EVALUATION OF *TUCUMANIA TAPIACOLA* DYAR (LEPIDOPTERA: PHYCITIDAE) FOR BIOLOGICAL CONTROL OF JOINTED CACTUS IN SOUTH AFRICA

by

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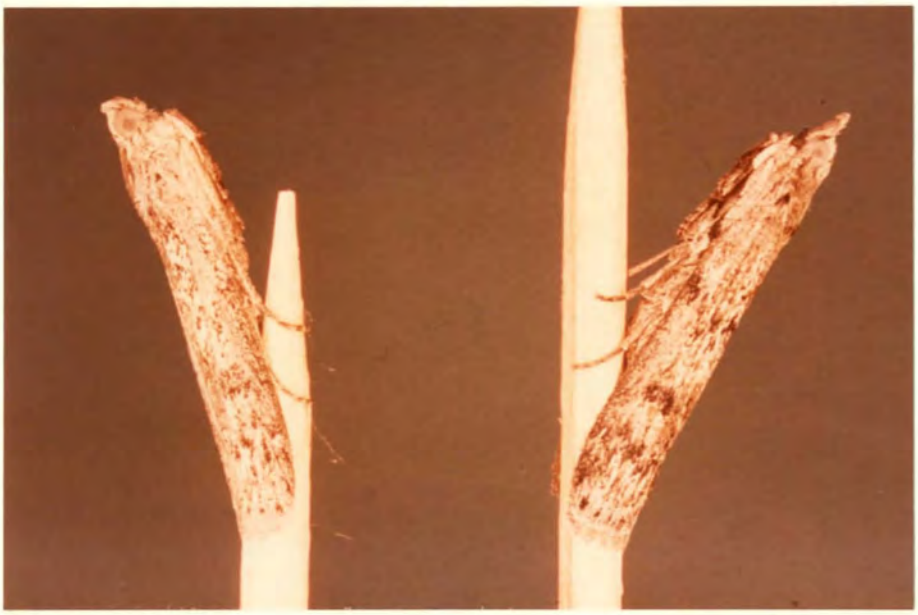
FRONTISPIECE

Final-instar larva of Tucumania tapiacola from Ibarreta, Argentina.



Male (left) and female (right) adults of
Tucumania tapiacola from Ibarreta, Argentina.

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RÉSUMÉ

Jointed cactus, Opuntia aurantiaca Lindley, remains a problem and continues to expand its range in South Africa, in spite of a mandatory herbicidal control programme. The feasibility of biologically controlling the weed is being explored because the cost of herbicides has escalated and, if it succeeds, biological control is permanent self perpetuating and relatively cheap. This thesis describes the introduction and release in South Africa of the phycitid moth, Tucumania tapiacola Dyar, as a potential biocontrol agent against jointed cactus.

A preliminary objective of the study was to resolve the taxonomic confusion within the genus Tucumania, so that the various populations of the moth from widespread localities and from different host plants could be identified.

The efficiency of mass-producing T. tapiacola in the insectary was continually improved through investigations of the insect's biology, and its response to various environmental parameters. Techniques were developed to manipulate the different life-stages of T. tapiacola so that every release was made with the maximum possible number of individuals, all in the same stage of development. Trials were made with various methods for transporting and releasing T. tapiacola in the field, and the most successful of these were employed during the establishment programme.

In all, approximately 830 000 T. tapiacola eggs, larvae and adults have been released at seven localities in South Africa, between May 1977 and February 1982. So far, the moth has failed to establish for more than three to five generations at any release site, for reasons that were not immediately apparent.

The mortality factors acting against the immature stages of T. tapiacola have been investigated and quantified. The accumulated data were used to construct partial-life-tables and survivorship curves. These show that survival of the eggs, larvae and pupae differed in shaded and exposed habitats, and on small, medium and

large O. aurantiaca plants. The overall mortality suffered by the immature stages alone did not account for the establishment failure. Alternatively, genetic problems that are commonly associated with the collection, mass production and release of biocontrol agents may have been responsible for the failure. Methods of overcoming these problems during future releases are discussed.

INTRODUCTION

Jointed cactus, Opuntia aurantiaca Lindley, is a low growing plant, from Argentina and Uruguay in South America (Arnold 1977), that has invaded large areas of South Africa, particularly in the eastern Cape Province (Neser & Annecke 1973). The weed is mainly a problem in natural pastures where, if unchecked, it forms impenetrable thickets that reduce the grazing capacity of the land (Zimmermann 1979).

Even in lightly infested areas, the potential threat caused by jointed cactus reduces the financial value of land. Also, joints are easily dislodged by animals that accidently brush against, or collide with, the inconspicuous bushes. When this happens, the long, barbed thorns become embedded in the animals and, in extreme cases, when the mouth or limbs are affected, they may starve or become lame. More usually the problem is less severe and is mainly one of inconvenience and discomfort. Sheep dogs that pick up joints become distracted and inefficient, and live-stock with joints in the fleece or hide are difficult to handle (Zimmermann & van de Venter 1981).

In most areas, jointed cactus is kept below an economic threshold through the application of herbicides (Zimmermann et al. 1974). Although populations of the weed are reduced by these chemicals, they are expensive, difficult to apply, damaging to desirable vegetation and only provide temporary relief because many small plants are not detected and remain to reinfest the treated area (Zimmermann 1979; Zimmermann & Malan 1980). Escalating costs and the shortage of rural labour have aggravated these problems and the search for cheaper, more efficient control methods has been intensified (Neser & Annecke 1973). Biological control is probably the only promising alternative that might provide a permanent solution to the problem.

This is not a new concept. In 1935, the cochineal, Dactylopius austrinus De Lotto from Argentina, via Australia, was released in South Africa for biological control of jointed cactus (Pettey 1948). The initial impact of this insect was spectacular and it almost eradicated the cactus over large areas (Pettey 1948). However, the cochineal was unable to maintain the high level of control and the

plant subsequently became re-established, although it never reverted to the original pre-introduction levels (Moran & Annecke 1979).

Several, mostly unsubstantiated, reasons were initially proposed for the reduced effectiveness of D. austrinus as a biological control agent. The cochineal was believed to have lost its toxicity, and attacks by the fungus, Empusa lecanii, and predators, including ants, beetles and rodents, apparently all hindered its progress (Pettey 1948; Karny 1972). The importance of these factors has recently been questioned (Zimmermann et al. 1974; Walter 1977). It now appears that inclement weather, especially prolonged periods of rain (Greathead 1971), and the inability of crawlers to locate new host plants at low densities, are the most important factors limiting the success of D. austrinus (Gunn 1979; Zimmermann 1981; Moran et al. 1982).

Another insect that colonises and damages an undetermined number of jointed cactus plants in South Africa is the phycitid moth, Cactoblastis cactorum (Berg). This moth was originally introduced into South Africa during 1933 to control Opuntia ficus-indica (L.) Miller (Annecke & Moran 1978).

Although D. austrinus and C. cactorum provide temporary control of jointed cactus in some localised areas, the combined damage caused by these insects is not sufficient to hold the weed permanently below an acceptable threshold (Moran & Annecke 1979). Recent attempts to improve the the current levels of biological control have been made from two directions.

The first approach involves an accurate evaluation of the impact that D. austrinus and C. cactorum are having on jointed cactus, and an investigation of the factors hindering their action in the field. Aspects of this work have been discussed by Gunn (1979), Zimmermann (1981) and Zimmermann & Moran (1983), and are not dealt with here. This thesis is concerned with the alternative approach, namely the introduction of additional control agents into South Africa, and in particular the phycitid moth Tucumania tapiacola Dyar.

T. tapiacola was selected from the five insect herbivores, excluding generalist polyphages, that attack jointed cactus over its native range in Argentina and Uruguay (Zimmermann et al. 1979). The other four insects include the phycitid moth, C. cactorum, the lonchaeid fly, Dasiops bourquini (Blanchard) and the homopterans, Diaspis echinocacti (Bouche) (Coccoidea) and Dactylopius ceylonicus (Green) (Dactylopiidae). The choice of T. tapiacola was not made on any theoretical grounds (Harris 1973; Wapshere 1975), but because C. cactorum, D. ceylonicus and D. echinocacti were already established in South Africa. D. bourquini was not selected because the fly could not be reared in the insectary, and its host specificity and safety for release could not be tested.

Dyar (1925) and Heinrich (1939; 1956) described the adults of T. tapiacola, while Gunn (1974) and Hoffmann (1976) describe the larval and egg stages. The morphological features of the different life-stages are not dealt with in this study, except briefly in the context of the taxonomic status of T. tapiacola in Chapter 2. Aspects of the life history of T. tapiacola were described by Dodd (1940), Mann (1969), Hoffmann (1976) and Hoffmann & Moran (1977). A brief summary of the life history is included here to provide the reader with a background to the insect.

Eclosion of the pupae occurs in the early evening. The moths are active at night when mating and oviposition occur. The eggs are usually laid on the thorns and glochids of the cactus host, although they are deposited on any rough surface when the moths are confined in cages. At the end of the incubation period, most of the eggs hatch in the four hours after sunrise. The mobile first instar larvae immediately move to the shaded areas on the host plant. Penetration of the plant cuticle almost invariably takes place at the base of a thorn or at the internode of two cladodes. Each larva spins a number of silk threads between the thorns (or any other suitable protrusion) and the plant cuticle, enclosing itself in a loose silk mesh. The larvae use the silk threads as a brace as they force their mandibles down into the plant epidermis. The larvae tunnel into the host plant and plug the entrance hole with silk and frass. During its development, each larva ingests and destroys approximately 30 g of host plant

tissue. The larvae complete at least six instars before spinning a cocoon and pupating, usually in the soil, but sometimes within the hollow husk of a destroyed cladode.

This is not the first time that T. tapiacola has been introduced into a new country for biological control of jointed cactus. During 1935, the moth was released in Australia where it became established but remained at low population levels (Dodd 1940; Mann 1969). In parts of New South Wales, the larvae periodically become locally abundant and destroy considerable amounts of cactus (Hosking 1982, personal communication). However, the populations of T. tapiacola in Australia are generally too low to inhibit the growth and spread of the weed significantly.

The fact that T. tapiacola has not played a major role in the biological control of jointed cactus in Australia, should not preclude it from release in South Africa. The combined action of a complex of interacting factors, including climate, host types (Dodd 1940; Annecke & Moran 1978), competitors, diseases, predators and parasitoids (Goeden & Louda 1976) determines whether or not an agent will be successful in a new country. In the case of T. tapiacola, the conditions in South Africa may be more suitable than they were in Australia for the development and progress of the moth.

During December 1973, the first consignment of T. tapiacola eggs was shipped from Argentina to South Africa. The eggs were used to start an insectary culture of the moth. Host specificity tests and the initial releases in South Africa were conducted using individuals from this colony (Hoffmann 1976; Hoffmann & Moran 1977). Subsequently, at irregular intervals, additional shipments of T. tapiacola eggs, larvae and pupae were sent to South Africa from the same and different localities in South America. The history of these introductions is outlined in the first chapter of this thesis.

The taxonomic status of T. tapiacola within the genus Tucumania, and the identification of the various populations that were introduced is clarified, as far as possible, in Chapter 2. The third and fourth chapters describe the mass production and releases with T. tapiacola

in South Africa. Finally, measurements of the mortality factors acting against the immature stages of T. tapiacola in its new habitat are presented in Chapter 5, and the reasons for the failure of the moth as a biocontrol agent of O. aurantiaca in South Africa are discussed. The wide range of materials and methods that were employed make a conventional chapter to describe these techniques inappropriate. Instead the various methods are explained, where applicable, throughout the text.

1. HISTORY OF INTRODUCTIONS OF T. TAPIACOLA INTO SOUTH AFRICA

During extended surveys for cactophagous insects by both Australian and South African entomologists, Tucumania spp. larvae have been collected from at least 18 species of cactaceous hosts, mostly Opuntia spp., over a wide geographic range in South America (fig. 1 and Appendix 1). The number of Tucumania spp. involved has not been finalised and this problem is addressed in Chapter 2 where I conclude that the six Tucumania colonies introduced into South Africa, from four localities in South America, were all different strains of T. tapiacola.

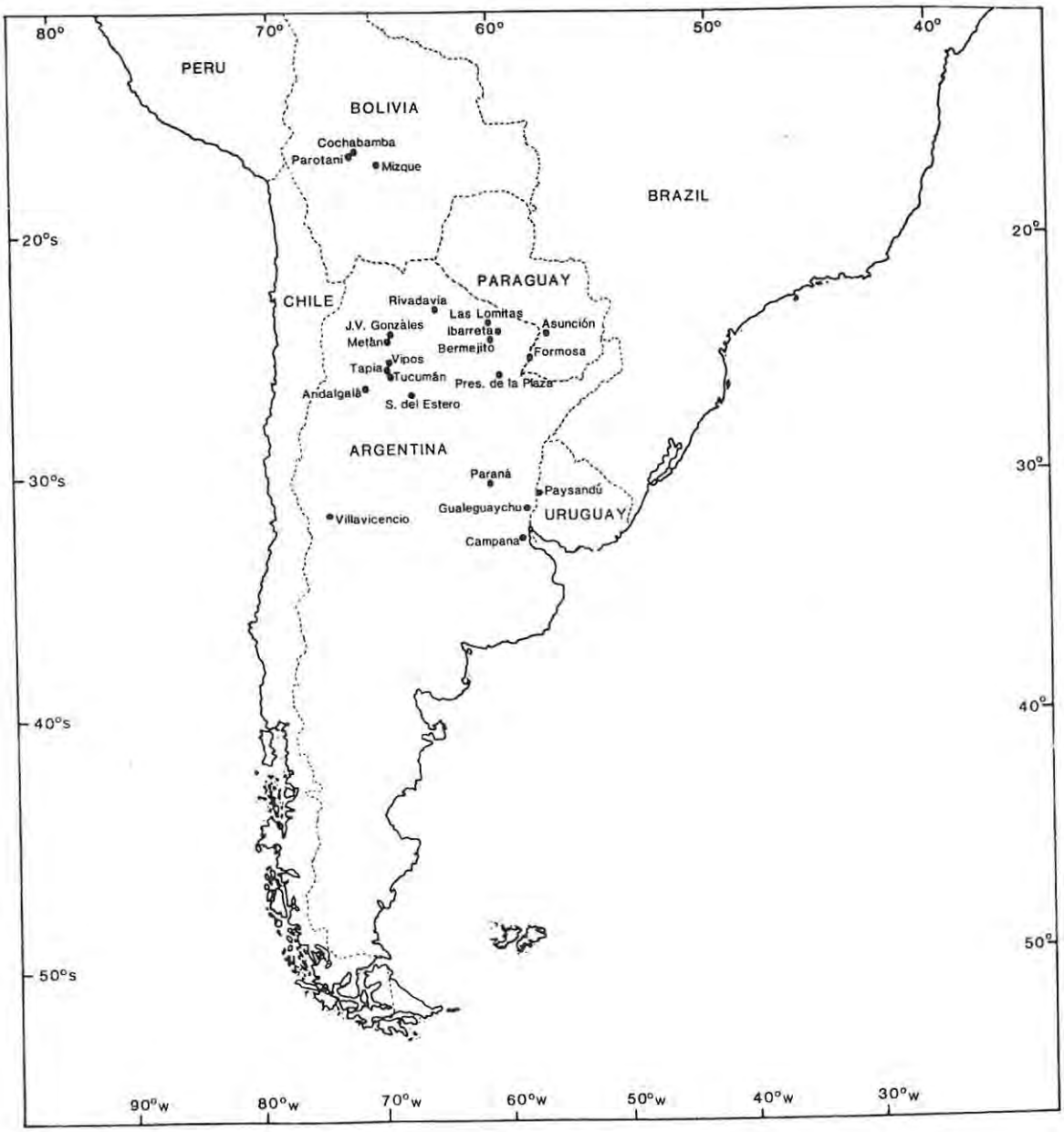

Fig. 1. The localities from which Tucumania spp. have been collected in South America.

1.1 Methods of shipment.

The first four shipments of T. tapiacola sent to South Africa, between 1973 and 1978, were of eggs and pupae. After June 1978, only actively feeding larvae were shipped. The methods used to obtain and transport the different life stages of the insect are described in turn.

(i) Eggs.

Larvae of T. tapiacola were collected in the field, in South America and transported in plastic tubes, with segments of host plant, to the insectary at the Instituto Miquel Lillo, Tucuman, Argentina. In the insectary the larvae were transferred to larger vials and provided with cactus cladodes for food, until they pupated, usually in the hollow husks of the destroyed cladodes.

Excessive mortality during transport to and in the insectary decreased the efficiency of this system. Transport delays increased larval mortality due to temperature extremes, suffocation, starvation and mechanical damage. In the insectary there was further mortality of the larvae, pupae and newly emerged adults, mainly due to unknown causes.

The moths were confined in glass jars, in which mating and oviposition took place. The gravid females laid their eggs on the frayed edges of thin mutton-cloth strips that were suspended in the jars. The strips with newly-laid eggs were removed from the jars, packed in cartons and sent by air directly to South Africa. A proportion of the fragile eggs was inevitably damaged during packing and in transit.

In spite of the losses that occurred during the initial collection of larvae and in handling the eggs, sufficient numbers were obtained for three successful shipments to South Africa. Insectary colonies were started with the imported eggs from each shipment.

(ii) Pupae.

Only one unsuccessful attempt was made to air-freight pupae of T. tapiacola from Tucuman to South Africa. On this occasion, eight pupae in silk cocoons were obtained from 30 larvae collected in O. aurantiaca at Campana, during June 1977.

Eight holes of approximately the same dimensions as the cocoons were punched in a 100 X 200 X 20 mm sheet of polystyrene. A cocoon was placed in each hole and the sheet was bound in stiff cardboard, to protect the pupae during shipment.

On arrival in South Africa, the pupae were incubated in separate glass vials at 25(±2)°C. Only three adults, two males and a female, eventually emerged from the pupae. The males emerged five and six days before the female and were held in continuous light at 15(±3)°C until she emerged. The three moths were then placed together in an oviposition cage. The virility of the males was apparently reduced by the cold storage, because neither mated with the female and no progeny were obtained.

No further attempts were made to transport pupae, although the method may have succeeded, especially if more pupae had been included in each shipment.

(iii) Larvae.

After June 1978, only larvae were air-freighted to South Africa, as this proved to be the most successful method of shipment.

The larvae that were collected in South America were placed directly in 10 or 20 ml plastic vials that were half filled with an agar plug of synthetic diet developed by Harley & Willson (1968). A folded piece of tissue paper was also placed in the tube to absorb excess moisture and to provide a refuge for the larvae. The tubes with larvae were placed in insulated boxes and air-freighted to South Africa as soon as possible after collection.

Mortality in the tubes was very low, and only three (3,7%) out of 81 Tucumania larvae died during the seven to ten days that they were in transit. The method was also successfully used to transport larvae of twelve other species of cactophagous Lepidotera. The overall loss from all these shipments was only 5,8% (n = 1331).

1.2 Introductions.

(i) Ibarreta (25.13S 59.50W), Argentina.

The first shipment of T. tapiacola to arrive in South Africa originated from Opuntia discolor Britton & Rose near Ibarreta, northern Argentina. An unspecified number of larvae were collected during October 1973 and were reared through to adults and allowed to oviposit in the insectary at the Instituto Miquel Lillo, Tucuman. In December 1973, approximately 1000 eggs were air-freighted to South Africa and used to start a culture of the moth in quarantine. The host specificity tests on T. tapiacola (Hoffmann 1976, 1977) and most of the releases in South Africa have been made with this strain, which was identified as T. porrecta by D.C. Ferguson, United States of America National Museum, Washington.

During June 1978, another four T. tapiacola larvae from Ibarreta were shipped directly to South Africa. These eventually produced one male and two female adults. The male was mated with one female and the other female was paired with a male from the insectary colony. The progeny from both females were reared through to adults before being crossed with and incorporated into the old insectary colony.

(ii) Cochabamba (17.26S 66.10W), Bolivia.

In September 1974, a shipment of approximately 400 viable Tucumania eggs laid by an unspecified number of females was received in South Africa. This material originated from larvae collected during May 1974, on Opuntia tayapayensis Cardenas near Cochabamba, Bolivia. This strain was identified as T. tapiacola by D.C. Ferguson.

The colony died during the fourth insectary generation when jointed cactus infested with C. cactorum larvae was accidentally introduced into the cages with the insect-free cactus, that was normally supplied to feed the larvae. The colony was lost because the C. cactorum larvae were larger and fed more vigorously than the T. tapiacola larvae and hence the latter starved.

(iii) Parotani (17.35S 66.20W), Bolivia.

Another 32 larvae were collected on Opuntia tayapayensis near Parotani, Bolivia, and air-freighted directly to South Africa during June 1978. The colony from this shipment was maintained for at least six generations, but became contaminated with Ibarreta larvae when their cages were accidently placed in the same insectary. The contaminated culture was reared as an inter-population hybrid until it was purposely destroyed in March 1981.

(iii) Campana (34.10S 58.55W), Argentina.

Two shipments of Tucumania larvae from Opuntia aurantiaca near Campana, Argentina were sent to South Africa. The first of these arrived during June 1978 and included eight larvae. An insectary culture was started with the three males and two females that eventually emerged. This colony was destroyed during July 1981 and was replaced by a colony started with 28 larvae received from Campana during April 1981. The Campana population was identified as T. tapiacola, and the most recent releases in South Africa were made with this stock.

2. THE TAXONOMIC STATUS OF T. TAPIACOLA

The genus Tucumania has received considerable attention because of its potential for biological control of O. aurantiaca in Australia and South Africa (Mann 1969; Hoffmann 1976). One of the main problems during this programme was to identify and name the populations of Tucumania from the Campana, Ibarreta and Parotani in South America, that were introduced and reared in South Africa.

The genus Tucumania was erected by Dyar (1925) for two new phycitid species he recognised and described. The descriptions were based on three adult moths reared from larvae that were collected from two unidentified Opuntia spp.. T. tapiacola is the type species of the genus and was described from one adult male, now the holotype, from Tapia, Tucuman Province, Argentina. The other species, T. porrecta, was described from two female adults from Paysandú, Uruguay, now the holotype and paratype. Roesler (1968) proposed that Tucumania Dyar should be sunk and the species placed in the genus Zophodia Hübner, along with a number of other cactophagous phycitids. However, no reasons were given to justify this proposed regrouping, and the genus Tucumania has been recognised throughout this study.

Apart from the original descriptions by Dyar (1925), Tucumania was included by Heinrich (1939; 1956) in his revisions of the subfamily Phycitinae. As well as the three specimens that were available to Dyar, Heinrich had received another male and female adult of T. tapiacola from Australia, where the moth had been reared for biocontrol of O. aurantiaca. Heinrich did not specify the South American origin of these additional specimens. However, they probably also came from Tapia, Argentina, as this was the apparent origin of the Australian stocks (Dodd 1940).

Dyar's (1925) description of the genus and two species of Tucumania runs to 36 lines of text and outlines, without any figures, the colour and patterns of markings on the moths. Heinrich (1939; 1956) included drawings that featured the male and female genitalia of T. tapiacola, and the female genitalia of T. porrecta.

Problems that are discussed below were encountered when attempts were made to identify and compare Tucumania spp. adults from Campana, Ibarreta and Parana using the descriptions of Dyar (1925) and Heinrich (1939; 1956). As a result, three series of moths that had been reared in the insectary, from Campana, Ibarreta and Parotani, were sent to the British Museum of Natural History for identification. These specimens were all identified as T. tapiacola, although the determinations were not conclusive because they were made without access to the type specimens (Schafer 1975 personal communication).

Tucumania specimens from 15 localities in South America were then sumbitted to Dr D.C. Ferguson at the United States of America National Museum, Washington, where the types of T. tapiacola and T. porrecta are held. His determinations are summarized in Appendix 1. The specimens from Parotani and Cochabamba, Bolivia were identified as T. tapiacola and the rest from Argentina as T. porrecta. Ferguson (1977 personal communication) was unable to identify all the specimens to species, even though some of the doubtful ones belonged to batches in which other individuals were classified as either T. tapiacola or T. porrecta.

The fact that some of the determinations from Washington and London conflicted, and that some of the moths could not be ascribed to either species, even with access to the types, suggested that the exact identity of the species within the genus Tucumania was confused. As a result, the diagnostic features used by Dyar (1925) and Heinrich (1939; 1956) were re-examined, using a series of moths from Campana, Ibarreta and Parotani. Unsuccessful attempts were made to borrow the types and to obtain specimens from the two type localities, Tapia and Paysandu, for comparison with the newly examined material. However, the evidence presented here strongly suggests that T. tapiacola and T. porrecta are not distinct species, and the genus Tucumania is probably represented by a single species.

2.1 Morphologiocal differences in the adults.

The differences in the coloration, size and genitalia of the adult

moths that were used by Dyar (1925) and Heinrich (1939; 1956) to separate T. tapiacola and T. porrecta are considered in turn.

(i) Coloration of the moths.

Dyar (1925) split the Tapia and Paysandu populations into two separate species, almost entirely on the grounds of subtle colour differences that he noted between the three adults he had at his disposal (Table 1). The two extra specimens sent to Heinrich (1939) from Australia apparently matched the T. tapiacola pattern and reinforced the arguments in favour of two species.

All the colour features outlined in Table 1 were recognised in the sample of 182 moths that was examined during this investigation. However, the differences between the individuals were not always as distinct as was originally proposed, and they could not be reliably used to distinguish the two species for the following eight reasons:

(a) The coloration on the moths from the three Tucumania populations under observation ranged from pale fawn, through various shades of grey, to almost pure black. There were four

Table 1. The main differences in the patterns of markings that were noted by Dyar (1925) and Heinrich (1939; 1956) in their descriptions of T. tapiacola and T. porrecta.

	T. tapiacola	T. porrecta
Forewings	Uniformly dark; luteous tint in median area.	Pale purplish fuscous
Discal dot	Large, distinct	Indistinct
Antemedial line	Broad; bidentate; continuous	Narrow, irregular dentate; interrupted
Subterminal line	Bordered outwardly by a pale line	Not bordered by a pale line
Hind wings	Strongly fuscous	Faintly fuscous
Thorax	Dark grey	Pale fawn coloured

basic colours in the scales that covered the moths, namely; white, fawn, grey and black. The ground colours of the moths were largely determined by the distribution of the fawn and grey scales, while the characteristic patterns of lines and spots on the wings resulted from the more regular arrangement of the black scales. The white scales were usually sparsely dispersed, and they did not contribute noticeably to the coloration of the moths.

The Tucumania sp. adults from Campana were generally light fawn coloured and the Parotani moths were mostly dark grey. The Ibarreta moths were more variable than either of the other two populations and ranged from light fawn to dark grey. Both fawn and grey scales were well represented in the Ibarreta population as a whole, although the proportions of each colour on the moths was variable, and this accounted for the continuum of different coloured phenotypes within the population.

Approximately half of the moths from Parotani, and approximately a quarter of the moths from Ibarreta, had patches of black scales on the forewings, apart from those that formed the lines and spots on the wings. The density and area covered by the black scales varied. In extreme cases, almost the entire forewings of the moths were covered and the normal wing markings were largely obscured. Black scales were rare on the Camapana adults.

Although the northern populations of Tucumania were generally darker than the southern Campana populations, the basic colours of the adults were highly variable. The two colour forms, "uniformly dark" and "pale, purplish fuscous", described by Dyar (1925) and Heinrich (1939; 1956), were present in all three populations, and did not appear to be characteristic of any particular population or species, as was originally suggested.

(b) The luteous tint in the median area of the forewings of T. tapiacola (Heinrich 1939; 1956) was noticable in some specimens from each of the three populations. In common with

most of the other wing markings, luteous tinting was absent in many of the phenotypes, and was more conspicuous in some moths than in others.

(c) The clarity of the discal spot at the end of the cell on the forewing varied considerably between the individual moths in each of the three populations. About 6% of the specimens were almost devoid of black scales and had no visible discal spot. In approximately 16% of the moths the spot was indistinguishable because of the predominance of black scales over the wings. In the rest of the moths the discal spot ranged from a small, faintly darkened area to a large distinct spot, and this character cannot be considered reliable.

(d) Apart from the discal spot, there was another spot between the base of the wing and the antimedial line in approximately 29% of the moths from the Ibarreta and Parotani populations. The distinctiveness of this spot also varied between individuals. The basal spot was never found on moths from Campana. Neither Dyar (1925) nor Heinrich (1939; 1956) mentioned this as a feature, and it was presumably absent from the five specimens they examined.

(e) The number and amplitude of the dentitions, and the distinctiveness of both the antemedial and subterminal lines, varied considerably between individual moths within all three populations. As a result, although some specimens fitted the description of either T. tapiacola or T. porrecta, many were different from both, or had features in the transverse lines that were common to both species.

(f) All the specimens examined during this study had subterminal lines that were bordered outwardly by a more or less distinct pale line. None of the moths had the T. porrecta condition (Dyar 1925) where this line was not discernable.

(g) The extent and intensity of the fuscous area of the hind-

wings varied between the individual moths in each population. Generally, the Campana individuals fitted the description of T. porrecta and had a small, faintly fuscous area restricted to the terminal edge of the hindwing. The Ibarreta and Parotani populations resembled T. tapiacola in this respect, and the fuscous area of the hindwing was darker and covered a larger proportion of the wing. However, there was a certain amount of overlap, and the darkest morphs from Campana were more fuscous than the lightest morphs from the northern populations.

(h) Lastly, the thorax of the Campana populations was of the light-fawn colour ascribed to T. porrecta, while the Ibarreta and Parotani populations had the dark-grey thorax of T. tapiacola.

Some of the observed differences in the colour patterns on the moths distinguished the northern Ibarreta and Parotani populations from the southern Campana population. Basal spots on the forewings, a general darkening of the forewings, a dark grey thorax and fuscous hindwings, were all characteristic features of the northern populations. However apart from these general differences, the Tucumania spp. adults could not be reliably identified by their colour and patterns of markings on the wings. The various morphs could not be clearly categorised because there was a gradation of phenotypes within each population, and most of the features recognised by Dyar (1925) and Heinrich (1939; 1956) were represented by their different expressions within each population. The situtation was complicated further because many individual moths from each population possessed features that were supposed to characterise either T. tapiacola or T. porrecta.

Apparently the features thought by Dyar (1925) and Heinrich (1939; 1956) to distinguish two species, were due to individual variation and geographic variation within a single species, although this was only resolved after a large number of specimens were examined. As a result, on the basis of colour, there are no consistent features that could serve to separate T. porrecta from T. tapiacola at the specific level.

(ii) Size.

With the five adults at his disposal, Heinrich (1939; 1956) measured alar expanses of 27 and 28 mm in the two males, and 30 mm in the female, of T. tapiacola. His T. porrecta females had alar expanses of 32 and 35 mm. He therefore concluded that the adults of T. tapiacola were smaller than those of T. porrecta, and incorporated this feature in a key he constructed to separate the species.

I measured and compared the alar expanses of 79 male moths and 103 female moths from the Campana, Ibarreta and Parotani populations. The expanse in the males was significantly smaller than that of the females in each population, but there were no differences between the populations for either sex (Table 2). The alar expanses of the males ranged from 19 to 32 mm and the females from 23 to 36 mm. The alar expanses of the male and female specimens measured by Heinrich (1939; 1956) all fell within these ranges and the validity of his conclusions on the relative size of the two species must be questioned.

Table 2. The mean (±1 standard error) alar expanse of Tucumania adults from three localities, reared in the insectary under the same conditions. n = number of moths that were measured. ns = not significant.

Locality	Wing span (mm) Males	n	Females	n	't'
Parotani	25,1 ±0,7	23	27,9 ±0,8	15	2,72 0,01<p<0,05
Campana	23,3 ±0,4	21	26,8 ±0,3	50	6,17 p<<0,001
Ibarreta	24,2 ±0,5	35	27,9 ±0,5	38	5,53 p<<0,001
ANOVA, F =	2,26 ns		2,20 ns		

(iii) The male genitalia.

Without having examined males of T. porrecta, Heinrich presumed that features of the male genitalia that were peculiar to T. tapiacola were; "the apex of harpe bluntly pointed; anellus with the apices of the arms appreciably broadened" (fig. 2A).

The male genitalia in Tucumania adults from Ibarreta, Campana and Parotani were alike, and all resembled those described by Heinrich (1939; 1956). However, the enlarged apices of the arms of the anellus as drawn by Heinrich (fig. 2A), were more pronounced than those seen in this study (fig. 2B). In an extreme example from Campana, the arms of the anellus were covered with many distinct scobinations (fig. 2C). Apart from this, the differences between individuals were minor and often difficult to distinguish, and do not seem to justify separation of the populations into two species.

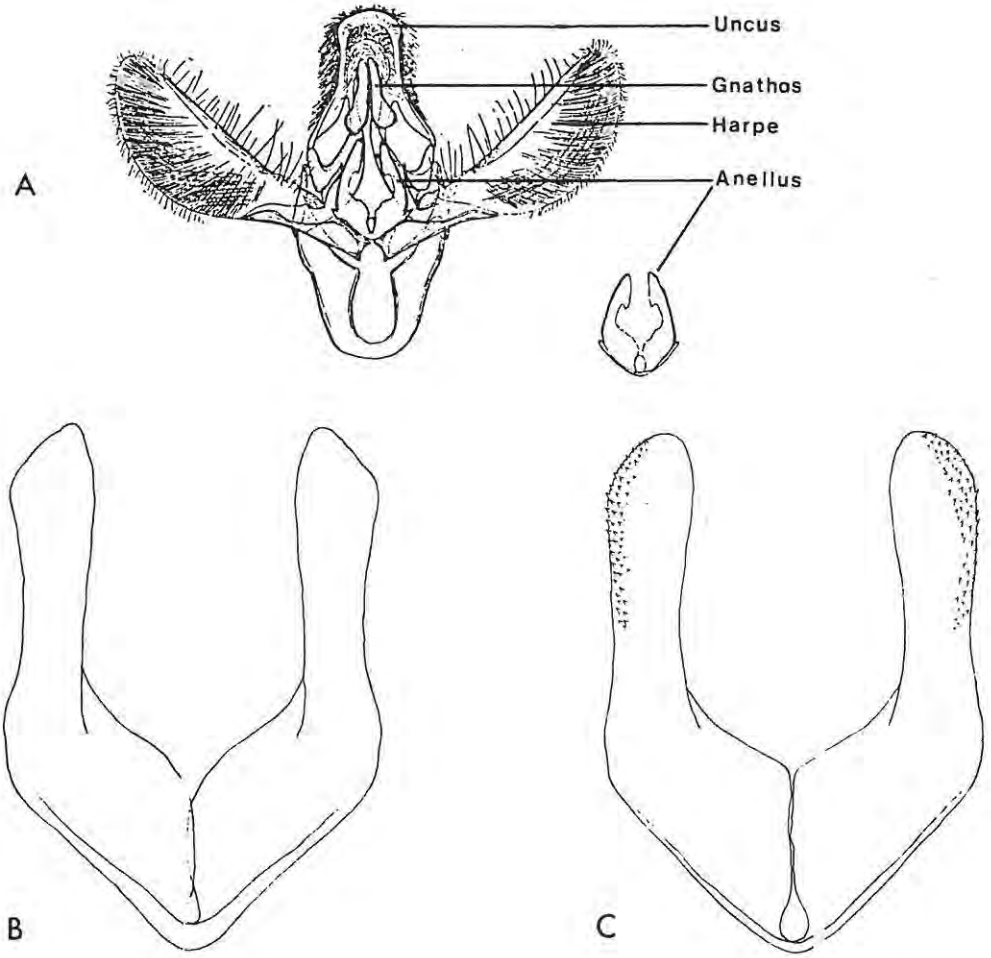

Fig. 2. The male genitalia of T. tapiacola with the anellus illustrated in situ and separately. A - After Heinrich (1939). B & C - The anellus as seen in this study.

(iv) The female genitalia.

Heinrich (1939; 1956) noted that the signum was keel-like and that scobinations were obvious and abundant in the neck of the bursa copulatrix of the two T. porrecta females at his disposal. In the single female considered by Heinrich to be T. tapiacola, the signum was granular and scobinations were sparse and reduced in the bursa copulatrix (fig. 3).

Within each population there was a gradation in the degree to which the scobinations in the bursa copulatrix were developed. Also, the signum ranged from being smooth and keel-like, to being a rough granular structure, and was reduced or almost absent in some specimens. This was therefore another example where features used by Heinrich (1939; 1956) to separate T. tapiacola from T. porrecta were found within single, isolated populations of freely interbreeding individuals.

