PRE-RELEASE STUDIES ON *ZOPHODIA TAPIACOLA* (DYAR) (PYRALIDAE : LEPIDOPTERA), A BIOLOGICAL CONTROL AGENT AGAINST JOINTED CACTUS, *OPUNTIA AURANTIACA* LINDLEY

by

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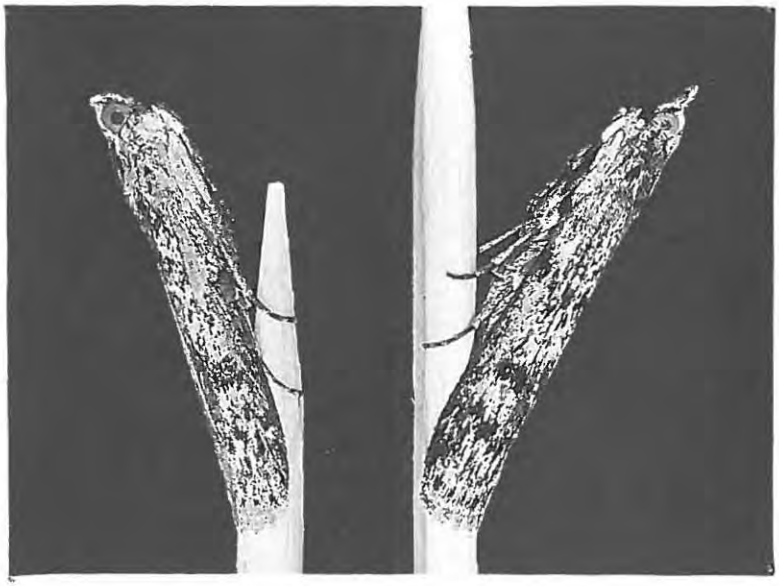

Male (left) and female (right) Z. tapiacola.
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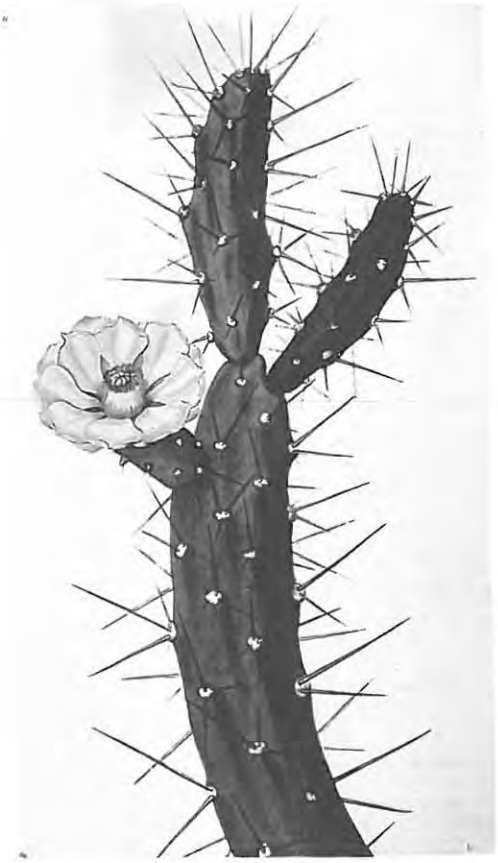

Photocopy of Miss Drake's painting of O. aurantiaca published in Lindley's description of the plant (1833).
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ACKNOWLEDGEMENTS

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RÉSUMÉ

Jointed Cactus, Opuntia aurantiaca Lindley (see frontispiece), is the most important weed plant in South Africa, infesting approximately, $1,2 \times 10^{10} M^2$ and costing approximately R240 000 per annum. Tordon herbicide effectively kills jointed cactus bushes to which it is applied. However, apart from being expensive and damaging to beneficial vegetation, spray programmes have not successfully controlled the weed because most small O. aurantiaca plants are impossible to detect in the field. Biological control may provide a solution to the problem. Two insects, the cochineal bug, Dactylopius austrinus De Lotto and the pyralid moth, Cactoblastis cactorum Berg., already exercise a degree of control over the weed. The introduction into South Africa of other natural enemies such as Zophodia tapiacola (Dyar) from Argentina, South America, may reduce the density of jointed cactus to below an acceptable economic threshold.

