.2118	N.S.
Waite	27.10.75	O	82	15	1				
		E	82.4	14.3	1.3	0.1735	0.1655	0.1122	N.S.
	12.10.76	O	82	14	2				
		E	81.6	15	1.5	0.1837	0.1927	0.2628	N.S.
	24.5.77	O	85	12	1				
		E	85	12	0.9	0.1429	0.1443	0.0152	N.S.

O = Observed.

E = Expected.

maximum likelihood method (Method 3) of Bliss and Fisher (1953). According to Bliss and Fisher (1953), the expectations with values of < 5 should be pooled together in applying the χ^2 test, so that no expectation remains < 5. However, Pahl (1969) discussed this commonly accepted rule and assessed the feasibility of grouping data into classes with expected frequencies considerably < 5, i.e., as low as 0.05. He concluded that the grouping of data into smaller classes was allowable. In applying the χ^2 test to the negative binomial distribution, all expectations with < 1.0 were, therefore, grouped so that no expected frequency was smaller than 1.0. This was necessary because, if the expectations with < 5.0 had been grouped, there would be too few classes to fit to the negative binomial distribution.

Of the 11 observations, 10 fitted the negative binomial distribution (Table 4.3 and Appendices XVIII A and B). This means that the distributions of colonizing *A. craccivora* alatae at these 10 observations were significantly clumped or aggregated. According to Southwood (1966) the value of the negative binomial parameter 'k' gives a measure of the degree of aggregation if the sampling units are of same size, and the smaller the value of 'k', the greater is the extent of aggregation (range > 0 to < 8.0). Since the sampling unit in the present study, i.e., a broad bean stem with a colonizable crown, was homogenous for all the sampling occasions, the value of 'k' can be regarded as a valid measure of the degree of aggregation of *A. craccivora* alatae. For the 10 distributions fitted to the negative binomial distribution, the values of 'k' ranged from 0.11 to 1.86 (Table 4.3).

Table 4.3. Results of fitting negative binomial distribution* to the aggregated distributions of colonizing *Aphis craccivora* alatae in the experimental plots - 1976-77.

Location	Date	Total stems N	Maximum alatae per stem	Mean alatae per stem ($\bar{x}$)	s^2	K	χ^2 value	d.f.	P (0.05)
Mortlock	13.10.76	98	4	0.3673	0.4822	1.092	0.4937	1	N.S.
	26.10.76	182	9	1.044	3.0699	0.4544	7.1944	6	N.S.
	3.11.76	123	11	2.1463	5.7489	0.9588	23.0281	8	0.01**
	18.11.76	195	7	0.1641	0.4368	0.1149	0.7072	2	N.S.
	24.11.76	50	10	2.86	9.1433	0.8617	10.1409	6	N.S.
	3.9.77	75	4	0.7467	1.1377	1.143	1.1004	2	N.S.
	13.9.77	95	3	0.4316	0.6096	0.7875	1.1313	1	N.S.
	7.10.77	143	8	0.7692	1.4745	1.1781	2.8069	3	N.S.
	13.10.77	129	10	1.6124	3.2548	1.8596	7.3943	6	N.S.
	27.10.77	263	3	0.2433	0.3375	0.5112	0.8374	1	N.S.
Waite	12.5.77	75	9	1.24	4.0768	0.4831	7.1998	5	N.S.

* See Appendices XVIII A and B also.

Table 4.4. Relationship between high rates of influx of *Aphis craccivora* alatae and the number of colonized stems in the experimental plots 1976-77.

Location	Date	No. of incoming alatae	Rate of influx/day	No. of colonized stems
Mortlock	Oct 13, 1976	36	5.1	31
	26	190	14.6	97
	Nov 3	582	72.8	174
	24	143	23.8	40
	Sept 3, 1977	56	8.0	34
	13	41	4.1	29
	Oct 13	207	34.5	107
Waite	May 12, 1977	93	5.8	61

It is interesting to note that all the aggregated distributions of colonizing *A. craccivora* alatae, were associated with higher rates of influx of alatae (Tables 4.3 and 4.4).

Although the wind direction, wind velocity, wind breaks, topography, height and spacing of plants may influence the deposition of colonizing alatae (see Section 4.1), it is unlikely that these physical factors had influenced the distribution of *A. craccivora* alatae, because of the small size of the experimental plots. The aggregated distributions may, nevertheless, be attributed to the colonization behaviour of *A. craccivora* alatae. This may mean that colonizing *A. craccivora* alatae seem to prefer stems already colonized by one or more alatae for settling, than alata-free stems. The higher rates of influx are prerequisite for the manifestation of aggregative colonization behaviour of the alatae. The aggregative behaviour of colonizing alatae, in part may explain the patchy infestations of this aphid in the field.

4.2.2-D: Colonization behaviour of alatae

Colonization behaviour of alatae is perhaps one of the most difficult aspects to study in the field. Extensive and direct observations in the field (Kennedy *et al.* 1959a, 1959b, 1961; Müller 1958; Farrell 1976), field cages (Woodford 1973) and glasshouse (Russell 1966) have revealed host selection and settling behaviour of a few aphid species which infest crop plants.

Although direct observations were not made on the colonization behaviour of *A. craccivora* alatae in the present study, however, indirect and circumstantial evidence could be obtained from the data regarding

this aspect. A comparison between the number of alatae and the corresponding number of stems colonized in the experimental plots (irrespective of aphid age and morph) between two consecutive observations, reflected the colonization behaviour of alatae (Appendices XV A, B, C and D).

Two conclusions are evident from these results. Firstly, the number of colonized stems exceeded the number of alatae on many occasions; and secondly, when the rate of influx of alatae was high, relatively fewer stems were colonized, indicating aggregation or clumping of colonizing alatae (Table 4.4). When all the observations were pooled together for each location, it became evident that, of the colonized stems, 45% (range 34 to 56) were lacking colonizing alatae and had either nymphs only or nymphs and apterae (Table 4.51). A further classification of the colonized stems according to morph-composition (Appendices XVI A and B) revealed that 23.7% of the colonized stems (range 7.9 to 40.7) had nymphs only (Table 4.52). Obviously these nymphs must have been laid by the incoming *A. craccivora* alatae, because there were no apterae to which to attribute these nymphs, on these stems. These isolated nymphs thus provide circumstantial evidence that *A. craccivora* alatae may have moved away after larviposition on these stems. It is also evident from Table 4.52 that, approximately 10% of colonized stems (range 4 to 20) had alatae only. These alatae were either new arrivals or they had moved from other stems after larviposition. As the proportion of stems colonized with nymphs only, is twice the proportion of stems colonized with alatae only, it can be inferred that either many alatae flew back from the stems after laying nymphs or the alatae which were present on these colonized stems (10% - without nymphs or apterae) had larviposited on

Table 4.51. Proportion of colonized broad bean stems with and without *Aphis craccivora* alatae in the experimental plots 1975-78.

Location	Year	Total colonized stems	Stems with alatae	%	Stems without alatae	%
Mortlock	1975-76	398	175	44.00	223	56.00
	1976-77	599	328	54.76	271	45.24
	1977-78	458	302	65.94	156	34.06
Waite	1975-76	85	48	50.47	37	49.53
	1976-77	140	79	56.43	61	43.57
Total		1680	932	55.48	748	44.52

Table 4.52. Proportion of broad bean stems colonized only by *Aphis craccivora* alatae and nymphs in the experimental plots 1975-78.

Location	Year	Total colonized stems	Stems with alatae only	%	Stems with nymphs only	%
Mortlock	1975-76	398	60	15.08	162	40.70
	1976-77	599	24	4.00	47	7.85
	1977-78	458	54	11.79	94	20.52
Waite	1975-76	85	17	20.00	46	54.12
	1976-77	140	15	10.71	49	35.00
Total		1680	170	10.12	398	23.69

more than one stem. In either case, the concept of the movement of alatae following larviposition, from one stem to another during colonization, has been well established by these results. Consequently, 82% additional stems are colonized due to this inter-plant movement by the colonizing alatae (Table 4.51). In other words, this behaviour increases the colonization efficiency of alatae, i.e., the ratio of the number of stems colonized by alatae to the total number of colonized stems would be 1 : 1.82.

The apparent inverse relationship between the rate of influx of *A. craccivora* alatae and their colonization behaviour seems advantageous to this species. When there are few colonizing alatae, colonization of approximately 82% more stems, is an appropriate compensation to ensure the establishment of the species in a new field or an area. When the rate of influx of alatae is higher, relatively fewer stems are colonized due to aggregative behaviour of the alatae, so that the colonies initiated by many alatae would ensure the establishment of the species in a new area, despite the activities of natural enemies. Such colonies would also produce alata progeny far earlier and also at a higher rate than those initiated with fewer alatae (see Section 3).

It is also evident from Appendix XVI A that the colonization of broad bean stems was consistent without any alatae at Mortlock in January 1976. The presence of apterae was also consistent in the colonized stems at that time. It is probable that some of the nymphs escaped attention when the plants were cleaned of aphids at these observations. Since the temperatures were higher, these nymphs became apterae and reproduced on the stems between two consecutive weekly observations. These results, nevertheless, indicate that apterae are

important for survival of this species through the summer months. This would be advantageous, because during hot and dry summer months the colonizing alatae may be either scarce or suffer high mortalities or may not be successful in locating the scarce and isolated patches of colonizable host plants.

4.2.2-E: Mortality of alatae during rainy periods

Mortality of colonizing *A. craccivora* alatae was observed during rainy periods. The alatae which were found dead on broad bean seedlings in the experimental plots were recorded (Table 4.6). The overall proportion of alatae which died due to rains is 5.7%. This proportion represents a partial estimate of the actual mortality, because it is likely that many alatae might have died and were washed away from the plants and could not be recorded.

Mortality due to rains may adversely affect the success of colonization of *A. craccivora*, especially in areas where the aerial densities of colonizing alatae are minimal, and where heavy falls occur in late autumn, at the time of primary infestation of newly germinated legume pastures.

4.2.2-F: Incidence of natural enemies

The incidence of natural enemies of *A. craccivora* in the experimental plots, is presented in Appendix XIX.

Of the predators, coccinellids and chrysopids were incidental at both the locations during spring of 1975, 1976 and 1977. Syrphids and chamaemyiids were scarce at Waite during spring of 1975 and 1977.

Table 4.6. Mortality of colonizing *Aphis craccivora* alatae in the experimental plots during rainy periods 1975-77.

Location	Date	Total alatae	Dead alatae
Mortlock	Sept 19,1975	3	1
	Oct 21	11	4
	28	17	1
	Nov 4	65	7
	18	15	1
	Oct 26, 1976	190	2
	Nov 3	422	13
	24	143	5
	Sept 3, 1977	56	1
	13	41	15
	Oct 7	114	5
	13	207	9
	Nov 2	19	2
Waite	Sept 11, 1975	6	1
	25	10	2
	Oct 27	17	3
	Nov 6	4	1
	Oct 12, 1976	18	4
Total		1358	77
	Percentage mortality =	5.67	

These predators were active at Mortlock only in spring of 1976 and 1977; the aphid population levels were also high during these years at Mortlock (see Table 4.12; Appendices XV B and C). As the interval between two observations ranged from 7 to 15 days for most of the sampling occasions during these years, the presence of eggs and young larvae of syrphids and chamaemyiids, indicates their active search for newly colonized stems. 1-15 eggs and larvae of these flies were seen on a colonized stem. The aphid population levels were low in spring of 1975 at Mortlock (see Table 4.11 and Appendix XV A) and these predators were also absent. Although the data are insufficient to make any valid conclusions, nevertheless, it appears that syrphids and chamaemyiids would be active and abundant only when the aphid populations are a common occurrence.

The incidence of parasite was also negligible at both the locations in spring of 1975, 1976 and 1977. However, in late autumn of 1977, parasites were active at Waite and approximately 30% colonized stems were parasitized.

The apparent absence of parasites can be explained in two ways. Firstly, *Aphidius colemani* Viereck (syn: *Aphidius platensis* Brethes) is a polyphagous species (Stary 1972; Carver and Stary 1974) and not hot-specific to *A. craccivora*. When *A. craccivora* populations are scarce in an area, it is likely that the parasite populations would be dependent upon the availability and the abundance of other species of host aphids. The isolated and newly established populations of *A. craccivora* in an area would therefore be liable to the parasite attack, only when the other host-aphids are harbouring the parasite populations. Secondly, the sampling interval between two observations

was too short for detection of the parasite activity. Whenever the sampling intervals were about 14 days or more, mummified aphids or aphids with late instar parasite larvae were easily detected on the colonized stems. When the sampling intervals were 7-9 days, parasites could not be detected. This is because it takes between 7 and 10 days at 20-21°C for a parasitized aphid to mummify (Johnson 1959; Gutierrez 1975 - personal communication). It is, therefore, probable that the actual parasite incidence in the experimental plots may have been greater, but could not be detected.

Activity of syrphid and chamaemyiid predators may be detrimental to the establishment and growth of a new colony of *A. craccivora*, merely because of their numbers on a per stem basis. The activities of parasites in late autumn, as noted in May 1977 at Waite, might be detrimental to the establishment and survival of newly founded colonies of *A. craccivora* through winter months. In this respect the parasites have a potential for biological control of this aphid in South Eastern Australia, more so than the predatory syrphids and chamaemyiids, because these predators increase in numbers following a build-up of the aphid populations and that too in late spring and early summer months (see also Section 2.2.3l-D).

4.2.2-G: Presence of alatiform progeny in colonies in the experimental plots

Table 4.7 shows the presence of alatiform nymphs in colonies in the experimental plots. The preceding sampling intervals for the two sampling occasions were 15 to 24 days and it can be inferred that alatiform nymphs appeared among second generation aphids. The proportion of

Table 4.7: Presence of alatiform progeny in *A. craccivora* colonies in the experimental plots 1976-77.

Date	Preceding sampling interval in days	Total number of colonized broad bean stems	No. of colonized stems with alatiform nymphs	Range of total aphids per colonized stem
November 18 1976	15	227	12	< 50 to > 200
October 7 1977	24	129	2	37 to 46

colonized stems with alatiform nymphs was very small - < 1 to 5%. The small size of colonies especially in 1977 (37 to 46 aphids per stem) is characteristic of alata production in *A. craccivora* (see also Section 2.2.34-D).

