THE ECOLOGY OF *CACTOBLASTIS CACTORUM* (BERG) (LEPIDOPTERA: PHYCITIDAE) IN RELATION TO ITS EFFECTIVENESS AS A BIOLOGICAL CONTROL AGENT OF PRICKLY PEAR AND JOINTED CACTUS IN SOUTH AFRICA

by

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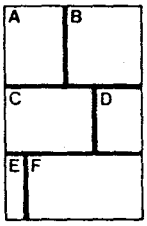


Life cycle of Cactoblastis cactorum (scale line = 5mm).

A. Eggs are laid in 'eggsticks', usually on the ends of cactus spines.

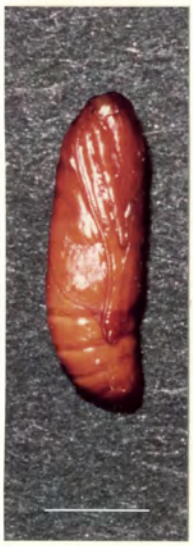
B. The larvae that hatch from the eggstick move to the base of the spine where, together, they attempt to penetrate the cactus cuticle. If penetration is initially unsuccessful (due to a tough cuticle or gum exudation), they attempt penetrating elsewhere on the plant.

C. Final instar larvae in an opened up, eaten cladode.

D. Once larval development is completed, the final instar larvae vacate the eaten cladode and search for a pupation site in the ground litter.

E. A pupa that has been removed from the cocoon.

F. A prickly pear Opuntia ficus-indica plant and a stand of jointed cactus O. aurantiaca plants damaged by C. cactorum larvae.



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RÉSUMÉ

The successful biological control of the shrub-like prickly pear Opuntia stricta Haworth in Australia by Cactoblastis cactorum (Berg) was not repeated when C. cactorum, derived from the Australian population, was released in South Africa in the 1930's against the tree prickly pear Opuntia ficus-indica (L.) Miller. Resistance of the woody portions of O. ficus-indica to attack by C. cactorum was regarded as the main reason for the poor performance of C. cactorum in South Africa. C. cactorum also oviposits and feeds on Opuntia aurantiaca Lindley, which is currently South Africa's most important weed and which is also considered to be partly resistant to attack by C. cactorum.

This study had three main objectives: (i) to compare the ecology and effectiveness of C. cactorum as a biological control agent on O. ficus-indica and O. aurantiaca; (ii) to reassess why C. cactorum has not been as effective a biological control agent in South Africa as it has been in Australia; and (iii) to evaluate whether inundative release or the importation of new biotypes of C. cactorum from South America (where it is indigenous) might be feasible methods of improving its effectiveness as a biological control agent of O. aurantiaca in South Africa.

All field work was undertaken at a site near Grahamstown in South Africa. The ecology and effectiveness of C. cactorum on O. ficus-indica and O. aurantiaca was assessed in terms of its oviposition behaviour, survival and feeding on these host plants.

The proportion of C. cactorum eggs laid on O. ficus-indica and O. aurantiaca was similar and was influenced by the size, conspicuousness and condition of the host plant as well as by the proximity of the host plant to moth emergence sites. Factors affecting oviposition site selection on the plant are also considered.

Life tables, compiled for a summer and a winter generation, showed that the survival of C. cactorum was greater on O. ficus-indica than on O. aurantiaca, mainly because higher egg predation by ants occurred on the latter host plant species. During the period of study, the

population size of C. cactorum was reduced by a number of mortality factors, of which egg predation and the effects of low temperatures on fecundity were the most important. Although there was evidence of a partial, positive response by predatory ants to C. cactorum egg densities on plants, the extent of egg predation was also affected by other factors, particularly seasonal effects.

C. cactorum destroyed a greater percentage of cladodes on O. ficus-indica than on O. aurantiaca, but even on O. ficus-indica it was unable to contain the growth of plants within the study area. C. cactorum larvae rarely killed the woody rooted cladodes of O. ficus-indica and O. aurantiaca and consequently whole plants were not often destroyed. The detrimental effects of host plant resistance, natural enemies and climate on the effectiveness of C. cactorum as a biological control agent all appear to be greater in South Africa than in most of the regions occupied by C. cactorum in Australia.

A field experiment conducted at the study site showed that inundative release methods for improving the effectiveness of C. cactorum on O. aurantiaca are not feasible. The importation of biotypes of C. cactorum from South America that might be better suited for destroying O. aurantiaca infestations in South Africa, is also not a viable option.

Results of a survey of a 218ha area that is regarded as being heavily infested with O. aurantiaca, illustrate how this cactus species has been overrated as a weed problem. It is argued that the present strategy for O. aurantiaca control in South Africa is not based on sound economic or ecological criteria.

1. INTRODUCTION

Cactoblastis cactorum (Berg) is one of at least 47 species in the family Phycitidae with larvae that are internal feeders in cacti (Mann 1969). Its life cycle is illustrated in the frontispiece. Particularly noteworthy is that eggs are laid as eggsticks usually on the ends of cactus spines. This form of egg clumping is characteristic of all the four or five species in the genus Cactoblastis and also of the genera Melitara and Olycella (Mann 1969).

The host plants of C. cactorum are predominantly species within the subgenus Platyopuntia of the genus Opuntia. Eleven native host plant species and 14 adopted host plant species have been recorded from this subgenus (Appendix 1). In addition, the Cylindropuntia Opuntia salmiana Parmantier and a species in the genus Cleistocactus have been recorded as native host plants (Appendix 1). Most of the adopted host plant species of C. cactorum and two of the native host plant species are weeds in some countries and C. cactorum has been used as a biological control agent against a number of these. Figure 1.1 shows that, from its origin in South America, C. cactorum was successfully introduced to Australia, then South Africa and from these two countries to various islands around the world where opuntias were a problem.

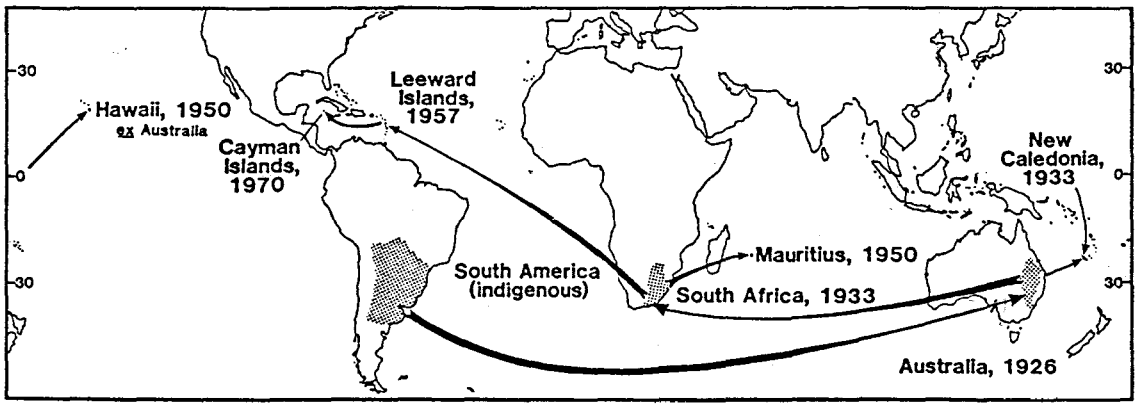

Fig. 1.1. World distribution of C. cactorum. C. cactorum is indigenous to South America and has been introduced to other regions as a biological control agent of Opuntia spp.. The origin (indicated by arrows) and year of release are shown for each region. Garcia Tuduri et al. (1971) give a detailed list of the islands occupied by C. cactorum within the Leeward Islands. C. cactorum has also been released in Israel and Kenya but establishment has apparently been unsuccessful (Bennett 1970). Information in map based on Julien (1982) and references cited therein.

In South Africa the two main weeds attacked by C. cactorum are the prickly pear Opuntia ficus-indica (L.) Miller and the jointed cactus O. aurantiaca Lindley. The origin, introduction, biological control and status of these two plants in South Africa has been reviewed by Annecke & Moran (1978), Moran & Annecke (1979) and Zimmermann & Moran (1982). O. aurantiaca is South Africa's most economically important weed because of a costly herbicidal control program which has been promoted by the government since 1957. The biological control agents that are established on O. aurantiaca in South Africa are C. cactorum, the cochineal insect Dactylopius austrinus De Lotto and the pyraustid Mimorista pulchellalis (Dyar) (Pettey 1948; Nieman 1983). The destruction caused by these three biological control agents has not been considered sufficient to warrant stopping or reducing the herbicidal control program. An attempt has also been made to establish the phycitid moth Tucumania tapiacola Dyar on O. aurantiaca in South Africa but this was unsuccessful (Hoffmann 1982). T. tapiacola is established on O. aurantiaca in Australia.

1.1 Description of O. ficus-indica and O. aurantiaca.

As is characteristic of the opuntias, O. ficus-indica and O. aurantiaca plants are made up of cladodes which are segments of stem modified primarily for water storage and photosynthesis. A cladode that falls to the ground has the ability to produce roots and form a new plant. Each cladode has small, barbed glochids and elongated spines arising in groups from areoles distributed over the surface. The two weeds are markedly different in growth form (Fig. 1.2). O. ficus-indica is a tree-like prickly pear which can grow to a height of over four metres. With age its cladodes change from being flattened and succulent to being more woody and rounded. This eventually results in a plant having thick, woody trunks and branches supporting green, succulent cladodes. Large, succulent, edible fruit are produced in summer. O. aurantiaca, on the other hand, is an inconspicuous plant that grows among the surrounding vegetation and is usually less than 0.5m in height although it can exceed this height by using adjacent scrub for support. The cladodes are much smaller and more elongate than those of O. ficus-indica and those that become rooted and buried develop into woody tubers that function as storage organs (Zimmermann 1981). The cladodes break off the plant easily and take root, often below the

Fig. 1.2. A small O. ficus-indica plant and a stand of O. aurantiaca plants (right foreground).

plant. This eventually results in the formation of stands of O. aurantiaca plants, sometimes covering more than $5m^2$ in ground area. Other cladodes become attached to animals or are carried away by water and in this way are distributed over large areas. The inedible fruits produced by O. aurantiaca can also take root easily. The seeds they contain are 99.95% sterile (Archibald 1936) and so reproduction is almost entirely vegetative in O. aurantiaca, whereas in O. ficus-indica fertile seeds are produced.

The woody cladodes of Opuntia plants are usually resistant to attack by C. cactorum larvae (Dodd 1940; Pettey 1948) and hence plants with a high proportion of woody tissue are rarely destroyed by C. cactorum. The woody composition of O. ficus-indica and O. aurantiaca is shown in Figs 1.3 & 1.4. The proportion of woody cladodes on O. ficus-indica in terms of mass increases with plant size, whereas in terms of cladode

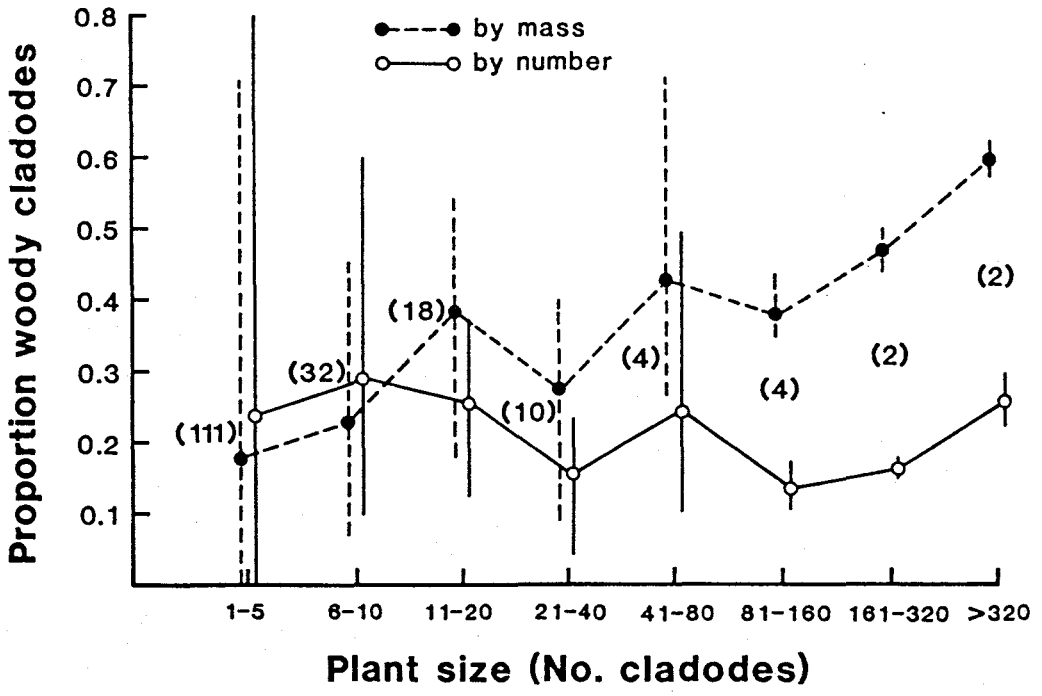

Fig. 1.3. Mean proportion of woody O. ficus-indica cladodes in relation to plant size. Proportions are expressed in terms of cladode numbers and cladode mass. Vertical lines indicate the range of values and numbers in brackets indicate the sample size of plants. The method for calculating cladode masses is given in Appendix 2.

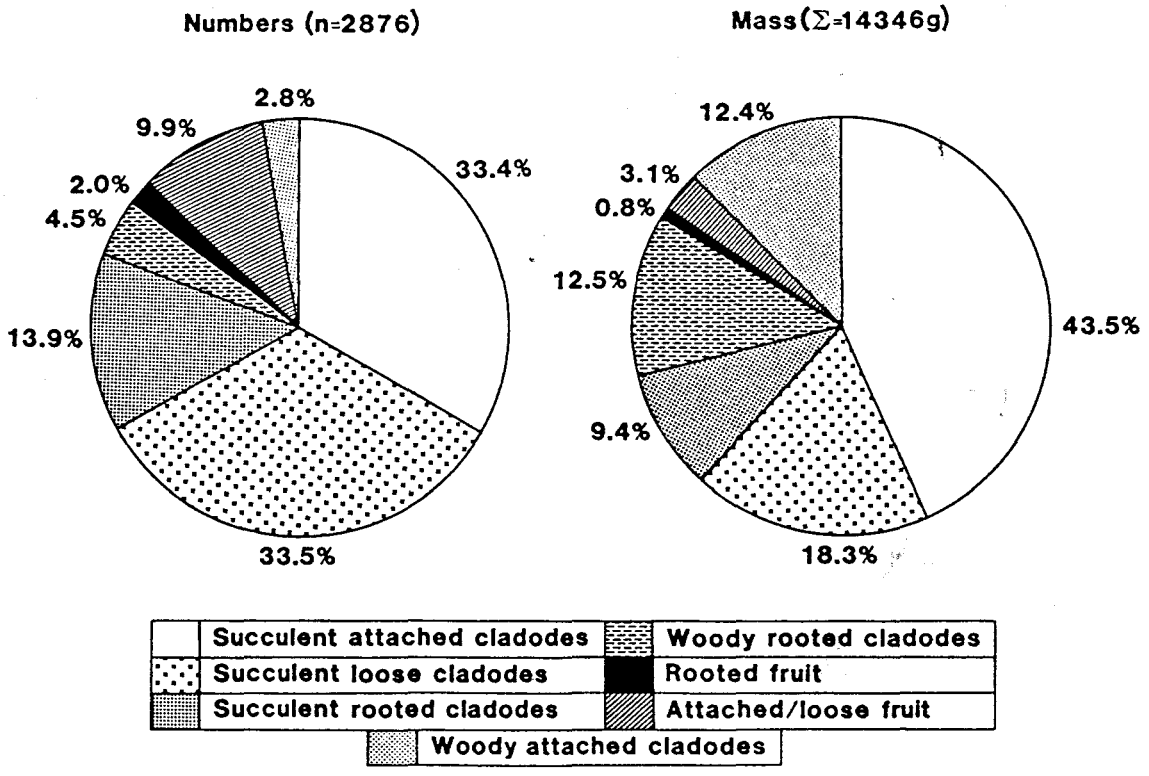

Fig. 1.4. Composition of O. aurantiaca stands in terms of numbers and mass of cladodes and fruit (see Appendix 3 for methods).

number it remains more or less the same (Fig. 1.3). This is because as plants become larger and more tree-like, their basal, woody cladodes increase markedly in size. Woody cladodes constituted 49.5% of the total mass and 23.7% of the total number of cladodes. The proportion of woody cladodes are underestimated in Fig. 1.3 because cladodes which were intermediate between succulent and woody were classed as succulent.

In O. aurantiaca stands, cladodes and fruit which were woody constituted 7.3% of the stand in terms of number but 24.9% in terms of mass because these cladodes are relatively large (Fig. 1.4). The total proportion of woody cladodes on O. aurantiaca in terms of number and mass respectively was therefore 16.4% and 24.6% lower than on O. ficus-indica. Succulent, attached cladodes constituted only 33.4% of the total number of cladodes and fruit. There was a large proportion of unattached succulent cladodes (33.5%) which was partly due to the time of year when these stands were sampled (see Appendix 3). Rooted cladodes and fruit in O. aurantiaca totalled 20.4% by number and 22.7% by mass.

O. aurantiaca plants have a number of different growth forms depending mainly on the amount of direct sunlight they receive (Hoffmann 1982). Three main growth forms of O. aurantiaca plants can be distinguished (Fig. 1.5): (i) exposed forms tend to be low growing and have small cladodes with long spines; (ii) semi-shaded forms have long spines, a high proportion of large cladodes and often exceed 0.5m in height by using the surrounding bush for support; and (iii) etiolated forms occur in the shade, also often exceed 0.5m in height, are characterized by elongated cladodes and in deep shade have short spines.

1.2 History of C. cactorum in Australia and South Africa.

The first use of C. cactorum for biological control was in Australia against the prickly pear Opuntia stricta Haworth (Dodd 1936, 1940, 1959) and is one of the world's outstanding examples of the successful biological control of a serious weed problem (DeBach et al. 1976). (Modern opinion is that Opuntia inermis De Candolle is a synonym of O. stricta, eg. Murray 1982). Prior to the initial release of C. cactorum in 1926, about 24 282 000 hectares of land in Australia

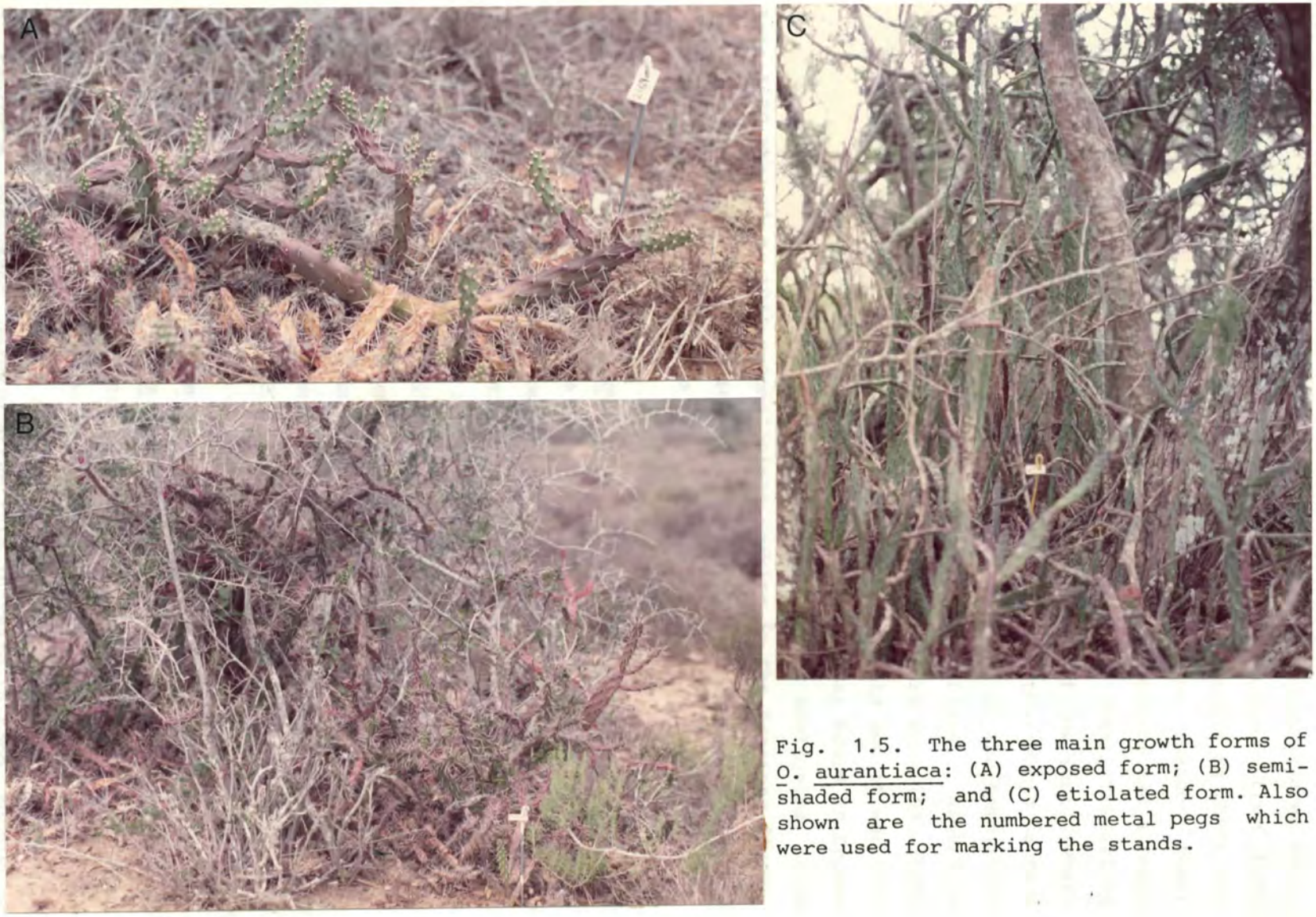

Fig. 1.5. The three main growth forms of O. aurantiaca: (A) exposed form; (B) semi-shaded form; and (C) etiolated form. Also shown are the numbered metal pegs which were used for marking the stands.

were infested by prickly pear, half of which were densely infested and agriculturally useless. Mechanical and chemical methods of control were not feasible, the cost of clearing a densely infested area being between 6.7 and 40 times the value of the land (calculated from Dodd 1940 p. 2). Many landholders could not keep the cactus in check and because of financial difficulties, were forced to abandon their properties (Dodd 1940 p. 2). The use of biological control had already been considered when in 1912 the Queensland Prickly Pear Travelling Commission was appointed and sent to various parts of the world where cacti occurred in an attempt to find natural enemies that would attack O. stricta (Mann 1970). In 1914 one of the members of the commission discovered C. cactorum in the Botanic Gardens at La Plata, Argentina but the larvae he sent across to Australia died before pupation (Dodd 1940 p. 108). The First World War interrupted events and it was only after the appointment of the Commonwealth Prickly Pear Board in December 1919 that more research on biological control was instigated. From late 1920 through to 1937 entomologists working in the Americas discovered about 150 different species of natural enemies on Opuntia spp. and related cacti, of which 50 were despatched to Australia.

In 1925, 2750 eggs of C. cactorum reached Australia. These eggs were derived from larvae that were collected from Opuntia delaetiana Weber and a similar species at Concordia, Entre Rios in Argentina (Dodd 1940 p. 109). C. cactorum satisfied host specificity requirements and in February-March 1926 eggs were first released. This was the start of a massive campaign to distribute C. cactorum eggs throughout the infested areas of Queensland and New South Wales. An impressive total of approximately 2750 million eggs (weighing a total of about 800 - 900 kg) was distributed between 1926 and 1931 by government authorities (Dodd 1940 p. 115). By 1932, most of the prickly pear plants were destroyed to ground level but were not necessarily killed because they had woody cladodes below ground level resistant to C. cactorum attack. During 1932 and 1933 the C. cactorum population was suddenly reduced in size because the larvae had consumed most of the available food supply. Consequently the plants that were not killed by C. cactorum during the first wave of attack sent up a vigorous regrowth. The population of C. cactorum recovered quickly after this increase in food supply so that by 1935 the regrowth was under control (Dodd 1940 p. 5). Repeated destruction of the above-ground portions eventually resulted in the

death of the woody rooted cladodes. Waves of prickly pear resurgence and then collapse continued but on a more localized level (Dodd 1940 p. 141). The end result was that in Queensland, complete biological control of prickly pear had been achieved. Widespread infestations of O. stricta had been reduced to isolated or widely scattered plants with only small patches of resistant prickly pear remaining. By 1940, 8 900 000 hectares of country were open for reoccupation by farmers. The benefit to the farmers was enormous but no statistics are available to show the economic recovery brought about by this biological control program (Dodd 1959 p. 576). In New South Wales C. cactorum was not as successful as in Queensland but infestations were nevertheless reduced by at least 80% (Dodd 1940 p. 8).

In South Africa, C. cactorum was first released in 1933 against O. ficus-indica from material derived from the Australian population. From 1933 to 1941 about 579 million eggs were distributed over an infested area in the Eastern Cape totalling about 598 300 hectares (Pettey 1948 p. 31). The effectiveness of C. cactorum on O. ficus-indica was not nearly as great as it was in Australia on O. stricta. The difference in performance was attributed mainly to the more tree-like and woody habit of O. ficus-indica. C. cactorum was effective in destroying young plants (below a height of about 0.6m) but with older plants only the first two or three terminal cladodes were eaten so that the woody stumps still remained. The latter still had a great capacity for producing regrowth. Pettey, in a report he made after a visit to Australia, had in fact predicted this state of events before C. cactorum was released in South Africa (Pettey 1948 p. 15).

C. cactorum occurs on O. aurantiaca in Australia as well as in South Africa. In neither country was O. aurantiaca the original target weed. Both Dodd (1940 p. 145) and Pettey (1948 p. 73) reported that C. cactorum readily oviposited on O. aurantiaca and the larvae flourished on it. However, they noted that the larvae were only effective in destroying the above-ground cladodes, rarely killing the rooted tubers. Consequently O. aurantiaca plants attacked by C. cactorum recovered quickly by producing a large amount of new growth. Both Dodd and Pettey therefore concluded that C. cactorum was not an effective biological control agent of O. aurantiaca.

1.3 The purpose and scope of this study.

Despite the lengthy account by Pettey (1948) on C. cactorum in South Africa, there is a lack of clarity about the reasons why C. cactorum has not been as effective in this country as it has been in Australia. Pettey (1948) and Annecke & Moran (1978) regarded incompatibility with the host plant as the major reason. Mortality from natural enemies and weather was also considered important but the overall contribution of these factors was uncertain. In addition, factors affecting the performance of C. cactorum as a biological control agent of O. aurantiaca in South Africa are unclear because the account by Pettey (1948) deals almost exclusively with the biology of C. cactorum on O. ficus-indica.

The purpose of this study has been to re-examine the ecological factors that influence the effectiveness of C. cactorum as a biological control agent of O. ficus-indica and O. aurantiaca in South Africa. The approach has been to make a detailed study of C. cactorum at one site rather than a more superficial analysis at a number of different sites.

Moran & Annecke (1979) discussed the possibility that there are races of C. cactorum in South America which are better suited to South African conditions and in particular, better adapted to feeding on low-growing O. aurantiaca plants. A further aim of the present study has therefore been to evaluate whether the introduction of a more appropriate strain (or biotype) of C. cactorum would increase its effectiveness as a biological control agent in South Africa.

The effectiveness of C. cactorum has been assessed in terms of: (i) oviposition behaviour (chapters 4 & 5); (ii) survival (chapters 6 & 7); and (iii) its ability to destroy O. ficus-indica and O. aurantiaca plants (chapter 8). These sections are prefaced by an introductory chapter on the general biology of C. cactorum (chapter 3), and followed by chapter 9 which is a digression to consider the economic importance of O. aurantiaca as a weed and the control methods used against it.

2. STUDY SITE AND METHODS

All field work was undertaken on Thursford Farm (33°12'S; 26°22'E), 21km NW of Grahamstown (Fig. 2.1 A). This area consists of False Karroid vegetation (Acocks 1975; Fig. 2.2), mainly Pentzia spp. and Relhania genistaefolia (L.)L'Herit. Interspersed amongst this low scrub are loose thickets of taller bushes and trees predominantly Ozoroa mucronata (Bern.)R. & A. Fernandes, Azima tetracantha Lam., Pappea capensis Ecklon & Zeyher, Grewia robusta Burch., Euclea undulata Th., Portulacaria afra Jacq. and Schotia afra (L.) Bodin. This site was chosen because it is near Grahamstown and because O. ficus-indica and O. aurantiaca both occur there. The exposed growth form of O. aurantiaca (Fig. 1.5 A) is predominant in the low scrub vegetation while the intermediate and, to a lesser extent, the etiolated growth forms (Fig. 1.5 B,C) exist among the loose thickets of bushes and trees.

Temperature at the study site was measured on a thermohydrograph kept in a Stevenson screen. Rainfall was recorded on a Hellman Type recording rain gauge kept near the farm house, 2.6 km from the study site. Fig. 2.3 shows the monthly rainfall for the entire study period and the average temperatures for the period covering the summer 1981/82 and winter 1982 generations which was when C. cactorum was studied most intensively. Rainfall was very erratic at the study site because it is near the border of the summer and winter rainfall regions. There was a drought from about November 1982 to June 1983.

Seven 50x50m adjacent quadrats (Figs 2.1 B & 2.2) were marked out and all O. ficus-indica plants (n=179) and O. aurantiaca stands (n=1316) in the quadrats were numbered and marked (Fig. 1.5). Within these quadrats the following data were gathered:

(i) The dimensions were taken of each O. aurantiaca stand and were later correlated with other information on the woody and succulent composition of the stands to determine the amount of O. aurantiaca in each quadrat (Appendix 3).

(ii) O. ficus-indica plants were surveyed at the end of each season from summer 1981/82 to summer 1983/84 inclusive to determine the number

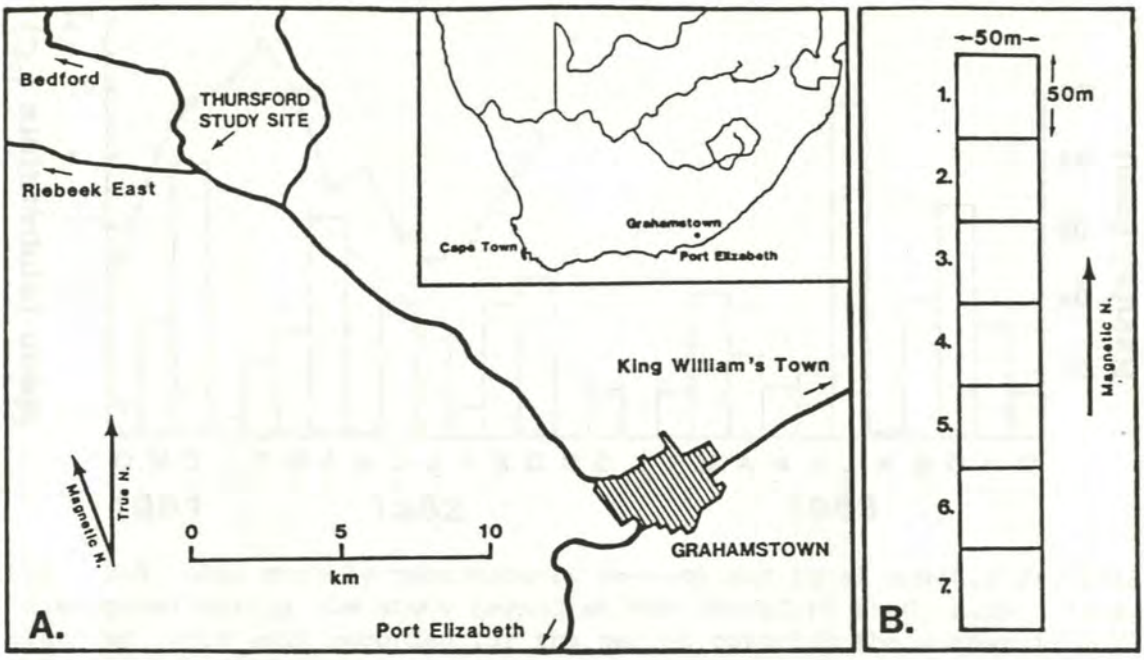

Fig. 2.1 A. The location of the study site on Thursford farm, in relation to Grahamstown. B. Diagram to show how the the quadrats at the study site were positioned. Quadrats 2-7 were positioned on the south facing slope of a hill and quadrat one was on top of the hill.

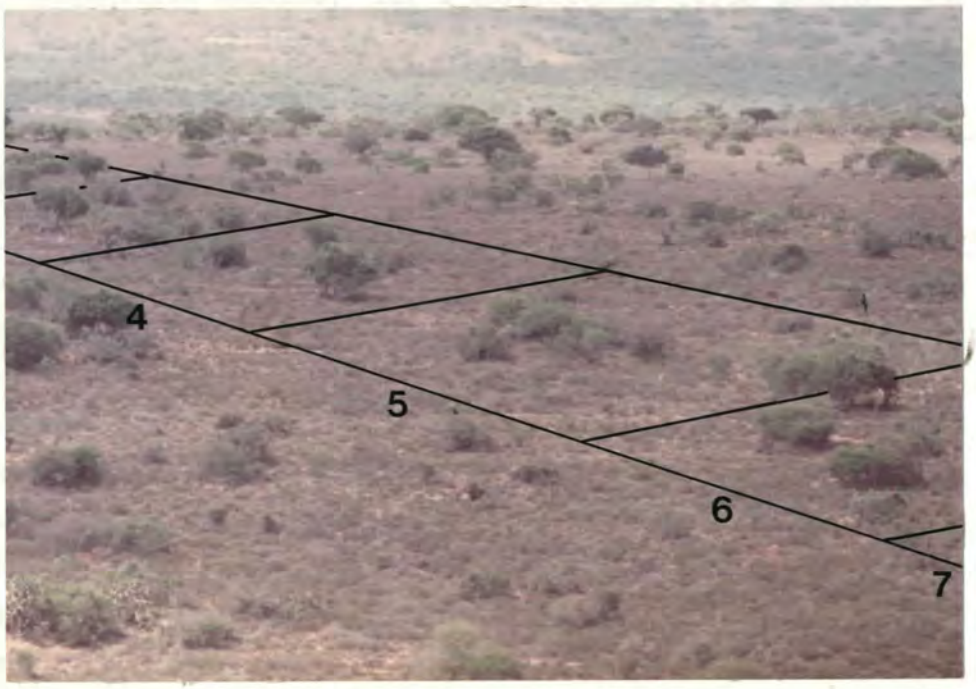

Fig. 2.2. View of quadrats 2-7 at the Thursford study site. Each quadrat measured 50X50m.

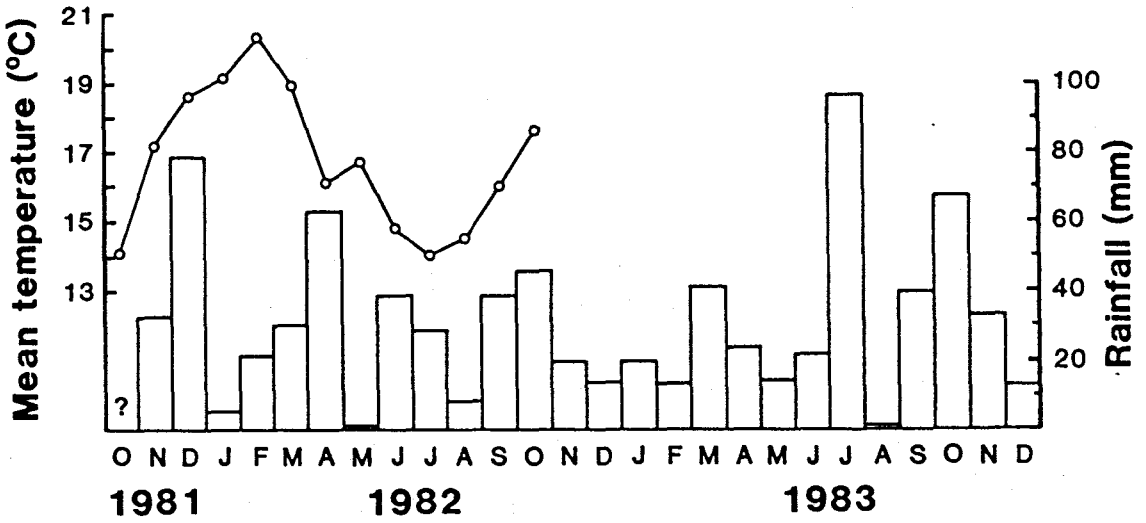

Fig. 2.3. Mean monthly temperatures (o——o) and total monthly rainfall (histogram) during the study period at the Thursford study site. Temperatures were only recorded for the period covering the summer 1981/82 and winter 1982 generations of C. cactorum because this was when C. cactorum was studied most intensively.

of cladodes destroyed by C. cactorum and other causes, and the number of undamaged cladodes remaining. This type of analysis was not feasible for O. aurantiaca because, for a sufficiently large sample, too many cladodes would have had to be counted.

(iii) On 85% and 70% respectively of the days in the summer and winter egg laying periods, all conspicuous O. ficus-indica plants and selected O. aurantiaca stands were searched for newly laid C. cactorum eggsticks. Six O. ficus-indica plants outside the quadrats were also searched for eggsticks. Plants were searched on an almost daily basis because firstly, egg mortality was high so it was important to search for newly laid eggsticks before they disappeared and secondly, by searching on consecutive days, the laying date of each eggstick was known. This was useful for calculating incubation periods (chapter 3), predation rates (chapter 7) and determining the effect of wind on oviposition (chapter 5). Each eggstick found was numbered (Fig. 2.4), characterized in terms of certain variables, and checked on subsequent days for signs of mortality. The number of eggs in each eggstick was determined either by counting directly or by estimating the number of eggs from the length of the eggstick ($y=2.87x-5.2$, $r^2=0.948$, $n=136$, where x is the eggstick length (mm) and y is the number of eggs in the eggstick). It was not possible to search all the O. aurantiaca stands daily as there were too many of them and they also took longer to

Fig. 2.4. A numbered eggstick on an O. ficus-indica cladode. When more than one eggstick was found on the same cladode, they were numbered on the cladode surface with a felt-tipped pen. This type of numbering was difficult on O. aurantiaca because of the high density of spines.

search than O. ficus-indica plants. At the end of each egg laying season, however, all O. aurantiaca stands were searched for hatched eggsticks and for evidence of the presence or absence of any eggsticks. These latter surveys each took about two weeks to complete.

Methods for other, more specific, surveys and experiments are mentioned in the text where appropriate.

3. GENERAL BIOLOGY OF C. CACTORUM

Six aspects of C. cactorum biology are dealt with in this chapter: (i) life cycle and general behaviour; (ii) phenology; (iii) the development periods of eggs, larvae and pupae; (iv) fecundity; (v) the number of eggs per eggstick and the number of eggsticks; and (vi) longevity and oviposition rate. These topics form a foundation for the chapters that follow. The results presented are compared with those obtained by Pettey (1948) in South Africa and by Dodd (1940) in Australia.

3.1 Life cycle and general behaviour.

C. cactorum adults emerge in the evening, usually within two hours after dusk. Mating takes place during the early morning from daylight until about 7.30am (Dodd 1940 p. 120) but otherwise adults usually remain inactive during daylight and sit motionless in the vegetation in the vicinity of their host plants. Oviposition, like emergence, usually occurs within two hours after dusk (Dodd 1940 p. 122) although oviposition can continue until about midnight (Pettey 1948 p. 42).

The most distinctive feature of C. cactorum biology is the clumping of the eggs in eggsticks. The first photograph in the frontispiece shows the stance of a female during the oviposition of an eggstick. The first egg in the eggstick is glued to the spine with an amber-coloured substance presumably derived from the accessory glands. The positioning of eggs on top of one another is guided by setae that surround the ovipositor. The sequence of events in the laying of an egg on an eggstick by a C. cactorum female is explained in the legend to Fig. 3.1. Pettey (1948 p. 41) recorded that during the oviposition of an eggstick, eggs are laid at a rate of about one every 16 seconds (range = 10-24) so that for eggsticks ranging in size from 61-102 eggs, each one takes 12-34 minutes to complete.

The larvae that hatch from an eggstick penetrate the plant together (frontispiece, B). The first larvae that emerge move down to the base of the spine where they surround themselves with a web of silk spun between the spine and the cladode surface. This web may protect them from predators such as ants. When the number of larvae reaches a

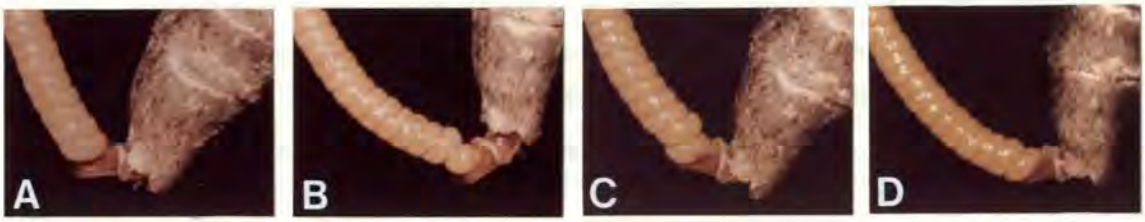

Fig. 3.1. Sequence of events in the oviposition of an egg on the end of an eggstick by a C. cactorum female. Only the end of the abdomen and the end of the eggstick are shown (see frontispiece for photograph of a female ovipositing an eggstick). The setae located round the perimeter of the ovipositor are used to position it over the last laid egg in the eggstick (A). The next egg is then extruded from the ovipositor (B) and pressed against the last egg in the eggstick (C,D). The process is then repeated for the next egg to be laid.

certain undetermined threshold level, the larvae begin penetrating, usually adjacent to the spine on which the eggstick was laid. At the Thursford study site, a colony of nine larvae was the smallest that successfully penetrated a cladode. To penetrate, the larvae chew away the cuticle at one spot on the cladode surface and deposit it in a ring around the penetration site (frontispiece, B). If penetration is prevented by a tough cuticle or because of gum exudation, the larvae usually attempt to penetrate elsewhere on the plant.

After successful penetration, the larvae feed gregariously on the parenchymous tissue inside the cladode. Fibres are not eaten. Larvae can tunnel from cladode to cladode thus avoiding having to move outside and start penetrating the plant elsewhere. However, larvae sometimes do have to vacate the cladode when (i) the cladode becomes detached from the plant and contains no more suitable tissue for consumption; (ii) they destroy the entire plant in which they are feeding; (iii) they are unable or unwilling to bore into adjacent cladodes, particularly when the adjacent cladode is woody; or when (iv) the internal cladode temperature becomes too high. Under the latter circumstances, larvae, when outside the cladode, sometimes suspend themselves on a web of silk that is spun in the shade beneath a cladode (similar behaviour has been recorded in Olycella subumbrella (Dyar) by Lummus & Wangberg 1981). Internal cladode temperatures can be very high. For instance, in cladodes of North American cacti under natural conditions, temperatures from 10°C to 22°C above air temperature can occur with a maximum recorded temperature of 65°C (Smith et al. 1984). When locating a new penetration site, larvae spin a silken path which presumably maintains

colony cohesion (see Long (1955) for other Lepidoptera) as well as enabling the larvae to retrace their route if necessary. After about the third instar, larvae in some colonies split up into smaller groups, especially when the cladodes are small.

Dodd (1940 p. 130) and G.C. Clark (in Pettey 1948 p. 52) recorded that there were six larval instars of C. cactorum. By rearing individual C. cactorum larvae throughout their development and collecting the head capsules after each moult, I have found that they can pass through as many as eight instars although six instars is the usual number. This increase in instar number is possibly partly because the larvae were reared individually. Long (1953) has shown for larvae of other lepidopteran species that aggregation of the larvae tends to result in a decrease in the number of instars.

By the time pupation occurs, C. cactorum larvae have noticeable aposematic orange and black banding (frontispiece, C) similar to that found in other lepidopteran larvae such as Tyria jacobaeae L. (aposematic colouration is often associated with gregariousness - see Harvey & Paxton 1981; Harvey et al. 1982). C. cactorum larvae pupate individually in the ground litter surrounding the plant although some do pupate inside the dried eaten cladodes.

3.2 Phenology.

C. cactorum normally has two generations a year, a short one in summer and a longer one in winter. However, C. cactorum is univoltine in some regions (eg. South-eastern Australia - Dodd 1940 p. 116; Murray 1982), and in parts of Central Queensland can complete three generations over a period of a year (Dodd 1940 p. 116).

The phenology of C. cactorum eggs, larvae and pupae at the Thursford study site for summer 1981/82 and winter 1982 generations is shown in Fig. 3.2. Pupation of C. cactorum larvae from O. aurantiaca was later than for larvae from O. ficus-indica because of slower larval development on O. aurantiaca (see next section). About 10% of larvae on O. aurantiaca in the summer generation overwintered instead of pupating and producing a winter generation.

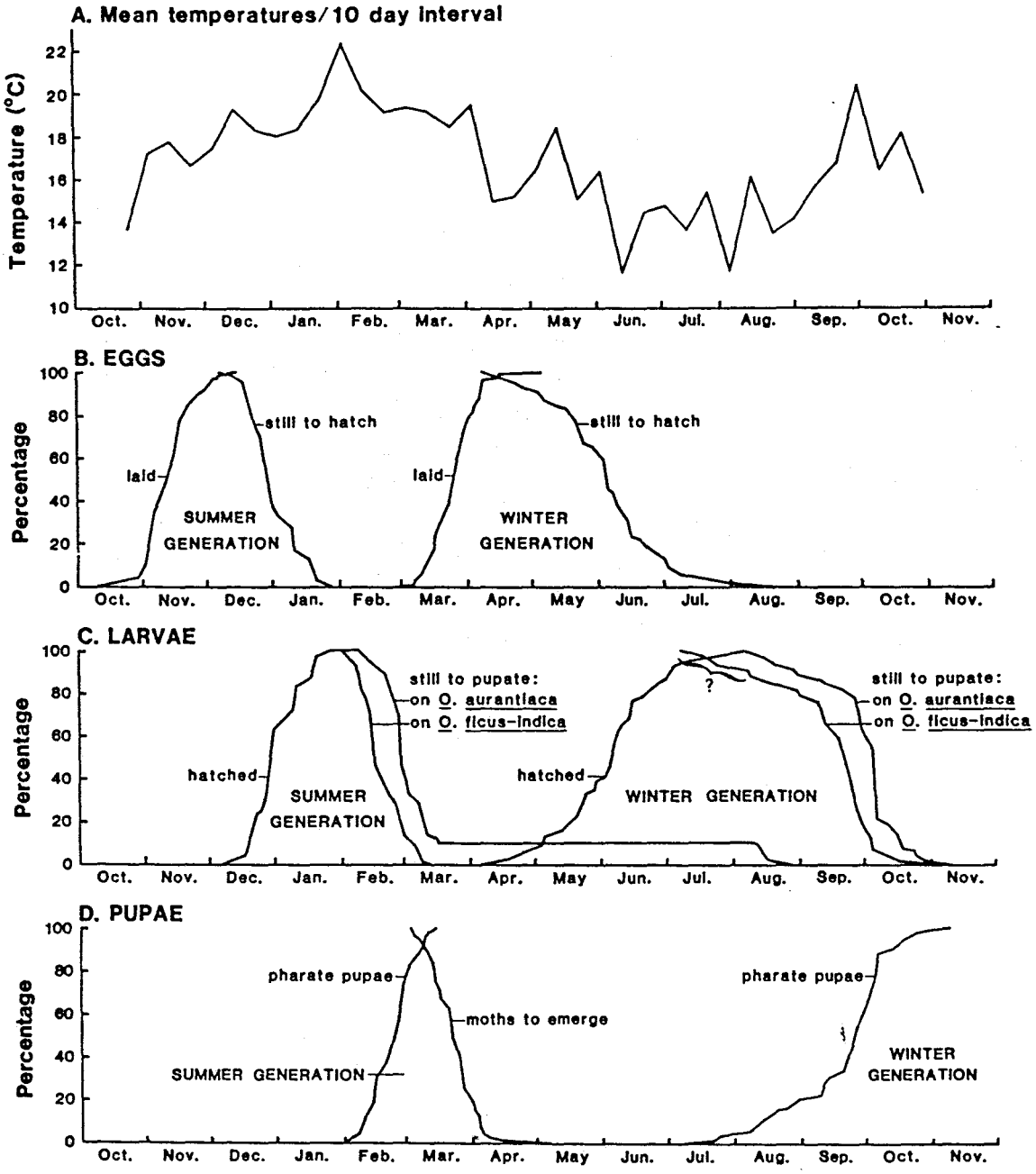

Fig. 3.2. Phenology of C. cactorum eggs, larvae and pupae at the Thursford study site over the summer 1981/82 and winter 1982 generations. Mean temperatures over this period are also shown. The seasonal presence of eggs and hatched larvae was recorded directly in the field. The pupation dates of larvae were calculated using the day-degree periods in Appendix 4. The seasonal presence of pupae was deduced from graphs B & C.