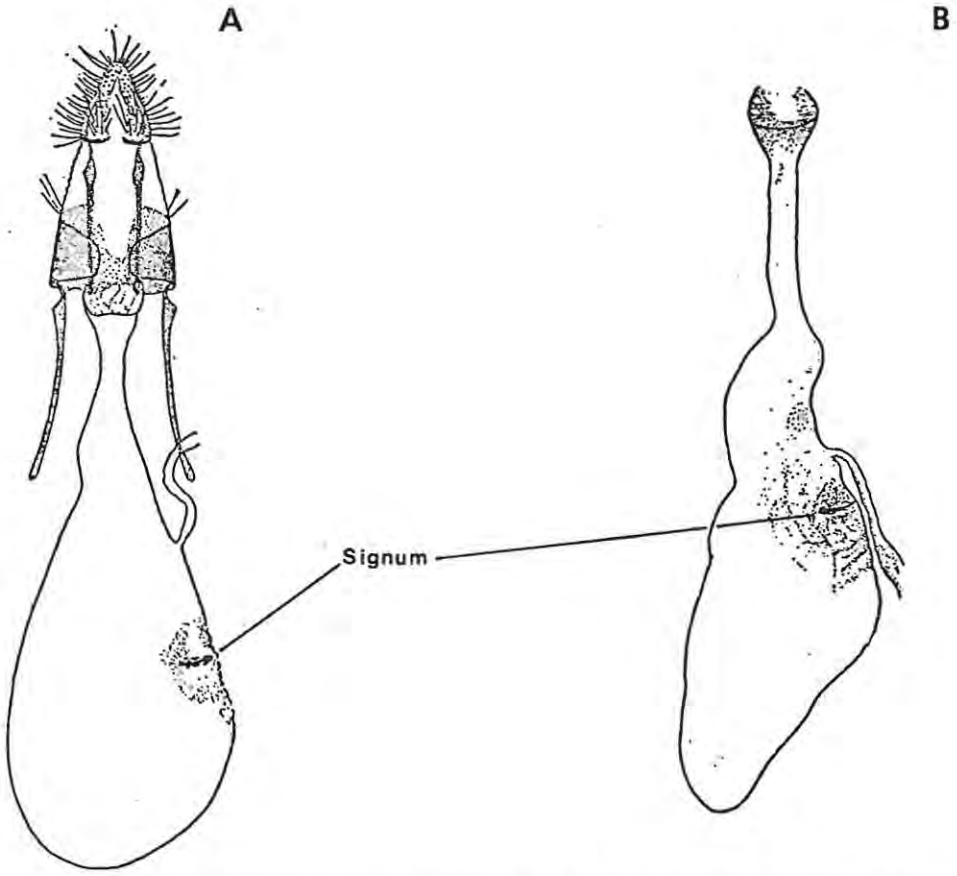

Fig. 3. The chitonised portion of the female genitalia of T. tapiacola (A) and T. porrecta (B). (After Heinrich 1939).

2.2 Morphological differences in the immature stages.

The immature stages of the Campana and Ibarreta populations were compared in an attempt to find consistent morphological differences that might justify splitting them into two species. The Parotani population was not included in this part of the study because the colony by this time had been lost.

The eggs and first-instar larvae were examined with a scanning electron microscope. The eggs were coated with gold before being placed in the electron beam. After being killed with CO_2, the first-instar larvae were placed directly in the microscope without coating. CO_2 was used in preference to other killing agents because the larvae died in a natural, extended state and did not contract and curl up. Larvae in the second and subsequent-instars were examined under conventional binocular and compound light microscopes. The setal patterns on the larvae were observed after the exoskeleton had been prepared using the technique of Hinton (1956).

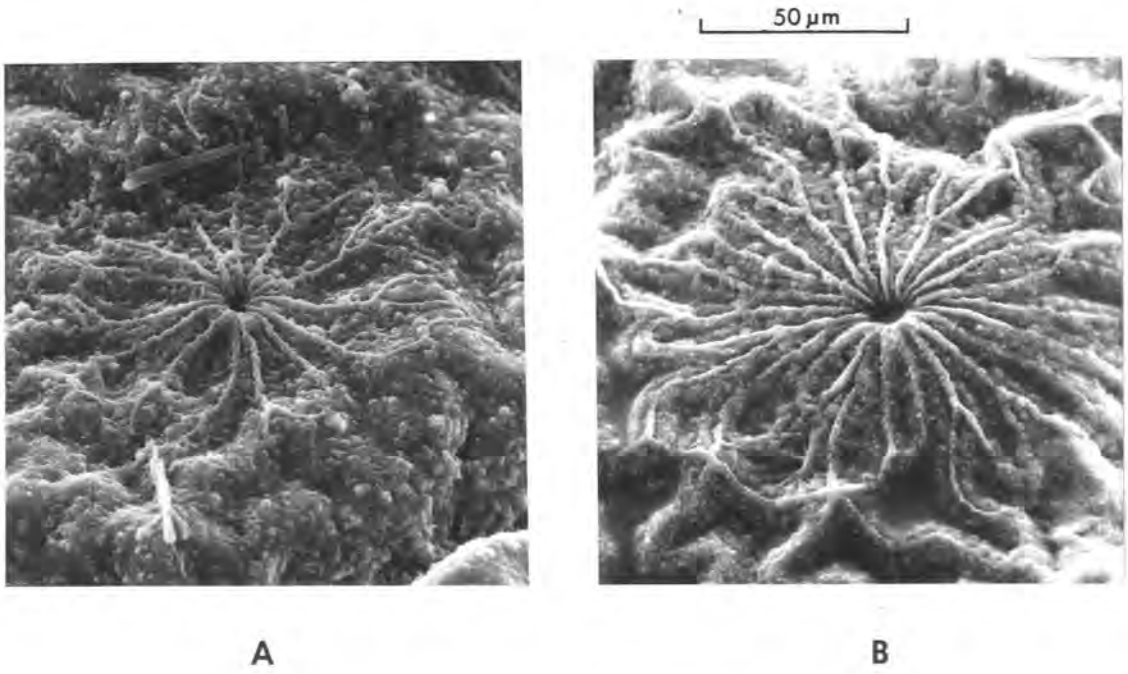

Fig. 4. The micropyle area of T. tapiacola eggs. A - Campana type. B - Ibarreta type.

(i) The eggs.

The eggs laid by the Campana and Ibarreta females were almost identical, except for slight differences in the area of the micropyle, which was situated at the anterior pole of the eggs and was surrounded by a rosette of converging ridges (fig. 4). Preliminary observations indicated that the Ibarreta eggs had more ridges converging on the micropyle than the Campana eggs. This trend was investigated further by examining eggs from four Campana females, eight Ibarreta females and 15 females from the F_1 generation of a Campana/Ibarreta cross (see below).

The micropylar ridges could not always be counted, either because they were incompletely developed, or because the micropyle was hidden in folds in the chorion. Together these constituted the deformed micropyles recorded in Table 3. Other micropyles were excluded from the counts because they were entirely, or partially, obscured by dirt, or by scales that had become dislodged from the female and attached to the egg during oviposition.

Table 3. The number of T. tapiacola eggs from different source populations that were examined for micropylar differences and the percentage of micropyles with entire, incomplete and obscured rosettes of ridges. F_1 C/I = F_1 generation of a Campana/Ibarreta cross.

	Source Populations		
	Campana	Ibarreta	F_1 C/I
Number of females	4	8	15
Number of eggs observed	84	101	298
% with entire rosette of ridges	48,8	39,6	73,2
% with ridging incomplete	41,7	48,5	22,1
% with ridges obscured	9,5	11,9	4,7

In each population, the percentage of eggs with "obscured" micropyles was low (Table 3). In the F_1 generation of the Campana/Ibarreta hybrid, the percentage of eggs with an entire rosette of ridges around the micropyle was highest and the percentage with "incomplete" rosettes was lowest. The lower percentage of eggs with entire rosettes around the micropyle in the two pure strains may have resulted from prolonged inbreeding. The Ibarreta population had completed approximately 44 generations in the insectary, and the Campana population was in its fifth insectary generation when the eggs were examined. The eggs from the hybrid population were laid by first generation adults. This point is elaborated further in the conclusions to this chapter.

The number of ridges per micropyle varied considerably within the batches of eggs laid by individual females and the ranges for 27 batches are shown in fig. 5. The mean number of ridges per micropyle also varied between females within the Campana and hybrid populations (Analysis of variance: $F = 5,13$; $0,001<p<0,01$ for Campana and $F = 13,6$; $p<<0,001$ for the hybrid population). This difference was not significant within the Ibarreta population ($F = 1,72$), possibly because the normal variation between females had diminished as a result of continued inbreeding over 44 generations.

The number of ridges per micropyle averaged 12,6 on eggs from Campana, 20,5 on eggs from Ibarreta and 16,2 on eggs from the hybrid population. There was no overlap between the Campana and Ibarreta populations. The average in the hybrid was midway between the average of the two parent populations, as would be expected for a polygenic character (Mayr 1963).

(ii) The larvae.

Presumably Dyar (1925) had no specimens of the immature stages of T. tapiacola and T. porrecta because these were not included in his descriptions. Heinrich (1939; 1956) restricted his comments to; "Larvae purplish or wine colored with sclerotised areas about body tubercles dark brown and large; two setae in group VII on abdominal segments 7 and 8." Apparently these are characteristic features of the

genus because Heinrich did not specify whether the above description applied specifically to either T. tapiacola or T. porrecta.

The only obvious morphological difference between the larvae of the populations that were introduced into South Africa was that the head-capsule in the Campana larvae was dark red, and in the Ibarreta larvae it was black. The real significance of the micropylar and larval head capsule differences cannot be ascertained without seeing geographically intermediate populations.

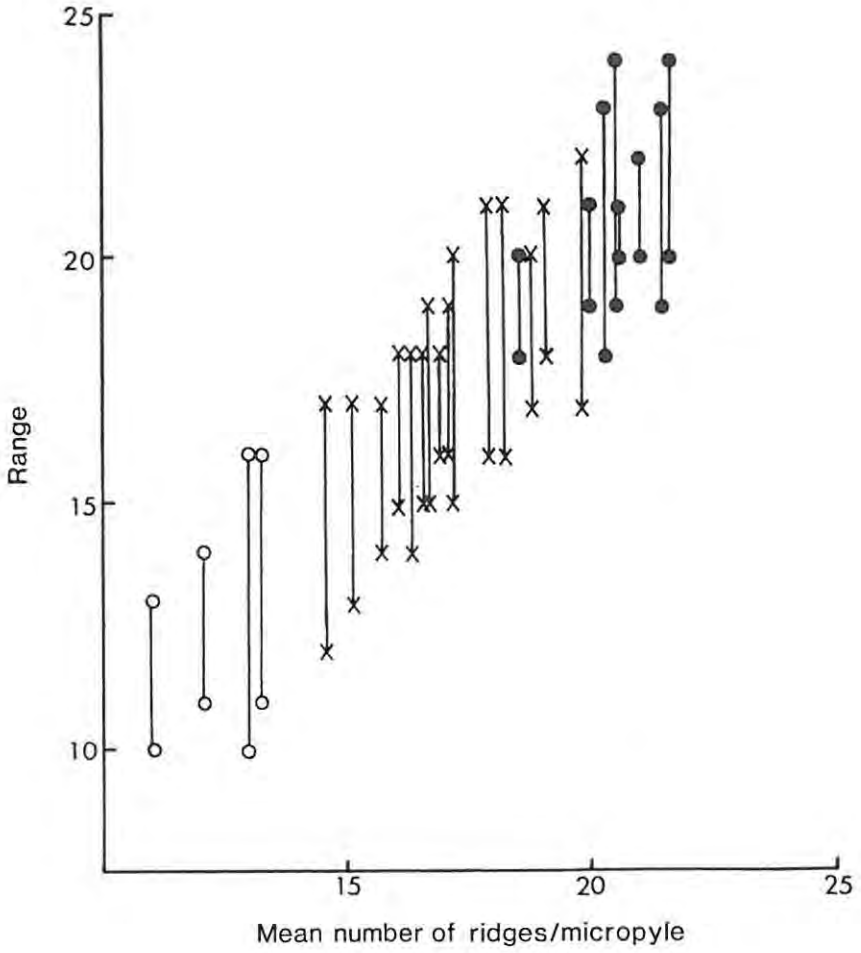

Fig. 5. The mean number of ridges per micropyle on T. tapiacola eggs laid by moths from Ibarreta (●), Campana (o) and the F_1 generation of a Campana/Ibarreta cross (×). The mean for each batch of eggs laid by single females is plotted along the horizontal axis, and the range within each batch is represented by the vertical bars.

2.3 Inter-population cross-breeding.

Apart from the variations in the micropylar area of the egg, larval head-capsule colour and vague features of the adult coloration, there was a lack of consistent morphological differences between the Tucumania populations from Campana, Ibarreta and Parotani, and there seemed to be no justification for classifying them as different species. This finding was investigated further by examining the reproductive compatibility of the adults from the three populations.

The tests were performed by isolating pupae in 35 ml glass vials, to ensure that the newly emerged adults remained virgin until they were placed together in the oviposition cages. One pair of moths was placed in each cage and, except for the controls, the males and females were from different sources. In the controls, males from Ibarreta were paired with females from Ibarreta, and males from Parotani were paired with females from Parotani. For each combination of cross-breeding populations, between 9 and 14 pairs of moths were crossed. After both adults in a cage had died, the females were dissected and examined for the presence of a spermatophore in the bursa copulatrix. The number of mated females that laid fertile eggs was also recorded.

In all the crosses, at least some of the pairs mated, and nearly all the mated females laid fertile eggs (Table 4). The percentage of pairs that mated varied from 30,0% for Parotani males crossed with Campana females, to 80,0% for Campana males crossed with Ibarreta females. The reasons for this difference were eventually resolved and are discussed in Chapter 3 under the sub-title "mating success". However, it should be emphasised that the low percentage of pairs that mated was probably not due to inter-population incompatibility.

The progeny of all the crosses were reared separately and the adults of the F_1 generation were back-crossed with each other and with the parent populations. For each back-cross, up to five males and five females were placed in the oviposition cages. No attempt was made to determine the percentage of pairs that mated by dissecting the females. Instead, the presence of fertile eggs in the cages showed

Table 4. The percentage of pairs of Tucumania adults that mated (and laid viable eggs) after males and females from different populations were confined singly in oviposition cages. n = number of pairs crossed in each combination.

Females from	Males from Campana	n	Ibarreta	n	Parotani	n
Campana	-		60,0 (60,0)	10	30,0 (30,0)	10
Ibarreta	78,6 (78,6)	14	33,3 (33,3)	9	33,3 (22,2)	9
Parotani	57,1 (57,1)	14	60,0 (60,0)	10	60,0 (50,0)	10

that at least some of the moths had mated and produced viable eggs. All the back-crosses that were performed are shown in Table 5 and every combination produced viable eggs.

Table 5. The combinations of Tucumania adults that were back-crossed during the F_1 generation, from the crosses shown in Table 4. x = Back cross made; - = no back cross made. C = Campana; I = Ibarreta; P = Parotani; I/C; I/P; P/C = F_1 generation hybrids.

Females from	Males from C	I	P	I/C	I/P	P/C
C	-	-	-	x	x	-
I	-	-	-	x	-	x
P	-	-	-	-	x	-
I/C	-	x	-	x	x	x
I/P	-	x	-	x	x	x
P/C	x	x	x	x	x	x

2.4 Conclusions.

The diagnostic features of adults used by Dyar (1925) and Heinrich (1939, 1956) to separate T. tapiacola from T. porrecta were inconsistent and variable in the moths from Campana, Ibarreta and Parotani, that were examined. Some of the moths fitted the description of T. tapiacola while others from the same source fitted the description of T. porrecta more closely. The situation was further confused because some individual phenotypes displayed characteristic features of both T. tapiacola and T. porrecta, and others had characters not described by either Dyar (1925) or Heinrich (1939; 1956).

The fact that the three populations cross-bred freely and produced viable offspring indicated that the minor inter-population differences (in adult and larval coloration and the micropylar area of the eggs) were probably due to geographic variation although this needs to be checked. The lower incidence of apparently "unnatural" deformities in the micropylar area of the eggs laid by the "hybrid" moths, compared to both the parent populations also indicated that the two populations were genetically compatible and therefore of the same species

These findings provide strong evidence that Dyar (1925) was not justified in dividing the genus Tucumania into two species. The variation that Dyar (1925) and Heinrich (1939; 1956) assumed to be interspecific was probably really intraspecific. There is thus no good reason to doubt that Tucumania has only one, widespread and geographically variable biological species, and T. tapiacola and T. porrecta are probably synonyms. As a result, all the Tucumania material so far introduced into South Africa has been classified as T. tapiacola.

The integrity of the separate populations of T. tapiacola has been maintained, in spite of the fact that they are all probably the same species. Clausen (1936) first emphasised the potential importance of subtle inter-population differences within species that can be manipulated for biological control. It is possible that even minor morphological, physiological or behavioural differences may allow some strains of a species to establish in a new area, while other, slightly different, strains of the same species fail to survive. Alternatively,

the ability of the different strains to control a pest may vary due to minor differences. As a result, the different populations of T. tapiacola have been maintained as separate colonies in the insectary, so that they can be released in turn, or in different areas, and the relative progress of each can be followed.

Although the differences between the populations of T. tapiacola from Parotani, Ibarreta and Campana were not investigated in detail, they form a basis for further investigations that may be required if the biocontrol potential of each population of T. tapiacola is to be evaluated independently. This may be immediately relevant because both Ibarreta and Campana colonies have been released in South Africa already, and it is possible that releases with populations from other sources will follow.

When more than one strain of a natural enemy is released on a target pest, and the relative progress of the strains is monitored, population markers are needed to recognise the source colony of individuals recovered during the second and subsequent generations in the field. Any morphological, physiological or behavioural feature peculiar to a particular population can serve as a marker for that population. Although many of the differences between allopatric populations of a species are difficult to detect, some morphological characters may be obvious and relatively easily recognised (Mayr 1970). These features make ideal markers, especially if they allow the source of a strain to be identified from single individuals in situ and without damage to the specimens that are examined. In T. tapiacola, the colour patterns of the adults and larvae meet these requirements. The ridges around the micropyles on the eggs require microscopic examination, but may also serve as useable markers for populations of T. tapiacola.

3. MASS-PRODUCTION OF T. TAPIACOLA

The chance of establishing a biocontrol insect on a target weed are enhanced if large numbers of individuals are deployed simultaneously at the release site (Myers & Sabath 1981). Although a release area may be suitable for the development of a particular biocontrol insect, the programme can fail because too few individuals are released. Releases of large numbers ensures that the adults that emerge from the first field generation are able to locate and mate with each other and produce a sufficiently large second field generation for survival and increase of the population. If the agent does not establish after large numbers have been released, then the failure may be due to other deficiencies in the release programme or other detrimental biotic and abiotic factors in the new environment.

Usually agents for release are mass-produced in insectaries. Alternatively, however, large numbers of the potential agent can be collected in the country of origin, shipped to the release area and liberated on the pest. This method has seldom, if ever, been used in biological control of weeds because agents are rarely abundant in their native ranges; there is a danger that undesirable diseases and parasitoids might be introduced with the insects; and there are many difficulties associated with the transport of large numbers of live insects between continents (Bartlett & van den Bosch 1964).

Almost without exception, therefore, biocontrol agents for establishment programmes have been mass-produced in insectaries. The process has the advantages that insectary colonies can be started with relatively few individuals and parasitoids can be eliminated, usually within one insectary generation. One of the main problems with insectary production is that the insects must often be reared for several generations before sufficient numbers of individuals can be obtained for release. Insectary rearing over long periods can result in the selection of laboratory ecotypes that are poorly suited to survive under field conditions (Mackauer 1976).

As a result, the effects of various insectary conditions on the development and survival of T. tapiacola were investigated. These

included the longevity, mating-success and fecundity of the adults; the incubation periods and percentage hatch of the eggs; survival and development of the larvae and cold storage of the eggs and adults. With this approach, the optimal conditions were provided during mass-production of T. tapiacola and large numbers of eggs, larvae and adults were obtained in the shortest possible time. This minimised the number of generations that T. tapiacola needed to be reared through in the insectary and reduced the chances of selecting undesirable, laboratory-adapted strains before releases commenced.

3.1 Material and methods.

(i) Rearing procedures.

Larvae of T. tapiacola were confined in flat, wooden cages with removable glass lids that lay in a sunken lip around the top of the cage (fig. 6). Each side of the cage had three, 60 mm diameter, aeration holes, that were covered on both inner and outer surfaces with fine mesh nylon gauze. These cages were designed to overcome four problems encountered with the conventional cages that were initially used to rear T. tapiacola in South Africa (Hoffmann 1976).

(a) The double gauze layers over the aeration holes of the cages prevented the braconid parasitoid, Bracon hebetor Say, from reaching the T. tapiacola larvae and prepupae in the cages. In the conventional cages, B. hebetor was able to immobilise and oviposit on the larvae by inserting its ovipositor through the single layer of gauze.

(b) The cages were easily stacked and allowed more efficient use of the limited amount of horizontal space in the insectaries.

(c) The newly emerged moths were difficult to collect from the far side of the conventional cages with side-opening doors. This problem was initially overcome by removing the destroyed cladodes with prepupae and pupae from the cages

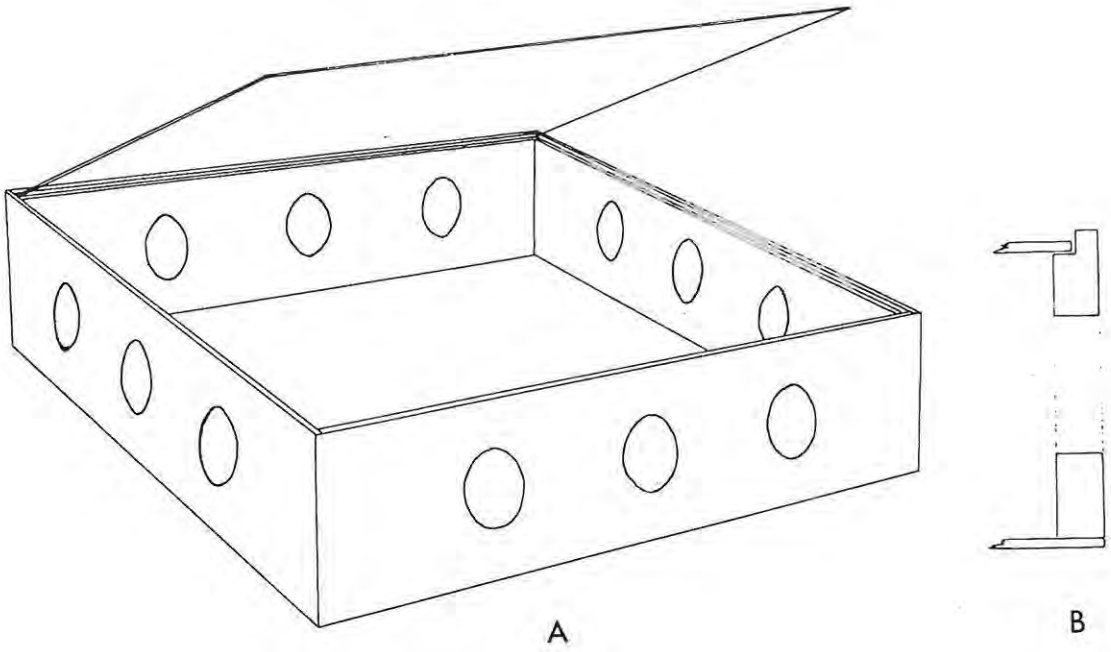

Fig. 6. The cages used to rear T. tapiacola larvae. A - complete cage, with partially raised lid. B - section through side, and part of the lid and base of the cage.

and placing them in light proof boxes, from which the adult moths emerged some time later (Hoffmann, 1976). During the transfer, however, a proportion of the pupae in the cladodes were inevitably killed or damaged, producing abnormal moths. The shallow, top-opening cages allowed easy access to the whole cage and the moths were harvested directly, without difficulty.

(d) Larvae and prepupae frequently escaped from the conventional cages by chewing through the single layer of gauze, almost always in the angle where the gauze was attached to the wooden frame. The escape holes made by the larvae created an additional problem because they allowed parasitoids easy access to and from the cages. The larvae never chewed through the inner layer of gauze covering the aeration holes of the flat cages, probably because the gauze lay flush over the holes. The larvae that had

vacated their cladodes aggregated in the lightest areas of the cages, especially along the edges of the glass lid.

Each cage was filled with approximately 3 kg of loose jointed cactus cladodes and inoculated with 200 newly-hatched larvae (less than twelve hours old). The cactus was collected from various infestations close to Grahamstown (33.18S 26.32E).

The cages were held in an insectary with alternating conditions of 28(±2)°C and 35(±5)% relative humidity during a 14 hour photophase and 22(±2)°C and 50(±10)% relative humidity during a ten hour scotophase. The relative humidity in the cages was usually higher than the rest of the room because moisture was given off by the damaged cactus cladodes.

The larvae completed their development in approximately 35 days and pupated in the cages, usually within the hollow husk of the cladodes they had destroyed.

Each day, the newly-emerged moths were removed from the larval cages and placed in 27 ℓ oviposition cages, made from clear 'perspex' thermoplastic and with fine mesh nylon gauze lids. Strips of coarse, 'mosquito-netting' gauze were suspended in the cages. The moths in the cages were held under the same alternating temperature (28/22°C) and light conditions as the larvae. A Philips GL5 'indicator-light' provided dim illumination in the insectary during the dark phase and the moths were never subjected to total darkness.

The moths mated during the scotophase and the females oviposited on the coarse-gauze strips. The strips with eggs were removed and replaced with fresh strips every day. The eggs on the strips were kept in petri dishes or 35 ml glass-vials and incubated at 25(±2)°C. After seven days, the eggs hatched and the first-instar larvae were transferred onto jointed cactus in the larval cages.

There was an overlap of generations within the insectary and all stages of the life cycle were available for experimentation most of the time.

Table 6. The range of relative humidities (%RH) and corresponding saturation deficits (SD) recorded at different temperatures (T°C) in the insectaries.

T°C	%RH	SD
40	18 - 25	41 - 45
35	20 - 28	31 - 33
30	25 - 35	19 - 22
25	35 - 45	13 - 15
20	50 - 60	7 - 9
15	65 - 75	3 - 5
10	75 - 85	2 - 3

(ii) Experimental conditions.

Most of the experimental and observational studies on T. tapiacola were made in the controlled environment of insectaries or incubators. Temperatures above 20°C were controlled to within ±2°C, and lower temperatures fluctuated through ±3°C. The temperature control was occasionally disrupted when the air conditioning to the insectaries malfunctioned and during electrical power failures, that seldom lasted more than two hours.

The relative humidity was not controlled in the insectaries and incubators, but it normally equilibrated within ranges that were dependant on the prevailing temperature regime. The approximate range of relative humidities (%RH) that were measured at seven different temperatures and the corresponding saturation deficits (= saturated vapour pressure minus actual vapour pressure) are recorded in Table 6.

Observations were also made on the moths, during summer and during winter, while they were held under more natural temperature regimes. These adults were held in cages in an open glass-house. The conditions then encountered by the moths are summarised in Table 7.

Table 7. The average conditions that T. tapiacola adults encountered in an open glass-house during summer and winter.

	Summer	Winter
Mean daily maximum temperature	24,8°C	18,3°C
Mean daily minimum temperature	13,9°C	8,7°C
Mean daily temperature	19,3°C	13,5°C
Average day length (sunrise - sunset)	14h.23m.	10h.52m

(iii) Measurements of adult size.

The size of the T. tapiacola adults used in various experiments was measured from their pupal mass just before eclosion.

Pupae in various stages of development were removed from their cocoons and placed in separate 35 ml glass vials. The pupae lost almost 25% of their mass between pupation and adult eclosion (fig. 7), and thus an unnecessary variable was introduced into the experimental procedure if the pupae were weighed at different stages of maturity. As a result, the pupae were checked daily and only weighed within 24 hours of adult eclosion. This was marked by the pupae turning from brown to almost black just before eclosion.

The weighed pupae were replaced in the vials and the adults usually emerged on the same night. The following day, the moths were sexed and sorted for observation. Allowing the adults to emerge in separate vials ensured that the moths were virgin at the start of each experiment.

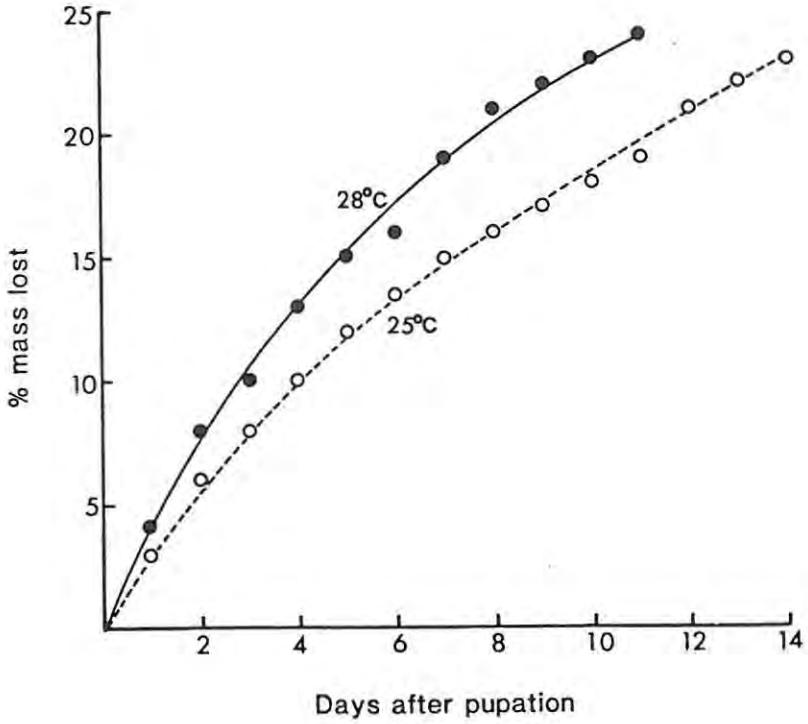

Fig. 7. The percentage mass lost by pupae of T. tapiacola during development at 25°C, 40(±5)%RH; SD = 13 -15 mm/Hg, and 28°C, 35(±5)%RH; SD = 16 -19 mm/Hg.

3.2 Longevity of adults.

The longevity of both mated and virgin, male and female adults of T. tapiacola was measured at 35°C and 25°C, and under the winter temperature regime described in the materials and methods. The size of each adult was recorded from its pupal mass at emergence.

(i) Effect of adult size on longevity.

In many insect species, adult longevity is directly proportional to size (Partridge & Farquhar 1981). However, there was no significant correlation between the size of T. tapiacola adults and the number of days that they lived at any of the three temperature regimes investigated (Table 8).

Table 8. The correlation coefficients (r) between longevity and adult size of virgin and mated, male and female adults of T. tapiacola, measured at different temperatures (see text). n - number of adults measured. In no case was r significant.

	Temperature regimes					
	Winter	n	25°C	n	35°C	n
Mated males	0,49	11	-0,16	12	-	-
Mated females	0,12	10	0,22	12	-	-
Virgin males	0,39	10	0,54	11	0,10	18
Virgin females	0,32	9	0,05	13	0,08	20

(ii) Effects of temperature on adult longevity.

The longevity of T. tapiacola adults was inversely related to temperature and was longest at the coldest temperatures. At 35°C the virgin female moths lived on average for only 4,7 days, while virgin females kept under winter conditions lived on average for 26 days (Table 9).

The differences in the developmental times of virgin males compared to mated males were not significant (Table 9). However, during winter and at 25°C the virgin females lived longer, on average, than the mated females. The fact that egg production and oviposition rapidly exhausts energy reserves has been used to explain the larger differences in the longevity of virgin and mated females compared to virgin and mated males (Griffiths & Tauber 1942; Bilewicz 1953). Males are apparently not as detrimentally affected by reproduction because they contribute proportionately less energy to the process.

The mated female adults generally lived longer, on average, than the mated males, and the virgin females always lived longer, on average, than the virgin males (Table 9). The one exception was when mated males held under winter conditions outlived mated females, under the same conditions, by an average of 2,1 days. This difference was not significant.

Table 9. The mean (±1 standard error) longevity in days of mated and virgin, male and female adults of T. tapiacola at three different temperature regimes (see text). The different longevities were compared with the Mann-Whitney U test. * = 0,01<p<0,05; ** = 0,001<p<0.01; ns = not significant. *[1] = 0,01<p<0,05 for a one tail test. n = number of moths treated.

Longevity of:	Temperature regimes Winter	n	25°C	n	35°C	n
Mated males	18,8 ±2,2	11	7,5 ±0,5	12	3,0 -	1
Virgin males	20,9 ±2,4	9	8,7 ±1,1	12	3,4 ±0,2	19
Mated females	16,7 ±2,4	11	9 5 ±0,8	12	4,0 -	1
Virgin females	26,0 ±3,1	9	13,6 ±1,0	12	4,7 ±0,4	19
Difference (in days) between:						
Virgin ♂♂ - mated ♂♂	2,1	ns	1,2	ns	0,4 -	
Virgin ♀♀ - mated ♀♀	9,3	*	4,1	*	0,7 -	
Mated ♀♀ - mated ♂♂	-2,1	ns	2,0	**	1,0 -	
Virgin ♀♀ - virgin ♂♂	5,1	*[1]	4,9	**	1,3 **	

3.3 Effects of Temperature on mating.

The effect of temperature on the percentage of T. tapiacola adult moths that mated was measured at five different temperatures. The moths were either caged as single pairs of one male and one female, or ten males and ten females were placed in each cage. The presence of fertile eggs in the containers with single females showed that the moths had mated. The genitalia were dissected from the single females that failed to lay fertile eggs and from the females in the communal cages with ten pairs of moths. The presence of a spermatophore in the bursa copulatrix confirmed whether these moths had mated or not.

Mate success in T. tapiacola was affected by high temperatures and by the number of pairs of moths that were placed in each cage (Table 10). Only one out of 20 single pairs mated at 35°C. The percentage of pairs that mated reached a peak of 59,5% at the alternating daily temperature regime of 28/22°C. However this was not significantly higher than the percentages of single pairs that mated at 25°C and under normal summer and winter temperature regimes.

Of the 113 pairs of adults that were caged singly at the four lower temperature regimes (Table 10), only 64 (56,6%) mated. In comparison, 94% of the females mated when ten pairs of moths were confined in each cage. Cullen (1981) also recorded a higher rate of successful matings in communal cages, as opposed to cages with single pairs of the phycitid, Bradyrhoa gilveolella (Treitschke), although the reasons for this difference were not explained. In the case of T. tapiacola size incompatibility between some of the single pairs of moths may have prevented mating.

Table 10. The percentage of T. tapiacola adults that mated under five different temperature regimes (see text). n = number of moth pairs subjected to each temperature. Sig. = Percentages with the same letter are not significantly different: those with different letters are significantly different at $p<0,05$ (G test; Sokal & Rohlf 1969).

Temperature °C	n	pairs/ cage	% mate	Sig.
35 Cont.	20	1	5,0	c
25 Cont.	24	1	50,0	b
	50	10	96,0	a
28Day/22Night	42	1	59,5	b
	50	10	92,0	a
Summer.	27	1	59,3	b
Winter.	20	1	55,0	b

3.4 Effect of adult size on mating success.

The pupal mass of the male moths was plotted against the pupal mass of the female moths for the 113 pairs of moths that were caged separately at the four lower temperature regimes (ie. excluding 35°C). The pairs that mated are represented with closed circles, and those that failed to mate with open circles (fig. 8).

The figure is divided into three sections.

Section A. Points below the horizontal line. The males of the 15 pairs of moths included in this section all weighed less than 43 mg and only four (26,7%) mated.

Section B. Points above the diagonal line. The male moths of the pairs in this section were larger than the females, and only eight out of the 24 (33,3%) mated.