Any insect considered for release should not colonise and destroy beneficial plants of which the culivated spineless cacti are the most vulnerable. Pre-release studies on Z. tapiacola have shown that it can only colonise a few species of low growing cacti and that it will not damage the large spineless cacti or other desirable plants. Further, the moths are relatively fecund and each larva destroys significant amounts of O. aurantiaca during its development. Consequently, Z. tapiacola is not only considered safe for release but it has the potential to act as a successful biological control agent of O. aurantiaca in South Africa.

INTRODUCTION

Jointed cactus, Opuntia aurantiaca Lindley (1833), is the major weed problem in the East Cape Province of South Africa where the plant invades valuable grazing pasture and, if not checked, forms dense, thorny, impenetrable thickets. The plants are generally low growing inconspicuous shrubs from which individual joints, or cladodes, are readily detached principally by passing animals, wind, rain and flowing water (Pettey, 1947). The height of each plant is determined by the surrounding vegetation and in semi-arid karoo scrub, jointed cactus seldom grows to more than one half meter while it may reach two to three meters when it is supported and protected by tall vegetation. Although the yellow O. aurantiaca flowers produce seed bearing fruits, reproduction is mainly vegetative because every loose joint and fruit that comes into contact with the soil can root to form a new bush. The ease with which joints are detached from the plants, coupled with the ability of each to form a new bush, facilitates spread and establishment of the weed in uninfested areas.

For many years, attempts have been made to eradicate, or at least control and check O. aurantiaca. Initially land-owners tried to rid their property of the weed by mechanical means. This, however, proved to be ineffective and time consuming. Expensive hormonal herbicide applications (initially 2,4,5-T, now replaced with Tordon 40) temporarily

reduce the weed density to levels acceptable to the landowners, although in the East Cape Province, jointed cactus is still spreading to uninfested areas at a rate of $1 \times 10^8 M^2$ per annum and eradication in already infested veld has never been achieved. Tordon 40 always kills O. aurantiaca plants onto which it is sprayed, however, its use never achieves satisfactory control because most small plants are not detected during herbicide application. Besides being inefficient, the herbicide programme is very expensive and R7 000 000 has been spent on 90 000 000 litres of herbicide alone between 1957 and 1975. This figure does not include the cost of transport estimated at R30 000 each year and the cost of labour for which there are no estimates available*. Another disadvantage of the method is that many beneficial plants in the proximity of jointed cactus bushes are also killed by the herbicide which may remain effective in the soil for a number of years. Rising costs coupled with labour shortages are making the application of herbicidal control so difficult that there is an increasing demand for cheaper, more efficient control methods.

Biological control is an alternative that may provide a solution to the jointed cactus problem (Nesser & Annecke, 1973). The practice of introducing natural enemies to combat cactus and other weeds has met with much success in many parts of the world, including South Africa (Dodd, 1940; Fullaway, 1954;

* Unpublished Data from, the Eastern Cape Region, Department of Agricultural Technical Services, Queenstown, South Africa.

Holloway, 1964; Wilson, 1964; Andres & Goeden, 1971; Nesøer & Annecke, 1973; Goeden et al., 1974; DeBach, 1975). Extensive surveys in South America where O. aurantiaca does not reach pest proportions (except on the island of Martin Garcia off Buenos Aires) have established that there are several natural enemies of jointed cactus and other closely related cacti in that area (Zimmermann, 1972). Two of these natural enemies, namely the cochineal bug, Dactylopius austrinus De Lotto and the pyralid moth, Cactoblastis cactorum Berg., have already been released in South Africa and are responsible for a significant but undetermined degree of control. Huffaker (1974) points out that it may be the total response of a number of natural enemies that controls a pest and not the response of any one. Consequently, the pressure already being exerted on O. aurantiaca may be increased if more natural enemies are introduced and adequate biological or intergrated control of jointed cactus may be achieved.