4.2.2-H: Relationship between area of a host crop and rates of settling of alatae

Does the area of a host crop affect rates of settling by colonizing alatae? In view of the individualistic nature of host plant selection behaviour of alatae (Kennedy *et al.* 1959a, 1959b, 1961), there is no good reason to presume that a smaller host crop area would reduce the rate of settling. This is because the decision by an alata to stay and reproduce following its arrival on a host plant, is determined by its previous flight experience as well as the degree of host plant suitability in the sense of feeding and reproducing stimuli, it receives from the host plant. Further, if the rate of settling of alatae is presumed to be a function of rate of alightment and aerial densities of alatae in a region, then it may be argued that their rates of settling would be unaffected by the area of a host crop and the number of host plants therein.

It is also well known that all alatae that land on host plants do not stay to feed and reproduce, but many do take off again (Kennedy *et al.* 1959a, 1959b). The later flights following a retake-off are less intense and last for shorter durations (Kennedy and Booth 1963a, 1964; Kennedy 1965, 1966). This flight behaviour of alatae implies that they would land in the vicinity of the host plant from which they

flew. According to Kennedy *et al.* (1959a, 1959b) the successive reduction in the flight duration would increase the probability that alatae would land again on a host plant. This implication is based on the tendency of the plants to grow together in patches or clumps in nature (Kennedy *et al.* 1959a, 1959b). However, if a patch of host plants is so small that even a trivial flight of a short duration would carry an alata away from that patch, then the smallness of the patch could be regarded as influencing the settling of alatae. Conversely, in a larger area of a host crop, the probability that an alata would land again on a host plant following one or many successive trivial flights, would be higher and consequently a higher number of alatae would settle ultimately than might be expected in a smaller area of a host crop.

The observations on settling of *A. craccivora* alatae indicate approximately equal numbers of alatae in the two adjacent plots (see Appendix XV-A, B, C and D). These results suggest that the number of settled alatae is positively related to the area of a host crop and the rate of settling and colonization is probably dependent upon the aerial abundance of alatae in a locality. It can be concluded from these results that the rate of settling and colonization by *A. craccivora* alatae is not influenced by the area of a host crop.

4.3: Infestations of mature broad beans at Mortlock and Port Clinton in late spring 1976

Mature stands of broad bean were sampled by stratified systematic sampling for *A. craccivora* infestations at Mortlock Experiment Station and Port Clinton in early November 1976.

The area of the plot at Mortlock was 800 square metre (50x16 m). Samples of 20 stems each were observed along 3 parallel transects (50 m each). The transects were 10 paces apart and 5 paces away from the border rows. Six samples were observed at intervals of 10 paces along each transect. The results are presented in Table 4.81.

It is evident from Table 4.81 that 68% of the sampled stems were infested. Each infested stem had 12 to 20 cm long colonies. The aphids were aggregated on basal leaves and developing pods also. The colonies were producing many alatae. The natural enemies of the aphid were also active but seemed to have little effect on aphid populations.

Two plots were sampled at Port Clinton. Eighteen samples, each comprising 20 stems, were observed along 3 transects in Plot I. In Plot II, eighteen samples of 10 stems each were observed along 6 transects. The transects were parallel to the length of the plots. The results are presented in Table 4.82.

Only 7% of the sampled stems were infested at Port Clinton. The infested stems had 5-10 cm long colonies. Many stems which had been infested previously were free of aphids. Syrphid and chamaemyiid larvae were abundant on colonized stems. The crop was stunted in growth due to poor soil moisture. It appeared that the poor plant growth due to lack of rains and natural enemy activities had influenced considerably the aphid incidence at Port Clinton.

4.4: Primary infestation of young broad beans at Mortlock in early spring 1977

Observations on the rates of primary infestation (colonization by

Table 4.81. Infestation of mature broad beans* by *Aphis craccivora* at Mortlock in early November 1976.

Sampling point	No. of infested stems
1	20
2	20
3	19
4	14
5	2
6	5
7	16
8	13
9	13
10	15
11	6
12	20
13	11
14	17
15	20
16	7
17	17
18	10

Total stems sampled	Total infested stems
20 x 18 = 360	= 245

Percentage infestation = 68.06

* Area of plot 832 sq m. (50 x 16 m).

Table 4.82. Incidence of *Aphis craccivora* in two plots of mature broad beans at Port Clinton in early November 1976.

Sampling point	Plot I*	Plot II**
1	0	2
2	0	0
3	2	0
4	10	0
5	2	0
6	3	0
7	3	4
8	2	0
9	3	0
10	1	0
11	0	0
12	0	1
13	0	2
14	0	0
15	0	1
16	0	2
17	0	0
18	0	0
Total	26	12

Total stems sampled = 540 Total infested stems = 38

Percentage infestation = 7.04

* 20 stems/point; Plot size 60 x 22 paces.
** 10 stems/point; Plot size 51 x 47 paces.

A. craccivora alatae) were made in August 1977 in a plot of 4 week old broad beans (78x50 m) at Mortlock Experiment Station. The beans germinated by 25th July. The young seedlings with 2-3 opened leaves were free of aphids on 6th August. The plants were sampled on 19th August by stratified systematic sampling. Samples of 20 stems each were observed along 4 parallel transects (78 m). The transects were 17 paces apart and 8 paces away from the border rows. Five samples were observed at intervals of 21 paces along each transect. The numbers of infested stems, alatae, apterae and total aphids per infested stem were recorded. The results are presented in Table 4.9.

It is evident from Table 4.9 that, of the 50 infested stems, only 8 had 1-2 first generation apterae each. These observations indicated that secondary infestation by apterae had not started until the sampling and the observed rates of infestation could be attributed with a greater probability to the primary infestation by colonizing alatae. The numbers of total aphids per infested stem ranged from 1 to 20. The colonized stems were free of natural enemies.

It is interesting to note that of the 50 total colonized stems (Table 4.9), the number of stems which had nymphs only was 28, compared to 14 stems which had colonizing alatae. This means that 200% additional stems (excluding those with first generation apterae) were colonized by the alatae. These observations thus support conclusions of the observations in the experimental plots that *A. craccivora* alatae may move away from one stem to another during colonization and that 82% additional stems are colonized due to the inter-plant movement by the alatae (see Table 4.51 and Section 4.2.2-D).

Table 4.9. Primary infestation of four-week old broad beans* by *Aphis craccivora* at Mortlock in late August 1977.

Sampling point	Total alatae	Total infested stems	No. of stems with alatae	No. of stems with first generation apterae
1	2 D	4	2	0
2	1	3	1	1
3	0	2	0	0
4	0	2	0	0
5	0	2	0	0
6	1	3	1	0
7	0	3	0	1
8	0	4	0	0
9	1 D	4	1	0
10	0	0	0	0
11	0	2	0	1
12	0	3	0	1
13	1	1	1	0
14	1 D	2	1	1
15	0	0	0	1
16	1 D	4	1	0
17	4	6	3	2
18	1 D	1	1	0
19	0	1	0	0
20	2	3	2	0
Total	15	50	14	8

Total stem sampled = 20 x 20 = 400	Total infested stems = 50	Percentage infestation = 12.5
	Total alatae = 15	Mean alatae per stem = 0.04

D = Alatae with distorted wings.

* Area of plot = 3900 sq m. (78 x 50 m).

The mean rate of primary infestation was very low - 0.04 alata per stem (Table 4.9). These results imply that multiple influxes of alatae together with recolonization by apterae and alatae which are produced later within an infested crop may be far more important in determining the extent of infestation of a crop by *A. craccivora*.

4.5: Observations on survival of the aphid in summers - 1976-77 and 1977-78

Dry and hot summer months (December to February) are crucial for the survival of *A. craccivora* populations in South Eastern Australia because of the scarcity of host plants (Gutierrez *et al.* 1971, 1974b). Observations on the summer survival of this aphid are therefore ecologically important.

Young broad beans were colonized by *A. craccivora* at Waite grounds in January and February during 1975, 1976 and 1977. Observations in January 1978 revealed survival of the aphid on barrel medic (*Medicago truncatula* var. *longispina*), common burr medic (*Medicago polymorpha* var. *vulgaris*) and subterranean clover (*Trifolium subterraneum*) in the irrigated lawns at Waite grounds. The aphids were recorded on isolated common burr medic plants also which were growing near the bases of irrigated grape vines in Claremont Orchard of the Waite Institute. Also, *A. craccivora* colonies were recorded in lucerne (*Medicago sativa* cultivar Hunter River) plots at Northfield Research Station (North East suburb of Adelaide) and on isolated lucerne plants in backyard gardens in Adelaide suburbs in January 1978 (Carver - personal communication). The aphid was breeding on young shoots of *Wisteria* vines also at the Waite in January 1978.

A visit to dairy towns of Jervois and Mypolonga along the River Murray (50-70 km South-east of Adelaide) in January 1978 did not indicate aphid incidence on white clover (*Trifolium repens*) and strawberry clover (*Trifolium fragiforum*) in flood-irrigated mixed pastures and sprinkle-irrigated lucerne. A small colony was observed on shaftal clover (*Trifolium resupinatum*) at Mypolonga . Observations in irrigated and non-irrigated lucerne at Mortlock Experiment Station in January 1977 and January 1978 did not indicate *A. craccivora* infestations. These plants were heavily infested with the newly introduced spotted alfalfa aphid (*Therioaphis trifolii* B.).

These observations indicate that *A. craccivora* survives the hot and dry summer on sheltered and irrigated patches of isolated host plants in lawns and backyard gardens in the suburbs around Adelaide.

4.6: Summary

Colonization of young broad bean seedlings in the experimental plots at Mortlock Experiment Station indicated peaks of influx of *A. craccivora* alatae in early November during 1975 and 1976, and in mid-October in 1977. Small numbers of colonizing alatae were also consistent during March to May. A similar pattern of alata influx was observed at Waite Institute also.

An analysis, based on the numbers of colonizing alatae per stem, indicated three features of their dispersion pattern in the experimental plots. Their distributions were random at many occasions ($P = 0.8$), due to their lower rates of influx; random distributions approximating

to the Poisson distribution were observed; and aggregated distributions approximating to the negative binomial distribution were also observed when the rates of influx of the alatae were higher.

A relationship between numbers of colonizing alatae and numbers of colonized stems in the experimental plots, reflects the colonization behaviour of *A. craccivora* alatae. Circumstantial evidence indicated inter-plant movement of colonizing alatae when their rates of influx were lower; at higher rates fewer stems were colonized due to their aggregative behaviour. Wing distortion and mortality of colonizing alatae were a common occurrence during rainy periods.

Syrphid and chamaemyiid flies were efficient in searching newly colonized stems in the experimental plots. These predators were active at Mortlock in late spring in 1976 and 1977 when the rates of influx of alatae were high. The Aphidiid parasite (*Aphidius colemani* V.) was active at the Waite in May 1977. Alatiform nymphs were recorded in colonies in the experimental plots at Mortlock in November 1976 and October 1977.

Stratified systematic sampling of mature broad beans at Mortlock and Port Clinton in early November 1976 indicated 68 and 7% infestation by *A. craccivora*. Observations on primary infestation of a 4 week old broad bean crop at Mortlock in mid-August 1977 indicated a very low rate of influx of alatae - 0.04 alata per stem. The number of colonized stems with isolated nymphs was twice the number of stems with colonizing alatae.

A. craccivora survives hot and dry summers in sheltered and irrigated patches of isolated host plants in lawns and backyard gardens in suburbs around Adelaide.

SECTION 5

DISCUSSION

The experiments reported in this thesis were designed to measure migration and define its role in the population system (Southwood 1972) of the cosmopolitan *Aphis craccivora* in the South Australian environment. The questions which gave rise to the present study (see Section 1.8) were answered by a systematic study of migration and dispersive behaviour of this insect. This required not only an assessment of the inherent migratory potential of this species, but also the probability of realisation of this potential within the environmental constraints of a given habitat. Secondly, it was also important to demonstrate that emigration could regulate the numbers of this aphid in its natural populations. Both immigration and emigration were studied. A study of flight behaviour of alatae was also necessary, as flight is a prerequisite for long distance migration and recolonization. The experiments on colonization (Section 4), migrant production (Section 2), and flight behaviour (Section 3) of *A. craccivora*, were thus inter-related and linked into a logical sequence.

The 'concept of colony' of aphids on a host plant as an independent and biologically functional unit (Way 1968, 1973) was basic to the hypothesis of the present study (Section 1.8). The unit of experimental population, selected for the study was, therefore, a colony of aphids on a host plant. This approach was not only simple but also realistic. After all, in the field, *A. craccivora* live in aggregates on spatially discrete host plants, each aggregate being a self-sustained and self-regulated unit of a local population system.

The principle implicit in such an approach was that the local abundance and population dynamics of a migratory aphid species, such as

A. craccivora in a crop, could be better understood by an integration of studies at two levels i.e., at the level of a colony and also at the level of groups of colonies which constitute a natural population in a field or an area. The genetical, physiological and ecological processes, at both an individual and a population level, which operate within a population unit i.e., a colony, would mainly determine the changes in the numbers of aphids of that population unit. For this reason, such a population unit i.e., a colony of aphids on a plant, may be regarded as a super-individual. The average number of such population units per unit area, their spatial distribution, their mean densities, their rates of population increase, the frequencies of establishment and extinction of these population units in time, and the movements of individual aphids among these population units, would determine the probability of survival and the local abundance of an aphid species in a geographically defined area.

Both these levels of studying aphid population dynamics are relevant to the present study, although more emphasis has been placed on studies at the level of a colony of *A. craccivora* as a unit of its population system (Section 2). The experiments and observations on the colonization behaviour of this aphid represent studies at the level of groups of its colonies in the field (Section 4). The relevance and profitability of such an approach to the study of population dynamics of *A. craccivora*, is discussed later.

The relationship between growth habit of broad bean plants and colonization by *A. craccivora* appears advantageous to this aphid in two ways (see Section 2.2.3l-A and Appendix II). Firstly, the crowns consist of meristematic tissue and the colonizing aphids and their progeny can feed on nutritionally superior sap; as a result, large and more fecund apterae can

be produced. From an ecological point of view, these apterae may be useful for early establishment of a colony in a new habitat. Secondly, as broad bean plants grow, they go on producing new axillary basal shoots for 8-12 weeks and thus provide the colonizing aphids with a continuous supply of meristematic crowns. Similar growth habits of other legume hosts such as groundnuts, medics and clovers, etc., would also be beneficial to *A. craccivora*.