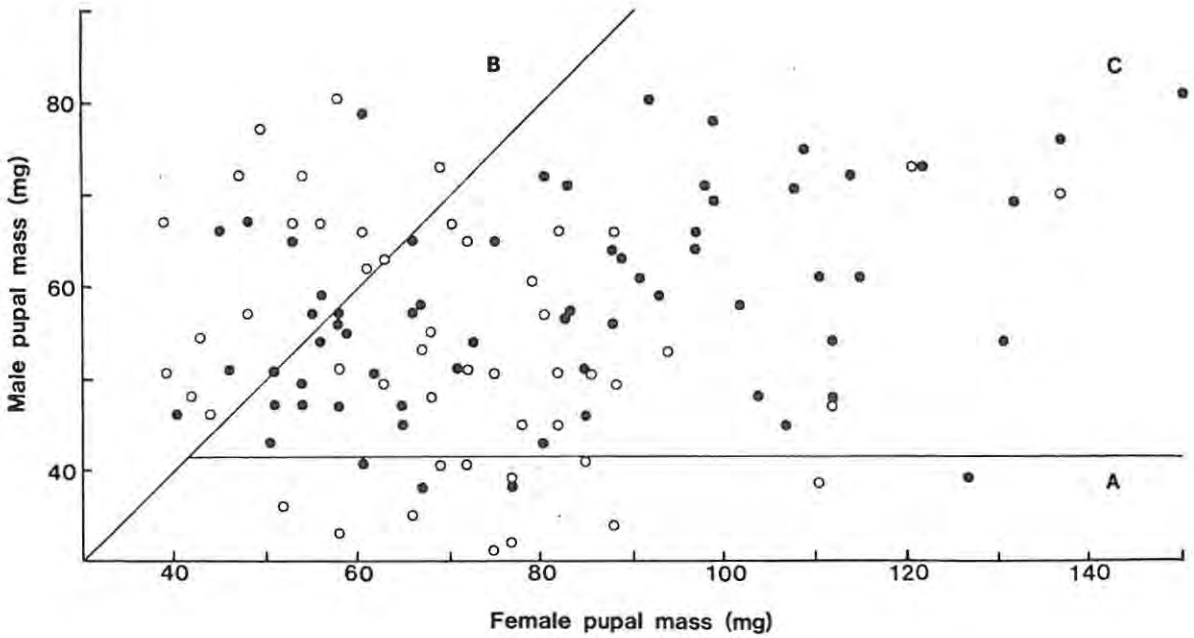

Fig. 8. Mate success in T. tapiacola. The male pupal mass was plotted against the female pupal mass for each of 113 pairs of moths. Closed circles represent pairs that mated; open circles represent pairs that did not mate.

Section C. Points between the horizontal and diagonal lines. The male moths in this section weighed more than 43 mg, but were lighter than their female partners. Fifty two out of the 74 (70,3%) pairs mated and this proportion was significantly higher than either of the other two sections (X^2 =16,4; p<<0,001).

These trends suggested that the small males were less virile than large males, and that when the males were larger than the females, the ability of the pairs to mate was reduced. This apparent incompatability due to size did not affect the mate performance of T. tapiacola when several pairs of moths were placed in each cage for two possible reasons: (a) The male and female moths in communal cages were able to 'choose' partners and most were able to find a compatible mate. (b) Males of T. tapiacola have the ability to mate with and fertilise more than one female. As a result some of the male moths probably mated two or more times and made up for the small males that were unable to mate.

3.5 Fecundity of T. tapiacola.

The fecundity of T. tapiacola was measured at five different temperature regimes (see materials and methods), for 57 females that mated when caged separately with single males. There was no size difference in the eggs laid by different females (Hoffmann 1976), but the total number of eggs laid per female was directly proportional to the pupal mass at eclosion (fig. 9), a phenomenon that is common among insects (Norris 1934; Shorey 1963; Martyn 1965; Engelmann 1970).

At 35°C only one out of twenty pairs of moths mated. This female had a pupal mass of 83 mg and laid 142 eggs. The point is plotted on fig. 9, but is excluded from further statistical analysis.

The T. tapiacola females held under winter conditions laid fewer eggs than those held at the three warmer temperatures (Analysis of covariance and Newman-Keuls Test: p<0,001 for winter v's summer and 28/22°C; 0,01<p<0,05 for winter v's 25°C). Egg production was also lower at 25°C than under the summer conditions (0,01<p<0,05), although

the differences between summer and 28/22°C and between 25°C and 28/22°C were not significant. The overall average fecundity of T. tapiacola at the five temperature regimes was 309 (range 53 - 737) eggs per female.

Mann (1969) recorded an average of 150 to 190 (maximum 376) eggs per female during mass-production of T. tapiacola in Australia. This is lower than the average of 309 recorded here and is probably due to the fact that Mann's averages were derived from the total number of eggs laid by two or more females in the same cage. Under those conditions, the average per female was reduced if some of them had not mated. Also, Mann (1969) did not relate fecundity to female size, and the insectary reared moths in Australia may have been smaller on average, and therefore less fecund, than those measured during this study.

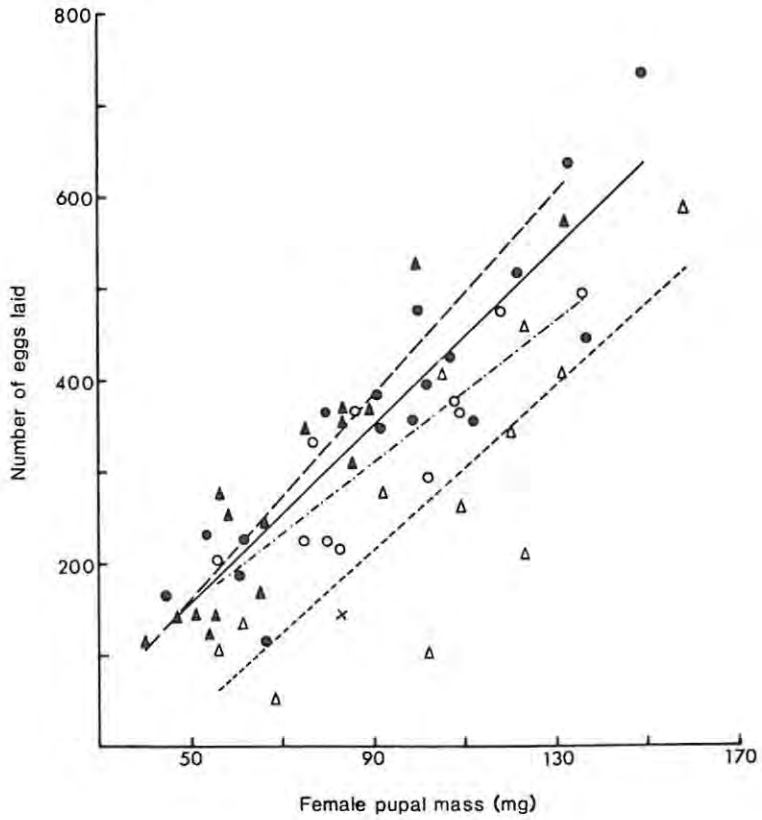

Fig. 9. Fecundity of T. tapiacola relative to pupal mass at 28/22°C (●——●; r = 0,91); 25°C (o-·-·-o; r = 0,86); Summer (▲--▲; r = 0,93); winter (Δ----Δ; r = 0,83) and 35°C (X).

3.6 The incubatiion period and percentage egg hatch.

The incubation periods and percentage hatch of T. tapiacola eggs were measured at seven different temperatures, ranging from 10°C to 40°C. The eggs subjected to each temperture were laid over a ten-hour period by eight gravid females that were less than three days old.

No eggs hatched at 10°C and 40°C, and the average incubation period was inversely related to temperature, ranging from 38 days at 15°C to three days at 35°C (fig.10). The time interval between the hatch of the first and last eggs in a batch was also affected by temperature. At temperatures of 25°C and higher, the eggs that had been laid on the same night all hatched within a 24 hour period. At the cooler temperatures the eggs laid on the same night hatched over two or more days and up to seven days at 15°C, as represented by the vertical lines in fig. 10.

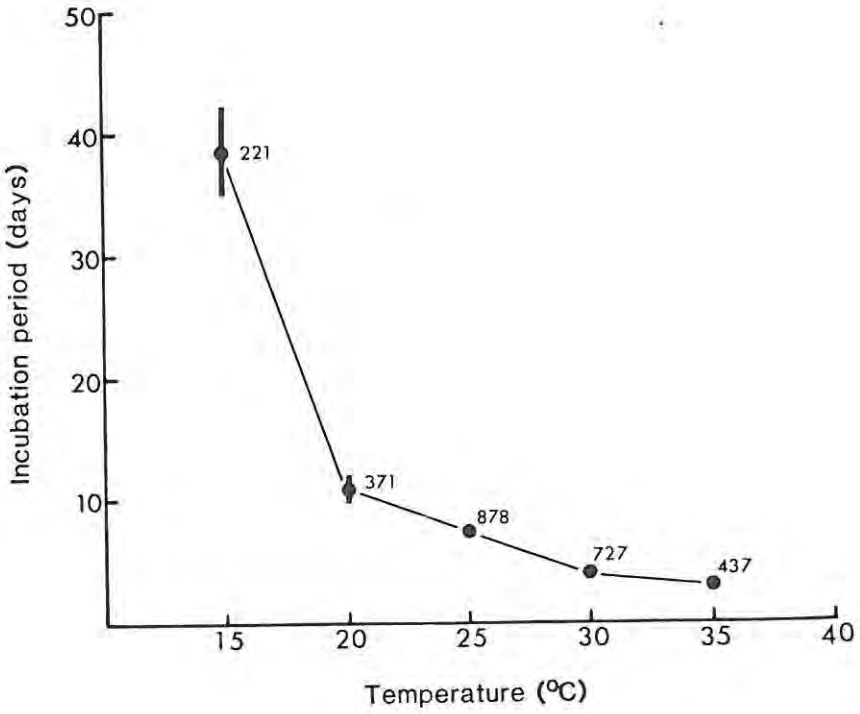

Fig. 10. The average incubation period of T. tapiacola eggs at different temperatures and the interval (vertical bars) between hatch of the first and last eggs in the batches. The number of eggs that were incubated is recorded next to each data point.

The protracted period over which the eggs hatched at the lower temperatures was probably due to the fact that the eggs in the batch were laid during a ten-hour scotophase at 22°C. Therefore, the first eggs laid in the batch developed for nearly ten hours at 22°C before they were subject to the cooler incubation temperatures. Thus these eggs were more developed than those laid later in the period, and this slight difference at the start was exaggerated by the time the eggs hatched at the lower temperatures.

After eclosion of the last larva, counts were made of the hatched and unhatched eggs in each batch. The shells of eggs that had hatched were translucent, almost colourless and had emergence holes left by the larvae as they chewed their way out of the egg. The unhatched eggs were placed in one of two categories:

(a) Embryonic larvae that had died in various stages of development were visible through the shells of some of the unhatched eggs. These were classified as fertile eggs that had failed to complete their development.

(b) The other unhatched eggs were opaque, brown coloured and were usually shrivelled by the time they were examined at the end of the expected incubation period. These eggs were either infertile, or were fertile, but the embryos had not differentiated into recognisable larval forms. As these eggs were indistinguishable, all the unhatched eggs without visible embryonic larvae were grouped together as infertile eggs.

The optimal temperatures for survival of eggs of T. tapiacola were around 20°C and 25°C. At these two temperatures 86,9% and 85,6% of the eggs hatched and less than half the unhatched eggs showed signs of larval development (fig. 11). At the higher and lower temperatures, there was a decrease in the percentage hatch of the eggs and the percentage of eggs that developed recognisable larvae, but failed to hatch, increased. No eggs hatched or showed signs of larval development at 40°C. At 10°C, 44,0% of the eggs developed recognisable larvae, but none of these hatched.

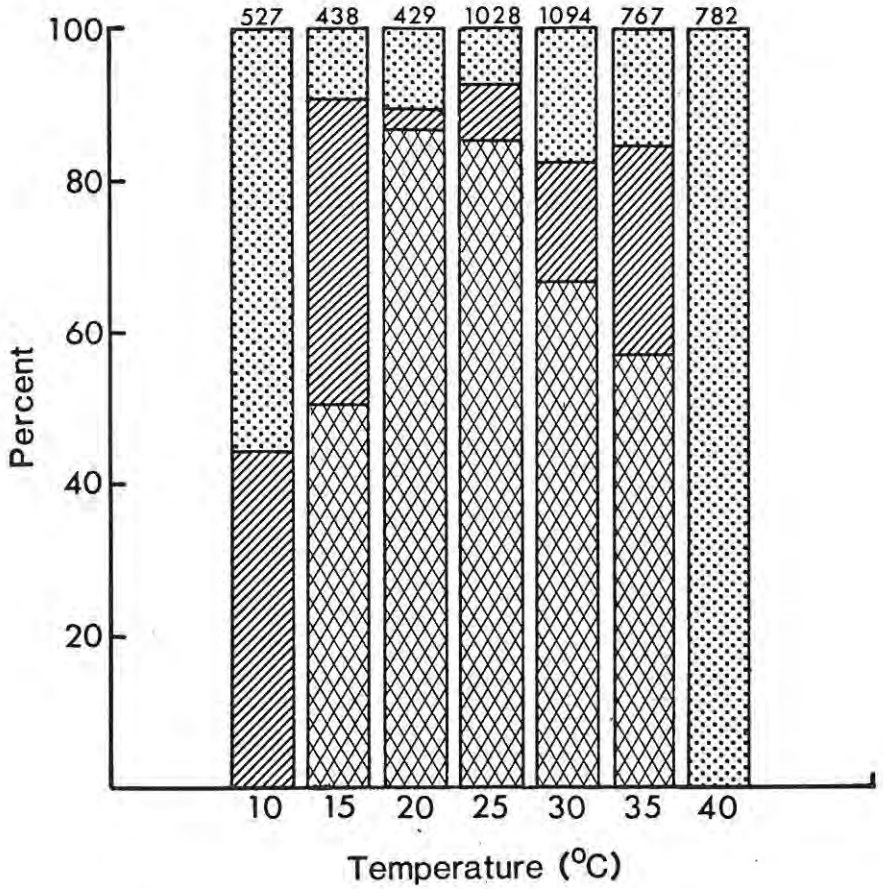

Fig. 11. The percentages of T. tapiacola eggs that hatched (cross-hatch) and that failed to hatch but contained recognisable, immature larvae (diagonal-hatch), or that showed no signs of larval development (stipple), at different temperatures. The number of eggs that were subject to each temperature is shown above each histogram bar.

3.7 Timing of larval eclosion.

Eggs of T. tapiacola were incubated under natural conditions of light, temperature and humidity to determine the time of day at which they normally hatched. Eggs that had been laid on 250 mm lengths of cotton thread were suspended horizontally over a revolving drum that completed one revolution every 24 hours. The surface of the drum was coated with "Formex" gum and was marked with 12 lines that ran parallel to the axis of the drum and divided the surface into 12 segments of equal size. Each segment took two hours to pass under the cotton thread.

Within ten minutes of hatching, the larvae of T. tapiacola lowered themselves on silk strands from the cotton thread and dropped into the glue on the revolving drum. The larvae were trapped in the glue and their position on the drum indicated in which two-hour-period accurate to within ten minutes, they had hatched. Using this method, the time of day that the eggs hatched was measured during summer (December) and during winter (August) (fig. 12).

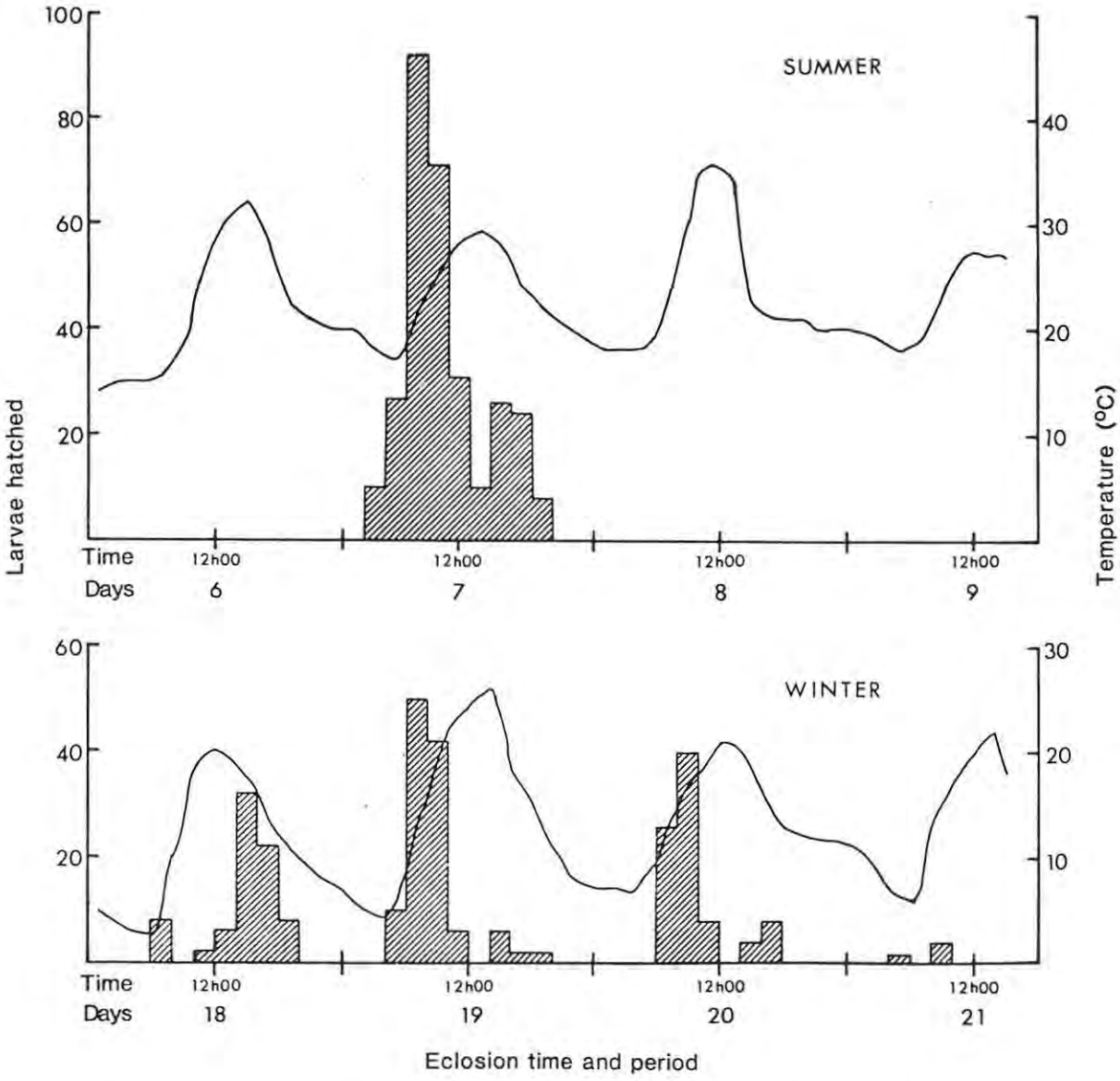

Fig. 12. The timing of larval eclosion from T. tapiacola eggs in summer (n = 301) and in winter (n = 290). A thermograph trace shows the temperatures over the eclosion period (Days = days after oviposition).

Although the time period over which the eggs of T. tapiacola hatched differed between summer and winter, the time of day at which most of the eggs hatched was the same for both seasons. During summer, larval eclosion occurred between 02h00 and 20h00 on the seventh day after the eggs were laid (fig. 12). Most of the eggs (54,2%) hatched in the four hour period between 06h00 and 10h00 as the temperature increased. In winter, the incubation period for eggs of T. tapiacola was longer (18 to 21 days) and the eggs hatched over a period of four days (fig. 12). The percentage of the eggs that hatched on each successive day in winter was 26,9%, 40,7%, 30,3% and 2,1%. On the first day of the eclosion period, the eggs hatched between 14h00 and 18h00 as the temperature was falling. On the three following days, most (77,1%) of the eggs hatched between 06h00 and 10h00, while the temperature was rising.

3.8 Effect of density on larval development.

The optimal number of larvae that could be reared in each larval cage during a single generation was determined by comparing survival and development of the larvae at densities of 50, 100, 150, 200, 250, 300, 350 and 400 larvae per cage (25 ℓ capacity). At each density, two larval cages were filled with 3 kg of fresh jointed cactus cladodes. A predetermined number of newly-hatched larvae (less than twelve hours old) were then placed in each of the cages in an insectary with a fluctuating temperature regime of 28/22°C. After the larvae had pupated, a number of pupae were removed from each cage and weighed. The sex and date of emergence of all the adults from each cage was recorded to determine the sex ratio, percentage larval survival and developmental duration of T. tapiacola at the different densities.

The sex ratio of the adults that emerged from the larval cages ranged from 0,95 males per female to 2,10 males per female (Table 11). Although the number of males that emerged per female varied considerably, there was no correlation between the sex ratio and the density at which the larvae were reared. Apart from the initial density of 50 larvae per cage, where the females that emerged outnumbered the males by one, none of the cages produced more female moths than males (ie: a

male:female ratio of less than one) and the average ratio from all the cages was 1.25 males per female (426:341).

The developmental time of T. tapiacola from egg hatch to adult eclosion, at the different larval densities are also presented in Table 11. An analysis of variance showed that some of the developmental times of both the males and females differed significantly. However the differences were too small to be resolved with multiple range tests (Zar 1974) and they had no implications for the mass-rearing programme. The overall average developmental time of 40,5 days for the males was significantly shorter than the 41,5 days for the females ($t = 2,49$; $0,01<p<0,05$). There was no correlation between the developmental times and the initial densities of larvae that were placed in the cages.

Table 11. Adult sex ratio and mean (±1 standard error) developmental time from egg hatch to adult eclosion in T. tapiacola reared at different larval densities. n = number of males and females that emerged at each density.

Larvae /cage	Sex Ratio ♂ : ♀	Developmental time (days) Males	n	Females	n
50	0,95	40,5 ±1,2	21	40,8 ±1,0	22
100	2,10	39,4 ±0,6	65	40,6 ±0,8	31
150	1,03	41,6 ±0,8	61	43,8 ±1,0	59
200	1,14	39,0 ±0,5	87	39,9 ±0,5	76
250	1,28	39,0 ±0,6	92	40,6 ±0,8	72
300	1,27	39,9 ±0,6	80	40,2 ±0,7	63
350	1,07	42,0 ±1,2	16	41,7 ±2,5	15
400	1,33	42,3 ±3,0	4	44,7 ±2,7	3
Total	1,25	40,5 ±0,3	426	41,5 ±0,3	341
ANOVA		F = 2,26 0,01<p<0 05		F = 2,51 0,01<p<0,05	

The percentage of larvae of T. tapiacola that survived to become adults was highest (49,0%) from cages with 100 larvae per cage (fig. 13). At initial larval densities up to 200 larvae per cage, crowding had little or no effect on larval survival, which fluctuated between 40% and 49%. Most mortality at these low larval densities was due to one of three causes: (i) some first-instar larvae failed to penetrate the cuticle of the cactus and never started feeding; (ii) other larvae penetrated into the cactus, but were either repelled by or encapsulated in gum exuded by the plant (Hoffmann 1976); (iii) some larvae died because they became trapped in the drying husk of the cladodes that they had destroyed. These three causes of mortality were unrelated to the initial densities of larvae that were placed in the cages and accounted for between 50% and 60% of the mortality suffered by the larvae, even at the lowest densities. At larval densities of 250 larvae per cage and higher, percentage survival decreased with increasing density. Starvation as a result of increased competition for food at the higher initial larval densities meant that fewer larvae survived to become adults.

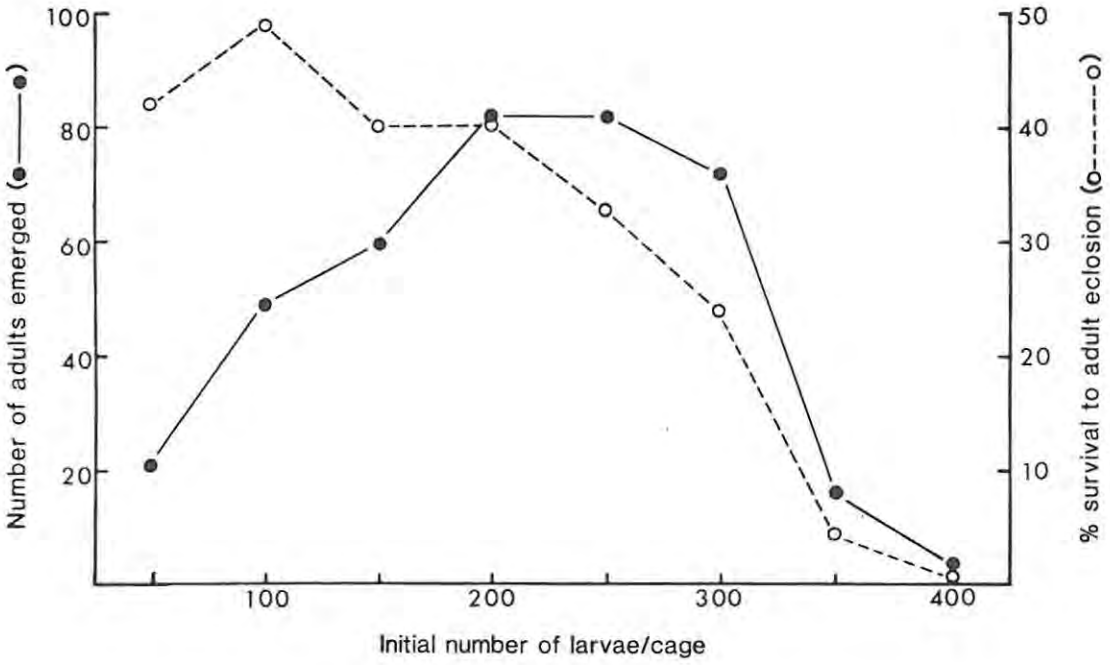

Fig. 13. The mean number of T. tapiacola adults that emerged in cages with different initial larval densities, and the corresponding percentage survival of larvae from egg hatch to adult eclosion.

Although the percentage survival of larvae was highest (49%) in cages with an initial density of 100 larvae, the total number of moths that emerged was highest (82 adults per cage) in cages that had an initial density of 200 and 250 larvae per cage (fig. 13).

The mean pupal mass of T. tapiacola decreased as larval densities increased, up to 250 larvae per cage for females and 300 larvae per cage for males (fig. 14). The decrease in pupal mass at initial larval densities of 200 per cage and lower was not due to starvation because there was an excess of food in the cages and not all the cactus was utilised by the larvae. Increased crowding apparently had other effects on the larvae.

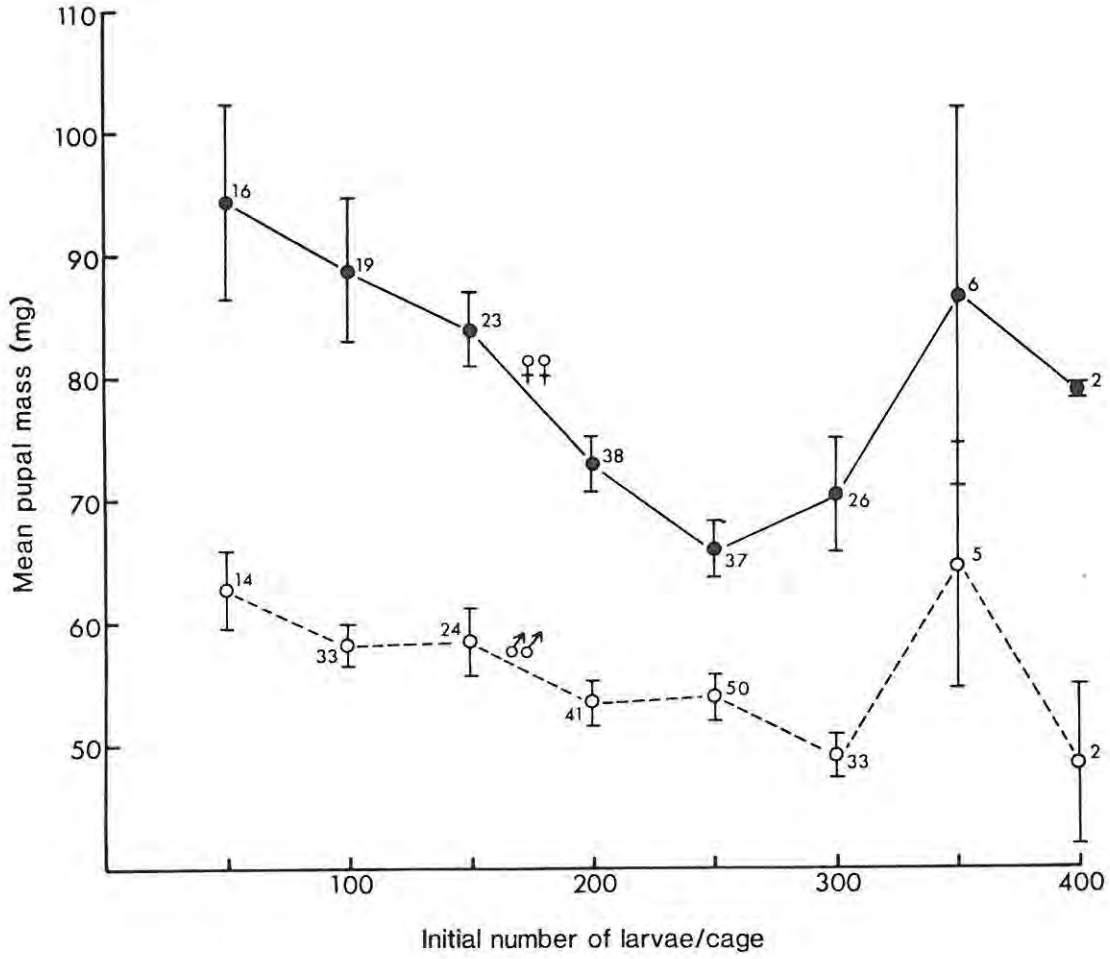

Fig. 14. The mean (±1 standard error) mass of male and female pupae of T. tapiacola from cages with different initial larval densities. The numbers of pupae that were weighed are shown next to each data point.

First-instar larvae of T. tapiacola are intolerant of other larvae in their proximity. When two larvae come into contact, one, or both, retreats and moves away from the other. Such contacts may cause the larvae that have started to penetrate the cactus to leave their feeding sites and restart the penetration process elsewhere. Although it was not measured, larval interference must have increased with the density of larvae that were placed in the cages, and this in turn would have delayed the settling time of the larvae.

Dempster (1971) showed that larvae of Tyria jacobeae L. (Lepidoptera: Arctiidae), that were starved of food for three days after egg hatch, weighed less at pupation than larvae that were not starved. Apparently the T. jacobeae larvae never recovered from the initial starvation and this effect may also have permanently retarded T. tapiacola in the larval cages. As a result, small adults emerged in the cages with higher initial larval densities, even though there was an excess of food available.

At initial densities of 200, 250 and 300 larvae per cage, there was no excess food and the average pupal mass was lowered further because the larvae completed their development with less food. The few adults that emerged in the cages with an initial density of 350 and 400 larvae per cage differed considerably in size as shown by the large standard errors at these densities in fig. 14.

The total number of eggs that were laid by all the adults that emerged per cage at each larval density was calculated using the equation:

$$E = N(4{,}88m - 100{,}7)$$

where E is the calculated total number of eggs; 4,88 and 100,7 are the common regression coefficients of pupal mass on fecundity at 25°C, 28/22°C and summer conditions (fig. 9); m is the mean female mass at any particular larval density (fig. 14); and N is the number of females that emerged per cage at that density (fig. 13).

Most eggs (9600 in total) were produced by the complement of females that emerged from cages with an initial density of 200 larvae/cage,

and there was therefore a 48 fold increase in numbers from one generation to the next. The increase per generation was higher in the cages with lower initial larval densities and was highest (61 fold) at 150 larvae/cage. For mass-production, however, the initial larval density that produced the largest number of individuals per generation (in this case 200/cage) was considered preferable to the initial larval density with the highest increase factor (ie. 150/cage). In other words, a density of 200 larvae/cage results in the maximum yield of eggs per unit of cactus.

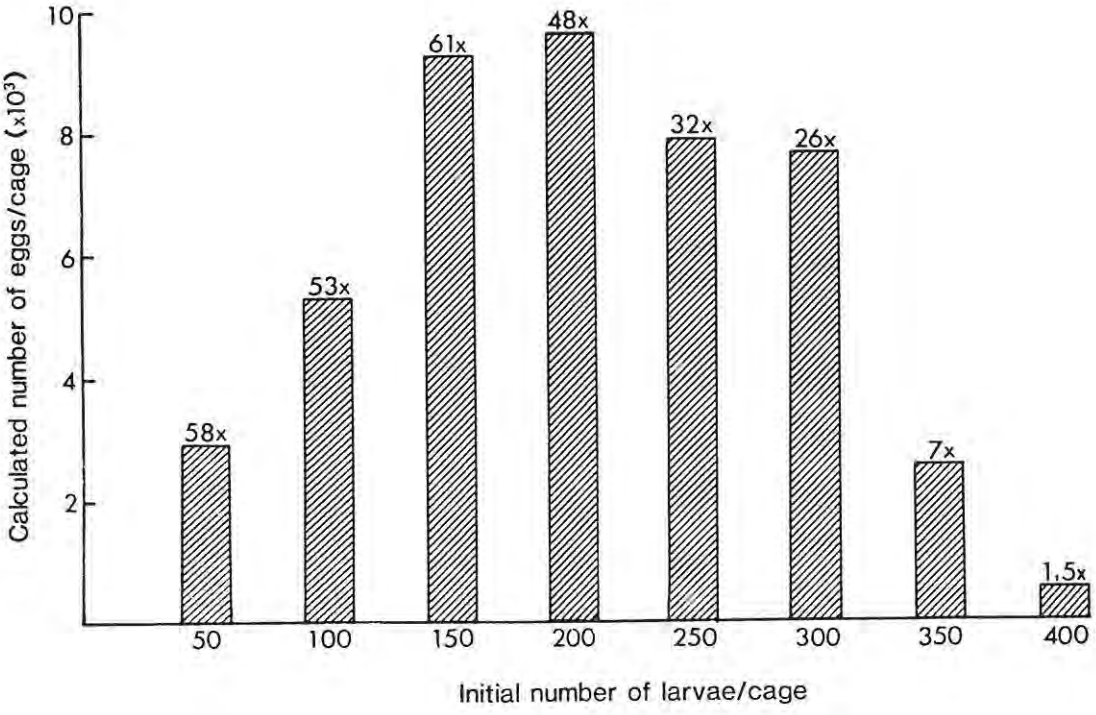

Fig. 15. The calculated egg production of T. tapiacola (see text) from cages with different initial densities of larvae. The potential increase in numbers from generation to generation at each density is shown by the number on top of each histogram bar.

3.9 Temperature effects on larval development.

The optimal temperature for larval development of T. tapiacola was measured by rearing larvae from egg hatch to adult eclosion at five

different temperatures; 20°C, 24°C, 28°C, 32°C and 36°C. At each temperature, 1000 newly-hatched larvae (less than twelve hours old) were placed in five cages in groups of 200 per cage. The sex and date of eclosion of all the adults were recorded and the percentage survival of both the male and female larvae was calculated for each temperature (fig. 16). No adults emerged from larvae held at 36°C.

At 24°C significantly fewer female adults emerged than males (paired 't' = 3,44; $0,01<p<0,05$). This does not imply that there was reduced survival of females because there is no way of determining the sex ratio of the first-instar larvae that were placed in the cages at the start of each experiment. At all the other temperatures there was no difference in survival of the male and female larvae. The survival of males and females combined was highest at 24°C and 28°C, and temperatures around this range were considered best for rearing the larvae.

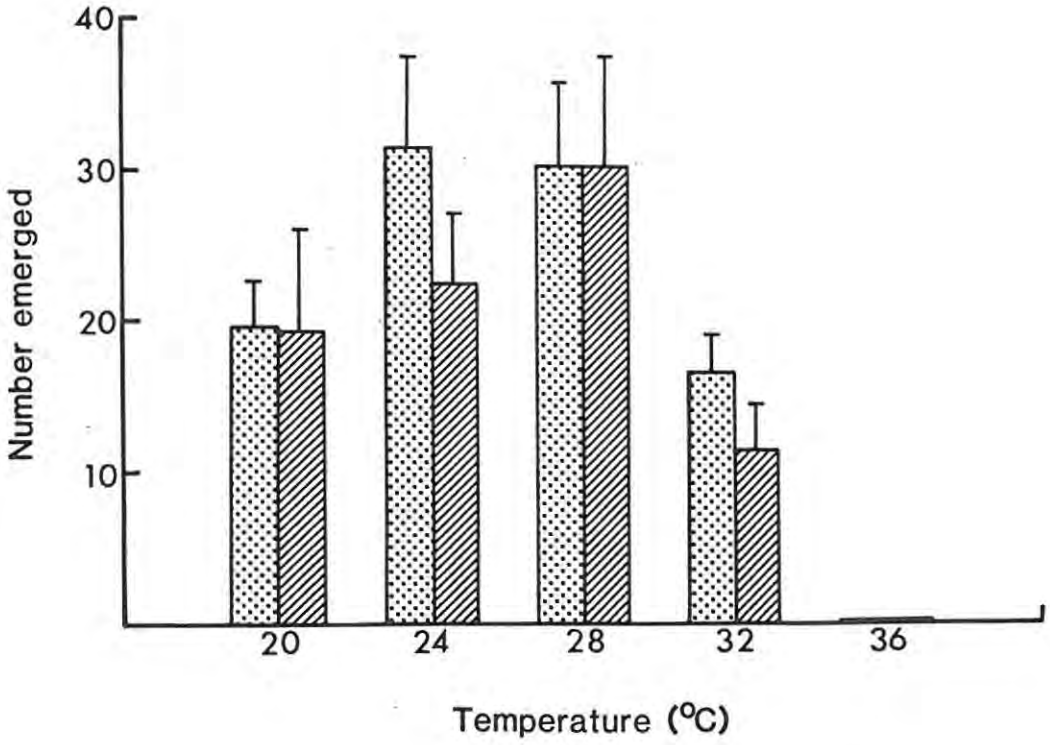

Fig. 16. The mean (+1 standard error) number of male (stipple) and female (diagonal hatch) adults of T. tapiacola that emerged per cage, at different temperatures, from an initial density of 200 larvae .