Before any organism can be transferred to a new country for biological weed control, its host range must be determined to ensure that beneficial plants will not be colonised and destroyed in its new environment (Huffaker, 1964). The cacti are usually very good candidates for biological control because they are seldom economically beneficial plants and almost without exception, insects that feed on cacti do not utilise other plant families and vice versa (Mann, 1969). However, although plants outside the Cactaceae might be safe from attack by cactophagous insects, in South Africa a problem

arises because not all cacti are weeds and there is a beneficial group known as the Burbank spineless cacti, Opuntia maxima Mill., which are grown as fodder crops in the drier areas of the country (de Kock & Aucamp, 1970). O. maxima, which embraces a wide variety of cultivars or forms, is closely related to the weed prickly-pear Opuntia megacantha Salm Dyk and they may not be botanically distinct from each other (Henderson & Anderson, 1966). However, the spineless cacti are generally referred to as O. maxima while the thorney weed is known as O. megacantha. O. maxima is already damaged by introduced American cactophagous insects, including C. cactorum, which were released to control other Opuntia weeds (Pettey, 1939; Pettey & Marais, 1950).Therefore, to prevent further damage, only insects that are unable to colonise O. maxima may be considered 'safe' for release and pre-release studies must be conducted to establish the host specificity of all potential control candidates.

The first and probably most conclusive indications of whether an insect will be a suitable, safe biological control agent come from surveys conducted in its indigenous habitat and from reviews of the literature (Zwolfer & Harris, 1971). Surveys of the pyralid moth, Zophodia tapiacola (Dyar), conducted in Argentina, South America, show that Z. tapiacola is an oligophagous species restricted to a few low growing O. aurantiaca type cacti (Mann, 1969; Zimmermann, 1972). Dodd (1940) records that in 1935, Tucumania tapiacola Dyar (= Z. tapiacola) was introduced into Australia as a control

agent of O. aurantiaca in that country. Extensive pre- and post-release examinations showed that the moth never colonised beneficial plants and it only survived on O. aurantiaca, H. martinii and young O. inermis plants. Dodd also noted that Z. tapiacola never exercised spectacular control over O. aurantiaca because the cochineal, Dactylopius sp. near confusus (= D. austrinus), had previously destroyed most of the available O. aurantiaca plants, thereby depriving the moth of suitable hosts. However, he also noted that the moth did seem to be inflicting an unspecified degree of damage to O. aurantiaca in certain areas.

Consequently, Z. tapiacola was considered to be a host specific species which, although not spectacular in its control of O. aurantiaca in Australia, was never-the-less amenable to introduction into new countries. As a result, in February, 1973 Z. tapiacola larvae were collected from Opuntia discolor and Opuntia retrosa host plants along road Number 81 between Pirané and Los Lomitas in the Formosa Province, Argentina, by Mr. H. Erb who was employed by the South African Department of Agricultural Technical Services for that purpose. The larvae were used to start a laboratory reared colony of Z. tapiacola which was maintained at the Institute of Miquel and Lillo, Tucuman, Argentina. In December, 1973, 500 to 1000 eggs on frayed cloth strips were sent by air to South Africa where they were received in Johannesburg by an officer of the Department of Agricultural Technical Services from Pretoria. The eggs were checked for

damage before being forwarded to Mr. H.G. Zimmermann at the Weed Laboratory, Department of Agricultural Technical Services, Uitenhage. Here the culture was maintained for one generation and on the 5th February, 1974, eggs of the F_1 generation were moved to Rhodes University, Grahamstown where the culture has since been maintained. In May, 1974 Mr. H. Erb collected more Zophodia sp. larvae from Opuntia tayapayensis plants around Cochabamba, Bolivia. These were reared through to adults in Tucuman and the eggs obtained were sent to South Africa in September, 1974. This colony was reared in Uitenhage until the 4th November, 1974 after which it was moved to Grahamstown. Initially it was suspected that the Formosa population and the Bolivian one comprised two seperate Zophodia species. However, Mr. P. Whalley, British Museum (Natural History), London, determined specimens from both colonies as all being Z. tapiacola. Unfortunately, in June, 1975 the Bolivian colony died when C. cactorum larvae, which are more vigorous feeders than Z. tapiacola, where accidentally introduced into the rearing cages with jointed cactus from the field.