Results of Experiment I on colony growth and alata production (Section 2.2.3) provide an insight into the changing age-structure and also provide a quantitative information on emigration potential of the experimental colonies. The total population and the number of the first and second instar nymphs in a colony prior to the start of dispersal by alatae and apterae, are dependent on the number of apterae (Figures 2.17 and 2.18). The term 'dispersal' in the context of Experiments I and II, has been used to describe the movements of adult aphids off the host plants in field cages. Dispersal by apterae, resulted in reduced production of new nymphs in the colonies (see Figure 2.14 and Appendix II). It is also interesting to note that the ratios of first instar nymphs to apterae, remained more or less constant prior to the start of dispersal by alatae and apterae, in the colonies which varied in size from about 35 to over 3,000 aphids (Figure 2.19). These results indicate two aspects of population growth in *A. craccivora* colonies. Firstly, the absolute numbers of apterae (not their percentage) determine total population of a colony. Secondly, the production of nymphs per aptera, remains more or less constant as the total population increases until after the start of dispersal. In other words, there is no evidence of density-dependent reduction of fecundity of apterae, in the colonies of *A. craccivora* in relation to increasing density, prior to the start of dispersal.

It can be concluded from these results (Figure 2.19) that reduction in the numbers of new nymphs in *A. craccivora* colonies is brought about by the emigration of apterae rather than by their reduced fecundity. So relatively fewer apterae stay in a colony and contribute to its nymphal population. This mechanism of decline of numbers in colonies of *A. craccivora* is not unexpected in view of the main thrust of its biology towards emigration, as an evolved adaptation. These results in *A. craccivora* are similar to those of Ito (1952a, 1952b, 1960) who suggested that *Aphis glycines* M., *A. maidis* F., *Macrosiphum avenae akebiae* S. and *Rhopalosiphum padi* L. (=*R. prunifoliae* F.) avoided intraspecific competition by emigrating as apterae, before crowding could decrease their fecundity.

These results are however different from the results of similar studies in *Aphis fabae* S. (Way and Banks 1967; Dixon and Wratten 1971) and *Brevicoryne brassicae* L. (Hughes 1963; Way 1968). Way and Banks (1967) reported slow multiplication rates of reproducing apterae in colonies of *A. fabae*, when the number of apterae increased to more than 16. Hughes (1963) maintained that reduced fecundity of apterae in dense colonies of *B. brassicae* was an intraspecific stabilising mechanism, which helped populations to persist. Way (1968) concluded that the changes in numbers of progeny of *B. brassicae*, were not due to the changing numbers of reproducing apterae but because of their reduced fecundity due to crowding. The proportion of apterae remained remarkably constant at about 7% in *B. brassicae* colonies with 100 to over 5,000 aphids. Reduced fecundity in relation to increasing populations, has been reported for other aphid species also, such as *Drepanosiphum platanoides* S. (Dixon 1975), *Eucallipterus tuliae* L. (Dixon 1971a) and *Microlophium carnosum* B. (Perrin 1976).

These contrasting results in *A. craccivora* and other aggregating aphids, such as *A. fabae* and *B. brassicae*, indicate that aphid species differ in their self-regulating mechanisms and these mechanisms perhaps reflect the differences not only in their biologies but also in their adaptations to the nature and growth habits of their host plants.

Results of Experiment I (Section 2.2.3) also provide a measure of emigration potential of *A. craccivora* colonies in the absence of natural enemies and in nearly-natural field conditions. The proportion of alatiforms among third instar nymphs in a colony of *A. craccivora* can be regarded as the best measure of its potential rate of emigration, for the reasons discussed earlier (see Section 2.2.34). The destructive sampling of the experimental colonies of same age, which were initiated with one alata, not only helped in pin-pointing the appearance of alatiform progeny in relation to age and size of a colony, but also provided a picture of changes in the potential rate of emigration. Alatiform nymphs were first observed in 18 day old colonies which had over 300 aphids (Figures 2.20 and 2.21). The potential rate of emigration varied between 75 and 97% in the colonies with 550 to over 4,000 aphids, until the colonies were 52 days old (Figures 2.20 and 2.21).

A relationship between crowding and alata determination, in the experimental colonies, was worked out by two methods (Figures 2.22 and 2.23). This relationship indicated that in a colony of *A. craccivora* on broad bean with 92 to 108 aphids, 50% of its first instar nymphs would probably become alatiform; at populations of more than 120 aphids per colony, approximately 90% of first instar nymphs would be alatiform.

These results indicate that *A. craccivora* colonies not only produce alatiform progeny within a short period after their inception, but also keep on producing a high proportion (> 85%) until the colonies begin to decline in numbers. Data in Appendix II show declining aphid populations in a few colonies, sampled at 45, 52 and 60 days, as the host plants had deteriorated considerably. The potential rates of emigration in these declining colonies varied between 54 and 85% (Figure 2.20). What is evident from these results is that the alata production in *A. craccivora* is not a density-dependent process (Figure 2.21).

Alata production in herbaceous aphids is a population process which manifests itself in response to various environmental factors, experienced by aphids within a colony. Johnson and Birks (1960) and Johnson (1959, 1959a, 1965, 1966a, 1966b) studied the effects of various environmental factors on wing determination in *A. craccivora* in laboratory. Johnson and Birks (1960) suggested that all aphids began development as presumptive alatae and that the course of development in *A. craccivora* was from winged to winglessness, and that it was an irreversible process. They also suggested that a decision whether an individual would become winged or wingless could be made between the embryonic stage (prenatal) and the second moult after birth (postnatal). Among the factors which may directly influence the course of development of an aphid, Johnson (1965, 1966a, 1966b) regarded temperature and photoperiod as primary factors. Lower temperatures (10 to 20^{o}C) and shorter photoperiods (8 to 12 hours) favoured wing development, whereas higher temperatures (25 to 30^{o}C) and longer photoperiods (12 to 16 hours) favoured the apterous condition. Tactile stimulation among the mothers as well as the young nymphs favoured wing development. Similarly, the condition of host plant also had

prenatal and postnatal effects. Young broad bean seedlings favoured apterous condition; matured and aged broad bean plants favoured wing development. Crowding and host plant influences were regarded as secondary factors. Starvation of mothers and young nymphs favoured apterous development. Ant attendance during first and second instars also favoured apterous development (Johnson 1959a). Mechanical injuries inflicted on nymphs after second moult and parasitization suppressed wing development (Johnson 1959) and resulted in intermediate adults which looked more like apterae but had rudimentary wings.

The theory of Johnson and Birks (1960) gets strength from the well planned experiments, in which a distinction between prenatal and postnatal diversion was well emphasized. Further, the theory rests heavily on histological evidence of the presence of wing analgens in each of a large number of fully formed embryos and first instar nymphs, which were laid by both apterae and alatae. The authors also showed that nearly all the progeny of alatae, laid during the first three days of their reproductive lives, developed into apterae on broad bean leaf discs. However, among the nymphs laid later until 15 days, 55 to 69% developed into alatae.

Lees (1975) gives a summary of experimental work on aphid dimorphism and concludes that, in general, the interactions between aphids and to a lesser extent the kind of food, are the factors usually associated with the control of alary dimorphism. He also concludes that both these factors act on the same endocrine system although routed through different sensory pathways i.e., tactile and gustatory. The findings of Johnson (1965, 1966a, 1966b) in *A. craccivora*, however, differ from this general conclusion (Lees 1975) and it is clear that aphid species

differ in their responses to environmental factors regarding alary dimorphism. Perhaps, the anholocylic nature of *A. craccivora* may also make this species different in this respect.

The observed high rates of emigration in the experimental colonies of *A. craccivora* (Figures 2.20 and 2.21) are not unexpected; these results provide field evidence in support of the findings of Johnson (1965, 1966a, 1966b). It is evident that the temperatures, the photoperiod, and the conditions of host plants, used in these experiments may have contributed to higher rates of emigration. Temperature and photoperiod not only have direct effects on morph determination but also affect growth and developmental physiology of host plants in the field. It is, therefore, difficult to distinguish between the direct and indirect effects of these factors in the field. The results of Experiment I, thus represent the outcome of an interaction of all the environmental factors (except ant attendance) which may influence alata determination in *A. craccivora* colonies in the field.

An interesting outcome of these results is the quantitative assortment of apterae and alatae in the colonies. The proportions of apterous nymphs mostly varied between 5 and 15% (Figure 2.20), and this small proportion not only maintained high rates of alata production, but also helped the persistence of the colonies until the host plants deteriorated.

There is another explanation for the observed high rates of emigration in *A. craccivora* colonies. Most of the nymphs laid by the colonizing alatae during their earlier phases of reproduction became apterae in the newly established colonies (see Appendix III). Alatiform nymphs appeared among the nymphs laid by the first generation apterae. It is also probable that the nymphs laid by the colonizing alatae during

later phase of their reproduction, may have also become alatiform. Generally, in parthenogenetic and viviparous herbaceous aphids, the appearance of alatiform nymphs among the progenies of apterous adults, is a common occurrence. This generalisation is relevant to *A. craccivora*, as Johnson and Birks (1960) observed well developed wing anlagen in the first instar nymphs laid by apterae. Also, it is less common to expect alatiform nymphs among the progenies of alatae viviparae. In this context, if apterae are the predominantly reproducing morph in a colony, because of emigration of their counterpart alatae away from that colony, then a constant high proportion of alatiform nymphs can be expected, until alatae also begin to reproduce in that colony. This is exactly what had happened. In some of the caged colonies which were sampled at 52 and 60 days, a considerable number of alatae were also reproducing and, their progenies were probably increasing the proportions of apterous nymphs; consequently the proportions of alatiform nymphs in third instar in these colonies declined from 75 to 55% (Figure 2.20). What becomes obvious from the foregoing discussion is that the flight behaviour of alatae is also an important factor which affects the potential rate of emigration of a colony. If alatae of an aphid species do not fly away and, instead, reproduce in a colony then high proportions of apteriform nymphs can be expected in that colony and consequently dense colonies with high aphid populations would result on host plants. This is true for the newly introduced spotted alfalfa aphid (*Therioaphis trifolii* M.), which forms dense colonies on lucerne in South Australia in summer months. Messenger and Force (1963) also reported poor alata dispersal and increased populations in *Therioaphis maculata* B. on alfalfa until the host plants collapsed.

Production of higher proportions of alatiform progeny at higher populations (Figure 2.21) would result in dispersal of many colonizers in a locality. The enormous numbers of the colonizers would increase the probability of success of colonization and establishment of this species elsewhere. These results (Figure 2.21) thus provide empirical evidence in support of the hypothesis that *A. craccivora* is a super-migrant species (Gutierrez *et al.* 1974a).

The relationship between population density per stem and the proportions of alatiform nymphs on subterranean clover (Figure 3 of Guttierrez *et al.* 1974a), however, does not support the preceding hypothesis. The proportion of alatiform nymphs shown by this relationship declines drastically to zero at higher aphid densities. Also, this relationship is one of the most important inputs in the model of *A. craccivora* populations in temperate legume pastures of South Eastern Australia (Gutierrez *et al.* 1974a). It may well be argued that the aphid would respond differently to different host plant species. However, it is unlikely that the sequence of population events during the growth of a colony of *A. craccivora* would be any different on different host plant species. The total population of a colony and the time of start of dispersal may vary according to host plant characteristics (see Section 2.3) but a drastic reduction in the proportions of alatiform progeny in relation to higher population of a colony may hardly be expected merely because of a different host plant species, under a given set of weather conditions. I, therefore, suggest that this relationship, given by the authors, needs a considerable improvement as the outputs of the model rest heavily on this single relationship. Two examples of such outputs are: the ratios of total

alatae and total apterae, produced at various times and with different initial rates of infestation, have been regarded as criteria for optimum alata production in *A. craccivora* populations on burr medic and subterranean clover; and the effects of different biotic mortality factors in reducing the total alata production have been regarded as criteria for a successful biological control agent.

A survey of literature shows that only a few aphid species produce higher rates of alatae than *A. craccivora* in their natural populations. For example, the maximum rates of alata production in *Brevicoryne brassicae* L. (Hughes 1963), *Microlophium carnosum* B. (Perrin 1976) and *Aulacorthum solani* K. (Kazino 1971) are 70%; 63% in *A. fabae* S. (Way and Banks 1967); 50% in *Melanaphis pyrarius forma sacchari* Z. (van Rensburg 1973); and 85% in *Macrosiphum rosae* L. (Maelzer 1977).

The maximum rates of alata production in laboratory studies were 80% in *Acyrthosiphon pisum* H. (Sutherland 1969) and *Rhopalosiphum insertum* H. (Dewar 1976); 94% in *Dysaphis devecta* H. (Forrest 1974); 69% in *Rhopalosiphum padi* L. (Dixon and Glen 1968); 66% in *Myzus persicae* S. (Kazino 1971); and 60% in *Therioaphis maculata* B. (Toba *et al.* 1967). The main question arising from these laboratory studies is: how often would these potentials for alata production be realized under natural field conditions? For example, at a density of nearly 1,000 aphids per rose bud, 85% alatae were produced in experimental colonies of *Macrosiphum rosae* in the field, but the numbers of aphids per rose bud rarely reach up to 500 in natural populations of this aphid (Maelzer 1977). The results of Experiment I on alata production (Figure 2.21) represent a more realistic situation.

Production of alatae in aphid colonies and their emigration has been regarded as a density-dependent and intraspecific stabilising mechanism by some ecologists (Hughes 1963; van Rensburg 1973; Gutierrez *et al.* 1974a; Farrell 1976). This is a sweeping generalisation and a thorough analysis of this statement is justified. It seems appropriate here to make a distinction between 'alata production and emigration' on one hand and a 'density-dependent intraspecific stabilising mechanism' on the other, in colonies of herbaceous aphids in general. These two terms are not to be confused with each other, as they represent two different processes.

Alata production and emigration, as discussed earlier, is an evolved adaptation and an integral part of the biology of an aphid species. Each aphid species has its own genetic mechanism which operates in response to its total and immediate environment i.e., temperature, photoperiod, condition of host plant and the extent of crowding, etc., and results in production of varying proportions of winged and wingless progeny. Further, the morph and generation status of reproducing aphids in a colony also influences the extent of production of alatae. The emigration of alatae involves a specialized behaviour, characteristic of migratory insects (Kennedy 1961, 1975), which takes them away from a colony through active and persistent flight. Prevailing temperatures and light intensities determine whether or not flight occurs (Taylor 1957, 1965). Neither the alata production nor the flight behaviour, which are the components of emigration in an aphid colony, appear to be influenced solely by the density of a colony.

Production of higher proportions of alatae in dense colonies on old and deteriorating host plants, has often been regarded as a density-dependent process (Hughes 1963). The quality and the quantity

of plant sap on which aphids feed in old and deteriorating host plants, may be as important a factor as crowding, experienced by aphids due to high density, for the production of high proportions of alatae. There is no good reason to emphasize the role of density at the expense of the role of nutrition, provided by the old and deteriorating host plants.