The average developmental durations of T. tapiacola from egg hatch to adult eclosion at the different temperatures are shown in Table 13. The developmental times decreased with increasing temperatures and the shortest times that were measured for a male and female respectively at 32°C were 25 and 26 days. At each temperature, the developmental time of the females was significantly longer than that of the males.

Table 13. The mean (±1 standard error) developmental time of T. tapiacola, from egg hatch to adult eclosion at different temperatures. n = the number of adults that emerged at each temperature.

Temperature °C	Developmental time (days) Males	n	Females	n	't'
20	100,9 ±0,9	97	104,6 ±0,7	96	2,35 0.01<p<0,05
24	57,7 ±0,6	156	61,6 ±0,8	112	4,30 p<<0,001
28	40,3 ±0,5	150	42,3 ±0,5	150	4,52 p<<0,001
32	32,4 ±0,5	84	33,6 ±0,4	58	2,87 0,01<p<0,001

3.10 Cold storage of eggs.

The optimal temperature at which eggs of T. tapiacola could be stored was calculated by measuring the percentage hatch of eggs that had been held at either 5°C, 10°C or 15°C for different lengths of time. At each temperature, approximately 8000 newly-laid eggs (less than 12 hours old) were divided into four batches of approximately 2000 eggs. One batch of 2000 eggs was placed directly in the cold cabinet at one of the above temperatures. The other three batches were incubated at 25°C for 2, 4 and 6 days respectively before being cooled. Every five days, a sample of approximately 50 eggs was taken from each batch in cold storage and returned to 25°C. After larval eclosion, the eggs were examined and the percentage that had hatched was recorded.

The percentage hatch of eggs that were stored at 5°C and 10°C declined more rapidly with storage time than the the eggs that were stored at 15°C (fig. 17). The difference in the percentage hatch of eggs stored at the three cold temperatures was most marked for eggs that were placed in the cold cabinets within 12 hours of being laid (fig. 17A) and least marked for eggs that were incubated at 25°C for 4 days before being cooled (fig. 17C). Storage at 5°C usually resulted in a lower percentage hatch of the eggs than storage at 10°C for an equivalent period of time. Storage at 15°C was always less detrimental than the two lower temperatures.

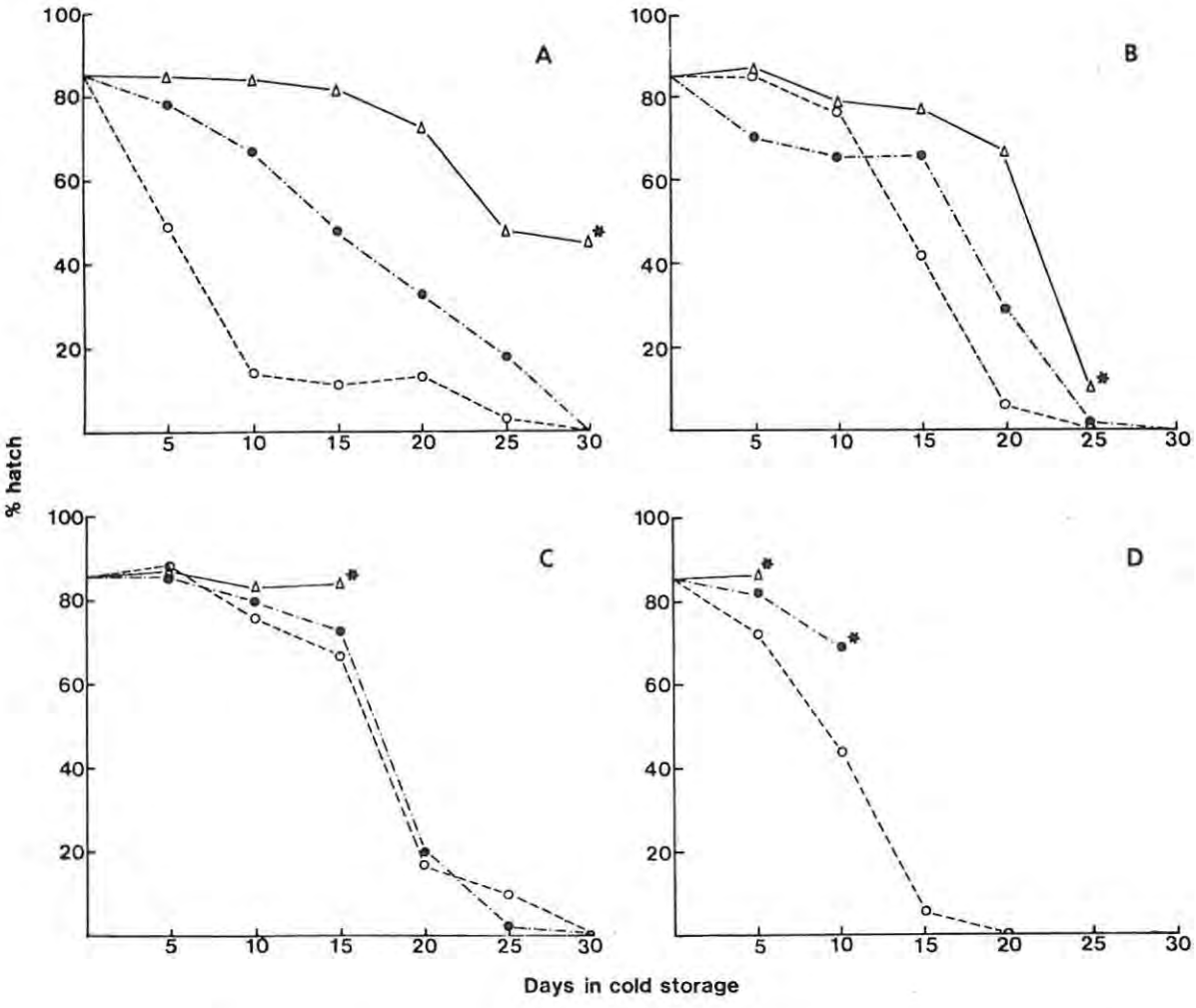

Fig. 17. The percentage hatch of T. tapiacola eggs after storage at 5°C (o------o), 10°C (●-·-·-●) and 15°C (Δ——Δ) for up to 30 days. The eggs were either placed in cold storage within 12 hours of being laid (A) or were incubated at 25°C for 2 days (B), 4 days (C) and 6 days (D) before being cooled. * = egg batches hatched while in cold storage.

The longest period that the eggs of T. tapiacola could be stored before the percentage hatch drastically decreased was for 15 days at 15°C, providing the eggs were not incubated for more than four days at 25°C before being placed in cold storage. Eggs that had been incubated for six days at 25°C before being cooled hatched within ten days, while still being held at 15°C (fig. 17D). The percentage hatch of the eggs that were cooled within two days of being laid decreased after they had been held at 15°C for twenty days (fig. 17A & B).

As a result, whenever eggs of T. tapiacola needed to be stored, newly laid eggs (less than 12 hours old) were kept at 15°C, usually for a maximum of 15 days, but occasionally for up to 20 days.

Most of the batches of eggs that were placed in cold storage were required for field releases. It was therefore essential that they all hatched within 24 hours of each other so that the releases could be made with the larvae all in the same stage of development. As a result, the period between removal of the eggs from cold storage and larval eclosion was measured in 20 batches of eggs that were held at 15°C for from one to 20 days. Approximately 2500 newly laid eggs were placed in cold storage within 12 hours of being laid. Every day for 20 days, a batch of between 67 and 141 eggs was removed from cold storage and incubated at 25°C. The eclosion time of the larvae from the eggs in each batch was recorded using the methods described in section 3.7.

The eggs of T. tapiacola hatched, on average, four hours earlier for each day they were held at 15°C (fig. 18). The time delay between the hatch of the first and last eggs of the batches ranged from 21 to 48 hours, but was not related to the number of days that the eggs were held at 15°C. Using these data, batches of eggs could be stored for up to 20 days, at 15°C, and the approximate time that the eggs would hatch after being returned to 25°C could be predicted. The eggs were then selectively removed from cold storage and returned to 25°C at staggered intervals to synchronise the time at which they hatched.

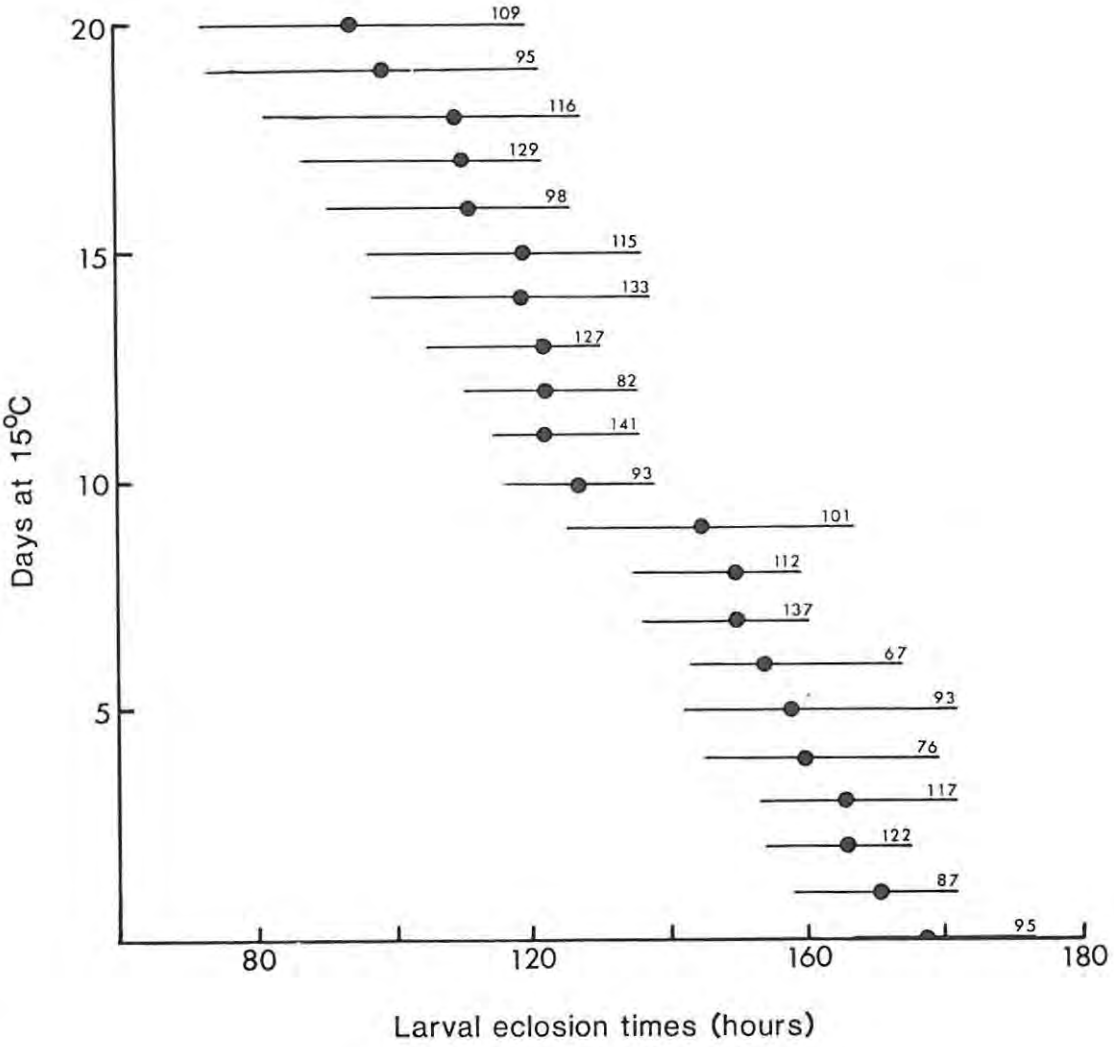

Fig. 18. The period between removal from cold storage and larval eclosion of T. tapiacola eggs that were stored at 15°C for from one to 20 days. The horizontal lines represent the interval between which the first and last eggs hatched in each batch. Points show the time taken for 50% of the eggs to hatch. The numbers of eggs in the batches are shown for each data point.

3.11 Cold storage of adults.

The fecundity, mating success and the percentage hatch of eggs laid by mated females were measured after the adults of T. tapiacola had been stored at 15°C in continuous light for 5, 10 or 15 days. The moths were placed in cold storage within 12 hours of emergence and before

Table 14. Mating success and percentage egg hatch in T. tapiacola after virgin adults had been held at 15°C in continuous light for up to 15 days. n = number of pairs subject to each treatment.

Days at 15°C	n	% of pairs that mated	% egg hatch
0	42	59,5	84,6
5	21	61,9	79,8
10	22	36 4	86,6
15	20	5,0	0,0

they had mated. After being removed from the cold-cabinet, the moths were paired singly in oviposition cages under an alternating temperature regime of 28/22°C with a 14 hour photophase. The eggs laid by the females were removed daily from the cages and incubated for ten days at 25°C. After larval eclosion, the hatched and unhatched eggs from each female were counted and the percentage of eggs that had hatched was recorded.

Mating success of T. tapiacola adults that were stored at 15°C for five days was not significantly different from the moths that were not cooled (Table 14). After ten days at 15°C, the percentage of pairs that mated decreased and after 15 days at 15°C only one pair out of twenty mated. The female from this particular pair laid only 47 eggs, none of which hatched. The percentage hatch of the eggs laid by the females held at 15°C for up to 10 days was not reduced.

Therefore, storage of adults of T. tapiacola for up to 10 days at 15°C did not effect the fecundity of the female moths (Analysis of covariance; F = 0,77 for comparison of slopes; F = 1,72 for comparison of elevations; ie. the slopes and elevations were not significantly different) (fig. 19).

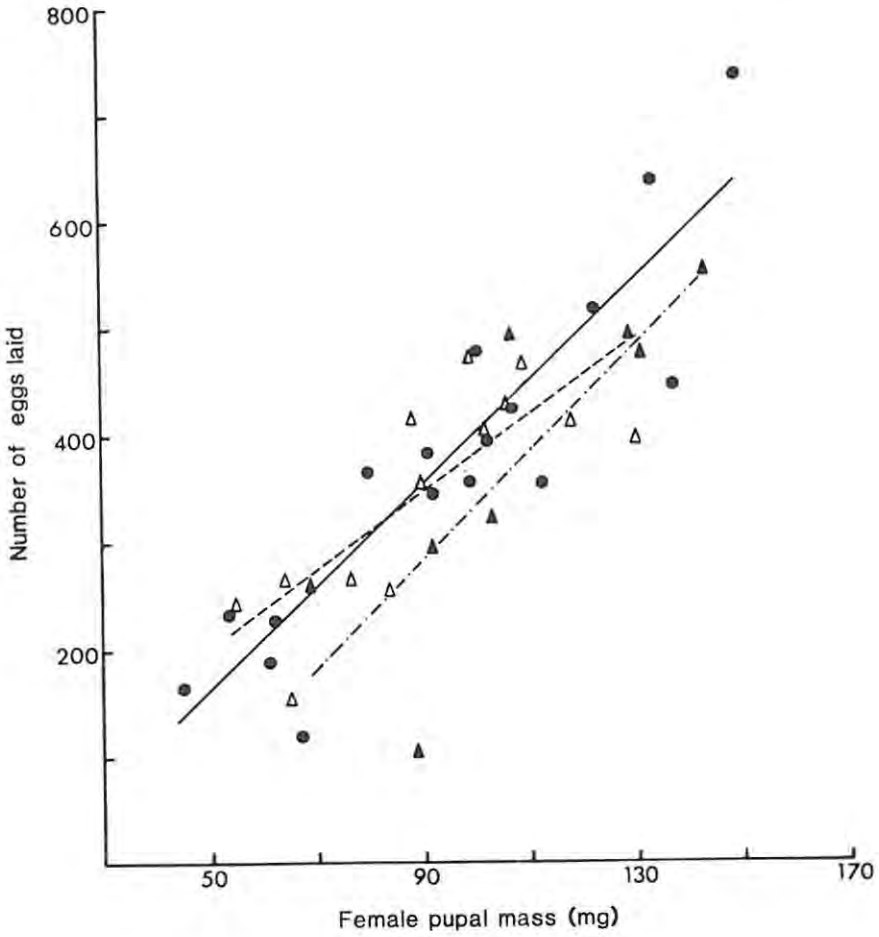

Fig. 19. Fecundity of T. tapiacola females that had been held at 15°C in continuous light for either 0 days (●——●; r = 0,90), 5 days (Δ-----Δ; r = 0,79) or 10 days (▲-·-·-·-▲; r = 0,81).

3.12 Conclusions.

The results reported here were used to rationalise and increase the efficiency of the mass-rearing programme with T. tapiacola. The following procedures were adopted as a result of these findings.

(a) The adult moths were held in communal oviposition cages with up to ten pairs of moths per cage, because this maximised the number of females that mated.

(b) The adults were held at an alternating temperature regime of 28(±2)°C during a 14 hour photophase and at 22(±2)°C during a ten hour scotophase. This regime was optimal for adult survival, mating and oviposition.

(c) The T. tapiacola eggs were usually incubated at 25°C, although higher and lower temperatures were used, when necessary, to enhance or suppress eclosion of the first-instar larvae.

(d) Two hundred T. tapiacola larvae were placed in each cage with 3 kg of jointed cactus cladodes and reared at the same fluctuating temperature regime (28/22°C) under which the adults were maintained. These conditions resulted in the maximum increase in numbers from one generation to the next.

(e) In addition, at the end of each generation, the insectaries were scrubbed and heated to 45°C for five to seven days to eliminate secondary colonisers (eg. ants, spiders, mites, aphids, mealybugs, etc.) that otherwise became common in the cages. The ability to hold eggs and adults in cold storage over this period facilitated the process.

A comparison of fig. 13 and fig. 16 shows that the overall survival of T. tapiacola larvae at 28°C and an initial density of 200 larvae per cage was 40,2% in fig. 13 and 35,5% in fig. 16. The only difference between the two sets of conditions was the time of the year at which the experiments were conducted. The data for fig. 13 were obtained during March/April, and the data for fig. 16 during August/ September. In winter (May to October), jointed cactus enters a dormant phase and the plant nutrients translocate to and concentrate in the underground tuber (Zimmermann & van de Venter 1981). As a result, the aerial parts of the 'dormant' overwintering jointed cactus plants were probably less nutritious than the growing plants collected during summer. In T. tapiacola, the change in the quality of the host plant was not critical, although it may have caused the lowered larval survival and the problem may assume more serious proportions when other cactophagous insect species are reared in the insectary.

4. RELEASES OF T. TAPIACOLA IN SOUTH AFRICA

In South Africa, jointed cactus grows over a wide area in a variety of habitats from moist areas of dense shade beside perennial rivers to dry, exposed areas of semi-desert and low scrub vegetation. The morphological appearance of O. aurantiaca varies considerably in the different habitats and is largely determined by the amount of direct sunlight the plants receive. Two basic growth-forms can be distinguished: plants in direct sunlight have a 'typical' growth-form, while plants in dense shade have an 'etiolated' growth-form. The two types are not always distinct and there is a continuum of intermediate forms, dependant on the degree to which the plants are shaded. The two main growth-forms were distinguished and described in Appendix 2.

4.1 The release sites.

T. tapiacola has been released at seven different localities in South Africa, mainly around Grahamstown and north of Kimberley (fig. 20). Each locality is characterised by a particular climate, natural vegetation and predominant growth-form of jointed cactus. Most (almost 85%) of the T. tapiacola eggs, larvae and adults that have been released were deployed at the first three release sites listed below.

(i) Andries Vosloo Kudu Reserve (33.08S 26.41E)

This is a state owned nature reserve situated near Fort Brown, on the Great Fish River and approximately 22,5km north-east of Grahamstown.

The jointed cactus on the reserve was not controlled with herbicides because the authorities were concerned about the detrimental side effects of the chemicals on the indigenous flora of the area. As a result, the jointed cactus plants were manually up-rooted from the soil and piled in large heaps of up to 20 m^3, then sprayed with herbicide.

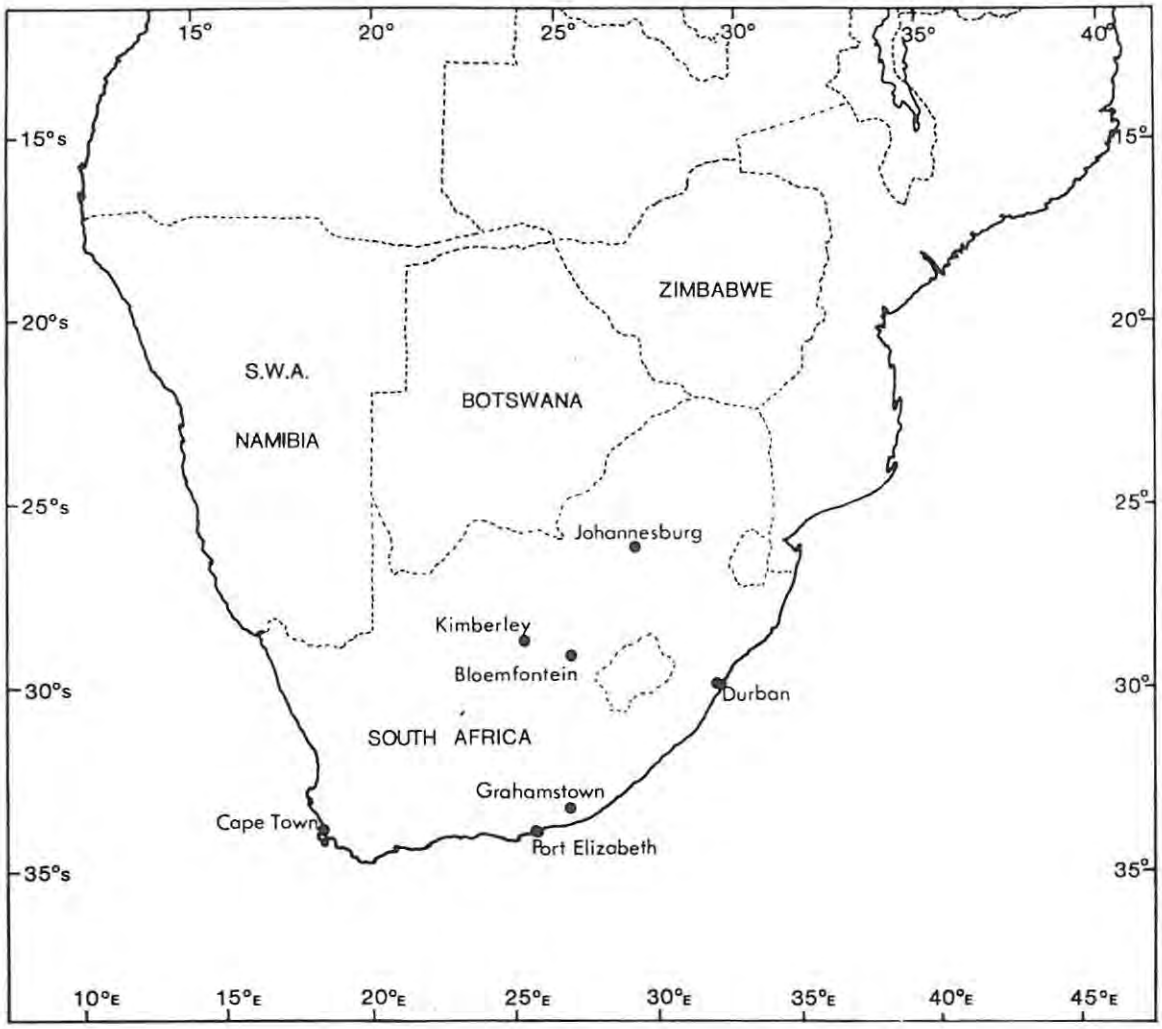

Fig. 20. Map of southern Africa showing the relative positions of Grahamstown and Kimberley, the main areas for releases of T. tapiacola.

The release site covered approximately 6 ha and followed a watercourse that only flowed after heavy or prolonged rains in the region. The release area was demarcated by two dirt tracks that ran parallel to each other, approximately 500 m apart on either side of the watercourse.

No control measures had been practised on the jointed cactus in the release area for at least fifteen years and large thickets of O. aurantiaca were common in patches. Large trees, mainly Combretum caffrum (Ecklon & Zeyher) Kuntze, were abundant along the watercourse and the jointed cactus bushes under the trees was mostly the 'inter-

mediate' growth-form, except for a few 'etiolated' plants under the denser thickets of bush, mainly Rhus refracta Ecklon & Zeyher. Between 20 and 50 m away from the watercourse, the trees gave way to open grassland and False Karroid Vegetation (Acocks 1975), where 'typical' jointed cactus was dominant.

(ii) Mosslands Farm (33.24S 26.26E)

Mosslands is a privately owned farm situated approximately 12,5 km south-west of Grahamstown.

The jointed cactus at Mosslands was mostly controlled with herbicides but a rectangular area of approximately 4 ha was set aside for biological control. The area was delimited by ploughed crop-lands on two sides and the boundary fence of the farm on the other.

The Kariga River flows through the plot and the dominant vegetation type is riverine Valley Bushveld (Acocks 1975). Most of the jointed cactus growing in the bare leaf litter, below the dense canopy that is typical of Valley Bushveld, was of the 'etiolated' growth-form. However, there was also approximately 1 ha of open grassland and low-growing False Karroid Vegetation on an east facing slope of the river bank. 'Typical' jointed cactus was abundant in this clearing and 'intermediate' growth-forms occurred around the edges and under the bushes and trees that had regrown in the area.

(iii) Thursford Farm (33.12S 26.22E)

Thursford is a privately owned farm situated approximately 19km west-north-west of Grahamstown.

The jointed cactus at Thursford is mostly the 'typical' growth-form, among the False Karroid vegetation in the area, mainly Pentzia spp. (Acocks 1975). 'Intermediate' growth-forms of jointed cactus also occur among the loose thickets of taller, indigenous bushes and trees, predominantly Papea capensis Ecklon & Zeyher and Acacia karroo Hayne.

A 2 ha release site within the infested area of the farm was marked off with fence poles and excluded from the herbicide spray programme. T. tapiacola was only released within the demarcated area, but because of the inherent deficiencies in the application of herbicides (Zimmermann 1979), jointed cactus was always available outside the release area for the natural spread of the moths.

(iv) Thomas Baines Nature Reserve (33.24S 26.30E)

This is a State owned nature reserve situated approximately 10,5 km south-south-west of Grahamstown.

The jointed cactus at Thomas Baines was also controlled manually because of the detrimental side effects of the herbicide. The uprooted jointed cactus plants were placed in pits, about 2 m deep, and sprayed with herbicide before being covered with approximately 0,5 m of soil.

An area of about 5 ha, bounded by the Settlers Dam reservoir on one side and the access road to the reservoir wall on the other, was set aside as a release site. The habitat was similar to Mosslands and all the cactus in the release area was of the 'etiolated' growth-form, growing in the shade of the Valley Bushveld vegetation.

(v) Gannahoek Farm (33.51S 26.15E)

Gannahoek is a privately-owned farm situated approximately midway between Grahamstown (33.18S 26.32E) and Adelaide (32.42S 26.17E).

No special area was demarcated for biological control, but releases were confined to a strip, approximately 100 m wide and 500 m long, along the banks of of the Koonap River.

Most of the cactus on the farm was the 'typical' growth-form, among Pentzia spp., except along the watercourses and river banks where 'intermediate' growth-forms were predominant under the larger bushes and trees.

(vi) Sydney-on-Vaal Estate (28.27S 24.18E)

Sydney-on-Vaal is a large privately owned area of farmland situated approximately 50 km north-west of Kimberley.

Most of the jointed cactus at Sydney-on-Vaal was restricted to an area of land between the Vaal River and the extensive irrigated croplands of the estate. There was no D. austrinus in the area when it was selected as a release site for T. tapiacola, and C. cactorum was only present at low levels and had very little impact on the weed. No chemical or mechanical control measures were practised against O. aurantiaca on the estate, and thickets of jointed cactus up to 100 m^2 in area were common. This was considered an ideal site to study the impact of T. tapiacola on O. aurantiaca in the almost complete absence of any other biological control agents.

(vii) Le Rouxrivier (26.23S 24.58E).

Le Rouxrivier is a private farm situated approximately 245 km north of Kimberley in the north western sector of the Cape Province.

There was no O. aurantiaca in this area and T. tapiacola was released onto an unidentified Opuntia sp., close to O. inermis De Candolle. The cactus covered an area of approximately 6 ha along the banks of a dry watercourse, below a weir. Parts of the infestation were impenetrable and there was no insect damage on the plants.

The release of T. tapiacola in this area was unplanned. A consignment of larvae destined for release at Sydney-on-Vaal, on 4th June 1980, were withheld, because the cactus in that area had been almost eradicated by the cochineal. On the following day, the larvae were released during an inspection of the Opuntia sp. infestation at Le Rouxrivier. The release was made on the off-chance that T. tapiacola might colonise the cactus. Six months later, the infestation was surveyed for signs of T. tapiacola damage, but there were no signs that the larvae had survived. Nothing further is reported on this release or release site.

4.2 Climate at the release sites.

The temperatures and relative humidities were recorded continuously for one year after the first releases of T. tapiacola at Thursford Farm and Andries Vosloo Reserve, and for 11 months at Mosslands Farm. The temperatures recorded at Kimberley, from Anon (1978), were used to compare Sydney-on-Vaal to the other release areas. The average rainfall for Mosslands was obtained from farm records and for the other sites from Anon (1978). These climatic statistics are summarised in fig. 21 and Appendix 3.

The temperatures at the three main release sites were relatively mild and never dropped below freezing, even after an exceptional snowfall at Mosslands on 20th June 1976. The highest temperatures recorded were at Andries Vosloo where 40°C was exceeded on eight days during the year, with a maximum of 44,5°C. At Thursford, the temperature once rose to 40°C and at Mosslands the maximum was 39°C, on three days out of the eleven months. Throughout the year, the average daily minimum temperatures were almost the same at all three release sites. However, between December and March, and in June, the average daily maximum temperature at Andries Vosloo was 3°C to 5°C higher than at Mosslands and Thursford Farms. Thus, the average summer temperatures at Andries Vosloo were higher than at the other two localities.

On average, Thursford received 690 mm of rain a year, 30 mm more than Mosslands and 139 mm more than Andries Vosloo. Although on average more rain fell during spring and autumn at all three localities, the pattern of rainfall throughout the year was erratic, and there was no distinct wet or dry season.

These climatic conditions may be compared with Ibarreta and Campana in South America where the two main stocks that were introduced into South Africa originated (fig. 21 and Appendix 3).

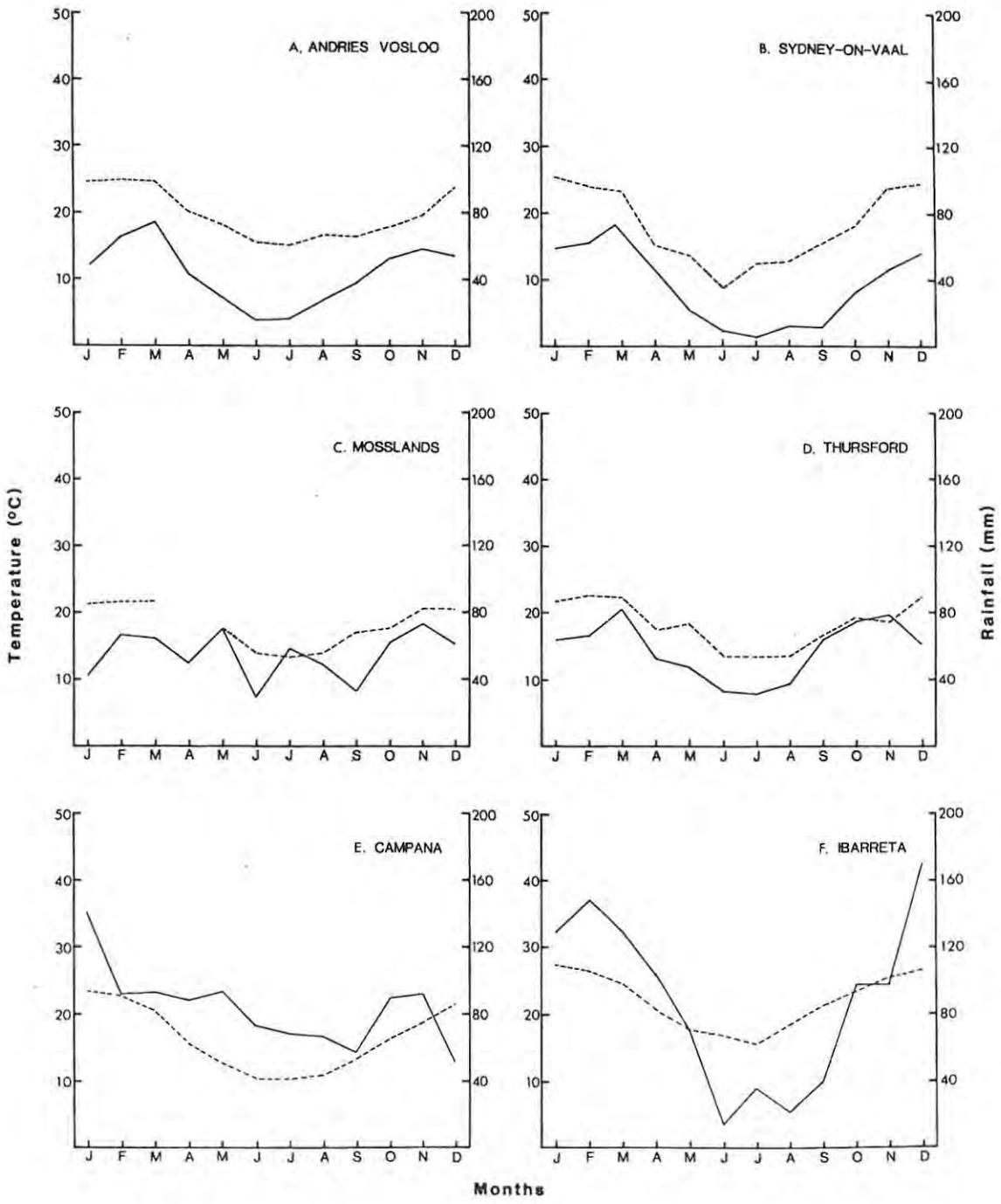

Fig 21. The mean monthly temperature (°C) (continuous lines) and rainfall (mm) (broken lines) at four of the release sites of T. tapiacola in South Africa (A - D) , and at the two source localities of T. tapiacola in South America (E & F).

4.3 The release methods.

Four different methods were developed to deploy T. tapiacola during releases in South Africa.

(i) Releases with eggs.

The first attempts to establish T. tapiacola on jointed cactus in South Africa were made by introducing the eggs of the moth onto the cactus in the field. Batches of five to twenty eggs on 20 x 20 mm squares of mosquito-netting gauze were placed in jointed cactus plants in the field.

To obtain the eggs, strips of mosquito-netting, approximately 300 mm long and 20 mm wide, were placed in oviposition cages in the insectary. The female moths oviposited on the strips which were removed from the cages each morning and cut into 20 mm sections with between five and 40 eggs attached to each section. The netting squares with eggs were transported to the release sites and pushed into place on the thorns of the jointed cactus plants, where it was anticipated they would hatch.

At Mosslands and Thursford, over 99% of the eggs were removed or destroyed by predators, especially ants and to a lesser extent mites, within one to two days of being placed out (Hoffmann 1977). As a result, although large numbers of eggs could be placed among jointed catus plants in the field in a relatively short time, the high mortality suffered by the eggs made this method impractical for mass-releases. It was therefore only used on five occasions, mainly for trials to determine the effectiveness of the method.