Individuals from the Formosa colony were used to study the life history, basic biology and host specificity of Z. tapiacola with a view to its release as a control agent of O. aurantiaca in South Africa.

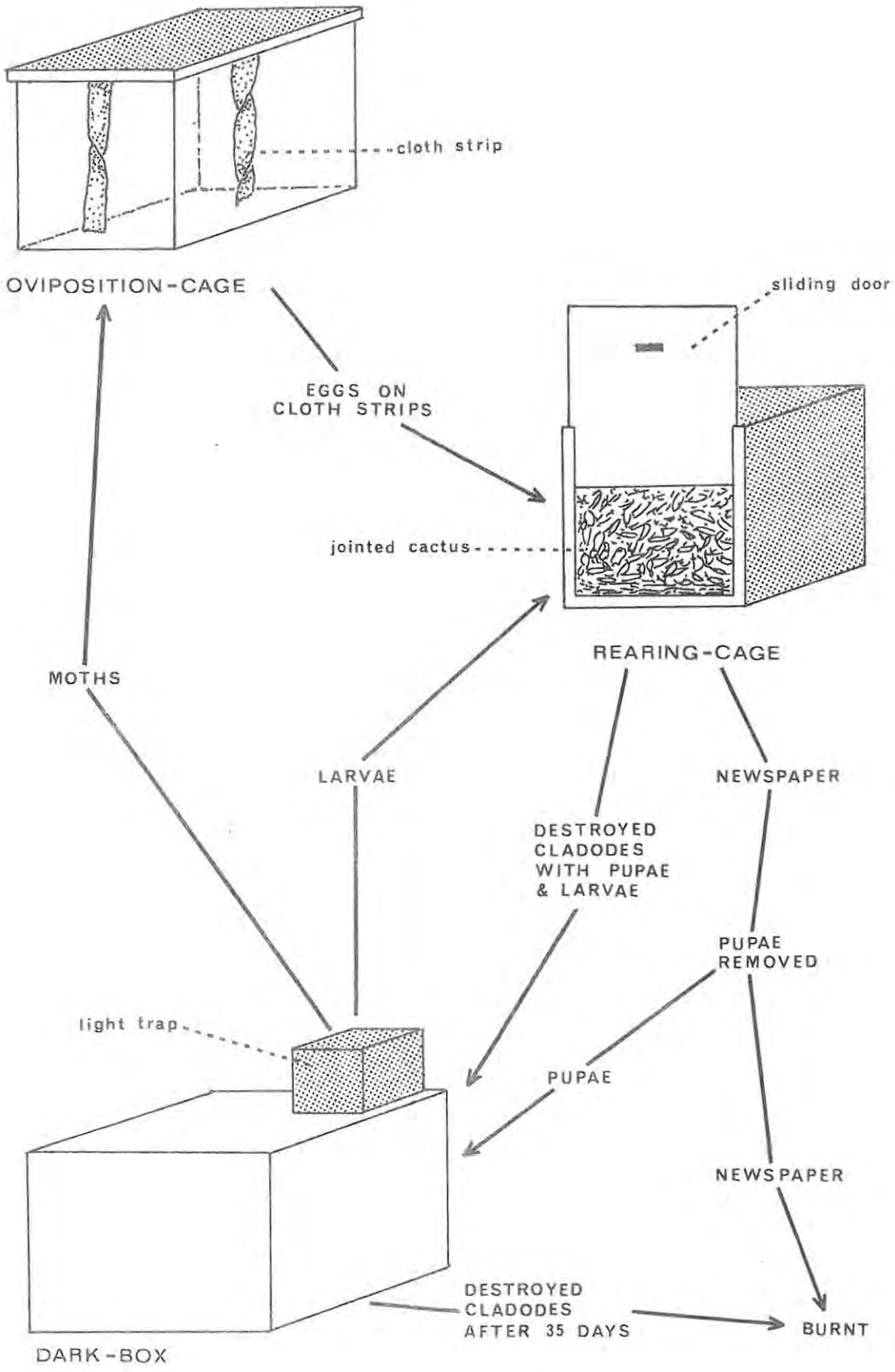

Fig. 1. Rearing techniques used to maintain a colony of Z. tapiacola in quarantine.