The egg-laying period of C. cactorum at Thursford was from early October to mid-December in the summer 1981/82 generation and from late February to early May in the winter generation (Fig. 3.2). Observations of the following four generations showed that there were slight shifts in the egg-laying periods between years. For example, in the winter

1983 generation, egg-laying began in early February and was nearing its peak by the beginning of March. The peaks in the egg-laying periods of C. cactorum in summer and winter generations at Thursford lie well outside the range of peaks recorded by Pettey (1948) for other sites in the Eastern Cape (Table 3.1) probably because of regional variations in temperature regimes.

Table 3.1. The peaks in the egg-laying periods of C. cactorum in South Africa and Australia. 'Summer' and 'winter' generations refer to the generation of the females, not the eggs.

Locality	°latitude S	Winter generation	Summer generation
South Africa:			
Thursford study site	33°	11 Nov.	24 March
Uitenhage, Fort Beaufort and Graaff-Reinet[1]	32°-34°	3 - 29 Oct.	3 Feb. - 9 March
Australia[2]			
Central Queensland	21°-25°	15 Sept. - 10 Oct.	9 - 28 Jan.
Southern Queensland	25°-29°	3 - 18 Oct.	22 Jan. - 10 Feb.
Hunter Valley (NSW)	32°	26 Oct. - 16 Nov.	17 Feb. - 13 March

[1]Pettey (1948 p. 64).

[2]Dodd (1940 p. 117).

In Australia, the peaks in egg-laying periods of C. cactorum are delayed with increasing latitude. In Central and Southern Queensland the peaks in egg-laying periods are earlier than in South Africa (Table 3.1). However, in Hunter Valley (New South Wales), which is at a similar latitude to the prickly-pear infested regions of the Eastern Cape, the peaks in egg-laying of C. cactorum are similar to those in South Africa. The performance of C. cactorum as a biological control agent of O. stricta in New South Wales was poor in comparison to its performance in Queensland (Dodd 1940) which might have been connected with differences in phenology. The latitudinal differences in the effectiveness of C. cactorum as a biological control agent are considered further in the discussion.

3.3 Development periods.

The differences in the phenology of C. cactorum in South Africa and Australia, discussed in the previous section, result in differences in development periods of eggs, larvae and pupae in the two countries.

1) Egg incubation periods: The incubation periods of naturally laid eggsticks at the study site were calculated from the laying and hatching dates, obtained from the daily surveys of eggsticks on O. ficus-indica and O. aurantiaca (chapter 2). The effect of temperature on egg development rates in C. cactorum is considered in Appendix 4. The mean egg incubation periods at the Thursford study site were 50.9 and 74.7 days in the summer and winter generations respectively, which are longer than the corresponding periods recorded elsewhere in South Africa by Pettey (1948) and in Australia by Dodd (1940) (Table 3.2). Even the shortest incubation periods recorded at the study site in each generation were longer than the mean incubation periods recorded by Pettey (1948) and Dodd (1940). In addition, the mean incubation periods recorded by Dodd are shorter than those recorded by Pettey (Table 3.2).

Table 3.2. Egg incubation periods (in days) of C. cactorum.

Locality	Summer generation			Winter generation		
	Mean ± SE	Range	n	Mean ± SE	Range	n
South Africa						
Thursford study site	50.9 ± 0.5	41-64	66	74.7 ± 1.2	58-114	98
Uitenhage[1]	39	?-73	-	53	-	-
Graaff-Reinet[1]	33	-	-	50	-	-
Australia[2]						
Southern Queensland	28-30	18-?	-	23-28	?-132	-
Hunter Valley (NSW)	28-32	-	-	40-45	23-70	-

[1] Pettey (1948 p. 64).

[2] Dodd (1940 p. 117).

During the summer generation, temperatures were increasing during the egg development period in the field whereas in the winter generation they were decreasing (Fig. 3.2). As a result, in the summer generation, incubation periods were longer for early-laid than for late-laid eggsticks whereas in the winter generation, early-laid eggsticks took a shorter time to develop than those laid later on (Fig. 3.3).

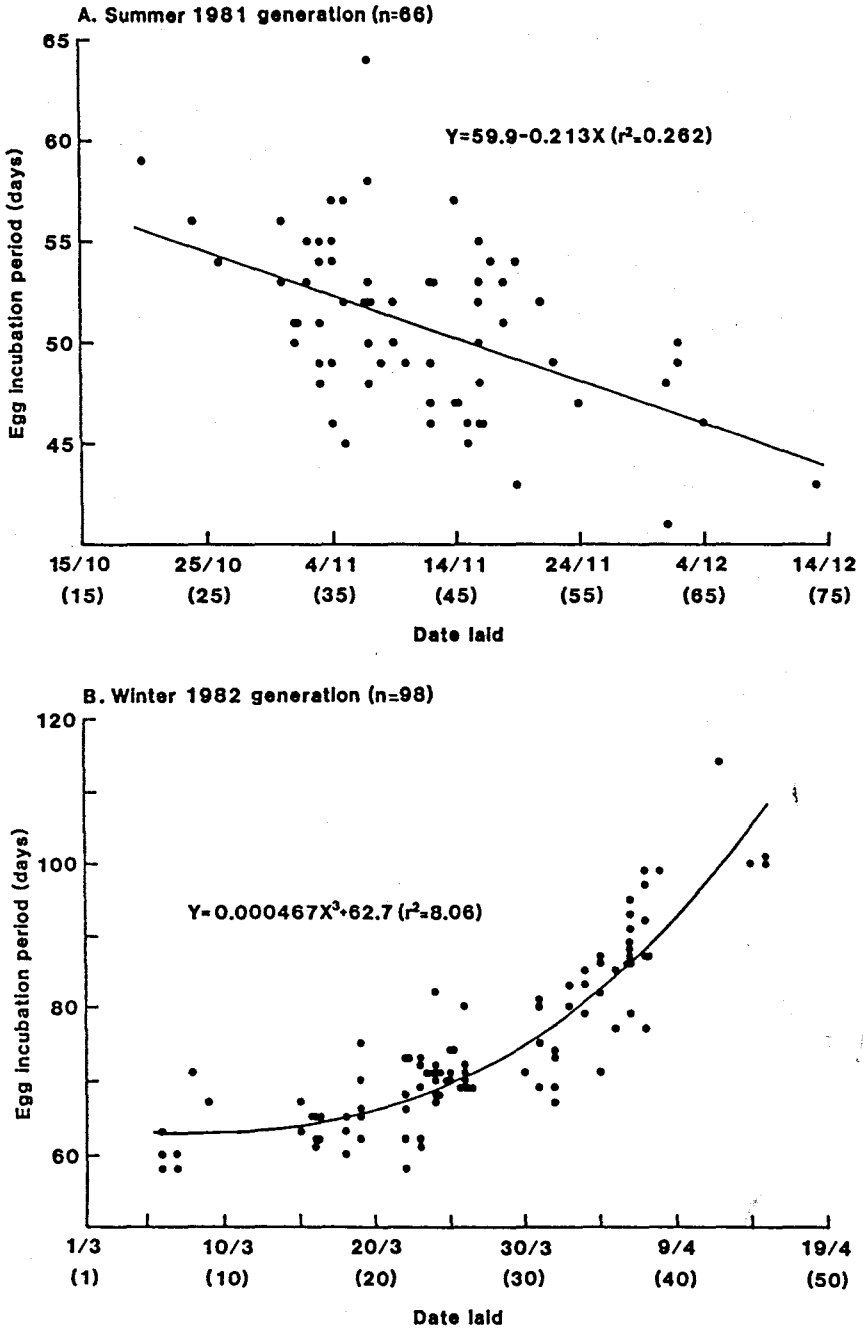

Fig. 3.3. Incubation periods of C. cactorum eggsticks laid at different dates at the Thursford study site in the summer 1981/82 (A) and the winter 1982 (B) generations. Note that the y-axis scales are different in the two graphs. The numbers in brackets on the x-axis are the date numbers for 'x' in the equations.

2) Larval development periods. Larval development periods were recorded for colonies on O. ficus-indica and O. aurantiaca during the course of the larval mortality determinations (section 6.6). They were not, however, determined for colonies on O. aurantiaca in the summer generation because in most instances the hatching dates of these colonies were not known. Expression of larval development periods in terms of day-degrees is considered in Appendix 4.

As a result of the lower temperatures, larval development was more than twice as long in the winter as in the summer generation (Table 3.3). In the winter generation, development periods were significantly longer on O. aurantiaca than on O. ficus-indica (paired t-test for colonies of similar hatching dates; $t=4.56$; $d.f.=8$; $P=0.0009$). This might have been because of poorer nourishment on O. aurantiaca or because the smaller cladodes of O. aurantiaca resulted in less efficient feeding. From the pupation dates, it was clear that in the summer generation, larval development was also slower on O. aurantiaca than on O. ficus-indica. As was shown in Fig. 3.2, about 10% of larvae in the summer generation from O. aurantiaca overwintered instead of producing a winter generation. Much of the time they spent as larvae must have been spent in a dormant state as their period of development was 1.7 times

Table 3.3. Larval development periods (in days) of C. cactorum. O. f.-O. ficus-indica; O. a. - O. aurantiaca; O. s. - O. stricta. The sample size indicates the number of colonies.

Locality	Host plant	Summer generation				Winter generation			
		Mean temp.(°C)	Mean ± SE	Range	n	Mean temp.(°C)	Mean ± SE	Range	n
South Africa									
Thursford study site	O. f.	19.4	49.3 ± 0.9	46-53	8	15.4	102.0 ± 2.3	90-120	13
	O. a.	-	-	-	-	15.3	123.6 ± 2.4	90-141	21
	O. a.[1]	16.7	206.8 ± 2.4	200-210	4	-	-	-	-
Uitenhage[2]	O. f.	21.2	64	52-82	-	16.2	130	99-167	-
Graaff-Reinet[2]	O. f.	22.2	56	47-73	-	16.4	122	104-164	-
Australia[3]	O. s.	23.3	51	27-?	-	-	180	?-200	

[1] Summer generation larvae that overwintered.

[2] Pettey (1948 p. 56).

[3] Dodd (1940 p. 130).

as long as that of winter generation larvae on O. aurantiaca (calculated from Table 3.3). In two of the colonies, a proportion of the larvae pupated for a winter generation whereas the rest overwintered as larvae. This suggests that the cues for overwintering were operative towards the end of larval development.

The time taken for C. cactorum colonies to pupate was longer on O. aurantiaca than O. ficus-indica. For instance, in the winter generation, in all colonies recorded on O. ficus-indica, it took less than a week for all the larvae in each colony to pupate whereas on O. aurantiaca, the colony pupation period ranged from two to three weeks. As Dodd (1940 p. 131) has suggested, larvae in different cladodes on a plant would tend to develop at different rates as there is likely to be variation in the nutritional qualities of the cladodes. On O. aurantiaca this variation would be particularly pronounced as the cladodes are small and consequently larvae in a colony have to feed in a large number of them. The number of cladodes consumed per colony ranged from 1-5 on O. ficus-indica and from 5-68 on O. aurantiaca (Table 8.1).

The larval development periods on O. ficus-indica recorded by Pettey (1948) at two localities, are all greater than the corresponding results obtained at the Thursford study site even though the mean temperatures recorded by Pettey are higher (Table 3.3). Pettey's results are based on colonies kept in cages and this could have prolonged the development periods in two ways: (i) the food quality and quantity might have been lower than that in the field; (ii) the internal temperatures of cladodes in cages might have been less than that of cladodes on plants in the field because they would not have been exposed to direct sunlight. In the field, under cold conditions, larvae use the sun to raise their body temperatures by clustering on the inside of the 'windows' of cladode cuticle which have resulted from their feeding activities.

In Australia, the larval development period of C. cactorum in the summer generation is similar to that in South Africa but in the winter generation, the larval development period is considerably longer (180 days compared with 102-130 days - Table 3.3). The winter generation of C. cactorum in Australia begins earlier in the year than in South

Africa (Table 3.1) and as a result larvae in Australia might have a period of dormancy in order to postpone pupation until spring arrives.

3) Pupal development periods. Pupal development periods of C. cactorum were not recorded at the Thursford study site. The pupal development periods recorded by Pettey (1948) and Dodd (1940), are compared in Table 3.4. The summer pupal development periods recorded in South Africa are similar to those recorded in Australia but the winter pupal development periods are considerably longer in South Africa than in Australia.

Table 3.4. Pupal development periods of C. cactorum (including the pharate period).

Locality	Summer generation		Winter generation	
	Mean	Range	Mean	Range
South Africa[1]				
Uitenhage	29	20-32	73	64-86
Graaff-Reinet	24	21-27	62	56-66
Australia[2]	21-28	13-?	35-42	?-90

[1]Pettey (1948 pp. 61,65).

[2]Dodd (1940 p. 135).

The results presented in this and the previous section show that there are marked differences in the phenology and development periods of C. cactorum in South Africa and Australia. This is a reflection of differences in the temperatures experienced by C. cactorum in the two countries which is an important aspect in considering the fecundity of C. cactorum.

3.4 Fecundity.

The following procedure was used to determine fecundity of C. cactorum females. Pupae from larvae that had fed on O. ficus-indica or on O. aurantiaca in the field, were placed in emergence cages in the laboratory. Each day, all females in the emergence cages were removed

and, from a random sample of these, each female was placed in a separate oviposition cage. Females were therefore given the opportunity of mating on the same night as emergence but not after this. Those which failed to oviposit were presumed not to have mated and were excluded from fecundity determinations. The oviposition cages measured 45 X 30 X 45 cm and each one contained two O. ficus-indica cladodes. Cages were checked daily for eggsticks that had been laid the previous evening and each eggstick found was collected and the number of eggs it contained was recorded. When a female died, it was dissected and the number of developed and undeveloped eggs in the oviducts was recorded. Developed eggs were regarded as those which were about as large as oviposited eggs. Fecundity could therefore be expressed in three ways: (i) total fecundity was the sum of all eggs, laid and unlaid; (ii) developed-egg fecundity was the sum of the number of eggs laid and of the unlaid developed eggs and; (iii) realized fecundity was the actual number of eggs laid.

The initial mass of a sample of the females was recorded and from this an equation was determined which allowed prediction of total fecundity from initial body mass (Fig. 3.4). The mean proportions of developed and laid eggs could then be used to calculate developed-egg and realized fecundity (Fig. 3.4).

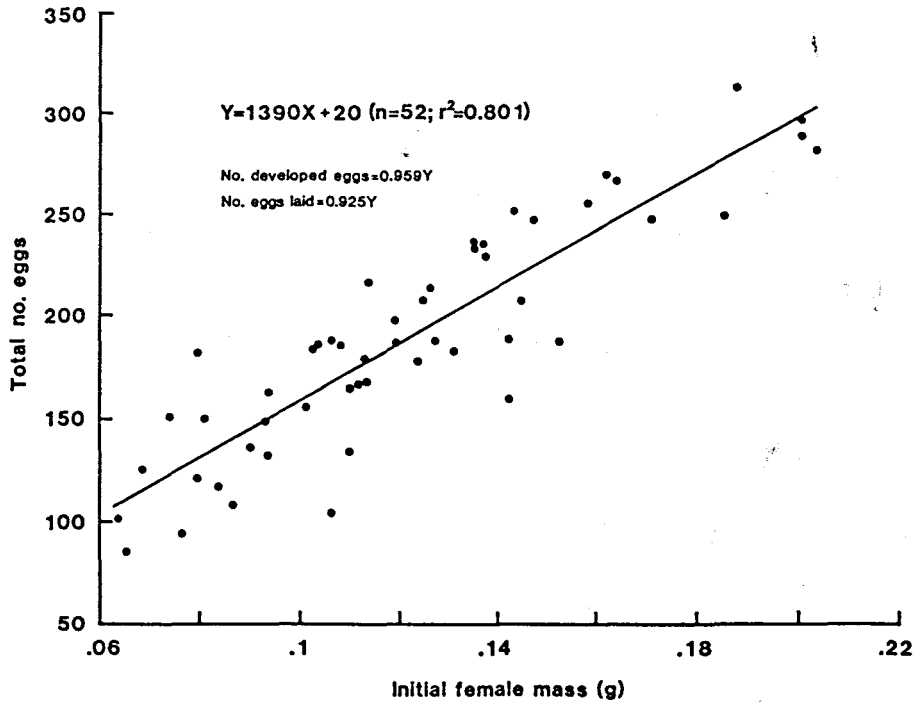

Fig. 3.4. Total number of C. cactorum eggs, laid and remaining in oviducts, in relation to initial female mass.

Fecundity of females reared on O. ficus-indica was significantly higher than on O. aurantiaca and significantly greater in winter than summer generations (Table 3.5). The lower fecundity on O. aurantiaca is possibly because of poorer nourishment or because the smaller cladodes of O. aurantiaca result in less efficient feeding. These reasons were also suggested for explaining the longer larval development period on O. aurantiaca than O. ficus-indica (section 3.3).

Table 3.5. C. cactorum fecundity, determined in the insectary, in relation to larval host plant and generation in the field at the Thursford study site. Probabilities for analysis of variance: n.s. - not significant ($P > 0.05$); * - $P < 0.05$; *** - $P < 0.001$.

	Summer generation		Winter generation	
	O. ficus-indica	O. aurantiaca	O. ficus-indica	O. aurantiaca
Mean ± SE	172.3 ± 4.8	138.4 ± 5.8	177.0 ± 4.7	159.4 ± 7.0
Range	54-277	63-262	100-281	58-260
n	66	49	75	57

Source of variation	d.f.	Mean square	F-ratio	P
Within cells	243	1877.91		
Host plant	1	38074.72	20.28	***
Generation	1	8365.83	4.45	*
Host plant x generation	1	3978.34	2.12	n.s.

The significantly greater fecundity in winter compared with summer (Table 3.5) is perhaps related to a difference in growth rates of larvae between these two generations. In Pieris rapae L. it has been shown that high temperatures during larval development increase growth rates but also tend to decrease fecundity (Gilbert 1984).

The fecundity values in Table 3.5 are higher than the means recorded by Pettey (1948) (Table 3.6). This is because Pettey's averages include females which did not oviposit and because his experiments were conducted outdoors where low temperatures tended to reduce fecundity. The effect of low temperatures on realized fecundity is an important component of C. cactorum population ecology. Based on results

Table 3.6. Comparison of C. cactorum fecundity measurements quoted or calculated from Pettey (1948) on O. ficus-indica in South Africa and Dodd (1940) on O. stricta in Australia. Non-laying females were included in the calculation of mean fecundities, whereas in Table 3.5, they were excluded.

	O. ficus-indica (Pettey 1948)	O. stricta (Dodd 1940)
Mean fecundity - summer[1]	168	?
Mean fecundity - winter[1]	90	?
Mean fecundity - total	126	135
Maximum mean fecundity	232	274
Maximum fecundity	328	392

[1]Dodd (1940 p. 125) does give fecundity values for summer and winter generations of C. cactorum in Australia but these are based on results for mass-reared moths and are therefore unreliable.

presented by Pettey (1948), there is a linear relationship between mean fecundity and the average minimum temperature recorded over the oviposition period (Fig. 3.5). All except one of the summer fecundity measurements in Fig. 3.5 are higher than those in winter because of the warmer temperatures. On average, realized fecundity recorded by Pettey (1948) in the winter generation was only 54% of that in the summer generation (Table 3.6).

To determine the effect of summer and winter temperatures on realized fecundity, moths were placed in oviposition cages on the roof of the Rhodes University Zoology Department during the egg-laying periods of the summer 1982/83 and winter 1983 generations. The cages were located in a place where night lighting from surrounding buildings could not interfere with oviposition. Low temperatures reduced fecundity by 2.0% and 12.8% in the summer and winter generations respectively (Table 3.7). Females which failed to oviposit were excluded from these results as it was not determined whether they had mated or not.

Fecundity of C. cactorum on O. stricta in Australia appears to be slightly higher than on O. ficus-indica in South Africa (Table 3.6) although a comparison of this kind is suspect because results in the two countries were measured and interpreted in different ways.

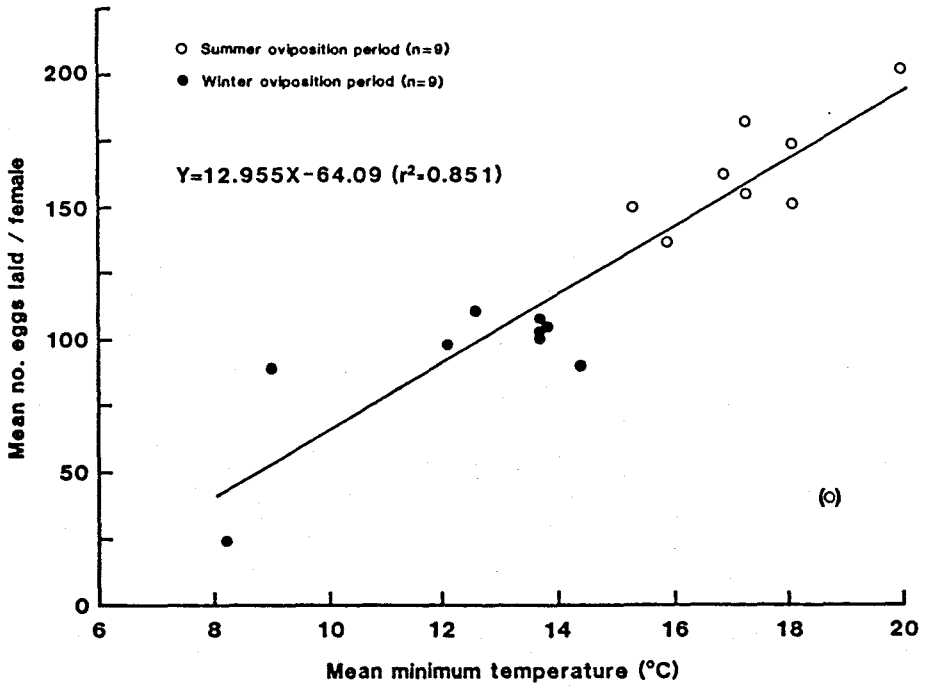

Fig. 3.5. Mean number of eggs laid per C. cactorum female in relation to the mean minimum temperature over the oviposition period. The data point in brackets was excluded in the calculation of the equation and is lower than expected because fecundity in that particular egg-laying period was adversely affected by high temperatures. (Calculated from raw data in Pettey 1948 pp. 47,48,50).

Table 3.7. Determination of the percentage unlaid C. cactorum eggs attributable to prevailing temperatures. Fecundity was measured in the insectary under optimal temperature conditions and outside on the Rhodes University Zoology Department roof under ambient temperatures conditions, for the summer 1983 and winter 1983 generation oviposition periods. Ambient temperatures are given in Table 3.10. C. cactorum females used in these experiments were derived from larvae which developed on O. ficus-indica at the Thursford study site. 'Total eggs' is the sum of all eggs, laid and unlaid. The potential number of eggs laid/female was calculated by multiplying the total eggs/female by the proportion of total eggs laid in the insectary.

	Summer generation		Winter generation	
	Insectary	Outside	Insectary	Outside
Total eggs/female (n)	181.3 (13)	187.8 (20)	198.9 (22)	193.8 (32)
Proportion total eggs laid	0.892	0.874	0.912	0.795
Actual no. eggs laid/female	161.7	164.1	181.4	154.1
Potential no. eggs laid/female	161.7	167.5	181.4	176.7
Difference (potential-actual)	0	3.4	0	22.6
% temperature mortality	0	2.0	0	12.8

Temperatures in the winter generation of C. cactorum in South Africa appear to be lower and have a more detrimental effect on fecundity than winter temperatures in Australia (comparison of Pettey 1948 p. 49 with Dodd 1940 p. 125). However, in the summer egg-laying period of C. cactorum in Australia, realized fecundity was often reduced by high temperatures (Dodd 1940 p. 127) whereas in South Africa this was rarely so (Pettey 1948 p. 50).

In summary, the fecundity of C. cactorum was significantly greater for females reared on O. ficus-indica than for those reared on O. aurantiaca. Realized fecundity of C. cactorum is affected by low and high temperatures. In South Africa, realized fecundity is reduced mainly in the winter generation by low temperatures whereas in Australia, realized fecundity is reduced mainly in the summer generation by excessively high temperatures.

3.5 The number of eggs per eggstick and the number of eggsticks.

From the information collected in the fecundity determinations, it was found that the number of eggs per eggstick was lower for later-laid eggsticks and the number of eggs per eggstick increased with fecundity (Fig. 3.6). Females with a high fecundity laid more eggs per eggstick and laid more eggsticks. Most females usually lay three or four eggsticks (mean = 3.8, Table 3.8).

Under both field and insectary conditions, the mean numbers of eggs per eggstick recorded for C. cactorum in this study were considerably lower than those recorded by both Dodd (1940) and Pettey (1948) (Table 3.9). Although increased fecundity and a decreased proportion of later-laid eggsticks might be factors that explain this discrepancy in results, another likely explanation is that the results and observations of Pettey and Dodd were biased towards larger eggsticks.

In the winter generation of C. cactorum, the mean number of eggs per eggstick on O. aurantiaca was significantly lower than that on O. ficus-indica (Table 3.9). This is possibly because the females were tending to lay a higher proportion of their initial, larger eggsticks on O. ficus-indica plants than on O. aurantiaca plants. However, why this difference in number of eggs per eggstick should occur in the

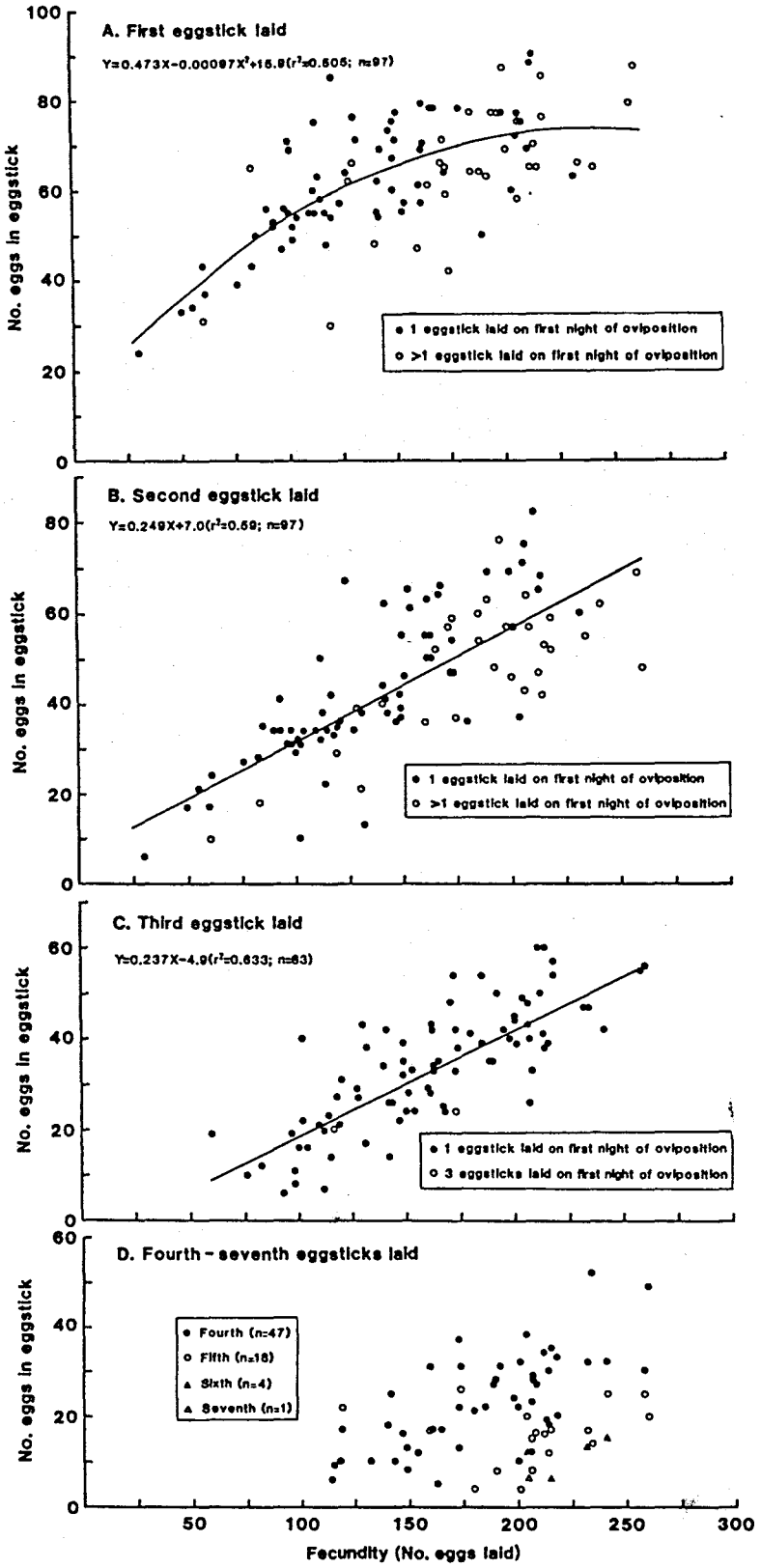

Fig. 3.6. The number of eggs in eggsticks of C. cactorum in relation to fecundity and the position of the eggstick in the female's eggstick laying sequence. (A) first eggstick laid; (B) second eggstick laid; (C) third eggstick laid; and (D) fourth, fifth, sixth and seventh eggsticks laid. On the first night of oviposition, females sometimes laid more than one eggstick so that it was not possible to determine in which order the eggsticks were laid. In these instances eggstick size was assumed to decrease according to oviposition order and these eggsticks are indicated by open dots in graphs A, B & C. Thirty-one females laid two eggsticks, and 2 females laid three eggsticks, on the first night of oviposition.

Table 3.8. Number of eggsticks laid per C. cactorum female. Females whose realized fecundity was reduced by low temperatures are excluded from these results.

	Larval host plant		
	O. ficus-indica	O. aurantiaca	Total
Mean ± SE	3.83 ± 0.14	3.75 ± 0.17	3.80 ± 0.11
Range	2-7	2-6	2-7
n	64	40	104

Table 3.9. The number of eggs in eggsticks laid by C. cactorum females in the field at the Thursford study site on O. ficus-indica and O. aurantiaca, and in the insectary by females which developed as larvae on O. ficus-indica and O. aurantiaca. Values given by Pettey (1948) and Dodd (1940) are also shown. Probabilities for t-test: n.s. - not significant ($P > 0.05$); *** - $P < 0.001$.

	O. ficus-indica			O. aurantiaca				Total[1]		
	Mean ± SE	Range	n	Mean ± SE	Range	n	t	Mean ± SE	Range	n
Field eggsticks										
Summer 1981/82	56.2 ± 1.6	4-102	176	54.7 ± 1.6	13-111	148	$0.64^{n.s.}$	55.5 ± 1.1	4-111	324
Winter 1982	56.5 ± 1.3	4-105	208	45.9 ± 1.2	2-84	158	5.95^{***}	50.1 ± 1.1	2-105	262
Insectary eggsticks	44.5 ± 1.4	4-93	245	42.3 ± 1.7	4-90	150	$1.01^{n.s.}$	43.7 ± 1.2	4-93	395
Pettey (1948 p. 45)	68.5	-	-							
	96.7	?-150	-							
Dodd (1940 p. 122)[2]	70-90	?-150	-							

[1] Sample size of O. ficus-indica eggsticks was lowered so that the ratio of O. ficus-indica to O. aurantiaca eggsticks was the same as that recorded in the field.

[2] Larval host plant = O. stricta.

winter but not in the summer generation is uncertain. Overall, the mean number of eggs per eggstick at the Thursford study site was lower in the winter than the summer generation (Table 3.9). The realized fecundity of females was greater in the summer than in the winter generation (Fig. 3.5, Table 3.7) which would have resulted in more later-laid eggsticks.

For eggsticks laid in the insectary, the mean number of eggs per eggstick was lower than that recorded in the field (Table 3.9). There would have been a higher proportion of later-laid eggsticks in the insectary than in the field because of more suitable temperature conditions for oviposition, and this would have lowered the mean number of eggs per eggstick.

3.6 Longevity and oviposition rate of female moths.

The adults of many Lepidoptera feed on nectar to supplement their energy supply and in some species such as the Heliconius butterflies, adults also feed on amino acids and pollen which enables them to generate new oocytes over a long life span (Dunlap-Pianka et al. 1977). C. cactorum adults, however, do not feed so that they emerge from the pupa with a limited supply of energy which is not supplemented in their life time. Their life span is therefore short, its length depending mainly on the prevailing temperatures (Table 3.10, Fig. 3.7). The rate

Table 3.10. Longevity of C. cactorum females in oviposition cages situated either outside, under ambient temperature conditions, or in an insectary. Females were derived from larvae which developed on O. ficus-indica at the Thursford study site. temp. - temperature; min. - minimum.

	Mean temp. (°C)	Mean min. temp. (°C)	% nights[1] unsuitable for oviposition	Female longevity (days)		
				Mean ± SE	Range	n
Ambient - summer	21.6	15.5	0	9.0 ± 0.8	4-18	20
Ambient - winter	18.1	13.4	11.7	15.0 ± 0.8	6-22	32
Insectary	22.9	21.0	0	7.0 ± 0.2	3-9	35

[1] ie. temperature during oviposition < 12°C.

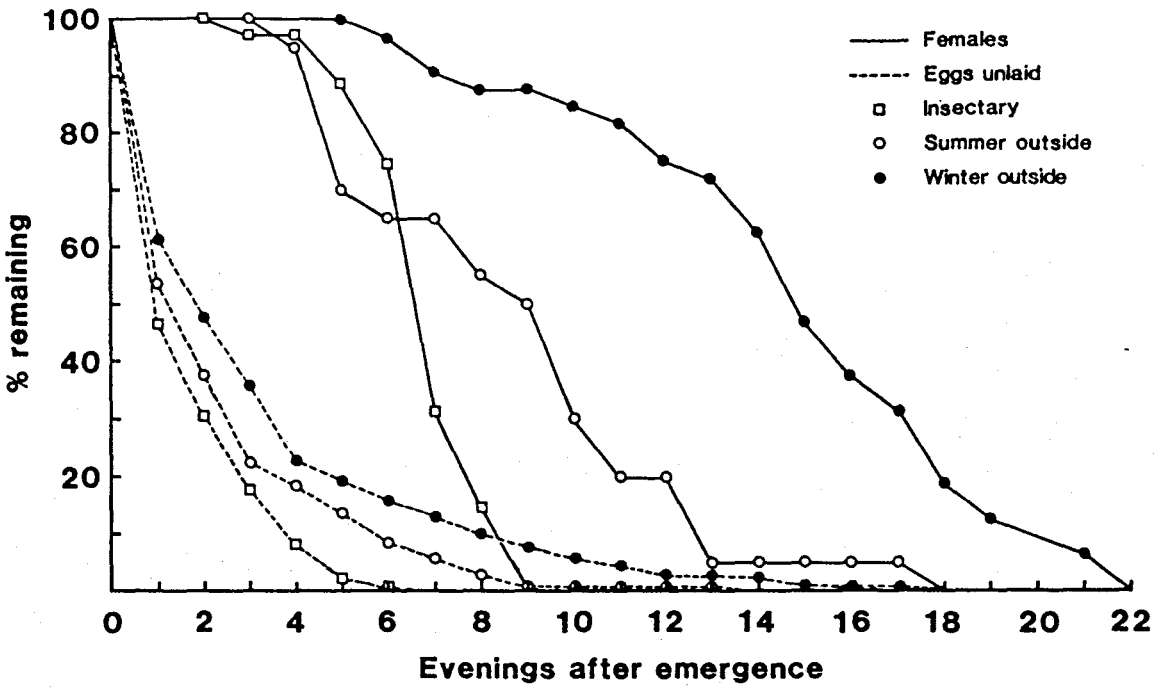

Fig. 3.7. Survivorship and oviposition rates of C. cactorum females in cages situated either outside, under ambient temperatures in the summer and winter oviposition periods, or in an insectary. The appropriate temperatures and sample sizes are given in Table 3.10.

of oviposition is also affected both by temperature, and by the age of the female (Fig. 3.7). Under summer, winter and insectary temperature regimes, more than 50% of eggs were laid on the two nights following the night of emergence and mating.

Temperatures can reduce the rate of oviposition by limiting the rate of egg maturation and by limiting the number of nights during which females can oviposit. Under winter temperature conditions, moths failed to oviposit on evenings when temperatures one hour after sunset were equal to or below 12°C. At this temperature threshold, 11% of the nights during the winter oviposition period were unsuitable for oviposition while in the summer generation, temperatures did not fall below 12°C. Reduced realized fecundity under low temperature conditions (Fig. 3.5, Table 3.7) might be a result of the rate of egg maturation exceeding the oviposition rate. Many of those moths which died with a high proportion of unlaid eggs, had a ball of up to 22 tightly packed eggs in the bulla seminalis (the duct linking the spermatheca with the median oviduct). These egg conglomerations might have been caused by a differential rate of egg maturation and oviposition.

Wing-loading (ie. the area of the wings relative to body mass) in C. cactorum females decreases markedly as eggs are oviposited. In this study, wing-loading of C. cactorum females was not measured but an indication of the relative changes in wing-loading over time was obtained by plotting egg mass as a percentage of total body mass over time (Fig. 3.8). These values were calculated from a knowledge of the

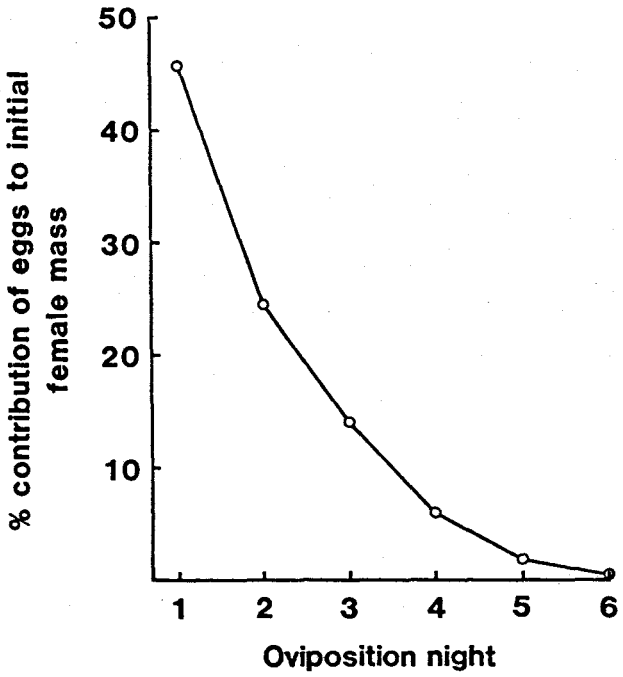

Fig. 3.8. Percentage contribution of eggs to the initial mass of C. cactorum females at the beginning of each night of oviposition. Based on data for 38 females.

initial body mass of each moth, the number of eggs laid each evening and the mean mass of a newly laid egg. These calculations do not account for evaporative water loss or for decreases in egg size over the egg-laying period. Overall, egg mass constituted 46% of initial body mass and the first evening of oviposition resulted in a body mass reduction of 21%. As more eggs are oviposited, the wing-loading would be decreased which would result in greater energetic efficiency of flight; this in turn would be likely to increase the tendency for flight and hence dispersal.

In summary, this chapter has introduced three important features of C. cactorum biology that have a direct bearing on the rest of this thesis. Firstly, the phenology and development periods of C. cactorum differ between South Africa and Australia, presumably because of

different temperature regimes in the two countries. Secondly, fecundity of C. cactorum is affected by host plant characteristics and by temperature. Thirdly, C. cactorum females have a high oviposition rate and a short life span. This third feature of C. cactorum biology is an important consideration in the two following chapters on oviposition behaviour in C. cactorum.

4. OVIPOSITION: HOST PLANT SELECTION

The selection by a C. cactorum female of a suitable oviposition site is critical for the survival of the eggs and the subsequent larvae. The oviposition of eggsticks at the beginning of each generation determines their spatial distribution in relation to one another and in relation to suitable penetration sites and food sources for emerging larvae. However, the selection of suitable oviposition sites would be constrained firstly by imperfections in the response of C. cactorum females to suitable oviposition cues, and secondly by factors affecting the survival of the female herself.

Fig. 4.1 shows the possible sequence of events in the life and oviposition behaviour of a female C. cactorum moth. The choice of an oviposition site is shown as a hierarchy consisting of three levels: (i) inter-plant; (ii) inter-cladode and (iii) intra-cladode. Listed beside each level are the variables considered in this study. Inter-plant oviposition is considered in this chapter and inter- and intra-cladode oviposition patterns in chapter 5. Fig. 4.1 shows that after the eggstick is oviposited, the female might lay another eggstick either on the same cladode or on the same plant as the previous eggstick or on a different plant, or she might cease oviposition for the evening and lay the eggstick another evening.

Host location and oviposition behaviour of C. cactorum is assessed in this study from an analysis of the positioning of eggs in the field. Stanton (1982) has emphasized the limitations of this approach in that the positioning of eggs in the field is really the nett result of the host plant selection process and not the actual behaviour of the female that produced these patterns. Consequently, inferences concerning actual behaviour need to be made with caution. As C. cactorum oviposits only after dark, it would obviously have been difficult to adopt a behavioural approach in this study.

A characteristic of C. cactorum oviposition behaviour is that, not only are eggs clumped in eggsticks, but the eggsticks themselves tend to be clumped. Monro (1967) found that whereas some O. stricta plants were "overloaded" with eggsticks, resulting in subsequent larval starvation, others had few if any eggsticks on them. He suggested that this could

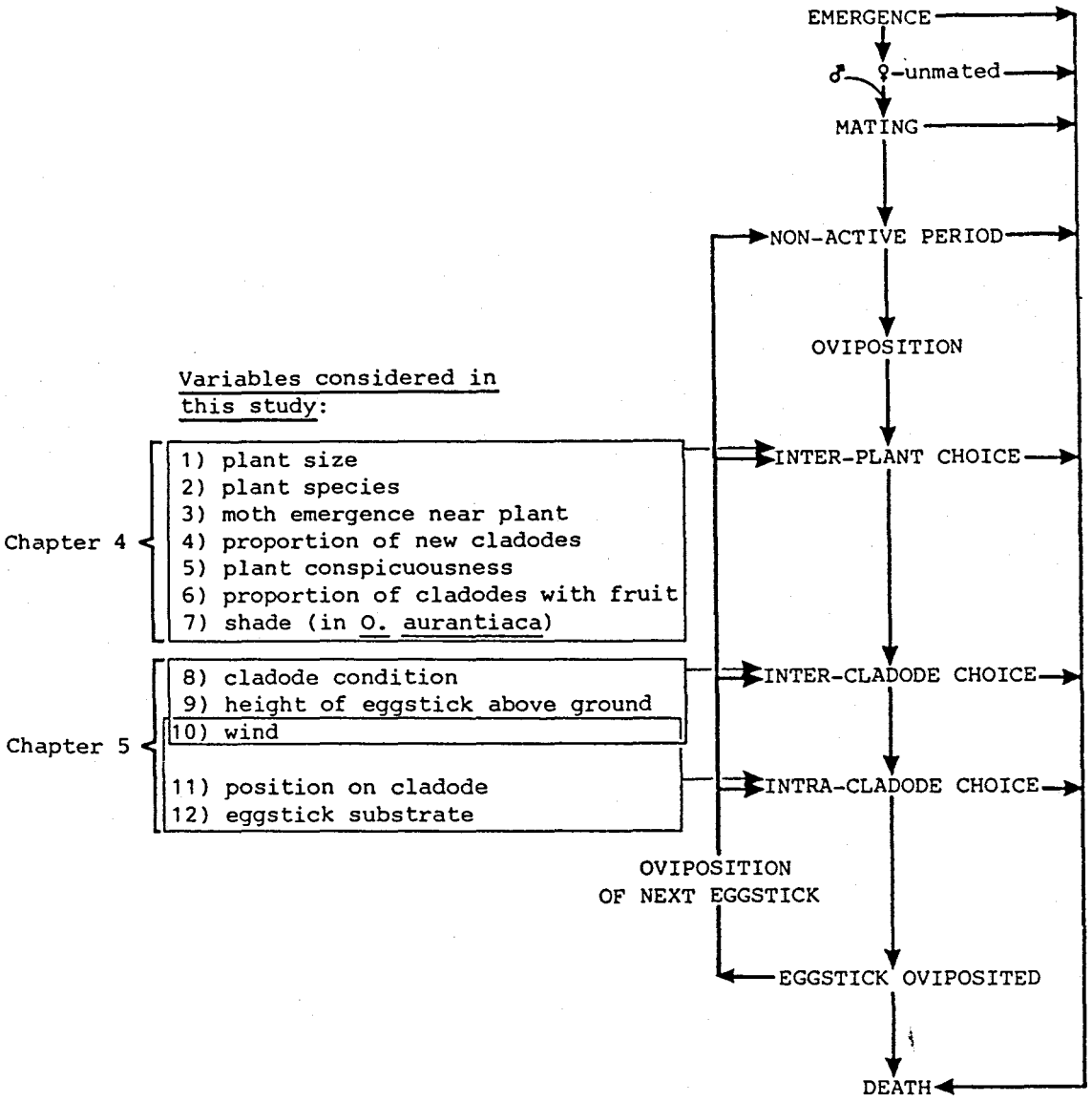

Fig. 4.1. Possible pathways in the life and oviposition behaviour of a C. cactorum female. Variables that could affect oviposition at each level of plant selection, and which are considered in this study, are shown.

be an adaptive trait in C. cactorum for conserving its food resources and this point of view is considered later in the discussion. Myers et al. (1981) found that properties of the plants such as size, previous damage by C. cactorum and nutritional status could also have caused clumping effects.

There was significant clumping of eggsticks on O. ficus-indica plants in both the summer and winter generations at the Thursford study site and the variance in the number of eggsticks per plant was considerably greater than the mean (Table 4.1). Clumping of eggsticks on O. aurantiaca stands was also clearly evident but could not be assessed accurately because the number of eggs laid was not known for all stands.

Table 4.1. Assessment of the degree of clumping of C. cactorum eggsticks on O. ficus-indica plants in the quadrats at the Thursford study site. Only plants with at least one cladode visible above the surrounding vegetation are included. The distribution of eggsticks per plant is compared with the expected Poisson distribution using the G-test. *** - $P < 0.001$.

Generation	No. eggsticks/plant			G
	Mean	Variance	n	
Summer 1981/82	1.97	89.40	93	163.1***
Winter 1982	2.54	84.51	95	163.7***

The primary aim of this chapter is to establish the factors that affect the number of eggs laid on O. ficus-indica and O. aurantiaca plants growing in sympatry. A preference for one host plant over the other could affect the degree to which each is brought under biological control by C. cactorum. Pettey (1948) does not mention whether either of these host plants was favoured for oviposition, but does mention that eggsticks were often laid on O. aurantiaca. In Australia, Dodd (1940 p. 145) observed that moths oviposited just as freely on O. aurantiaca as on O. stricta in field situations where they occurred together and in fact appeared sometimes to favour the former plant. Although C. cactorum oviposits on a wide range of Platyopuntia species including ones not found within its native distribution (Appendix 1, Moran & Zimmermann 1985), there is evidence of discrimination between some of these host plants. Mann (1969) comments that in Argentina, C. cactorum does not oviposit on large Opuntia quimilo Schumann plants and that the low-growing Opuntia sulphurea G. Don has not been recorded as a host plant. In Australia, Dodd (1940) recorded that eggs were laid infrequently on young Opuntia tomentosa Salm-Dyck plants that were less than 1.8m in height and never on older, taller plants.

The marked differences in the growth forms of O. ficus-indica and O. aurantiaca (Fig. 1.2) could affect oviposition preferences. These differences, however, also complicated the work reported in this chapter because different methods had to be used for eggstick searching and plant size quantification of each plant species (see chapter 2). Before considering whether egg densities of C. cactorum differed between O. ficus-indica and O. aurantiaca at the study site, oviposition patterns between individual plants/stands are first considered separately for each host plant species.

4.1 Oviposition patterns on O. ficus-indica plants.

Only plants that had at least one cladode visible above the surrounding vegetation (termed 'visible plants') are included in this analysis of oviposition by C. cactorum on O. ficus-indica. The excluded plants were hidden among the vegetation and therefore unavailable for oviposition.

Plant size was the most important factor affecting eggstick numbers on O. ficus-indica. Table 4.2 shows that in both summer and winter generations there was a highly significant positive correlation between

Table 4.2. Correlations between the number of C. cactorum eggsticks laid on O. ficus-indica plants and different estimates of plant size. Only plants with at least one cladode visible above the surrounding vegetation are included. See Appendix 2 for equations and methods used for estimating the different plant parameters. All correlations are highly significant ($P < 0.001$).