(ii) Releases of first-instar larvae.

Following the initial unsuccessful releases with eggs, first-instar larvae of T. tapiacola were deployed among the jointed cactus plants at the release sites.

Preparations for larval releases began up to twenty days in advance. Eggs that were laid over 15 days were accumulated and held in cold storage at 15°C to increase the numbers of larvae that were deployed on each occasion. The batches of eggs were removed from cold storage at approximately four-hour intervals and placed in an incubator at 25°C, starting with the last batch to be laid and ending with the first. The removal times were staggered in this way to bring all the eggs that had been accumulated over the 15-day period to more or less the same stage of development. Most of the eggs then hatched within 24 hours of each other. The newly-hatched larvae, less than 24 hours old, were transported to the release sites and spread among the jointed cactus plants.

The success of larval releases was gauged by following a release of approximately 2000 larvae onto 'etiolated' plants at Mosslands Farm. Ten days after the larvae had been placed among the cactus, the plants were uprooted and the number of larval entries was recorded. Of the 2000 larvae that were released, 733 (36,7%) had penetrated into and were developing in the cactus. Most of the 1267 larvae that failed to penetrate the cactus were probably preyed upon by ants and other predators.

A second release of 1000 larvae onto 'typical' jointed cactus plants at Thursford Farm was also followed to compare the relative success of the release method on the two types of jointed cactus. After ten days, only 146 (14,6%) of the larvae had penetrated these plants. The reasons for the difference in survival on the two cactus types are discussed in Chapter 5. However, because survival was lower on 'typical' plants, larval releases were concentrated on 'etiolated' and 'intermediate' jointed cactus plants.

(iii) Releases with larvae in cladodes.

The third release method developed during attempts to establish T. tapiacola on jointed cactus in South Africa, was to release larvae already feeding in loose jointed cactus cladodes.

Large numbers of first-instar larvae, all in the same stage of development, were obtained from eggs of T. tapiacola that were accumulated for up to 15 days as outlined in the previous section. The newly-hatched larvae were then spread onto trays filled with loose jointed cactus cladodes that had been collected in the field and brought back to the insectaries. The larvae were left to penetrate the cactus and start their development. They were then taken to the release site where the loose cladodes with the larvae were placed among the jointed cactus bushes.

This method was developed to preclude the large mortality suffered by the free-living, newly-hatched larvae before they penetrated into the cactus plants in the field. The method was also designed to overcome transport problems associated with trying to move large numbers of free-living larvae from the insectary to distant release sites, such as Sydney-on-Vaal. In these cases, many of the larvae would have starved to death or would have become considerably weakened during the long delay between egg hatch and arrival at the release site.

Two main problems made releases with larvae in cladodes an impractical method for large scale releases. Firstly, much time and effort was needed to collect sufficient amounts of suitable cactus for the larvae to penetrate. Secondly, the land-owners objected in principle to having jointed cactus brought onto their properties, in spite of the fact that O. aurantiaca was already abundant in the area and the T. tapiacola larvae eventually destroyed almost all the joints in which they were introduced.

As a result, this release method was only used on three occasions and no attempt was made to quantify the relative success of the method. However, many of the larvae successfully migrated from the loose cladodes into the jointed cactus plants growing in the field and continued their development.

(iv) Adult releases.

On a number of occasions T. tapiacola adults were released directly into the field in areas were jointed cactus was abundant.

Before each release, the newly emerged male and female moths were removed from the larval cages in the insectary and placed in oviposition cages for one night, at densities of up to ten pairs per cage. The following morning, after most of the moths had mated, they were removed from the oviposition cages and each was placed in separate 35 ml glass vials, with a gauze or cotton-wool stopper. Each vial was provided with a tooth-pick that served as a perch for the moth. The adults in the vials were kept in continuous light in a cold cabinet at 15°C. This regime inhibited activity and oviposition for up to five days without detrimental side affects.

The accumulated moths were transported in the vials to the release areas and liberated. Attempts to transport the moths in communal cages were unsuccessful because, almost invariably, the initial movements of one or two moths disturbed all the others in the cage and they damaged each other and themselves whenever activity started. The single moths, that became active during transport in the separate vials, usually resettled after a short time and without much damage, because there was no interference from other moths.

The behaviour of newly released moths was observed, as far as was possible, after a release on 3rd February 1980 of 146 males and 70 females. The toothpicks, on which the moths were perched, were removed from the glass-vials and placed upright on a polystyrene board, without disturbing the moths. The moths remained inactive on the toothpicks until ten minutes before sunset when two of the males flew away within thirty seconds of each other into the surrounding vegetation. The sun set at 18h40 at the release site and night fell at approximately 19h40 after a dusk period of approximately one hour. The moths on the board were checked at ten minute intervals and the number that had flown was recorded. Most of the moths only flew after dusk and the onset of activity in the females lagged 10 to 20 minutes behind the males (fig. 22). Two of the females adopted a mate calling posture between 19h50 and 20h00, without moving from their perches. At 20h50, when the last check was made, 98,6% of the males and 95,7% of the females had flown. The two 'calling' females had not moved and neither had attracted a mate. At least five moths, four males and one female, were eaten by bats within seconds of flying into the air.

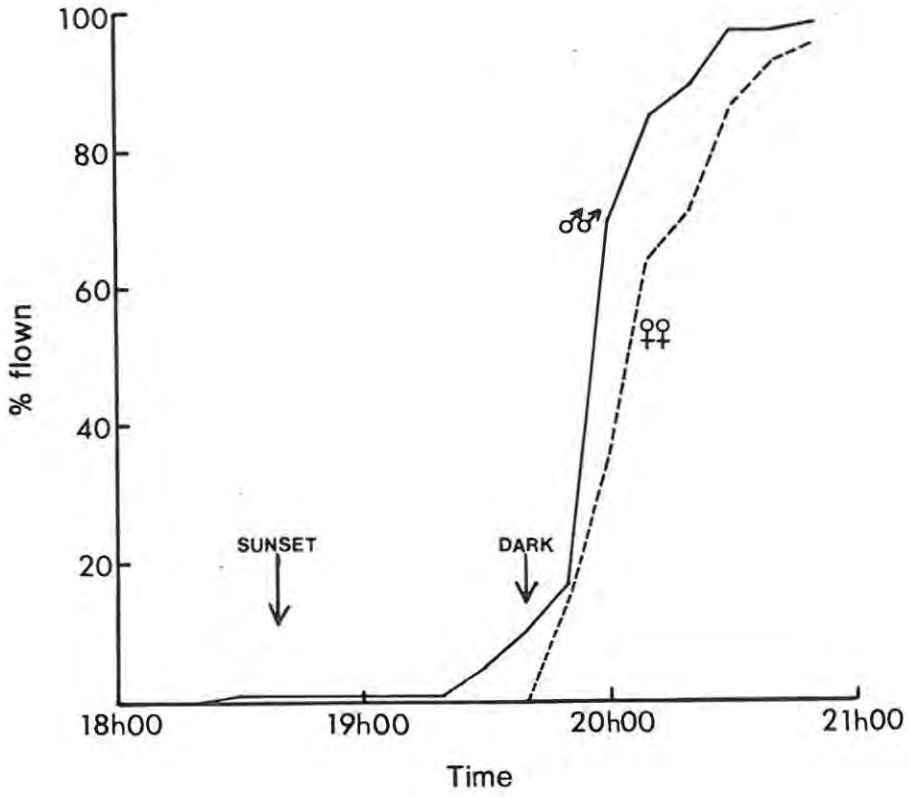

Fig. 22. The cumulative percentages of male and female T. tapiacola adults that became active between 18h00 and 20h50.

The relative success of adult releases was not measured quantitatively. However, the larval progeny of newly-released adults were usually found between thirty and sixty days after the moths had been released.

4.4 The releases.

Although the first trial releases with T. tapiacola were made at Mosslands Farm on 10th May 1976, large scale attempts to establish the moth on O. aurantiaca in South Africa did not commence until 27th May 1977. Since then, approximately 22500 eggs and 804250 larvae and exactly 3076 adults have been released at seven different localities (Appendix 4 and Table 15). Most releases were made with free-living, newly-hatched larvae and the other three release methods only accounted for 5,5% of the total numbers deployed.

Table 15. Approxiamate numbers of eggs and larvae, and the exact number of adults, of T. tapiacola released at various localities in south Africa between 27th May 1977 and 13th February 1982.

Locality	Stages released				Total
	Eggs	Free-living larvae	Larvae in cladodes	Adults	
Thursford	13000	239000	10250	-	262250
Mosslands	-	246000	-	1215	247215
A. Vosloo	9500	173000	-	1274	183774
T. Baines	-	28000	-	587	28587
Gannahoek	-	34000	5000	-	39000
S. on Vaal	-	40000	5000	-	45000
Le Rouxriv.	-	24000	-	-	24000
Total	22500	784000	20250	3076	829826

Almost all the eggs and larvae deployed in the field were placed among thickets of jointed cactus in the most heavily infested areas of the release sites. However, on 15th and 29th November 1979, at the Andries Vosloo Kudu Reserve, 25000 larvae were spread onto a large pile (approximately 20 m^3) of jointed cactus that had been stockpiled during manual clearing operations.

4.5 Methods used to monitor T. tapiacola populations in the field.

Two methods were used to monitor the presence of T. tapiacola at the release localities.

Most commonly, searches were made for larvae in the jointed cactus plants. The larvae were difficult to find because they almost always tunnelled into the lower basal parts of small plants and loose cladodes lying on the soil. Detection of the larvae was made more

difficult because the jointed cactus plants showed little or no signs of external damage until the larvae had almost completed their development. This is also true in the native range of T. tapiacola in South America. As a result, many O. aurantiaca plants had to be uprooted and dissected to collect even small numbers of T. tapiacola larvae. This made larval recoveries inefficient as a means of monitoring the populations, especially at the low levels at which the moth became established.

As a result, methods were developed to monitor the populations of T. tapiacola at the release sites. Water-bath, pheromone traps, baited with laboratory-reared, virgin females were constructed to trap T. tapiacola males in the field. The water bath of each trap measured 0,25 m^2 and was filled with water and a detergent wetting agent to a depth of 150 mm. A 500 ml, cylindrical, netting cage with virgin-female moths was placed on a stand just above the water level in the centre of the bath.

The effectiveness of the traps was tested in the field before they were used to monitor the populations of T. tapiacola at the release sites. Two traps were placed 5 m apart on the ground at Thomas Baines Nature Reserve on 3rd February 1980. Forty-three laboratory-reared, virgin, male moths were released around the traps at points on a circle with a radius of 10 m measured from a point equidistant between the two traps. The traps were checked each day for three days and the number of males that were recaptured was recorded (Table 16). The trial was repeated on 22nd February 1980 at Thursford Farm. In this case, 37 virgin males were released around the traps.

At both localities, most of the males that were recaptured were caught on the first night after release and more moths were caught in one trap than the other. A greater percentage of the moths were recaptured at Thomas Baines (67,4%) than at Thursford (24,3%). The reasons for this difference are not apparent, but it may have been due to the type of habitat in which the traps were set. The traps at Thursford Farm were placed among low karroid vegetation on an exposed plain. At Thomas Baines, the traps were placed among large bushes and trees on the side of a sheltered valley. The direction and strength of the

Table 16. The number, and percentage, of T. tapiacola males recaptured over three nights in pheromone traps baited with virgin females, at Thomas Baines Nature Reserve and Thursford Farm.

Night	Thomas Baines Trap A	Thomas Baines Trap B	Thursford Trap A	Thursford Trap B
1	23	6	7	-
2	-	1	1	-
3	-	-	-	1
Total recaptured	29		9	
% recaptured	67,4		24,3	

wind were not measured, but it was probably stronger and more unidirectional at the Thursford site than at Thomas Baines. This in turn may have resulted in a more rapid and greater dispersal of the male moths that were released at Thursford and thus less were recaptured.

The results of the trials indicated that the traps were suitable for monitoring the presence of T. tapiacola males in the field. Six traps were therefore set at Thursford farm on 10th March 1980 and six traps were set at Mosslands Farm on 25th March 1980. The virgin females in the traps were replaced every five to ten days depending on their availability from the insectary colony. The traps were maintained until 27th June 1980. Over this period, only one T. tapiacola male was caught in the traps, on 21st March 1980 at Thursford Farm. The low catch rate suggested that T. tapiacola was absent in the areas around the traps. However, recoveries of larvae in the area suggested that this was not the case. Consequently, the traps were discarded and larval searches were continued to monitor the populations of T. tapiacola.

4.6 Recoveries of T. tapiacola.

Throughout the release programme, the development of the populations of T. tapiacola was followed, as far as was possible, at all of the release sites, excluding Le Rouxrivier. Recoveries confirmed that T. tapiacola had become established in the area, and the number of generations that had been completed in the field was estimated from the time-lapse between the last release in the area and the recovery. The estimate was never entirely accurate because T. tapiacola has two to three generations per year and these overlap completely (Mann 1969). As a result, one year after release, it was not possible to determine whether recovered individuals were in the second or third generation. Most observations were made on the first generation of larvae in the field because they were most abundant and the numbers always declined in the subsequent generations.

The records of the time spent and the numbers of larvae recovered during the second generation are too incomplete to be meaningful and they are not included here. Thorough surveys were not made on second generation larvae to minimise disturbance of the survivors and conclusions about the success or failure of releases can only be made when populations survive for three and more generations. However, second generation larvae were encountered commonly at Mosslands and twice at Thursford. No second generation recoveries were made at Thomas Baines, Andries Vosloo or Gannahoek, in spite of searches that totalled approximately 235 man-hours.

The longest period between a release and recovery of T. tapiacola in South Africa was recorded at Sydney-on-Vaal. On 5th June 1980, during a four-man-hour search, a single, fifth-instar larva was found in the stem of a jointed cactus plant. T. tapiacola had last been released at Sydney-on-Vaal on 20th August 1978, one year and ten months or four to five generations before the recovery. No subsequent searches were made for T. tapiacola at Sydney-on-Vaal because the jointed cactus in the area was almost eradicated by the cochineal, D. austrinus, following its accidental introduction into the area, possibly with a release of T. tapiacola larvae in cladodes that was made on 24th January 1978.

The longest period between release and recovery of T. tapiacola at Mosslands Farm was 18,5 months. Two larvae in the fifth or sixth-instar were found during a six-man-hour search on 31st January 1980 after the last release in the area had been made on 15th July 1978. In this case the larvae were in at least the third and possibly the fourth generation.

The recapture of a single male moth in a pheromone trap at Thursford Farm on 20th March 1980 meant that T. tapiacola had completed at least two, and possible three, generations at the farm since the last release had been made on 8th January 1979. Besides this recapture of an adult male, five second generation larvae were also recovered on 18th December 1978. The larvae were all found in a single thicket of jointed cactus, approximately 5 m away from the periphery of a larger thicket in which 5000 larvae had been placed, on 7th June 1978.

4.7 Conclusions.

T. tapiacola has apparently failed to establish as a biological control agent of jointed cactus in South Africa, although large numbers of eggs, larvae and adults have been released at a variety of localities.

Confirmation that populations of the moth have survived for more than three generations has only been made at two of the release sites, namely Sydney-on-Vaal and Mosslands. However, in all the release areas, the moth has apparently dwindled to extinction, although the rate at which this has happened has varied between sites. Two alternative, but less likely, explanations are that the moth has survived, but only at very low levals, or the moth has dispersed and has established in areas that have not been surveyed, away from the original release sites.

If T. tapiacola has established at low levels, the populations may eventually build up and exert some pressure on the jointed cactus weed. In the mean time, any further releases with T. tapiacola in

South Africa should be made with free-living, newly-hatched, larvae deployed on large thickets of 'etiolated' plants, like those encountered at Sydney-on-Vaal and Mosslands.

5. MORTALITY OF *T. TAPIACOLA* IN SOUTH AFRICA.

Natural enemies intended for biological weed control may fail, either because they do not become established or because the populations do not increase to levels that supress the weed. Various reasons have been proposed for the failure of different agents. They have included: attacks by indigenous parasitoids and predators (Currie & Fyfe 1938; Williams 1950, 1960; Wilson 1960; Goeden & Ricker 1967, 1970; Peschken 1977); diseases (Bornemissza 1966; Harris 1967; Harris & Peschken 1971); the climate was unsuitable for development of the agent (Maddox *et al.* 1971; Baker *et al.* 1972; Schaber *et al.* 1975); too few individuals were released (Wilson 1960; Harris *et al.* 1971); rapid dispersal of the population following release (Peschken *et al.* 1970; Andres & Goeden 1971); the lack of alternate hosts when the target weed was dormant (Andres & Goeden 1971); the population lacked sufficient genetic variability (Force 1967), either because a 'laboratory-ecotype' was selected during mass rearing (Boller 1972; Mackauer 1972, 1976) or because too few individuals were collected (Mackauer 1972) possibly in the wrong areas (Remington 1968; Lucas 1969; Wapshere 1981).

Of the above reasons, predators and parasitoids have probably most often been implicated in the failure of biological weed control programmes (Goeden & Louda 1976). However, there are apparently only two cases were this has been demonstrated conclusively. The cassidid beetle, *Physonota alutacea* Boheman, never became established on Mauritius for the control of black sage, *Cordia machrostachya* (Jacq.) R. & S., because ants removed all the young larvae. Williams (1950) demonstrated, by exclusion techniques, that in the absence of ants, *P. alutacea* survived and developed normally. Annecke *et al.* (1969) showed that in areas where coccinellid predators were eradicated with applications of DDT, the prey cochineal, *Dactylopius opuntiae* (Cockerell), effectively controlled the prickly pear, *Opuntia ficus-indica* (L.) Miller, in South Africa (Zimmermann & Moran 1983).

All the other examples where predators have supposedly interfered with biological weed control agents after release have been treated in one of two ways. Firstly, predators have been seen to kill the introduced

natural enemies and, with no further evidence, the failure of the programmme has been blamed on the predators (Miller 1936; Currie & Fyfe 1938; Miller cited in Huffaker 1959). Secondly, after predation has been observed, attempts have been made to quantify the amount of predation caused by the major predator or predators. If, in the opinion of the observer, the mortality has appeared sufficiently high, this has been accepted as the prime cause for the failure of the agent (Currie & Fyfe 1938; Bornemissza 1966; Peschken 1971).

Meaningful conclusions cannot be drawn from either of the last two methods and there are cases where agents have proved successful in spite of apparently high predation (Bess & Haramoto 1958; Goeden & Ricker 1967; Hawkes 1973; Isaacson 1973). Only those predators that, alone or combined, cause the population of the natural enemy to remain static at a low level, or to decline to extinction, detrimentally effect the biocontrol programme. The amount of mortality needed to cause a negative population growth rate depends on the fecundity of the prey. As long as at least two offspring survive to breed from each female, the population will not decline. Hence an organism that lays ten eggs can only tolerate 80% mortality, while one that lays 1000 eggs can tolerate 99,8% mortality. Therefore, measurements of mortality alone cannot predict whether a population will decline or not and the measurements must be related to fecundity.

When an agent is surpressed by a single predator, as in the cases cited above of the cassidid, P. alutacea, and the cochineal, D. opuntiae, exclusion techniques can usually demonstrate the impact that the predator has on the prey. However, in most cases the situation is more complex and a number of predators and other factors act sequentially against the different stages of the life cycle of the insect. Under these circumstances, exclusion techniques are inadequate and a life-table analysis should be used to determine the overall mortality suffered by the agent and this balanced against fecundity.

Clausen (1951) suggested that agents that fail to establish or to provide satisfactory control should be ignored, and efforts should be made to find alternative strains, sub-species or species for the control programme. This approach, plus pressure to find successful

agents to control the target weed and the lack of funds to study unsuccessful ones, probably accounts for the paucity of thorough investigations into biocontrol ventures that have failed. Harris (1981) believes that post-release studies should be conducted on unsuccessful agents because the results may provide insight into which agents should be selected for future releases. Also, there has been considerable discussion about the genetic effects of rearing and recolonising insects (Mackauer 1981; Myers & Sabath 1981), but, to date, very little experimental evidence has been accumulated to support or refute the hypotheses. Detailed investigations of establishment attempts may help to rectify the situation and show the importance of genetic effects in biocontrol programmes.

There is another reason why such studies may be justified. In some cases, the failure of the programmme may be beyond control (eg: predators and unsuitable climate) while in other cases the agents may fail because of deficiencies in the release programme (eg: harmful genetic change and too few individuals released in the wrong areas). Therefore, unsuccessful agents cannot legitimately be discarded until the reasons for the failure have been positively identified and shown to be uncontrollable.

The lack of knowledge of why agents are unsuccessful, has led to the continuation of release programmes that might have been terminated sooner, with a corresponding saving in manpower and finance. A good example has been the attempts to establish the arctiid moth, Tyria jacobaeae L., on tansy ragwort, Senecio jacobea L., in Australia, where releases were first made in 1937, again from 1955 to 1959 and finally during 1961. The bittacid, Harpobittacus nigriceps (Selis), a latent virus and other predators have all been implicated in the establishment failure (Currie & Fyfe 1938; Bornemissza 1966; Schmidl 1972). However, no complete life-table study has been made on T. jacobaeae in Australia, and the overall reasons for its failure remain obscure.

In South Africa, T. tapiacola has so far apparently failed to become established, or, if it has survived, it has done so at undetectably low levels. The first releases with T. tapiacola failed because ant

predators rapidly removed 100% of the eggs that had been placed in batches among the jointed cactus (Hoffmann 1976). As a result the release methods were modified and several aspects of the mortality suffered by T. tapiacola were measured, both under natural conditions in the field, and under controlled laboratory conditions. The mortality of the different life-stages are discussed in turn, starting with the effects of climate and predators on the eggs of T. tapiacola. This is followed by the effects of host-plant types and predation on the survival of first-instar larvae on the surface of the plant and older larvae within the plant. Finally, the mortality of the pupal stage is discussed and partial-life-tables and survivorship curves are presented to summarize the overall mortality suffered by the immature stages of T. tapiacola in South Africa.

There were two limitations in the study. Firstly, because there was no natural population of T. tapiacola in the field, each stage of the life cycle had to be transferred from the insectary and placed as naturally as possible among, or in, the cactus plants. Secondly, no method could be found to measure adult mortality and this remained as a gap in the partial-life-tables. Both these limitations were taken into account in the interpretation of the mortality data.

5.1 Methods used to measure egg mortality.

The eggs of T. tapiacola are deposited singly by the female moths on the thorns or glochids of the cactus host plants (Mann 1969). Each egg is pressed against the thorn and glued in position during the oviposition process. Attempts were made to find the eggs of T. tapiacola in the field for mortality studies, but the small, cryptic, single eggs were never found on jointed cactus, even when they must have been most abundant following releases of large numbers of gravid female adults. Attempts were also made to obtain eggs laid naturally on the cactus by placing T. tapiacola moths in cages that enclosed a number of jointed cactus plants. However, this method failed because the females behaved atypically and laid nearly all their eggs on the gauze sides of the cages. As a result, mortality of eggs of T. tapiacola

could only be measured after eggs laid in the insectary had been transferred onto plants in the field using the following methods.

Mated T. tapiacola females were provided with loose cladodes of jointed cactus in smooth walled, perspex, oviposition cages in the insectary. The moths were left in the cages for one night while eggs were laid on the thorns of the cladodes. The eggs were then placed among the experimental plants in the field. The eggs were counted and the position of each was marked with a dot of red enamel paint on the cuticle of the cactus alongside the egg-bearing thorn. The joints, with eggs, were then transported to the experimental site and placed among the branches of jointed cactus plants. Alternatively, and more often, the thorns with eggs were detached from the cladodes, transported to the field and pushed into the areoles, among the thorns of the jointed cactus plants (fig. 23).

Fig. 23. Jointed cactus cladodes with artificially placed thorns bearing T. tapiacola eggs.

The number of eggs that were dislodged from the thorns and the percentage hatch of the remaining eggs were recorded on plants that had been cleared of predators and/or sheltered from rain. Ant and mite predators were excluded by spreading rings of Gamma BHC powder in furrows in the soil around the stems of the jointed cactus plants (fig. 24). Some of the jointed cactus was sheltered from rain by placing sheets of glass, supported horizontally on metal frames, 0,20 to 0,5 m above the topmost joints of the plants (fig. 25). A continuous rainfall recorder measured the amount of rain, and the number of hours that rain fell, while the eggs were exposed on the plants. The hardest rainfall, expressed as mm/hour, was calculated from the recordings.

Egg mortality was measured on 'typical' and 'etiolated' jointed cactus plants (see Appendix 2 for a description of the characteristic features of these two categories of O. aurantiaca).

Fig. 24. Jointed cactus plants surrounded with furrows filled with Gamma BHC insecticide to exclude ant predators.

Fig. 25. Jointed cactus sheltered from rain with a sheet of glass supported on a wire stand.

5.2 Egg mortality - predators excluded.

The percentage mortality of eggs of T. tapiacola was measured at six different times on jointed cactus plants from which predators had been excluded. Initially, the mortality of eggs on thorns projecting from the lower surfaces of the cladodes was measured separately from that of the eggs on the upward projected thorns. A potential difference in mortality between the two situations was expected on the assumption that the eggs on the lower surfaces of the cladodes would be more protected from climatic influences. However, 22,2% of 180 eggs were dislodged from thorns on the upper surfaces of the cladodes and 28,9% were dislodged from thorns on the lower surfaces. This difference was not significant ($X^2 = 2,50$). The length of the thorns compared to the diameter of the cladodes meant that most of the eggs on the lower surface, and especially those attached to the extremities of the thorns, were not effectively sheltered from the rain. As a result, the position of the eggs on the cladodes was not taken into account when the mortality data were analysed.

In the shelter of the insectary, no eggs of T. tapiacola fell from the thorns of potted jointed cactus plants and 87,0% of 200 eggs hatched.

In the absence of predators on jointed cactus plants that were sheltered from the rain, but exposed to the sun and wind, 8,9% out of 360 eggs were dislodged from the thorns and lost (Table 17). The buffeting action of the wind on the eggs, and on the jointed cactus plants, apparently loosened the cement attachment of these eggs and they dropped from the thorns.

On the jointed cactus plants that were exposed to rain, as opposed to sheltered plants, a significantly higher proportion (25,6%) of the eggs were dislodged from the thorns (paired 't' = 3,01; $0,01<p<0,05$).

Table 17. The percentage mortality and percentage hatch of T. tapiacola eggs on jointed cactus plants sheltered from, and exposed to, rain. n = 120 eggs for each replicate; 60 on sheltered plants and 60 on exposed plants.

Exposure period (Days)	Rain during period			Sheltered plants		Exposed plants	
	total mm	total hours	hardest rain mm/hour	% dislodged	% hatch	% dislodged	% hatch
9	46,9	17,0	22,9	15,0	53,1	56,7	80,8
13	121,0	67,5	5,9	13,3	96,1	26,7	88,6
13	37,1	49,5	1,2	5,0	93,0	21,7	80,9
19	44,3	49,0	1,8	5,0	93,0	8,3	78,2
14	18,5	15,5	2,5	3,3	72,7	10,0	81,6
21	21,3	20,5	5,2	11,7	84,9	30,0	85,7
Total				8,9	81,1	25,6	82,5

The bonding of the eggs to the thorns was apparently loosened by the rain. There was no correlation between the number of eggs that were dislodged from exposed plants during each of the six replicates and the total rainfall (r=0,15; ns) or the total hours of rainfall (r=0,31; ns). However, there was a significant correlation between the numbers dislodged and the hardest rainfall (expressed as mm/hour) during the period that the eggs were exposed (r=0,93; $0,001<p<0,01$). This analysis suggests that the direct impact of heavy raindrops was most damaging to the eggs and that light rainfall had little or no effect on the bonding that held the eggs on the thorns.

There was no difference between the percentage hatch of eggs that survived on the sheltered plants (81,1%) compared to the exposed plants (82,5%). The percentage hatch of the eggs in both cases was lower, although not significantly (X^2 = 0,29) than the average 87,3% of eggs that hatched in the insectary.

5.3 Egg mortality - with predators.

The eggs of T. tapiacola were removed from jointed cactus plants by at least nine species of ants, Monomorium albopilosum Emery, Monomorium delagoensis Forel, Tetramorium laevithorax Emery, Tetramorium quadrospinosum Emery, Technomyrmex albipes Smith, Pheidole megacephala Fabricius, Camponotus rufoglaucus Jerdon, Acantholepis capensis Mayr and Acantholepis sp. and two species of mites, Abrolophus meyerae van Huysteen and Abrolophus rusticus van Huysteen.

The combined effects of these predators overshadowed the climatically induced mortality suffered by T. tapiacola eggs. The overall percentage egg mortality on jointed cactus plants exposed to predators was almost exactly the same on plants sheltered from rain (80,0%) compared to plants exposed to rain (80,9%) (Table 18). The slight differences in mortality on 'typical' and 'etiolated' plants considered separately were not significant (X^2 = 0,24 in both cases). Predators seemed to be more active on 'typical' jointed cactus plants in the sun than on 'etiolated' plants in the shade, although the 5,7% difference in mortality between the two plant types was not significant (X^2 = 1,78).

Table 18. The percentage mortality (% mort.) of T. tapiacola eggs on 'typical' and 'etiolated' jointed cactus plants, both sheltered from and exposed to rain. n = number of eggs placed on the plants.

	'Typical' plants	n	'Etiolated' plants	n	Total	n
Sheltered	88,9	90	71,1	90	80,0	180
Exposed	82,3	2577	77,3	1025	80,9	3602
Total	82,5	2667	76,8	1115		

There was no correlation between the initial density of T. tapiacola eggs/plant and the percentage of eggs that disappeared from either 'typical' or 'etiolated' jointed cactus plants (Table 19).

Table 19. The percentage mortality of T. tapiacola eggs placed at different densities on 'typical' and 'etiolated' jointed cactus plants. n = total number of eggs at each density.

Initial number of eggs/plant	'Typical' plants	n	'Etiolated' plants	n
1	87,9	140	74,1	58
2	80,9	152	65,3	72
5	85,4	405	77,1	275
10	79,3	1020	80,0	220
20	85,5	860	78,5	400
Total	82,3	2577	77,3	1025

The incubation period of T. tapiacola eggs that were placed on 'typical' jointed cactus plants ranged on average from five days during February (summer) to 22 days during July (winter) (fig. 26A). On 'etiolated' jointed cactus plants in the shade, the eggs took an average of three to four days longer to hatch.

Peschken et al. (1970) and Peschken (1977) suggested that the slow development of prey species at cooler temperatures would result in higher mortality because the prey were exposed to predators for longer periods. However, this was not the case with T. tapiacola eggs and there was no correlation between percentage mortality and the time of the year that the eggs were exposed to predators on the plants (fig. 26B). As a result, the mean daily survival probability (see next paragraph) of T. tapiacola eggs followed a seasonal cycle (fig. 26C) and was low in winter, when the incubation period was long, and high in summer, when it was short. This indicates that the predators of T. tapiacola eggs were less active in winter and more active in summer. The mean daily survival probability of eggs on 'etiolated' plants was consistently higher than on 'typical' plants, because egg predators were more active in the exposed habitats than in the shade.

The mean daily survival probability (Px) was calculated for eggs of T. tapiacola using the formula (Rausher 1979):

$$Px = \sqrt[n]{\frac{lx+n}{lx}}$$

where lx is the number surviving at day x, lx+n is the number surviving at day x+n and n is the number of days between day x and day x+n. In this case, lx is the number of newly-laid eggs exposed at the start of each experiment and lx+n is the number of eggs that hatched after an incubation period of n days.

The rate at which eggs of T. tapiacola were removed from jointed cactus plants was measured at the Andries Vosloo Reserve during November and January, and at Thursford Farm during January only. Single eggs on thorns were placed out at initial densities of five eggs/plant. Counts of the eggs were made every day for five days, and

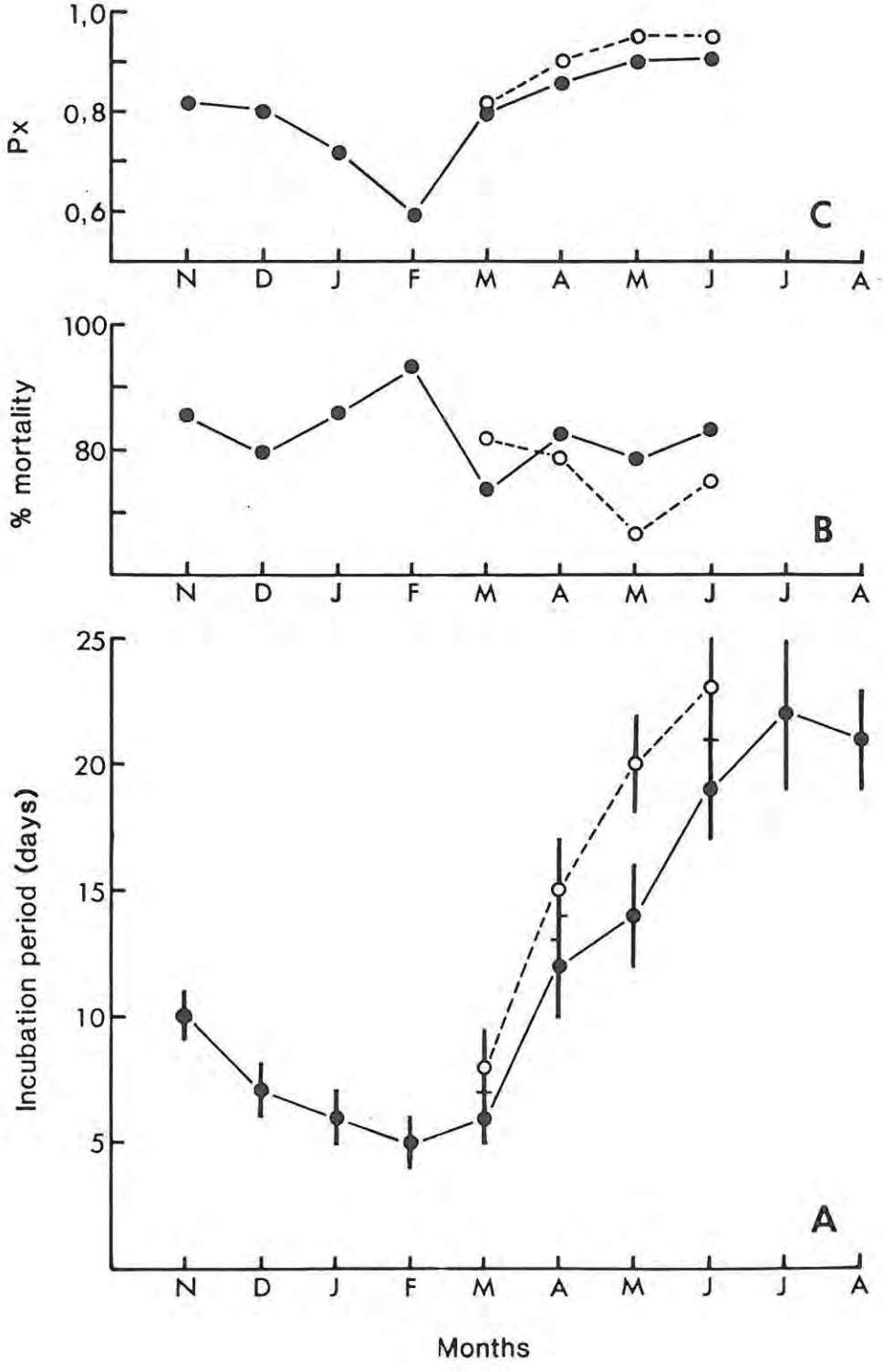

Fig. 26. The mean (and range) incubation period (A); percentage hatch (B); and mean daily survival probability (Px - see text) (C) of T. tapiacola eggs on 'typical' (●——●) and 'etiolated' (o-----o) jointed cactus at different times of the year.

the number that was missing each day was recorded and plotted as a percentage of the total number of eggs initially placed on the plants (fig. 27). All three curves show that the eggs were removed most rapidly at the beginning of the exposure period, and that the rate of removal decreased with time. This trend was investigated further under controlled laboratory conditions.