The term 'intraspecific stabilising mechanism' (Hughes 1963) necessarily has a connotation of suppressing or counteracting effect on the rate of increase of an aphid population, whereas 'emigration by alatae' may or may not contribute to suppression of a population. These two terms are, therefore, not synonymous with each other. It is not the nature of the emigration itself, but its intensity and the extent of this process, relative to birth rate and immigration, which is important as far as stability or decline of an aphid population is concerned. The need for stability or persistence of a population in time is also implicit in the term 'stabilising mechanism'. For example, when the host plants are scarce or too difficult to be located for initiation of new colonies, prolonged persistence of the existing colonies in an area would be an immediate need. Minimisation of over-exploitation of the existing host plants would be desirable; under such circumstances, emigration by alatae may contribute to decline of a population and can be regarded as a stabilising mechanism; consequently, the prolonged survival of declining colonies can be achieved.

A constant high rate of emigration in *A. craccivora* colonies until the host plants deteriorate and collapse (Figures 2.20 and 2.21), does indicate that the production of colonizers (alatae) is the immediate need in this aphid, rather than the persistence and prolonged survival

of its colonies on deteriorating host plants. In this context, the alata production and alata emigration in *A. craccivora* cannot be regarded as a density-dependent intraspecific stabilising mechanism, but that emigration can be regarded justifiably and in its own right, as an integral part of the life history of this aphid (Dingle 1972, 1974).

The consequences of emigration by *A. craccivora* alatae may be different in individual colonies. If the losses by emigration are equal to birth rate and immigration, emigration in a colony would then have a stabilising influence. If the losses by emigration exceed the birth rate, then emigration can be regarded as the regulating factor for population changes in a colony. Once emigration has a regulating influence, the aphid population in a colony would continue to decline and the colony would perish ultimately, rather than persisting at a more or less stable size. In this context, the size of a colony at which the losses by emigration equal its birth rate, can be regarded as its 'upper size'. The upper size of a colony depends on host plant characteristics (see Sections 2.2.3l-B and 2.3.5).

Results of Experiment I (Section 2.2.3) also provide an estimate of the numbers of alatae, which a colony of *A. craccivora* can produce on a two week old broad bean plant, colonized by one alata, in the absence of natural enemies (Table 2.2). These results indicate that broad bean is a favourable crop for the production of high densities of *A. craccivora* alatae per unit area, during winter in South Australia. The total number of alatae which can be produced on a broad bean plant under natural conditions, would however vary, depending on the presence and activities of natural enemies. Other factors such as cultivars

of broad bean, age at infestation and the interval between colonization and maturity of the crop in a season, would also influence the extent of alata production. The results in Table 2.2 get support from the observations of natural infestations of *A. craccivora* on mature broad beans at Mortlock in early November 1976 (see Section 4.3). On the basis of these results, I predict that *A. craccivora* has the potential of attaining a pest status in South Australia during winter-spring, if broad beans are grown on a large scale, especially so in the coastal areas of the state, where temperatures, from June to October, are such that this aphid can complete 4 generations during this period (Year Book of South Australia 1978).

However, whether or not a broad bean crop in South Australia can be infested heavily with *A. craccivora*, would depend to a greater extent on temperatures that would prevail soon after the germination of the crop. If the daily maximum temperatures remain > 16-17^{o}C for a considerable period, a greater probability of colonization of a young crop can be expected (see Section 3).

Results of Figure 2.30 indicate variation in the rates of dispersal of alatae among the six caged colonies. It is evident that individual colonies differed in this respect. These results imply that the extent of alata production and dispersal in *A. craccivora* is related to the size of its colonies. This means that the abundance of the alatae in an area would be dependent on the upper size of its colonies i.e., host plant species on which larger colonies can develop, would produce more alatae per unit area than those which can support smaller colonies. Results of Experiment II (Section 2.3.4) support this implication.

It is also evident from Figure 2.30 that the rate of dispersal of alatae is postively related to the age of the colonies. This means that in an area, higher aerial densities of *A. craccivora* can be expected at the maturity of its host crops. The observed peaks of colonizing *A. craccivora* alatae in the experimental plots at Mortlock in early November 1975 and 1976 and in mid October 1977 (see Tables 4.11 and 4.12) support this conclusion.

Results of Experiment II (Section 2.3.4) have been discussed briefly in their respective sections. These results are especially relevant to the hypothesis of this study. They describe the interactions of initial numbers of colonizing alatae and host plant species on the production and emigration of alatae and apterae.

These results provide additional field evidence in support of the theory of wing determination in *A. craccivora* (Johnson and Birks 1960), as alatiform nymphs among the first generation aphids were observed in most of the experimental colonies (Tables 2.31 and 2.32). Initial number of colonizing alatae had no effect on the time of appearance of alatiform progeny on common burr medic and broad bean plants. However, on lucerne and subterranean clover, alatiform nymphs appeared only in the colonies which were initiated by 4 and 8 alatae, at 19 days after colony inception. This indicated that the effect of initial number of colonizing alatae, had complementary effect on the production of alatiform progeny among the first generation aphids on these host plants.

Although the alatiform nymphs were seen in the colonies 19 days after start of the experiment, alata dispersal in the cages was not

observed until 39-42 days (Table 2.33). The reason for this apparent delay in alata dispersal is unknown. However, it seems likely that the alatae were prevented from flight by the prevailing low temperatures and settled on the plants without flight. It is also probable that the flight behaviour of first generation alatae (progeny of alatae viviparae) may be different from those alatae, laid by apterae viviparae. Even if the latter possibility was true, it would not have been ecologically significant because of the over-riding flight inhibiting influence of low temperatures, and the alatae would have eventually settled on the host plants without flight.

A meaningful understanding of the observed emigration in the experimental colonies (Sections 2.3.43 and 2.3.44), was made by two approaches. The parameters used in the first approach were the periods of dispersal and the rates of dispersal over those periods. In the second approach, the mean cumulative number of alatae, and apterae, which dispersed from a colony with the same colonization density on one host plant species, were compared statistically by two-way analysis of variance. It was, therefore, possible to compare the effects of colonisation densities on the rates of dispersal of alatae and apterae on different host plant species on one hand, and also to assess the interactions of the colonisation densities and the host plant species on the output of emigrants on the other.

It is evident from Figures 2.31, 2.32 and 2.33 that the rate of dispersal of alatae was related to initial numbers of colonizing alatae in the colonies. The period of alata dispersal in the colonies with 4 and 8 alatae was shorter than the period in the colonies with 1 and 2 alatae (Figures 2.34, 2.35 and 2.36). The combinations of high

rates of alata dispersal and shorter dispersal periods in the colonies with 4 and 8 alatae and lower rates of alata dispersal for longer periods in the colonies with 1 and 2 alatae, signified that the initial colonisation densities had influenced the rate and the pattern of alata dispersal on a host plant species without affecting the total output of alatae from a colony. Results of analysis of variance also indicated that initial colonisation densities had no significant effect on the output of dispersing alatae (Table 2.34). The implication of these results is that the output of *A. craccivora* emigrants from a crop would not be influenced by the colonization behaviour of the alatae but that the start of alata dispersal and the numbers of dispersing alatae in time would vary according to the number and the distribution of different sized colonies in the crop.

Significant differences in respect of total dispersing alatae were observed between the host plant species (Table 2.34). More alatae dispersed from the colonies on broad bean and common burr medic than from subterranean clover, and there were no significant differences in this respect between broad beans and common burr medic (Table 2.35). It is essential to point out here that in the colonies initiated with one alata on broad beans, *Macrosiphum euphorbiae* were also breeding. Further, these colonies were attacked by the parasites (*Aphidius colemani*) at a later stage (see Appendix XI). The colonies initiated with 8 alatae on broad beans were also attacked by the parasites (Appendix XI). If these colonies had not been contaminated with *M. euphorbiae* and the parasites, it is probable that many more alatae would have dispersed from broad beans. What these results imply is that under identical conditions of colonisation and weather, more alatae would disperse from a unit area of broad beans than from an equal area of subterranean clover. These differences between host plant species

in respect of their capacities to produce emigrants, point out the importance of their structure and surface area on which the aphids not only feed but also form colonies. Thus, in the context of the definition of resources as a component of environment of an animal species (Andrewartha and Birch 1954; Andrewartha 1961), a host plant should be regarded not merely as a source of nutrition for aphids but also as a place for them to live. As Dixon (1977) points out, the role of host plant in its entirety has often been ignored in the studies of population dynamics of herbaceous aphids. The foregoing results can be regarded as a step forward towards remedying this situation. Further, these results define also the concept of carrying capacity of a host plant which for aphid species such as *A. craccivora* can be regarded as a transient resource (Maelzer 1977). The results of Experiment II (Section 2.3.4), therefore, provide evidence in support of the hypothesis of this research project.

These results are strikingly similar to the findings of Way and Banks (1967) in *Aphis fabae* S. Way and Banks (1967) studied population growth and emigration in *A. fabae* colonies, which were initiated by 2, 4, 8, 16 and 32 apterae per plant on two sizes of broad beans and kept outdoors in field cages. Initial colonization densities had no striking influence on the total number of emigrants, whereas the size of the plants influenced their output enormously. The total number of emigrant aphids from small plants from the densities of 2, 8 and 32 initial apterae, were 3635, 2600 and 2706, whereas the outputs of emigrants from large plants from all the 5 densities were 19540, 17963, 17397, 14599 and 15099 aphids. The proportions of adult alatae among the emigrants varied between 26 and 56% on small plants and between 55 and 63% on large plants (Table 5, Experiment II of Way and Banks 1967).

The significance of the size of host plant (surface area and carrying capacity) in the build-up of *A. fabae* populations and alata dispersal is evident from these results.

Similar studies in *Hyperomyzus lactucae* L. (Boakye 1973) revealed different results. The output of emigrants increased with increasing initial colonization density and more alatae emigrated from small than from medium and large sowthistle plants. The mean populations on small, medium and large plants were 1735, 958 and 1231 aphids. The small numbers of *H. lactucae* emigrants from large plants can be attributed to small aphid populations on these plants, and to a lesser extent, to their larger surface areas and carrying capacities also. In this context, the dispersal of alatae in this aphid may be regarded as facultative in a sense because of its relationship with the state of crowding on small sowthistle plants.

Results of Experiment II also established apterous dispersal as an essential but facultative behaviour in *A. craccivora* (see Section 2.3.44). These results also confirm the results of Experiment I on apterous dispersal (see Section 2.2.36). Neither the initial numbers of colonizing alatae nor the host plant species had any significant effect on the total number of dispersing apterae (Tables 2.36 and 2.37). The rate of dispersal of apterae was related to the initial numbers of colonizing alatae and this relationship was more apparent on common burr medic and subterranean clover than on broad beans (see Figures 2.37, 2.38 and 2.39). This means that dispersal of *A. craccivora* apterae is a response to the extent of crowding and the shortage of space for apterous settling and larviposition on the host plants. Similar

results have been recorded in *Aphis fabae* (Way and Banks 1967) and in *Macrosiphum rosae* (Maelzer 1977).

The results in Figures 2.37, 2.38 and 2.39, provide additional evidence in support of the results of Experiment I, wherein apterous dispersal in a few declining colonies was associated with declining numbers of young nymphs and their total populations (see Section 2.2.3l-C and Figures 2.12 and 2.14). The early start of apterous dispersal and its facultative nature in response to smaller surface areas on common burr medic and subterranean clover plants, in contrast to the delayed dispersal (by approximately one generation time) on broad beans which had larger surface area for apterous feeding and larviposition, is additional direct evidence in support of the hypothesis of this study. The total population and the number of first and second instar nymphs in a growing colony of *A. craccivora* are dependent on the number of apterae (see Figures 2.17 and 2.18). Delayed apterous dispersal would result in increased reproduction by many apterae and hence a higher build-up of population on a plant i.e., a larger upper size of a colony. This would result in a larger output of emigrant alatae and increased recolonization in a crop. The ultimate result would be a higher level of abundance of this aphid in a field or an area. The influence of the size, surface area and carrying capacity of host plants on the start and the extent of apterous dispersal and hence on the upper size of colonies of *A. craccivora*, thus explains the importance of the host plant as a factor in the local abundance of this aphid (see also Section 2.3.5).

The concept of carrying capacity of host plants and its role in the abundance of aphid populations in nature, does not seem limited

to *A. craccivora* only. Perrin (1976) studied the causes of changes in the natural populations of the stinging nettle aphid (*Microlophium carnosum* B.) in three different nettle patches. He concluded that each nettle patch had a particular 'carrying capacity' for aphids, within which biennial fluctuations of the aphid numbers occurred. Studies on the causes of changes in the numbers of the rose aphid (*Macrosiphum rosae* L.) on rose bushes indicated that two peaks of abundance of this aphid in Spring were related to the numbers of available rose buds, suitable for colonisation. This was especially so, because of the transient nature of rose buds for this aphid (Maelzer 1977).

What is the significance of apterous dispersal in the survival of *A. craccivora* populations? Apterous dispersal may be advantageous to *A. craccivora* on two levels. On the level of a colony, apterous dispersal may prolong its survival on a deteriorating host plant and hence the period over which alatae may be produced. On the level of a group of colonies in an area, apterous dispersal may be an important means of colonizing and utilizing the nearby uninfested food plants efficiently; thus prolonging not only the survival of a local population as a whole until all the available plants mature, collapse or vanish, but also the period of alata production and dispersal in that area.

Results of experiments and observations on flight behaviour (Section 3) do not indicate any behavioural polymorphism among *A. craccivora* alatae as has been reported in *A. fabae* (Shaw 1970a). These results do emphasize the over-riding flight inhibiting effects of prevailing weather, particularly of low temperatures ($< 17^{o}C$) and also the adverse effects of rains, honey dew, parasitization and dropping off behaviour on wing distortion and thus on flight behaviour. What can

be concluded from these results is that, in the absence of any behavioural polymorphism among the alatae, the major emigration mechanism in *A. craccivora* seems to be its extreme sensitivity to produce alatiform progenies in its colonies. In other words, the thresholds of stimuli which determine alata development are very low in *A. craccivora*. The frequent occurrences of large numbers of intermediates in the natural populations of *A. craccivora* in South East Australia and South Australia (Carver 1974 - personal communication) can be attributed to the extreme sensitivity of this species to alata production.