	Summer 1981/82 (n=99) generation	Winter 1982 (n=101) generation
	r	r
Total no. cladodes[1]	0.7946	0.7372
No. succulent cladodes[1]	0.7818	0.7322
Total mass cladodes[1]	0.7923	0.7476
Mass succulent cladodes[1]	0.8012	0.7611
Total no. areoles[1]	0.7881	0.7413
Ground area covered by plant	0.7090	0.6328
Cross-sectional area of plant	0.7445	0.6474

[1]Transformed to $\log_{10}(x+1)$.

eggstick number and each of seven different plant size estimates. The mass of succulent cladodes gave the best correlation (see also Fig. 4.2) and is therefore used in the rest of the analyses. Large plants present a greater target area, and are therefore probably more likely to be located by females than small plants. To eliminate the effect of target area, egg numbers on plants were expressed in terms of egg densities. For all visible plants, egg densities expressed in terms of the number of succulent cladodes tended to increase with plant size while in terms of the mass of cladodes, they tended to decrease (Fig. 4.3). It is not possible to draw any firm conclusions from Fig. 4.3 regarding oviposition behaviour, especially as the sample sizes of large plants are so small. However, these results do show that for plants that had eggsticks laid on them, the density of eggs was highest on the smaller plants (1-5 cladodes). Because C. cactorum eggs are clumped, oviposition on a small plant automatically results in a high egg density on the plant.

Multiple regression analysis was used to determine factors additional to plant size that might explain the variation in eggstick number between plants (Table 4.3). The significance of the t-values in Table 4.3 gives an indication of the contribution of each variable in explaining the number of eggsticks laid on plants when the other variables are held constant. Multiple regression analysis helps reduce the effects of inter-correlation between independent variables. For example, the simple correlation between the number of eggsticks and plant conspicuousness is highly significant in both generations but it is also highly correlated with plant size (Table 4.4). When plant size is controlled for in the multiple regression analysis, plant conspicuousness was only significant in the winter generation. However, it is necessary to interpret the significance of variables in a multiple regression with care. Female C. cactorum moths are probably not responding to plant size per se but rather to plant size as a measure of plant conspicuousness. The plant conspicuousness variable is significant in the multiple regression equation in the winter generation because it explains variability in eggstick numbers additional to that explained by plant size.

Plant size and moth emergence near the plant were the only significant variables explaining numbers of eggsticks on plants in the summer

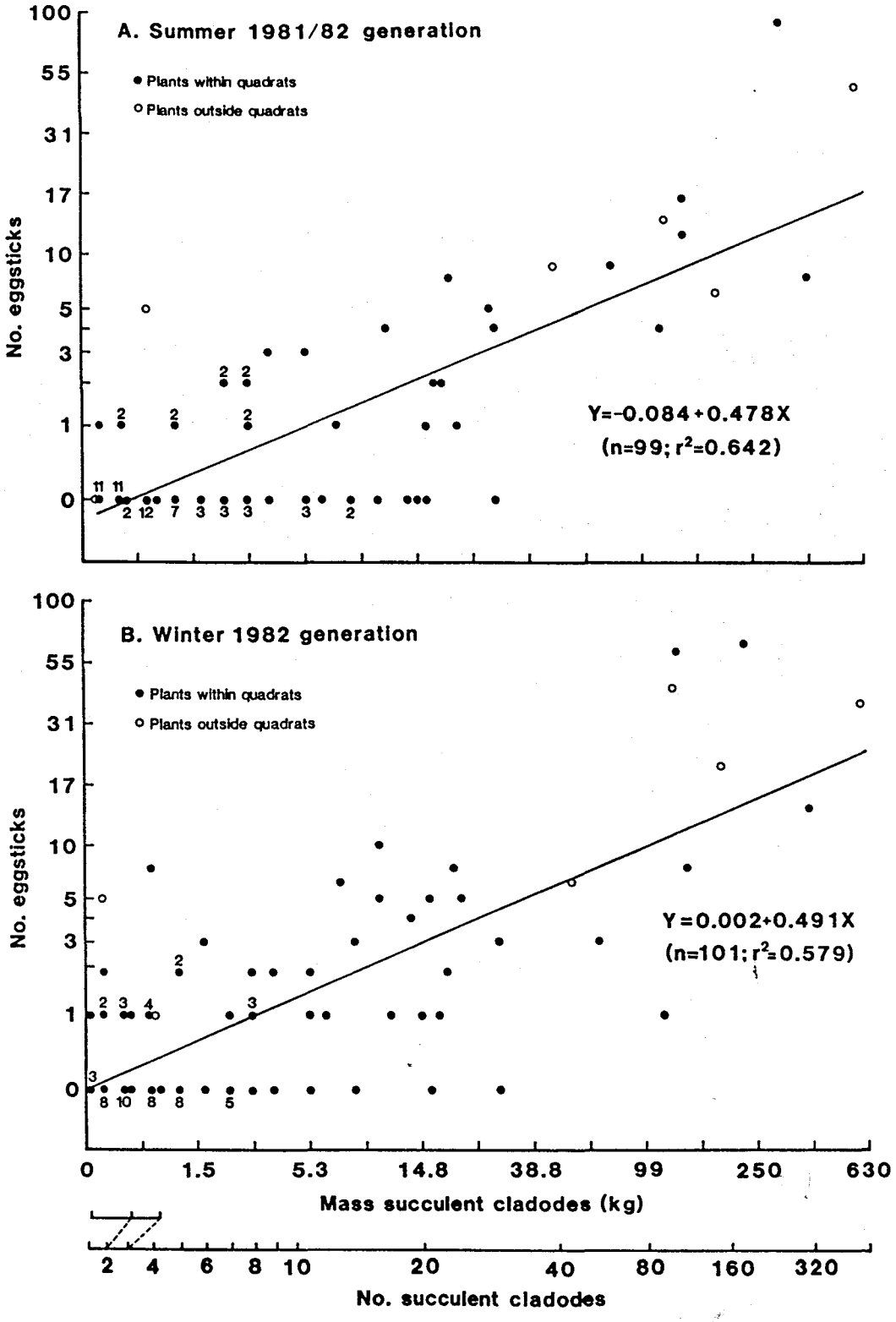

Fig. 4.2. Number of C. cactorum eggsticks laid on O. ficus-indica plants in relation to plant size (expressed as mass of succulent cladodes) in the summer 1981/82 (A) and winter 1982 (B) generations at the Thursford study site. Below the x-axis, the corresponding numbers of succulent cladodes are shown for small plants derived from broken off cladodes (short axis) and for seedling and large plants (long axis) (see Appendix 2 for details). Numerals accompanying the data points indicate the number of plants.

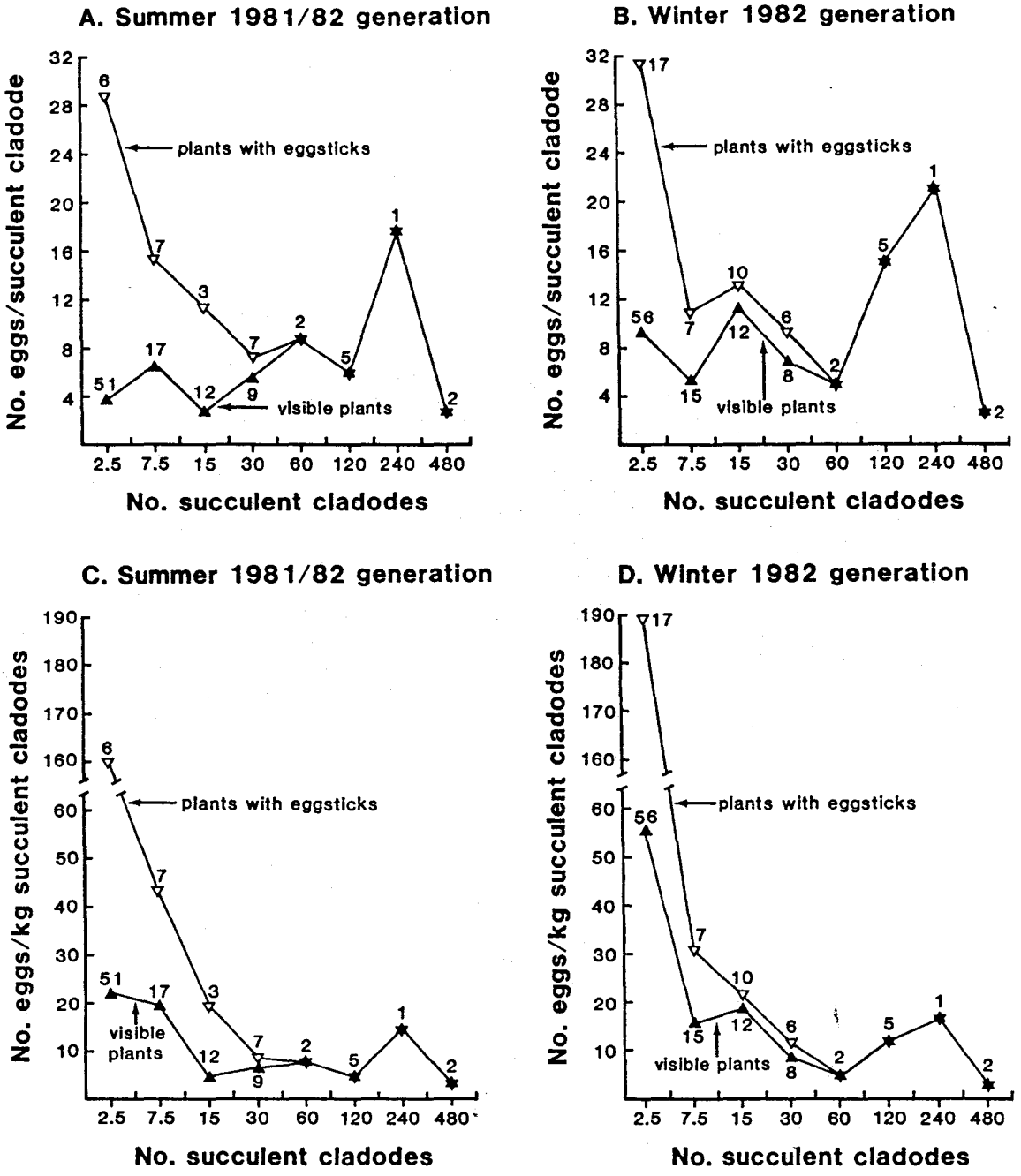

Fig. 4.3. The relationship of C. cactorum egg density with O. ficus-indica plant size. Density was calculated as the total number of eggs divided by the total number of succulent cladodes (A,B) or divided by the total mass of succulent cladodes (C,D), for each plant size category. Plant sample sizes are given next to each point.

Table 4.3. Multiple regression analysis of the relationship between the number of C. cactorum eggsticks laid on O. ficus-indica plants and some characteristics of the plants. n.s. - not significant ($P > 0.05$); * - $P < 0.05$; ** - $P < 0.01$; *** - $P < 0.001$.

	Summer 1981/82 generation (n=99)				Winter 1982 generation (n=101)			
	Slope (b) or constant	SE	t	r^2	Slope (b) or constant	SE	t	r^2
Mass succulent cladodes (kg)[1]	0.396	0.052	7.58^{***}	0.642	0.330	0.046	7.18^{***}	0.579
Moth emergence near plant[2]	0.225	0.106	2.13^{*}	0.658	0.402	0.092	4.36^{***}	0.644
Proportion new cladodes	-	-	$0.50^{n.s.}$	-	0.444	0.154	2.89^{**}	0.680
Plant conspicuousness[3]	-	-	$-1.43^{n.s.}$	-	-0.233	0.093	-2.51^{*}	0.700
constant	-0.068	0.034	-2.00^{*}	-	0.056	0.060	$0.94^{n.s.}$	-

[1]Transformed to $\log_{10}(x+1)$.

[2]Measured as $\log_{10}$(no. cladodes destroyed by larvae of the same generation as the moths).

[3]Measured as the proportion of the plant's perimeter obscured by vegetation one meter or less away from it.

Table 4.4. Simple correlations between variables used in multiple regression analysis of Table 4.3 and an additional variable, the proportion of cladodes with fruit, which was not significant in the multiple regression equation. The proportion of cladodes with fruit was not recorded in the winter generation because the fruiting season was over. n.s. - not significant ($P > 0.05$); * - $P < 0.05$; ** - $P < 0.01$; *** - $P < 0.001$.

Variable	Variable number					
	1	2	3	4	5	6
	Winter 1982 generation (n=101)					
1. No. eggsticks[1]		.761 ***	.656 ***	.288 **	-.423 ***	-
2. Mass succulent cladodes[1]	.801 ***		.592 ***	.142 n.s.	-.211 *	-
3. Moth emergence near plant	.673 ***	.732 ***		.057 n.s.	-.260 **	-
4. Proportion new cladodes	.139 n.s.	.138 n.s.	.097 n.s.		-.211 *	-
5. Plant conspicuousness	-.354 ***	-.330 ***	-.294 **	-.256 **		-
6. Proportion fruit cladodes	.500 ***	.620 ***	.449 ***	.028 n.s.	-.157 n.s.	
	Summer 1981/82 generation (n=99)					

[1]Transformed to $\log_{10(x+1)}$.

generation. In the winter generation, however, the proportion of new succulent cladodes and the conspicuousness of the plant were also significant. A possible reason why more variables were significant in winter than in summer is that whereas only 33% of the plants had eggsticks on them in summer, in winter 50% had eggsticks so that there

was a greater spread of variability in the latter generation. This should be kept in mind in the discussion of each variable that follows.

1) Moth emergence near plant. C. cactorum larvae usually pupate in close proximity to the plant they feed on (Pettey 1948 p. 55). The number of cladodes damaged by larvae of the same generation as the moths was therefore used as a measure of the number of moths that emerged in the vicinity of each plant. In both generations it was the next most important variable after plant size in explaining the number of eggsticks on plants (Table 4.3). Dodd (1940 p. 121) and Myers et al. (1981) also found that previously attacked O. stricta plants had a greater density of eggsticks than unattacked ones. Myers et al. (1981) showed that under controlled conditions, among a group of plants, those that had moths placed on them before evening commenced, were more likely to have eggsticks laid on them than those which did not. These results imply that females lay at least some of their egg complement before dispersing from the vicinity of their emergence site. Dispersal behaviour is an important aspect of both the oviposition behaviour and the population dynamics of C. cactorum and it is necessary here to digress and consider C. cactorum dispersal in greater detail.

There are a number of records of long distance dispersal by C. cactorum females. Dodd (1940 p. 121) remarks "many instances on record indicate that individuals have flown as far as fifteen miles to oviposit". In the Leeward Islands, C. cactorum appears to have dispersed naturally from some of the islands to others. For instance, it colonized the island of St Kitts from Nevis four miles away (Garcia Tuduri et al. 1971). Similarly, in the Hawaiian Island chain, C. cactorum has apparently dispersed naturally through these islands over a period of about seven years (C.J. Davis in Garcia Tuduri et al. 1971).

On the basis of the above evidence for short and long distance dispersal in C. cactorum, and as proposed by Osmond & Monro (1981), it is likely that the dispersal behaviour of C. cactorum females is age-related, with females laying their first eggstick(s) near the emergence site and then dispersing to lay the rest of their egg complement further afield. Osmond & Monro (1981) suggested that oviposition of eggs near the emergence site by C. cactorum "probably acts as an

insurance against flying into regions devoid of prickly-pear and thus dying without finding a host". Another possible reason for oviposition prior to dispersal is to reduce the energy cost of flight. In C. cactorum, a full egg complement constitutes about 46% of female mass (Fig. 3.8) and thus the tendency may be to reduce wing-loading by laying part of the egg complement before dispersal. This type of behaviour is commonly recorded in moths which emerge gravid from the pupa (Johnson 1969 pp. 181-182 and Baker 1978 pp. 336-337 and references therein; Sanders & Lucuik 1975; Greenbank et al. 1980; Bellows et al. 1984). In the European pine shoot moth, Rhyacionia buoliana (Schiff.), egg-laden females on a flight mill can fly up to 13 km in still air (Green 1962) but the tendency of females in the field is to deposit part of their egg complement before dispersal (Green & Pointing 1962). Sanders & Lucuik (1975) found that in the spruce budworm Choristoneura fumiferana (Clem.), the size of the female affects the tendency to oviposit before dispersal. Compared with females that were starved as larvae, those that were well fed as larvae were larger, had a higher wing loading when gravid and were more prone to ovipositing before flight. Sixty-eight percent of starved moths flew before ovipositing compared with 35% of those that were fully fed.

Dispersal behaviour of C. cactorum is also likely to be affected by other factors such as temperature that increase the energy cost of flight and hence dispersal (see Baker 1978 pp. 251-260 for other Lepidoptera). In addition, when host plants in the vicinity of the emergence site are heavily damaged by C. cactorum, the stimulus to disperse before oviposition might be greater because the likelihood of locating more suitable host plants elsewhere is increased. However, Pettey (1948 p. 43) remarks "...egg sticks are commonly found...on the spines of dead, dried up parts of damaged pear plants and on the spines of completely killed pear plants especially when the moth population is large". Possibly the extent of initial wing-loading in some females forces them to oviposit on plants in the vicinity of the emergence site even if the plants are in poor condition.

In summary, it appears that the tendency for dispersal by C. cactorum females increases as more eggs are oviposited because of the associated

decrease in wing-loading. In terms of the energetics of flight, there is therefore a sound reason for females to lay their first eggsticks prior to dispersal.

2) Proportion of new cladodes. Myers et al. (1981) have shown that the nutritional status of the host plant affects oviposition in C. cactorum. They found that significantly more eggsticks were laid on green- than on yellow-coloured O. stricta plants and that green plants had more crude protein than yellow plants. At Thursford, yellow-coloured plants also tended to have few eggsticks laid on them. Twenty-six percent of the 93 visible plants within the quadrats were yellow-coloured and, in both summer and winter generations, the density of C. cactorum eggs on these plants was significantly lower than that on the green-coloured plants (Table 4.5). There was a significantly lower

Table 4.5. Proportion of new cladodes and the density of C. cactorum eggs on 'green' and 'yellow' O. ficus-indica plants within the quadrats at the Thursford study site. Mann-Whitney U-test (Z = normal deviate of U): ** - $P < 0.01$; *** - $P < 0.001$. clads - cladodes; prop. - proportion.

	Green plants	Yellow plants	Z
Number	69	24	
Mean ± SE no. clads/plant	27.9 ± 8.7	9.9 ± 2.8	
Mean ± SE prop. new clads/plant	0.20 ± 0.02	0.08 ± 0.03	3.38^{***}
Mean ± SE density eggs/plant - summer[1]	3.6 ± 0.7	0.8 ± 0.6	2.65^{**}
Mean ± SE density eggs/plant - winter[1]	7.2 ± 1.5	2.4 ± 1.4	2.90^{**}

[1]Density = No. eggs/total no. cladodes on plant.

proportion of new-succulent cladodes on the yellow- than on the green-coloured plants (Table 4.5) which suggests that the number of new cladodes growing on a plant is related to the nutritional status of the plant. I therefore used the proportion of new cladodes on the plant as a measure of nutritional status as it provided a continuous variable that could be easily measured for all plants within the study area. The 'proportion of new cladodes' was significant in the multiple regression analysis for the winter but not for the summer generation (Table 4.3) and provides further evidence that oviposition behaviour in C. cactorum is affected by the nutritional status of the host plant.

3) Plant conspicuousness. This is a difficult factor to define and in this study was measured as the proportion of the plant's perimeter obscured by vegetation one metre or less away from it. Plants with less than one cladode visible were excluded from the multiple regression analysis, yet even without these, plant conspicuousness was still a significant factor explaining the number of eggsticks on plants in the winter generation (Table 4.3). The presence of surrounding vegetation near a prickly pear might reduce its chances of being located by C. cactorum. Myers et al. (1981) recorded the type of vegetation, if any, that surrounded each O. stricta plant and found that plants in the open did not have the highest C. cactorum egg density but rather the ones that were surrounded by "sticks and herbs". These results reflect the effect of surrounding vegetation type, rather than plant conspicuousness, on eggstick densities and therefore are not comparable to those presented in this study. In addition, measurement and interpretation of plant conspicuousness would depend largely on the type of habitat in which it is recorded. Myers et al. (1981) obtained their results from woodland populations whereas in this study observations were made in open vegetation interspersed with thickets (Fig. 2.2).

Host plants in habitats with dense vegetation probably stand the least chance of being located by C. cactorum females. Pettey (1948 p. 35) commented that in an extensive area of dense prickly pear intermingled with bush, eggsticks tended to be concentrated on prickly pears along the borders of stock paths and roads. Plant accessibility rather than conspicuousness is implied here although the two factors are related. The effect of dense bush on host plant location has important implications for biological control because O. ficus-indica and O. aurantiaca usually occur at high densities in this habitat type (see section 9.1).

4) Proportion of cladodes with fruit. C. cactorum females might respond to fruit quantity on a plant because, as with new cladodes, fruit might provide an index of the growth vigour of the plant and in addition they are often penetrated and fed on by newly hatched larvae. Although this variable is highly correlated with the number of eggsticks laid on plants, it is also highly correlated with plant size (Table 4.4). This factor was excluded from Table 4.3 because it is not significant in the multiple regression analysis, presumably because the variation it

explains in eggstick number is accounted for by plant size. It is still possible, however, that part of the reason why large plants have more eggsticks on them than small ones is because they have more fruit.

4.2 Oviposition patterns on O. aurantiaca stands.

In view of the sampling problems with O. aurantiaca (chapter 2), oviposition patterns on O. aurantiaca are analysed here in terms of firstly, the presence or absence of eggsticks and secondly, the number of hatched eggs. These results were collected at the end of each oviposition period when remains of eaten eggsticks were often still apparent. The results for eggstick presence on stands must however be conservative because eggsticks on some stands would have disappeared by the time the survey took place and therefore escaped detection. There was no significant difference between small ($< 0.25\ m^2$) and large ($> 0.25 m^2$) O. aurantiaca stands in the proportion of eggs laid that hatched ($G=0.012$, $0.90 < P < 0.95$, $n=110$). Consequently the relationship between oviposition and stand size can be reliably assessed in terms of the number of eggs hatched. For subsequent analyses, because of the small numbers of hatched eggsticks in each generation (65 in summer and 105 in winter), stands were classed according to the ground area they covered.

The log-size frequency distribution of O. aurantiaca stands, with and without eggsticks, is shown in Fig. 4.4. For summer and winter generations combined, the percentage of stands with eggsticks increased with stand size. Only 10.7% of the stands were recorded with eggsticks laid on them and eggsticks were never recorded on stands smaller than $0.0031 m^2$.

The number of hatched eggs also increased with stand size, although this is only evident above the $0.079 m^2$ size category (Fig. 4.5 A). When the results are expressed in terms of density, there is a weak positive correlation with stand size although this is only significant in the summer generation (Fig. 4.5 B). There are three possible reasons why egg densities are greatest on large O. aurantiaca stands and these are discussed separately below.

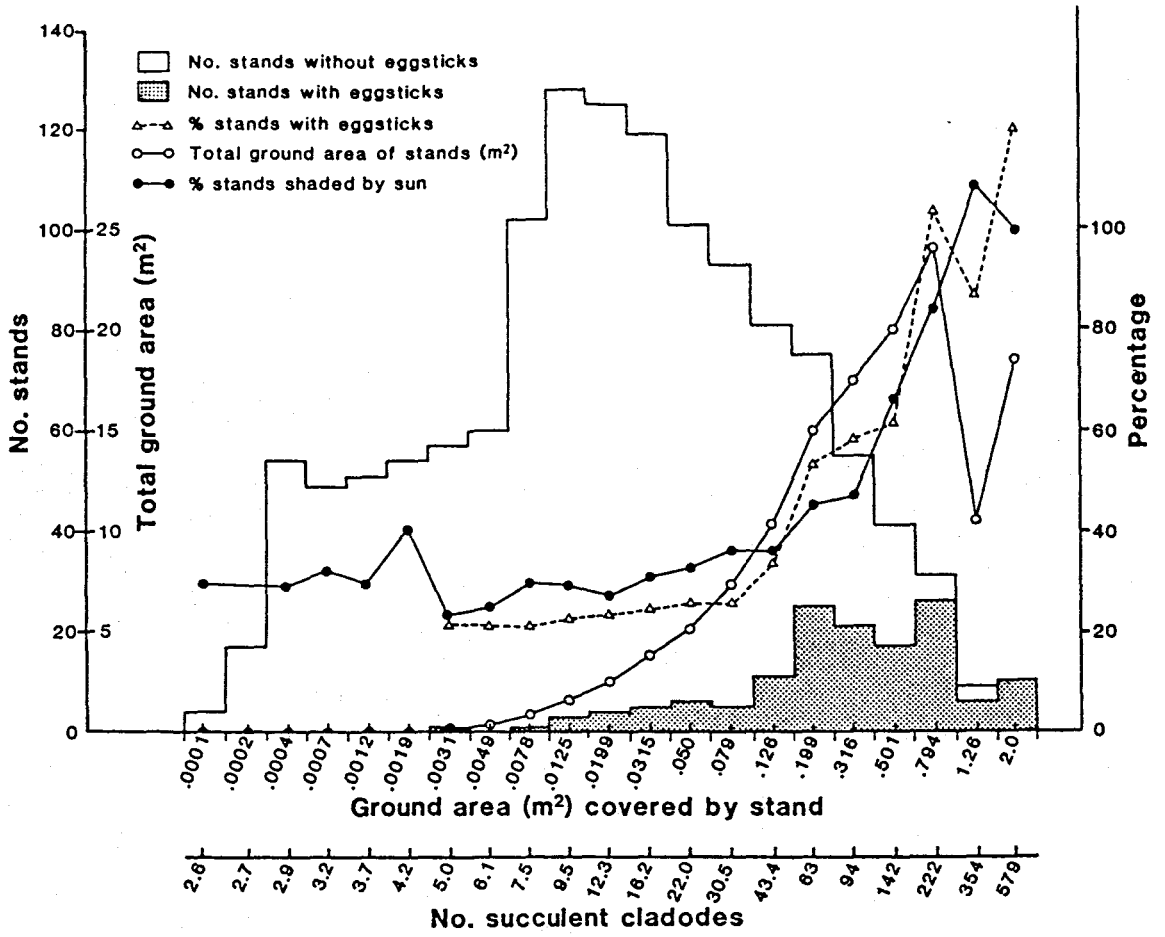

Fig. 4.4. The histogram shows the log-size frequency distribution of O. aurantiaca stands in the quadrats at the Thursford study site, recorded without C. cactorum eggsticks (unshaded) in both the summer 1981/82 and winter 1982 generations or with eggsticks (shaded) in either of the generations (also plotted as the percentage of clumps with eggsticks). O. aurantiaca stands are classed according to ground area covered by each stand and the corresponding median number of succulent cladodes is also shown for each area class (the number of succulent cladodes was calculated from equation 7 in Appendix 3). The total ground area of stands in each class and the percentage of stands that are shaded from the sun, are also shown.

1) Shade. The percentage of shaded O. aurantiaca stands was positively correlated with stand size (Fig. 4.4, $r_s = .9790$, $P < 0.001$, n=12, stands $> 0.0078m^2$ only). Large O. aurantiaca stands therefore tend to be found in shaded places and tend to have either a semi-shaded or etiolated growth-form (see Fig. 1.5). Although not actually measured, fecundity and larval survival in C. cactorum appeared to be greater in the shaded than in the exposed growth-forms of O. aurantiaca, possibly because the shaded plants were more nutritious and had larger cladodes. Oviposition on the large shaded O. aurantiaca stands might therefore be advantageous in terms of increasing fecundity and larval survival.

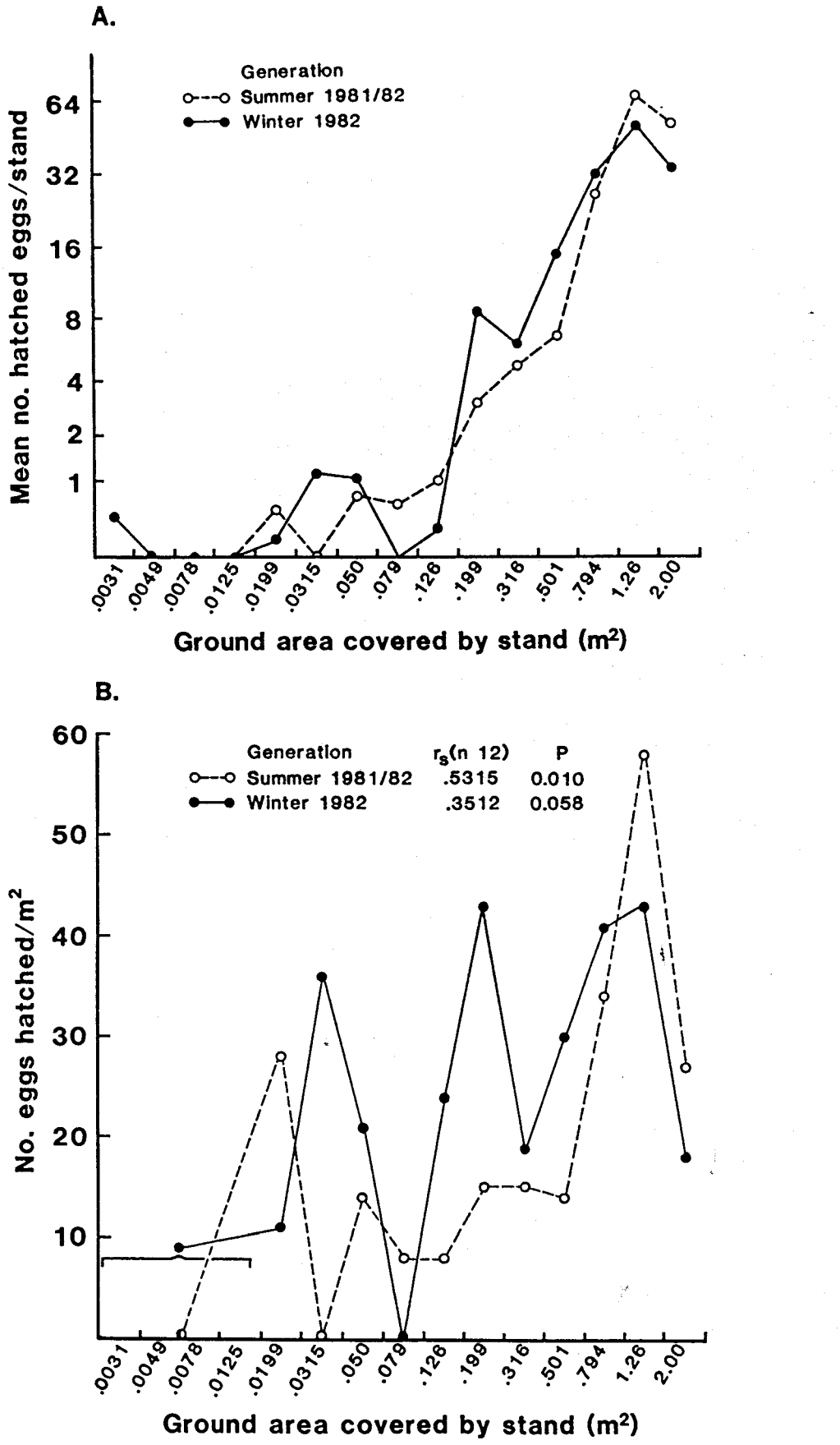

Fig. 4.5. Number (A) and density (B) of hatched C. cactorum eggs on O. aurantiaca stands in relation to stand size. r_s - Spearman rank correlation.

2) Food quantity. An average-sized colony of C. cactorum larvae on O. aurantiaca requires about 30 succulent cladodes to complete development (Table 8.1). On average, only stands greater than 0.077 m^2 have this number of succulent cladodes (calculated from equation 5 in Appendix 3). This illustrates that oviposition on small O. aurantiaca stands can be disadvantageous in terms of the amount of food available for larval development. In the absence of larger host plants, females probably do lay eggsticks on small stands and in oviposition cages, they lay eggsticks even if there is no cactus at all.

3) Conspicuousness of stands. This factor would affect the outcome of inter-stand choice as smaller stands are usually hidden among the surrounding vegetation and therefore would probably not be apparent to the moth. In a sample of small stands (with < 30 succulent cladodes each) it was found that the mean height of the surrounding vegetation was significantly greater than the maximum height of the stand (paired t-test, t=2.41, P=0.022, n=35).

To summarize, both the number and density of C. cactorum eggs tended to be greatest on large O. aurantiaca stands. Fecundity and larval survival appear to be highest on the larger stands probably because they have better quality cladodes and there is less likelihood of food being limiting to the larvae. Large stands would also be more apparent to a female C. cactorum moth locating a host plant for oviposition.

4.3 Comparison of oviposition patterns on O. ficus-indica and O. aurantiaca.

A comparison of the number and density of C. cactorum eggs laid on O. ficus-indica and O. aurantiaca in the quadrats at Thursford is shown in the series of bar graphs in Fig. 4.6. Differences in egg densities were tested statistically with Wilcoxon's paired-sample test using the seven quadrats as cases. Because of the small sample size, the probability of a Type II error (Sokal & Rohlf 1981) is very high. The T-values give an indication of the extent of the differences in egg densities between the two species (small T-values indicate a large difference).

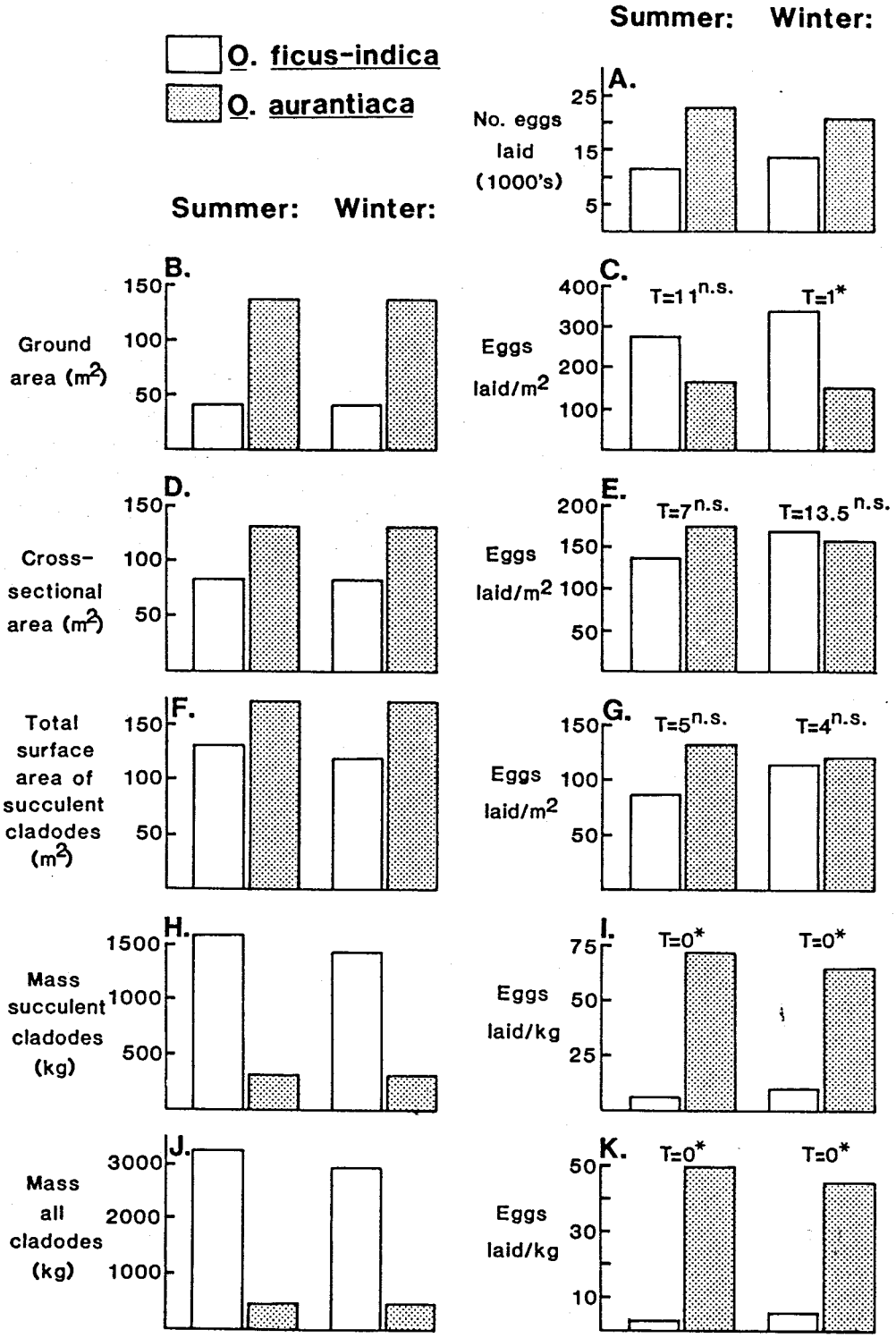

Fig. 4.6. The proportion of C. cactorum eggs laid on O. ficus-indica and O. aurantiaca within the quadrats at the Thursford study site. The numbers of eggs laid on each host plant species are shown in bar graph A. Plant parameter estimates for O. ficus-indica and O. aurantiaca are given in bar graphs B,D,F,H & J on the left and the corresponding egg densities are given in bar graphs C,E,G,I & K on the right. Each plant parameter and egg density value is based on total values for all quadrats. Values for each quadrat are given in Appendix 5. Methods and equations used for estimating the plant parameters are given in Appendices 2 & 3. Differences in egg densities between O. ficus-indica and O. aurantiaca were tested using Wilcoxon's paired sample test (a small T-value indicates a large difference in densities). n.s. - not significant ($P > 0.05$); * - $P < 0.05$.

In both summer and winter generations, more eggs were laid on O. aurantiaca than on O. ficus-indica (Fig. 4.6 A). However, the ground area, cross-sectional area, and cladode surface area were all greater for O. aurantiaca than for O. ficus-indica (Fig. 4.6 B,D,F). In Fig. 4.6 C,E,G egg densities are expressed in terms of these three measurements of target area. There were more eggs laid/m^2 ground area on O. ficus-indica than on O. aurantiaca and this difference was significant in the winter generation (Fig. 4.6 C). Ground area is a poor measure of the area of cactus presented to a host-locating female as it does not account for the considerable differences in height between O. aurantiaca and O. ficus-indica. Cross-sectional area is probably the best measure of the area presented to a host-locating female as it accounts for target area in both horizontal and vertical dimensions. In terms of this variable, there was little difference between the two species of host plants (Fig. 4.6 E). There was also little difference in egg densities when they were expressed in terms of cladode surface area (Fig. 4.6 G), although in both generations the value was higher for O. aurantiaca than for O. ficus-indica.

Whereas O. aurantiaca covers a greater area in the quadrats than O. ficus-indica (Fig. 4.6 B,D,F), in terms of mass, the situation is the reverse (Fig. 4.6 H,J) because O. ficus-indica has a much greater density of cactus per unit area than O. aurantiaca. For example, in O. ficus-indica there are 19kg succulent cladode/m^2 cross-sectional area whereas there are only 2.4 kg/m^2 in O. aurantiaca. The effect of target area on oviposition combined with the smaller mass of cactus per unit target area therefore results in O. aurantiaca having a greater density or load of eggs than O. ficus-indica (Fig. 4.6 I,K). This could affect the efficiency of C. cactorum as a biological control agent on each host plant species but with the higher egg and larval mortality on O. aurantiaca (Chapter 6), the nett effectiveness of C. cactorum on this host plant is not necessarily greater than on O. ficus-indica. In addition, eggsticks tend to be clumped on plants (Table 4.1) so that although the density of eggs on O. ficus-indica was low overall (Fig. 4.6 I,K), some plants, especially small ones (Fig. 4.3), did have a high density of eggs on them.

4.4 Conclusions.

The factors found to be important in inter-plant oviposition patterns can be categorized on two levels. Firstly, there are those which affect the chances of the host plant being encountered (eg. host plant size, conspicuousness and proximity to moth emergence sites). Secondly, there are those concerning plant quality which influence oviposition behaviour by the female on the encountered host plant (eg. nutritional status).

In terms of the target area presented to a female C. cactorum searching for an oviposition site, there was little difference in the proportion of eggs laid on O. ficus-indica and O. aurantiaca plants at the study site (Fig. 4.6 E). It was not possible to control for factors other than target area which would influence host plant location. The most important of these is probably plant conspicuousness as it is lower for O. aurantiaca than for O. ficus-indica because stands of the former species tend to be low-growing and intermingled with the surrounding vegetation. The results shown in Fig. 4.6 E therefore still do not necessarily give a true measure of the discrimination by C. cactorum between the two host plant species. They do suggest, however, that under typical field conditions, there is no evidence of a marked preference for ovipositing on either host plant species. Janzen (1979) and Rausher & Papaj (1983) have stressed that the species of host plant is not necessarily the unit of discrimination by herbivorous insects. Neither O. ficus-indica nor O. aurantiaca are intrinsically unfavourable host plants to C. cactorum for oviposition. The criteria for host plant selection by C. cactorum appears to be not so much in terms of the host plant species (ie. O. ficus-indica or O. aurantiaca) but rather in terms of the particular characteristics of the individual plants within each species.

5. OVIPOSITION: FACTORS AFFECTING SITE SELECTION ON THE PLANT

Oviposition patterns of C. cactorum on O. ficus-indica and O. aurantiaca plants were considered in the previous chapter. In this chapter, oviposition patterns between and on cladodes of plants are considered (see Fig. 4.1). One of the reasons given for the poor performance of C. cactorum as a biological control agent of O. ficus-indica is that many eggsticks are laid on the woody cladodes so that consequently larval mortality is high. According to Pettey (1948 p. 43), "...the moth shows no preference for the portion of the pear plant most suitable to its progeny". He said this because eggsticks were commonly found on the spiny woody segments and on the spines of dead, dried up parts of damaged O. ficus-indica plants. Monro (1975 p. 209) wrote: "In South Africa, Cactoblastis is limited by the ratio of suitable to unsuitable food... Food is not short but only a proportion of the larvae are laid on the succulent parts of the host-plant". In this chapter, the preference shown by C. cactorum for ovipositing on the more succulent portions of the host plant is assessed. The choice of cladodes for oviposition is possibly also influenced by factors that affect the survival and mobility of the moth and in this regard the importance of height and wind are investigated in this chapter.

5.1 Cladode condition.

Cladodes were classed into three categories (Fig. 5.1).

(i) New-succulent: cladodes less than a year old.

(ii) Old-succulent: succulent cladodes more than a year old. Old-succulent cladodes which had eggsticks laid on them were classed in two groups; those that were entirely succulent with completely green cuticles (group 1) and those that were becoming woody and had cuticles that were only partly green (group 2).

(iii) Woody: cladodes with cuticle completely or almost completely grey-brown due to the development of woody tissue.

The proportion of C. cactorum eggsticks laid on each cladode type is shown in Table 5.1. There was a highly significant difference between summer and winter generations in the number of eggsticks laid on new-succulent cladodes (O. ficus-indica: $G=142.4$, $P<0.001$; O. aurantiaca: $G=96.5$, $P<0.001$). In summer, the new-succulent cladodes are still

Fig. 5.1. Classification of cladode condition in O. ficus-indica (top row) and O. aurantiaca (bottom row). L-R: new-succulent, old-succulent group 1, old-succulent group 2, and woody. Scale line = 25cm.

Table 5.1. The number and percentage of C. cactorum eggsticks laid on succulent and woody cladodes (clads) of O. ficus-indica and O. aurantiaca in the summer 1981/82 and winter 1982 generations. Also shown are the percentage of cladodes with eggsticks that had new-succulent cladodes or fruit attached to them. The classification of cladode condition is shown in Fig. 5.1 and explained in the text. succ. - succulent.

Cladode condition	O. ficus-indica			O. aurantiaca		
	No. egg-sticks	%	% clads with new-succ. clads /fruit attached	No. egg-sticks	%	% clads with fruit/new-succ. clads attached
Summer 1981/82						
New-succulent	6	2.3	0	1	0.6	-
Old-succ. (1)	185	69.8	79.5	142	85.5	66.4
Old-succ. (2)	67	25.3	59.7	19	11.5	15.8
Woody	7	2.6	0	4	2.4	25.0
Total	265	100.0	-	166	100.0	-
Winter 1982						
New-succulent	136	39.7	1.5	45	46.4	72.7
Old-succ. (1)	172	50.1	57.6	52	53.6	82.4
Old-succ. (2)	34	9.9	44.1	0	0	-
Woody	1	0.3	0	0	0	-
Total	343	100.0	-	97	100.0	-

growing and were avoided for oviposition, possibly because their spines are not fully developed. In winter, however, the new-succulent cladodes are fully grown and became the favoured sites for oviposition.

Eggsticks were rarely laid on woody cladodes. Twenty-four percent of O. ficus-indica cladodes were woody (section 1.1, Fig. 1.3) yet less than 3% of eggsticks were laid on these cladodes (Table 5.1). Old-succulent group 2 cladodes were oviposited on frequently but these cladodes often had new-succulent cladodes or fruit attached to them which larvae could use for penetration. The majority of eggsticks were therefore laid in sites where larval penetration was possible.

To assess whether C. cactorum females discriminated between O. ficus-indica succulent cladodes of different ages, the proportion of new-succulent cladodes with eggsticks was compared with the proportion of old-succulent cladodes with eggsticks, for different plant sizes, in the winter generation (Table 5.2). Overall, there was a highly

Table 5.2. Number of new- and old-succulent O. ficus-indica cladodes with and without C. cactorum eggsticks (winter 1982 generation) for different plant sizes. Plants without new-succulent cladodes are excluded. Probabilities for G-test: n.s. - not significant ($P > 0.05$); ** - $P < 0.01$; *** - $P < 0.001$.

Plant size (No. of cladodes)	No. plants	No. cladodes				G^1
		with eggsticks		without eggsticks		
		New	Old	New	Old	
1-10	15	8	14	22	25	$0.65^{n.s.}$
11-20	10	9	13	24	73	$0.10^{n.s.}$
21-40	8	1	24	34	117	
41-80	2	5	2	21	72	17.59^{***}
81-160	4	38	37	91	217	
161-320	2	29	26	65	154	9.84^{**}
321+	2	14	21	311	709	$1.349^{n.s.}$
Total	43	104	137	568	1367	18.128^{***}

[1] with William's correction.

significant preference for oviposition on new-succulent cladodes but preference for these cladodes depended upon the size of the plant. There was no significant preference for new-succulent cladodes on plants with up to 40 cladodes nor on very large plants with more than 320 cladodes. New-succulent cladodes on plants with between 40 and 320 cladodes, however, had significantly more eggsticks laid on them than expected from the the null hypothesis that the oviposition site was independent of the condition of the cladodes. The reason why preference for new-succulent cladodes changes with plant size probably relates to the average age of the old succulent cladodes in each plant size category. The average age of succulent cladodes on large plants would be greater than on small plants. However, it is uncertain why there was no significant preference for new-succulent cladodes on the large plants with more than 320 cladodes. The method of analysis in Table 5.2 is limiting because old succulent cladodes of different ages are grouped together. It does show, however, that C. cactorum female moths do appear to respond to the age of a succulent cladode and do not merely oviposit on any non-woody cladode.

There are two possible ways in which a female C. cactorum moth might distinguish between cladodes of different condition: (i) visually by ovipositing on the more terminal cladodes which are the youngest, and (ii) by using chemosensory cues. Myers et al. (1981) observed that a C. cactorum female would tap the plant surface with her labial palps and wave her antennae while walking around on the plant in search of an oviposition site. In this way C. cactorum females might be able to assess the suitability of a cladode for oviposition.

The results in Tables 5.1 & 5.2 show that although some of the eggsticks were laid on woody cladodes unsuitable for the larvae, the majority were laid on the succulent cladodes and that there was a preference for oviposition on young, full-grown succulent cladodes. The unsuitable positioning of some eggsticks suggests that there are factors other than cladode condition affecting the selection of a site for oviposition and two of these, namely height of the eggstick above the ground and wind, are considered below.

5.2 Height.

The height of eggsticks above the ground was obviously considerably greater on average on O. ficus-indica than on O. aurantiaca (Fig. 5.2) because O. ficus-indica grows to a greater height than O. aurantiaca. Whereas on O. aurantiaca, 98% of eggsticks were laid within 0.4m of ground level, on O. ficus-indica, only 37% of eggsticks were within this height range.