MATERIAL AND METHODS

The colony of *Z. tapiacola* from the Formosa Province, Argentina was maintained at Rhodes University in a quarantine insectary at a constant temperature of 25°C (± 3°C) and a relative humidity of 50% (± 10%) with a 12 hour light/12 hour dark photoperiod. During the dark period a Philips GL 45 B indicator bulb provided dim illumination in the room so that the moths were not subject to unnatural total darkness.

Adult moths were provided with a honey-water feed and frayed cloth strips in perspex thermoplastic 'oviposition-cages' (fig. 1). The moths mated in these cages, after which the females deposited most of their eggs on the cloth strips. Eggs were transferred on the strips to 'rearing-cages' and placed among *O. aurantiaca* cladodes collected at Thursford farm, Grahamstown, South Africa. The base of each 'rearing-cage' was lined with five to ten sheets of newspaper and then filled with cladodes. Young *Z. tapiacola* larvae hatching from the eggs crawled onto and tunnelled into the jointed cactus in which they developed and pupated. At weekly intervals, all dead cladodes and the newspaper were removed and replaced with fresh ones. The dead cladodes were placed in a 'dark-box' with a 20mm diameter 'escape-hole' located in the one top corner and covered with a gauze 'light-trap-cage'. Adult moths emerging from the pupae in the dead cladodes were attracted through the escape hole to the dim insectary "night light". Consequently, they aggregated in

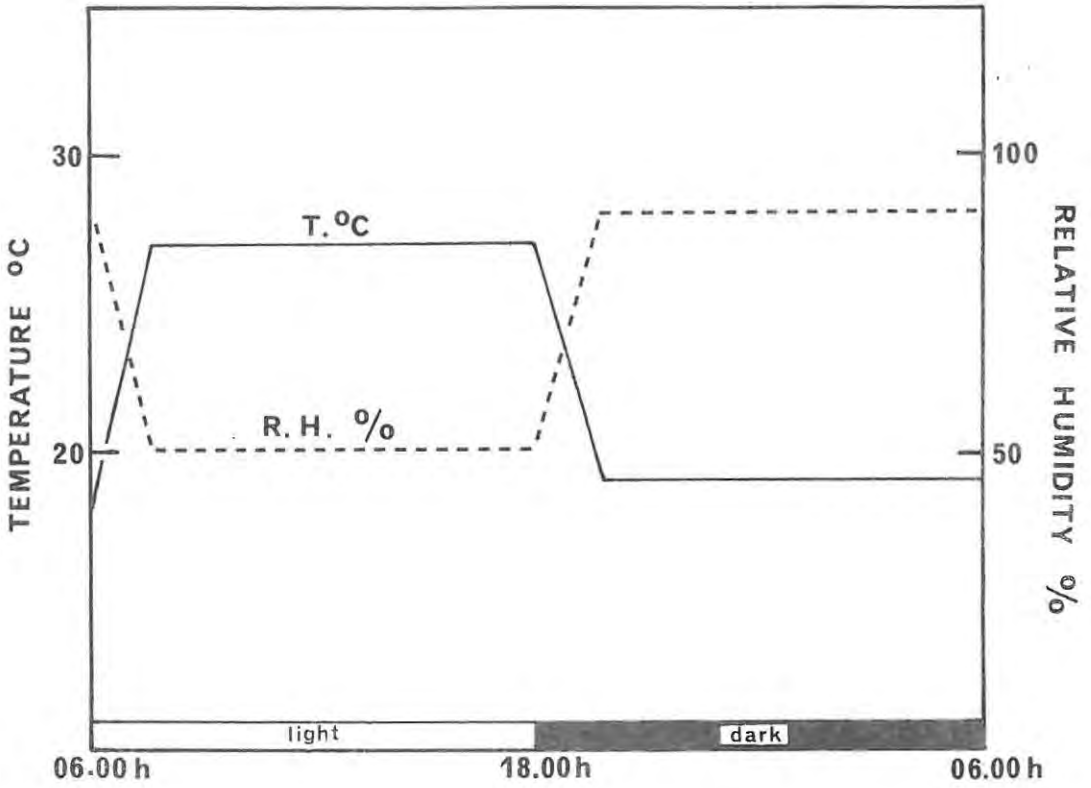

Fig. 2. Temperature, relative humidity and photoperiod maintained in the controlled environment room during all observations on Z. tapiacola.