Behavioural polymorphism among *A. craccivora* alatae would not be ecologically useful to the species. Firstly, the mechanism of wing determination (Johnson and Birks 1960) and its physiological sensitivity to various environmental factors (Johnson 1965, 1966a, 1966b) would make any behavioural polymorphism (among its alatae) superfluous, and such a polymorphism would only reduce the extent of actual emigration. Secondly, the over-riding and synchronising nature of prevailing weather on alata emigration on one hand, and the intensities of other factors in the immediate environment of the alatae, such as the extent of honey dew secretion, rains, parasitization, and wind velocities which may blow the alatae off the plants, on the other, would also render any behavioural polymorphism ineffective. More importantly, behavioural polymorphism among the alatae would be counter-productive to the migratory life history of this aphid since the main thrust of its field biology is to produce many colonizers and achieve a high degree of colonization, rather than to prolong the survival of the existing colonies.

The usefulness of behavioural polymorphism in *A. craccivora* alatae may also be judged by its consequences in a colony. If a proportion of flight mature alatae does not fly away but reproduces in a colony, the number of reproducing apterae would increase (see Figure 2.21) and this would result in the early collapse of the host plant. The output of emigrant alatae from that colony would be reduced, because many alatiform nymphs would fail to become adults due to the early death of the host plant (Way and Banks 1967).

The very idea of behavioural polymorphism among winged aphids, rests heavily on the laboratory experiments in *A. fabae* (Shaw 1970a). Low tempratures (< 16^{o}C) and low light intensities inhibit take-off and flight in *A. fabae* (Taylor 1957, 1965). Shaw (1970a) conducted his experiments at a cycle of 16 hr light and 8 hr dark. Temperature during the light period was 20$\pm$1^{o}C and 15$\pm$1^{o}C during the dark (Shaw 1970). Under these experimental conditions it is likely that flight mature alatae which completed their teneral period during the dark, would have been prevented from taking off and would be liable to settle on host plant and reproduce on it without flight (Johnson 1958). Further, there was no provision in the experimental set-up to distinguish between the flying alatae and those which walked or dropped off the host seedling. The alatae could also come back to the seedling after leaving it once, because the sticky trapping surface (to trap the flying alatae) was provided only at the top of the lantern lamp cage; the transparent walls of the lantern lamp were devoid of any trapping area. The interpretations and conclusions derived from the observations under these experimental conditions may, therefore, remain questionable.

The experiments and observations on flight behaviour of *A. craccivora* (Section 3) explain the occurrences of autumn and spring

flights (Gutierrez *et al.* 1971, 1974b) and the swarms of this aphid, observed in South Eastern Australia in 1948 and 1950 (Dyce 1951; Johnson 1951, 1957), in terms of the dominating and synchronising influence of the prevailing temperatures on alata dispersal.

Observations on colonization of broad beans (Sections 4.2, 4.3 and 4.4) indicate that *A. craccivora* has a potential to attain pest status in South Australia. Observations on the infestation of mature broad beans at Mortlock (Table 4.81) and at Port Clinton (Table 4.82) were made at the same time in early November 1976. About 68% of the sampled stems were infested at Mortlock and 7% at Port Clinton. Prolonged rains and cool weather up to early November at Mortlock, had not only delayed the maturity of broad beans, but also resulted in high aphid populations on plants probably because of the reproduction by alatae in the parent and nearby colonies. Natural enemies were also active but seemed to have little effect on aphid population build-up. The crop at Port Clinton was suffering from moisture stress for want of rains. Many infested stems were free of aphids as natural enemies had probably exterminated the aphids. The presence of dead aphids, their moulting skins (exuviae), empty parasite mummies, larval exuviae and pupal cases of the predators were indicative of the past presence of aphids and natural enemies on these stems. These observations interestingly indicated the interactions of components of weather, crop growth and natural enemy activity, on the build-up of *A. craccivora* populations on broad beans in natural conditions.

Results on colonization behaviour of alatae (see Section 4.2.2-D) and their distribution patterns (see Section 4.2.2-C) provide an insight

into the ecological significance of colonisation in this species. The inter-plant movement by colonizing alatae is certainly beneficial to the establishment of new populations as it increases the colonizing efficiency of alatae up to nearly 82% (see Section 4.2.2-D). This is significant especially in view of observed lower rates of infestations of broad bean plants by the alatae (0.04 alata per stem) in the field (Table 3.9). As mentioned in the foregoing, it is the number of colonies and not the pattern of colonization in a field, which determines the output of emigrant alatae, hence the importance of inter-plant movement of colonizing alatae is evident.

The significance of aggregative behaviour of colonizing alatae (Table 4.3 and Appendices XVIII A and B) is evident from the effects of initial colonization densities on the rates of alata dispersal (see Section 2.3.43 and Figures 2.31 to 2.36). In a natural situation, the proportions of colonies initiated by one alata and those initiated by more than one alata, would determine not only the extent of alata dispersal but also the rates of alata dispersal.

Is *A. craccivora* a super-migrant species? Several aspects of its biology and behaviour suggest that it is so. Studies on reproductive physiology of *A. craccivora* (Elliot and McDonald 1976) revealed a delayed ovarian development in alatae compared to apterae. The maximum number of oocytes and embryos, together with the maximum lengths of terminal ovarian follicles, were observed in nine day old alatae. The pattern of fecundity of alatae is also different from that in apterae. The rate of production of nymphs in alatae reached its maximum at 7-10 days and also alatae reproduced over a longer period (35 days) than apterae (25 days) on broad bean plants in a glasshouse

(Elliot and McDonald 1976). These results in association with the results of obligatory and pre-reproductive migratory behaviour (see Section 3.5) indicate that *A. craccivora* alatae migrate at a stage of life history when their reproductive values (Dingle 1972, 1974) are maximum with reference to the establishment of the species in a new habitat. What this means is that *A. craccivora* alatae are morphologically, physiologically, behaviourally and ecologically adapted as migrants and any criteria for the success of migration in this species can, therefore, be related justifiably to the production of alatae in its natural populations (Gutierrez *et al.* 1974a). The significance of the results of Experiments I and II (Section 2) is, therefore, evident in understanding the migration ecology of *A. craccivora*. The production of > 85% alatiform progeny, starting within 2-3 generations' time (Section 2) until the host plants deteriorate, is certainly an empirical evidence of the super-migrant nature of this aphid. Further, *A. craccivora* fits neatly in the behavioural scheme of migrant insects (Kennedy 1961, 1975; Dingle 1972, 1974). Even the movement of young apterae, which changes the spatial pattern of colonies in a field, may also be regarded as migratory in the sense that these apterae defer their reproduction and, by their movement, ensure the success of establishment of a new colony on an uninfested plant (Kennedy 1961, 1975).

Does emigration regulate population numbers in *A. craccivora* colonies? The consistently high rates of alata production for a considerable time in the life of a colony and the flight behaviour of alatae together with the sensitivity of apterae to the interactions of size, surface area of host plant and population of a colony, and their consequent movement away from the plant, establish emigration as a key factor in the decline of *A. craccivora* population on a plant. There

is no evidence of reduced rate of reproduction by apterae in the colonies of *A. craccivora* until the start of emigration (see Figure 2.19) and reduction in birth rate is brought about by apterous emigration.

In the absence of such an internal mechanism for population decline, the external mortality factors i.e., physical, micro-climatic and biotic, may also play an important role in determining aphid numbers, especially on crop plants, where the upper size of a colony is small. The external mortality factors may slow down the growth of newly established colonies to such an extent that many colonies would not reach the stage of producing alatae. This is not impossible in view of the activities of natural enemies, which can exterminate small populations (up to 50 aphids) on individual stems or plants (see Sections 1.7, 2.2.3l-D and 4.2.2-F). In other words, the natural enemies and micro-climatic factors would reduce the rate of survival of new and juvenile colonies so that fewer colonies would reach the stage of alata production. As emigration has a regulating influence on the populations of colonies after the start of dispersal by alatae and apterae, the extinction of juvenile colonies cannot be attributed to and explained by the role of emigration. The role of external mortality factors in this respect, therefore, cannot be ignored. The effectiveness of natural enemies (predators) in reducing aphid numbers in natural populations of species which form small colonies, has been well demonstrated in the aphid, *Pterocomma populifoliae* F. (Sanders and Knight 1968) and the rose aphid, *Macrosiphum rosae* L. (Maelzer 1977).

Do the host plant characteristics and initial colonization densities have any influence on the survival of juvenile colonies of *A. craccivora*? On plants with larger carrying capacities and surface

areas, emigration by apterae would be delayed (see Figures 2.37, 2.38 and 2.39) and despite the activities of natural enemies and other external mortality factors, the juvenile colonies would reach maturity i.e., to the stage of producing emigrant alatae. Similarly, colonies initiated by more than one alata would also reach maturity, despite mortality by external mortality factors, more so than the colonies initiated with one alata.

Why does *A. craccivora* not attain pest proportions in temperate legume pastures in South East Australia? There are two aspects to an answer of this question. Firstly, it is postulated that the pasture plants are not colonized extensively by *A. craccivora* alatae. The observed rate of primary infestation of a broad bean crop in early spring 1977 at Mortlock (see Table 3.9) was 0.04 alata per stem. In view of the extensive field studies on the influence of spacing and densities of groundnut plants on the landing, settling and colonization by *A. craccivora* alatae in the African continent (Booker 1963; A'Brook 1964, 1968; Davies 1972; Farrell 1976, 1976a), it is unlikely that the rate of primary infestation of temperate legume pasture plants would be equal to or more than the observed rate on broad beans (Table 3.9). Secondly, it is also postulated that *A. craccivora* fails to attain high population densities (per unit area) in temperate legume pastures. The physical and micro-climatic factors such as high plant densities, high humidity, low light intensity and lower temperatures, prevalent in the wet and dense legume pastures would seriously slow down the population increase in individual colonies (Wyatt and Brown 1977). Natural enemies would also exterminate small colonies on the pasture plants. As a result many newly established colonies would perish before reaching the stage of alata production and emigration. Further, the early dispersal by

apterae (see Figures 2.37 and 2.38) and the consequent small upper sizes of colonies in the legume pastures would also result in reduced production of alatae per unit area. Reduced production and emigration of alatae would thus keep the aphid populations at low levels in the temperate legume pastures. By early spring when temperatures are favourable for population growth and alata dispersal, the plants would be reaching maturity and would not be suitable for recolonization and establishment of new colonies on a large scale.

An examination of the model of *A. craccivora* populations in the temperature legume pastures in South Eastern Australia (Gutierrez *et al.* 1974a), in view of results of the present study, indicates that considerable improvements can be made in the model by incorporating quantitative information regarding several aspects of biology and behaviour of this aphid. These aspects would comprise empirical data on the rate of primary infestation of pasture plants by the alatae; dispersal by apterae; recolonization by apterae and alatae; a realistic relationship between the populations of colonies and alata production; role of natural enemies in the extermination of small colonies; empirical data on rates of reproduction and survival of aphids on pasture plants in field conditions; and the effect of low temperatures on alata dispersal and its consequences for the population of colonies.

Any future study on the population dynamics of *A. craccivora*, especially on plants with small carrying capacities such as groundnuts and temperate legume pastures, I suggest, would be more revealing if the concurrent estimates of the rates of establishment and extinction of juvenile colonies in an area are made. If the rates of extinction are equal to the rates of establishment within a given period, the aphids

would be scarce and would be exterminated. Conversely, if the balance is in favour of survival of juvenile colonies to maturity i.e., to the stage of alata dispersal, *A. craccivora* populations would not only persist but attain higher levels of abundance also. Further studies on spatial aspects of the dispersive and post-flight behaviour of alatae in the field, under varying weather conditions, are necessary for a fuller understanding of the role of prevailing weather on the build-up of local populations.

What is the adaptive significance of migration in its totality, in the life history of *A. craccivora*? This question can be answered in the context of the stability of the habitat (Southwood 1962, 1975; Southwood *et al.* 1974) on one hand, and the spread of risk of extinction in both time and space (den Boer 1968; Taylor 1975) on the other. The discontinuity of host plants in both time and space, demands a continuous migratory activity, so that the survival and the persistence of populations on a regional basis is achieved (Way 1973; Roff 1974, 1975). As Taylor (1977) suggests, population changes in aphid numbers on a regional basis may be better understood if spatial aspects of population dynamics are also taken into account. Migration in insects has been regarded as serving the same functions as diapause (Southwood 1962; Dingle 1968), since both these adaptations allow the escape of an insect population from extinction in space and time respectively. In *A. craccivora* and possibly in other migratory aphids, such as *A. fabae* and *Mysuz persicae*, I suggest that temporal survival is achieved by a change of spatial pattern through migration.

The usefulness of the 'concept of colony' in understanding the

abundance and the causes of changes in the numbers in *A. craccivora* populations, is, therefore, evident from the present study. I suggest that this approach would be equally applicable to the studies of other herbaceous aphids which form small and discrete colonies on their host plants, and those which survive at low levels of abundance. The studies on the causes of changes in numbers of rose aphids (*Macrosiphum rosae* L.) which form small colonies on rose buds (< 500 aphids per bud; Maelzer 1977) and studies on the natural regulation of *Pterocomma populifoliae* F. on the big tooth aspen (Sanders and Knight 1968) are examples of this approach.

The objectives of ecological research are ecological understanding and practical utility (Gilbert *et al.* 1976). I think the present study has achieved these objectives. I conclude that *A. craccivora* is not adapted to reach pest proportions in temperate legume pastures in South Eastern Australia.

Appendix I: A key for the identification of nymphal instars of *Aphis craccivora* for ecological studies.

1.0 Antennae 4-segmented ..... First instar

1.1 Antennae 5-segmented 2.0

1.2 Antennae 6-segmented 5.0

2.0 Third antennal segment 1.2 to 1.5 times longer than the fourth segment 3.0

2.1 Third antennal segment > 1.5 times (up to 1.8 times) longer than the fourth segment 3.1

3.0 Width of cauda > length and distal end not pointed .. Second instar

3.1 Third antennal segment imperfectly divided, cauda triangular, width of cauda equal to length and distal end pointed 4.0

4.0 Body rectangular shaped with well developed mesothoracic shoulders, body width at mesothorax more than the width of the head, antennae may appear six segmented ..... Third instar alata

4.1 Body oval shaped, mesothoracic shoulders absent, width of meso and metathorax in confirmity with the width of the head and the width of first abdominal segment ... Third instar aptera

5.0 Cauda characteristically wedge shaped, length of cauda > width, antennal segments 3, 4 and 5 nearly equal, antennae and hind legs slender and longer 5.1

5.1 Well developed overlapping wing buds on lateral sides of meso and metathorax ..... Fourth instar alata

5.2 Wing buds absent, body oval shaped ..... Fourth instar aptera

Appendix II: Progress of infestations of *Aphis craccivora* on broad bean seedlings.