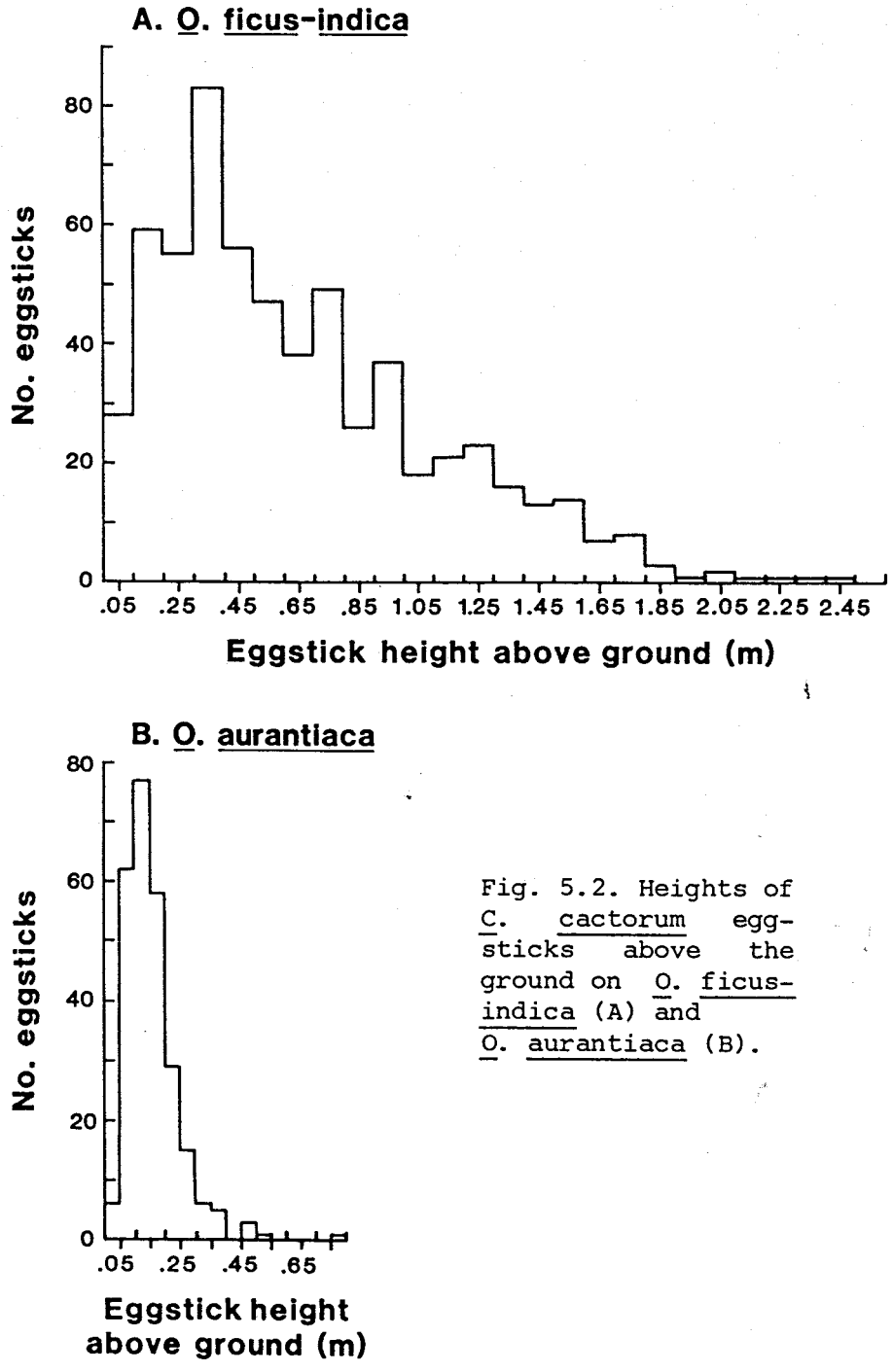

Fig. 5.2. Heights of C. cactorum eggsticks above the ground on O. ficus-indica (A) and O. aurantiaca (B).

Pettey (1948 p. 44) commented that the majority of eggsticks on O. ficus-indica plants were found on cladodes within 3 ft (ie. 0.9m) of the ground surface. This was substantiated in this study in which 73% of eggsticks occurred within this height range. To determine statistically whether this is because moths favour oviposition lower down on the plant, requires a knowledge of the height distribution of cladodes on the plants which was not obtained in this study. The impression gained in the field, however, is that on large O. ficus-indica plants, eggsticks are rarely laid on the cladodes high up on the plant. On O. ficus-indica plants up to 1.8m high, eggsticks are laid at an average of between 50% and 60% of the total plant height, but for plants higher than this, they are laid at an average of only about 31% of total plant height (Fig. 5.3 A). The height of O. ficus-indica

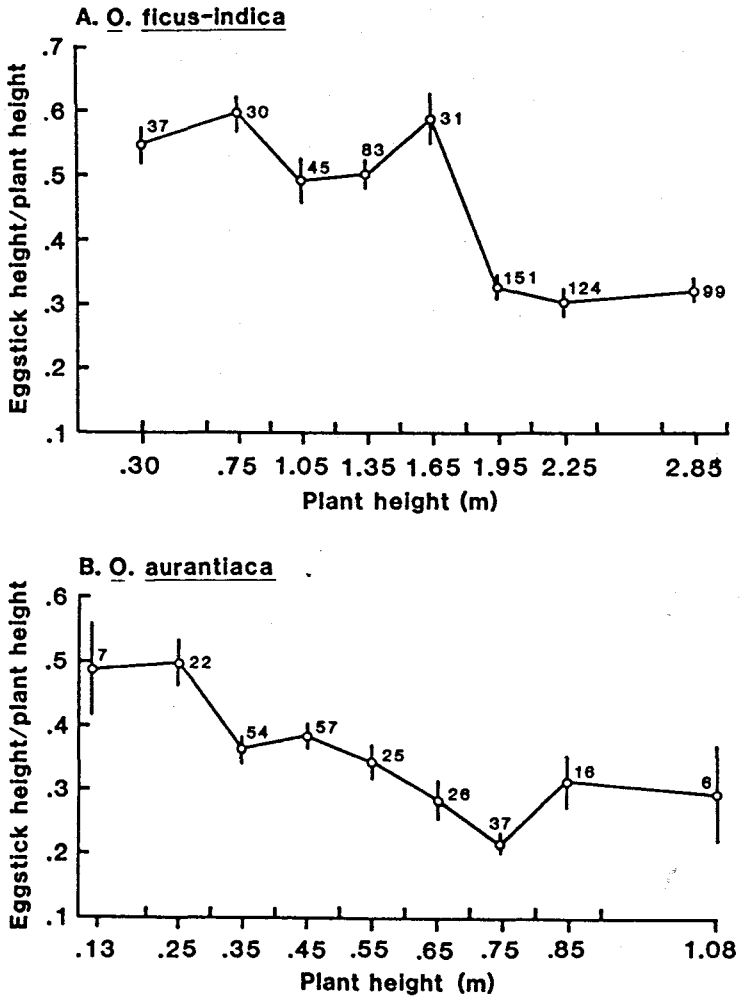

Fig. 5.3. Height of C. cactorum eggsticks above the ground, expressed as a fraction of plant height (mean ± SE) for different plant height categories on O. ficus-indica (A) and O. aurantiaca (B). Sample sizes are shown next to each data point.

plants therefore appears to affect the selection of particular cladodes for oviposition mainly on those plants greater than about 1.8m in height. A similar plot for O. aurantiaca (Fig. 5.3 B), shows that eggstick height as a ratio of plant height also decreases with increasing plant height even though O. aurantiaca is so much lower than O. ficus-indica. The height distribution of cladodes on O. aurantiaca, however, is entirely different from that of O. ficus-indica. Some of the plants in O. aurantiaca stands are often supported by surrounding vegetation which increases the overall height of the stand even though the majority of cladodes are near the ground.

The results in Figs 5.2 and 5.3 therefore show that (i) the height at which eggsticks of C. cactorum are laid is obviously dependent on the height of the host plant; and (ii) on large O. ficus-indica plants (> 1.8m in height), cladodes located low down on the plant are more likely to have eggsticks laid on them.

5.3 Wind.

The influence of wind on the positioning of eggsticks on O. ficus-indica plants was investigated indirectly for the winter 1982 generation of C. cactorum by determining the correlation between the wind direction prevailing during oviposition and the directions from which each eggstick would be sheltered from the wind by the surroundings. To record wind velocity and direction, a Woelfe Type mechanical wind recorder was set up near the farm house 2.6km from the study site. Eggsticks are laid mostly in the evening within two hours of dusk (section 3.1) and so the average wind direction and speed was measured for the period from 19h30 to 21h30 on each night of oviposition. Because O. ficus-indica plants were searched daily for newly laid eggsticks, the exact evening of oviposition was known for most of the eggsticks. A compass, divided into the eight cardinal sectors, was placed over each of these eggsticks, orientated towards north and the sectors (direction) from which shelter from wind could be provided, were recorded (Fig. 5.4 A). These 'shelter sectors' were recorded in three categories according to the shelter provided by: (i) the cladode on which the eggstick was laid and any other cladodes in close proximity to the eggstick; (ii) the host plant and; (iii) the surrounding vegetation other than the host plant itself. The deviation of each

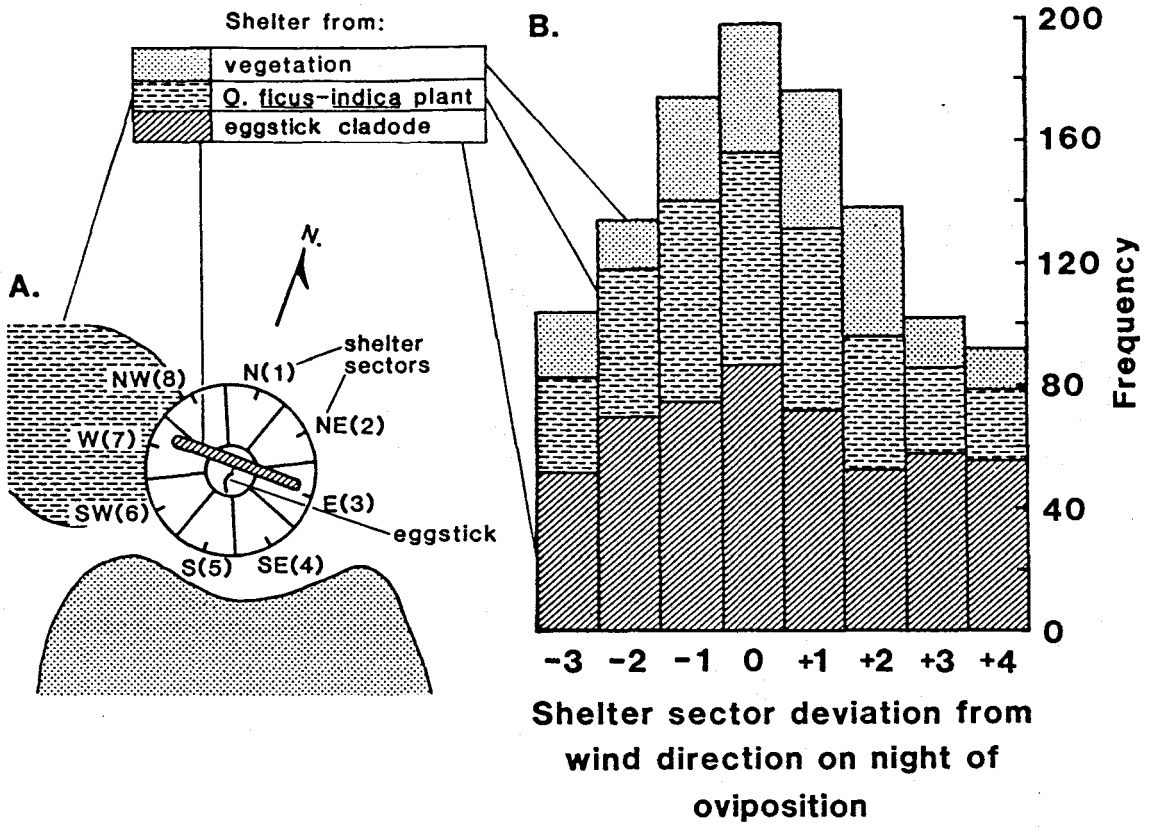

Fig. 5.4. Oviposition site selection by C. cactorum in relation to shelter from wind. A. Schematic diagram, looking vertically down on an eggstick and its surroundings showing how 'shelter sectors' were recorded. The circle represents a compass divided into the eight cardinal sectors and orientated in a northerly direction. In this instance, the eggstick will be sheltered by: (a) the cladode, if the wind blows from the NW, N or NE (ie. in sectors 8, 1 or 2); (b) by the rest of the O. ficus-indica plant, if the wind blows from the W (ie. sector 7) and; (c) by other vegetation, if the wind blows from the SE or S (ie. sectors 4 & 5). The wind direction and speed at the time of oviposition was known for each eggstick recorded. B. Frequency of shelter sectors in relation to their deviation from the wind direction on the night of oviposition. For all three categories of shelter, the frequency of shelter sector deviations are significantly biased towards low deviations (Surrounding cladodes, $G=16.48$, $0.025 < P < 0.05$; O. ficus-indica plant, $G=48.19$, $P < 0.001$; Surrounding vegetation, $G=45.76$, $P < 0.001$; Total, $G=77.97$, $P < 0.001$).

shelter sector from the direction from which the wind was blowing on the night of oviposition, was determined. For instance, if the wind direction during the evening of oviposition was in the north sector, shelter sectors also in the north sector would be recorded as having no deviation, shelter sectors in the east sector would have a deviation of +2 sectors, in the west sector -2 sectors and in the south sector a deviation of +4 sectors. The less the deviation of the shelter sector,

the more likely it is that the sector would provide wind protection to an ovipositing moth.

If C. cactorum moths were not responding to wind, it could be expected that shelter sector deviations would be random and, for large sample sizes, the frequencies of the deviation categories would be similar. However, for all three categories of shelter, the frequencies of shelter sector deviations were not similar but significantly biased towards low deviations (Fig. 5.4 B). C. cactorum females therefore tend to oviposit in sites on the host plant which are sheltered from the wind at the time of oviposition. There are three possible reasons for this.

(i) Available evidence suggests that moths tend to fly upwind when searching for host plants for oviposition. Andrews et al. (1980) found that when wind direction was fairly constant, females of the navel orangeworm moth Amyelois transitella (Walker) tended to fly upwind towards oviposition traps. Green & Pointing (1962) showed that for the European pine shoot moth Rhyacionia buoliana (Schiff.), when winds were less than the moths' flight speed, flight between ovipositions was upwind. If C. cactorum females tended to fly upwind when searching for suitable host plants, a bias of eggsticks on the leeward side of the plant could be expected.

(ii) A flying moth searching for an oviposition site on a plant would probably have more flight control on the leeward than on the windward side of the plant because firstly, wind strength would be lower on the leeward side and secondly, the moth would be flying into the wind.

(iii) C. cactorum females would tend to oviposit in sheltered localities because the process of laying an eggstick is precarious (frontispiece, A) and would be affected by the wind.

At low wind velocities, shelter from the surroundings would be expected to be of less importance to an ovipositing moth than at high wind velocities. However, the frequency distribution of shelter sector deviations was independent of wind velocity ($G=14.56$; $df=28$; $0.975 < P < 0.99$). Eggsticks tend to be laid in sheltered positions even at low wind velocities (< 5 km/h).

To summarize, C. cactorum eggsticks tend to be laid in positions where, at the time of oviposition, there is shelter from the wind provided by the surrounding vegetation, the plant, or the cladode on which the eggstick is laid. Wind can therefore affect both inter- and intra-cladode oviposition patterns. In the following two sections, intra-cladode oviposition patterns are considered further in terms of the positioning of eggsticks on the cladodes and the substrate chosen by the female for oviposition

5.4 Position on cladode.

The majority of C. cactorum eggsticks on O. ficus-indica and O. aurantiaca were positioned on the sides of cladodes rather than underneath or on top (Table 5.3). This is because most cladodes are in an upright position so that most of the cladode surface is orientated vertically. Of the eggsticks not positioned on the sides of cladodes, more were laid under the cladodes than on top, this difference being highly significant on O. aurantiaca but not significant on O. ficus-indica (Table 5.3). Cladodes are more often horizontally positioned on

Table 5.3. Position of C. cactorum eggsticks on O. ficus-indica and O. aurantiaca cladodes, for summer 1981/82 and winter 1982 generations combined. Eggsticks were laid either on the side, underneath or on top of the cladode, or in a position intermediate between the side and underside, or intermediate between the side and the top of the cladode. Probabilities for G-test: n.s. - not significant ($P > 0.05$); *** - $P < 0.001$.

Position	O. ficus-indica			O. aurantiaca		
	Absolute frequency	% frequency	G[1]	Absolute frequency	% frequency	G[1]
Side	507	83.2		155	59.2	
Under	25	4.1	$0.19^{n.s.}$	47	17.9	15.81^{***}
Top	22	3.6		16	6.1	
Side-under	29	4.8	$0.16^{n.s.}$	34	13.0	13.68^{***}
Side-top	26	4.3		10	3.8	
Total	609	100.0		262	100.0	

[1] with William's correction.

O. aurantiaca than on O. ficus-indica which explains the higher frequency of eggsticks recorded underneath and on top of O. aurantiaca cladodes.

It is apparent from Table 5.3 that although the positioning of eggsticks on cladodes is largely dictated by the orientation of the cladodes, C. cactorum tends to oviposit preferentially under the cladode rather than on top. Dodd (1940 p. 129) commented that eggsticks were laid on the underside of cladodes as a protection from excessive heat caused by direct sunlight. Many eggsticks at Thursford farm were in positions that were exposed to the direct rays of the sun for long periods, yet there was no record of egg mortality from excessive heat. A more likely explanation for preferential oviposition beneath cladodes is that in that position they are less exposed to hail, heavy rain and predators.

5.5 Eggstick substrate.

Ninety-eight percent of eggsticks on O. ficus-indica and 99% of eggsticks on O. aurantiaca were laid on spines. The remaining eggsticks were laid on glochids, no eggsticks being laid on the cladode surface itself (Table 5.4). In Fig. 5.5, the frequency distribution of lengths of spines chosen for oviposition is compared, for each host plant species, with the distribution of a random sample of naturally occurring spine lengths. On both O. ficus-indica and O. aurantiaca

Table 5.4. Number and percentage of C. cactorum eggsticks laid on the spines, glochids and cuticle of O. ficus-indica and O. aurantiaca cladodes.

Eggstick substrate	O. ficus-indica		O. aurantiaca	
	Absolute frequency	% frequency	Absolute frequency	% frequency
Spines	596	97.7	261	99.2
Glochids	14	2.3	2	0.8
Cuticle	0	0	0	0
Total	610	100.0	263	100.0

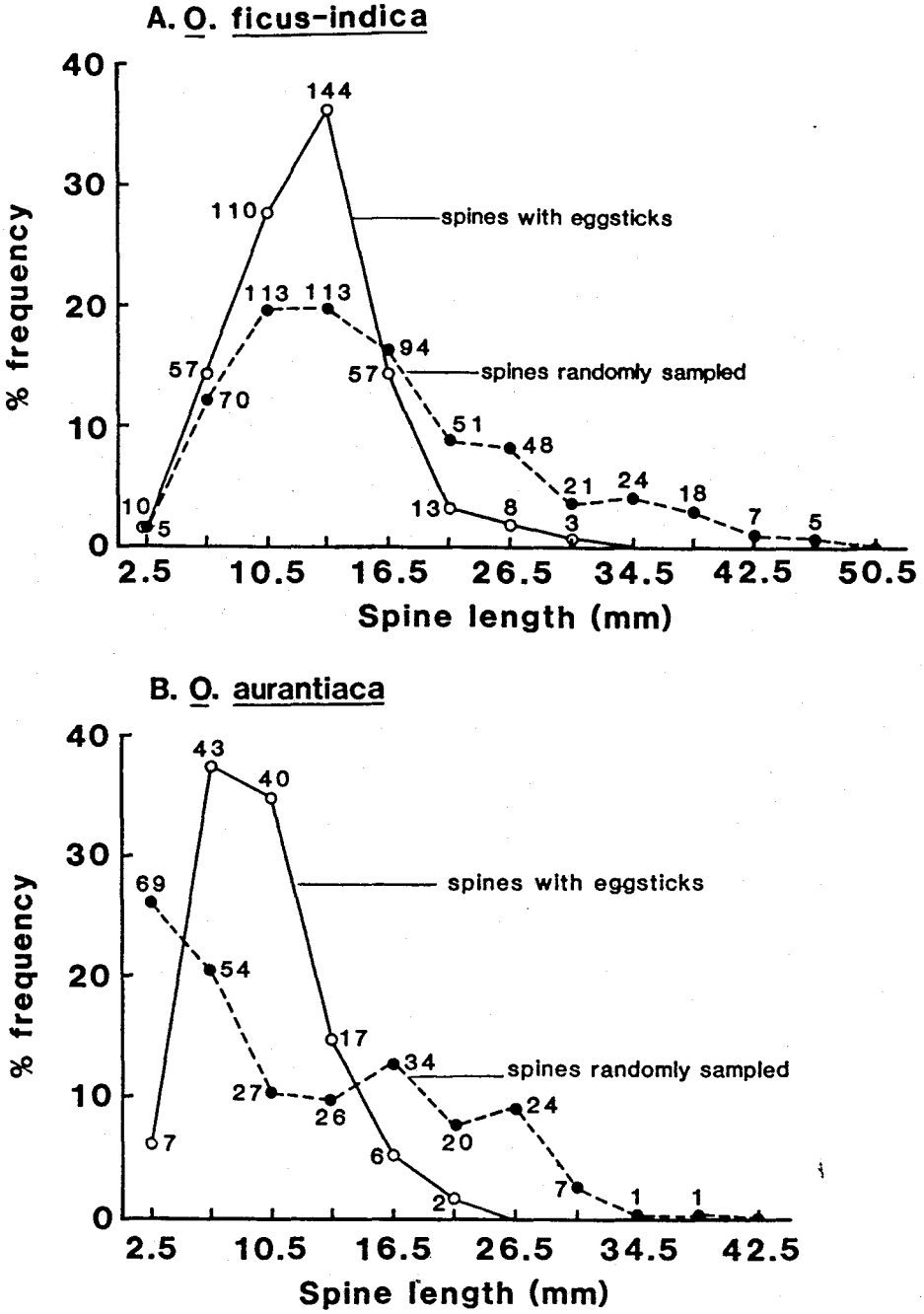

Fig. 5.5. Lengths of spines with C. cactorum eggsticks compared with the actual, randomly measured frequency of spine lengths, on O. ficus-indica (A) and O. aurantiaca (B). Sample sizes are shown next to the data points. On each host plant, there was a significant difference in the frequency distributions of spines with eggsticks compared with the spine lengths randomly measured (Kolmogorov-Smirnov two-sample test: O. ficus-indica, $D=0.266$, $K=4.07$, $P<0.001$; O. aurantiaca, $D=0.279$, $K=2.50$, $P<0.001$).

there was a highly significant difference in the frequency distribution of spines on which eggsticks were laid compared with the actual frequency distribution of spine lengths (Fig. 5.5). Fewer eggs than

expected were laid on long spines (> 18mm) of O. ficus-indica and on short spines (< 5mm) of O. aurantiaca. A comparison of Figs 5.5 A and 5.5 B suggests that for intermediate spine lengths (5-18mm), the length of spine is chosen randomly depending on availability.

5.6 Conclusions.

The results presented in this chapter suggest that, contrary to the statements of Pettey (1948) and Monro (1975), C. cactorum eggsticks are laid preferentially on young, succulent cladodes and only rarely on woody cladodes unsuitable for larval survival. The occasional oviposition of eggsticks on woody cladodes is possibly because factors such as wind and height of cladodes above ground limit the range of sites available for oviposition on the plant. There are presumably also imperfections in the response of C. cactorum to the oviposition cues.

A theme of this and the previous chapter has been that oviposition site selection is influenced by proximate factors that affect the behaviour and survival of the moth and ultimate factors that affect the survival of the eggs and larvae. The possible conflict between proximate and ultimate factors will be considered in the discussion because the results on oviposition in this and the previous chapter can then be compared with those on C. cactorum survival which are presented in the following two chapters.

6. COMPARATIVE LIFE TABLES FOR C. CACTORUM ON O. FICUS-INDICA AND O. AURANTIACA

These life tables were assembled for three main reasons: (i) to compare the survival of C. cactorum on O. ficus-indica and on O. aurantiaca; (ii) to assess the relative effect of weather, host plant and natural enemies on C. cactorum survival; and (iii) to gain an understanding of why C. cactorum has fared better as a biological control agent of O. stricta in Australia than of O. ficus-indica in South Africa. Data on C. cactorum survival in Australia are limited, but those that exist (Dodd 1940), enable some comparisons to be made between the two countries.

Pettey (1948) gathered a considerable amount of information on C. cactorum survival in South Africa but it is incomplete and was often collected under artificial conditions that cannot be related to the natural field situation. His data on pupal mortality are extensive but there are no reliable field-collected results about egg, larval and adult mortalities. Survival of eggs and larvae depends on where the eggs were originally oviposited, yet results presented by Pettey are based on eggsticks which had been placed on plants in paper quills. The results for egg and larval mortality presented below were all obtained from eggsticks and larval colonies that occurred naturally in the field.

In this chapter, results for egg, larval and pupal mortality are discussed separately. The complete life tables are then presented from which adult mortality (ie. pre-oviposition egg mortality) is deduced.

6.1 Causes of egg mortality.

The main cause of egg mortality was predation by at least eight species of ants. Recorded species were: Crematogaster liengmei Forel (Fig. 6.1 A), Pheidole sp. (megacephala Forel and/or capensis Mayr) Tetramorium erectum Emery, T. bacchus Forel, Tetramorium sp., Monomorium albopilosum Emery, M. (?)minutum Mayr and Camponotus niveosetosus Mayr. Species recorded foraging on O. ficus-indica and O. aurantiaca and suspected as egg predators were: Technomyrmex albipes Smith, Monomorium delegoensis Forel, Camponotus eugeniae Forel and

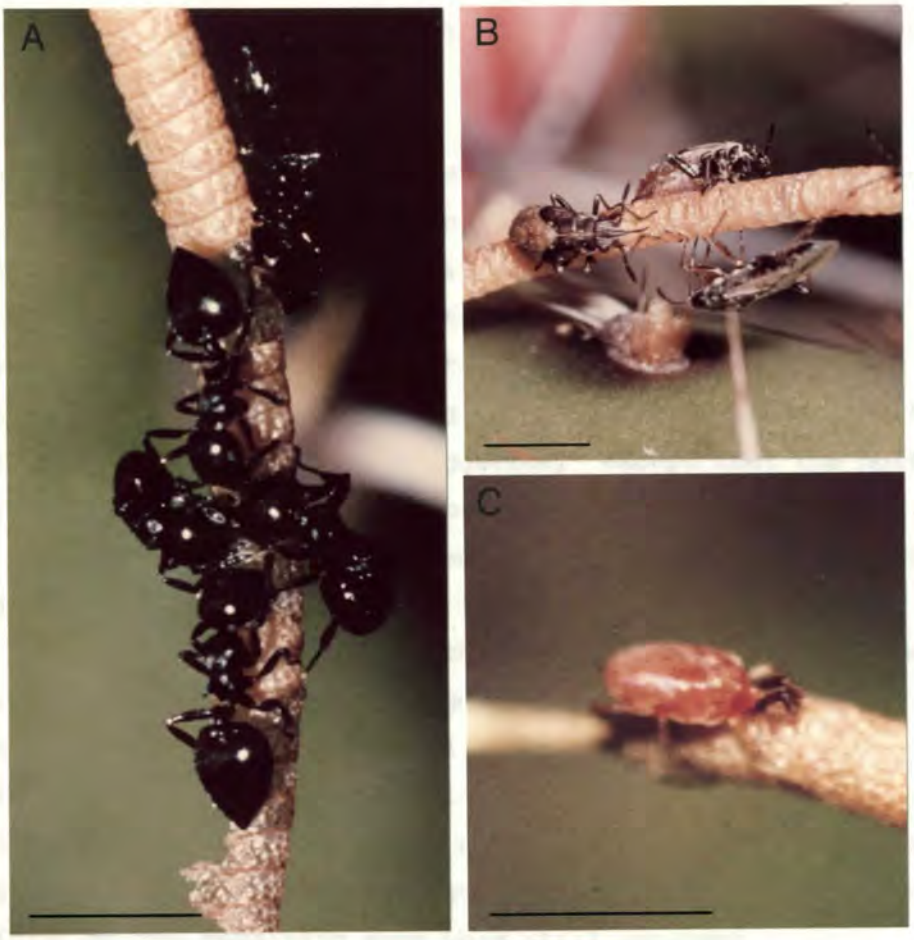

Fig. 6.1. Some predators of C. cactorum eggs: Crematogaster liengmei (A); Nysius sp. (Lygaeidae) (B); and an unidentified mite (C). Scale line = 2mm.

C. rufoglaucus (Jerdon). T. albipes was recorded feeding on C. cactorum eggs by Pettey (1948 p. 78). A lygaeid, Nysius sp. (Fig. 6.1 B) and an unidentified mite (Fig. 6.1 C) were also recorded as egg predators and Trichogrammatoidea sp. occasionally parasitized eggs, but in relation to ants they are of minor importance. The parasitoid apparently is not T. lutea Girault (G. Prinsloo pers. comm.) which is the species Pettey (1948 p. 86) recorded from C. cactorum eggs in South Africa. In addition to egg predation, mortality of eggs sometimes occurred when eggsticks were broken off, either partly or completely, by adjacent vegetation brushing against them, or by hail, heavy rain and wind.

6.2 Methods for determining egg mortality.

The methods used to locate eggsticks and check for mortality are outlined in chapter 2. Only eggsticks that were found one or two days

after being laid are included in the results. Five categories of mortality were distinguished.

1) Predation. The nature of the damage caused to eggsticks by predators varied according to the different predatory species responsible. It was not possible, however, to distinguish between the types of damage caused by each species. Some of the smaller ants made a small hole in each egg and extracted the contents from it. They frequently removed the contents of all eggs in the eggstick but left it intact so that it had the appearance of an emerged eggstick, except that the holes had a more ruptured appearance than those made by emerging larvae. Other ants, for instance C. liengmei, tended to make large holes in the eggs so that undamaged eggs distal to those eaten were more likely to be broken off by wind, etc. When this occurred, mortality from these broken-off eggs was ascribed to egg predation, not breakage. Ants frequently destroyed the proximal eggs first so egg breakage due to predation was a common occurrence. Some ants (eg. C. niveosetosus) removed eggs from the end of the eggstick but this type of predation could be distinguished from breakage mortality because fragments of the most distal of the remaining eggs were still apparent.

2) Breakage. When eggs are broken off an eggstick, they shear between two eggs leaving a clean break. The original number of eggs in the eggstick was always recorded, so the number of eggs broken off could be calculated.

3) Disappearance. When eggsticks disappeared between surveys without leaving evidence of the cause, they were assigned to this category. In the winter generation, for each eggstick that disappeared, a guess was made of the factor responsible (predation or breakage), based on weather and prevailing circumstances.

4) Parasitism. Eggs turn black when parasitized. Eggs also darken in the few days prior to hatching but these are grey in colour and could be easily distinguished from those that had been parasitized.

5) Unhatched. All eggsticks that hatched successfully were removed, placed in numbered vials, and taken back to the laboratory where the number of hatched and unhatched eggs was counted. The unhatched eggs

were divided into those that were undeveloped (eggs still cream-coloured) and those that were partially or fully developed (eggs either partly or completely darkened).

6.3 Results for egg mortality.

Egg predation was responsible for 56.6% and 53.5% mortality of eggs laid on O. ficus-indica in the summer and winter generations respectively. Egg predation was significantly higher on O. aurantiaca, accounting for 74.0% and 72.4% mortality respectively in each generation (Table 6.1). In addition, in the winter generation, 32.3% of the eggs that disappeared from O. ficus-indica and all those from O. aurantiaca were considered to have been destroyed by predators rather than broken off by environmental factors. The number of disappeared eggs that were eaten by predators and the number that were

Table 6.1. Mortality of C. cactorum eggs at the Thursford study site in the summer 1981/82 and winter 1982 generations. Only those eggsticks found within two days of being laid are included. The G-test (with William's correction) was used to test for differences in mortality on O. ficus-indica and O. aurantiaca and for differences in mortality between summer and winter generations. To calculate cell frequencies for the G-tests, egg numbers were divided by the mean number of eggs/eggstick (Table 3.9) because mortality normally occurs in units of eggsticks. O. f. - O. ficus-indica; O. a. - O. aurantiaca; pred. - predation; break. - breakage; n.s. - not significant ($P > 0.05$); * - $P < 0.05$; ** - $P < 0.01$.

Mortality factor	Summer 1981/82 generation					Winter 1982 generation					Summer vs. winter	
	O. f.		O. a.			O. f.		O. a.			O. f.	O. a.
	No.	%	No.	%	G	No.	%	No.	%	G	G	G
Predation	5153	56.6	2008	74.0	5.53^{*}	4612	53.5	2101	72.4	7.40^{**}	$0.33^{n.s.}$	$0.06^{n.s.}$
Disappeared pred.	270	3.0	71	2.6		90	1.0	158	5.4			
break.	567	6.2	0	0		189	2.2	0	0			
Breakage	1379	15.1	265	9.8	$0.76^{n.s.}$	605	7.0	46	1.6	$3.11^{n.s.}$	5.35^{*}	3.99^{*}
Parasitism	4	0.04	0	0		11	0.1	0	0			
Unhatched	90	1.0	15	0.5		345	4.0	52	1.8			
Total mortality	7463	81.9	2359	86.9		5852	67.9	2357	81.2			
Hatched	1649	18.1	355	13.1	$0.77^{n.s.}$	2770	32.1	544	18.8	$3.75^{n.s.}$	8.40^{**}	$0.85^{n.s.}$
Total	9112	100.0	2714	100.0		8622	100.0	2901	100.0			

broken off has been estimated in Table 6.1 for both generations. With the inclusion of the disappeared eggs, the values for predation mortality are increased by between 1% and 5.4% (Table 6.1).

In both generations of C. cactorum, a higher proportion of eggsticks were broken off on O. ficus-indica than on O. aurantiaca although this difference was not significant (Table 6.1). With the high rate of egg predation on O. aurantiaca, many eggsticks were not exposed to the causes of breakage for as long as they were on O. ficus-indica. Eggsticks on O. aurantiaca were also less exposed to wind, rain and hail because they were close to the ground and were more frequently located beneath cladodes than they were on O. ficus-indica (Table 5.3).

Eggstick breakage was significantly greater in the summer than winter generation (Table 6.1). This was mostly because three hail storms and one heavy rain storm occurred at the Thursford study site during the summer but none during the winter generation.

Parasitism by Trichogrammatoidea sp. was only an incidental mortality factor and caused 0.04% and 0.1% mortality of eggs on O. ficus-indica in the summer and winter generations respectively (Table 6.1). No parasitism was recorded from eggs laid on O. aurantiaca probably because with the small sample size, it was less likely to be recorded. In Hawaii, Hinckly (1961) recorded 2% and 7.5% parasitism by T. semifumatum of naturally laid C. cactorum eggsticks.

Failure to hatch was a minor cause of egg mortality (Table 6.1). Of the eggs in the eggsticks remaining after predation and breakage, 2.2% and 2.9% were undeveloped in the summer and winter generations respectively, while 0.6% and 1.7% were developed but unhatched (Table 6.2). There was no significant difference between summer and winter generations in the number of undeveloped eggs per remaining eggstick, but there was a highly significant difference between generations in the number of developed unhatched eggs per eggstick (Table 6.2). This was probably because the prolonged cold spells in the latter part of the winter generation (Fig. 3.2) prevented some larvae from emerging from their eggs.

Table 6.2. The number of hatched and unhatched eggs of C. cactorum in remaining eggsticks from O. ficus-indica and O. aurantiaca, compared between summer and winter generations at the Thursford study site. Mann-Whitney U-test (Z = normal deviate of U): n.s.- not significant ($P > 0.05$); * - $P < 0.05$; *** - $P < 0.001$. undev. - undeveloped; dev. - developed.

	Summer 1981/82 (n=106)			Winter 1982 (n=198)			Z
	Mean ± SE	Range	%	Mean ± SE	Range	%	
Hatched	50.3 ± 1.9	4-111	94.8	44.5 ± 1.3	7-95	90.6	2.50^{*}
Unhatched - undev.	2.2 ± 0.3	0-30	4.1	2.9 ± 0.3	0-21	5.9	$-1.16^{n.s.}$
- dev.	0.6 ± 0.1	0-9	1.1	1.7 ± 0.2	0-27	3.5	-4.28^{***}

6.4 Egg predation by ants.

Egg predation by ants was an important factor preventing the establishment of Tucumania tapiacola on O. aurantiaca in South Africa (Hoffmann 1982) and the results in Table 6.1 show that it can also be an important factor detrimentally affecting C. cactorum in South Africa.

The diversity and density of ants was visibly greater on O. aurantiaca than on O. ficus-indica and might explain why predation of C. cactorum eggs was greater on the former plant. The difference in ant densities between the two host plant species is most likely attributable to differences in height and extrafloral nectar production.

(i) Height. As a result of the differences in height of the two host plant species, eggsticks were laid nearer the ground on O. aurantiaca than on O. ficus-indica (Fig. 5.2). Ants would be more likely to forage closer to the ground because it is less exposed to wind, temperatures are higher, and the foraging distance from the nest would be shorter. Except for C. liengmei, the ants are all ground-nesting species (C. liengmei sometimes nests in cladodes that have previously been hollowed out by C. cactorum larvae). On O. ficus-indica in the summer generation, the mean height above ground of eaten eggsticks was significantly lower than that of hatched eggsticks whereas in the winter generation the mean heights of these two eggstick categories were similar (Table 6.3). The reason for the difference in results between generations is uncertain.

Table 6.3. Comparison of the mean height above ground (metres) of C. cactorum eggsticks that hatched compared with those that were eaten by ants, on O. ficus-indica at the Thursford study site. Mann-Whitney U-test (Z = normal deviate of U): n.s. - not significant ($P > 0.05$); *** - $P < 0.001$.

Generation	Hatched eggsticks		Eaten eggsticks		Z
	Mean ± SE	n	Mean ± SE	n	
Summer 1981/82	0.80 ± 0.05	71	0.54 ± 0.04	129	4.56^{***}
Winter 1982	0.69 ± 0.04	137	0.67 ± 0.04	161	$0.79^{n.s.}$

(ii) Extrafloral nectar production. Ants are attracted onto O. ficus-indica and O. aurantiaca by extrafloral nectar that is produced at the base of the areoles. This extrafloral nectar is possibly a source of both carbohydrate and protein for the ants. Pickett & Clark (1979) in a study conducted in Arizona, found that the extrafloral nectar from Opuntia acanthocarpa Engelm. & Bigelow contained a greater variety of amino acids than has been recorded in floral or extrafloral nectar from other plant species. In addition, the concentration of amino acids was "extremely high". Nectar production in O. ficus-indica and O. aurantiaca is particularly high on fruit and growing cladodes. From observations of ants foraging on plants it appears that extrafloral nectar production is greater on O. aurantiaca than on O. ficus-indica which might explain why C. cactorum egg predation by ants is greater on O. aurantiaca. Pickett & Clark (1979) found that extrafloral nectar production on O. acanthocarpa was greater than on Opuntia phaeacantha Engelm., and that this tallied with greater ant activity and lower numbers of Chelinidea vittiger Hamlin and Narnia inornata Distant (Coreidae) on O. acanthocarpa.

Predation of C. cactorum eggs by ants appears to be widespread in the Eastern Cape. I have observed extensive egg predation in a valley-bushveld site near Uitenhage and in Fish River scrub vegetation near Fort Brown. Pettey (1948) found that ants attacked all stages of C. cactorum except the adult and considered that ants had probably caused more mortality of C. cactorum in South Africa than any other predators. He recorded that several species of small ants removed eggsticks from the paper quills in which they had been placed for

distribution purposes. He described an experiment in which predation of eggsticks in paper quills was measured at seven sites. At five of these sites, only 2-7% of the eggsticks were removed from the quills whereas at the other two sites ants were responsible for 30% and 59% removal. These results are underestimates for two main reasons. Firstly, eggsticks of unknown age were used so that they were not exposed to predation for their entire development period during Pettey's experiment. Secondly, these tests were conducted in May when winter temperatures were already prevailing. Predation of C. cactorum eggs by ants is strongly influenced by season (Chapter 7). At the Thursford study site, of the eggs remaining on O. ficus-indica plants at the beginning of May, only 16% were eventually destroyed by ants.

Predation of C. cactorum eggs by ants also occurs in Australia, but available evidence suggests that it is not as severe as in South Africa. Dodd (1940) recorded egg predation by Iridomyrmex ants but regarded this as being unusual. He mentions that small ant species such as Crematogaster may eat some of the eggs in a stick but does not detail the extent of this predation. Monro (1967) and White (1981) determined eggstick densities at a number of sites in Australia yet make no mention of egg predation affecting their estimates of eggstick densities. In a later paper, Monro (1975 p. 207) mentions that in the southern part of the range of C. cactorum in Australia, there is "an almost classic two species interaction with little interference from predators or competitors".

In Hawaii, ants destroyed 30% of C. cactorum eggs laid on O. ficus-indica (Fullaway 1954). There are no records of predation by ants of C. cactorum eggs in South America but in North America, Lummus & Wangberg (1981) recorded 57% mortality by Crematogaster punctulata Emery ants of Olycella subumbrella (Dyar) eggs which are laid in small eggsticks on Opuntia spines.

6.5 Causes of larval mortality.

The behaviour of larvae during penetration of the cladode cuticle and their subsequent feeding activity is described in section 3.1. The main factors preventing larval penetration of cladodes are tough, impenetrable cuticles and gum exudation (Fig. 6.2). On O. ficus-

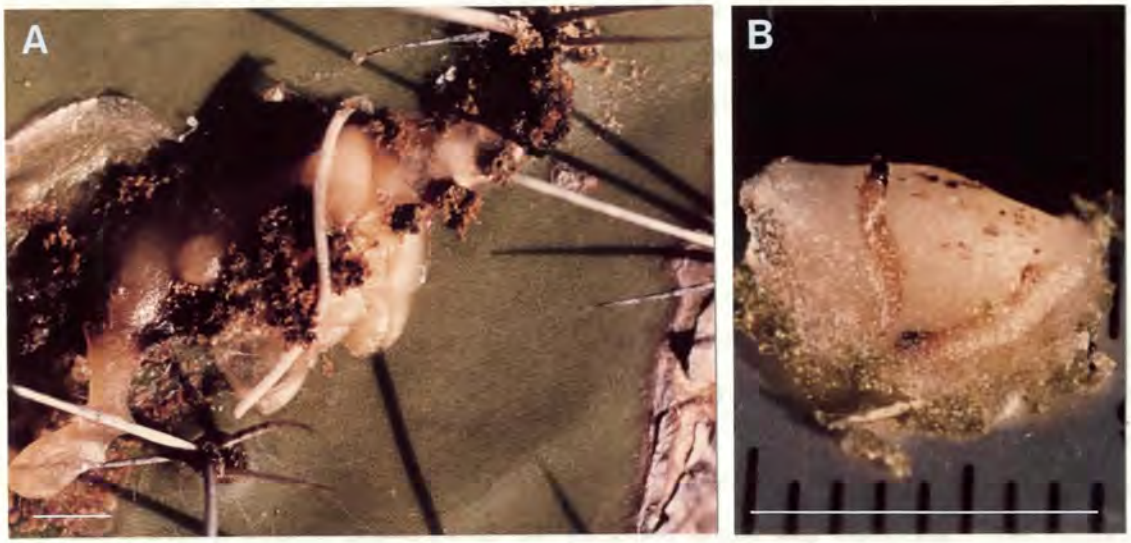

Fig. 6.2. A: gum exudation from an O. ficus-indica cladode at the penetration site of C. cactorum larvae. The eggstick from which the larvae emerged has broken off the spine and become embedded in the gum. B: second instar larvae embedded in gum. Scale line = 8mm.

indica, larvae often had to attempt penetrating at a number of different sites before they were successful. They normally managed to feed at each penetration site and larvae in some colonies were already in the third instar by the time they had successfully penetrated. On O. aurantiaca, larvae were usually successful in their first penetration attempt but a number of colonies died, for an unknown reason, soon after penetrating. Prior to and during penetration, C. cactorum larvae are exposed to attack by predators. Dodd (1940 p. 151) recorded that Crematogaster sp. ants attacked small larvae, and I observed on one occasion a C. liengmei ant removing a first instar larva soon after it had hatched. In this study, penetration mortality includes mortality of whole colonies during penetration and mortality within colonies from emergence to soon after successful penetration.

During the post-penetration period, larval mortality was caused by dispersal, food shortage, disease, predation by ants (Pheidole sp. and Anoplolepis steingroeveri (Forel) have been observed attacking larvae) and temperature extremes. In addition to these mortality factors the tachinid Pseudoperichaeta sp. was recorded as an incidental parasitoid of C. cactorum larvae. Three categories of post-penetration mortality were distinguished in this study: (i) mortality of whole colonies following unsuccessful trivial migrations in search of food (termed dispersal mortality); (ii) mortality of whole colonies from unknown

factors; and (iii) mortality of individuals within colonies from unknown factors. Dispersal mortality is probably underestimated but the balance is incorporated in the second category as 'unknown factors'.

6.6 Methods for determining larval mortality.

O. ficus-indica and O. aurantiaca plants outside the experimental quadrats, were searched for eggsticks near the end of the egg development period. As a result of the high egg predation, location of sufficient hatched eggsticks was difficult. When all the larvae from each eggstick had emerged, the eggstick was removed and taken back to the laboratory where the number of hatched eggs was counted. The colony derived from each eggstick was numbered and its progress followed throughout its development. All colonies were checked at least every week in the summer generation and at least every fortnight in the winter generation. This was necessary in order to keep track of the colonies and to record those which had died out. Colonies that successfully penetrated the same plant often had to be combined in the results because their dispersion overlapped. Shortly before pupation, the cladodes containing each colony, or collection of colonies, were placed in a cage (Fig. 6.3) together with a plentiful supply of fresh

Fig. 6.3. Determination of larval mortality: the cages in which C. cactorum colonies were placed shortly before they started pupating. The O. aurantiaca stands on which the colonies were originally feeding are next to the cages.

cladodes. An accurate record could then be kept of the number of larvae which pupated. Results for some of the colonies were discarded because the larvae started pupating prior to placement in the cages. These colonies were, however, included in calculations of the proportion of colonies that successfully pupated. During these larval mortality determinations, records were also kept of the number of cladodes destroyed (chapter 8) and the development period of each colony (chapter 3). Larval mortality was determined in both the 1981/82 and 1982/83 summer generations in order to increase sample sizes.

In addition to the above procedure, destructive sampling was used to determine the proportion of individual larvae that successfully penetrated within colonies: cladodes containing colonies that had recently penetrated successfully were cut open and the number of larvae they contained was counted. The number of larvae that were alive prior to penetration was determined from the number of hatched eggs in the eggstick that the colony had originated from. The results of this destructive sampling were pooled with the results from the other sampling method to calculate the 'within-colony' penetration mortality.

6.7 Results for larval mortality.

Both within- and whole-colony penetration mortality were greater on O. ficus-indica than on O. aurantiaca but these differences were statistically insignificant (Table 6.4, within-colony penetration mortality, $G=0.077$, $P>0.70$; Table 6.5). However, the main factors causing penetration mortality were different on each host plant. Mortality of larvae on O. ficus-indica was caused mostly by gum exudation whereas on O. aurantiaca some colonies died out for an unknown reason soon after penetration. This difference in penetration mortality factors is illustrated by the fact that on O. aurantiaca, no colonies were recorded re-penetrating after their first penetration attempt whereas on O. ficus-indica, 28% of colonies did so. One colony of C. cactorum on O. ficus-indica succeeded in penetrating only after the fifth attempt.

Fig. 6.4 shows the penetration mortality of C. cactorum colonies on O. ficus-indica in relation to plant size. Penetration mortality of colonies was greatest on plants with 41 to 320 cladodes (35-39%).

Table 6.4. Mortality of C. cactorum larvae on O. ficus-indica and O. aurantiaca at the Thursford study site in summer and winter generations. C. - whole colonies; W. - within colonies; pen. - penetration; lar. - larvae; col. - colonies.

Mortality factor	Summer 1981/82 + 1982/83						Winter 1982					
	O. ficus-indica			O. aurantiaca			O. ficus-indica			O. aurantiaca		
	No. lar.	No. col.	% lar.	No. lar.	No. col.	% lar.	No. lar.	No. col.	% lar.	No. lar.	No. col.	% lar.
Penetration - C. No pen.	11	1	0.4	96	3	3.9	192	6	5.4	65	5	7.3
During pen.	513	11	16.3	283	6	11.4	491	10	13.8	100	2	11.3
Penetration - W.[1]	383	-	12.2	234	-	9.4	419	-	11.8	81	-	9.1
Dispersal - C.	162	5	5.1	0	0	0	77	3	2.2	0	0	0
Other - C.	0	0	0	599	18	24.1	33	1	0.9	17	1	1.9
Other - W.	703	(41)	22.3	413	(26)	16.6	668	(50)	18.8	195	(18)	21.9
Total mortality	1772	17	56.3	1625	27	65.4	1880	20	52.9	458	8	51.5
Pupated	1374	41	43.7	861	26	34.6	1671	50	47.1	431	18	48.5
Total	3146	58	100.0	2486	53	100.0	3551	70	100.0	889	26	100.0

[1]Calculated separately using destructive sampling (see text).

Table 6.5. Larval mortality within C. cactorum colonies on O. ficus-indica and O. aurantiaca, for summer and winter generations combined: (i) penetration mortality within colonies that penetrated successfully (determined from destructive sampling of colonies, see text); and (ii) total mortality within colonies that pupated. Mann-Whitney U-test (Z = normal deviate of U): n.s. - not significant ($P > 0.05$).