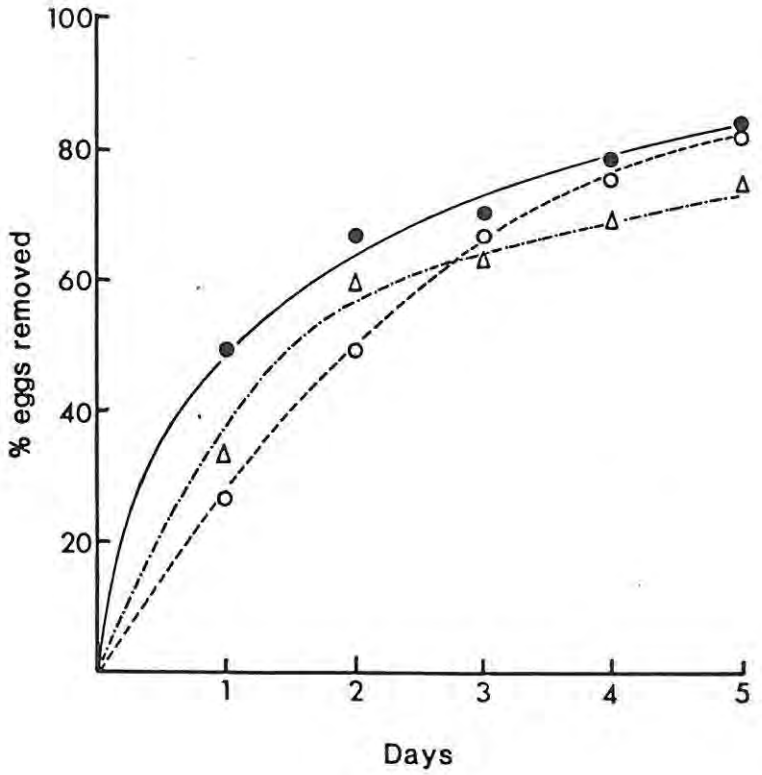

Fig. 27. The rates (plotted as % removed with time) at which T. tapiacola eggs were removed from O. aurantiaca plants at Andries Vosloo Reserve during November (O-----O; n = 395) and January (●——●; n = 520), and at Thursford Farm during January (Δ-·-·-Δ; n = 230). n = initial number of eggs placed on the plants, at a density of 5/plant. Curves fitted by eye.

5.4 Predation of eggs by ants in the laboratory.

The ant, Monomorium albopilosum Emery, appeared to be the most widespread and common ant species found feeding on eggs of T. tapiacola at the Andries Vosloo Reserve, and it was therefore selected for

laboratory investigation. A colony of M. albopilosum was excavated from the soil and was placed in a 27 ℓ perspex box filled with soil. The box with the ant nest was sealed and the only escape that the ants had was through a 10 mm diameter glass tube that led onto a feeding-table (Skaife 1961). The foraging area of the table covered 0,25 m^2 and was surrounded by a trough filled with water that confined the ants. The ants were fed each day with dead moths and sugar water.

Every four to five days, ten loose jointed cactus cladodes, with T. tapiacola eggs on the thorns, were placed on the table instead of the dead moths. For each experiment, the density of eggs on all the cladodes was fixed at either one, two, eight or 16 eggs/cladode, and each density was tested three times. The density of eggs was controlled by placing up to 20 cladodes in an oviposition cage with between two (when low densities of eggs were required) and ten (when high densities of eggs were required) gravid female moths. After one

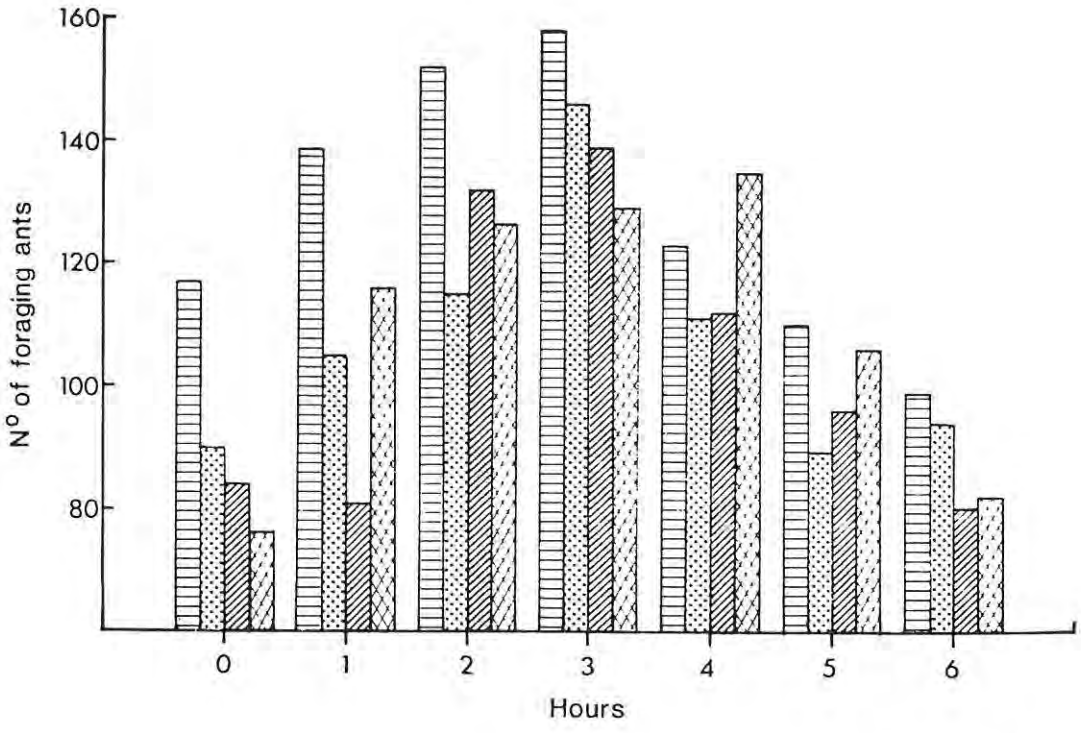

Fig. 28. The number of M. albopilosum ants foraging on a feed-table during the first six hours after T. tapiacola eggs had been placed on the table at densities of 1 (horizontal hatch), 2 (stipple), 8 (diagonal hatch) and 16 (cross hatch) eggs/cladode.

night, the cladodes were removed from the oviposition cages and those with the required number of eggs, or more, were singled out. The excess eggs were scraped from the thorns of cladodes with a surplus, until ten cladodes with the selected density of eggs/cladode were obtained, and these were then placed on the feeding-table. The number of ants that were foraging was counted every hour for the first six hours that the cladodes were in place. The missing eggs were also counted every hour for six hours and again after 24 and 48 hours.

The number of M. albopilosum ants foraging on the table when no food was present varied, on average, between 76 and 117 (time 0 in fig. 28). When the cladodes with eggs were placed on the feeding table, ants were recruited from the nest and the numbers foraging increased. The number of eggs per cladode did not influence the rate of forager recruitment and the increase in the number of ants that were recruited was similar at each egg density. The duration of the period over which ants continued to be recruited was longest (four hours) at a density of 16 eggs per cladode. At densities of eight eggs per cladode and lower, the number of foraging ants on the table started to decline after three hours.

The percentage of eggs removed by M. albopilosum at each density is shown in fig. 29. Most of the eggs were removed during the first five to six hours and only a small proportion of the eggs were removed after six hours. The percentage of eggs removed after 48 hours was highest (84 %) at an initial density of eight eggs per cladode. The eggs that survived were located by the foraging ants, but they were apparently unable to dislodge them, although they were frequently seen trying to do so. The field and laboratory situations are not directly comparable, but there is a remarkable similarity between the rates of removal and the final proportion of eggs removed, although this was measured in days in the field and in hours in the laboratory (fig. 27 and fig. 29).

The inability of M. albopilosum to remove all of the eggs from the thorns could account, in part, for the survival of some of the eggs of T. tapiacola in the field. However, the large number of ant and mite species that attack the eggs under natural conditions have different

foraging strategies and abilities to remove the eggs. It therefore seems likely that the eggs that escaped predation in the field did so mainly because they were not detected by predators, or at least were only detected by predators that were unable to remove them.

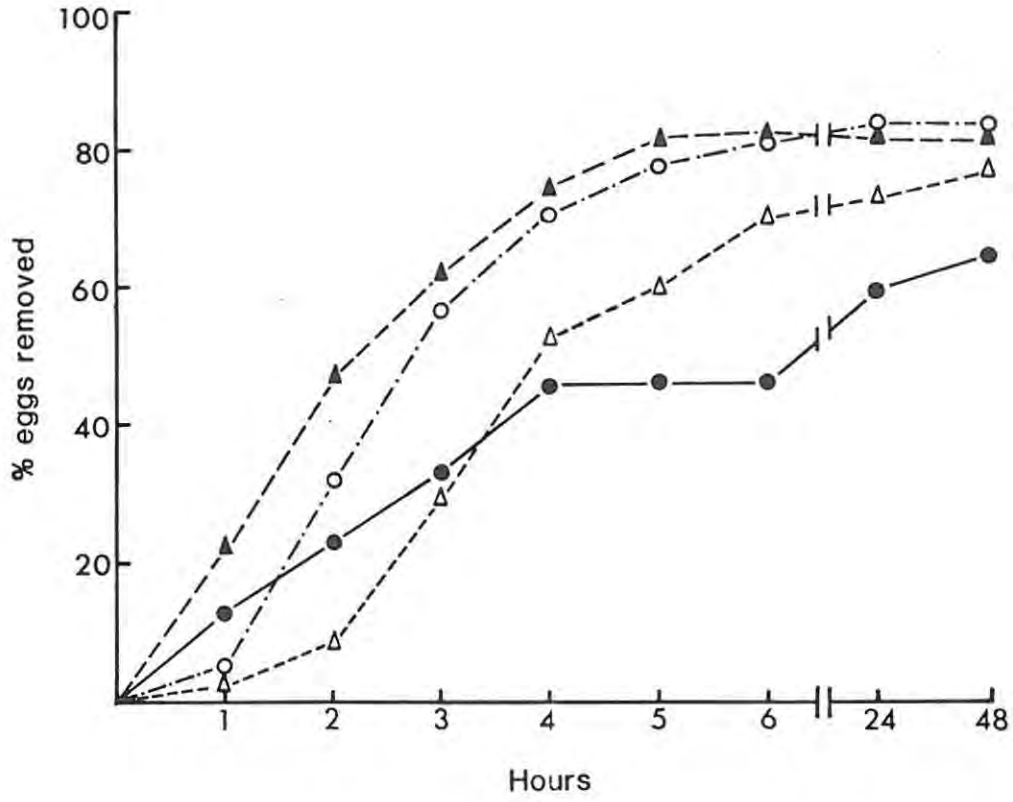

Fig. 29. The percentage of T. tapiacola eggs removed from the thorns of ten O. aurantiaca cladodes by M. albopilosum, on a feeding-table, over 48 hours. The initial density of eggs on the cladodes was 1 (●——●), 2 (○-·-·-○), 8 (Δ-----Δ) and 16 (▲---▲) eggs/cladode.

5.5 Methods used to measure larval mortality.

The mortality factors acting on newly-hatched larvae of T. tapiacola before they tunnelled into the jointed cactus differed from those acting on the larvae after they had tunnelled into the jointed cactus and started feeding. As a result, these two stages were separated and the mortality of each was measured independently of the other.

Larvae of T. tapiacola were transferred from the insectary and placed on plants in the field using the following methods. A fine paintbrush was used to transfer the first-instar larvae from the petridishes in which they hatched, into gelatin capsules. One larva was placed in each capsule and the transfer was made within six hours of larval eclosion from the egg. The capsules with larvae were transported to the experimental sites, opened, and impaled on the thorns of the jointed cactus plants. The larvae moved from the open capsules, down the thorns and onto the jointed cactus, in the same way as larvae that hatched from eggs on the thorns. On the plant, the larvae searched for penetration sites and those that were successful started feeding.

The mortality of the larvae was measured separately on 'typical' and 'etiolated' jointed cactus plants (Appendix 2), and the 'typical' plants were further subdivided into three size categories (fig. 30). The first category included 'small' plants that were usually less than one year old, had less than five joints and were without a distinct

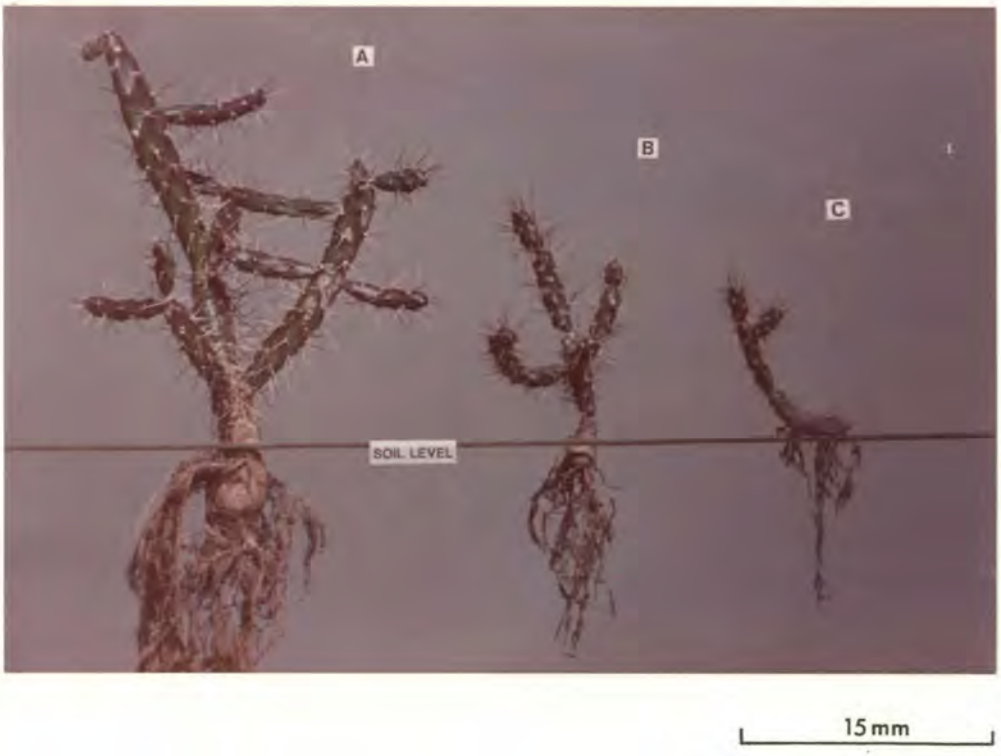

Fig. 30. The three size categories of 'typical' jointed cactus plants. A = large; B = medium; C = small.

stem or an underground tuber. 'Medium' size plants had from eight to 12 joints, were usually between one and two years old and had developing tubers and more or less distinct woody stems. 'Large' plants had more than 15 joints, were usually more than two years old and had distinctly woody stems and well developed underground tubers. The 'etiolated' plants were not subdivided on the basis of size because they never grew more than three or four joints tall before they collapsed and new vertical stems grew from the fallen joints.

Predators could not be excluded from the plants using Gamma BHC, as they were for the egg mortality investigation, because the larvae were sensitive to the small amounts of insecticide that often drifted onto the plants in the wind. Other methods that were tried, such as surrounding the plants with a metal hoop or rope coated with Formex glue, were unsuccessful in keeping the plants predator-free. As a result, mortality of the first-instar larvae in the absence of predators was measured on potted jointed cactus plants in a greenhouse.

In both the the greenhouse and field situations, eighty jointed cactus plants from each category (small, medium and large, 'typical' plants and 'etiolated' plants) were selected and marked with a numbered metal stake pushed into the soil alongside the plants. The first-instar larvae were released on the plants at four different densities, so that of the 80 plants in each category, 20 had one larva/plant, 20 had two larvae/plant, 20 had five larvae/plant and 20 had ten larvae/plant. Five to ten days after the larvae had been released, the number of larval entry holes was counted and the position of each on the plants was noted.

5.6 Mortality of first-instar larvae on the outside of the plant.

The behaviour of the first-instar larvae of T. tapiacola during plant penetration was described by Hoffmann (1976). Briefly, each larva selects an entry site, usually at the internode of two cladodes or at the base of a thorn. The larva then spends up to 30 minutes spinning a loose covering of silk around itself. The silk threads are used as a

brace to push against while the larva forces its mandibles into the plant epidermis and chews a tunnel into the plant. The time taken by the first-instar larvae of T. tapiacola to penetrate the jointed cactus and start feeding ranged from one hour, up to forty-eight hours. The delay depended mainly on how rapidly the larvae found suitable entry sites. Some larvae penetrated the plant epidermis at the first attempt, while others only succeeded after trying at two or more positions on the plants.

The number of T. tapiacola larvae that penetrated into jointed cactus differed on the four categories of plants. In the greenhouse, without predators (fig. 31A & B), most larvae penetrated medium-size, 'typical' plants while only a few larvae penetrated the large plants. In the field, with predators (fig. 31C & D), larval penetration was highest on the 'etiolated' plants and low on all three size categories of 'typical' plants.

In both the greenhouse and field situations, larval penetration of large-size, 'typical' jointed cactus plants was consistently low over the range of densities at which the larvae were released. On the other three categories, the number of larvae that penetrated the plants increased with the numbers that were initially released onto each plant. This trend was less marked in the field than in the greenhouse (fig. 31). Although the number of larval penetrations increased, the percentage of larvae that penetrated the plants decreased as the numbers released onto the plants was increased (fig. 31A & C). The highest survival recorded was when single larvae were released onto small-size 'typical' plants in the greenhouse and 100% of the larvae penetrated into the plants.

There were significantly more larval penetrations in the greenhouse than in the field on small-size (paired 't' = 5,26; $0,001<p<0,01$) and medium-size (paired 't' = 3,85; $0,01<p<0,05$), 'typical' jointed cactus plants. However, the number of larval pentrations did not differ significantly between the greenhouse and the field on large-size, 'typical' plants (paired 't' = 0,60) and 'etiolated' plants (paired 't' = 0,17). Apparently, predators were active on and removed larvae from typical plants in the field, but predation did not affect the the

larvae on etiolated plants in the shade. Predators were never seen removing larvae from jointed cactus plants in the field, but spiders and ants that were accidently introduced into the insectaries frequently fed on young T. tapiacola larvae. Presumably these species also preyed on the larvae in the field.

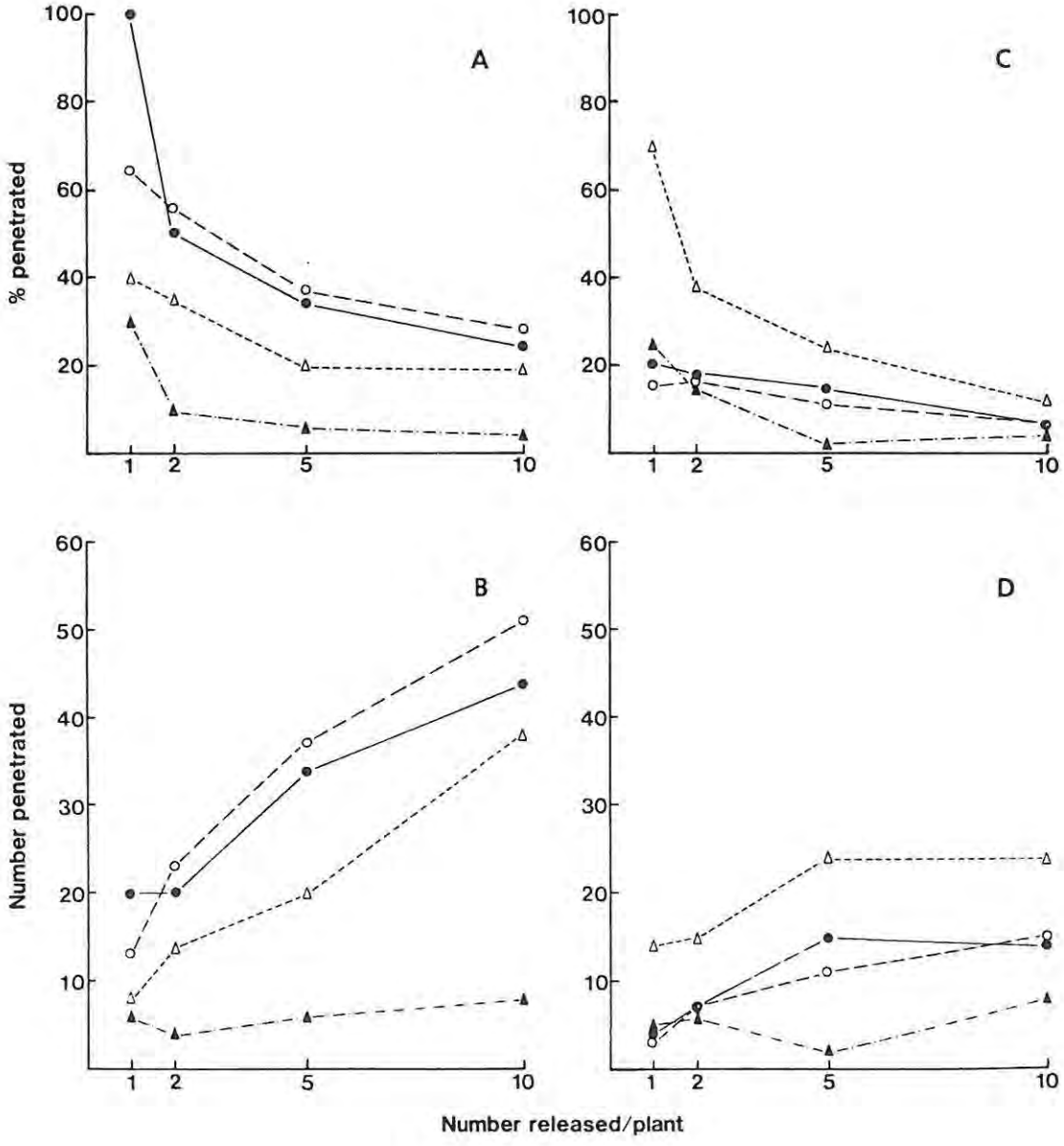

Fig. 31. Mortality of T. tapiacola first-instar larvae on the surface of jointed cactus plants. The larvae were released, at densities of 1, 2, 5 and 10/plant, on small (●———●), medium (O----O) and large (▲-·-·-▲) 'typical' plants and on 'etiolated' plants (Δ------Δ), in a greenhouse (A & B) and in the field (C & D).

The low number of larvae that penetrated large jointed cactus plants, even in the absence of predators in the greenhouse, indicated that these plants were least suitable for colonisation by T. tapiacola. Although predators may have accounted for the low number of larvae that penetrated large plants in the field, this does not explain the low number of larval penetrations in the greenhouse. The inability of newly hatched T. tapiacola larvae to penetrate the tough cuticle and epidermis of old jointed cactus plants (Hoffmann 1976) probably prevented the larvae from colonising these plants.

The negative phototactic movements of the larvae (Hoffmann 1976), as shown by the position of the larval entry sites on the plants, may have contributed to this mortality. Almost equal numbers of T. tapiacola larvae penetrated the stems (183 larvae) compared to the terminal joints (163 larvae) of the potted jointed cactus plants in the greenhouse (Table 20), and only on medium size plants did more larvae penetrate into the terminal joints. On average, each jointed cactus stem supported approximately eight terminal cladodes and therefore, there were almost eight times as many terminal cladodes

Table 20. The number (n) of T. tapiacola larvae that penetrated the stems and terminal joints of four different categories of potted jointed cactus plants in a greenhouse. The number of stem and terminal joints on the plants, and the proportions that were penetrated are shown. Tn = the total number of larval penetrations on each plant category.

Plant category	Tn	Stem joints			Terminal joints		
		n	No. of stems	No./ stem	n	No. of joints	No./ joint
Small	118	65	80	0,81	53	206	0,26
Medium	124	45	80	0,56	79	631	0,13
Large	24	20	80	0,25	4	1432	0,01
'Etiolated'	80	53	80	0,66	27	256	0,11
Total	346	183	320	0,57	163	2525	0,07

available for larval penetrations (2525:320). However, the proportion of larval penetrations was over eight times higher on the stems than on the terminal joints (0,57:0,07). On large-size 'typical' plants alone, the proportion of stems penetrated was approximately 25 times higher than the proportion of terminal joints. The downward movement of larvae on these plants was most marked, possibly because the terminal joints were higher and more exposed than on the smaller plants. On small, medium and 'etiolated' plants, the stem joints were less differentiated from the terminal joints, and were more penetrable than the woody stems of large plants. As a result, the first-instar T. tapiacola larvae were at a greater disadvantage on large-size, 'typical' plants, and this may account for the low percenatge of penetrations recorded on these plants.

In spite of the apparent disadvantages of moving down the plant before penetrating the cuticle, the larvae of T. tapiacola derive at least four possible advantages from tunneling into the stem at the base of the plant, as opposed to the terminal joints:

(a) Lummus and Wangberg (1981) measured temperatures of up to 53°C in the terminal cladodes of Opuntia polycantha Haworth and noted that the larvae of Olycella subumbrella Dyar moved onto the outside of the plant during the hottest part of the day to avoid the lethal temperature conditions within the cladodes. At this stage the larvae were vulnerable to predators. The temperature in the terminal joints of O. aurantiaca has been measured at 43,7°C, while the ambient air temperature was 32°C and the shaded basal parts of the plant were 33,9°C. Under these conditions, the cooler basal parts of the plant presumably provided the most suitable habitat for larval development.

(b) The terminal joints of O. aurantiaca readily dropped from the plant, especially when they were damaged. Most of the terminal joints that were attacked by T. tapiacola dropped from the plants while only partially destroyed. The larvae continued to develop in the fallen joints and completely ingested all the edible tissue. Larvae that had not

completed their development then had to leave the destroyed cladodes and search for new suitable host plants. During this period they were vulnerable to predators.

(c) The basal parts of the stem and the underground tuber are the main storage organs in jointed cactus (Zimmermann & van de Venter 1981) and larvae feeding in this part of the plant were presumably in the nutritionally most rewarding area.

(d) Finally, larvae feeding in the tuber could tunnel directly into the soil to pupate.

The solitary behaviour of T. tapiacola larvae, and the intolerance they have of other larvae in their vicinity, may have accounted for the generally low percentage penetrations per plant on the small, medium and 'etiolated' jointed cactus plants. As most of the larvae placed on jointed cactus moved downward and attempted to penetrate into the stems of the plants, larval contacts would have been frequent, especially at the higher larval densities of five and ten larvae per plant. The encounters between the larvae would probably have caused most of them to leave the heavily infested plants and search for other uncolonised plants.

Population levels exceeding two first-instar larvae per plant are most unlikely under natural conditions because the females of T. tapiacola lay single eggs at low densities (Mann 1969), and because egg predation is high. As a result, meaningful conclusions concerning the suitability of the different categories of jointed cactus for colonisation by T. tapiacola could only be drawn following releases of larvae at densities of one, and possibly two, larvae per plant. At that density in the greenhouse, small-size, 'typical' plants were most suitable (with 67% of the larvae able to penetrate the plants), followed by medium plants (60%), 'etiolated' plants (37%) and large-size, 'typical' plants were least suitable (17%). In the field, 'etiolated' plants were more suitable than all three categories of 'typical' plants, although this was probably due to the lower level of predation in the shaded habitat, compared to the exposed habitat.

5.7 Mortality of larvae feeding in the plant.

The causes of larval mortality in T. tapiacola changed after the larvae had penetrated the epidermis and tunnelled into the jointed cactus plants. Normally, the larvae completed their development within one tunnel that they excavated in the cactus. As a result, direct observations of the larvae were not possible unless the cladodes were cut open and the larvae extracted. This procedure could not be used for mortality studies because the development and defences of the larvae were detrimentally affected each time they were disturbed. Larval development was therefore followed indirectly through observations of the external damage that was evident on cladodes infested with larvae. The approximate extent of the larval tunnels was usually discernable through the plant epidermis and the damaged areas appeared as dark, rotting regions.

The progress of a total of 208 larvae of T. tapiacola was followed on the four different categories of jointed cactus plants. The larvae were observed at least twice a week from the time they started feeding until they died or pupated. When the damaged area of the cladode was not noticeably different from one examination to the next, a search was made for the larva in the cladode and an attempt was made to determine its cause of death.

Gum produced by the jointed cactus plants accounted for most of the mortality suffered by small T. tapiacola larvae soon after they penetrated the plant epidermis (Table 21). Gum induced mortality was easily recognised because the gum flowed out of the entry holes made by the larvae and solidified as a conspicuous plug on the outside of the plant. Besides repelling insect herbivores, gum serves a number of possible functions in plants. Carbohydrates are stored as gums; they may help to retain water; injured parts of the plant are sealed by gum to prevent microbial infection and water loss (Smith & Montgomery 1959). The amount of gum produced by Opuntia spp. varies from species to species (Pettey 1948), and within each species, old and water-stressed plants generally produce more gum than those growing under more favourable conditions (McGarvie & Parolis 1979).

Table 21. Percentage mortality of T. tapiacola larvae during development in different categories of O. aurantiaca. <III = larvae in 1st to 3rd-instar; >IV = larvae in 4th to 6th-instar. (n) = number of larvae observed.

Cause of Mortality	Plant categories: Small <III	Small >IV	Medium <III	Medium >IV	Large <III	Large >IV	Etiolated <III	Etiolated >IV
Gum	6,6	0,0	50,0	7,4	41,2	0,0	0,0	0,0
Starvation	1,3	39,4	0,0	3,7	0,0	14,3	15,8	57,2
Other	5,3	19,7	3,4	22,2	17,6	28,6	10,5	9,5
Total	13,2	59,1	53,4	33,3	58,8	42,9	26,3	66,7
(n)	(76)	(66)	(58)	(27)	(17)	(7)	(57)	(42)

No larvae were repelled by gum from etiolated plants and only 6,6% of the larvae were repelled by gum on small-size, 'typical' plants. On medium and large-size, 'typical' plants, mortality due to gummosis was much higher and this accounted for most of the mortality of first to third-instar larvae (<III) on these plants (Table 21).

The second major cause of mortality during larval development of T. tapiacola was starvation and this was highest during the third to sixth larval-instars (>IV; Table 21). Starvation occurred when the larvae had insufficient food and were unable to locate suitable host plants to support them through to pupation.

On 'typical' plants, this was most common when the larvae initially penetrated very small plants and loose cladodes lying on the soil. Also, when larvae tunnelled into the terminal joints of larger jointed cactus bushes, the cladodes usually dropped from the plants in response to the larval damage. Larvae in these dislodged joints were in the same predicament as those that had initially colonised small plants and loose joints.

On 'etiolated' plants the larvae penetrated the long, narrow joints at a point anywhere along the length of the joint. Once inside the cactus, the larvae tunnelled in one direction leaving behind damaged tissue that shrivelled as it dried, causing the larval tunnel to collapse. The larvae were then unable to move back along the tunnel to feed on the fresh plant tissue beyond the entry hole. The larvae were therefore forced to tunnel in one direction only and some reached the end of the cladode before they were due to pupate.

The larvae were able to move from the destroyed joints and search for fresh food sources. However, of 67 larvae that ran short of food, only five managed to find and recolonise suitable cladodes. The others disappeared and most were probably taken by predators. However, because a shortage of food had initially caused them to leave the shelter of the cladodes and become vulnerable to predators, this mortality was grouped under the heading of starvation.

On all four categories of jointed cactus, a number of larvae also died from unknown causes (Table 21). All but four of these larvae disappeared from the plants, even though there was still food available and the feeding area seemed to be suitable for the continued development of the larvae. The four larvae that died within their tunnels showed symptoms of microbial infection. Whether this was the cause of death, or secondary, after death, was not apparent.

On medium and large-size, 'typical' plants, larval mortality was highest during the first three larval instars (Table 22). The major mortality factor on these plants was gummosis, a process that was initiated soon after the larvae penetrated the plants. The larvae that were not repelled by gum on medium and large plants had a higher survival probability after the third-instar than larvae on small and 'etiolated' plants. Larval mortality on these plants was higher after the third-instar (Table 22), mainly as a result of starvation.

Table 22. The number of T. tapiacola larvae that survived to the 3rd-instar and pupation, on different categories of jointed cactus plants, and the percentage mortality between the stages. (Data derived from Table 21).

Plant category	No. initial penetrations	% mortality	No. alive at 3rd instar	% mortality	Number pupated
Small	76	13,2	66	59,1	27
Medium	58	53,4	27	33,3	18
Large	17	58,8	7	42,9	4
Etiolated	57	26,3	42	66,7	14

5.8 Pupal mortality.

The larvae of T. tapiacola almost invariably tunnell downwards as they feed through the stems of the jointed cactus plants. As a result, they usually complete their development in the subterranean parts of the stem and tuber. At some stage before pupation, most of the maturing larvae chew their way out of the plant below ground level and tunnel into the soil for distances of up to 30 mm. The soil displaced by the larvae during this process is ingested and either regurgitated, or defaecated as frass, in the hollowed tuber and stem of the cactus. During the final stages of development, when disturbed and during periods of extreme heat (Mann 1969), the larvae withdraw into the tunnels. At the end of the larval stage, the prepupae retreated into the tunnels in the soil, spun a cocoon and pupated. In this position the pupae were protected from predators and the effects of inclement weather.

Pupal mortality in T. tapiacola was measured in an exposed habitat, among 'typical' plants, and in a shaded habitat, among 'etiolated' plants. Initially the parasitoids and predators that attacked T. tapiacola pupae were collected for identification and the type of damage that each caused was noted. This was achieved by taking 400 cocoons, with pupae, from the insectaries and placing them among the

leaf litter at Thursford and Mosslands Farms. The pupae were checked in situ every day for the first four days and samples of 20 pupae were then returned to the laboratory at four to five day intervals. The recollected pupae were confined in stoppered, glass-vials, to collect any parasitoids that emerged.

Almost half (47%) of the cocoons disappeared within twenty-four hours of being placed in the field. These were presumably removed by rodents and birds. A single ant species, Oligomyrmex sp., was found feeding on the pupae at Mosslands Farm. Pupae that had been damaged in a similar way to those that were killed by Oligomyrmex sp. were also found at Thursford Farm, but the actual predators involved were never discovered. Five adult parasitoids, representing two undescribed chalcidoid species from the genera Hockeria (3 adults) and Invreia (2 adults) were collected from the pupae placed at Thursford farm. No parasitoids emerged from the pupae placed at Mosslands.

The methods described above were only used to identify the predators and parasitoids of T. tapiacola pupae. The mortality that T. tapiacola pupae suffered under more natural conditions was measured as follows. In the insectary, first-instar larvae were placed on jointed cactus plants growing in asbestos trays filled with soil. The trays measured 0,15 m^2 and 200 mm in depth. Each contained from four to six growing, jointed cactus plants. Single first-instar larvae were placed on each plant and held in the insectary until they had developed to approximately the fourth-instar. Larvae that failed to penetrate the plants, or died while still being held in the insectary, were replaced with larvae of an equivalent age. The trays, with plants and larvae, were then transported to the field and buried so that the soil in the trays was flush with the surface of the surrounding soil. The larvae eventually pupated in the field and were left until all the adults had emerged. The trays were then lifted and the cocoons with pupal remains were sieved from the soil.

The pupal castes were removed from the cocoons and the fate of each was determined. Pupae that produced adults had characteristic emergence splits in the cuticle and scales from the moth were visible on the silk of the cocoons. Pupae that had been parsitised had

distinct emergence holes through which the adult parasitoids emerged. Very few pupal remains were found in the cocoons of pupae that had been killed by ants. Some of the pupae showed none of the above characteristics and remained as entire but desiccated and shrivelled pupae within the cocoons. The cause of death in these pupae was unknown and was classified as mortality due to 'other-causes'.

Pupal mortality was generally low and the difference between exposed and shaded habitats was not significant (X^2 = 1,76). Ant predators were active at both localities but parasitoids only killed larvae in the exposed habitat at Thursford Farm (Table 23).

Table 23. Mortality of T. tapiacola pupae in exposed and shaded habitats. (n) = number of cocoons retrieved and examined.

Cause of Mortality	Percentage pupal mortality in: Exposed habitats	Shaded habitats
Parsitoids	4,7	0,0
Predators	6,6	4,1
Other	8,6	9,0
Total (n)	19,9 (151)	13,1 (145)

5.9 Life tables for T. tapiacola in South Africa.

A series of four partial-life-tables (Table 24A - D) and survivorship curves (fig. 32) have been constructed to summarise the cumulative mortality suffered by the immature stages of T. tapiacola on small, medium and large jointed cactus plants in exposed habitats, and on 'etiolated' jointed cactus plants in the shade. These tables have been updated from Hoffmann (1981).