Age of colony in days**	Plant number	Shoot M/A*	Shoot length in cm	Shoot length with aphids (cm)	Total No. of leaves	Leaves with aphids F/O+	Number of aphids
6	1	M	21	0	8	2 F	12
		A	3	0	2	2 F	3
		A	3	0	1	0	0
	2	M	26.5	0	8	2 F	7
		A	2.5	0	2	0	0
		A	3.0	0	2	0	0
		A	2.5	0	2	0	0
	3	M	20	0	8	1 F	9
		A	1.5	0	1	0	0
10	1	M	27	0	9	2 F	14
		A	4.5	0	4	0	0
		A	2.5	0	3	0	0
		A	2.5	0	2	0	0
	2	M	28.5	0	9	3 F	19
		A	2.5	0	1	0	0
		A	3.0	0	1	0	0
	3	M	24	0	8	2 F	19
		A	4.5	0	3	0	0
		A	2.5	0	1	0	0
		A	2.5	0	1	0	0
12	1	M	27	0	8	1 F	20
		A	3.5	0	2	0	0
		A	3.5	0	2	0	0
	2	M	26	0	9	2 F	32
		A	3.5	0	3	0	0
		A	3.5	0	2	0	0
		A	2.5	0	2	0	0
	3	M	24	0	9	2 F	19
		A	3.5	0	2	0	0
		A	2.5	0	2	0	0
15	1	M	25.5	0	10	2 F	60
		A	3.5	0	3	1 F	1
		A	2.0	0	2	0	0
	2	M	27	0	10	2 F + 1-0	34
		A	4.0	0	4	0	0
		A	3.5	0	3	0	0
		A	2.5	0	3	0	0
	3	M	25	0	10	2 F + 2-0	97
		A	6.5	0	5	0	0
		A	7.0	0	5	0	0
		A	3.0	0	4	0	0

Appendix II: *(continued)*

** Age of colony in days	Plant number	Shoot M/A*	Shoot length in cm	Shoot length with aphids (cm)	Total No. of leaves	Leaves with aphids F/O+	Number of aphids
18	1	M	31	0	11	3 F	388
		A	10	0	4	0	0
		A	7.5	0	4	0	0
		A	3.0	0	1	0	0
	2	M	30	0	11	2 F + 1-0	394
		A	8	0	5	0	0
		A	6.5	0	5	0	0
	3	M	31	0	10	2 F	3 + 4 M***
		A	6.5	0	5	1-0	1 M
		A	6.5	0	5	1-0	1 M
		A	5	0	4	0	0
21	1	M	26.5	0	11	2 F + 2-0	314
		A	14	0	7	0	0
		A	11	0	6	0	0
	2	M	33	1.5	11	2 F + 4-0	848
		A	10	0	6	0	0
		A	14	0	6	2 F	2
	3	M	30.5	0	12	2 F + 1-0	361
		A	8	0	5	0	0
		A	8.5	0	5	0	0
		A	8	0	5	0	0
24	1	M	31.5	5.5	12	1 F + 1-0	858
		A	21	0	8	2 F	32
		A	15	0	6	2 F	40
		A	15	1.5	5	1 F	75
	2	M	27.5	4.5	11	2 F + 2-0	614
		A	13	1.5	6	2 F	124
		A	13.5	0	6	2 F	26
	3	M	28	4	11	1 F + 4-0	393
		A	13	0	5	0	0
		A	12	0	6	0	0
27	1	M	37	6	13	2 F + 2-0	1375
		A	14	0	6	0	0
		A	15	0	6	0	0
		A	9	0	5	0	0
	2	M	31	0	12	1 F + 1-0	573
		A	15	0	7	0	0
		A	10	0	5	0	0
		A	7	0	5	0	0
	3	M	27	6.5	11	2 F + 1-0	825
		A	12	0	6	2 F	156
		A	11	0	4	2 F	244

Appendix II: *(continued)*

Age of colony in days**	Plant number	Shoot M/A*	Shoot length in cm	Shoot length with aphids (cm)	Total No. of leaves	Leaves with aphids F/O+	Number of aphids
30	1	M	25	7	12	1 F + 3-0	676
		A	10.5	2	6	2 F + 1-0	650
		A	9.5	3	5	2 F + 1-0	610
	2	M	31	7	12	1 F + 2-0	1386
		A	17	4	7	2 F + 3-0	510
		A	15	4	6	2 F + 1-0	522
		A	2	1	1	1 F	85
	3	M	32	2	14	3 F	519 + 15 M
		A	20	0	8	0	1 M
		A	16	0	7	2 F	5 + 2 M
		A	13	0	6	0	0
33	1	M	32.5	8.5	11	1 F + 10-0	2374
		A	24	6	10	2 F	621
		A	19	0	8	2 F	203
		A	7	0	3	2 F	146
		A	7	0	3	2 F	126
	2	M	35	9	13	1 F + 4-0	1632
		A	24.5	2	10	2 F	202
		A	16	3	7	1 F	197
		A	13	0	6	1 F	140
39	1	M	32	14	13	1 F + 12-0	2109
		A	23	6	9	2 F	1234
		A	23	4.5	8	2 F	802
		A	2	0	2	2 F	53
	2	M	32	7	12	2 F + 10-0	1035
		A	23	7	9	2 F	605
		A	20	7	8	2 F	664
		A	17	0	6	2 F	263
		A	14	0	6	2 F	398
	3	M	32	14	13	2 F + 11-0	2873
		A	20	10	8	2 F	565
		A	22	4	9	2 F	419
		A	13	0	6	2 F	322
45	1	M	32	8	12	1 F + 7-0	1341
		A	21	6	9	2 F + 2-0	1483
		A	17	0	7	2 F	891
	2	M	31	18	12	2 F + 10-0	1700
		A	32	9	12	1 F + 6-0	986
		A	18	5	7	2 F	195
		A	23	0	10	2 F	159

Appendix II: *(continued)*

Age of colony in days**	Plant number	Shoot M/A*	Shoot length in cms	Shoot length with aphids (cm)	Total No. of leaves	Leaves with aphids F/O+	Number of aphids
45	3	M	28	22	12	1 F + 11-0	1348
		A	16	11	9	2 F + 7-0	750
		A	14	9	7	1 F + 6-0	669
		A	16	11	8	2 F + 6-0	840
52	1	M	38	14	17	1 F + 9-0	4164
		A	31	0	13	2 F	782
		A	22	0	10	2 F	441
	2	M	32	24	12	9 D + 3-0	1319
		A	21	14	6	3 D + 3-0	441
		A	15	13	6	3 D + 3-0	612
		A	11	10	6	4 D + 2-0	180
	3	M	29	13	11	4 D + 7-0	2549
		A	28	11	13	4 D + 9-0	2392
		A	30	10	12	8-0	1636
		A	20	9	10	2 F	640
		A	13	9	5	2 F	839
60	1	M	26	20	10	8 D + 2-0	482
		A	22	18	9	2 D + 7-0	2809
		A	15	10	6	4 D + 2-0	303
		A	7	4	6	3 D + 3-0	140
	2	M	31	25	12	2 D + 10-0	4756
		A	30	16	11	11-0	1450
		A	28	12	11	11-0	2675
		A	15	6	6	6-0	729
	3	M	40	37	15	15-0	7247
		A	26	26	11	11-0	3880
		A	25	25	11	11-0	4406

* M = Main Shoot
A = Axillary Basal Shoot

\+ F = Folded Top Leaves of Crown
O = Opened Leaves

*** M = Mummified Aphids

** Age of Plants at Colonization = 18 days

D = Dried Leaves

Appendix III: Age-structure in the experimental colonies of *Aphis craccivora* on broad bean seedlings - 1977.

Age of colony in days	Plant No.	Shoot M/A*	% Nymphs counted	Number of aphids per instar and morph								Total
				I	II	III Apt	III Al	IV Apt	IV Al	Apt	Al	
3	1	M	100	7	0	0	0	0	0	0	1	8
	2	M	100	5	0	0	0	0	0	0	1	6
	3	M	100	3	0	0	0	0	0	0	1	4
6	1	M	100	5	3	4	0	0	0	0	0	12
		A		1	1	0	0	0	0	0	1	3
	2	M	100	3	3	0	0	0	0	0	1	7
	3	M	100	4	3	1	0	0	0	0	1	9
10	1	M	100	2	4	1	0	6	0	0	1	14
	2	M	100	6	8	2	0	2	0	0	1	19
	3	M	100	4	7	4	0	4	0	0	1	19
12	1	M	100	4	4	4	0	5	0	2	1	20
	2	M	100	9	5	7	0	5	0	5	1	32
	3	M	100	5	4	4	0	5	0	0	1	19
15	1	M	100	34	8	6	0	5	0	6	1	60
		A		1	0	0	0	0	0	0	0	1
	2	M	100	14	5	5	0	7	0	2	1	34
	3	M	100	60	12	9	0	9	0	6	1	97
18	1	M	100	222	110	23	3	10	0	19	1	388
	2	M	100	185	139	28	11	10	0	20	1	394
	3	M	100	0	0	0	0	1	0	2+3M	1M**	7
		A		0	0	0	0	0	0	1M	0	1
		A		0	0	0	0	0	0	1M	0	1
21	1	M	100	136	116	6	36	4	2	14	0	314
	2	M	100	215	306	45	165	25	58	34	0	848
	3	M	100	121	116	43	47	17	2	14	1	361
24	1	M	100	455		10	243	7	109	33	1***	858
		A	100	30		0	0	0	0	2	0	32
		A	100	37		0	0	0	0	3	0	40
		A	100	70		0	0	0	0	4	1	75
				297	295							
	2	M	100	263		27	255	18	39	12	0	614
		A	100	115		0	0	0	0	8	1	124
		A	100	23		0	0	0	0	3	0	26
				230	171							
	3	M	100	133	128	9	59	17	27	19	1	393

Appendix III: *(continued)*

Age of colony in days	Plant No.	Shoot M/A*	% Nymphs counted	Number of aphids per instar and morph								Total
				I	II	III Apt	III Al	IV Apt	IV Al	Apt	Al	
27	1	M	100	413	390	28	225	66	177	74	2	1375
	2	M	100	121	122	17	129	14	133	32	5	573
	3	M	100	259		8	242	40	238	28	10	825
		A	100	145		0	0	0	0	11	0	156
		A	100	225		0	0	0	0	19	0	244
				406	223							
30	1	M	100	251	37	0	3	13	288	55	29	676
		A	100	193	167	9	210	13	46	12	0	650
		A	100	243	127	16	150	20	44	10	0	610
	2	M	100	506	483	2	99	1	163	38	94	1386
		A	100	142	86	10	113	21	114	24	0	510
		A	100	162	104	34	110	34	52	26	0	522
		A	100	75	0	0	0	0	1	8	1	85
	3	M	100	165	70	13	73	48	74	54+15M	22	534
		A		0	0	0	0	0	0	1M	0	1
		A		4	0	0	0	0	0	2M	1	7
33	1	M	100	654	587	1	444	1	507	38	142	2374
		A	100	409	114	3	15	1	32	45	2	621
		A	100	72	45	1	23	5	52	5	0	203
		A	100	46	44	7	21	6	18	4	0	146
		A	100	88	29	0	0	0	0	7	2	126
	2	M	100	244	322	34	328	12	512	61	119	1632
		A	100	190						11	1	202
		A	100	180						16	1	197
		A	100	126						12	2	140
				270	202	3	14	1	6			
39	1	M	50	206	191	3	153	10	364	44	211	2109
		A	50	221	192	21	124	13	15	46	16	1234
		A	100	307	252	9	126	17	49	24	18	802
		A	100	17	7	3	16	2	4	2	2	53
	2	M	50	127	97	4	36	0	188	29	102	1035
		A	100	178	195	24	132	21	31	21	3	605
		A	100	220	197	14	126	21	49	28	9	664
		A	100	77	90	11	75	0	2	8	0	263
		A	100	126	95	10	80	8	47	30	2	398
	3	M	50	297	403	7	280	4	300	59	232	2873
		A	100	175	200	4	80	27	31	33	15	565
		A	100	171	108	5	43	12	43	29	8	419
		A	100	164	88	8	27	3	7	14	11	322

Appendix III: *(continued)*

Age of colony in days	Plant No.	Shoot M/A*	% Nymphs counted	Number of aphids per instar and morph								
				I	II	III Apt	III Al	IV Apt	IV Al	Apt	Al	Total
45	1	M	50	197	168	23	127	1	106	29	68	1341
		A	50	198	194	3	139	3	144	28	93	1483
		A	100	230	220	11	117	9	204	38	62	891
	2	M	50	109	200	16	209	8	223	40	130	1700
		A	50	74	121	2	59	1	152	21	147	986
		A	100	28	50	30	17	30	24	4	12	195
		A	100	32	48	3	15	10	28	6	17	159
	3	M	50	69	124	7	105	1	232	23	249	1348
		A	50	4	17	3	66	2	240	1	85	750
		A	100	8	45	6	97	1	426	0	86	669
		A	100	4	41	0	100	2	445	0	248	840
52	1	M	50	563	447	52	306	75	418	147	295	4164
		A	100	201	193	95	33	130	39	47	44	782
		A	100	209	61	34	11	41	2	40	43	441
	2	M	100	101	118	12	75	18	565	21	481	1391
		A	100	131	53	2	18	6	166	2	63	441
		A	100	186	86	12	30	10	225	3	60	612
		A	100	27	17	4	5	5	66	0	56	180
	3	M	50	143	191	35	189	154	401	69	254	2549
		A	50	149	183	64	194	117	368	40	202	2392
		A	50	135	148	72	81	114	160	107	109	1636
		A	100	225	137	26	37	47	75	53	40	640
		A	100	113	123	6	180	18	310	27	62	839
60	1	M	100	95	34	12	11	13	169	7	141	482
		A	100	1427	718	70	86	38	125	11	334	2809
		A	100	115	25	7	10	7	91	0	48	303
		A	100	17	14	8	7	2	79	0	13	140
	2	M	50	1121	434	56	323	77	175	137	247	4756
		A	100	347	264	47	149	74	329	45	195	1450
		A	50	170	133	22	239	61	567	42	249	2675
		A	100	249	131	20	102	15	163	13	36	729
	3	M	50	1319	731	303	184	78	412	112	1081	7247
		A	50	596	284	88	195	37	484	56	456	3880
		A	50	951	370	113	175	24	259	91	531	4406

* M = Main Shoot
A = Axillary Basal Shoot

** M = Mummified Aphids

*** Teneral Alata.

Appendix IV: Experimental colonies of *Aphis craccivora* on broad beans with stable-instar distributions and tests of goodness of fit to a geometric progression - 1977.