	O. ficus-indica			O. aurantiaca			Z
	Mean ± SE	Range	n	Mean ± SE	Range	n	
% larvae surviving penetration	16.1 ± 4.2	0-70.8	19	11.2 ± 2.4	0-27.0	12	$0.45^{n.s.}$
% total larval mortality	43.4 ± 3.8	5.7-96.2	40	38.9 ± 2.9	12.5-80.0	31	$0.54^{n.s.}$

On smaller plants, (1-40 cladodes), and on the large plants (>320 cladodes), penetration mortality was considerably lower (7-17%) (Fig. 6.4). There is a striking similarity between these results and those presented in Table 5.2 on the preference of C. cactorum females for ovipositing on new-succulent growth. The results in Table 5.2

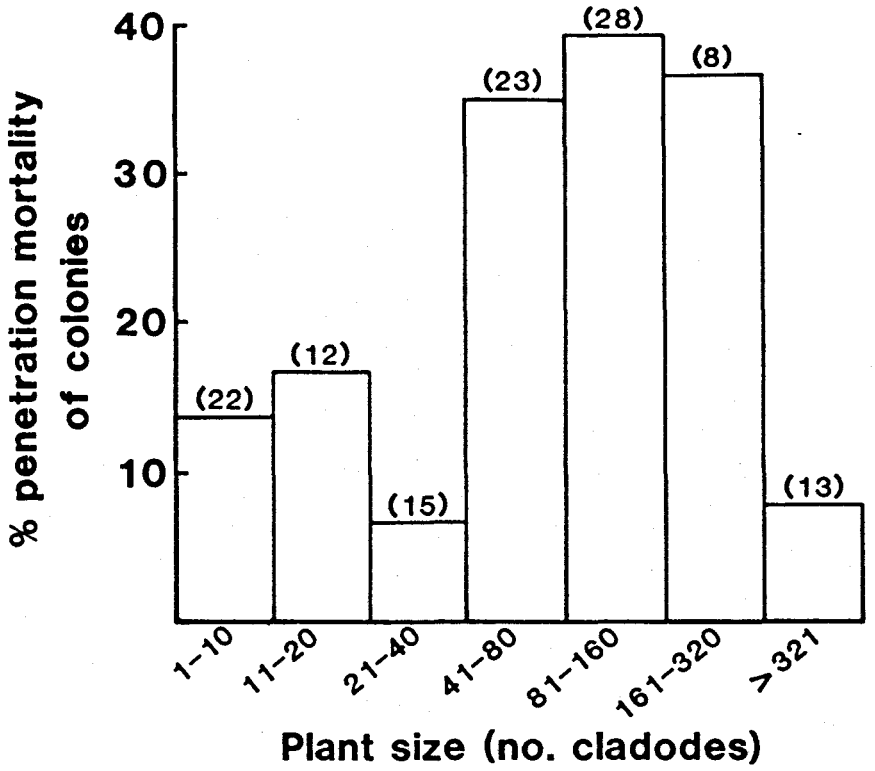

Fig. 6.4. Penetration mortality of C. cactorum colonies on O. ficus-indica in relation to plant size. Numbers in brackets indicate sample sizes of eggsticks.

showed that there was a significant preference for ovipositing on new-succulent cladodes on plants with 41-320 cladodes whereas there was no significant preference on smaller plants (1-40 cladodes) and on large plants (> 320 cladodes).

Dispersal mortality affected C. cactorum colonies on O. ficus-indica but not those on O. aurantiaca (Table 6.4). This was because O. ficus-indica has a tree-like habit so that cladodes or fruits containing larvae, fall to the ground usually away from the plant's trunk, whereas on O. aurantiaca, when cladodes containing larvae broke off the plant they usually fell among other plants in the stand and the larvae were able to penetrate new cladodes.

On O. aurantiaca, mortality of C. cactorum colonies after penetration was high during summer (24.1% - Table 6.4). This was consistent for both the 1981/82 and 1982/83 generations. The cause of this mortality is uncertain but possibly relates to dehydration of O. aurantiaca plants during the summer larval development periods. The surface to mass ratio of O. aurantiaca cladodes is about 5.4 cm^2/g whereas for

O. ficus-indica it is about 0.8 cm^2/g (calculated from Appendix 5). Consequently, under conditions of low rainfall and high evaporative water loss, cladodes of O. aurantiaca are likely to dehydrate faster than those of O. ficus-indica. During these periods, cladodes of O. aurantiaca are visibly more wrinkled from dehydration than those of O. ficus-indica. Little rain fell during both the summer generations (1981/82 and 1982/83), when larval mortality was measured (Fig. 2.3). Ambient temperatures were also highest during this time (Fig. 2.3) and therefore evaporative water loss would have been at a maximum.

Of the colonies that pupated, there was no significant difference between O. ficus-indica and O. aurantiaca in the percentage larval mortality per colony (Table 6.5). The results in Table 6.5 include within-colony mortality both during and after penetration whereas in Table 6.4, these two categories are expressed separately.

Overall, 9.1% more larvae pupated from O. ficus-indica than from O. aurantiaca plants in the summer generation (43.7% minus 34.6%: Table 6.4) mostly because of the high post-penetration mortality of whole colonies on O. aurantiaca. In the winter generation, the percentage of larvae that pupated from each host plant was similar (47.1% and 48.5% for O. ficus-indica and O. aurantiaca respectively: Table 6.4). In other words, mortality of C. cactorum larvae on O. ficus-indica totalled 56.3% and 52.9%, and on O. aurantiaca totalled 65.4% and 51.5%, for summer and winter generations respectively (Table 6.4).

6.8 Causes of pupal mortality.

Pupal mortality at the Thursford study site was a consequence of: (i) predation by Dorylus helvolus (L.) ants; (ii) parasitism by the chalcids Invreia sp. and Euchalcidia sp.; (iii) factors, such as disease, that killed pharate pupae inside their cocoons; and (iv) factors such as disease and temperature extremes, that did not externally damage pupae but prevented moth emergence.

6.9 Methods for determining pupal mortality.

Two methods were used to determine pupal mortality.

(i) In the summer 1981/82 and winter 1982 generations, after all moths had emerged, the ground around damaged O. ficus-indica and O. aurantiaca plants was systematically searched for C. cactorum pupae. Pupae are most easily collected from high density areas immediately surrounding heavily attacked plants. However, care was taken to search for pupae in both high and low density areas as predation and parasitism of pupae is likely to be spatially density-dependent. Pupae were taken back to the laboratory where their fate was analysed from the remains. D. helvolus ants made large holes in the cocoon and pupa, while each emerging parasitoid left a small round hole in both the pupa and cocoon.

(ii) The second method involved placing cocoons containing pharate pupae in the field and recording their fate. Final instar larvae, collected from the field, were placed in cages to complete their development. A layer of dry soil, collected from the study site, was placed in the bottom of each cage so that the cocoons would have soil particles attached to them. When the cocoons were almost complete, they were taken to the study site where, around each of 17 damaged plants, ten cocoons were hidden in likely pupation sites. Knowledge of the most likely sites where C. cactorum larvae would pupate had been gained from the collection of many old pupae. Occasionally, the site chosen for concealing a pupa happened to have a pupae there already. A one-and-a-half inch (3.8cm) nail was hammered in immediately beside each cocoon and a large six inch (15cm) nail with a numbered metal tag was hammered in approximately 15cm away from the hidden cocoon. Shortly after the pupae should have emerged, they were relocated in the field, and taken back to the laboratory for analysis. A cocoon was recorded as having disappeared if the small nail that was next to it was located but not the cocoon itself.

Although the second method was useful for determining the proportion of pupae that disappeared, it had two disadvantages. Firstly, the pupation site was not naturally chosen by the pharate pupa although care was taken to conceal the cocoons in likely pupation sites. Secondly, the

pharate pupa was not exposed to mortality, especially from parasitism, while spinning the cocoon. In addition, this method was not used for the generations that were studied for the construction of the life tables. The results from the first method of determining pupal mortality have therefore been used for the life tables but the proportion of cocoons that disappeared was calculated using the results from the second method and incorporated into the overall life table (Table 6.6).

6.10 Results for pupal mortality.

Predation by D. helvolus ants was the most important pupal mortality factor at the study site (Table 6.6) . These are minimum figures for predation because 'disappeared' pupae were also partly attributable to predation by D. helvolus. Workers of D. helvolus sometimes dismembered

Table 6.6. Pupal mortality of C. cactorum at the Thursford study site in summer and winter generations, determined using two different sampling methods (see text for details).

Mortality factor	Sampling method							
	Collection (method 1)				Placement (method 2)			
	Summer 1981/82		Winter 1982		Summer 1982/83		Winter 1983	
	No.	%	No.	%	No.	%	No.	%
Dead pharates	2	1.1	8	4.2	3	1.8	8	4.9
Parasitism[1]	70	40.0	10	5.2	0	0	2	1.2
Predation			25	13.1	47	28.3	56	34.1
Disappeared[2]	18	10.3	20	10.5	16	9.6	18	11.0
Dead, undamaged	5	2.9	13	6.8	2	1.2	21	12.8
Total mortality	95	54.3	76	39.8	68	41.0	105	64.0
Emerged	80	45.7	115	60.2	98	59.0	59	36.0
Total	175	100.0	191	100.0	166	100.0	164	100.0

[1] In the summer 1981/82 generation, the technique had not yet been developed for distinguishing parasitism and predation, hence these mortalities are combined for this generation.

[2] Results for method 1 were calculated from results in method 2.

the entire cocoon and pupa so that they could not be found among the ground debris. The highest percentage parasitism recorded was 5.2% in the winter 1982 generation. Parasitism was underestimated, however, as parasitized pupae that were attacked by ants could not be distinguished in the analysis and were recorded as 'predation'.

The percentage of dead pharate and undamaged pupae was significantly greater in the winter than summer generations (results for all four generations combined - Pharates: $G=5.66$, $0.01 < P < 0.025$. Undamaged pupae: $G=19.10$, $P < 0.001$) probably because of adverse effects of low temperatures. Overall, pupal mortality totalled 54.3% and 39.8% in the summer 1981/82 and winter 1982 generations respectively.

Pettey (1948) gave considerable attention to pupal mortality of C. cactorum in South Africa. Pettey and co-workers recorded pupal mortality at nine different sites over a period of five years by collecting pupae in the field shortly before emergence and determining in the laboratory the proportion of pupae that emerged, were parasitized, or were killed by other factors. Comprehensive though Pettey's results are, the methods used to obtain them have two drawbacks: (i) the pupae appear to have been collected from high density areas immediately surrounding plants that had been heavily attacked by larvae, because these were the easiest to find. The main objective of Pettey and his assistants was to collect as many pupae as possible for egg production and distribution purposes, rather than to collect them randomly for an unbiased estimate of pupal mortality; (ii) pupae that disappeared before they could be collected are not included in Pettey's mortality calculations.

Pettey (1948 p. 79) recorded D. helvolus as an important mortality factor at the Uitenhage commonage but not elsewhere. Instead, he recorded parasitism as the most important factor, causing on average 16% mortality. He listed eighteen species of parasitoids of which Brachymera sp. was the most important (see also Taylor 1943).

6.11 Presentation of life tables.

Life tables were compiled for C. cactorum on O. ficus-indica and O. aurantiaca in the summer 1981/82 and winter 1982 generations from

the results presented above and from the fecundity results presented in chapter 3 (Tables 6.7 & 6.8).

Absolute population numbers were determined from surveys of the number of emerged larvae on all plants within the seven quadrats (see chapter 2 for methods). To account for the slight overlap in summer and winter generations (Fig. 3.2), an overwintering category was included in the life tables. The summer generation larvae from O. aurantiaca that overwintered (=10%), were removed from the summer generation life table and added to that of the winter generation. This adjustment was made at the beginning of the larval period and not later because the summer generation larvae that overwintered would have experienced mainly winter conditions in the larval stage. A consequence of the incorporation of this factor is that k-values which cover total mortality before and after the overwintering stage cannot be directly calculated from the figures in the 'alive' columns.

Pre-oviposition egg mortality, termed adult mortality for convenience, was calculated from the difference between the potential number of eggs that could have been laid (= number of emerged females X mean fecundity) and the actual number that were laid within the quadrats. Conventionally, these egg numbers would be divided by mean fecundity and multiplied by two, in order to keep the life table balanced (Harcourt 1969). However, the resulting figures are artificial because it is assumed that females either lay their full egg complement or do not lay at all. Mortality in the adult stage on C. cactorum has therefore been expressed in terms of egg numbers in Tables 6.7 and 6.8. This method is preferable because it also shows the proportion of eggs laid on each host plant (see below).

The sex ratio of emerging moths was not measured in this study and was assumed to be 50% females. Differential mortality of sexes in larvae of C. cactorum can occur and results in skewed sex ratios (Pettey 1948 p. 37). Pettey (1948 p. 36) recorded an overall average of 50.6% females in summer and 45.2% females in winter generations. However, his extensive records (for nine different sites over eight generations) show that sex ratios above and below 50% occurred in both generations and so it is reasonable to assume a 50% ratio.

Table 6.7. Life table for the summer 1981/82 generation of C. cactorum on O. ficus-indica and O. aurantiaca in the seven 50X50m quadrats at the Thursford study site. C. - whole colonies; W. - within colonies; pred. - predation; par. - parasitism.

Stage	Factor	O. ficus-indica				O. aurantiaca				Total			
		No. alive	No. killed	% killed	k	No. alive	No. killed	% killed	k	No. alive	No. killed	% killed	k
EGGS		11062				22836				33898			
	Predation[1]		6588	59.6	0.719		17493	76.6	0.865		24081	71.0	0.812
	Breakage	2111	2363	21.4		3113	2230	9.8		5224	4593	13.5	
	Unhatched	2002	109	5.2	0.023	2987	126	4.0	0.018	4989	235	4.5	0.020
LARVAE	Overwintering	2002	0	0	-	2688	299	10.0	-	4690	299	6.0	-
	Penetration - C.	1668	334	16.7	0.079	2278	410	15.3	0.072	3946	744	15.9	0.075
	Penetration - W.	1424	244	14.6	0.069	2025	253	11.1	0.051	3449	497	12.6	0.058
	Other - C.	1321	103	7.2	0.033	1377	648	32.0	0.167	2698	751	21.8	0.107
	Other - W.	874	447	33.8	0.179	930	447	32.5	0.170	1804	894	33.1	0.175
PUPAE	Pharates	864	10	1.1	0.005	920	10	1.1	0.005	1784	20	1.1	0.005
	Pred. & Par.	425	439	50.8	0.308	453	467	50.8	0.308	878	906	50.8	0.308
	Non-emergence	399	26	6.1	0.027	426	27	6.0	0.027	825	53	6.0	0.027
	Sex-ratio	200	199	49.9	-	213	213	50.0	-	413	412	49.9	-
			(X fecundity=172.3)				(X fecundity=138.4)				(X fecundity=154.8)		
EGGS[2]		34460				29479				63939			
Unlaid:	temperature		620	1.8	0.262		531	1.8	0.262		1151	1.8	0.262
	other	18850	14990	43.5		16124	12824	43.5		34974	27814	43.5	
Laid:	O. ficus-indica		14134	75.0			0	0			14134	40.4	
	O. aurantiaca		4716	25.0			16124	100.0			20840	59.6	

[1]Egg parasitism is included with predation. [2]See text for explanation.

Table 6.8. Life table for the winter 1982 generation of C. cactorum on O. ficus-indica and O. aurantiaca in the seven 50X50m quadrats at the Thursford study site. C. - whole colonies; W. - within colonies; pred. - predation; par. - parasitism.

Stage	Factor	O. ficus-indica				O. aurantiaca				Total			
		No. alive	No. killed	% killed	k	No. alive	No. killed	% killed	k	No. alive	No. killed	% killed	k
EGGS		14134				20840				34974			
	Predation[1]		7722	54.6	0.442		16228	77.9	0.687		23950	68.5	0.571
	Breakage	5110	1302	9.2		4282	330	1.6		9392	1322	3.8	
	Unhatched	4541	569	11.1	0.051	3908	374	8.7	0.040	8449	943	10.0	0.046
LARVAE	Overwintering	4541	0	0	-	4207	+299	-	-	8748	+299	-	-
	Penetration - C.	3668	873	19.2	0.093	3426	781	18.6	0.089	7094	1654	18.9	0.091
	Penetration - W.	3132	536	14.6	0.069	3043	383	11.2	0.051	6175	919	13.0	0.060
	Other - C.	2991	141	4.5	0.020	2963	80	2.6	0.012	5954	221	3.6	0.016
	Other - W.	2138	853	28.5	0.146	2040	923	31.2	0.162	4178	1776	29.8	0.154
PUPAE	Pharates	2048	90	4.2	0.019	1954	86	4.2	0.019	4002	176	4.2	0.019
	Pred. & Par.	1432	616	30.1	0.155	1366	588	30.1	0.155	2798	1204	30.1	0.155
	Non-emergence	1286	146	10.2	0.047	1227	139	10.2	0.047	2513	285	10.2	0.047
	Sex-ratio	643	643	50.0	-	613	614	50.0	-	1256	1257	50.0	-
			(X fecundity=177.0)				(X fecundity=159.4)				(X fecundity=168.4)		
EGGS[2]		113811				97712				211523			
Unlaid:	temperature		13316	11.7	0.795		11432	11.7	0.795		24748	11.7	0.795
	other	18239	82256	72.3		15659	70621	72.3		33898	152877	72.3	
Laid:	O. ficus-indica		11062	60.7			0	0			11062	32.6	
	O. aurantiaca		7177	39.3			15659	100.0			22836	67.4	

[1]Egg parasitism is included with predation. [2]See text for explanation.

The actual number of eggs laid in the quadrats by C. cactorum females of the winter 1982 generation was not measured and was assumed to be the same number as were laid by females of the winter 1981 generation. These figures are probably in excess of what was actually laid because the number of larvae that hatched on O. ficus-indica from the summer 1982/83 generation eggs was counted and found to be 72% of that in the previous summer generation. However, this might have been the result of higher egg predation or a shift in the ratio of eggs laid on each host plant.

There are three main aspects of C. cactorum population ecology at the Thursford study site that can be assessed from the life tables in Tables 6.7 & 6.8 and which are discussed below: (i) adult mortality; (ii) total mortality on O. ficus-indica and O. aurantiaca; and (iii) the contribution of weather, host plant and natural enemies to C. cactorum mortality.

6.12 Adult mortality.

Adult mortality was assumed to be the same for each host plant and was calculated from the total mortality figures in each life table (Tables 6.7 & 6.8). With the inclusion of temperature effects on realized fecundity, adult mortality was 46.5% and 83.9% in the summer and winter generations respectively. Even after accounting for the effect of temperature on fecundity (see Table 3.7) adult mortality was still 28.8% greater in the winter than summer generations (Tables 6.7 & 6.8). This difference between generations was probably caused by the effects of low temperatures on other aspects of adult survival such as emergence, mating and oviposition. Listed below are the factors other than temperature which are likely to contribute to adult mortality in C. cactorum.

(i) Emergence mortality. Females are sometimes unable to emerge successfully from a cocoon because of obstructions between the cocoon and ground surface. In addition, the moth is exposed to predation during the critical period of expansion and drying of wings.

(ii) Mating success.

(iii) Predation. This would affect moths both by day, when cryptically hidden in the surrounding vegetation, and by night when in flight. Moths are rarely encountered in the field so it has not been possible to find out which predators are important. On one occasion, however, I found a dead female C. cactorum moth in a spider web, suspended in front of an O. aurantiaca plant.

(iv) Emigration and immigration. If emigration of females from the quadrats exceeded immigration, it would raise the adult mortality. This, however, is unlikely to be of any great importance because of the large area covered by the quadrats and because the density of cactus within the quadrats was similar to that of the surroundings (Figs 2.1 B & 2.2).

6.13 Total mortality on O. ficus-indica and O. aurantiaca.

Survival of C. cactorum on O. aurantiaca was 55% and 60% of that on O. ficus-indica in summer and winter generations respectively (calculated from Tables 6.7 & 6.8). This difference was mainly because of the higher egg predation on O. aurantiaca. Mortality of whole colonies on O. aurantiaca during the summer generation also markedly reduced survival on this host plant. As a consequence of this difference in mortality and also in fecundity, it can be calculated that in summer and winter generations respectively, the number of eggs laid by O. ficus-indica-reared moths was in excess of the actual number laid on this host plant. In Tables 6.7 and 6.8 it has been calculated that in summer and winter generations respectively, 25.0% and 39.3% of eggs laid by O. ficus-indica-reared females were laid on O. aurantiaca. The lower survival and fecundity of C. cactorum on O. aurantiaca therefore indirectly reduced egg densities on O. ficus-indica and, conversely, the higher survival and fecundity on O. ficus-indica increased egg densities on O. aurantiaca.

6.14 The contribution of weather, host plant and natural enemies to C. cactorum mortality.

The relative contribution of weather, host plant and natural enemies to mortality of C. cactorum in each generation was analysed from the k-values in Tables 6.7 and 6.8 (Table 6.9).

Table 6.9. The relative contribution of weather, host plant and natural enemies to mortality of C. cactorum (expressed as k-values) on O. ficus-indica (O. f.) and O. aurantiaca (O. a.) at the Thursford study site in the summer 1981/82 and winter 1982 generations. pred. - predation; par. - parasitism.

	Summer 1981/82			Winter 1982		
	O. f.	O. a.	Total	O. f.	O. a.	Total
Weather						
Egg breakage	0.190	0.098	0.130	0.064	0.014	0.030
Unhatched eggs	0.023	0.018	0.020	0.051	0.040	0.046
Pharate pupae	0.005	0.005	0.005	0.019	0.019	0.019
Non-emergence	0.027	0.027	0.027	0.047	0.047	0.047
Adults	0.262	0.262	0.262	0.795	0.795	0.795
Total	0.507	0.410	0.444	0.976	0.915	0.937
Host plant						
Larvae	0.360	0.461	0.415	0.327	0.314	0.321
Lowered fecundity[1]	0.201	0.297	0.248	0.190	0.235	0.211
Total	0.561	0.758	0.663	0.517	0.549	0.532
Natural enemies						
Egg predation	0.529	0.767	0.682	0.378	0.673	0.541
Pupal pred. & par.	0.308	0.308	0.308	0.155	0.155	0.155
Total	0.837	1.075	0.990	0.533	0.828	0.696
Grand total	1.905	2.243	2.097	2.026	2.292	2.165

[1] k-value = $\log_{10}$(maximum mean fecundity/mean fecundity in life table). Maximum mean fecundity = 274 eggs/female (Table 3.6).

The mortality factors were divided among the three categories, and their k-values were summed for each. All larval mortality was attributed to the host plant although as mentioned earlier, weather and natural enemies both reduce survival in this stage. Physiologically related mortality (eg. unhatched eggs, dead pharate pupae and non-emerged pupae) was all assigned to the weather category. In addition to the k-values from the life tables, a k-value was calculated for

fecundity which was based on the maximum mean fecundity that has been recorded for C. cactorum.

From Table 6.9 it is clear that the estimate for host-plant-related mortality has not been conservative, that that for natural enemies is a minimum figure, while direct mortality from weather is probably slightly overestimated. Even with these distortions in mortality estimates, in both summer and winter generations, for both O. ficus-indica and O. aurantiaca, the total k-value for natural enemies was greater than that for host-plant-related mortality (Table 6.9). In the summer generation, natural enemies were also more important than weather factors while in the winter generation, weather was of overriding importance, mainly because of the high adult mortality caused by low temperatures.

The importance of a mortality factor in regulating population levels is generally regarded as depending not so much on its magnitude but on its degree of response to population density (Nicholson 1933, Morris 1957). The extent of density-dependent mortality in the egg and larval stages is discussed in chapters 7 and 8 respectively. Factors affecting fluctuations in pupal mortality were not determined in this study because of the extensive work done by Pettey (1948) and his co-workers. Pettey (1948 pp. 100-101) included density in a list of factors which affect the dynamics of pupal mortality and regarded it as impossible to explain variations in pupal mortality with any certainty because of the large number of influencing factors.

Survival of C. cactorum eggs, larvae and pupae at the Thursford study site was higher in the winter generation yet this generation produced fewer eggs than that in summer because of the high adult mortality (Tables 6.7 & 6.8). Pettey (1948 p. 29) recorded that in the collection of eggsticks for redistribution, there were many more eggsticks in the field in the winter than summer generations. Zimmermann & Malan (1980, 1981), from sites in South Africa, consistently recorded considerably greater damage to O. ficus-indica plants in the winter than the summer generations (their results are reproduced in Fig. 6.5). They attributed this to high mortality of late larvae and pupae in the winter generation but from Fig. 3.5 it is apparent that population fluctuations between summer and winter generations are rather the

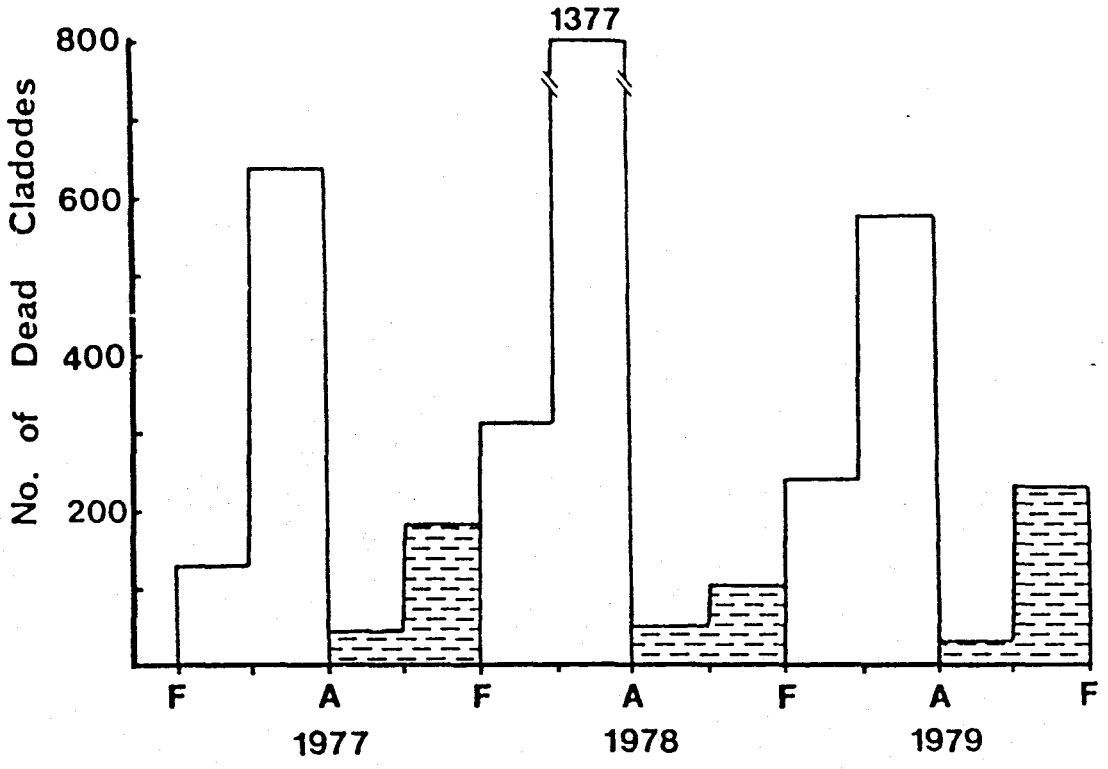

Fig. 6.5. The number of O. ficus-indica cladodes destroyed by winter, and summer (horizontal broken lines) generations of C. cactorum, based on data from three sites in the Eastern Cape. F - February; A - August (from Zimmermann & Malan 1981).

result of inhibitory effects of low temperatures on realized fecundity in the winter oviposition period.

The number of hatched eggsticks on O. ficus-indica plants within the quadrats was recorded over six generations at the Thursford study site (Fig. 6.6). These numbers are not proportional to the number of eggsticks laid by C. cactorum because egg predation varied between generations. In the winter 1983 generation egg predation was noticeably high and in the summer 1983/84 and winter 1984 it was lower than usual. The fluctuations in hatched eggstick numbers in Fig. 6.6 are therefore largely a result of low realized fecundity in the winter generations and changes in the extent of egg predation between generations.

6.15 Mortality of C. cactorum in South Africa and Australia.

A comparison of available results for mortality of C. cactorum in South Africa (this study and Pettey 1948) and Australia (Dodd 1940), is shown

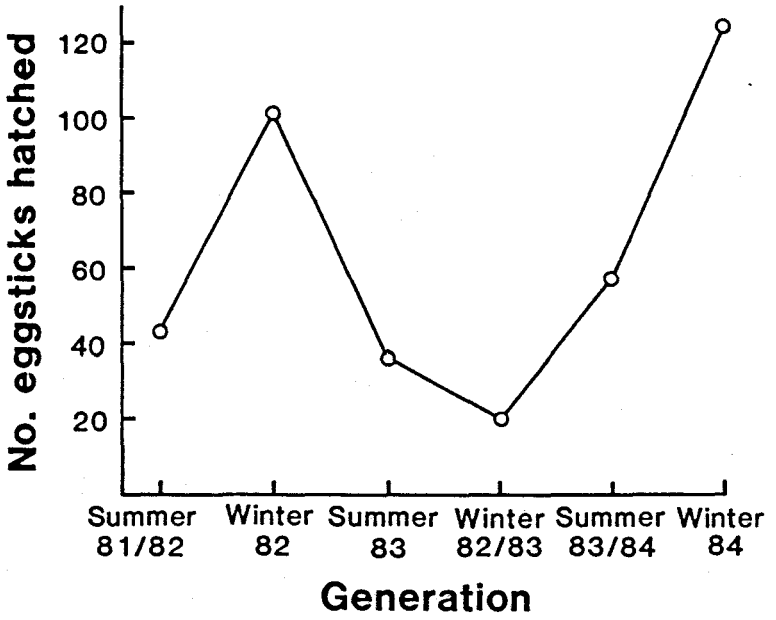

Fig. 6.6. Number of hatched C. cactorum eggsticks on O. ficus-indica plants within the quadrats at the Thursford study site, over six generations.

in Table 6.10. The following trends are apparent.

(i) Larval mortality of C.cactorum is similar on O. ficus-indica in South Africa and O. stricta in Australia. In chapter 3 it was shown that the fecundity of C. cactorum might be slightly greater on O. stricta in Australia. These differences in host-plant-related survival parameters are not sufficiently great to solely explain the difference in performance of C. cactorum between the two countries.

(ii) Pupal mortality is, on average, 13% higher in South Africa than in Australia.

(iii) Egg mortality, from egg predation by ants, was most important at the study site in South Africa, but unfortunately there are no comparable figures for Australia although available evidence (section 6.3; Robertson in press) suggests that it is not as great in Australia as in South Africa. The dynamics of egg predation are considered in greater detail in chapter 7.

(iv) Adult mortality was high at the study site in South Africa but there are no comparable figures for Australia. However, the discussion

Table 6.10. Comparison of C. cactorum mortality in South Africa on O. ficus-indica and in Australia on O. stricta.

	South Africa on O. ficus-indica		Australia on O. stricta
	This study	Pettey (1948)	Dodd (1940)
% egg mortality	74	-	-
% penetration mortality[1]	19	-	16
% total larval mortality	54	-	40-60
% pupal parasitism	5	16	13
% other pupal mortality	35	35	25
% adult mortality-summer	45	-	-
% " " -winter	84	-	-

[1] Only includes mortality of whole colonies and not mortality within colonies.

in section 3.4 about the different temperature regimes operating during the oviposition periods in the two countries, and their effect on realized fecundity, suggests that inhibitory effects of temperature might have been greater in South Africa than in Australia (see chapter 10).

Clearly, more information is required on C. cactorum mortality and survival in Australia, but the available data suggest that the effect of host plant incompatibility on C. cactorum population levels in South Africa is not as great as formally supposed by Monro (1975) and Annecke & Moran (1978). Natural enemies and climate considerably reduce the effectiveness of C. cactorum as a biological control agent of O. ficus-indica and O. aurantiaca in South Africa. However, the inefficiency of C. cactorum in destroying the basal woody cladodes of O. ficus-indica and O. aurantiaca is the ultimate factor that limits the effectiveness of C. cactorum as a biological control agent on these host plants and this is considered in chapter 8.

7. SPATIAL AND TEMPORAL PATTERNS OF C. CACTORUM EGG PREDATION BY ANTS

The results presented in the previous chapter showed that there was heavy predation of C. cactorum eggs by ants at the Thursford study site (Tables 6.7 & 6.8). However, the effects of egg predation by ants on the population dynamics of C. cactorum depend on the type of response by ants to egg densities and the extent to which their response is affected by other factors such as the season and weather. In most studies concerned with the assessment of insect population dynamics, the density-dependence of the different mortality factors is assessed over a number of generations by correlating the extent of mortality with the associated density (see Varley et al. 1973). As the study at Thursford was conducted over only two generations, this approach has not been possible. Instead, in this chapter, the response of ants to egg densities is assessed within each of the two generations on a spatial level between plants and on a temporal level over the period that eggs were present in the field.

Spatially density-dependent mortality can have a strong stabilizing effect on the host population (Hassell and May 1973, 1974; Hassell 1978, 1980) and is caused by predators or parasitoids searching for longer periods in patches of high prey density. Density-dependent searching behaviour by parasitoids has frequently been shown in laboratory experiments (see Hassell 1978; Waage 1979) and although it usually results in spatially density-dependent mortality of the prey, under certain circumstances density-independent or inverse density-dependent mortality occurs (Hassell 1982). Among parasitoids, most field examples show that host density and the intensity of parasitism are negatively correlated or not correlated at all (Morrison & Strong 1980; Morrison & Lewis 1984) although there are examples of positive correlations (eg. Hassell 1968; McClure 1977; Washburn & Cornell 1979). In a field situation, the performance of predators is affected by a large number of factors of which host density is just one. For instance, predator-prey interactions can be markedly affected by temperature (eg. Burnett 1949, 1970; Baumgaertner et al. 1981; Dreisig 1981; Cockrell 1984) and differential effects of temperature on predator and prey have been implicated in causing outbreaks of the prey (eg. Readshaw 1964; Clark 1964). Other factors affecting predator-prey interactions are discussed by Hassell (1978) and Hassell & Waage (1984).

Delayed density-dependent mortality is sometimes encountered in predator-prey population dynamics and can result in instability of the prey population (Varley *et al.* 1973). Delayed density-dependent mortality is normally assessed over a number of generations and can be shown to occur if, in a plot of host density with percentage mortality, the points when joined in a time sequence form an anti-clockwise spiral. In the results presented in this chapter, a similar method of joining points in a time sequence is used, except that the object is to assess delayed effects within and not between generations.

Past studies on the spatial and temporal dynamics of predation have concentrated on solitary predators and parasitoids. A solitary predator shows an individual behavioural response to prey density by tending to concentrate its searching in areas of high prey density. Ants, however, co-operate in foraging and there is therefore likely to be a marked group behavioural response to prey density because a worker which locates a patch of high prey density would recruit other workers to the patch (Carroll & Janzen 1973; Cammaerts & Cammaerts 1980).

Results in this chapter are based on the daily surveys which were undertaken of *C. cactorum* eggsticks on *O. ficus-indica* plants at the study site (chapter 2, section 6.2). All except five of these plants were located inside the quadrats. Results for egg predation on *O. aurantiaca* are not included because sample sizes were inadequate for such a detailed analysis.

7.1 Spatial patterns.

C. cactorum egg density and predation mortality were calculated as follows:

$$\text{Egg density} = \log_{10}\left(\frac{\text{No. eggs laid on plant}}{\text{No. cladodes on plant}}\right)$$

$$\text{Percentage eggs eaten} = \frac{\text{No. eggs eaten}}{\text{No. eggs eaten + hatched}} \times 100$$

Eggs that were broken off or which disappeared were excluded from the mortality calculations because they would have caused an underestimation

of predation mortality but were included in density calculations. Only eggsticks whose laying date was known to the nearest two nights were included in mortality determinations, also to avoid underestimation of egg predation.

A sample size of 12 or more eggsticks was regarded as sufficient for calculating predation mortality. Predation mortality could usually not be measured for each plant as sample sizes of eggsticks were too small; only four plants in the summer and five in the winter generations had a sufficiently large number of eggsticks to be considered separately. The data for the remaining plants were treated as follows: (i) eggstick densities for each plant were arranged in ascending order; (ii) within this order, plants were grouped so that each group contained at least 12 eggsticks; (iii) mean density and percentage mortality were calculated for each group.

In the summer generation there was no significant correlation between egg density and predation mortality (Fig. 7.1 A) but in the winter generation, excluding one aberrant point, there was a highly significant positive correlation between these two variables (Fig. 7.1 B). The three lower data points in Fig. 7.1 in the summer generation may be masking a direct density-dependent relationship.

The results presented in Fig. 7.1 suggest that on many of the O. ficus-indica plants, ants responded positively to increases in C. cactorum egg densities. Egg predation on some plants, however, was lower than would be expected if ants were responding to the density of eggs present. There are four possible reasons why predation was not correlated with egg density on some plants.

(i) An abundant alternative food source in the region of these plants might have made searching on spines for eggsticks a relatively 'unprofitable' method of food gathering. This proposition assumes that the alternative food source was not equally available near all O. ficus-indica plants.

(ii) Extrafloral nectar production (see section 6.4) might have been lower on these plants and would have resulted in lower ant densities.

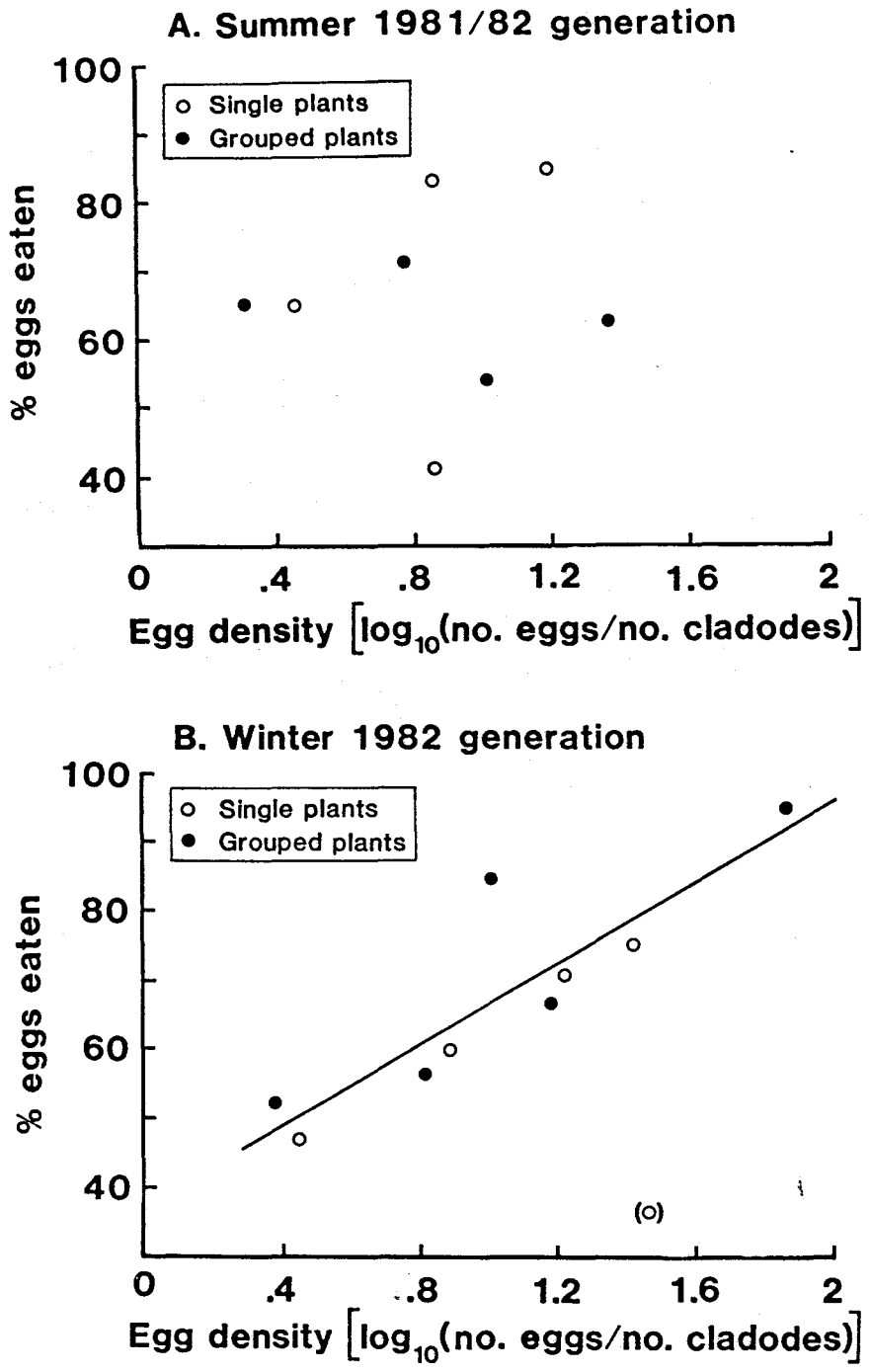

Fig. 7.1. The density of C. cactorum eggs on O. ficus-indica plants in relation to the corresponding predation mortality. A: summer generation; $r=0.063$, $P > 0.25$. B: Winter generation; $Y=37.6 + 29.3X$, $r=0.877$, $0.001 < P < 0.0025$ (data point in brackets excluded).

(iii) Egg predation might have been affected by the differential distribution, interaction and searching behaviour of the eight or so ant species within the study area. I noticed that the ant species composition tended to vary between plants. Presumably this was mainly because of differences in the proximity of each plant to the nests of the relevant ant species. Heterogeneity in ant species distribution has

been shown in a number of studies on the ant fauna of cocoa plantations (Leston 1970; Room 1971, 1975; Majer 1972, 1976; Taylor 1977; Taylor & Adedoyin 1978). Tilman (1978) and Laine & Niemala (1980) have shown that survival of lepidopteran larvae on trees is positively correlated with distance from Formica ant nests.

(iv) The method for determining egg density might not match the density of eggs that ants would encounter. In this study the O. ficus-indica plant has been considered as a single entity and the vegetation surrounding it has been ignored. This surrounding vegetation might form part of the ants' foraging area and if so, should theoretically have been included in the egg density calculations.

7.2 Temporal patterns.

Analysis of the effects of temporal changes in C. cactorum egg densities on the intensity of egg predation by ants was as follows: from the daily surveys of eggsticks on O. ficus-indica plants, the laying date and change in the number of eggs over time was known for each eggstick. For each generation, this information was assembled in a large table in which the columns represented the days of the egg development period, and each row showed the change in the number of eggs in an eggstick over this time. The total number of eggs available for predation and the total number of eggs destroyed by predators were then calculated for each day. Only hatched and eaten eggs were included in the analysis and once an eggstick had hatched, the eggs were excluded from the number of eggs available for predation. The egg development period in each generation was divided into five-day periods and the total number of eggs destroyed and the mean number of eggs available for predation, was calculated for each period. The percentage egg predation for each period was calculated as follows:

$$\% \text{ egg predation} = \frac{\text{No. eggs eaten in the five-day period}}{\text{Mean no. eggs available}} \times 100$$

Percentage predation of C. cactorum eggs by ants in relation to the number of eggs available for predation is shown in Fig. 7.2 for each generation. Data points have been linked in a time sequence. In the summer generation, this sequence moves in an anticlockwise direction

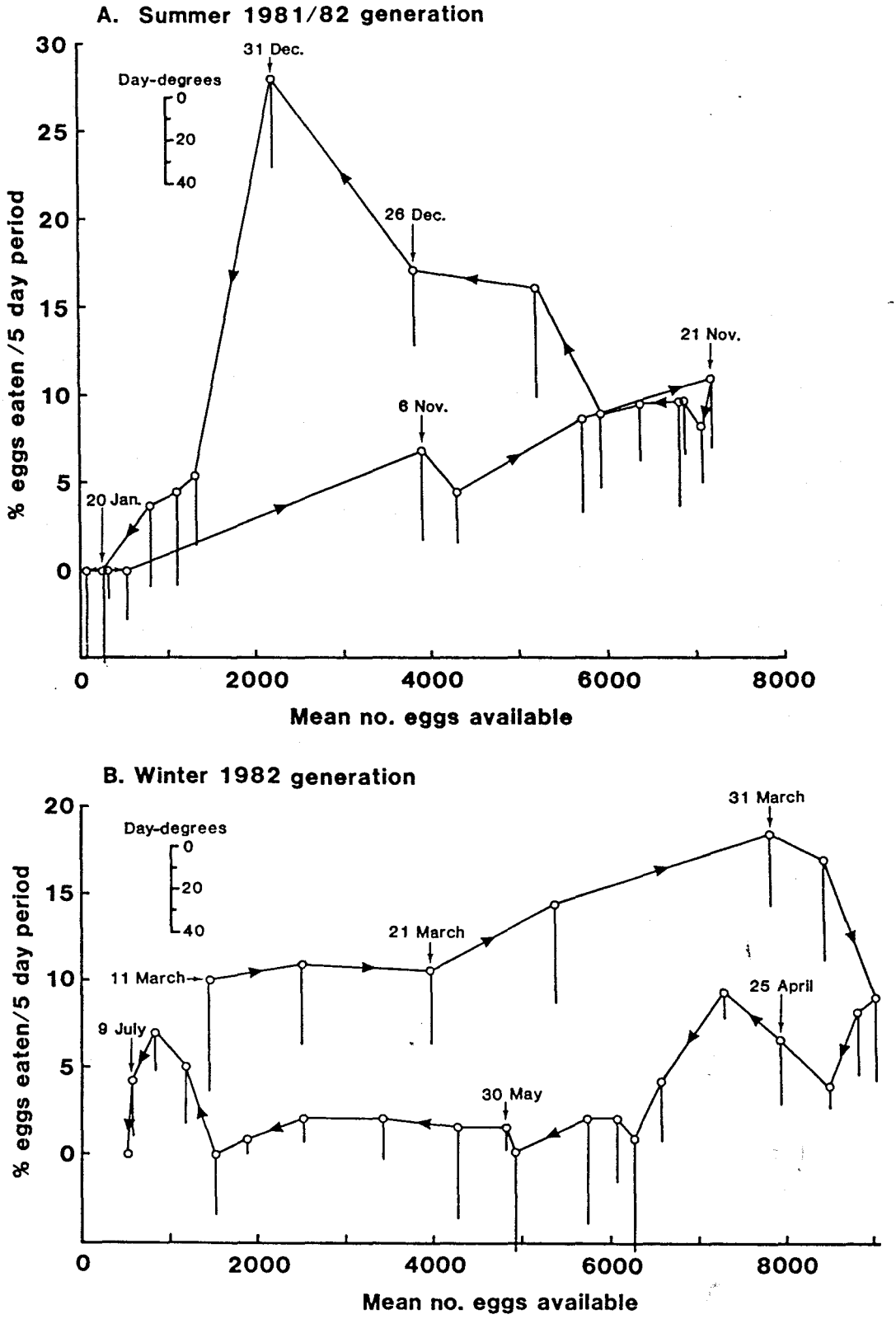

Fig. 7.2. Percentage C. cactorum eggs eaten by ants on O. ficus-indica plants in relation to the number of eggs available. Each point covers a period of five days and the points are linked in a time sequence. Each date refers to the last day of the particular five-day period. Eggs which eventually hatched are included in the number of eggs available. Vertical lines indicate the total day-degrees (at threshold=11°C) for each five-day period.

which suggests that there is a delayed density-dependent response. For instance, in each of the five-day periods ending on the 6 November and the 26 December, there were about 3800 eggs available for predation, yet in the earlier period only 6.8% of eggs were destroyed whereas in the later period 17.1% were destroyed. In the winter generation, the pattern is the reverse of that in the summer generation as the points joined in a time sequence move in a clockwise direction (Fig. 7.2 B). For instance, in each of the five-day periods ending on the 31 March and the 25 April, there were about 7800 eggs available for predation yet egg predation was 18.4% in the earlier period but only 6.6% in the later period.

In the summer generation, it could be argued that the anti-clockwise direction of the time sequence (Fig. 7.2 A) is caused by the rapid decrease in the number of eggs available for predation as the hatching rate of eggs increases. In order to avoid this possible bias, only eggs that were eaten were selected and the rate of predation was plotted against the number of eggs available (Fig. 7.3). Predation rate would obviously increase as more eggs became available but if there was no delayed density-dependent response, it would decrease at a similar rate as the number of eggs available decreased. In the summer generation, however, the rate of predation was greater as the number of eggs available decreased, and the points joined in a time sequence move in an anticlockwise direction thus confirming that there was a delay in the response of ants to C. cactorum egg densities. In the winter generation, the rate of predation in relation to egg availability increased and decreased at similar rates (Fig. 7.3 B) thus showing that there was no evidence of a delayed response.

In the summer generation, temperatures were increasing over the egg development period whereas in the winter generation they were decreasing (Fig. 3.2). In Fig. 3.3 it was shown that these increasing and decreasing temperature regimes affected the incubation periods of eggsticks laid at different stages during the oviposition period. They might also have affected the rate of predation of C. cactorum eggs by ants. In Fig. 7.2 the total day-degrees for each five day period is indicated by a vertical line. The threshold for these day-degree measurements was 11^{o}C and was based on table 4 in Bernstein (1979) which summarizes the literature on temperatures at which ants forage.