the 'light-trap' and were transferred daily to 'oviposition-cages'. Some larvae pupated between the newspaper sheets from which they were removed and placed in the 'dark-boxes'. Usually, a number of immature larvae were accidently removed from the 'rearing-cages' with the dead cladodes. In the 'dark-box' they were attracted to the light and they also accumulated in the 'light-trap' from which they were returned to the 'rearing-cages'. After four to five weeks, moths ceased emerging from the 'dark-box' which was then fumigated for six hours with ethyl acetate before the dead cladodes were removed and burnt. There was a complete overlap of generations in the colony and all stages were continuously available for investigation.

Observations on the life history and control potential of Z. tapiacola were conducted in a controlled environment room with diurnal temperature, relative humidity and light fluctuations as shown in fig. 2. Most of the specificity studies were also conducted on potted plants in the environment room although field tests were also carried out on caged plants. O. maxima plants used in the experiments were supplied by Mr. G. de Kock, Grootfontein Agricultural College, Middleburg, Cape Province, South Africa and also collected at Thorneycroft farm, Grahamstown, South Africa. Ornamental cacti tested were obtained from Bosch Nurseries, Port Elizabeth, South Africa. Most other plants were supplied by the Botany Department, Rhodes University, although some were collected at various places in the East Cape Province, South Africa.

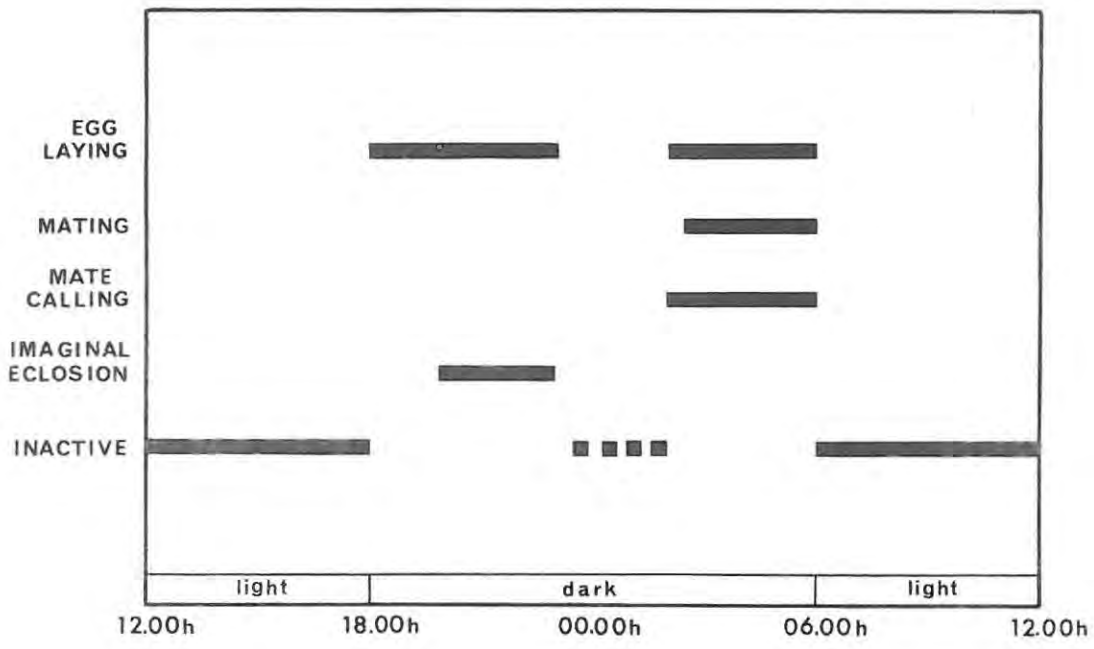

Fig. 3. Behavioural activity of Z. tapiacola adults over a 24 hour period in the controlled environment room. Dark bands represent the times at which each behaviour pattern was noted.