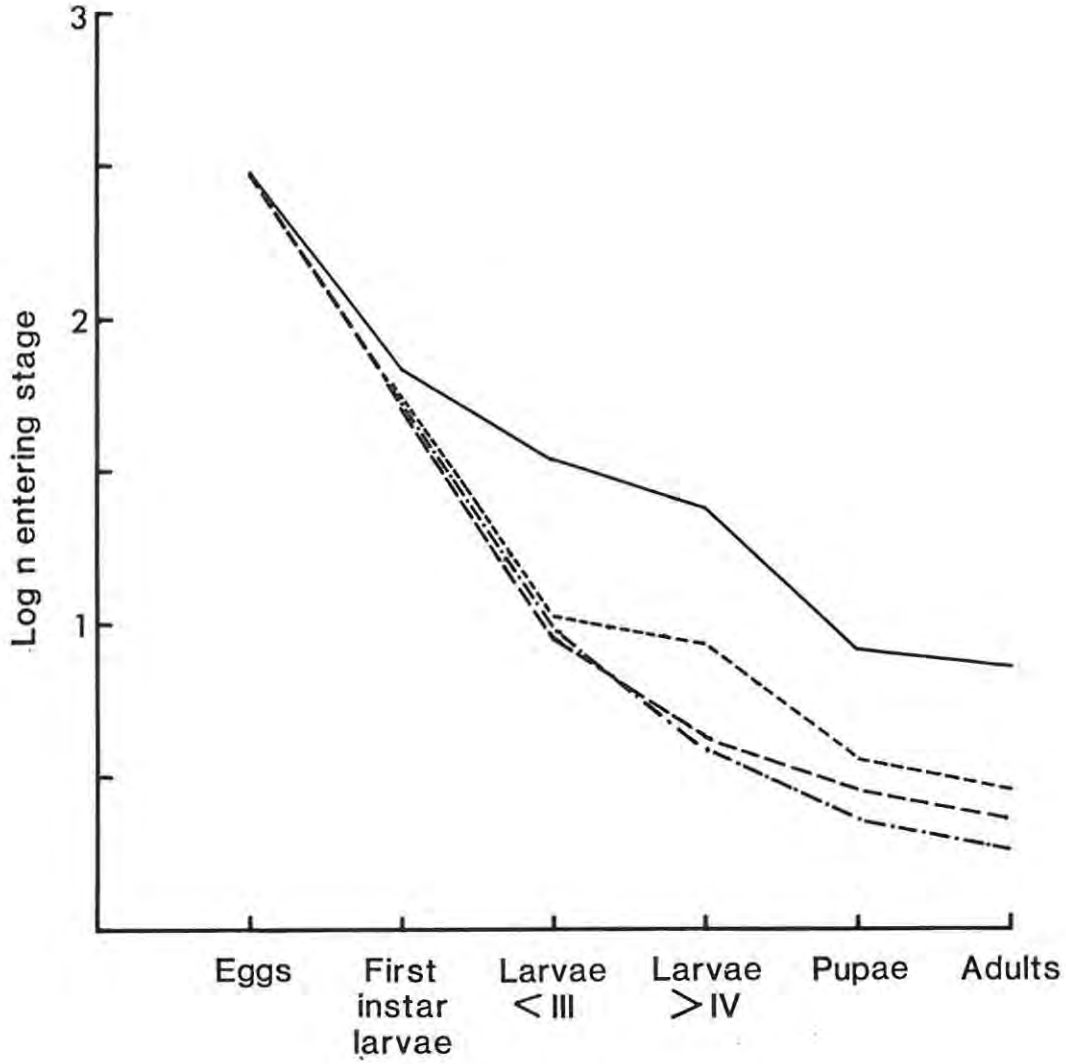

Fig. 32. Survivorship curves for the immature stages of T. tapiacola on 'etiolated' plants (————) and on small-size (-------), medium-size (— — —) and large-size (—·—·—) 'typical' plants of O. aurantiaca in South Africa. <III = 1st to 3rd-instar larvae in plant; >IV = 4th to 6th-instar larvae in plant.

Survival was lowest (0,6%) on large, 'typical', O. aurantiaca plants. At an average fecundity of 309 eggs per female, mortality of 99,4%, during the immature stages, results in only two adults emerging from the eggs laid by each female. Therefore, all the females that emerge from large plants would have to mate and lay their full complement of eggs to ensure survival of the population in this habitat. On small

and medium 'typical' O. aurantiaca survival was slightly higher, 0,9% and 0,7% respectively. At these levels, 71,9% of the females from small plants, and 92,5% of the females from medium plants would have to mate and lay their full complement of eggs to prevent a negative population growth rate. It was not possible to measure adult mortality during this study, but if less than 70% of T. tapiacola moths survived (as the case may well have been), the populations of T. tapiacola would eventually decline to extinction on 'typical' plants in exposed habitats.

In shaded situations, overall mortality of the immature stages was 97,7% and, on average, seven adults emerged from the 309 eggs laid by each female. Since only two of these females need to mate and lay eggs for the population to survive, in shaded habitats T. tapiacola could tolerate an adult mortality of 71,9% before the population declined. No figures were obtained for adult mortality, but an adult survival rate of 28,1% does not seem unrealistic, and this would allow T. tapiacola populations to survive in shaded habitats in South Africa.

The partial-life-tables for T. tapiacola in South Africa need to be interpreted with caution. Although the methods used to place the different life-stages of T. tapiacola in the field were designed to approximate natural conditions as closely as possible, they were unavoidably artificial. As a result, the conditions under which mortality was measured, were to a certain extent unnatural, and mortality may have differed from what it would have been in self-perpetuating populations in the field. Under these circumstances, the mortality of the artificially implanted life-stages may be expected to be higher than that of naturally occurring life stages, as was found by Girling (1978) in an egg mortality study of Eldana saccharina Walker on sugar cane. If this is the case, then the mortality factors acting on the immature stages alone probably do not account for the failure of T. tapiacola to become established in South Africa.

Table 24. Partial-life-tables for the immature stages of T. tapiacola on O. aurantiaca in South Africa. <III = 1st to 3rd-instar larvae in plants; >IV = 4th to 6th-instar larvae in plants.

(A) Small-size, 'typical' plants.

Life stage	Cause of mortality	% Mortality	Total % mortality during stage	Cumulative % Mortality
EGGS	Weather & predators	82,3	82,3	82,3
LARVAE				
1st-instar (pre-feed)	Predators & unsuitable plants	81,6	81,6	96,7
<III	Gum	6,6		
	Starvation	1,3		
	Other	5,3	13,2	97,2
>IV	Starvation	39,4		
	Other	19,7	59,1	98,8
PUPAE	Parasitoids	4,7		
	Predators	6,6		
	Other	8,6	19,9	99,1

(B) Medium-size, 'typical' plants.

Life stage	Cause of mortality	% Mortality	Total % mortality during stage	Cumulative % Mortality
EGGS	Weather & predators	82,3	82,3	82,3
LARVAE				
1st-instar (pre-feed)	Predators & unsuitable plants	83,3	83,3	97,0
<III	Gum	50,0		
	Other	3,4	53,4	98,6
>IV	Gum	7,4		
	Starvation	3,7		
	Other	22,2	33,3	99,1
PUPAE	Parasitoids	4,7		
	Predators	6,6		
	Other	8,6	19,9	99,3

Table 24 (continued)

(C) Large-size, 'typical' plants.

Life stage	Cause of mortality	% Mortality	Total % mortality during stage	Cumulative % Mortality
EGGS	Weather & predators	82,3	82,3	82,3
LARVAE				
1st-instar (pre-feed)	Predators & unsuitable plants	81,7	81,7	96,8
<III	Gum	41,2		
	Other	17,6	58,8	98,7
>IV	Starvation	14,3		
	Other	28,6	42,9	99,2
PUPAE	Parasitoids	4,7		
	Predators	6,6		
	Other	8,6	19,9	99,4

(D) 'Etiolated' plants.

Life stage	Cause of mortality	% Mortality	Total % mortality during stage	Cumulative % Mortality
EGGS	Weather & predators	77,3	77,3	77,3
LARVAE				
1st-instar (pre-feed)	Predators & unsuitable plants	51,7	51,7	89,0
<III	Starvation	15,8		
	Other	10,5	26,3	91,9
>IV	Starvation	57,2		
	Other	9,5	66,7	97,3
PUPAE	Predators	4,1		
	Other	9,0	13,1	97,7

6. DISCUSSION

In spite of a release programme during which over 830 000 individuals were deployed, the Ibarreta strain of T. tapiacola has apparently failed to become established in South Africa as a biological control agent of jointed cactus. This failure is not surprising in view of the fact that approximately 66% of the natural enemies released against arthropod pests failed to establish (Hall & Ehler 1979). The success rate may be higher for agents introduced against weeds, but this percentage has not yet been calculated.

Clausen (1951) noted that most successful biological control agents establish easily and exert pressure on the target pest within a short period of time. As a result he recommended that time and effort not be wasted on natural enemies that are difficult to establish. If his advice is followed, the release programme with T. tapiacola should probably be terminated and research emphasis switched to other cactophagous insects and pathogens. However, this decision should only be made after the following questions have been answered: (1) What are the factors that have prevented T. tapiacola from becoming established and is there anything that can be done to rectify the situation? (2) If any of the strains of T. tapiacola eventually establish, can the species become at least a partially effective control agent? Attempts are made to answer these questions in this discussion and the findings are used to suggest future strategies that might improve the biocontrol potential of T. tapiacola.

6.1 Factors preventing establishment.

Biological control agents can fail to establish for any one of several possible reasons (Andres et al. 1976). Those most likely to have hindered the progress of T. tapiacola in South Africa are discussed under three separate sub-headings below.

(i) Excessive mortality in the new environment.

The establishment failure of newly-released natural enemies has often

been attributed to parasitism, predation and disease-induced mortality in the new environment (Goeden & Louda 1976). If a newly released agent does suffer excess mortality due to natural causes, there is a limited amount that can be done to rectify the situation (Rabb et al. 1976) and the insect must usually be discarded as unsuitable for that particular programme. It is therefore important to determine the mortality suffered by an agent that has apparently failed to establish, and to calculate whether this is sufficient to cause the populations to dwindle to extinction.

The partial-life-tables for T. tapiacola show that in shaded habitats the mortality suffered by the immature stages alone probably does not account for the failure of the moth to become established. In exposed situations, survival is lower and it seems less likely that the species can exist in this habitat, especially if the moths oviposit mostly on large jointed cactus plants. However, the impact of mortality on the establishment programme with T. tapiacola cannot be conclusively determined without measurements of adult mortality. Southwood (1978) reviews methods of measuring mortality in natural populations but none of these could be applied, nor other methods be devised, to measure the mortality of T. tapiacola adults. There is no forseeable chance of adult mortality ever being accurately measured, even if populations of the insect become permanently established.

The mortality suffered by T. tapiacola between egg deposition and adult emergence, as measured in this study, was compared to that measured for populations of other insects, during the same portion of the life-cycle (Table 25). The table shows the lowest and highest mortality that was measured in different generations for each species. Adult mortality between generations is not included in Table 25 because none of the studies measured this directly. Adult mortality was inferred from the difference between potential fecundity and the numbers of progeny that were actually counted in the next generation. Emigration from and immigration into the sample areas were unavoidably included and reduced the accuracy of these etimates.

Table 25. The percentage mortality suffered by various insect species. For each species, the range of mortalities, from egg deposition to adult emergence, during different generations is shown.

Species	% mortality	References
Choristoneura fumiferana (Clem.) (Lepidotera: Tortricidae)	99,5 - 99,9	Morris & Miller (1954)
Operophtera brumata (L.) (Lepidoptera: Geometridae)	92,3 - 99,7	Varley & Gradwell (1968)
Bupalus piniarius L. (Lepidoptera: Geometridae)	82,2 - 99,9	Klomp (1968)
Operophtera brumata (L.) (Lepidoptera: Geometridae)	96,5 - 99,7	Embree (1971)
Tyria jacobaeae (L.) (Lepidoptera: Arctiidae)	80,6 - 100	Dempster (1971)
Saccharosydne saccharivora (Westw.) (Homoptera: Delphacidae)	96,8 - 97,6	Metcalfe (1972)
Leptoterna dolabrata (L.) (Homoptera: Miridae)	91,7 - 98,0	McNeill (1973)
Tucumania tapiacola Dyar (Lepidoptera: Phycitidae)	97,7 - 99,8	This study.

Although Table 25 does not include adult mortality, it serves to emphasise that the average generation mortality of relatively fecund insects must be high (close to 100%) if the population numbers are to remain reasonably stable in the long-term (Solomon 1976) and that insect populations do survive in spite of this high mortality, which superficially may seem to be excessive.

The adult mortality that will reduce the average fecundity of the females to a level below which the population can no longer maintain itself, can be calculated. This may be expressed as the percentage adult mortality, although it includes failure to mate, as well as

mated females that fail to lay any eggs and those that lay only a portion of their eggs before dying. In the case of a population of T. tapiacola in a shaded habitat, adult mortality must exceed 71,9% to raise the average generation mortality from 97,7% (as measured in this study) to an overall mortality of 99,4% (the level above which the population cannot sustain itself). Because there is no way of determining whether adult mortality in T. tapiacola will exceed 70% or not, the implications of both these alternatives must be considered.

If it is assumed that adult mortality exceeds 70%, the moth populations would not be able to survive and the logical step would be to terminate the release programme. If this happened, the real reasons for the establishment failure of T. tapiacola would be unresolved and the potential of the moth as a biological control agent would remain in doubt. This in turn could lead to the insect being repeatedly re-introduced in the future by workers who may be justifiably sceptical that the moth had been correctly handled during these establishment attempts. Alternatively, if it is assumed that adult mortality is lower than 70%, the populations will survive, at least in shaded habitats and other reasons must be sought to explain the establishment failure of the insect.

There are no valid reasons for accepting or rejecting either of the above alternatives. However, because there are a number of other possible reasons for the establishment failure, it is preferable at this stage to assume that T. tapiacola can survive under South African conditions, and to give the insect the benefit of the doubt, at least until the other possible causes for the failure have been investigated, or until releases have been attempted that avoid these potential pitfalls.

(ii) Too few individuals released.

The numbers of individuals released can determine whether or not an insect will establish in the release area. The critical phase occurs when the adults that emerge in the field need to locate partners and mate (Messenger & van den Bosch 1971). The proportion of adults that mate successfully increases with the number that are available for

pair formation. Therefore, there is a critical threshold below which too few adults mate, so that each successive generation is smaller than the preceeding one and the population eventually becomes extinct. This threshold probably varies from species to species and the minimum numbers of a natural enemy that must be released to achieve establishment tends to be characteristic for each species (DeBach & Bartlett 1964). Agents with a highly variable developmental time in the immature stages, coupled with short-lived adults that disperse rapidly will have a higher threshold than those with a closely synchronised adult eclosion period and long-lived adults that have a low tendency to disperse.

The number of adults that emerge in the first field generation is determined by the number of eggs or larvae that are initially released and if this level is below the critical threshold, establishment will not be achieved. The maximum number of first-instar T. tapiacola larvae released at any one time was 43000 and the number per release averaged 18000 - 19000. Following 89,7% mortality of T. tapiacola during the larval and pupal stages in shaded habitats, approximately 2000 adults would have emerged from an average release. Without the relevant information on adult mortality and dispersal, there is no way of knowing whether the adults at this density were above or below the critical threshold for mating success. As a result, future releases should strive to establish as many adults as possible in the first generation. This may be achieved by increasing the numbers of larvae that are deployed during each release, although the numbers that can be produced is limited by the available insectary facilities, space and time.

The adult population can also be boosted if the development of the insectary and field generations is synchronised (by raising or lowering the insectary temperature), so that adult eclosion in the insectary coincides with adult eclosion in the field. The insectary reared adults are then liberated in the release areas at the same time that adults emerge in the field. The proportion of females that mate should be higher in the larger populations and this in turn should increase the chances of establishment success. This practise should not be continued for extended periods, and may even be detrimental

after only one generation, because the less-fit insectary adults might genetically 'swamp' the progeny of the first releases, that have become better adapted to the new habitat (Messenger et al. 1976).

(iii) Genetically maladapted strains released.

Clausen (1936) emphasised the important bearing that inter-population variation may have on the chances of a species becoming a successful biological control agent. Wapshere (1975, 1981) has proposed methods for selecting, before release, the strains of a species that are most likely to provide effective control of the target weed. The successful biological control of skeleton weed, Chondrilla junicea L., was attributed to the use of these techniques and the careful selection of the most effective agents before releases commenced (Cullen 1974; Wapshere 1975, 1981). However, van Lenteren (1980) has warned that pre-release selection techniques can never be entirely relied on and when they are used, there is always a danger that potentially useful agents or strains might be discarded prematurely. Also, long-term research projects, to evaluate the most promising species or strains, may be expensive and may cause unnecessary delays in ultimately achieving control of the pest (DeBach 1971; Zwolfer et al. 1976). As a result, populations from many localities should be introduced and released on a trial and error basis to exploit fully and efficiently the intraspecific variation within species of natural enemies (Simmonds 1963; Wilson 1965).

Almost all the releases with T. tapiacola in South Africa were made with only one strain of the moth from Ibarreta. In South America, T. tapiacola occurs over a wide geographic range and on a number of cactaceous hosts. Thus there is a reasonable chance of intraspecific differences occurring between the isolated populations. Some of these differences have already been detected between the populations from Ibarreta and Campana; notably adult coloration, larval head capsule colour and the micropylar area of the eggs. Exploitation of this potential variation has already commenced with releases of the Campana strain of T. tapiacola and will be continued if other strains are obtained.

Simmonds (1963) proposed that genetic variation within species can be enhanced for biological control releases by cross-breeding a number of strains in the insectary and releasing the resultant hybrid strain. Natural selection should then benefit the genotypes best adapted to the new environment. However, cross-breeding either before or after release may have detrimental side effects (Hoy 1975). The vigour of the hybrid may be lower than that of the parent strains or, if the hybrid has the same or increased vigour, it is often lost within one or a few generations (Vetukhiv 1954, 1956, 1957). Also hybridization may disrupt the co-adaptation of gene complexes so that the fitness of the hybrid population is reduced, even though genetic variability is increased (Force 1967; Levins 1969).

Initially at least, future releases with T. tapiacola should adopt a conservative approach and the different strains should be released either sequentially at one locality or simultaneously at separate localities. This will discourage cross-breeding between the strains and allow them to be evaluated independently. If all the pure strains fail to establish or fail to contribute to the control of the weed, consideration should be given to mixing the strains before release.

Selective breeding in the insectary has been proposed as a technique to improve the performance of strains that are poorly adapted to the new environment (DeBach 1958). However, the method has not been proved in practice (Roush 1979). Its potential usefulness in biological control has been questioned because laboratory-selected strains usually revert to the wild-type once they are exposed to 'natural' selection pressures (Roush 1979). Also, there is a danger of inadvertently selecting undesirable traits that offset the beneficial effects of the desired traits (Simmonds 1963). These objections are particularly valid when attempts are made to establish the natural enemy on the target pest, as opposed to innundative releases (Roush 1979). As a result, selective breeding does not seem a viable option to improve the biological control potential of T. tapiacola.

Harris (1982 personal communicationa) recommended a technique used by Harris & Alex (1971), Harris et al. (1975) and Harris (1982) that

might enhance the chances of eventually establishing T. tapiacola. The technique indirectly exploits the natural variation within species and was proposed specifically to assist species that establish for one or a few generations in the new habitat, but then dwindle to extinction. The few individuals that survive to the second or subsequent generation in the field are presumably those that are genetically best adapted to the conditions of the new environment. However, when the selection process reduces the population to critically low levels, successful pair formation and mating are impaired and the population is unable to maintain itself in spite of its genetic adaptation to the habitat.

The survivors can be assisted during this critical phase by returning some of them to the insectary for mass-production through a number of generations. The individuals of this insectary colony are presumably better adapted to the environment in the release area than those that were originally released. As a result, selection pressures account for a smaller proportion of the re-released individuals than after the initial releases, and the chances that enough survive to allow normal mating are enhanced. T. tapiacola is a good candidate for this type of manipulation, especially as it may result in the eventual establishment of the moth, and at the same time demonstrate the practical usefulness of a technique for release of other cactophagous insects in the future.

The mass-production programme can have a critical bearing on the success of a biological control venture (Bush 1975). Populations of insects reared under insectary conditions loose 'fitness' as a reult of inbreeding and the inadvertent selection of laboratory adapted ecotypes (Mackauer 1976, 1981; Nei et al. 1975; Chambers 1975,1977; Pashley & Proverbs 1981). The nett result is diminished survival among the individuals that are eventually released in the field and the chances of successful establishment are decreased (Myers & Sabath 1981).

The Ibarreta population of T. tapiacola was reared through approximately 30 generations in the insectary before it was initially released. This delay almost certainly provided sufficient time for

the selection of laboratory traits, which can occur within a few generations (Boller 1972) and the Ibarreta strain was probably better adapted to survive in the insectary than in the field at the time of release. This alone may have contributed significantly, if not entirely, to the establishment failure.

Now that host specificity studies have been completed, any strains of T. tapiacola that are introduced from the same or different localities in South America should be mass-produced and released without delay. The Campana strain of T. tapiacola was only reared through two generations in the insectary before 1215 adults and 11000 larvae were released. The success of this approach with the Campana strain has not yet been assessed. However, in view of the inherent problems of prolonged mass-production in the insectary, the interval between introduction and release should routinely be kept at a minimum.

6.2 Future strategies with T. tapiacola.

At this stage, the exact reasons (or reason) for the establishment failure of T. tapiacola remain unknown, although a number of possibilities have been identified. Further investigations into the causes of the failure will probably require considerable finance and effort, with no guarantee of success, or guarantee that the study will lead to the eventual establishment of the insect. Instead therefore, a more efficient release programme is now proposed that avoids the problems already outlined in this discussion. The revised programme is summarised in fig. 33. Attempts should be made to establish T. tapiacola using these procedures. If the insect still fails to survive, it can then be concluded, almost beyond doubt, that the insect can never become a control agent of jointed cactus in South Africa.

The revised programme has already commenced (step 1) with releases of the Campana strain of T. tapiacola. This colony was obtained, at very little cost, during routine surveys for other cactophagous insects and pathogens in South America. This approach should be adopted in the future, so that additional strains from other geographic regions

(including Ibarreta) and host plants can be obtained with a minimum of additional expense.

The new strains can be reared from relatively small founder colonies into sufficient numbers for release within three insectary generations (step 2), as was achieved with the Campana colony. The optimal conditions for rearing T. tapiacola have been determined and, apart from the insectary space required, the insect can be mass-produced easily and cheaply.

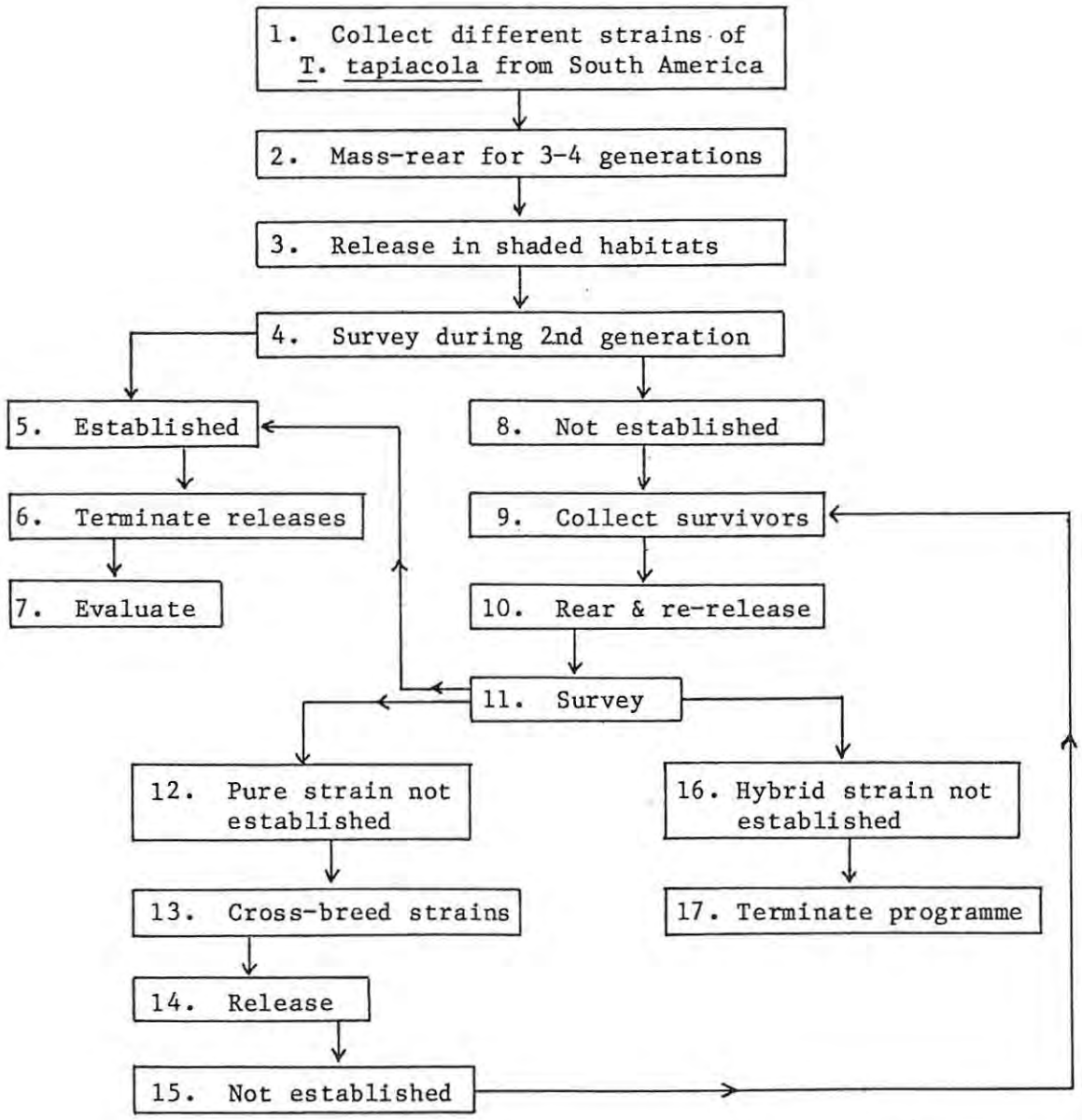

Fig. 33. Planned programme for future releases with T. tapiacola in South Africa.

Once releases have been made in suitable, shaded habitats (step 3), the insect requires no further attention until the larvae of the second generation are beyond the third-instar. At this stage, surveys need to be made in the release areas (step 4) to locate the older-instar larvae in the plants. If the second generation larvae are abundant and easy to find, the population may have established (step 5) and no further release efforts are required (step 6), except perhaps to add insectary reared adults to the population when the adults start to emerge. If the moth then survives into subsequent generations, its establishment is confirmed and an evaluation of the impact it has on the weed is needed at some later date (step 7).

If the larvae are scarce and difficult to find during the initial survey (step 4), the establishment attempt has probably failed again (step 8). In this eventuality, some of the surviving larvae should be collected and returned to the insectary (step 9) for mass-production and re-release (step 10) after a maximum of three or four insectary generations. This colony should be better adapted to the environment of the release site and therefore has a better chance of becoming established. Surveys during the second generation (step 11) should indicate whether the re-released population is increasing or decreasing in numbers.

Colonies of all the strains that are released should be maintained in isolation in the insectary. If none of the available pure strains become established (step 12), the insectary colonies should be mass-reared and cross-bred (step 13) before release (step 14). If this hybrid population also fails to become abundant in the second generation (step 15), some of the progeny can also be returned to the insectary (step 9) for mass-production and re-release (step 10). The failure of this strain (step 16) will have exhausted all the possible avenues for manipulation of T. tapiacola, and the programme should then be terminated (step 17).

The duration of this release programme will be determined largely by the development time of the insects in the insectary and in the field, and whether success is achieved sooner or later, if at all. The man-hours required will be mostly restricted to limited periods when

releases, larval surveys and collections are made. These tasks can probably be performed by workers primarily involved with other programmes. Thus, the time and finances required to continue the programme with T. tapiacola can be kept to a minimum and are justified because there is still a reasonable chance that the insect may become established and contribute to the control of jointed cactus.

6.3 The potential of T. tapiacola for control of jointed cactus.

If it is assumed that the modified release programme may result in the eventual establishment of T. tapiacola in South Africa, what impact could the insect have on the weed? These predictions may influence the decision to continue or discontinue releases with T. tapiacola. It is therefore important to consider the potential impact that T. tapiacola might have as a biological control agent of jointed cactus in South Africa. Sellers (1953) criticised Clausen's (1951) hypothesis that successful agents always establish easily and pointed out that agents that are difficult to establish may become at least partially effective. Also, Hall et al. (1980) have warned against generalising about predicting probabilities of success from previously recorded successes and failures.

Certain features of the biology of T. tapiacola hold promise that the insect may yet fulfil a role as a biological control agent against jointed cactus. The larvae are nearly always found in the basal parts of small plants or loose joints lying on the soil and they seldom attack large old host-plants, either in South America or following releases in South Africa. Also, survival of T. tapiacola larvae is higher in shaded habitats than in the open exposed areas. These observations have important implications when all the biological and chemical control measures against jointed cactus are considered together.

At present almost all of the factors that contribute to the control of jointed cactus in South Africa exert pressure on the larger, established plants in exposed habitats. The phycitid moth, C. cactorum, only attacks large jointed cactus plants (Moran & Annecke 1979) and

the cochineal, D. austrinus, is more abundant on large plants and thickets than on small plants, except when populations of the insect reach epidemic proportions (Zimmermann 1979). Almost 100% of the large plants and thickets are sprayed during herbicide applications, while up to 32% of the loose joints and small plants remain undetected and are not sprayed (Zimmermann 1979). The 'etiolated' jointed cactus growing in the dense shade of Valley Bushveld vegetation is hardly subject to any control measures because both C. cactorum and D. austrinus seldom occur in that habitat. Also, herbicides are more difficult to apply in Valley Bushveld and secondary damage to the dense thickets of indigenous flora is more severe than in the exposed False Karroid vegetation. As a result, the jointed cactus infestations in Valley Bushveld remain largely untouched and the plants provide a resevoir of joints that contribute to the spread and reinfestation of the weed.

If T. tapiacola becomes established, most of the larval damage will probably occur on loose joints and small plants, where the entire cladode or plant can be destroyed by a single larva. The larvae will therefore not compete with C. cactorum and only marginally with D. austrinus. T. tapiacola is also expected to be less detrimentally affected by herbicides than the other two insects because many small plants escape the application of chemicals.

Jointed cactus reproduces vegetatively when joints are dislodged from the parent plant and come to rest on the soil (Zimmermann & van de Venter 1981). Zimmermann (1981) has shown that up to 46,3% of the loose joints and small plants are killed by cochineal or desiccate under drought conditions and this mortality probably accounts for the slow rate of increase of jointed cactus in the drier parts of its range. T. tapiacola may further increase the mortality of loose joints and could contribute to slowing the rate of increase and dispersal of the weed. Thus, even at relatively low population levels of the insect, T. tapiacola might provide financial benefits by reducing the recovery time of the weed after herbicide applications.

In shaded habitats were jointed cactus remains practically untouched by either insects or chemicals, the impact of T. tapiacola on the weed

would almost certainly be significant only if the moth reached very high population levels. However, an agent at low densities may increase the stresses already operating against the weed and contribute to its control (Harris 1981). Harris (1979) noted that it takes an average of four agents to reduce a weed species to below an economic threshold. T. tapiacola may therefore contribute to the stress already exerted on jointed cactus by the insects, C. cactorum and D. austrinus, as well as by environmental factors. Ultimately, releases with other cactophagous insects and pathogens are planned and the combined impact of this complex of species may exert enough pressure to bring the weed under control.

6.4 Conclusions.

Although this discussion has been largely speculative, it seems reasonable to conclude that there is a chance that T. tapiacola can be established in South Africa. If this is achieved, the insect may contribute to the overall control of jointed cactus. Therefore, T. tapiacola should still be collected whenever larvae are encountered during routine surveys and collecting trips for other cactophagous insects. The material should be introduced into South Africa and released as soon as large enough numbers have been reared in the insectary. Close monitoring of the newly released populations would probably be wasted effort, although this may be justified if the insect becomes established at reasonable levels. I therefore propose that T. tapiacola should not be discarded as a potential biocontrol candidate, but that efforts to establish the moth should continue at a reduced level, utilising the mass-rearing and release techniques described in this thesis.

APPENDIX 1

The host plants and localities where Tucumania Dyar has been collected in South America. The numbers of the references (Refs) are decoded at the end of the list.

Host Plant	Locality	Remarks	Refs
Eriocereus bonplandii (Parmentier) Riccobono	Ibarreta (25.13S 59.50W) Argentina	-	7
Eriocereus martinii (Labouret) Riccobono	Ibarreta (25.13S 59.50W) Argentina	T. porrecta - Det. D.C. Ferguson 1977	7
	Rio Bermejo, Chaco, Argentina	T. porrecta - Det. D.C. Ferguson 1977	7
Eriocereus pomanensis (Weber) Berger	Joaquin V. Gonzáles (25.06S 64.12W) Arg.	-	7
	San Miquel de Tucumán (26.47S 65.15W) Arg.	T. porrecta - Det. D.C. Ferguson 1977	7
Eriocereus sp.	Paraná (31.45S 60.30W) Argentina	T. porrecta - Det. D.C. Ferguson 1977	7
Eriocereus tephracanthus (Link & Otto) Berger	Parotani (17.35S 66.20W) Bolivia	-	7
Monvilea sp.	Ibarreta (25.13S 59.50W) Argentina	Tucumania sp. - Det. D.C. Ferguson 1977	7
	Pres de la Plaza (27.00S 59.50W) Arg.	T. porrecta - Det. D.C. Ferguson 1977	7
Opuntia aurantiaca Lindley	Campana (34.10S 58.55W) Argentina	Released in South Africa.	7
	Gualeguaychu (33.03S 59.31W) Argentina	-	5,7
Opuntia bonaerensis Spegazzini	Campana (34.10S 58.55W) Argentina	-	7
Opuntia chakensis Spegazzini	Bermejito (25.38S 60.21W) Argentina	-	7

Host Plant	Locality	Remarks	Refs
Opuntia discolor Britton & Rose	Bermejito (25.38S 60.21W) Argentina	-	7
	Ibarreta (25.13S 59.50W) Argentina	T. porrecta - Det. D.C. Ferguson 1977	6,7
	Las Lomitas (24.41S 60.35W) Argentina	-	7
	Metan (25.30S 65.00W) Argentina	Tucumania sp. - Det. D.C. Ferguson 1977	7
	North West Argentina	Possible origin of Australian stock.	4
	Rivadavia (24.08S 62.54W) Argentina	T. porrecta - Det. D.C. Ferguson 1977	7
	Tapia (26.38S 65.17W) Argentina	T. porrecta - Det. D.C. Ferguson 1977	7
	Vipos (26.28S 65.21W) Argentina	T. porrecta & Tucumania sp. - Det. D.C. Ferguson 1977	7
Opuntia retrosa Spegazzini	Ibarreta (25.13S 59.50W) Argentina	-	7
	Formosa (26.07S 58.14W) Argentina	-	7
	Fortin Lavalle (25.41S 60.13W) Arg.	-	7
	Vipos (26.28S 65.21W) Argentina	-	7
Opuntia russelli Britton & Rose	Villavicencio (32.48S 69.00W) Argentina	Possibly not Tucumania.	5
Opuntia sp.	Tapia (26.38S 65.17W) Argentina	Type locality of T. tapiacola.	1,2,3
	Paysandú (33.21S 58.05W) Uruguay	Type locality of T. porrecta.	1,2,3
	Metań (25.30S 65.00W) Argentina	-	5
	Santiago del Estero (27.47S 64.15W) Arg.	-	5

Host Plant	Locality	Remarks	Refs
Opuntia stenartha Schuman	Asunción (25.15S 57.40W) Paraguay	-	5
Opuntia sulphurea G. Don	Andalgalá (27.33S 66.18W) Argentina	T. porrecta - Det. D.C. Ferguson 1977	7
Opuntia tayapayensis Cardenas	Cochabamba (17.26S 66.10W) Bolivia.	T. tapiacola - Det. D.C. Ferguson 1977 & reared in South Africa, but not released.	7
	Parotani (17.35S 66.20W) Bolivia		7
	Mizque (17.57S 65.17W) Bolivia	T. tapiacola - Det. D.C. Ferguson 1977	7
Opuntia utkilo Spegazzini	North West Argentina	-	4

REFERENCES: 1. Dyar (1925); 2. Heinrich (1939); 3. Heinrich (1956); 4. Dodd (1940); 5. Mann (1969); 6. Hoffmann & Moran (1977); 7. Unpublished reports, Weed Laboratory, Uitenhage, South Africa.

Zimmermann et al. (1979) also recorded that Tucumania larvae were collected from Opuntia salmiana Paramentier and Oputia pampeana Spegazzini, as well as three other doubtful records from Opuntia delaetiana Weber, Opuntia chakensis Spegazzini and Opuntia canina Spegazzini. The localities of these collections were not specified and therefore they are not included in the list.