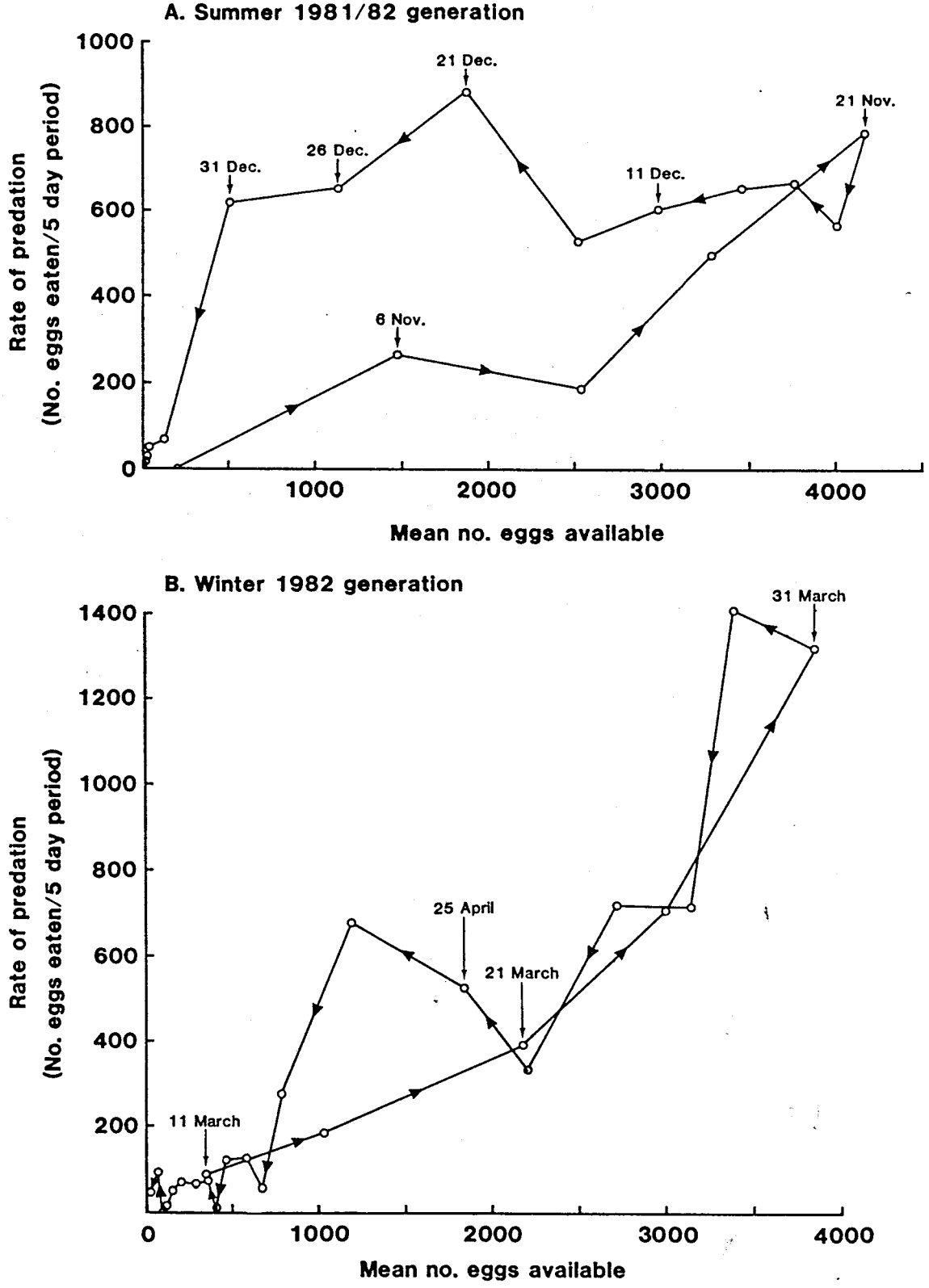

Fig. 7.3. Rate of predation of C. cactorum eggs by ants on O. ficus-indica plants, in relation to the number of eggs available that were destined to be eaten. Each point covers a period of five days and the points are linked in a time sequence. Each date refers to the last day of the particular five-day period.

Fig. 7.2 shows that although the total day-degrees in each period tended to increase over time in the summer generation and decrease over time in the winter generation, there is no clear correlation between the total day-degrees during a five-day period and the associated predation mortality. For example in the summer generation, the total day-degrees for the period ending on the 6 November was greater than for the period ending on the 26 December yet, with approximately equal numbers of eggs available, the percentage predation was lower in the earlier than the later period.

The differences in predation rate between the two generations is reflected in the frequency distributions showing the number of days that elapsed before eggsticks were first damaged by ants (Fig. 7.4). In both the summer and winter generations, the greatest number of eggsticks were attacked within two days of being laid. However, the mean number of days that elapsed before eggsticks were first eaten was less in the winter than in the summer generation because of the initially high rate of egg predation during the oviposition period of the winter generation. In the summer generation, the intensity of egg predation increased over the egg development period so that more days tended to elapse before eggsticks were first eaten.

MacDonald and Cheng (1970) developed a novel and practical method of testing for synchrony between host and parasitoid populations which can be adapted to the results presented in this study and which does control for temperature effects on the rate of predation. Their method involves a comparison of the cumulative frequency distributions over time of parasitized and unparasitized hosts which have just completed their period of susceptibility to parasitism. MacDonald and Cheng give an example, based on results collected for winter moth Operophtera brumata (L.) populations in Whytam Wood near Oxford, in which they compare the cumulative frequency of healthy prepupae falling from the oak trees each day with the cumulative frequency of parasitized prepupae falling per day. If the intensity of parasitism had been constant over the period of host susceptibility, then the cumulative distributions of unparasitized and parasitized prepupae falling each day would have been similar. If, however, the parasitoids had been poorly synchronized with their host and the intensity of parasitism had increased over the period of host susceptibility, then the later

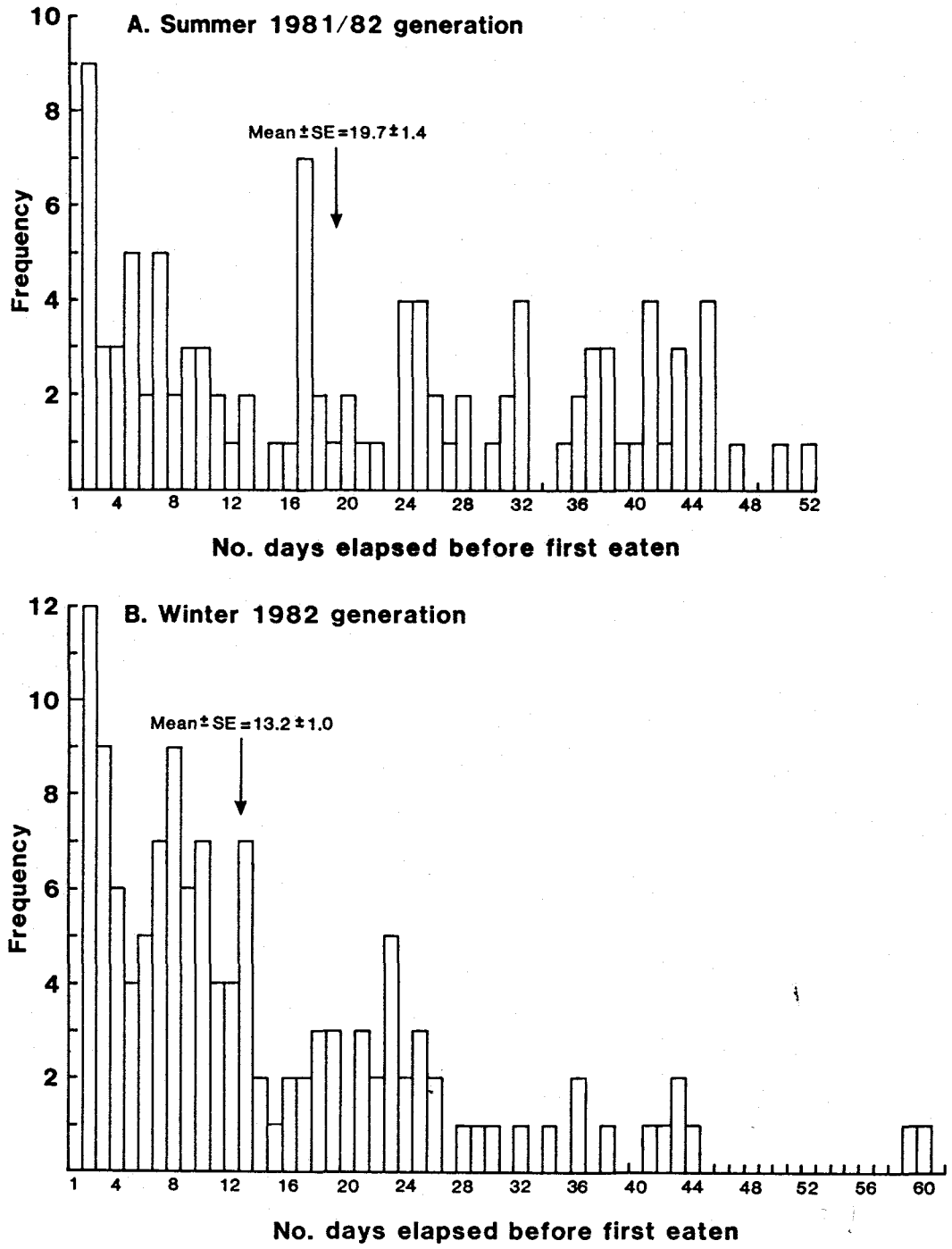

Fig. 7.4. Number of days elapsed before C. cactorum eggsticks on O. ficus-indica plants were first damaged by ants.

developing larvae would have a greater chance of being parasitized. Consequently the proportion of parasitized prepupae would tend to be greater towards the end of the prepupal period. This would result in a discrepancy between the cumulative frequency distribution of unparasitized and parasitized prepupae falling during the prepupal period. MacDonald & Cheng suggested the use of the Kolmogorov-Smirnov Test or

the X^2 test to determine whether these frequency distributions were significantly different.

The above method can be adapted to the results presented in this study by comparing the cumulative frequency distributions of laying dates for eaten and hatched C. cactorum eggs (Fig. 7.5). If the intensity of predation had been constant over the period of egg susceptibility to predation, then the cumulative frequency distributions of laying dates for hatched and eaten eggs would be similar. Fig. 7.5, however, shows that in the summer generation, predation was initially low but increased over the egg-development period whereas in the winter generation, predation was low at first, then increased markedly, and then steadily decreased over the rest of the egg development period.

One advantage of using MacDonald and Cheng's method is that it more or less controls for temperature effects on predation rate. Their method shows the degree of synchrony between predator and prey on an arbitrary but unbiased time scale which in this instance is the laying dates. Provided that temperature affects the searching rate of ants and the egg development rate in a similar way, eggs laid early in the oviposition period are exposed to a similar potential amount of predator searching time (in physiological time units) to those laid later in the oviposition period. The deviations between the cumulative frequency distributions of hatched and destroyed eggs is therefore likely to be caused by factors other than temperature.

Even though Fig. 7.5 shows that there were changes in the intensity of predation over time, there was no significant difference in the cumulative frequency distributions in each generation (Fig. 7.5). Nevertheless, the differential rates of predation within each generation did affect the extent of predation of eggs laid at different stages in the oviposition period (Fig. 7.6). As a result of the increase in predation rate over time in the summer generation, the percentage predation of C. cactorum eggs laid early on was less than the predation of eggs laid later on in the oviposition period (Fig. 7.6 A). In the winter generation, except for the eggsticks laid at the beginning of the oviposition period, the percentage predation of later-laid eggs was lower than the predation of eggs laid earlier on (Fig. 7.6).

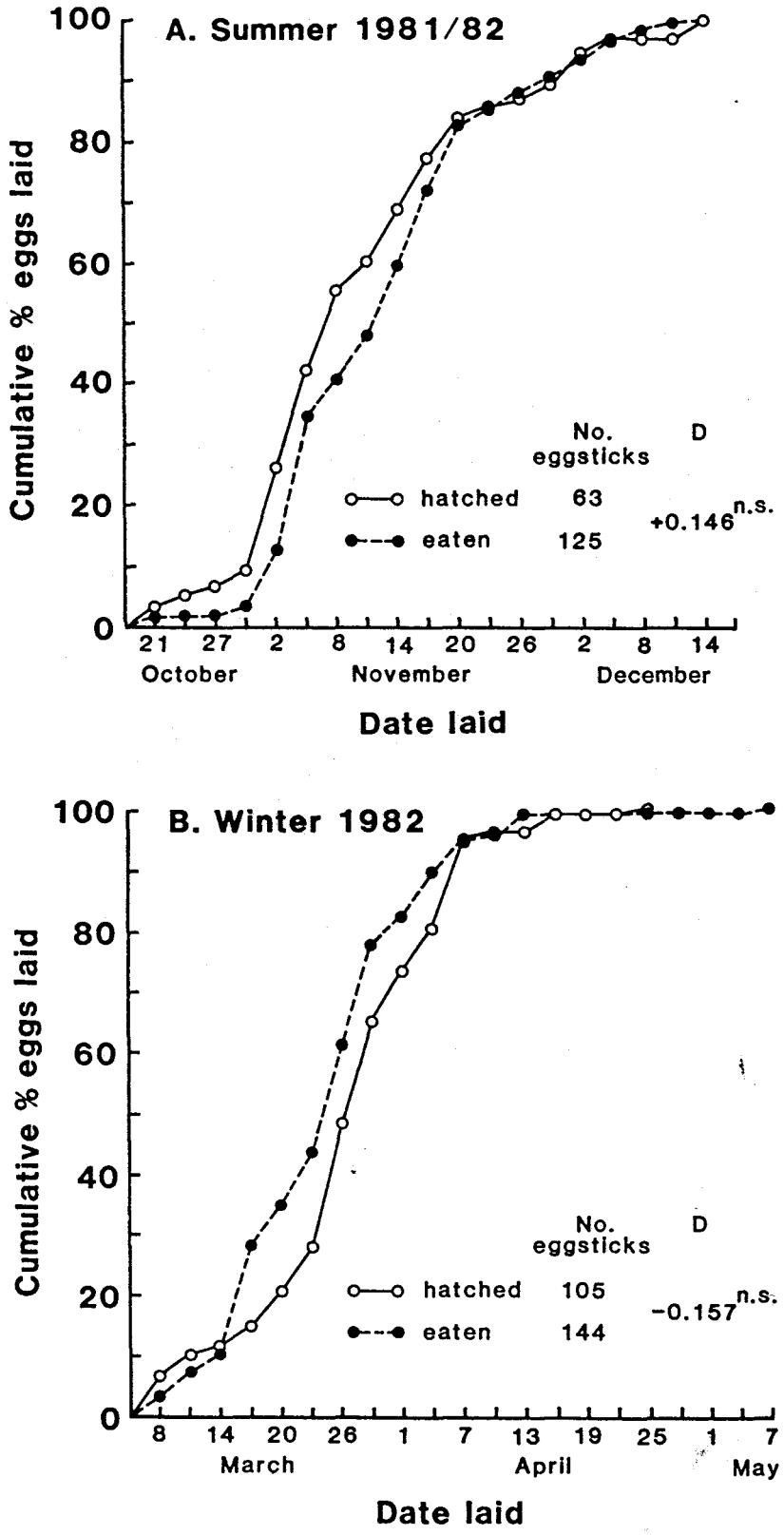

Fig. 7.5. Cumulative percentage of C. cactorum eggs laid over the oviposition period compared, for each generation, between eggs that were destined to hatch and eggs that were destined to be destroyed by ants. Kolmogorov-Smirnov Test (D=maximum deviation of cumulative distributions): n.s. - not significant ($P > 0.05$).

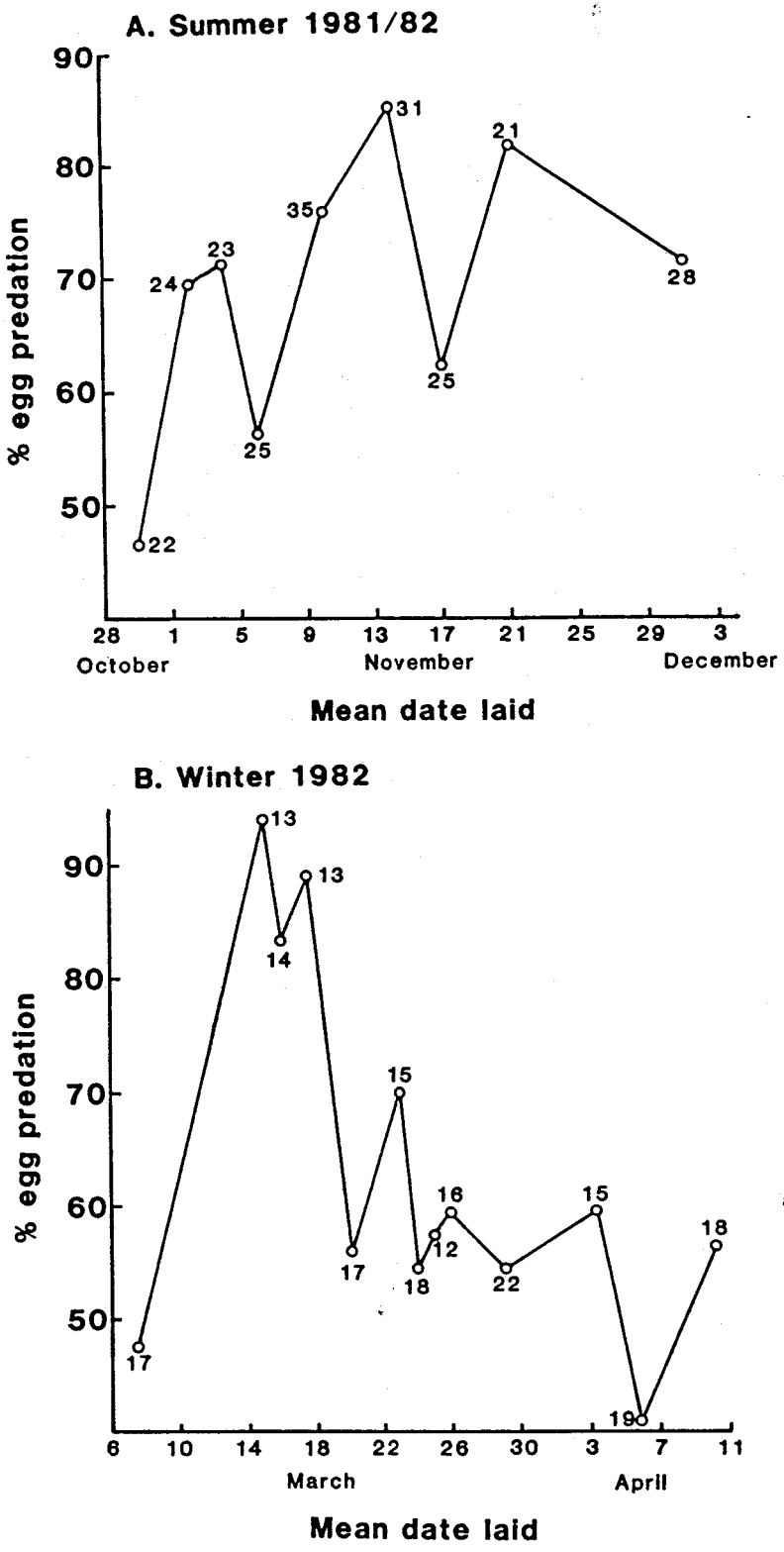

Fig. 7.6. Percentage predation of C. cactorum eggs by ants in relation to laying date. Only eggs that either hatched or were destroyed by ants were included in the calculations of percentages. Numbers adjacent to points indicate the sample sizes of eggsticks. Eggsticks were classed so that the sample size was greater than or equal to 12 for each data point (this minimum sample size was arbitrarily chosen).

Seasonal changes in ant foraging behaviour, and egg density, are the two most likely factors to have caused the observed changes in egg predation through time (Figs 7.2-7.6). In many ant species, summer is the main reproductive period of the year (Skaife 1961) and as the summer season progresses, recruitment of new workers and feeding rates are likely to increase. In addition, during the period of larval production in ants, there is an increase in the proportion of animal food collected by the workers (Pętal 1978). Consequently, over the summer egg development period of C. cactorum, the intensity of foraging for protein-rich foods by ants on a general level is probably increasing. The anti-clockwise time sequence in the summer generation (Fig. 7.2 A and 7.3 B) is more likely to have been caused by these seasonal effects on ant foraging behaviour than by a true delayed density-dependent response. During the winter generation of C. cactorum, the intensity of foraging for protein-rich foods by ants would be high at first but, when the autumn period commences, the main reproductive period of ants would come to an end and foraging activity and the proportion of protein in the diet could be expected to decrease markedly. This curtailment of activity and change in feeding preferences would account for the clockwise time sequence in the winter generation (Fig. 7.2 B).

Seasonal changes in the intensity of predation by ants has been shown by Kajak et al. (1972) and Pętal et al. (1971) for Myrmica ants in a meadow in Poland. The dominant component in the diet of these ants, the nymphs of Auchenorryncha (Homoptera), have a summer and an autumn hatching period. Myrmica preyed heavily on nymphs of the summer hatching period but not on those of the autumn period because the summer hatching period of the homopteran nymphs coincided with the maximal larval production by the ants whereas the autumn period did not. Similarly, another major component in the diet of Myrmica was newly emerged flies, which had a spring and an autumn emergence period. The ants preyed heavily on newly emerged flies in the spring emergence period but not in the autumn period. Spiders were another prey item of these Myrmica colonies and were most intensively eaten by ants during summer. From these findings of Kajak et al. (1972) and Pętal et al. (1971) and the results presented in this chapter on C. cactorum egg predation by ants, it seems that the degree of temporal coincidence of the prey with the peak larval production periods of the ants can have an important effect on the intensity of predation of the prey by the ants.

Although the seasonal changes in ant foraging behaviour appear to be the predominant factor affecting temporal patterns of egg predation by ants, it is possible that temporal changes in egg densities do affect egg predation, especially as the results for spatial predation patterns suggest that ants do sometimes respond positively to egg density. For instance, the increase in egg predation from the five-day period ending on the 11 March till the five-day period ending on the 31 March (Fig. 7.2) is possibly related to the increase in egg densities.

If the seasonal changes in predation by ants are of major importance, then presumably overall survival of C. cactorum eggs could be partly dependent upon how early or late in the season the eggs were laid. The peak egg-laying dates for C. cactorum can vary widely from year to year (Table 3.1). In the summer generation, if the oviposition period of C. cactorum occurred early on, lower than usual egg predation might be expected because the eggs would have been exposed to intensive predation by ants for a shorter period. In the winter generation, an early oviposition period could result in higher egg predation because eggs would have been exposed to intensive predation by ants for a longer period. The eggs of the winter 1983 generation of C. cactorum at the Thursford site were laid earlier than in the winter 1982 generation and this coincided with visibly higher egg predation by ants in the 1983 generation although this was not measured.

7.3 Conclusions.

The results presented in this chapter show that although there was a partial, positive response by ants, on both a spatial and temporal level, to C. cactorum egg densities, seasonal changes in ant foraging behaviour appear to be of overriding importance in affecting the extent of egg predation. The response by ants to C. cactorum egg densities on O. ficus-indica plants is also clouded by other factors such as alternative food sources and the degree of extrafloral nectar production. Therefore, although egg predation by ants considerably reduces C. cactorum egg densities (Table 6.7 & 6.8), it is unlikely to have a strong stabilizing influence on C. cactorum population dynamics because of the predominant effects of density-independent factors on the intensity of predation by ants. The full implications of these density-independent effects on population stability can only be assessed by

doing a study of C. cactorum egg predation over a greater number of generations.

The dynamics of predation of C. cactorum eggs by ants is complex because of the large number of ant species responsible (section 6.1) and because ants are generalists. The population dynamics of the ants would probably only be negligibly affected by fluctuations in the density of C. cactorum eggs as these would form only a small component of the ants' diet. Fluctuations in other more important food resources of ants could affect the extent of predation of C. cactorum eggs, firstly by affecting the population numbers of the ants and secondly by increasing or decreasing the relative importance of C. cactorum eggs in the ants' diet.

In chapter 4 it was shown that oviposition behaviour by C. cactorum resulted in a high degree of clumping of eggsticks on plants (Table 4.1). This clumping increased the density of eggsticks on individual plants and consequently might have increased the extent of density-dependent egg mortality by ants.

In the following chapter, results are presented to show the amount of destruction caused to O. ficus-indica and O. aurantiaca plants by C. cactorum larvae. The extent of this destruction is of course affected by the density of larvae present, which in turn is partly affected by the extent of egg predation. Predation of C. cactorum eggs by ants could be pre-empting density-dependent mortality of larvae (from food shortage) and this matter is considered at the end of the next chapter.

8. EFFECTIVENESS OF C. CACTORUM AS A BIOLOGICAL CONTROL AGENT ON O. FICUS-INDICA AND O. AURANTIACA

One of the notable features of the successful control of O. stricta in Australia by C. cactorum was that the woody, basal cladodes were usually not directly destroyed by larval attack but indirectly by the repeated destruction of the succulent regrowth. Repeated destruction of the succulent cladodes lowered the resistance of the whole plant so that eventually the woody butts disintegrated, this destruction being aided by associated fungi (Dodd 1940 pp. 49,141). Both O. ficus-indica and O. aurantiaca have a high proportion of woody tissue (Figs 1.3 & 1.4) and even at high population levels of C. cactorum, appear to be more resistant to repeated destruction than O. stricta in Australia (Pettey 1948 p. 69; Dodd 1940 pp.108,145).

In this chapter results are presented to show: (i) the level of damage to O. ficus-indica and O. aurantiaca cladodes by C. cactorum colonies and individual larvae; (ii) the impact of C. cactorum on the O. ficus-indica and O. aurantiaca populations at Thursford; (iii) the extent of density-dependent mortality of C. cactorum larvae (from food shortage) on O. ficus-indica and O. aurantiaca, and the estimated increase in density-dependent mortality that would have resulted had there been no predation of eggs by ants; and (iv) the feasibility of improving the effectiveness of C. cactorum as a biological control agent of O. aurantiaca by using an inundative release method.

8.1 Destruction of O. ficus-indica and O. aurantiaca cladodes.

During the sampling program to determine C. cactorum larval mortality (section 6.6), the number of cladodes destroyed by larval colonies was recorded. In addition, the dimensions were taken of a sample of eaten cladodes in order to calculate their initial mass. In Table 8.1, the number and mass of cladodes destroyed are expressed per colony, per emerging larva and per pupating larva. In both O. ficus-indica and O. aurantiaca, there was a wide range in the size of eaten cladodes (Table 8.2) and this contributed substantially to the variation in the number of cladodes destroyed. The mean mass of cladodes destroyed was calculated for each host plant as the product of the mean number of

Table 8.1. Number and mass of O. ficus-indica and O. aurantiaca cladodes destroyed by C. cactorum colonies that pupated. Fractions of partially eaten cladodes are included. Sample sizes refer to the number of colonies.

	O. ficus-indica				O. aurantiaca			
	No. cladodes			Mass (g)	No. cladodes			Mass (g)
	Mean ± SE	n	Range	Mean	Mean ± SE	n	Range	Mean
Per colony	2.8 ± 0.2	36	1-5	1453	29.6 ± 3.3	30	5-68	482
Per hatching larva	0.051 ± 0.004	36	0.019-0.116	26.5	0.60 ± 0.06	29	0.12-1.25	9.8
Per pupating larva	0.097 ± 0.010	34	0.039-0.286	50.3	1.02 ± 0.09	29	0.25-1.72	16.6

Table 8.2. Initial mass of cladodes (grams) destroyed by C. cactorum larvae. Mass was calculated from the cladode dimensions using equation 1 in Appendices 2 and 3.

	O. ficus-indica	O. aurantiaca
Mean ± SE	519 ± 34	16.3 ± 0.9
n	112	346
Range	9-1770	0.6-165

cladodes eaten and the mean initial mass of an eaten cladode (Table 8.1).

The mass of cladodes destroyed per larva was 33-37% lower for larvae feeding on O. aurantiaca than for those feeding on O. ficus-indica (calculated from Table 8.1). This difference illustrates the important role of bacterial rotting in increasing the destruction caused by C. cactorum. On O. ficus-indica, because of its large cladodes, bacterial rotting frequently sets in before the larvae finish eating the cladode. O. aurantiaca, however, has much smaller cladodes (Table 8.2) and therefore cladodes are usually eaten by C. cactorum larvae before rotting can set in. Another possible reason why the mass of tissue destroyed per larva is greater on O. ficus-indica than on O. aurantiaca could merely be that larvae consume more of the former host plant, but this appears to be of minor importance in comparison to bacterial rotting.

Dodd (1940 p. 48) recognized the importance of bacteria and fungi in aiding the destruction of prickly pears by C. cactorum. In O. stricta, bacterial soft rots are restricted to the succulent growth and the disease is transported between cladodes on the cuticle of the larva. There is one fungus species that occurs in association with C. cactorum larvae in succulent cladodes of O. stricta but otherwise the action of fungi is restricted to the woody basal cladodes.

On O. ficus-indica and O. aurantiaca respectively, only 2.0% and 3.3% of the cladodes destroyed were woody and only 2.6% and 0.6% of the cladodes destroyed were rooted. Pettey (1948 p. 38-39) showed that the 'fitness' of C. cactorum was considerably reduced (lowered fecundity and larval survival, higher proportion of males) when larvae were reared on woody cladodes. In the field, woody cladodes are usually only consumed when no alternative succulent cladodes can be located by the larvae. I have observed larvae searching for new food when there were uneaten woody cladodes remaining on their original host plant. Using their silken trails, they can retrace their tracks to the original host plant if no better food sources can be located.

To test the extent to which C. cactorum could destroy the different types of cladodes and fruit in O. aurantiaca stands, I artificially inundated a sample of stands with large numbers of larvae. After the larvae had pupated, a sample from each stand was collected and the proportion of eaten and uneaten cladodes and fruit was determined. This investigation formed part of an experiment which aimed to assess the feasibility of releasing C. cactorum inundatively on O. aurantiaca in problem areas (see section 8.5). The percentage destruction that was recorded for each cladode and fruit category is shown in Table 8.3. Only the attached, succulent cladodes were destroyed to any great extent. Combining the maximum values in Table 8.3 with the results presented in Fig. 1.4, only about 40% of cladodes and fruit are available for destruction by C. cactorum in O. aurantiaca stands.

A mean of 1.2% and a maximum of 6.9% of woody rooted cladodes of O. aurantiaca were destroyed in the inundative release stands (Table 8.3). The remark by Pettey (1948 p. 73) that C. cactorum larvae in South Africa do not penetrate or kill the woody rooted cladodes of O. aurantiaca plants is therefore incorrect. In South America,

Table 8.3. Percentage of cladodes and fruit destroyed by C. cactorum larvae in 11 O. aurantiaca stands which had been artificially inundated with larval colonies.

	% destroyed	
	Mean ± SE	Range
Succulent cladodes - attached only	38.5 ± 6.1	8.1-86.2
- unattached included	23.1 ± 4.0	6.4-55.6
Succulent, rooted cladodes	0.6 ± 0.3	0- 2.7
Woody, attached cladodes	5.5 ± 2.0	0-18.3
Woody, rooted cladodes	1.2 ± 0.8	0- 6.9
Attached & loose fruit	11.7 ± 8.3	0-85.7
Rooted fruit	0.5 ± 0.3	0- 2.6

C. cactorum larvae have also been recorded feeding on the woody rooted cladodes of O. aurantiaca (D.C. Lloyd, letter on file, Uitenhage Weed Laboratory, dated 3 August 1962; Silveira Guido 1964). Because of Pettey's remark, C. cactorum on O. aurantiaca in South America has been regarded as being more effective in destroying the woody rooted cladodes of O. aurantiaca than the C. cactorum population established in South Africa (letters of D.C. Lloyd cited by Moran and Annecke 1979). Silveira Guido (1964) recorded that of 135 woody rooted cladodes of O. aurantiaca collected at Carmelo, Uraguay, 1.9% were attacked by larvae of C. cactorum. On the basis of this evidence and the results presented in Table 8.3, it is unlikely that C. cactorum on O. aurantiaca in South America is better able to destroy the woody rooted cladodes of O. aurantiaca than C. cactorum in South Africa. This matter is raised again in the discussion on biotypes of C. cactorum (section 10.3).

C. cactorum larvae tend to feed on the larger succulent cladodes in O. aurantiaca stands. The initial mean mass of an eaten cladode was 16.3g (Table 8.2) whereas the mean mass of all succulent cladodes in O. aurantiaca stands was 8.0g (Appendix 3). This apparent preference for larger cladodes was confirmed by the significantly smaller mean size of the remaining uneaten succulent cladodes in the inundative release stands compared with cladodes of similar but unattacked stands

($Mean_1 \pm SE = 3.0 \pm 0.8$, n=9; $Mean_2 \pm SE = 7.9 \pm 0.9$, n=12; Mann-Whitney U-test, U=9.5, P=0.0007).

8.2 Impact of C. cactorum on the O. ficus-indica population

O. ficus-indica plants within the quadrats at Thursford were surveyed at the end of each season (chapter 2) and the numbers of woody, old-succulent, new-succulent and destroyed cladodes were recorded for each plant. Cladodes were destroyed by C. cactorum, Dactylopius opuntiae, vertebrate herbivores, and senescence. This latter category included old cladodes on large plants which fell to the ground and rotted, as well as cladodes which died from dehydration.

C. cactorum was the most important cause of cladode mortality on O. ficus-indica and over the five C. cactorum generations studied, destroyed 8.3% of available cladodes (Fig. 8.1). The percentage of cladodes destroyed on small plants (ie. with 1-5 cladodes) was not high

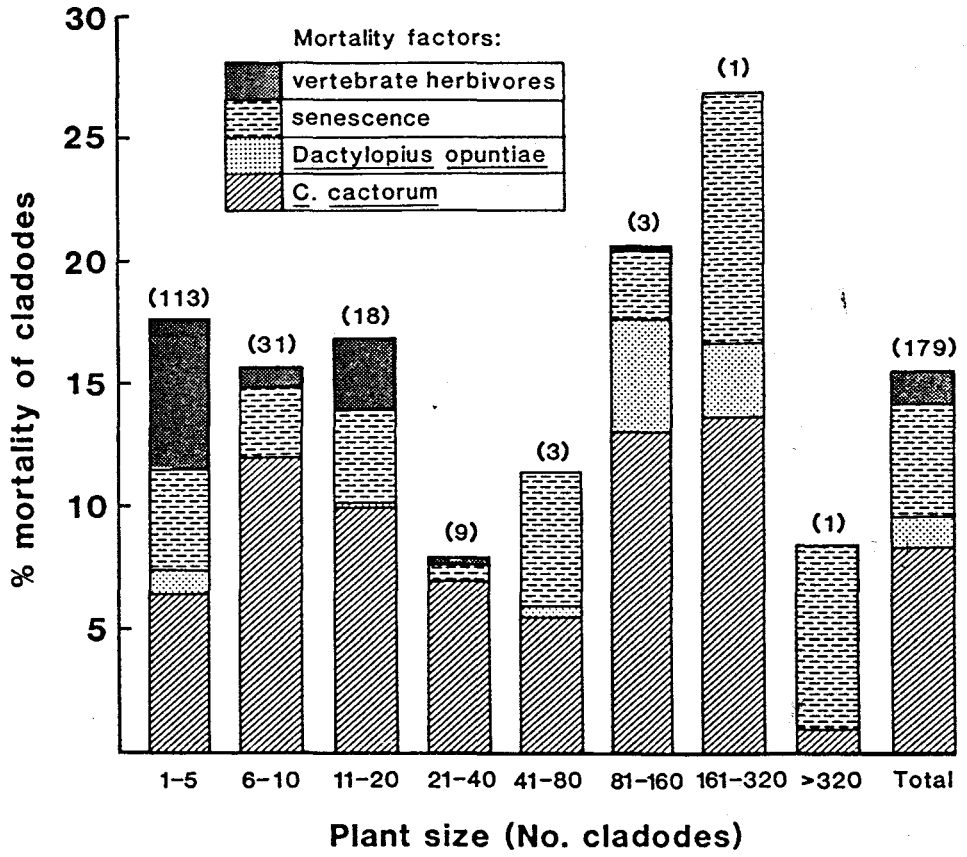

Fig. 8.1. Mortality of O. ficus-indica cladodes in the quadrats at the Thursford study site from summer 1981/82 - summer 1983/84 inclusive. The total number of cladodes available was calculated as the initial number of cladodes plus the number of new cladodes grown within the study period. The numbers in brackets indicate sample sizes of plants.

because a large proportion of them did not have eggsticks laid on them (Figs 4.2 & 4.3). The largest plant, with 498 cladodes, was minimally damaged because few eggsticks were laid on it. D. opuntiae was not an important mortality factor during the study period and only destroyed 1.3% of the available cladodes. However, after the end of the study period, in the winter 1984 and the summer 1984/85 seasons, D. opuntiae became particularly prominent. Senescence caused 4.6% and vertebrate herbivores 1.3% mortality of available cladodes. The vertebrate herbivores affected particularly the small plants and frequently tore them out of the ground. This was especially so during the winter 1982 drought.

Within the study period, no plants with more than five cladodes were totally destroyed by C. cactorum or any other cause. Of the plants with five or less cladodes, only 13.3% were entirely destroyed (Table 8.4). Dehydration (included in senescence) and vertebrate herbivores were the main causes of this plant mortality. C. cactorum and D. opuntiae only destroyed two plants each.

Table 8.4. Mortality of O. ficus-indica plants with five or less cladodes, within the quadrats at the Thursford study site from summer 1981/82 - summer 1983/84 inclusive. No plants with more than five cladodes were totally destroyed.

Cause	No. plants destroyed	% destroyed (n=113)
C. cactorum	2	1.8
D. opuntiae	2	1.8
Senescence	6	5.3
Vertebrate herbivores	5	4.4
Total	15	13.3

Neither C. cactorum alone nor all factors combined kept the O. ficus-indica population in check within the study period (Fig. 8.2). The numbers of new cladodes that grew over the six generations was 1.5 times more than the number of cladodes that were destroyed by all factors combined. New cladodes developed mainly during summer and the number that grew each season was closely related to the amount of

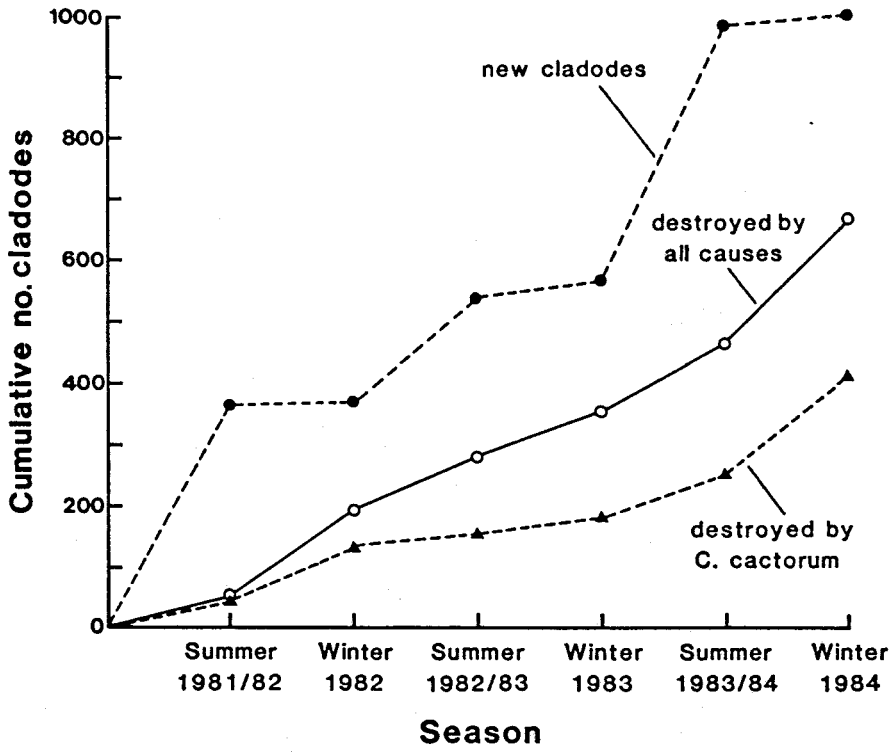

Fig. 8.2. Determination of whether there was a nett increase in the number of cladodes on O. ficus-indica plants within the quadrats at the Thursford study site. The cumulative number of new cladodes that developed over the study period is compared with the cumulative number of cladodes that were destroyed by C. cactorum and by all mortality causes combined. The winter 1984 value for C. cactorum damage was estimated from the number of larvae that entered that generation. The total number of cladodes destroyed in that generation was also estimated.

rainfall. In the summer 1982/83 generation, relatively few new cladodes were produced because of the drought.

Plants which have been attacked by C. cactorum normally compensate by producing regrowth. I do not know to what extent the cumulative increase in new cladodes (Fig. 8.2) was affected by C. cactorum attack. Some plant species overcompensate regrowth in response to herbivory, so that low levels of herbivore attack can result in an apparent increase in plant 'fitness' (Harris 1972, McNaughton 1983). In O. ficus-indica and O. aurantiaca, however, plant 'fitness' is ultimately reduced by C. cactorum attack because the amount of regrowth can be less than the amount of old growth destroyed and because fruit production appears to be lowered when there is compensatory cladode regrowth.

Zimmermann & Malan (1980, 1981), at three sites elsewhere in the Eastern Cape, recorded considerably greater damage to O. ficus-indica

plants by C. cactorum than that recorded above. Between 4.5% and 24.5% of small plants (1-5 cladodes), and between 4.5% and 23.8% of medium-sized plants (6-10 cladodes), were destroyed by C. cactorum larvae each season. Plants with 10-13 cladodes were also sometimes destroyed. There are four possible reasons why C. cactorum caused greater damage to cladodes at these sites than at Thursford: (i) Zimmermann & Malan chose sites where O. ficus-indica was known to have been well controlled by C. cactorum and D. opuntiae; (ii) the size distribution of O. ficus-indica plants at these sites was smaller than that at Thursford. A high proportion of C. cactorum eggs at the Thursford site were laid on large, tree-like plants that could not be destroyed by larvae; (iii) the presence of O. aurantiaca at Thursford appears to lower eggstick densities on O. ficus-indica plants (section 6.13); and (iv) mortality of C. cactorum at Thursford might be greater than at these other study sites.

8.3 Impact of C. cactorum on the O. aurantiaca population.

The total number of O. aurantiaca cladodes destroyed by C. cactorum within the quadrats was estimated for the summer 1981/82 and winter 1982 generations. Less than 5% of the total number of succulent cladodes were destroyed by each generation of C. cactorum (Table 8.5). Clearly, in these two generations, C. cactorum was not an effective biological control agent of O. aurantiaca although it did reduce the chances of cladode dispersal by destroying large succulent cladodes.

Table 8.5. Estimation of the extent of damage by C. cactorum larval colonies to O. aurantiaca succulent cladodes within the quadrats at the Thursford study site.

	Summer 1981/82	Winter 1982
No. hatched colonies	65	105
No. colonies surviving to pupation[1]	32	73
No. cladodes destroyed[2]	947	2161
No. succulent cladodes in quadrats[3]	46105	46105
% of succulent cladodes destroyed	2.1	4.7

[1] Estimated from Table 6.4.

[2] No. cladodes destroyed per colony=29.6 (Table 8.1).

[3] Estimated using equation 7 in Appendix 3.

8.4 Extent of density-dependent larval mortality.

The results presented above show that only a small proportion of O. ficus-indica and O. aurantiaca cladodes were destroyed by C. cactorum larvae at the Thursford study site. The poor performance of C. cactorum was mainly because severe mortality in the other stages of the life cycle (Tables 6.7 & 6.8) lowered larval densities considerably. However, density-dependent larval mortality (from food shortage) could still occur because eggsticks tended to be clumped on plants.

The extent of density-dependent larval mortality was assessed by comparing the number of cladodes required by C. cactorum larvae for development on individual plants/stands of O. ficus-indica and O. aurantiaca, with the actual number of cladodes available. In addition, the theoretical number of cladodes that would have been required on each plant/stand if egg predation had not occurred, was compared with the actual number of cladodes available. When the food requirements of the larvae exceeded the available supplies on the plant, the larvae were regarded as being overcrowded. Woody cladodes have been excluded from the number of cladodes available because of the increased mortality of C. cactorum larvae in these cladodes (section 8.1). Density-dependent mortality of larvae on overcrowded plants could be caused by (i) larvae being forced to feed on the unsuitable woody cladodes; (ii) starvation; and (iii) disease, which tends to be more prevalent under crowded conditions (see Pettey 1948 p. 84).

On O. ficus-indica, overcrowding of larvae only occurred on plants with fewer than five cladodes (Fig. 8.3). No plants were overcrowded in summer and only three were overcrowded in the winter generation. If egg predation had not occurred, a greater proportion of small plants would have been overcrowded (three in summer and seven in winter: Fig. 8.3) but all plants with more than ten succulent cladodes would have had sufficient cladodes for C. cactorum larval development.

Corresponding results for O. aurantiaca (Fig. 8.4) only include those plants which were searched daily for eggsticks and which had eggsticks laid on them. One stand in the summer and three in the winter generation had fewer succulent cladodes than were required for larval

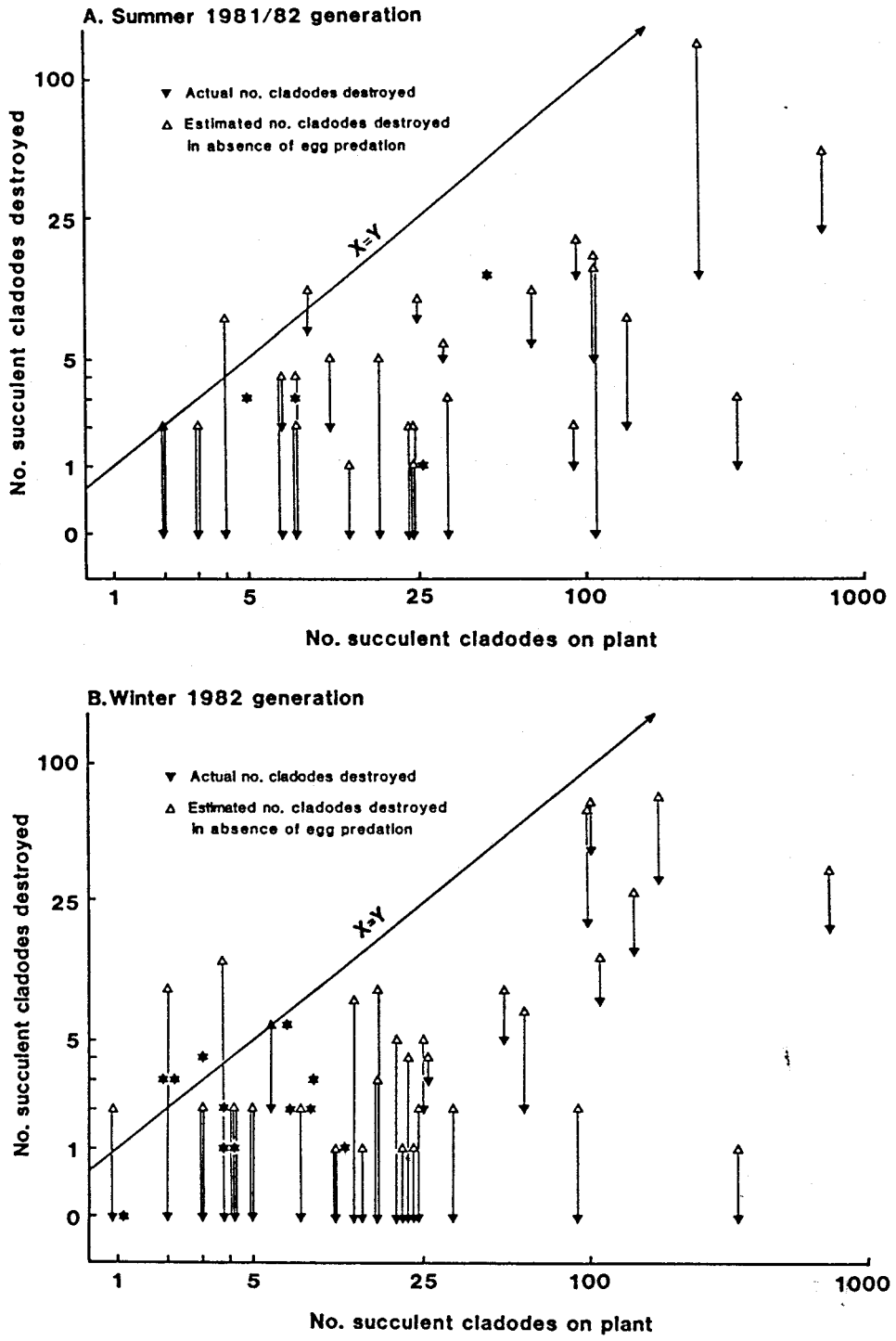

Fig. 8.3. The degree of overcrowding of C. cactorum larvae on O. ficus-indica plants at the Thursford study site in the summer 1981/82 (A) and winter 1982 (B) generations. Overcrowding is assessed by comparing the number of succulent cladodes required for development by larvae on each plant with the number of succulent cladodes that were available on the plant. The line in each graph shows where the number of succulent cladodes required is equal to the number of succulent cladodes on the plant. Points above the line indicate that overcrowding, and consequently density-dependent larval mortality, would have been likely. For each plant, the number of succulent cladodes required by C. cactorum larvae for development (▼) is compared with the estimated number that would have been required if egg predation had been absent (Δ). Each vertical line links a pair of symbols for one plant. Where there was no egg predation on a plant, the pair of symbols have the same location and form a star shape (✱).