1. THE LIFE HISTORY OF ZOPHODIA TAPIACOLA

Dyar (1925), Heinrich (1939; 1956), Dodd (1940), Mann (1969) and Gunn (1974) describe the adults and larva of Tucumania tapiacola Dyar (= Z. tapiacola) in some detail. However, their descriptions of the life history and biology of the moth are patchy. Consequently a more detailed account of the life history is presented here as a preliminary to further studies on the biological control potential of this insect.

ADULTS

The adults of Z. tapiacola (see frontispiece) are dark grey coloured with white hind wings and black patches on the legs. The fore wings have broken black transverse lines which contrast only slightly with the dark ground colour. There is a row of black dots along the terminal edge of the wing. The measured alar expanse of 80 moths varied from 22 to 33mm, and the females are generally larger than the males (Mean female alar expanse = 28,7mm, minimum = 25mm, maximum = 33mm; mean male alar expanse = 25,0mm, minimum = 22mm, maximum = 29mm). The sexes are readily differentiated because the male's labial palps curl up around the head while those of the female are porrect (see frontispiece)

Observations were made on the behaviour of 20 pairs of Z. tapiacola adults in cages in the controlled environment room and the periods of activity are shown in fig. 3. Eclosion of the imago occurred in the evening at any time

between 19.30h and 23.00h. The newly emerged moths took approximately 30 minutes to dry their wings, after which they became very active, flying and walking around the cages. Between 23.30h and 02,00h the moths settled down and very little activity occurred. After 02,00h they became active again and during this period mating occurred. The Z. tapiacola females initiated courtship by adopting a typical lepidopteran calling posture which exposed the sex pheromone membranes in the abdomen (Wigglesworth, 1972). As a result, pheromone was released into the cages and males were attracted to the calling females. While approaching its prospective mate, each male beat its wings and waved its antennae until the two moths came into contact. Immediately, the females dropped their abdomens and copulation commenced. During sperm transfer, which lasted for approximately 25 minutes, both moths gripped the substrate with their legs while they joined end to end, heads pointed in opposite directions. After mating the males left the females who remained stationary until the following night.

After mating the males remained active for a short while, but when the lights came on in the room they settled down and both sexes were inactive throughout the day. The male moths were never seen to mate with more than one female and they died two to three days after mating. During the day, the moths adopted a vertically upright, cryptic posture (see frontispiece). Moths that were touched on the posterior part of their body jumped away from the stimulus and fell to the floor of the cage