Age of colony in days	Plant No.	O/E*	Number of nymphs in instars I	II	III	e^{λ}	μ	$\chi^{2**}_{1\ d.f.}$
6	1	O	6	4	4			
		E	5.7	4.6	3.7	1.25	0.8	0.1183
	2	O	4	3	1			
		E	4.2	2.4	1.4	1.75	0.571	0.2758
10	1	O	2	4	1			
		E	2.8	2.3	1.9	1.20	0.833	1.911
	2	O	6	8	2			
		E	7.2	5.1	3.7	1.40	0.714	2.630
	3	O	4	7	4			
		E	5	5	5	1.00	1.00	1.20
12	1	O	5	4	4			
		E	4.9	4.3	3.8	1.125	0.889	0.0335
	2	O	9	5	7			
		E	8.9	7.6	6.5	1.167	0.857	0.9291
	3	O	4	4	4			
		E	4	4	4	1.0	1.0	0.0
15	1	O	35	8	6			
		E	34.2	11.2	3.6	3.07	0.326	2.5329
	2	O	14	5	5			
		E	13.3	7	3.7	1.90	0.526	1.065
21	3	O	121	116	90			
		E	124.6	108.3	94.1	1.151	0.8692	0.8301
24	1	O	297	295	253			
		E	303.7	281.1	260.2	1.08	0.9257	1.0344
27	1	O	121	122	146			
		E	117.2	129.3	142.5	0.907	1.1029	0.6213
33	1	O	1269	819	515			
		E	1271.5	812.4	519.1	1.565	0.6389	0.0909
52	1	O	1536	1148	889			
		E	1530.2	1161.4	881.4	1.318	0.7589	0.2421
	2	O	445	274	158			
		E	447	268.6	161.4	1.664	0.6008	0.1891
	3	O	1192	1304	1519			
		E	1177.4	1331.6	1505.9	0.884	1.131	0.8671

* O = Observed
E = Expected

** $\chi^2_{1\ d.f.} < 3.84$ = Non significant P = 0.05

Appendix V: Number of alatae of *Aphis craccivora* which dispersed from single-caged colonies on broad beans - 1977.

Date	Age of colony in days	Number of alatae collected and removed from Cage 2	Cage 3	Cage 5	Cage 7	Cage 16	Cage 20
25 May 1977	27	0	15	0	0	0	17
26	28	4	24	15	3	0	25
28	30	8	76	55	8	2	71
29	31	3	36	14	4	3	9
31	33	40	129	83	29	23	96
1 June	34	44	38	30	19	11	48
2	35	11	42	22	12	19	20
3	36	54	130	80	50	30	86
4	37	93	184	52	61	39	114
5	38	74	132	31	24	34	75
6	39	62	142	74	49	38	110
7	40	50	138	66	43	48	92
8	41	31	88	52	28	20	67
9	42	80	164	68	42	47	121
10	43	47	105	68	24	31	57
12	45	122	364	159	91	34	92
15	48	420	698	222	162	169	446
17	50	433	664	155	135	111	252
21	54	532	434	259	249	103*	484
23	56	496	593	312	306	N.R.	420
30	63	1116	573	665	664	N.R.	1104*
4 July	67	861*	90D	531	409	1300	1271
7	70	650	-	442	458	598	888
9	72	523	-	313	375	514	800
12	75	N.R.	-	74D	N.R.	462	771

* = Parasite mummies seen in colonies.

D = Death of host plant.

N.R. = Aphids not removed.

Appendix VI. Number of apterae of *Aphis craccivora* which dispersed from single-caged colonies on broad beans - 1977.

Date	Age of colony in days	Number of apterae collected and removed from					
		Cage 2	Cage 3	Cage 5	Cage 7	Cage 16	Cage 20
28 May 1977	30	0	0	0	0	0	4
29	31	17	87	19	3	3	0
31	33	4	5	1	0	2	2
1 June	34	3	0	0	0	1	3
2	35	0	0	1	1	0	2
3	36	1	10	1	2	1	1
4	37	1	25	1	1	1	0
5	38	3	10	1	1	0	0
6	39	2	7	5	0	0	1
7	40	0	7	2	0	1	0
8	41	1	9	4	0	1	0
9	42	2	2	9	1	0	0
10	43	2	4	2	0	2	0
12	45	0	0	2	0	2	1
15	48	5	4	6	3	2	1
17	50	36	3	6	1	0	5
21	54	20	2	10	21	5*	134
23	56	10	20	27	26	N.R.	170
30	63	8	8	38	21	N.R.	221*
4 July	67	8*	10D	21	25	14	123
7	70	5	-	14	9	9	46
9	72	11	-	18	14	3	18
12	75	N.R.	-	N.R. D	N.R.	30	45

* = Parasite mummies seen in colonies.

D = Death of host plant.

N.R. = Aphids not removed.

Appendix VII: *Number of alatae of *Aphis craccivora* which dispersed from different sized colonies on lucerne *Medicago sativa* cultivar 'Hunter River' - 1978.

Date	Age of colony in days	Initial colonisation density (alatae/plant) 1	2	4
27 June 1978	42	0	2	0
30	45	0	4	0
3 July	48	1	3	0
7	52	3	2	4
9	54	3	5	6
11	56	0	7	0
13	58	1	1	1
16	61	2	10	4
20	65	0	4	2
29	74	0	5	0

* Number per 4 plants.

Appendix VIII: *Number of apterae of *Aphis craccivora* which dispersed from different sized colonies on lucerne *Medicago sativa* cultivar 'Hunter River' - 1978.

Date	Age of colony in days	Initial colonisation density (alatae/plant) 1	2	4
27 June 1978	42	0	0	1
30	45	1	3	3
3 July	48	3	2	2
7	52	2	0	5
9	54	3	3	3
11	56	0	3	3
13	58	2	2	1
16	61	4	2	6
20	65	0	3	5
29	74	0	1	0

* Number per 4 plants.

Appendix IX: *Number of alatae of *Aphis craccivora* which dispersed from different sized colonis on common burr medic *Medicago polymorpha* var. *vulgaris* - 1978.

Date	Age of colony in days	Initial colonisation density (alatae/plant) 1	2	4	8
27 June 1978	42	14	40	186	306
30	45	46	51	205	211
3 July	48	44	65	156	206
7	52	62	81	255	263
9	54	38	47	156	188
11	56	34	40	166	152
13	58	78	69	144	206
16	61	165	204	301	418
20	65	426	647	421	661
25	70	438	606	203-3D	105-2D
29	74	79	202	82	413
31	76	219	789	163	232-3D
10 August	86	412-1D	414-3D	8-4D	6-4D
15	91	110-2D	525	-	-
17	93	328	686	-	-
25	101	618	645	-	-
28	104	323	185-4D	-	-
30	106	158	-	-	-

* Number/plant.

D = Death of host plant.

Appendix X: *Number of alatae of *Aphis craccivora* which dispersed from different sized colonies on subterranean clover, *Trifolium subterraneum* cultivar 'Clare' - 1978.

Date	Age of colony in days	Initial colonisation density (alatae/plant) 1	2	4	8**
27 June 1978	42	4	6	16	135
30	45	3	16	32	121
3 July	48	4	25	36	105
7	52	8	45	55	192
9	54	5	25	48	85
11	56	3-P	27	36	47
13	58	4	33	43	38
16	61	14	137	138	163
20	65	85	211	235	334
25	70	86	199	126-1D	73-1D
29	74	18	60	25-3D	229
31	76	123	250	288	144
10 August	86	263	425-1D	223	361-2D
15	91	111	237	115	-
17	93	240	162	50-4D	-
25	101	497	100-4D	-	-
28	104	220-1D	-	-	-
30	106	203	-	-	-

* Number/plant.

** 2 plants only.

D = Death of host plant.

P = Parasitized aphids seen.

Appendix XI. *Number of alatae of *Aphis craccivora* which dispersed from different sized colonies on broad bean *Vicia faba* (L.) 'Culture 127' - 1978.

Date	Age of colony in days	Initial colonisation density (alatae/plant) 1	2	4	8
27 June 1978	42	6	57	70	110
30	45	15	140	72	195
3 July	48	15	92	79	209
7	52	17	150	111	229
9	54	29	128	57	196-P
11	56	17	125	49	121
13	58	6	141	62	181
16	61	20	256	142	245
20	65	79-P	781	375	910
25	70	71	734	333	775
29	74	27	219-2D	140	172-1D
31	76	89	609	526	530
10 August	86	330	119-4D	1942-2D	724-3D
15	91	247	-	775	886
17	93	334	-	320-4D	257-4D
25	101	311-1D	-	-	-
28	104	220-2D			
30	106	122-3D			

* Number/plant

D = Death of host plant

P = Parasitized aphids seen.

Appendix XII. *Number of apterae of *Aphis craccivora* which dispersed from different sized colonies on common burr medic *Medicago polymorpha* var. *vulgaris* - 1978.

Date	Age of colony in days	Initial colonisation density (alatae/plant) 1	2	4	8
27 June 1978	42	5	90	42	178
30	45	6	5	17	111
3 July	48	12	32	12	37
7	52	106	124	34	64
9	54	33	95	40	45
11	56	31	68	26	32
13	58	14	74	28	75
16	61	22	40	52	53
20	65	31	45	133	126
25	70	68	52	76-3D	136-2D
29	74	31	33	44	84
31	76	41	90	60	360-3D
10 August	86	146-1D	110-3D	0-4D	0-4D
15	91	50-2D	52	-	-
17	93	22	38	-	-
25	101	276	205	-	-
28	104	98	78-4D	-	-
30	106	154	-	-	-

* Number/4 plants.

D = Death of host plants.

Appendix XIII: *Number of apterae of *Aphis craccivora* which dispersed from different sized colonies on subterranean clover *Trifolium subterraneum* cultivar 'Clare' - 1978.

Date	Age of colony in days	Initial colonisation density (alatae/plant) 1	2	4	8**
27 June 1978	42	0	14	39	8
30	45	2	2	10	26
3 July	48	4	10	52	50
7	52	4	14	84	82
9	54	3	5	38	48
11	56	4-P	3	24	31
13	58	8	8	51	92
16	61	9	61	68	109
20	65	29	61	82	96
25	70	25	45	30-1D	66-1D
29	74	5	55	20-3D	41
31	76	41	160	40	45
10 August	86	27	292-1D	76	31-2D
15	91	24	160	118	0
17	93	30	197	46-4D	-
25	101	208	0-4D	0	-
28	104	53-1D	-	-	-
30	106	242	-	-	-

* Number/4 or 2 plants.

** 2 plants only.

D = Death of host plant.

P = Parasitized aphids seen.

Appendix XIV. *Number of apterae of *Aphis craccivora* which dispersed from different sized colonies on broad bean *Vicia faba* (L.) 'Culture 127' - 1978.

Date	Age of colony in days	Initial colonisation density (alatae/plant) 1	2	4	8
27 June 1978	42	1	10	2	5
30	45	2	4	2	5
3 July	48	0	5	4	9
7	52	0	4	3	7
9	54	0	3	2	10-P
11	56	1	4	4	9
13	58	0	5	5	12
16	61	3	89	9	56
20	65	8-P	241	107	420
25	70	2	680	258	561
29	74	7	326-2D	222	223-1D
31	76	30	236	503	336
10 August	86	126	58-4D	1072-2D	250-3D
15	91	50	-	46	86
17	93	46	-	22-4D	23-4D
25	101	378-1D	-	-	-
28	104	54-2D	-	-	-
30	106	25-3D	-	-	-

* Number/4 plants.

D = Death of host plant.

P = Parasitized aphids seen.

Appendix XV-A. Colonization of broad bean stems in the experimental plots by *Aphis craccivora* at Mortlock 1975-76.

Date	Preceding interval in days	Plot I**		Plot II**	
		No. of alatae	No. of stems with aphids+	No. of alatae	No. of stems with aphids+
Sept 19, 1975	10	3	4	0	2
23	4	3	3	5	6
Oct 2*	9	7	14	6	10
10	8	1	2	3	5
21	11	6	11	5	12
28	7	6	14	11	16
Nov 4	7	34	49	31	40
11*	7	0	2	0	5
18	7	11	12	4	9
27	9	1	8	5	14
Dec 5	8	2	12	0	3
23*	18	3	34	3	32
30	7	0	4	0	5
Jan 6, 1976	7	0	3	0	4
13	7	0	5	0	0
19	6	0	3	0	2
Feb 3*	15	0	9	0	0
9	6	1	2	0	0
16	7	1	2	0	0
Mar 2	15	0	2	0	0
9*	7	2	2	0	1
16	7	4	3	0	1
23	7	0	2	1	2
30	7	0	5	1	3
Apr 13	14	2	6	3	8
20	7	1	8	2	6
May 4*	14	0	5	1	5
11	7	3	3	1	3
25	14	0	4	0	1
June 3	9	0	2	0	0

* New Planting + Alatae/apterae/nymphs

** Plot size = 3 x 3 m. Total plants 49/plot.

Appendix XV-B. Colonization of broad bean stems in the experimental plots by *Aphis craccivora* at Mortlock 1976-77.

Date	Preceding interval in days	Plot I		Plot II		
		No. of alatae	No. of stems with aphids+	No. of alatae	No. of stems with aphids+	
Oct 13, 1976	7	15	14	21	17	A
26	13	105	51	85	46	A
Nov 3	8	262	92	320	82	A
18*	15	27	122	5	105	A
24	6	25	15	118	25	B
Dec 13	19	1	9	0	6	B
23	10	0	3	0	1	B
May 5, 1977	7	0	0	1	1	B
14	9	1	1	2	2	B
21	7	2	2	2	2	B
30	9	0	0	1	3	B

* New planting.

A = Plot size 3 x 3 m. Total plants 49/plot.
B = Plot size 2 x 2 m. Total plants 25/plot.

\+ Alatae/apterae/nymphs.

Appendix XV-C. Colonization of broad bean stems in the experimental plots by *Aphis craccivora* at Mortlock 1977-78.