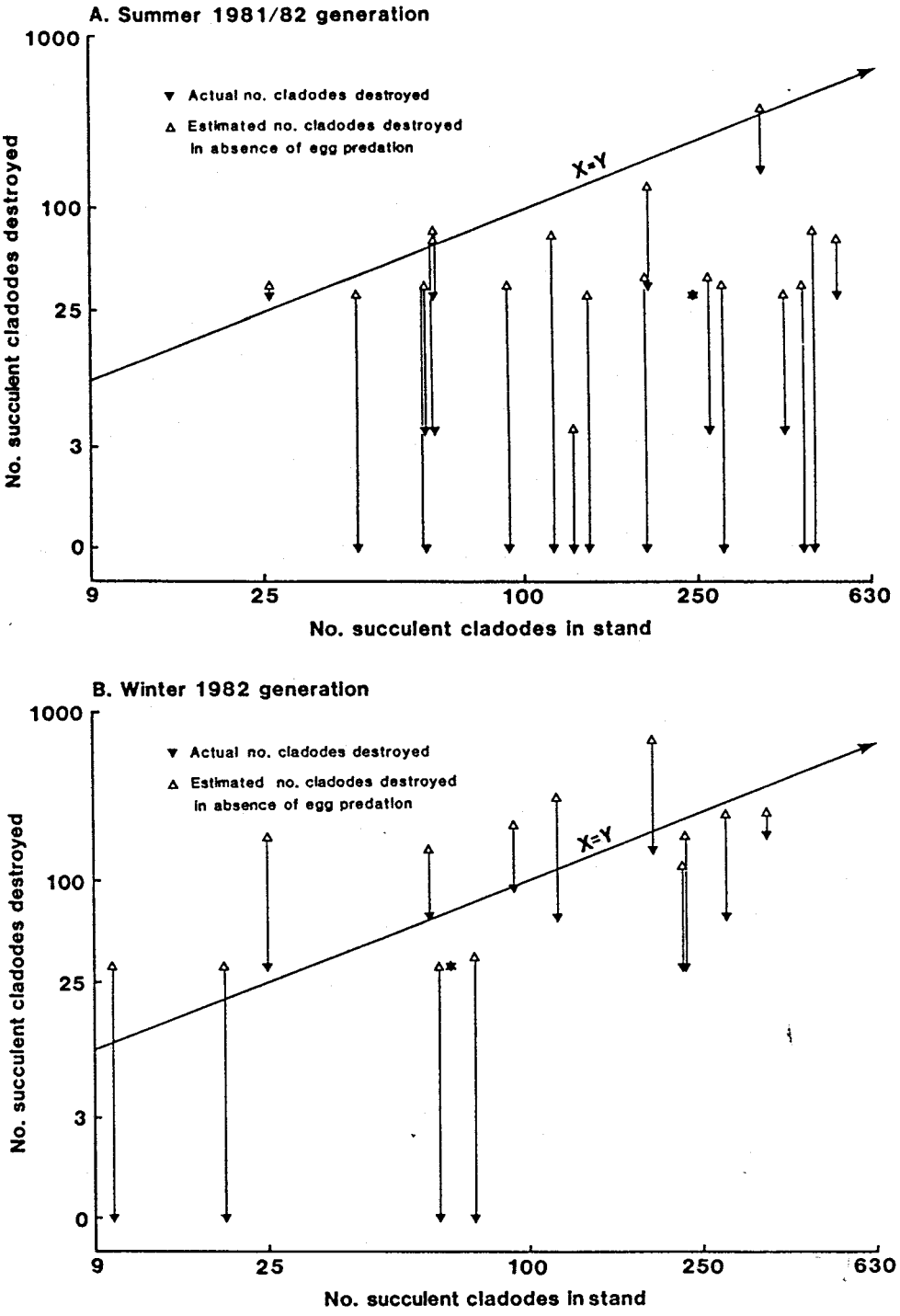

Fig. 8.4. The degree of overcrowding of C. cactorum larvae on O. aurantiaca stands at the Thursford study site in summer 1981/82 (A) and winter 1982 (B) generations. See caption to Fig. 8.3 for a fuller explanation.

development. If egg predation had not occurred, there would have been extensive overcrowding of larvae in the winter but not in the summer generation. The reduced level of damage in summer on O. aurantiaca was a result of the high percentage of colonies that died out after penetration (Table 6.4). Without this larval mortality factor, damage to O. aurantiaca would have been similar in summer and winter.

The results presented in Figs 8.3 and 8.4 therefore suggest that density-dependent larval mortality was not prominent on O. ficus-indica and O. aurantiaca plants at the Thursford study site. If egg predation had not occurred, the extent of damage to O. ficus-indica and O. aurantiaca plants would have been considerably greater but only on O. aurantiaca in the winter generation would density-dependent mortality of C. cactorum larvae have been prominent. In the absence of egg predation, overcrowding of larvae is more likely on O. aurantiaca than on O. ficus-indica plants because of the greater density of eggs oviposited per unit mass of plant (Fig. 4.6 I).

8.5 Inundative release of C. cactorum.

During the winter 1982 C. cactorum generation, I did an experiment at Thursford to investigate whether the inundative release of C. cactorum would be a feasible way of improving its effectiveness as a biological control agent. There were three reasons why this method was considered a possibility.

(i) In section 8.3 it was shown that C. cactorum caused relatively little damage to O. aurantiaca because of its low population numbers and its ineffectiveness in destroying high proportions of the woody rooted cladodes. C. cactorum does, however, destroy the easily dispersed large succulent cladodes. By artificially increasing the population density of C. cactorum, the severity and spread of O. aurantiaca infestations could therefore be considerably reduced.

(ii) O. aurantiaca occurs in high densities in regions with dense bush (section 9.1) yet C. cactorum tends to be rare in these regions,

possibly because of poor dispersal (see p. 49). Inundative release could therefore be used to improve the dispersion of C. cactorum.

(iii) The large-scale distribution campaigns of C. cactorum in Australia and South Africa have illustrated how easily C. cactorum can be reared and released in large numbers. This is mainly because of its colonial habits and especially because of the eggsticks it lays which can be easily handled and distributed (Dodd 1940 p. 115).

A different method from that of Dodd (1940) and Pettey (1948) was employed to rear C. cactorum in large numbers. Final instar larvae were collected from the field in February 1983 and taken back to Rhodes University where they were housed outside in large cages similar to those used by Pettey (1948). Prolonged maintenance of these colonies was not necessary because they were nearing pupation. After pupation, emergence, mating and oviposition, eggsticks were harvested. Shortly before the eggs hatched, they were put onto individual O. aurantiaca cladodes which larvae could then penetrate. The penetrated cladodes were taken into the field and distributed on O. aurantiaca stands.

One of the advantages of the above method was that it avoided the high mortality that occurs during the adult and egg stages of C. cactorum in the field (Tables 6.7 & 6.8). The cladodes containing C. cactorum larvae were also easily handled and could be easily distributed in the field. Dodd (1940) and Pettey (1948) distributed eggsticks placed in paper quills. As they were working with prickly pears, the distribution of larvae in cladodes would not have been feasible because the cladodes are too large.

The possible advantages of inundative release of C. cactorum were assessed in terms of (i) the rate at which larval colonies could be produced and released in the field and (ii) the effectiveness of the method in reducing O. aurantiaca infestations. A total of 2252 eggsticks (=99088 larvae) were produced at an overall rate of 96 eggsticks per active working hour (calculated from Table 8.6). The distribution of the penetrated cladodes in the field was the most time-consuming aspect of the release program (Table 8.6). Penetrated cladodes were distributed on 483 stands and a mean of 4.7 eggsticks were distributed per stand.

Table 8.6. Active working time taken to rear and release C. cactorum larval colonies for the inundative release experiment conducted at Thursford farm.

Activity	Time/100 eggsticks yielded (minutes)	%
Collection of colonies	6.4	10.3
Collection of food for colonies	1.1	1.8
Housing of colonies	2.3	3.7
Collection of eggsticks	9.1	14.6
Collection of cladodes in the field	9.0	14.4
Laying out of cladodes and eggsticks	14.5	23.2
Collection of the penetrated cladodes	2.9	4.6
Release of the penetrated colonies	17.1	27.4
Total	62.4	100.0

The results for mortality of cladodes and fruit on inundative release stands were given in Table 8.3. Although some of the stands were severely damaged, the performance of C. cactorum was disappointing. The larvae might have been detrimentally affected by the drought at the time (Fig. 2.3) but there was no evidence that this was so. In the generation following the inundative release experiment, eggstick densities were higher within the inundative release area than outside it, although this difference was not significant (Table 8.7).

Table 8.7. A comparison of C. cactorum eggstick densities on O. aurantiaca stands inside and outside the inundative release area at Thursford, based on a survey undertaken on 7 December 1983. Only stands greater than $0.2m^2$ were searched. Mann-Whitney U-test (Z=normal deviate of U): n.s. - not significant ($P > 0.05$).

	Inside	Outside
No. of stands searched	20	20
Total no. eggsticks found	90	43
Range	0-29	0-11
Mean no. eggsticks/m^2 ground area of O. aurantiaca	7.3	3.1
Z	$1.45^{n.s.}$	

The emigration of moths from the inundative release area would have 'diluted' this difference in egg density. The results in Table 8.7 suggest that the effects of the released larvae did extend into the next generation. A large proportion of the eggsticks were, however, destroyed by ants. Larvae produced from the surviving eggs attacked some of the regrowth that had resulted from C. cactorum damage in the previous generation.

8.6 Conclusions.

C. cactorum larvae effectively destroy the succulent cladodes of O. ficus-indica and O. aurantiaca plants. Bacterial rotting aids destruction, especially on O. ficus-indica where the cladodes are large enough for rotting to set in before the cladode is completely consumed by the larvae. Both O. ficus-indica and O. aurantiaca have a high proportion of woody basal cladodes which C. cactorum larvae seldom attack. Larval densities on O. ficus-indica and O. aurantiaca plants were rarely at high enough levels to force larvae to feed on the woody portions. C. cactorum population levels were also not high enough to destroy the woody portions of plants indirectly by repeatedly destroying the succulent cladodes over a number of generations. Because of its ineffectiveness in destroying the woody cladodes, C. cactorum rarely killed entire plants.

It must be emphasized that the results presented in this chapter were collected at only one site over a relatively short period. Casual observations suggest that in other parts of the Eastern Cape, the destruction of O. ficus-indica and O. aurantiaca plants can be greater than or less than that determined in this study. For instance, the destruction of O. aurantiaca by C. cactorum at the Andries Vosloo Kudu Reserve is considerably greater than that recorded at Thursford. Most of the O. aurantiaca plants at this locality are in large shaded stands which are favourable for C. cactorum survival. In other parts of the Eastern Cape, C. cactorum appears to be even less effective on O. aurantiaca than at Thursford. This is especially so in areas with a high proportion of small O. aurantiaca stands which are in the open. As far as O. ficus-indica is concerned, the results of Zimmermann and Malan (1980, 1981) have shown that in some areas of the Eastern Cape, C. cactorum is effective in destroying small O. ficus-indica plants.

The inundative release of C. cactorum considerably increased the destruction of O. aurantiaca cladodes but even so only a small proportion of the woody cladodes were destroyed. The inundative release of C. cactorum is not an economically viable control method although it could be useful for improving the dispersion of C. cactorum in certain areas.

9. BIOLOGICAL AND HERBICIDAL CONTROL OF O. AURANTIACA WITHIN THE CONTEXT OF ITS ECONOMIC IMPORTANCE AS A WEED.

This chapter is an attempt to put into perspective the status of C. cactorum as a biological control agent of O. aurantiaca by assessing the status of the target weed itself. One reason for doing this is that it has been assumed throughout this thesis that O. aurantiaca is an economically serious weed to the farmer and yet in most instances I do not believe that this is so. To illustrate this point, a survey was undertaken of Roux's Camp at Thursford to determine the overall extent and density of the O. aurantiaca infestations. The results of this survey were used to make an assessment of the severity of these infestations and the economic feasibility of controlling them with herbicides. In South Africa, herbicides have been the main method of controlling O. aurantiaca and since 1957 have been subsidized by the government at considerable cost (Zimmermann & Moran 1982).

The survey of Roux's Camp was undertaken during the period June-August 1983. The camp was divided into five sectors (Fig. 9.1). Sectors 1-3

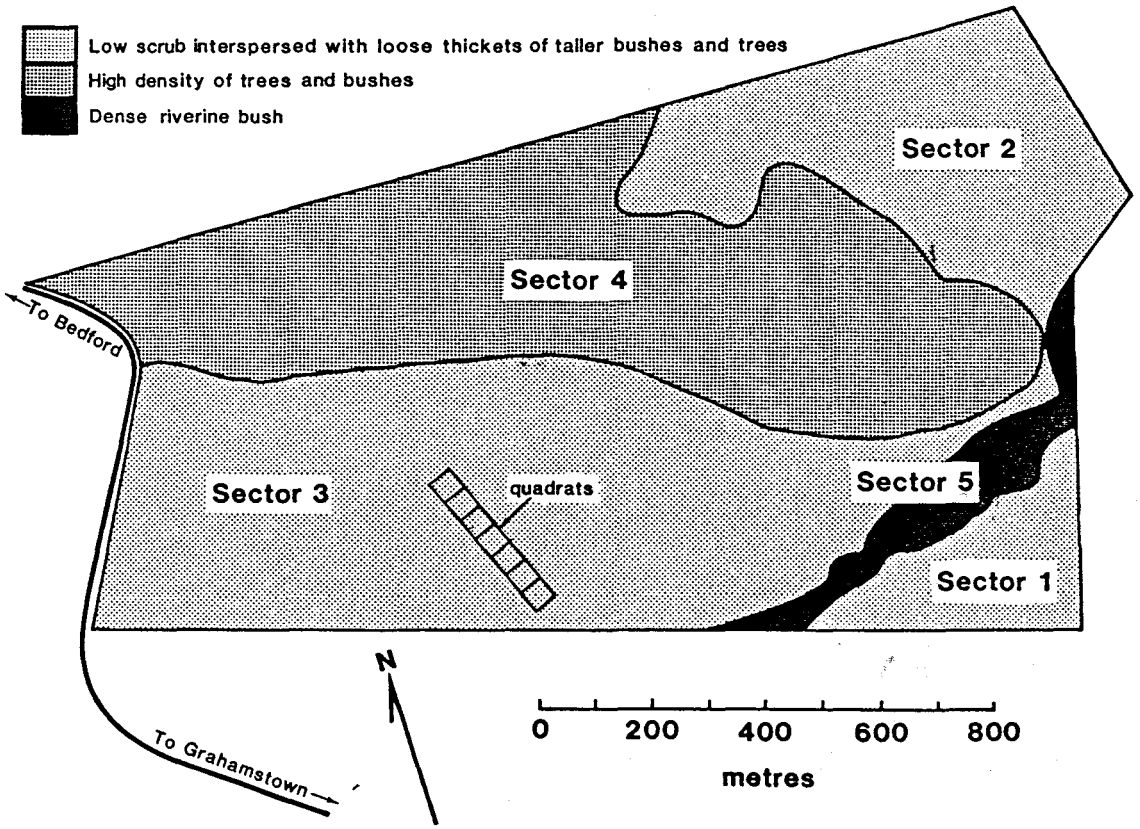

Fig. 9.1. Map of Roux's Camp at Thursford, showing the five sectors it was divided into for the survey of O. aurantiaca infestations. The seven 50X50m quadrats at the study site are also shown.

consisted mainly of low scrub but were interspersed with loose thickets of taller bushes and trees (Fig. 9.2 A & B). The seven 50x50m quadrats were in sector 3 (Figs 9.1 & 2.2). Sector 4 (Fig. 9.2 C) was mostly on a north facing slope, consisted of valley bushveld, and had a higher density of trees and large bushes than sectors 1-3. Sector 5 (Fig. 9.2 A) consisted of dense riverine bush and trees.

The extent of O. aurantiaca infestations was determined separately for each sector using a systematic random sampling method. I walked 50 paces in a specific direction and then threw a sling-shaped object ahead of me. At the site where it landed, a 2x5m quadrat was measured out and the area of each O. aurantiaca stand within the quadrat was determined, as well as a number of other variables (see below). Another 50 paces were taken and the process repeated. After each day's sampling, the results were entered into a computer and in this way it was possible to determine rapidly whether more quadrats were necessary to bring the variability down to an acceptable level. It was decided beforehand that sampling in each sector would continue until the standard error was less than 30% of the mean of the ground area of O. aurantiaca per quadrat. Consequently, sectors with low densities of O. aurantiaca had to be sampled more than those with high densities.

A device for measuring area, illustrated in Fig. 9.3, was used for demarcating each quadrat and for measuring the size of each O. aurantiaca stand. This device consisted of two arms which pivoted on a central, cross-shaped hinge. The distance from the centre of the hinge to the tip of each arm measured one metre and each arm was marked at 0.25m intervals, each 0.25m interval being further sub-divided into 2.5cm segments. At the site of each quadrat, the apparatus was positioned over the place where the sling-shaped object had landed and to avoid biased sampling, was orientated in a northerly direction (direction arbitrarily chosen) using the compass positioned on the apparatus (Fig. 9.3). With the arms of the apparatus positioned at 180^{o} and forming the one side of the quadrat, five metres were paced out from the hinge centre in a northerly direction and from this the perimeter of the quadrat could be determined visually. In dense bush, a tape measure was used to measure the five metres. It was sometimes necessary to peg out the corners of the quadrats, especially when there were many O. aurantiaca stands present. To measure the area of a

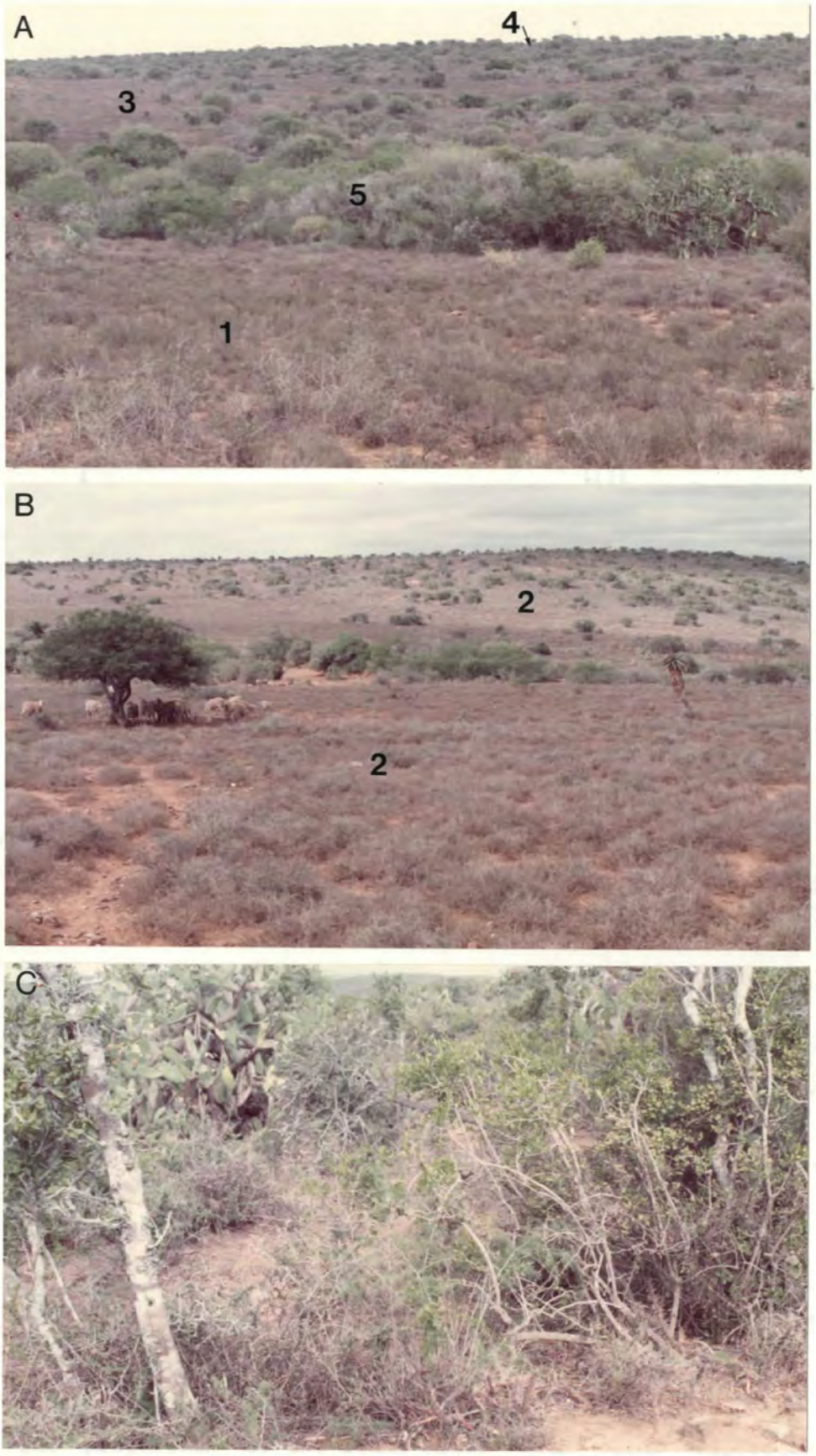

Fig. 9.2. The vegetation in the five sectors of Roux's Camp (see Fig. 9.1). A: sectors 1, 5, 3 & 4. B: Sector 2. C: Sector 4 (an O. aurantiaca stand is in the foreground).

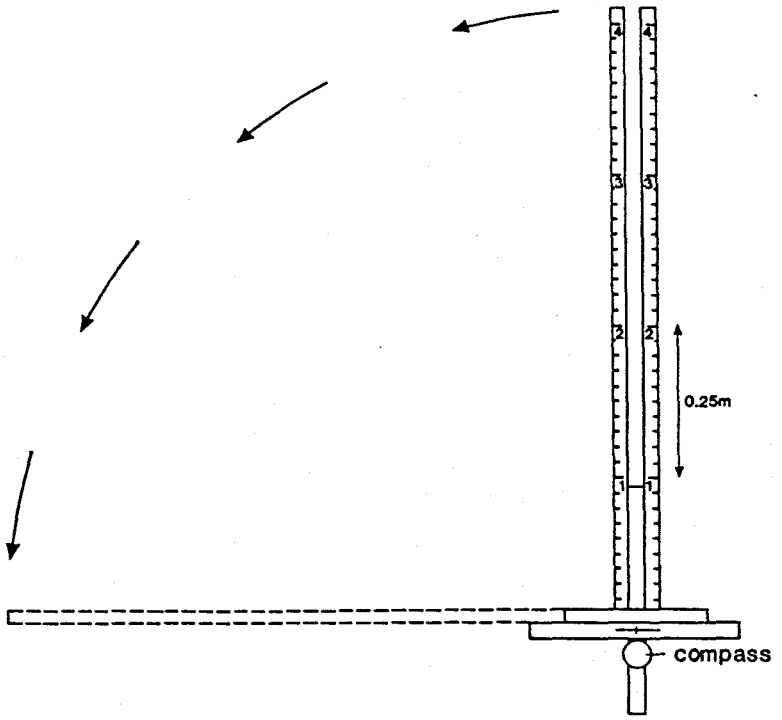

Fig. 9.3. The device used for measuring the areas of quadrats and O. aurantiaca stands.

stand, the apparatus was placed over the stand with the arms perpendicular to one another and the dimensions which contained the stand were noted and multiplied together to give the area in 25X25cm squares. Metal pegs were used to mark one metre distances in the large stands.

The following measurements were recorded for each O. aurantiaca stand found fully or partly within the quadrats.

(i) Area. From this measurement it was later possible to estimate other stand parameters using the equations in Appendix 3.

(ii) The proportion of the O. aurantiaca stand located within the quadrat. Proportions were scored according to five classes: (1) 0.125; (2) 0.125-0.375; (3) 0.375-0.625; (4) 0.625-0.875; (5) 0.875-1.

(iii) The proportion of the stand mixed with other vegetation. A scoring system was used: (1) pure stand; (2) 0.2-0.5 mixed; (3) 0.6-0.9 mixed; (4) completely mixed; (5) pure stand beneath trees.

(iv) The proportion of the stand shaded by trees or large bushes. Proportions were scored according to three classes: (1) open; (2) partially shaded; (3) completely shaded.

In addition to these measurements that were taken of each stand, the percentage vegetation cover in each quadrat was estimated according to seven classes: (1) 0-10%; (2) 11-20%; (3) 21-40%; (4) 41-60%; (5) 61-80%; (6) 81-90%; (7) 91-100%.

The results of this survey are summarized in Table 9.1. Altogether 460 quadrats were set up and 506 stands measured. The total area covered by each sector was calculated from an aerial photograph and from this, results could be expressed as absolute values for each sector.

9.1 O. aurantiaca density in relation to habitat.

The percentage of each sector covered by O. aurantiaca ranged from 0.39-4.09% (Table 9.1) and was closely related to the density of trees and large bushes. This relationship is shown in the significant negative correlation between the percentage area covered by O. aurantiaca in each sector and the percentage of stands that were in the open or among low scrub vegetation (r_s=-0.900; P=0.05; n=5). In sector 5, which consists of riverine bush, soil and water conditions are probably better for plant growth than in the other sectors and would partly explain why the density of O. aurantiaca was highest in this region. However, another likely reason why O. aurantiaca densities are greater in areas of dense bush and trees is that C. cactorum and D. austrinus densities appear to be lower in these habitats (perhaps because of poor dispersal), and mortality of cladodes from dehydration (Zimmermann 1981) is probably also lower because of the more shaded conditions. Large infestations of O. aurantiaca in areas of dense bush commonly occur in the Eastern Cape but are often not noticed because the stands are inaccessible and cryptic.

9.2 Assessment of the severity of O. aurantiaca infestations.

Although as much as 85.4 tonnes of O. aurantiaca were estimated for the entire 218ha camp, this amount covered only 1.1% of the total ground area. The area covered by O. aurantiaca was small in comparison with

Table 9.1. Survey of Roux's Camp at Thursford to determine the extent of O. aurantiaca infestations. The camp was divided into five sectors, shown in Figs 9.1 & 9.2. succ. clads - succulent cladodes.

	Sector no.					
	1	2	3	4	5	Total
SECTOR PARAMETERS						
Area (ha)	12.33	36.41	83.95	76.64	8.67	218.00
% vegetation cover	73	77	66	69	78	72
SAMPLING						
No. $10m^2$ quadrats surveyed	58	133	144	70	55	460
No. stands measured	48	103	123	134	98	506
Standard error as % of mean area O. aurantiaca per quadrat	28.1	27.3	27.2	21.6	29.2	-
O. AURANTIACA POPULATION SIZE						
No. stands -total	10 199	28 199	71 710	146 714	15 446	272 268
-per ha	827	774	854	1 914	1 782	1 249
Ground area (m^2) -total	479	1 683	4 126	14 427	3 546	24 261
- %	0.39	0.46	0.49	1.88	4.09	1.11
No. clads and fruit[1] -total	354	1 203	2 922	9 806	2 910	17 195
(1000's) -per ha	28.7	33.0	34.8	127.9	335.6	78.9
Mass clads & fruit (kg)[2] -total	1 415	5 304	12 927	47 763	18 033	85 442
-per ha	115	146	154	623	2 080	392
No. succ. clads[3] -total	199	639	1 547	4 867	1 226	8 478
(1000's) -per ha	16.1	17.6	18.4	63.5	141.4	38.9
Mass succ. clads (kg)[4] -total	1 086	3 873	9 430	33 278	11 206	58 873
-per ha	88	106	112	434	1 293	270
No. medium & large plants/($20m^2$)[5]	3	3	3	6	30	7
O. AURANTIACA SITUATION						
% stands in the open or among low scrub	88	86	83	74	38	76
% area mixed with other vegetation	67	70	68	67	90	70
% stands completely mixed with other vegetation	54	28	15	43	52	44

[1]Calculated using eq. 8 in Appendix 3. [2]Calculated using eq. 6 in Appendix 3.

[3]Calculated using eq. 7 in Appendix 3. [4]Calculated using eq. 5 in Appendix 3.

[5]Calculated from the total number of cladodes and fruit and the percentage of woody rooted cladodes (=4.5%: Fig. 1.4).

the 28% of ground area that was completely bare (Table 9.1). Although these results suggest that O. aurantiaca has not reduced the carrying capacity of the camp to any great extent, according to weed inspector reports this camp is considered to be "heavily infested" with O. aurantiaca and in need of herbicidal control (Reports on file, Extension Office, Dept. of Agriculture, Grahamstown). The assessment of O. aurantiaca infestations by weed inspectors is based on the non-quantitative criteria proposed by Serfontein (1961). Zimmermann (1981) suggested a more objective method of assessing infestations and his criteria are based on the number of medium- and large- sized plants per $20m^2$ (< 1 plant = light infestation; 1-5 plants = medium infestation; > 5 plants = heavy infestation). According to his criteria, sectors 1-3 have medium infestations, sectors 4 and 5 have heavy infestations and overall there is a heavy infestation of O. aurantiaca in Roux's Camp (Table 9.1). One of the problems with Zimmermann's method of assessment is that although he stresses that quadrats should be taken at random, this is unlikely to occur in practice unless a fixed method of random sampling is specified. As both O. aurantiaca plants and stands have a clumped distribution (Zimmermann 1981), there is a tendency for the human eye to 'home in' on the clumped areas and ignore the fact that there are large areas of uninfested land.

The disparity between the low percentage cover of O. aurantiaca recorded in Roux's Camp (Table 9.1) and the heavy infestation level it has been designated by weed inspectors, brings into question the economic validity of the criteria that have been set for assessing these infestations. A complication in setting these criteria however, is that the severity of an infestation is not only considered in terms of its effect on the carrying capacity of the land but also on the detrimental effect of O. aurantiaca on animals and its potential for dispersal to adjacent camps and farms.

The damage caused by O. aurantiaca cladodes which attach themselves to animals has been overrated. According to the owner of Thursford, he has never had any livestock deaths resulting from injuries from O. aurantiaca spines during the 22 years that he has managed the farm (G.J.H.C. Willetts pers. comm.).

Regarding the degree of dispersal of O. aurantiaca cladodes from infested to non-infested camps, there has been no research done on this subject. Wild animals, especially kudu, are generally blamed by farmers for dispersing cladodes between farms but it is unlikely that this factor is important. In a detailed study of kudu undertaken at the Andries Vosloo Kudu Reserve near Fort Brown, an area which is heavily infested with O. aurantiaca, T. Allen-Rolandson never once found or observed cladodes attached to kudu (pers. comm. to J.H. Hoffmann). A much more important dispersal factor is that cladodes from plants growing beside streams, are washed downstream to other farms during floods (Hosking & Deighton 1979; J.H. Hoffmann pers. comm.). O. aurantiaca densities tend to be highest around river courses as shown by the results for sector 5 (Table 9.1, and see Hosking & Deighton 1979 for New South Wales in Australia). There were some large stands on the banks of the stream running through sector 5 that could be sources for dispersal of cladodes downstream (Fig. 9.4).

Fig. 9.4. An O. aurantiaca stand overhanging a dry stream-bed in sector 5 of Roux's Camp at Thursford.

9.3 Economics and effectiveness of herbicidal control.

Based on the results obtained from the survey of Roux's Camp, the cost of herbicidal control was compared with the value and productivity of the land. (Table 9.2). Land prices for farms in the Eastern Cape are currently highly inflated, for two reasons (J.L. Clacey pers. comm.): (i) with the boom in the angora goat industry, profits of farmers are being spent on buying more land so as to avoid being heavily taxed; (ii) farmers who had their land expropriated by the government for incorporation into the Ciskei, are now wanting to use the money they were paid to buy farms elsewhere in the Eastern Cape. O. aurantiaca infestations on farms apparently have no adverse effect on land prices (J.L. Clacey pers. comm.).

If, theoretically, a herbicidal program was instigated to spray all O. aurantiaca infestations within Roux's camp, at a conservative estimate it would cost about US$7 500 (=R15 000) for labour and herbicides

Table 9.2. The estimated cost of herbicidal control of all O. aurantiaca stands in Roux's Camp (=218ha) compared with the value and productivity of the land. 1 US$ = R0.50.

	Cost per hectare (US$)	Total (US$)
EXPENDITURE ON HERBICIDAL CONTROL		
Labour[1]	6.4	1 395
Herbicides[2]	28	6 104
TOTAL	36	7 499
INCOME		
Value of land[3]	200-250	43 600-54 500
Nett income/year[4]	5	1 090

[1] About 16 man hours spent/ha (H.G. Zimmermann pers. comm.) @ $0.40 per active working hour (G.J.H.C. Willetts pers. comm.).

[2] 223 cladodes sprayed per litre ready mix herbicide (H.G. Zimmermann pers. comm.); 78 876 cladodes/ha therefore 354 l required per ha=1.7 drums (209 l/drum); total cost of each drum = $16.50.

[3] Based on selling prices of nearby farms with similar vegetation (J.L. Clacey pers. comm.).

[4] Based on average nett farm income for farms in the area (J.L. Clacey pers. comm.).

(Table 9.2). This amount is about seven times the nett income that would be derived per year from the camp (Table 9.2). A large-scale program such as this would still not result in the 'eradication' of O. aurantiaca because spray operators are inefficient in locating small stands (Zimmermann 1981). This inefficiency would be further compounded by the dense bush which exists in the camp and the ineffectiveness of herbicides in destroying all the plants in large stands.

Herbicides have been used in Roux's Camp since 1957 and in total 812 forty-gallon (200 l) drums have been applied (Fig. 9.5). Even in 1957, this camp was considered by weed inspectors to have a "heavy infestation" of O. aurantiaca (report on file, Extension Office, Dept. of Agriculture, Grahamstown) and it is still considered to be "heavily infested". It is therefore doubtful whether much benefit has been derived from this expensive herbicidal program. The total of 812 drums that have been used over the 28 years in Roux's Camp is more than twice the estimated amount of 371 drums (Table 9.2) required to spray all present infestations which emphasizes the fact that the estimate in Table 9.2 is a minimum figure.

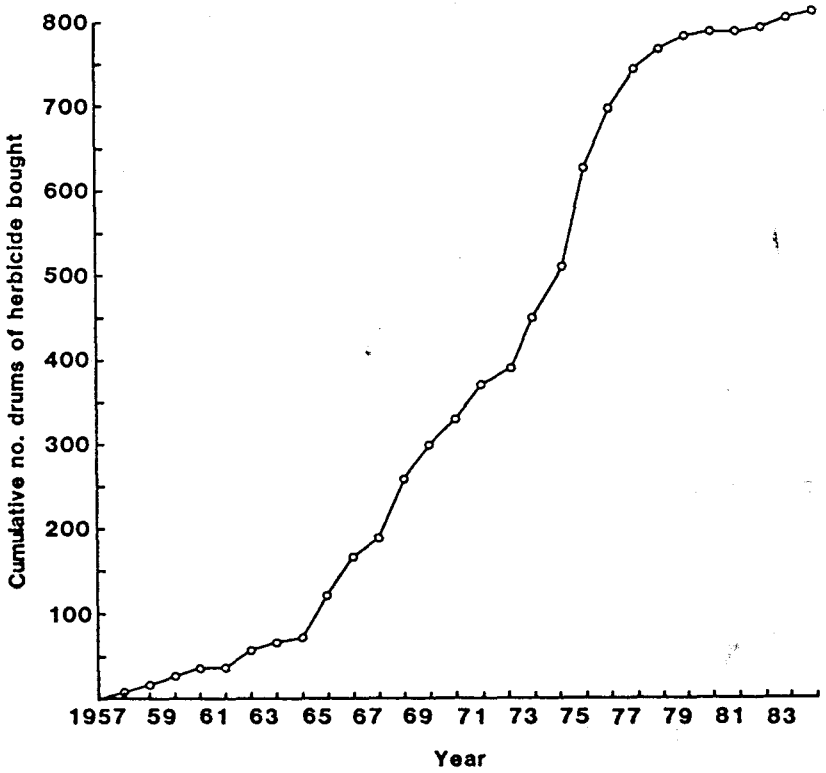

Fig. 9.5. Cumulative number of drums of herbicides used at Thursford since 1957 when herbicidal control was first implemented in South Africa by the State (1 drum = 200 l (1957-1981) or 209 l (1982+)). The decreased use of herbicides after 1975 was because from that time on this site was used for biological control experiments and the farmer was asked not to use herbicides within the study area.

Besides the expense of using herbicides, their effect on the surrounding vegetation needs to be considered. Overall, 70% of the area covered by O. aurantiaca in the camp was mixed with surrounding vegetation (Table 9.1). The use of herbicides is also in conflict with biological control because the large stands sprayed are also the ones which have the highest densities of D. austrinus (Zimmermann 1979, 1981) and C. cactorum (Fig. 4.5).

9.4 Conclusions.

O. aurantiaca is overrated as a weed problem and the present 'strategy' for its control is not based on sound economic criteria. The results presented above show that the so-called heavy infestation of O. aurantiaca in Roux's Camp at Thursford covers only 1.1% of the total surface area and therefore has a negligible effect on the carrying capacity for grazing animals. On the other hand, the high percentage of bare ground (28%) illustrates that overgrazing is of much greater concern as it has severely reduced the carrying capacity and has also increased soil erosion. If the efforts and expenditure that are devoted to the herbicidal control of O. aurantiaca were instead redirected to this much greater problem, the economic benefits would probably be considerably greater. Final succession shrubs that appear after overgrazing and which are inedible to livestock (eg. Relhania genistaefolia (L.) l'Herit. and Elytropappus rhinocerotis (L.f.) Less.) form a high percentage of the surface area in Roux's camp (pers. obs.). The importance of O. aurantiaca is insignificant in comparison to these 'indigenous weeds'. The situation at Roux's Camp is not exceptional but one which is common throughout the Eastern Cape.

It could be argued that although herbicidal control is not cost-effective in the short term, it is an investment in that it is preventing O. aurantiaca infestations from reaching levels where control would be essential but considerably more expensive. However, biological control by D. austrinus is particularly effective at high densities (Pettey 1948; Zimmermann 1981) provided that the insect is well dispersed.

Herbicidal control is considered important as a means of reducing the dispersal of O. aurantiaca from infested to non-infested areas. As

discussed above, the main dispersal agent appears to be water. An effective way to reduce this dispersal would be to spray all O. aurantiaca stands along the flood margins of rivers. In Roux's Camp, these stands appear to have escaped both herbicides and biological control as they are hidden among the riverine bush. This is probably so in other O. aurantiaca-infested regions. The use of herbicides in riverine situations however, could cause water pollution.

Zimmermann (1981) has stressed the need for an integrated approach to the control of O. aurantiaca. As far as possible, biological control should be given priority to herbicidal control as it is cheap and not destructive to the environment. D. austrinus has proved to be an effective biological control agent (Pettey 1948; Zimmermann & Moran 1982) and if the levels of acceptability for O. aurantiaca infestations were based on economic criteria, the value of D. austrinus would be more widely recognized. When C. cactorum in Australia reduced the vast, dense O. stricta infestations to isolated plants and small stands, it was considered an enormous success. O. aurantiaca in South Africa, in most infested areas, is at similarly low levels already and yet even more is expected from the biological control agents. Probably the main reason for these unrealistic expectations is that many landowners and government officials still believe that O. aurantiaca can be 'eradicated'. The results in Tables 9.1 & 9.2 show that eradication of O. aurantiaca is an impractical and unfeasible control strategy. If herbicides were not subsidized by the government, and a more flexible policy was adopted by the government towards the control of O. aurantiaca, a realistic economic threshold for O. aurantiaca would soon be set by the land owners themselves. O. aurantiaca is South Africa's most expensive pasture weed (Zimmermann & Moran 1982) but probably not its most serious. The strategy for O. aurantiaca control in the future should centre on enhancing the effectiveness of D. austrinus and using more specialized methods for curbing cladode dispersal such as destroying the much-neglected streamside infestations.

10. DISCUSSION

The successful establishment of C. cactorum in different parts of the world (Fig. 1.1) has shown that it is able to survive a wide range of environmental conditions. The findings in this study, however, have shown that although C. cactorum is established on O. ficus-indica and O. aurantiaca in South Africa, its performance as a biological control agent has been detrimentally affected by characteristics of the climate, host plants and natural enemies.

Three topics are considered in this discussion. The first concerns the oviposition behaviour of C. cactorum in relation to its survival. This subject has bearing on the second topic which is an assessment of the factors affecting the population dynamics of C. cactorum in Australia and South Africa. The population dynamics of C. cactorum have been discussed extensively in the literature and an attempt is made to summarize the various viewpoints that have been expressed and relate these to the findings in this study. The final topic considered is the possible use of alternative biotypes of C. cactorum for the biological control of O. aurantiaca in South Africa.

10.1 Oviposition behaviour of C. cactorum in relation to its survival.

Selection for traits in the oviposition behaviour of a lepidopteran would presumably be affected by how well the eggs were positioned for maximizing juvenile survival and by how much of the female's total egg complement was laid. It was suggested in chapters 4 and 5 that these two aspects might be in conflict with one another: greater discrimination in oviposition site selection could decrease the oviposition rate which, if time and energy were limiting and adult mortality was high, could decrease the chances of the female laying her full egg complement. A number of oviposition models have been proposed in which the optimization of oviposition has been considered in terms of both foodplant suitability for the progeny and the searching time available for oviposition (Levins & MacArthur 1969; Jaenike 1978; Courtney 1982 b, 1983).

Theoretically, oviposition rates could be increased by: (i) timing emergence to coincide with favourable weather conditions; (ii) mating

soon after emergence; (iii) emerging with well-developed eggs so that the onset of oviposition is not prolonged; (iv) clumping the eggs (egg clumping could increase oviposition rate because it reduces the number of times that a female has to locate new oviposition sites - Stamp 1980; Courtney 1984); and by (v) increasing the range of host plant species on which eggs are laid (Courtney 1982 a,b).

The traits listed above that could increase oviposition rate, occur in C. cactorum. Emergence of C. cactorum usually occurs on warm evenings (Dodd 1940 pp. 117,119; Pettey 1948 pp. 63, 64). Females emerge with a high proportion of well-developed eggs, thus avoiding a prolonged delay in the onset of oviposition (Fig. 3.7). Eggs are clumped so that usually only 3-4 oviposition sites need to be located by each female (Table 3.8) thus possibly decreasing searching time. In addition, egg clumping probably decreases 'handling time' of each egg because the number of times that a female has to position herself over a spine is considerably reduced. Another likely reason for egg clumping in C. cactorum is that it enables larvae to penetrate the plant together (frontispiece, B) which probably increases larval penetration efficiency.

Oligophagy in C. cactorum may partly be an adaptation for increasing oviposition rate. If at the Thursford study site, C. cactorum had only oviposited on the more suitable host plant, O. ficus-indica, and not on O. aurantiaca, the density of host plants (in terms of cross-sectional area) would have been decreased by 61% (calculated from Appendix 5). This could increase the time taken by the moth to locate a host plant and hence increase the probability of pre-oviposition egg mortality. Group penetration of the host plant, a consequence of egg clumping, probably facilitated the expansion of the host range of C. cactorum as it enabled larvae to penetrate successfully most of the tree-like Opuntia species.

The absence of feeding in adults of C. cactorum might be an evolutionary consequence of high adult mortality. High adult female mortality could have resulted in selection for a high oviposition rate over a short period. The need for females to supplement their energy resources would therefore diminish and would explain why they have non-feeding

mouthparts. Non-feeding in males could also presumably have resulted from high adult mortality.

Hebert (1983), in an analysis of the degree of clumping of forest moth larvae, found that the larvae of nearly one third of the species with non-feeding adults were regularly found in large aggregations (ie. eight or more larvae per group), whereas larvae of species with feeding adults were usually either solitary or in small groups. An analysis by Hebert (1983) of the moth fauna in the British Isles showed a similar pattern. Hebert's findings suggest that non-feeding in the adult stage evolved in response to reduced energy requirements for oviposition, resulting from egg clumping. Although the biology of C. cactorum supports the findings of Hebert, within the cactus phycitids there are species which lay their eggs singly yet have non-feeding adult stages. This is so in Tucumania tapiacola which in addition has a higher fecundity than C. cactorum (see Hoffmann 1982).

The clumping of eggs in eggsticks is found in the phycitid genera Cactoblastis, Melitara and Olycella (Mann 1969). Two reasons can be suggested to explain why eggs are clumped on top of one another to form 'sticks' rather than being clumped in some other shape. Firstly, the positioning of eggs on top of one another is probably the best way of fitting a large number of eggs on the end of a cactus thorn (predation by ants is probably lower for eggs oviposited on spines rather than on the cladode surface) and secondly, Birch (1971) suggested that the shape of the eggstick camouflages it so that it resembles a cactus spine. Of course there might not be any adaptive reason for the shape of the eggstick and it could merely be the consequence of selection for egg clumping per se.

In summary, C. cactorum females have a high rate of oviposition, possibly an adaptation for reducing the chances of them dying before laying their full egg complement. Time limitations on the female might limit the extent to which eggsticks can be laid in sites where the probability of progeny survival is greatest. Poor oviposition site selection might also occur because females are not ideally adapted to responding to good oviposition cues and because oviposition behaviour could be detrimentally affected by proximal factors such as wind (see chapter 5). The limited supply of energy available to the female could

also affect oviposition behaviour. For instance, in chapter 4 it was suggested that one of the reasons why eggsticks were clumped on plants was that females laid their first eggstick(s) before dispersing because the mass of these eggs increased the energy cost of flight. The clumping of eggsticks on plants has also been construed as a population regulation mechanism in C. cactorum and this viewpoint is discussed in the following section.

10.2 The population dynamics of C. cactorum in Australia and South Africa.

The population dynamics of C. cactorum on O. stricta in Australia have been widely discussed in the literature (eg. Nicholson 1947, 1958; Andrewartha & Birch 1954; Andrewartha 1957; Pimentel et al. 1963; Monro 1967, 1975; Birch 1971; Osmond & Monro 1981; Wiens 1976; Caughley & Lawton 1981; Murray 1982). This is because C. cactorum is a spectacular field example of the density-dependent interrelationship between a herbivore and its host plant (interpreted by some authors as the inter-relationship between a predator and its prey). Although this is such a famous example, the initial spectacular fluctuations of C. cactorum and O. stricta in Australia soon after C. cactorum was initially released, were never quantified, and instead reliance has had to be placed on descriptions and before-after photographs. Dodd (1940 pp. 4-5) described the sequence of population changes in C. cactorum and O. stricta as follows:

"1925-27: The introduction of Cactoblastis cactorum; its large scale rearing, and first liberations...
1928-30: The mass distribution of Cactoblastis throughout the pear areas and its rapid multiplication.
1930-32: The general collapse and destruction of the original stands of prickly-pear, brought about by enormous numbers of Cactoblastis...
1932-33: Heavy regrowth replaces the original prickly-pear; the Cactoblastis population suddenly diminishes as a result of starvation following the collapse of the primary pear.
1933-35: The recovery of Cactoblastis and the consequent destruction of the regrowth...
1935-40: The virtual complete control of the major pest pears by

Cactoblastis. The former dense pear country reclaimed and brought into production."

Caughley & Lawton (1981) attempted to model the initial fluctuations of C. cactorum and O. stricta in the 10 years after C. cactorum was released, but their model is inadequate because it fails to show the fluctuation(s) in the C. cactorum population that resulted from the regrowth of O. stricta plants that were not destroyed during the first wave of attack.

Two explanations have been proposed to explain why, after the crash of O. stricta to much lower levels, C. cactorum has apparently remained in equilibrium with O. stricta, rather than totally exterminating it.

(i) Nicholson (1947, 1958) and later Andrewartha & Birch (1954) interpreted the equilibrium between C. cactorum and O. stricta as a "game of hide and seek" between herbivore and plant. For instance Nicholson (1947) remarked:

"The end result which still persists, is that prickly pear is scattered in small isolated groups, with wide intervals between them. In a few of these Cactoblastis is still to be found, and these are generally doomed to complete destruction because Cactoblastis is able to increase rapidly in numbers on them. In other groups of prickly pear, which have not so far been found by Cactoblastis the pear tends to spread; but sooner or later is found by the moth, and the destruction of these groups is achieved shortly afterwards. In the meantime seed is scattered in new places, so maintaining the existence of prickly pear. Consequently, within Queensland as a whole, there is a low density of prickly pear, and a low density of Cactoblastis, which vary little from year to year; but at the same time is in continual fluctuation in space."

(ii) Monro (1967) showed that C. cactorum eggsticks were clumped on O. stricta plants. He suggested that:

"...Cactoblastis cactorum conserves its food by clumping its egg-sticks rather than laying them at random. As a result, more larvae die of starvation and more plants escape completely or with a light infesta-

tion than expected if eggs were laid at random. The proportion of eggs wasted by clumping increases rapidly with population per unit-resource and thus tends to stabilize the numbers of herbivore and host-plant...The behavioural response which produces egg-clumping most probably has a conservative genetic basis which prevents individual selection from favouring egg-spreading over egg-clumping genotypes."