APPENDIX 2

The features used to distinguish the 'typical' and 'etiolated' growth-forms of jointed cactus.

(i) 'Typical' Plants (fig. 34)

'Typical' plants grow mostly among the low False Karroid vegetation (Acocks 1975), which is the predominant floral type of large areas of the East Cape Province of South Africa.

The aerial parts of the plants receive direct sunlight for most of the day and they have well developed spines on short (100 -150 mm long) cladodes. The old plants (three years or more) flower annually and have substantial underground 'tubers' and hard woody stems. During winter and periods of drought, the terminal joints loose water, shrivel and are easily dislodged or drop from the parent plant. As a result, when no control measures are practised, dense thickets of jointed cactus develop, consisting of large parent plants surrounded by numerous smaller plants.

Fig. 34. The 'typical' growth-form of O. aurantiaca.

(ii) 'Etiolated' plants (fig. 35)

'Etiolated' jointed cactus plants grow mostly in the dense shade under larger bushes and trees and are commonly associated with the Valley Bushveld vegetation type (Acocks 1975).

The plants have poorly developed spines on narrow, elongate (200 - 300 mm long) joints which arise from succulent prostrate joints lying on the soil or leaf litter. The plants never flower and seldom produce underground tubers or woody stems. The stems usually grow to 0,5 - 0,6 m (two to three joints) in height and then collapse under their own weight. The fallen stems take root and produce new joints which grow into tall stems and in turn collapse, so that, eventually, dense mats of fallen stems accumulate on the shaded ground. Joints neither drop, nor are easily dislodged from 'etiolated' plants, which do not usually suffer the same water stress as plants growing in direct sunlight.

Fig. 35. The 'etiolated' growth-form of O. aurantiaca.

APPENDIX 3

Temperature and rainfall records from four of the localities at which Tucumania tapiacola was released in South Africa, and from the two source localities at which the release material was originally collected in South America.

The temperature was recorded in the field at Mosslands, Thursford and Andries Vosloo. The rainfall at Mosslands was obtained from the farm records. All the other temperature and rainfall data for the South African sites were extracted from Anon (1978). Temperatures and rainfall for the Argentinian localities were extracted from Anon (1969). In each case the extracted records are from the closest weather station to the release site, and they therefore do not necessarily reflect the exact conditions at the release sites.

The abbreviations used in the tables are as follows:

T.Max - The maximum temperature during the specified period.
Av.Max - The average daily maximum temperature.
Aver. - The average daily temperature.
Av.Min - The average daily minimum temperature.
T.Min - The minimum temperature recorded.

The release sites in South Africa.

(i) Mosslands Farm (33.24S 26.26E), Grahamstown.

Month	T E M P E R A T U R E °C T.Max	Av.Max	Aver.	Av.Min	T.Min	RAIN mm
Jan.	38,0	26,2	21,3	16,4	8,0	41
Feb.	39,0	28,5	21,6	14 7	10,0	67
March	33,0	27,7	21,9	16,1	11,0	65
April	-	-	-	-	-	49
May	32,0	24,8	17,8	10,9	3,0	73
June	29,0	21,3	14,0	6,7	0,0	28
July	28,0	20,5	13,4	6,3	1,0	57
Aug.	31,0	2[illegible],0	13,9	6,8	1,0	48
Sept.	34,0	23,5	17,0	10,5	1,0	33
Oct.	36,0	23,0	17,9	12,7	3,0	62
Nov.	39,0	26,2	20,4	14,7	7,0	75
Dec.	39,0	26,2	20,4	14,7	9,0	62
Year	39,0	24,4	18,1	11,9	0,0	660

(ii) Thursford Farm (33.12S 26.22E), Grahamstown.

Month	T E M P E R A T U R E °C T.Max	Av.Max	Aver.	Av.Min	T.Min	RAIN mm
Jan.	39,0	27,6	21,9	16,3	12,0	63
Feb.	39,5	28,8	22,8	16 7	13,0	66
March	33,5	28,2	22,4	16,6	10,0	81
April	32,0	23,4	17,3	10,6	5,0	53
May	32,0	24,5	18,4	12,3	8,0	49
June	27 0	19,8	13,6	7,4	3,0	33
July	28 0	20,6	13,6	6,6	2,0	32
Aug.	27,0	20,6	13,8	7,0	1,0	37
Sept.	32,0	22,3	16,3	10,4	6,0	62
Oct.	36,0	25,1	19,2	13,3	6,0	75
Nov.	36,0	24,9	18 9	12,9	8,0	78
Dec.	40,0	28,8	22,2	15,6	14,0	61
Year	40,0	24,6	18,4	12,1	1,0	690

(iii) Andries Vosloo Nature Reserve (33.08S 26.41E), Fort Brown

Month	T E M P E R A T U R E °C T.Max	Av.Max	Aver.	Av.Min	T.Min	RAIN mm
Jan.	44,0	32,9	24,5	16 2	10,0	52
Feb.	44,0	33,0	24,8	16 7	10,0	65
March	40,0	31,8	24,6	17,5	15,0	74
April	38,0	26,5	20,0	13,4	7,0	43
May	33,0	24,5	18,0	11,6	5,0	29
June	29,0	21,6	15,4	9,1	3,0	16
July	30,0	24,1	15,0	5,9	1,0	17
Aug.	33,0	22,3	16,7	11,1	6,0	28
Sept.	33,0	23,1	16,6	10,1	7,0	39
Oct.	39,0	24,0	17,8	11,7	6,0	50
Nov.	38,0	25,8	19,8	13,8	8,0	55
Dec.	43,0	32,5	23,8	15,0	11 0	53
Year	44,0	26,8	19,8	12,7	1,0	521

(iv) Sydney-on-Vaal (28.27S 24.18E). Weather station at Kimberley (24.48S 24.46E).

Month	T E M P E R A T U R E °C T.Max	Av.Max	Aver.	Av.Min	T.Min	RAIN mm
Jan.	36,3	32,5	25 1	17,8	7,1	55
Feb.	36,0	31,0	24,0	17,0	10,9	62
March	35,0	30,0	23,2	16,4	10,1	73
April	27,5	21,5	15,0	8,6	2,6	46
May	24,9	21,8	13,3	4,9	-3,6	20
June	21 8	17,9	8 8	-0,3	-6,0	9
July	26,8	20,8	12,5	4 2	-3,0	6
Aug.	29,1	22,4	12,6	2,8	-3,9	12
Sept.	32,1	23,5	15,2	6,9	-4,3	11
Oct.	33,4	27,4	18,8	8,5	2,0	32
Nov.	37,3	32 5	23,8	15,0	5,7	46
Dec.	37,8	32,5	24,4	16,3	10,5	57
Year	37,8	26,2	18,1	9,8	-6,0	429

The source localities in South America.

(i) Campana (34.10S 58.55W). Weather station at El Palomar (34.36S 58.36W), Argentina.

Month	T E M P E R A T U R E °C T.Max	Av.Max	Aver.	Av.Min	T.Min	RAIN mm
Jan.	41,9	30,7	23,2	17,0	6,6	141
Feb.	36,6	28,3	22,8	16,5	8,8	91
March	32,7	26,6	20,6	14,8	5,5	73
April	28,4	21,1	15,5	10 0	1,1	77
May	31,0	18,8	12,9	7,9	0,4	79
June	27,8	15,5	10,2	6,5	-4,7	82
July	27,8	15,9	10,2	6 2	-5,7	68
Aug.	29,6	16,6	11 0	6,0	-2,6	67
Sept.	31,0	18,8	13,1	8,2	-2,4	57
Oct.	31,1	21,3	16,1	10,8	0,5	89
Nov.	32,6	24,5	18,8	13,1	1,2	92
Dec.	35,0	27,5	21,1	14,8	5,45	51
Year	41,9	22,1	16,3	11,0	-5,7	967

(ii) Ibarreta (25.13S 59.50W). Weather Station at Los Lomitas (24.42S 60.35W), Argentina.

Month	T E M P E R A T U R E °C T.Max	Av.Max	Aver.	Av.Min	T.Min	RAIN mm
Jan.	43,4	34,2	27,1	21,5	9,4	128
Feb.	41,0	33,5	26,5	21,2	10,3	148
March	37,9	31,6	24,6	18,6	9,8	128
April	37,9	27,4	20,7	15,1	0,8	103
May	34,6	24,7	17,9	12,3	-2,6	74
June	32,9	23,5	17,0	11,9	-2,4	15
July	33,7	23,2	15,7	9,6	-7,0	36
Aug.	39,7	27,1	18,4	10,9	-5,3	21
Sept.	41,2	29,3	21,2	14,2	-2,1	40
Oct.	42,6	30,3	23,3	17,0	5,5	96
Nov.	43,2	33,0	25,3	18,2	5,8	96
Dec.	43,1	34,1	26,7	20,0	8,9	170
Year	43,4	29,3	22,0	15,9	-7,0	1055

APPENDIX 4

Diary of releases with *Tucumania tapiacola* in South Africa including dates, localities and life stages deployed on each occasion.

Date	Site	Numbers released			
		Eggs	Larvae	Adults ♂	Adults ♀ Tot.
27/05/77	A. Vosloo	2000			
30/05/77	"	2500			
09/06/77	"	5000			
14/06/77	Thursford	8000			
16/06/77	"	5000			
21/06/77	"		1250*		
11/07/77	"		3000		
06/10/77	Mosslands		18000		
26/10/77	"		33000		
27/10/77	Thursford		5000*		
03/11/77	Mosslands		35000		
14/11/77	"		35000		
22/11/77	Thursford		28000		
02/12/77	"		43000		
06/12/77	"		17000		
06/12/77	"		4000*		
23/12/77	Mosslands		33000		
11/01/78	"		19000		
24/01/78	S.-on-Vaal		5000*		
06/02/78	Thursford		15000		
15/02/78	Gannahoek		5000*		
12/03/78	Thursford		25000		
25/04/78	"		15000		
19/05/78	"		31000		
07/06/78	"		27000		
16/06/78	Mosslands		16000		
15/07/78	"		11000		
09/08/78	S.-on-Vaal		40000		

Date	Site	Numbers released				
		Eggs	Larvae	Adults ♂	♀	Tot.
13/10/78	Gannahoek		34000			
15/10/78	A. Vosloo		19000			
02/11/78	"		15000			
15/11/78	"		15000			
27/11/78	"		13000			
18/12/78	Thursford		23000			
08/01/79	"		12000			
24/01/79	A. Vosloo		18000			
02/02/79	"		5000			
23/02/79	"		8000			
14/03/79	"		12000			
18/04/79	"		5000			
10/05/79	"		8000			
29/10/79	T. Baines			71	50	121
15/11/79	A. Vosloo		15000	60	56	116
22/11/79	"			78	55	133
29/11/79	"		10000			
30/12/79	T. Baines			63	40	103
04/01/80	A. Vosloo			90	73	163
08/01/80	"			75	69	144
15/01/80	A. Vosloo			103	82	185
18/01/80	"			73	47	120
23/01/80	"			123	70	193
29/01/80	"			121	99	220
03/02/80	T. Baines			146	70	216
10/02/80	"			87	60	147
05/06/80	Le Rouxriv.		24000			
25/06/80	Mosslands		22000			
22/07/80	T. Baines		18000			
02/10/80	A. Vosloo		12000			
20/10/80	"		18000			
17/11/80	T. Baines		10000			

Date	Site	Numbers released				
		Eggs	Larvae	Adults ♂	♀	Tot.
21/10 - 19/11/81	Mosslands			683	532	1215
08/11/81			11000			
13/02/82			13000			
Totals		22500	804250	1773	1303	3076

Notes:

(i) * - Larvae released after they had infested cladodes in the insectary.

(ii) The larvae released at Andries Vosloo Nature Reserve on 15th May 1979, were placed in large piles (approximately 20 m^3) of jointed cactus plants that had been removed manually from the soil and stacked during clearing operations.

(iii) The larvae released on 5th June 1980, at Le Rouxrivier, were deployed on Opuntia sp., close to O. inermis De Candolle.

(iv) All the releases up to 17th November 1980 were made with material from the Ibarreta colony. Subsequent releases were made with the Campana stock.

REFERENCES

ACOCKS, J.P.H. 1975. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa. No. 40; 128pp.

ANDRES, L.A., C.J. DAVIS, P. HARRIS & A.J. WAPSHERE. 1976. Biological control of weeds. In: Theory and practice of biological control. Eds C.B. Huffaker & P.S. Messenger. Academic Press, New York; pp. 481-499.

ANDRES, L.A. & R.D. GOEDEN. 1971. The biological control of weeds by introduced natural enemies. In: Biological control. Ed. C.B. Huffaker. Plenum Publ. Corp., New York; pp. 143-164.

ANNECKE, D.P., M. KARNY & W.A. BURGER. 1969. Improved biological control of the prickly pear, Opuntia megacantha Salm-Dyck, in South Africa through the use of an insecticide. Phytophylactica 1: 9-13.

ANNECKE, D.P. & V.C. MORAN. 1978. Critical reviews of biological pest control in South Africa. 2. The prickly pear, Opuntia ficus-indica (L.) Miller. Journal of the Entomological Society of southern Africa 41: 161-188.

ANON. 1969. Estadisticas climatologicas 1951-1960. Servicio Meteorologico Nacional, Argentina.

ANON. 1978. Monthly weather report. Weather Bureau, Department of Transport, South Africa.

ARNOLD, T.J. 1977. The origin and relationships of Opuntia aurantiaca Lindley. Proceedings of the Second National Weeds Conference of South Africa, Stellenbosch, South Africa (1977). A.A. Balkema, Cape Town; pp. 269-286.

BAKER, C.R.B., R.L. BLACKMAN & M.F. CLARIDGE. 1972. Studies on Haltica carduorum Guerin (Coleoptera: Chrysomelidae) an alien beetle released in Britain as a contribution to the biological

control of creeping thistle, Cirsium arvense (L.) Scop.. Journal of Applied Ecology 9: 819-830.

BARTLETT, B.R. & R. VAN DEN BOSCH. 1964. Foreign exploration for beneficial organisms. In: Biological control of insect pests and weeds. Ed. P. DeBach. Chapman & Hall, London; pp. 283-304.

BESS, H.A. & F.H. HARAMOTO. 1958. Biological control of pamakani, Eupatorium adenophorum, in Hawaii by a tephretid gall fly, Procecidochares utilis. 1. The life history of the fly and its effectiveness in the control of the weed. Proceedings of the Tenth International Congress of Entomology. Montreal, Canada (1956) Vol 4; pp. 543-548.

BILEWICZ, S. 1953. Experiments on the effects of reproductive functions on the length of life of Drosophila melanogaster. (In Polish). Folia Biologica 1: 177-194.

BOLLER, E. 1972. Behavioral aspects of mass-rearing of insects Entomophaga 17: 9-25.

BORNEMISSZA, G.F. 1966. An attempt to control ragwort in Australia with the cinnabar moth, Callimorpha jacobaeae (L.) (Arctiidae: Lepidoptera). Australian Journal of Zoology 14: 201-243.

BUSH, G.L. 1975. Genetic variation in natural insect populations and its bearing on mass-rearing programmes. In: Controlling fruit flies by the sterile male technique. International Atomic Energy Agency (IAEA-PL-582/2); pp. 9-17.

CHAMBERS, D.L. 1975. Quality in mass-produced insects. In: Controlling fruit flies by the sterile male technique. International Atomic Energy Agency (IAEA-PL-582/3); pp. 19-32.

CHAMBERS, D.L. 1977. Quality control in mass rearing. Annual Review of Entomology 22: 289-308.

CLAUSEN, C.P. 1936. Insect parasitism and biological control. Annals of the Entomological Society of America 29: 201-223.

CLAUSEN, C.P. 1951. The time factor in biological control. Journal of Economic Entomology 44: 1-9.

CULLEN, J.M. 1974. Seasonal & regional variation in the success of organisms, imported to combat skeleton weed, Chondrilla juncea L. in Australia. Proceedings of the Third International Symposium on Biological Control of Weeds. Montpellier, France (1973). Commonwealth Institute of Biological Control. Miscellaneous Publications No. 8; pp. 111-117.

CULLEN, J.M. 1981. Considerations in rearing Bradyrrhoa gilveolella for control of Chondrilla juncea in Australia. Proceedings of the Fifth International Symposium on Biological Control of Weeds. Brisbane, Australia (1980). Ed. E.S. Del Fosse; pp. 233-239.

CURRIE, G.A. & R.V. FYFE. 1938. The fate of certain European insects introduced into Australia for the control of weeds. Journal of the Council for Scientific and Industrial Research 11: 289-301.

DEBACH, P. 1958. Selective breeding to improve adaptations of parasitic insects. Proceedings of the Tenth International Congress of Entomology, Montreal, Canada (1956). Vol 4; pp. 759-768.

DEBACH, P. 1971. The use of imported natural enemies in insect pest management ecology. Proceedings of the Tall Timbers Conference on Ecological Animal Control by Habitat Management 3: 211-233.

DEBACH, P. & B.R. BARTLETT. 1964. Methods of colonization, recovery and evaluation. In: Biological control of insect pests and weeds. Ed. P. DeBach. Chapman & Hall, London; pp. 402-426.

DEMPSTER, J.P. 1971. The population ecology of the Cinnabar moth Tyria jacobaeae L. (Lepidoptera, Arctiidae). Oecologia 7: 26-67.

DODD, A.P. 1940. The biological campaign against prickly pear. Commonwealth Prickly Pear Board Bulletin. Government Printer, Brisbane, Australia; 177pp.

DYAR, H.G. 1925. Notes on some American Phycitinae (Lepidoptera, Pyralidae). Insecutor Insectiae Menstruus 13: 220-226.

EMBREE, D.G. 1971. The biological control of the winter moth in eastern Canada by introduced parasites. In: Biological control. Ed. C.B. Huffaker. Plenum, New York; pp. 217-226.

ENGELMANN, F. 1970. The physiology of insect reproduction. Pergamon Press, Oxford; 307pp.

FORCE, D.C. 1967. Genetics in the colonisation of natural enemies for biological control. Annals of the Entomological Society of America 60: 722-729.

GIRLING, D.J. 1978. The distribution and biology of Eldana saccharina Walker (Lepidoptera: Pyralidae) and its relationship to other stem borers in Uganda. Bulletin of Entomological Research 68: 471-488.

GOEDEN, R.D. & S.M. LOUDA. 1976. Biotic interference with insects imported for weed control. Annual Review of Entomology 21: 325-342.

GOEDEN, R.D. & D.W. RICKER. 1967. Geocoris pallens found to be predaceous on Microlarinus spp. introduced to California for the biological control of puncturevine, Tribulus terrestris. Journal of Economic Entomology 60: 725-729.

GOEDEN, R.D. & D.W. RICKER. 1970. Parasitization of introduced puncturevine weevils by indigenous Chalcidoidea in southern California. Journal of Economic Entomology 63: 827-831.

GREATHEAD, D.J. 1971. A review of biological control in the Ethiopian region. Commonwealth Institute of Biological Control, Technical Communication No. 5; 162pp.

GRIFFITHS, J.T. & O.E. TAUBER. 1942. Fecundity, longevity, and parthenogenesis of the american roach, Periplaneta americana L. Physiological Zoology 15: 196-209.

GUNN, B.H. 1974. Chaetotaxy of the first and final instar larvae of the phycitid moth Tucumania tapiacola Dyar (Lepidoptera: Pyralidae). Unpublished report, Rhodes University, Grahamstown.

GUNN, B.H. 1979. Dispersal of the cochineal insect Dactylopius austrinus De Lotto (Homoptera: Dactylopiidae). Unpublished Ph.D. Thesis, Rhodes University, Grahamstown, South Africa.

HALL, R.W. & L.E. EHLER. 1979. Rate of establishment of natural enemies in classical biological control. Bulletin of the Entomological Society of America 25: 280-282.

HALL, R.W., L.E. EHLER & B. BISABRI-ERSHADI. 1980. Rate of success in classical biological control of arthropods. Bulletin of the Entomological Society of America 26: 111-114.

HARLEY, K.L.S. & B.W. WILLSON. 1968. Propagation of a cerambycid borer on a meridic diet. Canadian Journal of Zoology 46: 1265-1266.

HARRIS, P. 1967. Suitability of Anaitis plagiata (Geometridae) for biocontrol of Hypericum perforatum in dry grassland of British Columbia. Canadian Entomologist 99: 1304-1310.

HARRIS, P. 1973. The selection of effective agents for the biological control of weeds. Canadian Entomologist 105: 1495-1503.

HARRIS, P. 1979. Cost of biological control of weeds by insects in Canada. Weed Science 27: 242-250.

HARRIS, P. 1981. Evaluating biocontrol of weeds projects. Proceedings of the Fifth International Symposium on Biological Control of Weeds. Brisbane, Australia (1980). Ed. E.S. Del Fosse; pp. 345-353.

HARRIS, P. 1982. Euphorbia esula L., leafy spurge, and E. cyparissias L., cypress spurge (Euphorbiaceae). In: Biological control programmes against insects and weeds in Canada. Commonwealth Institute of Biological Control, Technical Communication (In Press).

HARRIS, P. & J. ALEX. 1971. Euphorbia esula L., leafy spurge, and E. cyparissias L., cypress spurge (Euphorbiaceae). In: Biological control programmes against insects and weeds in Canada 1959 - 1968. Commonwealth Institute of Biological Control, Technical Communication No. 4: 83-88.

HARRIS, P. & D.P. PESCHKEN. 1971. Hypericum perforatum L., St John's wort (Hypericaceae). In: Biological control programmes against insects and weeds in Canada 1959 - 1968. Commonwealth Institute of Biological Control, Technical Communication No. 4: 89-94.

HARRIS, P., A.T.S. WILKINSON, M.E. NEARY & L.S. THOMPSON. 1971. Senecio jacobaea L., Tansy ragwort (Compositae). In: Biological control programmes against insects and weeds in Canada 1959 - 1968. Commonwealth Institute of Biological Control, Technical Communication No. 4: 97-104.

HARRIS, P., A.T.S. WILKINSON, M.E. NEARY, L.S. THOMPSON & D. FINNAMORE. 1975. Establishment in Canada of the cinnabar moth, Tyria jacobaeae (Lepidoptera: Arctiidae) for controlling the weed Senecio jacobaea. Canadian Entomologist 107: 913-917.

HAWKES, R.B. 1973. Natural mortality of cinnabar moth in California. Annals of the Entomological Society of America 66: 137-146.

HEINRICH, C. 1939. The cactus feeding Phycitinae: a contribution towards a revision of the American pyralidoid moths of the family Phycitidae. Proceedings of the United States National Museum 86: 331-413.

HEINRICH, C. 1956. American moths of the subfamily Phycitinae. United States National Museum Bulletin 207; 581pp.

HINTON, H.E. 1956. The larvae of the species of Tineidae of economic importance. Bulletin of Entomological Research 47: 251-346.

HOFFMANN, J.H. 1976. Pre-release studies on Zophodia tapiacola (Dyar)(Pyralidae: Lepidoptera), a biological control agent against jointed cactus, Opuntia aurantiaca Lindley. Unpublished M.Sc. Thesis, Rhodes University, Grahamstown, South Africa.

HOFFMANN, J.H. 1977. The pyralid moth, Tucumania tapiacola Dyar (Lepidoptera), imported into South Africa from Argentina for jointed cactus control. Proceedings of the Second National Weeds Conference of South Africa. Stellenbosch, South Africa (1977); pp. 297-302.

HOFFMANN, J.H. 1981. Release of Tucumania tapiacola (Lepidoptera: Pyralidae) in South Africa against Opuntia aurantiaca: The value of detailed monitoring. Proceedings of the Fifth International Symposium on Biological Control of Weeds. Brisbane, Australia (1980). Ed. E.S. Del Fosse; pp. 367-373.

HOFFMANN, J.H. & V.C. MORAN. 1977. Pre-release studies on Tucumania tapiacola Dyar (Lepidoptera:Pyralidae), a potential biocontrol agent against jointed cactus. Journal of the Entomological Society of southern Africa. 40: 205-209.

HOY, M.A. 1975. Forest and laboratory evolutions of hybridized Apanteles melanoscelus (Hym.: Braconidae), a parasitoid of Prothetria dispar (Lep.: Lymantriidae). Entomophaga 20: 261-268.

HUFFAKER, C.B. 1959. Biological control of weeds with insects. Annual Review of Entomology 4: 251-276.

ISAACSON, D.L. 1973. A life table for the cinnabar moth, Tyria jacobaeae, in Oregon. Entomophaga 18: 291-303.

KARNY, M. 1972. Comparitive studies on three Dactylopius species (Homoptera: Dactylopiidae) attacking introduced opuntias in South Africa. Department of Agricultural Technical Services. Republic of South Africa. Entomology Memoir No. 26; 19pp.

KLOMP, H. 1968. A seventeen-year study on the abundance of the pine looper, Bupalus piniarius L. (Lepidoptera: Geometridae). In: Insect abundance. Ed. T.R.E. Southwood. Symposia of the Royal Entomological Society of London, No. 4. Blackwell, Oxford; pp. 98-108.

LENTEREN, J.C. van 1980. Evaluation of control capabilities of natural enemies: Does art have to become science? Netherlands Journal of Zoology 30: 369-381.

LEVINS, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237-240.

LUCAS, A.M. 1969. The effect of population structure on the success of insect introductions. Heredity 24: 151-157.

LUMMUS, P.F. & J.K. WANGBERG. 1981. Biology of Olycella subumbrella Dyar (Lepidoptera: Pyralidae) a borer of prickly pear cactus. Journal of the Kansas Entomological Society 54: 161-170.

MACKAUER, M. 1972. Genetic aspects of insect production. Entomophaga 17: 27-48.

MACKAUER, M. 1976. Genetic problems in the production of biological control agents. Annual Review of Entomology 21: 369-385.

MACKAUER, M. 1981. Some aspects of quality and quality control of biological control agents during insectary propagation. Proceedings of the Fifth International Symposium on Biological Control of Weeds. Brisbane, Australia (1980). Ed. E.S. Del Fosse; pp. 207-220.

MADDOX, D.M., L.A. ANDRES, R.D. HENNESSEY, R.D. BLACKBURN & N.R. SPENCER. 1971. Insects to control alligatorweed an invader of aquatic ecosystems in the United states. BioScience 21: 985-991.

MANN, J. 1969. Cactus-feeding insects and mites. United States National Museum Bulletin 256; 158pp.

MARTYN, E.J. 1965. Studies on the ecology of Oncopera intricata Walker (Lepidoptera: Hepialidae) 1. Fecundity of the female moths. Australian Journal of Zoology 13: 801-805.

MAYR, E. 1963. Animal species and evolution. Harvard University Press, Massachusetts; 797pp.

MAYR, E. 1970. Populations, species, and evolution. Harvard University Press, Massachusetts; 453pp.

McGARVIE, D. & PAROLIS, H. 1979. The mucilage of Opuntia ficus-indica. Carbohydrate Research 69: 171-179.

McNEILL, S. 1973. The dynamics of a population of Leptoterna dolabrata (Heteroptera: Miridae) in relation to its food resources. Journal of Animal Ecology 42: 495-507.

MESSENGER, P.S. & R. VAN DEN BOSCH. 1971. The adaptability of introduced biological control agents. In: Biological control. Ed. C.B. Huffaker. Plenum, New York; pp. 68-92.

MESSENGER, P.S., F. WILSON & M.J. WHITTEN. 1976. Variation, fitness, and adaptability of natural enemies. In: Theory and practice of biological control. Eds C.B. Huffaker & P.S. Messenger. Academic Press, New York; pp. 209-232.

METCALFE, J.R. 1972. An analysis of the population dynamics of the Jamaican sugar-cane pest Saccharosydne saccharivora (Westw.) (Hom., Delphacidae). Bulletin of Entomological Research 62: 73-85.

MILLER, D. 1936. Biological control of noxious weeds. New Zealand Journal of Science and Technology 18: 581-584.

MORAN, V.C. & D.P. ANNECKE. 1979. Critical reviews of biological pest control in South Africa. 3. The jointed cactus, Opuntia aurantiaca Lindley. Journal of the Entomological Society of southern Africa 42: 299-329.

MORAN, V.C., B.H. GUNN & G.H. WALTER. 1982. Wind dispersal and settling of first-instar crawlers of the cochineal insect Dactylopius austrinus (Homoptera: Coccoidea: Dactylopiidae). Ecological Entomology 7: (in press).

MORRIS, R.F. & C.A. MILLER. 1954. The development of life tables for the spruce budworm. Canadian Journal of Zoology 32: 283-301.

MYERS, J.H. & M.D. SABATH. 1981. Genetic and phenotypic variability, genetic variance, and the success of establishment of insect introductions for the biological control of weeds. Proceedings of the Fifth International Symposium on Biological Control of Weeds. Brisbane, Australia (1980). Ed. E.S. Del Fosse; pp. 91-102.

NEI, M., T. MARUYAMA & R. CHAKRABORTY. 1975. The bottleneck effect and genetic variability in populations. Evolution 29: 1-10.

NESER, S. & D.P. ANNECKE. 1973. Biological control of weeds in South Africa. Department of Agricultural technical Services, Republic of South Africa. Entomology Memoir No. 28; 27pp.

NORRIS, M.J. 1934. Contributions towards the study of insect fertility. III. Adult nutrition, fecundity and longevity in the genus Ephestia (Lepidoptera, Phycitidae). Proceedings of the Zoological Society of London 1934: 333-360.

PARTRIDGE, L. & M. FARQUHAR. 1981. Sexual activity reduces lifespan of male fruitflies. Nature 294: 580-582.

PASHLEY, D. & J. PROVERBS. 1981. Quality control of codling moth lab colonies: Loss of genetic variation. Annals of the Entomological Society of America 74: 20-23.

PESCHKEN, D.P. 1971. Cirsium arvense (L.) Scop., Canada thistle (Compositae). In: Biological control programmes against insects and weeds in Canada 1959 - 1968. Commonwealth Institute of Biological Control, Technical Communication No. 4; pp. 79-83.

PESCHKEN, D.P. 1977. Biological control of creeping thistle (Cirsium arvense): Analysis of the releases of Altica carduorum (Col.: Chrysomelidae) in Canada. Entomophaga 22: 425-428.

PESCHKEN, D., H.A. FRIESEN, N.V. TONKS & F.L. BANHAM. 1970. Releases of Altica carduorum (Chrysomelidae:Coleoptera) against the weed Canada thistle (Cirsium arvense) in Canada. Canadian Entomologist 102:264-271.

PETTEY, F.W. 1948. The biological control of prickly pears in South Africa. Scientific Bulletin of the Department of Agriculture, Union of South Africa. No. 271; 163pp.

RABB, R.L., R.E. STINNER & R. VAN DEN BOSCH. 1976. Conservation and augmentaion of natural enemies. In; Theory and practice of biological control. Eds C.B. Huffaker & P.S. Messenger. Academic Press, New York; pp. 233-254.

RAUSHER, M.D. 1979 Larval habitat suitability and oviposition preference in three related butterflies. Ecology 60: 503-511.

REMINGTON, C.L. 1968. The population genetics of insect introduction. Annual Review of Entomology 13: 415-426.

ROESLER, U. 1968. Das neue systematische verzeichnis der deutschen Phycitinae (Lepidoptera, Pyralidae). Nachrichtenblatt der Bayerischen Entomologen 17: 1-9.

ROUSH, R.T. 1979. Genetic improvement of parasites. In: Genetics in relation to insect management. Eds M.A. Hoy & J.J. McKelvey. Working papers of the Rockerfeller Foundation; pp. 97-105.

SCHABER, B.D., E.U. BALSBAUGH & B.H. KANTACK. 1975. Biology of the flea beetle, Altica carduorum (Col.: Chrysomelidae) on Canada thistle (Cirsium arvense) in South Dakota. Entomophaga 20: 325-335.

SCHMIDL, L. 1972. Studies on the control of ragwort, Senecio jacobaea L., with the cinnabar moth, Callimorpha jacobaeae (L.) (Arctiidae: Lepidoptera), in Victoria. Weed Research 12: 46-57.

SELLERS, W.F. 1953. A critique of the time factor in biological control. Bulletin of Entomological Research 83: 230-240.

SHOREY, H.H. 1963. The biology of Triochoplusia ni (Lepidoptera: Noctuidae). II. Factors affecting adult fecundity and longevity. Annals of the Entomological Society of America 56: 476-480.

SIMMONDS, F.J. 1963. Genetics and biological control. Canadian Entomologist 95: 561-567.

SKAIFE, S.H. 1961. The study of ants. Longmans, London; 178pp.

SMITH, F. & R. MONTGOMERY. 1959. The chemistry of plant gums and mucilages. Reinhold, New York; 627pp.

SOKAL, R.R. & F.J. ROHLF. 1969. Biometry. Freeman, San Francisco; 776pp. .

SOLOMON, M.E. 1976. Population dynamics. Edward Arnold, London; 67pp.

SOUTHWOOD, T.R.E. 1978. Ecological methods. Chapman & Hall, London; 391pp.

VARLEY, G.C. & G.R. GRADWELL. 1968. Population models for the winter moth. In: Insect abundance. Ed. T.R.E. Southwood. Symposia of the Royal Entomological Society of London, No. 4. Blackwell, Oxford; pp. 132-142.

VETUKHIV, M. 1954. Integration of the genotype in local populations of three species of Drosophila. Evolution 8: 241-251.

VETUKHIV, M. 1956. Fecundity of hybrids between geographic populations of Drosophila pseudoobscura. Evolution 10: 139-146.

VETUKHIV, M. 1957. Longevity of hybrids between geographic populations of Drosophila pseudoobscura. Evolution 11: 348-360.

WALTER, G.H. 1977. The role of wax in predation of cochineal by coccinellid beetles Exochomus flaviventris Mader (Coleoptera: Coccinellidae). Unpublished report. Rhodes University, Grahamstown.

WAPSHERE, A.J. 1975 A protocol for programmes for biological control of weeds. PANS 21: 295-303.

WAPSHERE, A.J. 1981. Recent thoughts on exploration and discovery for biological control of weeds. Proceedings of the Fifth International Symposium on Biological Control of Weeds. Brisbane, Australia (1980). Ed. E.S. Del Fosse; pp. 75-79.

WILLIAMS, J.R. 1950 The introduction of Physonota alutacea Boheman (Col., Cassid.) into Mauritius. Bulletin of Entomological Research 40: 479-480.

WILLIAMS, J.R. 1960. The control of black sage (Cordia machrostachya) in Mauritius: The introduction, biology and bionomics of a species of Eurytoma (Hymenoptera: Chalcidoidea). Bulletin of Entomological Research 51: 123-132.

WILSON, F. 1960. A review of the biological control of insects and weeds in Australia and Australian New Guinea. Commonwealth Institute of Biological Control, Technical Comminication No. 1; 102pp. .

WILSON, F. 1965. Biological control and the genetics of colonizing species. In: The genetics of colonizing species. Eds H.G. Baker and G.L. Stebbins. Academic Press, New York; pp. 307-329.

ZAR, J.H. 1974. Biostatistical analysis. Prentice Hall, London; 620pp.

ZIMMERMANN, H.G. 1979. Herbicidal control in relation to distribution of Opuntia aurantiaca Lindley and effects on cochineal populations. Weed Research 19: 89-93

ZIMMERMANN, H.G. 1981. The ecology and control of Opuntia aurantiaca in South Africa in relation to the cochineal insect, Dactylopius austrinus. Unpublished Ph.D. thesis, Rhodes University, Grahamstown, South Africa.

ZIMMERMANN, H.G., W.A. BURGER & D.P. ANNECKE. 1974. The biological control of jointed cactus in South Africa. Unpublished proceedings of the First National Weeds Conference. Pretoria, South Africa; pp. 204-211.

ZIMMERMANN, H.G., H.E. ERB & R.E. McFADYEN. 1979. Annotated list of some cactus-feeding insects of South America. Acta Zoologica Lilloana 33: 101-112.

ZIMMERMANN, H.G. & D.E. MALAN. 1980. A modified technique for the herbicidal control of jointed cactus, Opuntia aurantiaca Lindley, in South Africa. Agroplantae 12: 65-67.

ZIMMERMANN, H.G. & V.C. MORAN. 1983. The ecology and management of cactus weeds in South Africa. South African Journal of Science. (In press).

ZIMMERMANN, H.G. & H.A. VAN DE VENTER. 1981. Jointed cactus. Division of Agricultural Information, South Africa. Weed Series A.1.

ZWOLFER, H., M.A. GHANI & V.P. RAO. 1976. Foreign exploration and importation of natural enemies. In: Theory and practice of biological control. Eds C.B. Huffaker & P.S. Messenger. Academic Press, New York; pp. 189-207.