Date	Preceding interval in days	Plot I**		Plot II**	
		No. of alatae	No. of stems with aphids+	No. of alatae	No. of stems with aphids+
Aug 27, 1977	8	3	3	5	6
Sept 3	7	18	13	38	21
13	10	19	14	22	15
Oct 7*	24	49	65	65	64
13	6	116	55	91	52
27	14	22	31	42	44
Nov 2	6	10	14	9	12
24	22	10	28	3	12
Feb 13, 1978	11	0	0	0	0
20	7	0	0	0	0
Mar 2	10	1	1	0	0
9*	7	0	0	0	0
31	22	1	4	0	4

* New planting.

** Plot size 2 x 2 m. Total plants 25/plot.

\+ Alatae/apterae/nymphs.

Appendix XV-D. Colonization of broad bean stems in the experimental plots by *Aphis craccivora* at Waite 1975-77.

Date	Preceding interval in days	Plot I**		Plot II**		
		No. of alatae	No. of stems with aphids+	No. of alatae	No. of stems with aphids+	
Sept 11, 1975	9	2	3	4	4	
18	7	0	1	0	1	
25	7	5	5	5	8	
Oct 6	11	0	2	3	6	
20*	14	0	3	3	8	
27	10	3	4	14	19	
Nov 6	10	2	9	2	4	
May 17, 1976	2	0	0	-	-	
18	1	3	3	-	-	
19	1	3	3	-	-	
20	1	0	2	-	-	
22	2	0	8	-	-	
July 6*	42	0	6	0	2	
Aug 24	49	0	0	0	0	
Oct 12	7	9	11	9	9	
20	8	4	10	6	10	
Mar 3, 1977	17	0	3	4	12	
May 12	16	45	33	48	28	A
24	12	6	11	8	13	A

* New planting.
** Plot size 3 x 3 m. Total plants 49/plot.
A = Plot size 2 x 2 m. Total plants 25/plot.
\+ Alatae/apterae/nymphs.

Appendix XVI-A. Morph-composition of *Aphis craccivora* in colonized stems in the experimental plots at Mortlock 1975-78.

Date	Number of colonized stems				
	With alatae		Without alatae		
	Alatae only	Alatae and nymphs/apterae	Apterae only	Nymphs only	Apterae and nymphs
Sept 19, 1975	0	3	0	3	0
23	3	5	0	1	0
Oct 2	7	6	0	11	0
10	0	4	0	3	0
21	2	9	0	11	1
28	7	10	0	13	0
Nov 4	18	42	0	29	0
11	0	0	0	7	0
18	10	4	0	7	0
27	3	3	3	12	1
Dec 5	0	2	4	5	4
23*	2	2	2	14	14
30	0	0	2	6	1
Jan 6, 1976	0	0	0	5	2
13	0	0	1	2	2
19	0	0	2	1	2
Feb 3	0	0	0	0	9
9	1	0	0	0	1
16	0	1	0	0	1
Mar 3	0	0	0	0	2
9	0	2	0	0	1
16	2	1	0	1	0
23	0	1	0	3	0
30	0	1	0	5	2
Apr 13	4	1	1	4	4
20	0	3	1	7	3
May 4	0	1	1	6	2
11	1	3	0	1	1
25	0	0	0	4	1
June 3	0	0	1	1	0
Oct 13	7	21	0	3	0
26	5	71	0	20	1
Nov 3	4	157	1	6	6
18	2	16	0	2	207
24	4	31	0	4	1
Dec 13	0	1	0	10	4
23	0	0	1	1	2
May 5, 1977	0	1	0	0	0
14	0	3	0	0	0
21	2	2	0	0	0
30	0	1	0	1	1
Aug 27	0	8	0	1	0
Sept 3	2	31	0	1	0
13	12	15	0	2	0
Oct 7	4	63	0	21	41
13	4	86	0	17	0
27	18	29	0	27	1
Nov 2	12	4	0	10	0
24	2	10	6	14	8
Feb 13, 1978	0	0	0	0	0
20	0	0	0	0	0
Mar 2	0	1	0	0	0
9	0	0	0	0	0
31	0	1	1	1	5

* Data from one plot only.

Appendix XVI-B. Morph-composition of *Aphis craccivora* in colonized stems in the experimental plots at Waite 1975-77.

Date	Number of colonized stems				
	With alatae		Without alatae		
	Alatae only	Alatae and nymphs/apterae	Apterae only	Nymphs only	Apterae and nymphs
Sept 11, 1975	2	4	0	1	0
18	0	0	0	2	0
25	3	7	0	3	0
Oct 6	0	3	0	4	1
20	1	3	1	4	2
27	6	9	0	8	0
Nov 6	2	2	0	9	0
Mar 17, 1976*	0	0	0	0	0
18*	2	1	0	0	0
19*	1	2	0	0	0
20*	0	0	0	2	0
22*	0	0	0	8	0
July 6	0	0	0	5	3
Aug 24	0	0	0	0	0
Oct 12	3	13	0	4	0
20	5	5	0	10	0
Mar 3, 1977	0	4	1	4	6
May 12	7	29	3	20	2
24	0	13	0	11	0

* Data from one plot only.

Appendix XVII - A. Random distributions (with two classes only) of colonizing *Aphis craccivora* alatae in the experimental plots at Mortlock 1975-78.

Date	No. of stems (f) with indicated No. of alatae (x)		Mean alatae per stem ($\bar{x}$)	s^2	$s^2/\bar{x}$
	0	1			
Sept 19, 1975	95	3	0.0306	0.0299	0.9793
23	139	8	0.0544	0.0518	0.9521
Oct 2	183	13	0.0663	0.0622	0.9384
10	94	4	0.0408	0.0396	0.9691
21	185	11	0.0561	0.0532	0.9487
28	228	17	0.0694	0.0648	0.9344
Nov 27	132	6	0.0435	0.0419	0.9635
Dec 5	136	2	0.0145	0.0144	0.9927
23	164	6	0.0353	0.0343	0.9704
Feb 9, 1976	95	1	0.0104	0.0104	1.0
16	135	1	0.0074	0.0074	1.0
Mar 9	154	2	0.0128	0.0127	0.9935
23	52	1	0.0189	0.0189	1.0
30	146	1	0.0068	0.0068	1.0
Apr 13	191	5	0.0255	0.0250	0.9800
20	242	3	0.0122	0.0121	0.9918
May 4	293	1	0.0034	0.0034	1.0
11	94	4	0.0408	0.0396	0.9691
Dec 13	74	1	0.0133	0.0133	1.0
May 5, 1977	49	1	0.02	0.02	1.0
14	72	3	0.04	0.0389	0.9730
21	96	4	0.04	0.0388	0.9697
30	99	1	0.01	0.01	1.0
Aug 27	42	8	0.16	0.1371	0.8571
Mar 2, 1978	81	1	0.0122	0.0122	1.0
31	52	1	0.0189	0.0189	1.0

Appendix XVII-B. Random distributions (with two classes only) of colonizing *Aphis craccivora* alatae in the experimental plots at Waite 1975-77.

Date	No. of stems (f) with indicated No. of alatae (x)		Mean alatae per stem ($\bar{x}$)	s^2	$s^2/\bar{x}$
	0	1			
Sept 11, 1975	92	6	0.0612	0.0581	0.9485
18	146	1	0.0068	0.0068	1.0
25	186	10	0.0510	0.0487	0.9539
Oct 6	242	3	0.0122	0.0121	0.9918
20	291	3	0.0102	0.0101	0.9931
Nov 6	143	4	0.0272	0.0267	0.9795
Mar 18, 1976*	46	3	0.0612	0.0587	0.9583
19*	46	3	0.0612	0.0587	0.9583
Oct 20	137	10	0.068	0.0638	0.9384
Mar 3, 1977	69	3	0.0417	0.0405	0.9718

* Data from one plot.

Appendix XVIII-A. Observed and expected frequencies of colonized stems for negative binomial distributions of colonizing *Aphis craccivora* alatae in the experimental plots at Mortlock 1976-77.

Date	No. of alatae per stem (x)	Observed number of stems (f)	Expected number of stems (f)
13.10.76	0	71	71.4
	1	20	19.6
	2	6	5.2
	> 2	1	1.8
26.10.76	0	106	105.8
	1	36	33.5
	2	9	17.0
	3	14	9.7
	4	5	5.8
	5	5	3.6
	6	3	2.3
	7	2	1.5
	> 7	2	2.9
3.11.76 (data from one plot only)	0	45	39.9
	1	14	26.4
	2	19	17.9
	3	13	12.2
	4	18	8.3
	5	3	5.7
	6	3	3.9
	7	2	2.7
	8	2	1.9
	9	3	1.3
	> 9	1	2.8
18.11.76	0	176	176.1
	1	12	11.9
	2	5	3.9
	3	1	1.6
	> 3	1	1.5
24.11.76	0	16	14.2
	1	6	9.4
	2	4	6.7
	3	9	4.9
	4	2	3.7
	5	2	2.7
	6	4	2.0
	7	3	1.5
	> 8	4	3.7
3.9.77	0	43	42.2
	1	17	19.1
	2	8	8.1
	3	5	3.3
	> 3	2	2.3

Appendix XVIII-A (continued).

Date	No. of alatae per stem (x)	Observed number of stems (f)	Expected number of stems (f)
13.9.77	0	68	67.3
	1	16	18.8
	2	8	5.9
	> 2	3	3.0
7.10.77	0	77	79.1
	1	42	36.8
	2	16	15.8
	3	3	6.6
	4	3	2.7
	> 6	2	1.9
13.10.77	0	39	40.4
	1	35	34.9
	2	29	23.2
	3	12	13.8
	4	6	7.8
	5	2	4.2
	6	1	2.3
	7	3	1.2
	> 7	2	1.2
27.10.77	0	216	215.5
	1	33	35.5
	2	11	8.7
	> 2	3	3.3

Appendix XVIII-B. Observed and expected frequencies of colonized stems for a negative binomial distribution of colonizing *Aphis craccivora* alatae in the experimental plots at Waite 1977.

Date	No. of alatae per stem (x)	Observed number of stems (f)	Expected number of stems (f)
12.5.77	0	40	40.6
	1	17	14.1
	2	3	7.5
	3	7	4.5
	4	2	2.8
	5	2	1.8
	> 6	3	1.3
	> 8	1	1.2

Appendix XIX. Incidence of natural enemies of *Aphis craccivora* in the experimental plots at Mortlock and Waite 1975-77.

Date	No. of colonized stems	No. of colonized stems with				
		Syrphid E/L	Chamaemyiid E/L	Coccinellid E/L/A	Chrysopid L	Parasitized aphids
Mortlock						
Oct 2, 1975	24	0	0	0	0	1
Nov 4	89	0	0	0	0	5
11	7	0	0	0	2	0
27	22	0	0	0	0	1
Dec 5	15	0	0	0	0	1
23*	34	7	19	1	0	0
Feb 3, 1976	9	1	0	0	0	0
Nov 3*	92	9	1	0	0	0
18	227	116	95	1	0	2
24	40	0	0	2	2	0
Oct 7, 1977	129	42	5	1	0	17
13	107	15	0	1	0	0
27	75	1	5	3	3	6
Nov 2	26	0	0	1	1	0
24	40	1	6	0	0	0
Waite						
Sept 11, 1975	7	0	0	0	1	1
25	13	0	0	0	0	1
Oct 6	8	0	0	0	0	1
27	23	1	0	0	0	0
Oct 12, 1976	20	0	0	0	2	0
May 12, 1977	61	0	0	0	0	22
24	24	0	0	0	0	9

* Data from one plot only.
E = Eggs
L = Larvae
A = Adults

Appendix XX: Temperatures inside field cages for the first 46 days during Experiment II - 1978.

Day	Date	Maximum temperature (°C)	Minimum temperature (°C)	Cumulative day-degrees above 8.3°C
1	May 17	21	8	
2	18	19	6	
3	19	18	7.5	
4	20	18.5	8	
5	21	23	7	
6	22	21	9	
7	23	17	8	
8	24	16.5	6	
9	25	20.5	11	
10	26	23	8	
11	27	24	9	
12	28	25	9	
13	29	19	12	
14	30	23	5	72.4*
15	31	21	4	
16	June 1	23	4	
17	2	22	3.5	
18	3	16	4	82.6**
19	4	26	9	92.0**
20	5	25	7	
21	6	20.5	8	
22	7	19	9	
23	8	15	8	
24	9	20	8	
25	10	17	8	
26	11	15	8	
27	12	14.5	5	
28	13	23	5	
29	14	16	8.5	
30	15	15	4	
31	16	19	6	
32	17	24	7	
33	18	17	5	
34	19	18	3.5	
35	20	17	4	142.3A
36	21	20	4.5	
37	22	18	5	
38	23	25	10.5	
39	24	18	11	162.7B
40	25	15	5	
41	26	16	5.5	
42	27	25	10.5	
43	28	24	7.5	
44	29	25	6	
45	30	25.5	5	
46	July 1	16.5	4.5	192.1C

* First generation apterae seen.
** Alatiform nymphs and teneral alatae seen.
A = No alata dispersal until 35 days.
B = The start of alata dispersal.
C = Plants harvested for population counts.

Appendix XXI: Total populations and numbers of apterae in the experimental colonies (in the big cages), sampled at 46 days after the start of experiment - 1978.

Host plant species	Initial* number of colonizing alatae	T/A**	Colonies (replicates) 1	2	3	4	5
Common burr medic	1	T	1112	804	1062	-	-
		A	42	38	24	-	-
	2	T	1604	1102	1718	-	-
		A	33	44	43	-	-
	3	T	3253	2340	-	-	-
		A	80	81	-	-	-
	7	T	1004	-	-	-	-
		A	44	-	-	-	-
Subterranean clover	1	T	202	388	415	-	-
		A	16	29	8	-	-
	2	T	188	187	563	360	-
		A	18	16	38	11	-
	3	T	792	568	1126	638	860
		A	29	32	65	26	43
	5	T	1568	1174	-	-	-
		A	65	47	-	-	-
	6	T	1304	-	-	-	-
		A	65	-	-	-	-
Broad bean	1	T	3484	1058	436	1272	1466
		A	82	44	44	77	48
	2	T	930	4320	5088	-	-
		A	45	160	236	-	-
	3	T	1548	-	-	-	-
		A	88	-	-	-	-
	4	T	1280	3028	-	-	-
		A	63	155	-	-	-
	6	T	1066	2120	-	-	-
		A	84	83	-	-	-
	7	T	3776	-	-	-	-
		A	110	-	-	-	-

* Number of colonizing alatae alive at 4 days after colonization.

** T = Total aphids; A = Apterae.

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