While it is clear that clumping of eggs on plants can increase population stability by increasing the extent of density-dependent mortality (see Myers 1976), it is doubtful that, as Monro (1967) suggested, clumping evolved as a population regulation mechanism. In later papers, Monro and co-workers refrain from mentioning this group-selectionistic argument (see Monro 1975; Osmond & Monro 1981; Myers, Monro & Murray 1981) and instead interpreted the clumping of eggsticks in terms of other factors which would affect oviposition behaviour. Myers et al. (1981 p. 12) state:

"The contagious distribution of Cactoblastis eggs can be accounted for by more frequent oviposition on large, green plants in the vicinity of previously attacked plants. Heterogeneity in the "quality" of food plants can lead to a clumped egg distribution which may be associated with stabilization of the insect population. However, the oviposition choices can be explained by individual selection. Moths choose plants of better quality for oviposition, even though at high density many plants will still be overcrowded. There is also a large random component in the oviposition behaviour and many smaller and yellower plants also receive eggs. This "noise" prevents the extinction of the moths which would occur if they were too good at selecting the highest quality plants."

The view expressed by Myers et al. (1981), quoted above, provides a more realistic assessment of the behavioural basis for egg clumping, although the last sentence still implies the operation of group selection. The "noise" which is mentioned is probably not a random effect or an evolved population stabilization mechanism but is more likely due to proximal limitations imposed on the oviposition behaviour of C. cactorum females, discussed in the previous section of this chapter.

Although the results presented by Monro (1967) show that eggstick clumping would increase larval density-dependent mortality, his estimates of "eggstick wastage" are probably in excess of the wastage that would actually have occurred. Monro calculated that a C. cactorum larval colony from an average sized eggstick requires four O. stricta cladodes for development. On this basis, Monro assumed that if there were fewer than four cladodes per eggstick on each plant, all the larvae would die. This is an invalid assumption for two reasons. Firstly, not all colonies that emerge from eggsticks survive penetration. Dodd (1940 p. 134) recorded that 15% of hatched colonies on "green succulent" O. stricta died during penetration. Secondly, the hatching of eggsticks on plants does not occur simultaneously because the eggsticks were originally laid at different times (see Dodd 1940 pp. 117-119). Consequently, on overcrowded plants (ie. plants with insufficient food for the number of larvae present), larvae that hatch early are more likely to be able to complete their development than those hatching later. Even if larvae on a plant do emerge synchronously, they tend to develop at different rates (Dodd 1940 pp. 130-131) so that, on overcrowded plants, those larvae developing at a high rate are more likely to survive than those developing at a slower rate. It is therefore unlikely that all larvae would die from starvation on over-crowded plants.

The "hide and seek" model proposed by Nicholson (1947, 1958) and Andrewartha & Birch (1954) and the clumped distributions of C. cactorum eggs observed by Monro (1967), are probably both factors that contribute to stabilization of C. cactorum and O. stricta populations. Myers et al. (1981) remark that in Australia, O. stricta populations occurring in pastures are more transient than those in woodland situations apparently because the pasture plants have a higher nitrogen content than those in woodlands. Myers et al. (1981 p. 12) conclude that "perhaps the Cactoblastis are able to temporarily exterminate Opuntia in the open pastures. Therefore the dynamics of pasture populations might better be described by the "hide and seek" model while the woodland populations are at "equilibrium" and serve as refuges for the Cactoblastis". Osmond & Monro (1981) did a simulation of the C. cactorum-O. stricta populations in which they showed that both eggstick clumping and adult dispersal were necessary to stabilize the system.

In summary, it seems that the main factors contributing to the stability and persistence of the C. cactorum-O. stricta populations are: (i) eggstick clumping on plants (not an adaptation for population stabilization but a consequence of other factors affecting oviposition behaviour); (ii) temporary survival of populations of O. stricta resulting from temporary reductions in C. cactorum densities (the "hide and seek" model); and (iii) the resistance of some plants to attack, especially those with low nitrogen levels (see also Pimentel et al. 1963; White 1981).

At Thursford, in South Africa, the population ecology of C. cactorum appears to be markedly different from that occurring in most parts of Australia. Low evening temperatures during the winter generation oviposition period can severely reduce the realized fecundity of females (Fig. 3.5, Table 3.7) and, throughout the Eastern Cape, this appears to be the key factor causing fluctuations in C. cactorum populations between summer and winter generations (see Fig. 6.5). Natural enemies cause "imperfect density-dependent mortality" (sensu Milne 1957) in the egg and pupal stages (p. 110, p. 92) and in addition markedly reduce the overall abundance of C. cactorum (Tables 6.7 & 6.8). Egg predation by ants was a particularly important mortality factor that markedly reduced initial larval densities. Food limitation (compounded by egg clumping) is the main density-dependent factor that would limit C. cactorum population size at Thursford, but food was rarely limiting to larvae because mortality in other stages of the life cycle considerably reduced larval densities (Figs 8.3 & 8.4). The findings of Zimmermann & Malan (1980, 1981) suggest that at other sites in the Eastern Cape, density-dependent larval mortality might operate to a greater extent than at Thursford.

The population dynamics of C. cactorum in South Africa are therefore complex and contrast with the apparently simple herbivore-plant interaction, portrayed in the literature and discussed above, that occurs between C. cactorum and O. stricta in Australia. Host plant resistance and natural enemies do reduce C. cactorum population numbers in Australia but apparently not to the same extent as in South Africa (see section 6.15).

Monro (1975) considered that the effects of climate on C. cactorum populations were similar in South Africa and Australia but this is not so. The phenology of C. cactorum in South Africa differs from that in Australia (Table 3.1). As mentioned above, the realized fecundity of C. cactorum females in South Africa is reduced by low evening temperatures in the winter generation (Fig. 3.5, Table 3.7) and is rarely reduced by lethally high temperatures in the summer generation. In most parts of Australia, however, realized fecundity is not severely affected by low evening temperatures in the winter generation but is quite often affected by lethally high temperatures in the summer generation (p. 31, Dodd 1940 p. 127).

Although there are clearly differences in the effect of climate on C. cactorum biology in South Africa and Australia, the overall effect of climate on C. cactorum population dynamics in these two countries is difficult to assess on the basis of available evidence in Dodd (1940), Pettey (1948) and this study. Indirect evidence, however, based on a comparison of the distribution of C. cactorum in South Africa and Australia, suggests that climate may affect the population dynamics of C. cactorum differently in each country. C. cactorum has a wide distribution in Eastern Australia, ranging from about 21°-38°S (Dodd 1940, Murray 1982). The effectiveness of C. cactorum in destroying O. stricta tends to be lower in its more southerly range in Australia. For instance, C. cactorum was considerably more effective in destroying O. stricta in Queensland than in New South Wales (Dodd 1940 p. 8). Wilson (1960) states: "In isolated areas in the north of the State (New South Wales) and in all areas below about 32° south, Cactoblastis cactorum was quite ineffective". This poor performance of C. cactorum in its southerly range has been attributed both to poor host plant condition (Dodd 1940 p. 142) and to climate (Dodd 1936; Dodd 1940 p. 142; Anon. 1967; Sands & Harley 1981). It is remarkable that in South Africa, the main concentration of O. ficus-indica and C. cactorum is in the Eastern Cape, mainly south of 32°S. The poor performance of C. cactorum on O. ficus-indica in the Eastern Cape therefore matches the poor performance of C. cactorum on O. stricta at a similar range of latitudes in Australia.

The inefficiency of C. cactorum in destroying the basal woody cladodes of O. ficus-indica and O. aurantiaca plants is the ultimate factor that

would prevent C. cactorum from being an effective biological control agent of these weeds in South Africa. However, except on small plants, larval densities are rarely at levels where larvae are forced to feed on the woody cladodes (Figs 8.3 & 8.4). Natural enemies and the effects of climate reduce larval densities to the extent that plants are not usually repeatedly heavily attacked and weakened as is the case with O. stricta plants in Australia. The adverse effects of host plant resistance, climate and natural enemies all appear to be greater on average in South Africa than Australia and all these factors have therefore been important in explaining the poorer performance of C. cactorum in South Africa.

10.3 The possible use of alternative biotypes of C. cactorum for the biological control of O. aurantiaca in South Africa.

In the context of this study, 'biotypes' are loosely defined as populations of the same species that are genetically different, especially with regard to biological attributes important in biological control (González et al. (1979) and Diehl & Bush (1984) review the usage of the term biotype). There have been a number of cases in both insect and weed biological control where selection of a suitable biotype has increased the effectiveness of biological control (Smith 1941; Messenger & van den Bosch 1971; MacKauer 1976; Messenger et al. 1976; Room et al. 1981).

Several entomologists have observed in South America that C. cactorum causes extensive destruction to O. aurantiaca plants. This has led to the suggestion, first proposed in 1962 by D.C. Lloyd (letter on file, Weeds Laboratory, Uitenhage) that there are biotypes of C. cactorum in South America that are more effective at destroying O. aurantiaca (especially the underground woody cladodes) than the populations presently established in South Africa and Australia.

R.E. McFadyen has examined variation in morphological characters of C. cactorum larvae collected from different sites and from different host plants in South America. In a letter to H.G. Zimmermann dated 13 January 1982 she included a key which distinguished four different biotypes of C. cactorum. The morphological differences between the four biotypes are based firstly on whether the black dorsal bands on

the abdomen are complete or divided and secondly, on the presence or absence of dorsal, lateral, ventral, mesothoracic and prothoracic spots. Differences between larvae from different C. cactorum populations are not surprising in view of the wide distribution of this insect in South America (Fig. 1.1).

Even though there are morphologically distinguishable biotypes of C. cactorum in South America, there is no proof that any of these are more effective in destroying O. aurantiaca than the biotype that occurs in South Africa and Australia. In section 8.1, it was shown that C. cactorum in South Africa can destroy the woody rooted cladodes of O. aurantiaca plants. The extent of this destruction was not great but it was similar to the destruction of O. aurantiaca cladodes by C. cactorum recorded in South America by Silveira Guido (1964). C. cactorum has been recorded causing extensive mortality of the above-ground portions of O. aurantiaca plants in South America (Moran & Annecke 1979), but this could be because of favourable environmental conditions rather than because these larvae are better adapted genetically to O. aurantiaca than the larvae in South Africa. According to J.H. Hoffmann (pers. comm.) the destruction of O. aurantiaca by C. cactorum at the Andries Vosloo Kudu Reserve in the Eastern Cape of South Africa is comparable to the destruction of this plant by C. cactorum that he observed in South America.

The effectiveness of a new biotype of C. cactorum on O. aurantiaca in South Africa would not only depend on its ability to destroy the woody rooted cladodes of O. aurantiaca but would also depend on its ability to survive natural enemies and weather. It is unlikely that any biotype of C. cactorum could avoid the heavy predation of eggs by ants on O. aurantiaca in South Africa (see Table 6.1). E.C.G. Bedford, in a letter to D.C. Lloyd (dated 16 August 1962, on file at the Weeds Laboratory, Uitenhage), expressed the opinion that it was not worth importing new biotypes of C. cactorum to South Africa because of the detrimental effects of natural enemies. There might possibly be a biotype of C. cactorum in South America that is climatically better suited to South African conditions than the established biotype. However, density-dependent mortality by natural enemies might reduce the advantages of such a trait.

If a biotype of C. cactorum was discovered that was more effective on O. aurantiaca than that already established in South Africa, there would be considerable problems in establishing it successfully. In all likelihood this new gene pool would be absorbed into the large established gene pool and there would be little change in the status of C. cactorum on O. aurantiaca.

In summary, the investigation of alternative biotypes of C. cactorum in South America for possible introduction to South Africa against O. aurantiaca does not seem to be a feasible option for improving the level of biological control of this weed. The considerable expense that would be incurred in an attempt to locate and establish an alternative biotype would not be warranted in view of the low probability of such a project being successful.

10.4 Conclusions.

Neither the use of inundative control methods nor the importation of new biotypes of C. cactorum are feasible methods for improving the performance of C. cactorum as a biological control agent of O. aurantiaca in South Africa. In chapter 9 it was argued that O. aurantiaca is overrated as a weed problem in South Africa and that the government-sponsored herbicidal control programme for controlling this weed is not based on economically or ecologically sound criteria. While there are some aspects of research on the biological control of O. aurantiaca that still require attention (Moran 1981; Moran & Zimmermann 1985), the ultimate solution to the "problem" of O. aurantiaca as a weed lies in better land management and more realistic government policies, rather than in expectations for improved biological control.

11. SUMMARY

1) In this study, the effectiveness of C. cactorum as a biological control agent of O. ficus-indica and O. aurantiaca was assessed in terms of its oviposition behaviour, survival, and ability to destroy its host plants.

2) All field work was undertaken on Thursford farm, 21km NW of Grahamstown. O. ficus-indica and O. aurantiaca both occur at this site.

3) The oviposition behaviour of C. cactorum was assessed from the position of eggsticks on O. ficus-indica and O. aurantiaca plants in the field. The following factors were found to influence the number of C. cactorum eggsticks laid on plants: (i) plant size; (ii) proximity of plant to moth emergence sites; (iii) cladode condition; and (iv) plant conspicuousness. Eggsticks were significantly clumped on plants and this was thought to be a consequence of the host plant searching behaviour of C. cactorum females and not an evolved population regulation mechanism as proposed by Monro (1967).

4) The selection of a site for oviposition by C. cactorum on O. ficus-indica and O. aurantiaca plants was found to be affected by (i) height of cladodes above ground; (ii) cladode condition and (iii) shelter from wind. Succulent cladodes were the favoured sites for oviposition; 24% of O. ficus-indica cladodes were woody yet less than 3% of eggsticks were laid on these cladodes.

5) Life tables were compiled for C. cactorum on O. ficus-indica and O. aurantiaca in the summer 1981/82 and winter 1982 generations. Predation by at least eight species of ants caused 55-78% mortality of eggs. Adult mortality (=pre-oviposition egg mortality), calculated from the life tables, was 45% and 84% in summer and winter generations respectively. The detrimental effect of low temperatures on realized fecundity was the main reason for the high adult mortality in the winter generation and, throughout the Eastern Cape, appears to be the major cause of the fluctuations in C. cactorum densities between summer and winter generations.

6) Although there was evidence of a partial, positive response by ants to C. cactorum egg densities on both a spatial and temporal level, season appeared to be of overriding importance in affecting the extent of egg predation.

7) A comparison of the ecology of C. cactorum on O. ficus-indica and O. aurantiaca showed that: (i) while there was no significant difference between the host plants in the density of C. cactorum eggs laid per unit cross-sectional area of host plant, the density of eggs laid per unit mass of host plant was significantly greater on O. aurantiaca than on O. ficus-indica; (ii) the mass of cladodes destroyed per C. cactorum larva was 33-37% lower on O. aurantiaca than on O. ficus-indica, probably because the smaller cladodes on O. aurantiaca reduced the amount of bacterial rotting associated with larval feeding; (iii) the larval development period and the period taken for all larvae in each colony to pupate, was significantly longer on O. aurantiaca than on O. ficus-indica; (iv) fecundity was significantly higher on O. ficus-indica than on O. aurantiaca although the range of fecundities recorded for each host plant was similar; (v) egg predation by ants was significantly greater on O. aurantiaca than on O. ficus-indica; (vi) larval mortality on the two host plants was similar in the winter generation but in the summer generation, it was greater on O. aurantiaca because 24% of larval colonies on this host plant died out. Overall, the survival of C. cactorum on O. aurantiaca was 55% and 60% of that on O. ficus-indica in summer and winter generations respectively. Because of this difference in survival between host plants and because C. cactorum females show no marked preference for either host plant species, a greater density of eggs was laid on O. aurantiaca than would have been the case if O. ficus-indica plants had not been present at the site.

8) Over six generations, C. cactorum larvae destroyed 8.3% of the O. ficus-indica cladodes and only two of the plants. The number of new O. ficus-indica cladodes that appeared over these six generations was 1.5 times as many as the number of cladodes destroyed by C. cactorum and other mortality factors. On O. aurantiaca, an estimated 2.1% and 4.7% of succulent cladodes were destroyed by C. cactorum in summer 1981/82 and winter 1982 generations respectively.

9) The inundative release of C. cactorum on O. aurantiaca infestations was investigated but found to be unfeasible because the increased destruction caused by C. cactorum did not warrant the effort that was involved.

10) The investigation of alternative biotypes of C. cactorum in South America for possible introduction to South Africa against O. aurantiaca is not considered to be a viable option for improving biological control because of (i) the detrimental effect of generalist predators, particularly ants, on C. cactorum populations in South Africa and (ii) the problems involved in establishing a new biotype among the established C. cactorum populations. There is also no clear evidence that there are biotypes of C. cactorum in South America that are better adapted for destroying C. cactorum infestations than the biotype currently established in South Africa.

11) The woody basal cladodes of O. ficus-indica and O. aurantiaca plants are resistant to C. cactorum attack and are rarely destroyed by the larvae. Host plant resistance is the ultimate factor limiting the performance of C. cactorum as a biological control agent in South Africa. However, the findings in this study show that as a result of natural enemies and weather, larval densities at the study site rarely reached levels where larvae were forced to feed on the resistant woody cladodes. The detrimental effects of host plant resistance, natural enemies and weather all appear to be greater in South Africa than in most of the regions occupied by C. cactorum in Australia.

12) Results of a survey of a 218ha camp on Thursford farm illustrate how O. aurantiaca has been overrated as a weed problem. The present strategy for O. aurantiaca control is not based on sound economic or ecological criteria. It is suggested that a solution to the O. aurantiaca problem in South Africa lies in better land management and more realistic government policies, rather than in expectations for improved biological control.

APPENDIX 1.

Recorded host plants of Cactoblastis cactorum showing for each species: (i) the region of origin (see Britton & Rose (1919) for details); (ii) the regions in which it has been recorded as a host of C. cactorum; and (iii) the main references to it as a host plant of C. cactorum. The native host plant species of C. cactorum are listed separately from other plant species adopted as hosts. Opuntia is in the tribe Opuntieae and Cleistocactus in the tribe Cereeae. Opuntia salmiana is in the subgenus Cylindropuntia whereas all the other Opuntia host plants are in the subgenus Platyopuntia.

Host plant species	Origin	Regions where recorded as host plant of C. cactorum	References
NATIVE HOST PLANTS:			
1) Opuntia salmiana Parmentier	South America	South America	Dodd (1936); Mann (1969)
2) O. aurantiaca Lindley	South America	South America Australia South Africa	Dodd (1936); Mann (1969) Dodd (1940); Mann (1970) Pettey (1948)
3) O. retrorsa Spegazzini	South America	South America	Mann (1969)
4) O. utkilio Spegazzini	South America	South America	Dodd (1936); Mann (1969)
5) O. discolor Britton & Rose	South America	South America	Dodd (1936); Mann (1969)
6) O. brunnescens Britton & Rose	South America	South America	Dodd (1936); Mann (1969)
7) O. delaetiana Weber	South America	South America	Dodd (1936); Mann (1969)
8) O. vulgaris Miller (includes O. monacantha Haworth)	South America	South America Australia South Africa Mauritius	Mann (1969) Moran & Zimmermann (1985) Pettey (1948) Greathead (1971)
9) O. bonaerensis Spegazzini	South America	South America	Dodd (1936); Mann (1969)
10) O. canterai Arechavaleta	South America	South America	Mann (1969)
11) O. cordobensis Spegazzini	South America	South America	Dodd (1936); Mann (1969)
12) O. quimilo Schumann	South America	South America	Dodd (1936); Mann (1969)
13) Cleistocactus sp.	South America	South America	Mann (1969)
ADOPTED HOST PLANTS:			
14) O. repens Bello	West Indies	West Indies	Garcia Tuduri et al. (1971)
15) O. triacantha (Willdenow) Sweet	West Indies	West Indies	Simmonds & Bennett (1966); Garcia Tuduri et al. (1971)
16) O. tuna (L.) Miller	West Indies	Mauritius	Greathead (1971)
17) O. antillana Britton & Rose	West Indies	West Indies	Garcia Tuduri et al. (1971)
18) O. tardospina Griffiths	North America	South Africa	Pettey (1948)
19) O. stricta Haworth (includes O. inermis De Candolle)	North America	Australia South Africa	Dodd (1940); Mann (1970) Moran & Zimmermann (1985)
20) O. dillenii (Ker-Gawler) Haworth	North America West Indies Northern-South America	West Indies	Simmonds & Bennett (1966); Garcia Tuduri et al. (1971)
21) O. lindheimeri Engelmann	North America	West Indies	Simmonds & Bennett (1966)
22) O. tomentosa Salm-Dyck	North America	Australia	Dodd (1940); Mann (1970)
23) O. ficus-indica (L.) Miller (includes O. megacantha Salm-Dyck)	North America	South America Australia South Africa West Indies Hawaii	Dodd (1936); Mann (1969) Pettey (1948) Pettey (1948) Garcia Tuduri et al. (1971) Fullaway (1954)
24) O. spinulifera Salm-Dyck	North America	South Africa	Pettey (1948)
25) O. streptacantha Lemaire	North America	Australia	Dodd (1940); Mann (1970)
26) O. moniliformis (L.) Haworth	West Indies	West Indies	Garcia Tuduri et al. (1971)
27) O. rubescens Salm-Dyck	West Indies	West Indies	Garcia Tuduri et al. (1971)

APPENDIX 2. ESTIMATION OF O. FICUS-INDICA PARAMETERS

1) Estimation of cladode parameters. Method: (i) succulent and woody cladodes were collected in the field and taken back to the laboratory; (ii) the dimensions and mass of each cladode were recorded as well as the number of areoles; (iii) the data was filed on computer and equations were determined for estimating each parameter. The equations are listed below.

(i) Estimation of the mass of cladodes.

Succulent cladodes: $y/x = 0.680 \pm 0.010$ SE (n=54) therefore

$$y = 0.6795x \quad (1)$$

Woody cladodes: $y/x = 0.774 \pm 0.035$ SE (n=12) therefore

$$y = 0.7737x \quad (2)$$

where x = (length X breadth X height) of cladode (cm^3) and
y = mass of cladode (g).

(ii) Estimation of the number of spined areoles on cladodes.

Succulent cladodes:

$$y = 53.6(\log_{10}x) - 40.3 \quad (3)$$

(r^2=0.638; n=51)

where x = mass of cladode (g) and
y = number of spined areoles.

(iii) Estimation of the surface area of cladodes.

Mean ($\pm$ SE) no. spined areoles/100cm^2 cladode surface =
15.4 ± 1.3 (n=12) (4)

(Measured by placing a 10X12cm square randomly on each cladode and determining the number of areoles it contained).

Therefore $y = x/0.154$ (5)

where x = number of spined areoles (equation 3) and
y = surface area of cladode (cm^2).

2) Estimation of plant size parameters. Method: (i) dimensions of cladodes were measured in situ on 25 selected plants in the field (for large plants, the dimensions were taken of cladodes on one branch and of the woody trunk cladodes); (ii) the mass of each of these cladodes was estimated using equations 1 & 2 above; (iii) the mean mass of new-succulent, old-succulent and woody cladodes on each plant was calculated; (iv) the mean mass and the number of each cladode type was recorded on computer and equations were determined for estimating the mass of succulent cladodes and all cladodes on plants. The total number of spined areoles on the succulent cladodes was estimated using equation 3. To determine the proportionate mass of woody cladodes for Fig. 1.3, the mean mass of woody and succulent cladodes was calculated for each plant size class and multiplied by the respective number of cladodes in each class; the equations listed below were not used because they are not sufficiently accurate for small plants.

Equations were determined for two plant categories: (i) seedling plants and plants with more than three cladodes; (ii) plants derived from broken off cladodes, that had less than four cladodes. This approach was necessary because small plants derived from broken off cladodes had larger cladodes than seedling plants with a similar number of cladodes. The derived equations are listed below.

(i) Estimation of the mass of succulent cladodes.

For seedling plants and plants with more than 3 cladodes:

$$\log_{10}y = 2.588(\log_{10}x) - 0.374(\log_{10}x)^2 - 1.564 \qquad (6)$$
$(r^2=0.936;\ n=25)$

For plants derived from broken off cladodes, that had less than 4 cladodes:

$$y = 0.42x \qquad (7)$$

where x = number of succulent cladodes and
y = mass of succulent cladodes (kg).

(ii) Estimation of the mass of all cladodes.

For seedling plants and plants with more than 3 cladodes:

$$\log_{10}y = 2.919(\log_{10}x) - 0.398(\log_{10}x)^2 - 1.959 \quad (8)$$
$(r^2=0.960;\ n=25)$

For plants derived from broken off cladodes, that had less than 4 cladodes:

$$y = 0.42x \quad (9)$$

where x = total number of cladodes and
y = total mass of cladodes (kg).

(iii) Estimation of the number of spined areoles.

For seedling plants and large plants:

$$\log_{10}y = 1.454(\log_{10}x) - 0.110(\log_{10}x)^2 - 0.356 \quad (10)$$
$(r^2=0.985;\ n=25)$

For plants derived from broken off cladodes, that had less than 4 cladodes:

$$y = 0.1x \quad (11)$$

where x = number of succulent cladodes and
y = number of spined areoles (100's).

(iv) Estimation of the surface area of succulent cladodes.

$$y = x/1540 \quad (12)$$

where x = number of spined areoles on plant (calculated from equations 10 or 11) and
y = surface area of cladodes (m^2).
The value of 1540 is derived from equation 5.

APPENDIX 3. ESTIMATION OF O. AURANTIACA PARAMETERS

1) Estimation of cladode parameters. Method: same as that used for O. ficus-indica cladodes (see Appendix 2). The equations are listed below.

(i) Estimation of the mass of cladodes.

Succulent cladodes: $y/x = 0.660 \pm 0.012$ SE (n=40) therefore

$$y = 0.66x \quad (1)$$

where x = (length X breadth X height) of cladode (cm^3) and
y = mass of cladode (g).

Mean mass of a succulent cladode = 8.0g
(range of means for 39 stands= 1.9-24.9)

(ii) Estimation of the number of spined areoles on cladodes.

Succulent cladodes: $y = 1.35x - 0.00716x^2 + 20.12$ (2)
(r^2=0.867; n=40)

where x = mass of cladode (g) and
y = number of spined areoles.

Therefore, an average-sized cladode of 8g has an estimated 30.5 areoles.

(iii) Estimation of the surface area of cladodes.

Mean ($\pm$ SE) no. spined areoles/100 cm^2 cladode surface =
81.7 ± 6.0 (n=12) (3)

(Measured by placing a 1.5X10cm square randomly on each cladode and determining the number of cladodes it contained).

Therefore $y = x/0.817$ (4)

where x = number of spined areoles (equation 2) and
y = surface area of cladode (cm^2).

Therefore an average-sized cladode of 8g has an estimated surface area of $37cm^2$.

2) Estimation of stand size parameters. The following method was used for analysing each of fifty-nine O. aurantiaca stands in the field: (i) the ground area of the stand was measured using the apparatus illustrated in Fig. 9.3; (ii) all the cladodes and fruit in the stand were collected and placed in paper packets. Seven categories of cladode and fruit were distinguished (depending on their condition and type - see Fig. 1.4) and a packet was allocated for each category; (iii) in the laboratory the total number and mass of cladodes in each category was recorded; (iv) data was recorded on computer from which equations were determined for estimating size parameters of stands from the ground area. The stands were collected in the field during July 1983 when there was no new growth of cladodes and there was a high proportion of unattached cladodes (Fig. 1.4). In the determination of equations for estimating parameters for succulent attached cladodes, half the unattached cladodes (proportion arbitrarily chosen) were therefore included as compensation.

(i) Estimation of the mass of succulent cladodes.

$$\log_{10}y = 0.1516(\log_{10}x)^2 + 0.9511 \quad (5)$$
($r^2=0.929$; n=59)

where x = ground area of stand (cm^2)
y = total mass succulent attached cladodes plus half the mass of succulent unattached cladodes (g).

(ii) Estimation of the total mass of cladodes and fruit.

$$\log_{10}y = 0.1613(\log_{10}x)^2 + 0.9835 \quad (6)$$
($r^2=0.960$; n=59)

where x = ground area of stand (cm^2)
y = total mass of cladodes and fruit (g).

(iii) Estimation of the number of succulent cladodes.

$$\log_{10} y = 0.1266(\log_{10} x)^2 + 0.4205 \quad (7)$$
$(r^2=0.890;\ n=59)$

where x = ground area of stand (cm^2)
y = total number succulent attached cladodes plus half the number of succulent unattached cladodes.

(iv) Estimation of the total number of cladodes and fruit.

$$\log_{10} y = 0.1408(\log_{10} x)^2 + 0.5550 \quad (8)$$
$(r^2=0.926;\ n=59)$

where x = ground area of stand (cm^2)
y = total number cladodes and fruit.

(v) Estimation of the number of spined areoles.

$$y = 0.305x \quad (9)$$

where x = number succulent cladodes (equation 7)
y = number spined areoles (100's).
The value of 0.305 is the mean number of areoles per cladode (100's) and is derived from equation equation 2.

(vi) Estimation of the surface area of succulent cladodes.

$$y = x/0.817 \quad (10)$$

where x = number spined areoles (equation 9)
y = surface area of succulent cladodes (cm^2).
The value of 0.817 is the mean number of areoles/cm^2 and is derived from equation 3.

APPENDIX 4. THE EFFECT OF TEMPERATURE ON EGG AND LARVAL DEVELOPMENT PERIODS IN C. CACTORUM

Results for egg and larval development periods of C. cactorum at the Thursford study site were presented in chapter 3. An attempt was made to express these development periods in temperature time-units (ie. physiological time), the methods of calculation and results of which are presented below.

The following method was used to express development periods of eggs and larvae in temperature units. Hourly temperatures for each day, measured on the thermohydrograph at Thursford over the summer 1981/82 and winter 1982 generations, were entered into the computer. From this data set, a program was designed to determine the total day-degrees for each day, at different temperature thresholds. The temperature threshold is the temperature below which no development of the insect takes place. Egg and larval development periods, determined in the field, were calculated in terms of day-degrees at each of the thresholds. The true threshold of development was regarded as that which resulted in the least variation in the day-degree development periods between summer and winter generations (over a range of thresholds from 7-15^{o}C). This empirical method assumes a linear relationship between rate of development and temperature which is not always found in insect development (eg. Hilbert & Logan 1983 a,b).

1) Egg development periods.

For temperature thresholds ranging from 7-15^{o}C, mean day-degree incubation periods of winter generation C. cactorum eggs were from 1.18-1.26 times longer than those of the summer generation. This failure to equate summer and winter egg incubation periods in terms of day-degrees was possibly because egg development rate was not a linear function of temperature.

In order to determine the relationship between egg development rate and temperature, incubation periods were measured at five different constant temperatures ranging from 17.5 to 34.4^{o}C, under constant lighting conditions. It was not possible to keep relative humidity constant

over this temperature range but it was maintained at at least 40%. An attempt was also made to measure the incubation period at 13°C but this was unsuccessful because the eggs all failed to hatch.

Egg incubation periods decreased curvilinearly with increased temperature except at 34.4°C where there was a slight increase (Fig. A4.1). Only 19.3% of the eggs at 34.4°C hatched. The slight increase in incubation period at this temperature might have been because of stress on the developing embryos, possibly from desiccation, rather than because of a temperature effect. Dodd (1940) recorded a minimum incubation period of 18 days for C. cactorum whereas the minimum period recorded in Fig. A4.1 is only 22 days (at 29°C) which suggests that the incubation period could perhaps decrease further above 29°C. Murray (1982) presents some puzzling results in which he

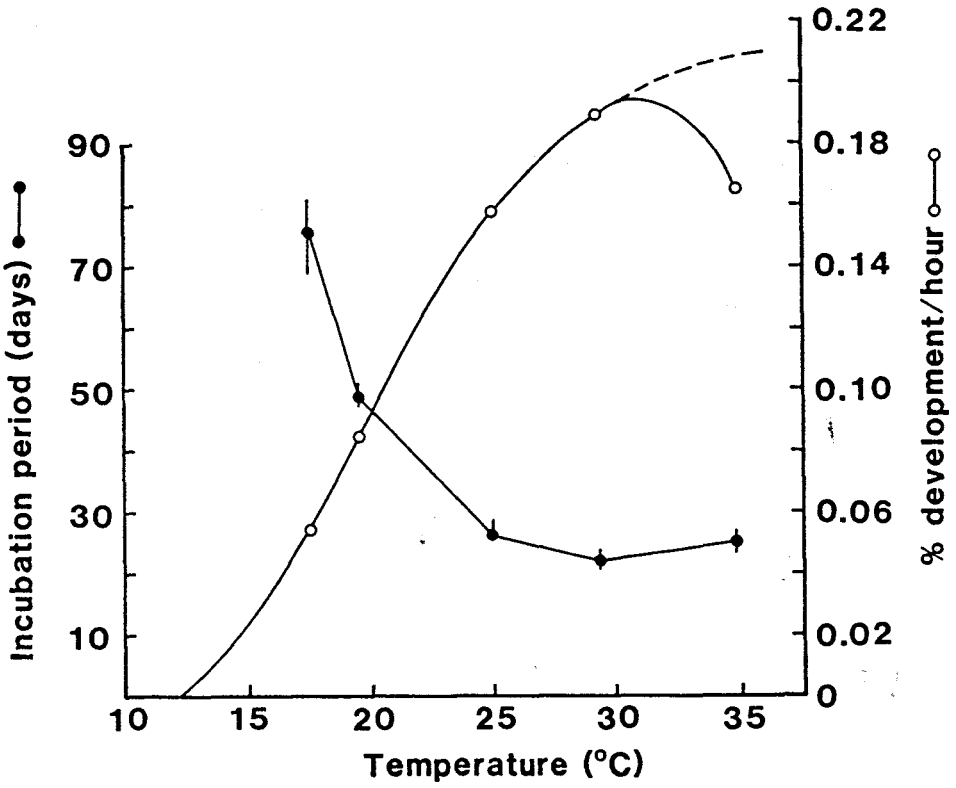

Fig. A4.1. Incubation periods of C. cactorum eggs under constant temperature conditions (•——•). Vertical lines indicate ranges. The reciprocal of the development period in hours, expressed as a percentage, has been plotted to show the rate of development (o——o). The extrapolation of the development rate curve below 17.5°C and above 30°C is based on arbitrary decisions (see text). Above 30°C, the broken line represents the maximum probable rate of development, assuming that the value recorded at 34.4°C was reduced by a non-temperature factor (see text), while the solid line represents the probable rate of development above 30°C, assuming that the value at 34.4°C was solely due to temperature.

recorded a minimum egg incubation period of seven days for an isolated C. cactorum population located in Victoria, Australia. This value lies well below the minimum possible incubation period that could realistically be extrapolated from the curve in Fig. A4.1. Under controlled alternating temperature conditions in the laboratory (12 hours dark/12 hours light, 11°C/28°C) he recorded a minimum of 14 days for this Victoria population but 27 days for the population from further north in Hunter Valley, N.S.W.. He considered genetic divergence to be the cause of this difference. At a constant 18°C, Murray recorded an incubation period of 62 days for the Victoria population which is comparable with the results in Fig. A4.1. Murray's results are therefore not consistently lower than the results in Fig. A4.1 and the reason for these discrepancies is uncertain.

Expressed as percentage development per hour, the development rate of C. cactorum eggs was not linear but decreased slightly from between 20 and 30°C and markedly above 30°C (Fig. A4.1). The form of the development rate curve below 17.5°C and above 30°C was uncertain but, for the purposes of fitting these results to those obtained in the field, an attempt has been made in Fig. A4.1 to extrapolate the incubation period and development rate curves over these ranges. The lower threshold of development is assumed to be 12°C. Above 30°C, the broken line represents the maximum probable rate of development, assuming that the value at 34.4°C was decreased by a non-temperature factor.

The results for development rate in Fig. A4.1 were fitted to the field data on egg incubation periods by substituting each hourly temperature recorded at Thursford with the corresponding percentage egg development shown in Fig. A4.1. Thus if an hourly temperature at Thursford was 25° the corresponding percentage egg-development for that hour according to the results in Fig. A4.1 would be 0.16%. The hourly development rates were then summed for the period of development of each eggstick. If the effects of ambient temperature on C. cactorum egg development in the field were the same as those measured under constant temperature conditions, then the sum of the hourly development rates over the incubation period of an eggstick in the field would be 100%.

In Fig. A4.2, the estimated percentage development of each field eggstick is plotted against the mean temperature recorded over the egg development period. The mean estimated 'percentage development' of summer generation eggsticks was 78.9% and that of winter generation eggsticks, 97.2%. From these results it is clear that even after accounting for the non-linear relationship of C. cactorum egg development rate with temperature (Fig. A4.1), it has still not been possible to equate the summer and winter egg development periods with one another. The estimated percentage development of winter generation eggsticks is close to 100% but that in summer is well below this level. This was so even though the egg development rate was assumed to continue increasing above 30°C (see broken line in Fig. A4.1). A probable explanation for the variability in results in Fig. A4.2 is that the ambient temperatures recorded on the thermohydrograph were different from those experienced by the eggsticks. Eggsticks would have received a greater amount of radiation from the ground and the sun than the thermohydrograph because they are positioned closer to the ground and are usually unshaded. The effects of ground radiation and direct

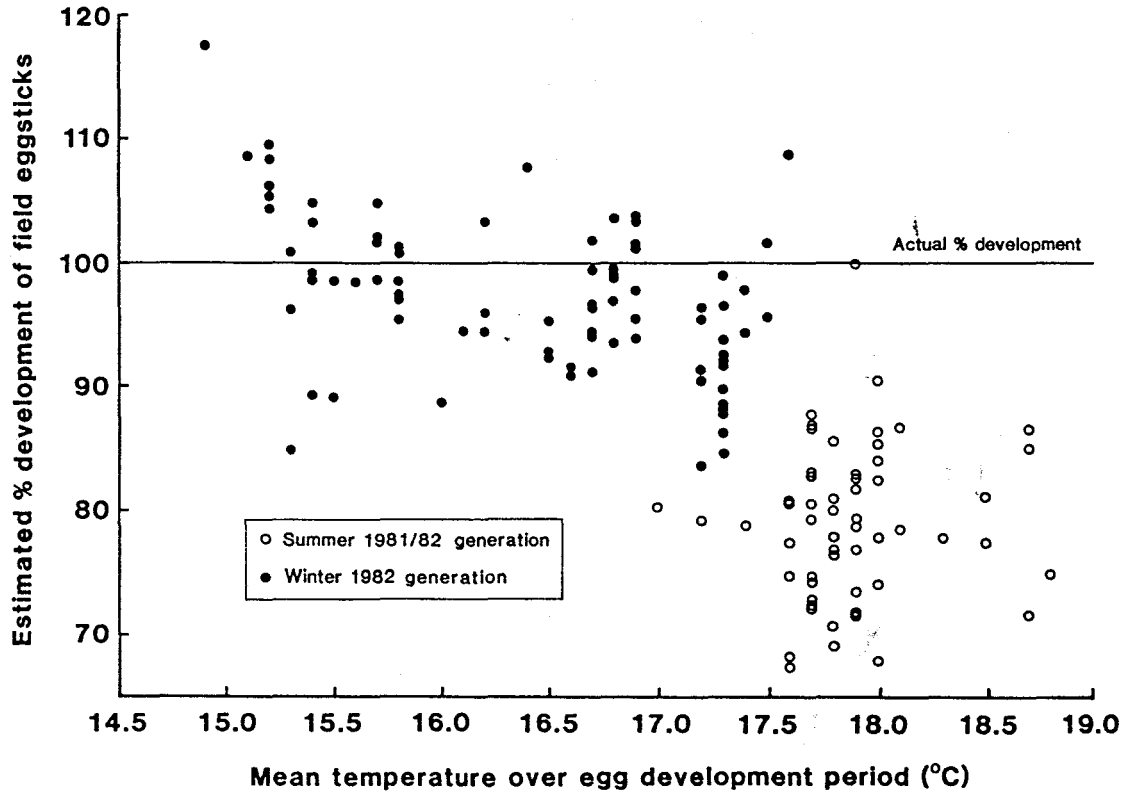

Fig. A4.2. The percentage development of C. cactorum eggsticks at Thursford, estimated from the incubation periods of eggsticks in the field and the development rate curve in Fig. A4.1. (see text for details), and shown in relation to the mean temperature over the egg development period.

sun on egg temperatures presumably do not increase uniformly with ambient temperature and are more pronounced at higher than at lower temperatures. This is suggested by the way the estimated percentage development decreases with mean temperature even within the winter generation (Fig. A4.2). The estimated percentage development of some eggsticks was greater than 100%, possibly because (i) cool temperatures towards the end of the development period delayed hatching and (ii) the temperatures experienced by these eggsticks were lower than the temperatures in the vicinity of the thermohydrograph.

The results on C. cactorum egg development in Fig. A4.2 show that it is not possible to predict egg incubation periods of C. cactorum on the basis of ambient temperature records alone; knowledge on the effects of microclimate are also required.

2) Larval development periods.

The day-degree development periods of C. cactorum larvae on O. ficus-indica were compared between summer and winter generations (Fig. A4.3, Table A4.1). At a threshold of 12°C there was a difference of only one day-degree between the mean day-degree development period for each generation (Table A4.1). At thresholds above and below 12°C, the difference between summer and winter generations was greater

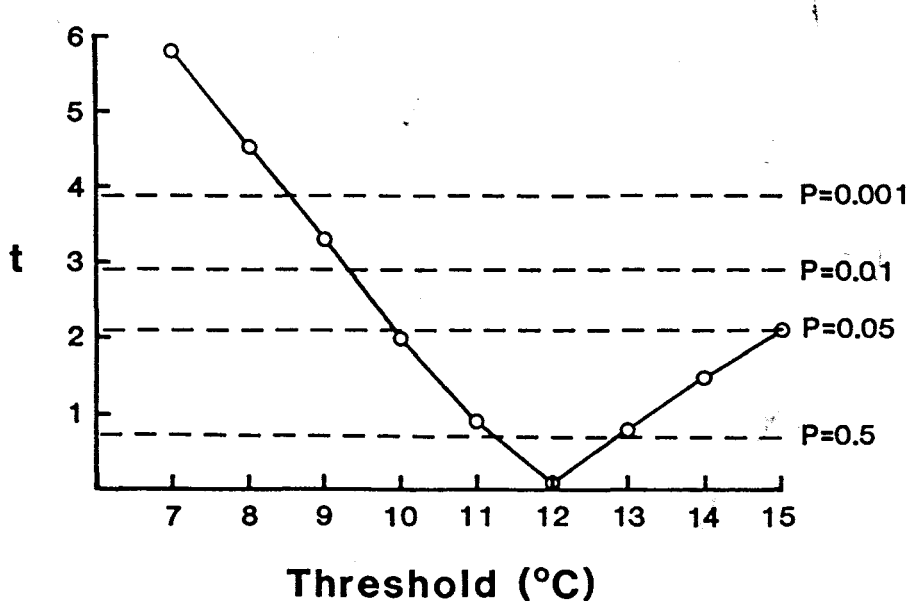

Fig. A4.3. Results of t-tests comparing day-degree larval development periods of C. cactorum at Thursford between summmer 1981/82 and winter 1982 generations at nine different temperature thresholds ranging from 7-15° (see text for details).

Table A4.1. Larval development periods of C. cactorum at Thursford, in day-degrees (threshold=12°C). Sample sizes indicate the number of colonies.

	Summer 1981/82 generation			Winter 1982 generation		
	Mean ± SE	Range	n	Mean ± SE	Range	n
O. ficus-indica	377 ± 10	339-415	8	376 ± 11	313-448	13
O. aurantiaca	-	-	-	461 ± 11	339-562	21
O. aurantiaca-overwintering	1104 ± 17	1061-1139	4	-	-	-

(Fig. A4.3). The method for determining the temperature threshold for development was therefore successfully used for larval development periods but not for those of eggs. Although the microclimatic temperatures experienced by the larvae were probably seldom the same as the ambient temperatures recorded on the thermohydrograph, the results in Fig. A4.3 suggest that, in contrast to egg incubation periods, the effects of microclimatic temperatures on larval development were roughly proportional to the effects of ambient temperatures.

The day-degree development period of overwintering summer generation larvae on O. aurantiaca was 2.4 times that of winter generation larvae on the same host plant. This confirms that the summer generation larvae that overwintered must have spent a considerable period of time in a dormant state (see pp. 24-25).

APPENDIX 5

The proportion of C. cactorum eggs laid on O. ficus-indica (O. f.) and O. aurantiaca (O. a.) within the seven 50x50m quadrats at the Thursford study site. Proportions are expressed in terms of five different plant parameters and compared using Wilcoxon's paired-sample test. A summary of these results is given in Fig. 4.6. The equations in Appendices 2 and 3 were used for estimating the plant parameters. n.s. - not significant (P>0.05); * - P<0.05. S - summer 1981/82; W - winter 1982.

Variable	Generation	Host plant	1	2	3	4	5	6	7	Total	T
No. eggs hatched	S	O. f.	1057	0	305	114	0	375	151	2002	-
		O. a.	600	688	534	534	204	374	53	2987	
	W	O. f.	3232	0	247	398	97	269	298	4541	-
		O. a.	1004	753	1082	515	146	342	66	3908	
Mortality factor[1]	S	O. f.	6.424	0	x	x	x	3.626	x	-	-
		O. a.	7.645	7.645	7.645	7.645	7.645	7.645	7.645	-	
	W	O. f.	2.646	x	x	2.531	x	5.500	x	-	-
		O. a.	5.333	5.333	5.333	5.333	5.333	5.333	5.333	-	
No. eggs laid[2]	S	O. f.	6790	0	1160	1018	445	1360	543	11316	-
		O. a.	4587	5260	4082	4082	1560	2859	405	22835	
	W	O. f.	8552	326	499	1007	273	1480	1686	13823	-
		O. a.	5354	4016	5770	2746	779	1824	352	20841	
Ground area (m^2)	S&W	O. f.	19.77	.45	1.24	3.52	1.37	9.31	5.52	41.18	-
		O. a.	19.90	40.64	35.81	20.95	8.21	9.44	2.69	137.6	
Eggs laid/m^2	S	O. f.	343	0	935	289	325	146	98	275	$11^{n.s.}$
		O. a.	231	129	114	195	190	303	151	166	
	W	O. f.	433	724	402	286	199	159	305	336	1^{*}
		O. a.	269	99	161	131	95	193	131	151	
Cross-sectional area (m^2)	S&W	O. f.	25.3	1.1	5.1	6.9	5.5	24.9	15.1	83.9	
		O. a.	21.9	37.0	30.1	20.9	9.3	7.9	3.8	130.9	
Eggs laid/m^2	S	O. f.	268	0	227	148	81	55	36	135	$7^{n.s.}$
		O. a.	209	142	136	195	168	362	107	174	
	W	O. f.	338	296	98	146	50	59	112	165	$13.5^{n.s.}$
		O. a.	244	109	192	131	84	231	93	159	
Total surface area of succulent cladodes (m^2)	S	O. f.	64.0	4.1	6.0	11.7	6.9	25.1	12.9	130.7	-
	W	O. f.	55.5	4.1	4.6	11.7	6.9	24.3	12.7	119.8	
	S&W	O. a.	28.7	51.6	41.6	25.8	9.9	11.2	3.3	172.1	
Eggs laid/m^2	S	O. f.	106	0	193	87	64	54	42	87	$5^{n.s.}$
		O. a.	160	102	98	158	158	255	123	133	
	W	O. f.	154	80	108	86	40	61	133	115	$4^{n.s.}$
		O. a.	187	78	139	106	79	163	107	121	
Mass succulent cladodes (kg)	S	O. f.	909	27	42	153	44	298	120	1593	-
	W	O. f.	791	27	28	153	44	286	117	1446	
	S&W	O. a.	45	92	86	48	19	23	6	319	
Eggs laid/kg	S	O. f.	7.5	0	27.6	6.7	10.1	4.6	4.5	7.1	0^{*}
		O. a.	101.0	57.2	47.6	84.9	83.4	122.2	69.8	71.6	
	W	O. f.	10.8	12.1	17.8	6.6	6.2	5.2	14.4	9.6	0^{*}
		O. a.	117.9	43.7	67.3	57.1	41.7	77.9	60.7	65.3	
Mass all cladodes (kg)	S	O. f.	2057	37	66	285	65	557	176	3243	-
	W	O. f.	1821	37	47	285	65	536	172	2963	
	S&W	O. a.	61	130	129	69	27	35	8	459	
Eggs laid/kg	S	O. f.	3.3	0	17.6	3.6	6.8	2.4	3.1	3.5	0^{*}
		O. a.	74.7	40.4	31.8	58.8	57.6	81.0	49.4	49.6	
	W	O. f.	4.7	8.8	10.6	3.5	4.2	2.8	9.8	4.7	0^{*}
		O. a.	87.2	30.8	44.9	39.6	28.7	51.7	42.9	45.3	

[1] ie. the ratio of eggs laid to eggs hatched, for eggsticks found within two days of being laid. An 'x' indicates that the mortality factor for that particular quadrat was not used for calculating the number of eggs laid.

[2] Derived either by multiplying the number of eggs hatched by the mortality factor or by using the actual number of eggs counted in the quadrat, depending on which was the larger value. This method was used to account for eggsticks that disappeared.

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