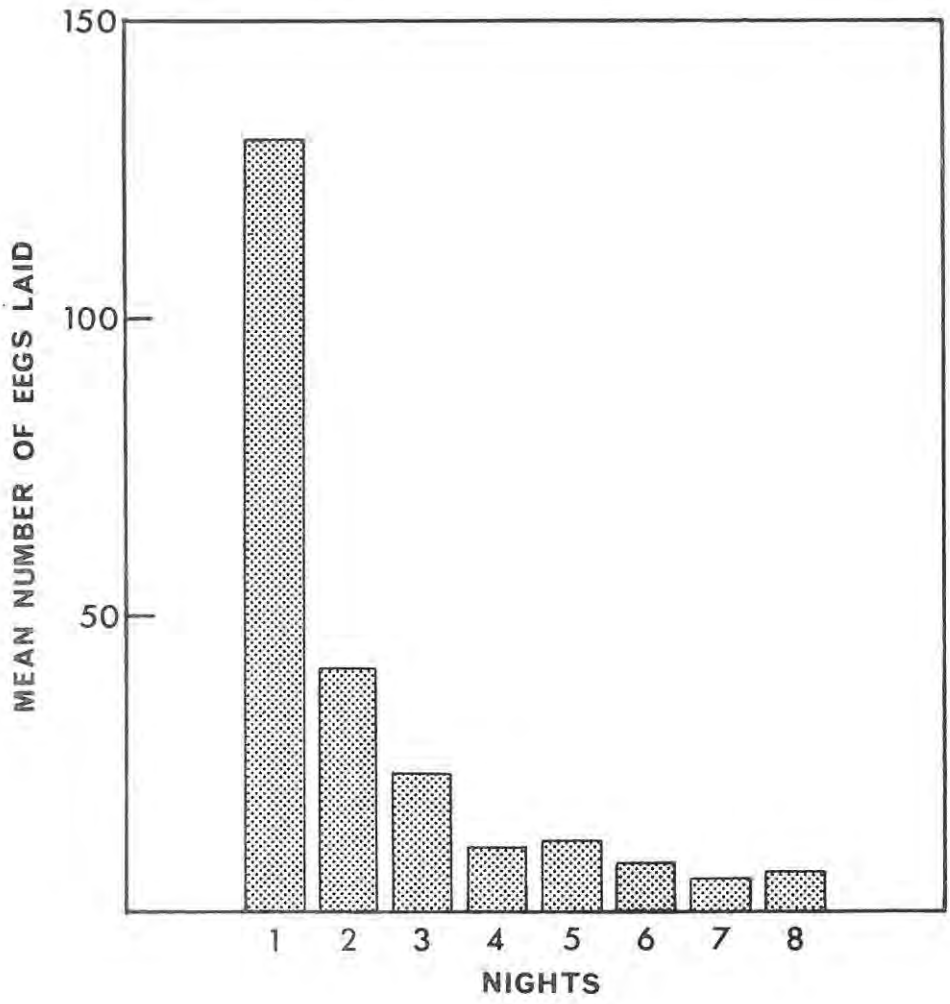

Fig. 4. The mean number of eggs laid by each of eight Z. tapiacola females on eight consecutive nights.

in a cateleptic state. They remained motionless for five to ten minutes before making a brief flight to regain a perch.

At approximately 18.30h the moths once again became active and egg laying commenced. The females walked about the cages, depositing eggs on any rough projection, although most were laid on the hanging frayed cloth strips provided. The females always wandered for a time between each egg deposition, which took 3 to 7 seconds, although they often came back to the same spot and laid eggs close to and on top of each other. Eggs were laid throughout the night except during the midnight period of inactivity. Oviposition usually continued for about eight nights. The mean number of eggs laid by eight females was 231 (minimum - 127; maximum - 284) of which 56% were deposited on the first egg laying night, 18% on the second, 10% on the third and the remaining 16% on the last five nights (fig. 4). The fecundity and egg laying pattern noted here was very similar to that recorded for T. tapiacola (= Z. tapiacola) by Mann (1969).

Many observations showed that, virgin Z. tapiacola adults were able to mate successfully on any of the first four nights after emergence. However, they loose the ability as they age and none of ten male or ten female moths were able to copulate when provided with young mates after being kept in isolation for six nights. All the virgin males died within nine days, while the females lived for ten to thirteen days. Virgin females always discharged 50 to 100 infertile eggs in the 48 hours preceding death.

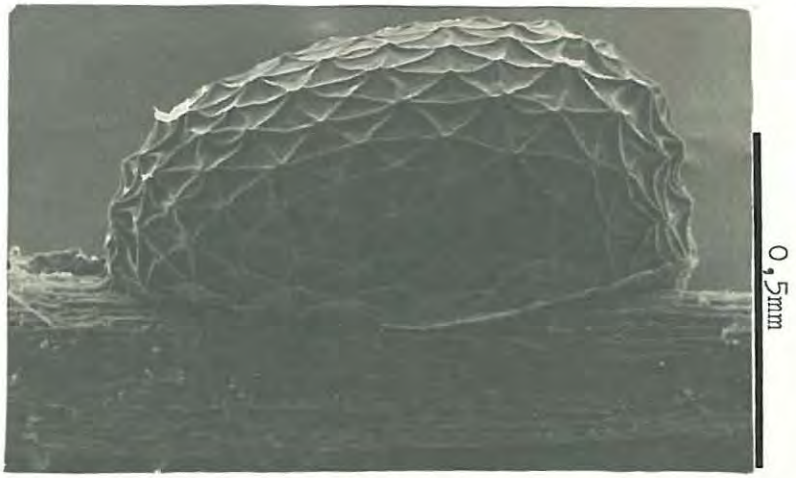

Fig. 5. Scanning electron micrograph of a Z. tapiacola egg on an O. aurantiaca thorn.

Fig. 6. Composite scanning electron micrograph of a first instar Z. tapiacola larva. Lateral aspect.

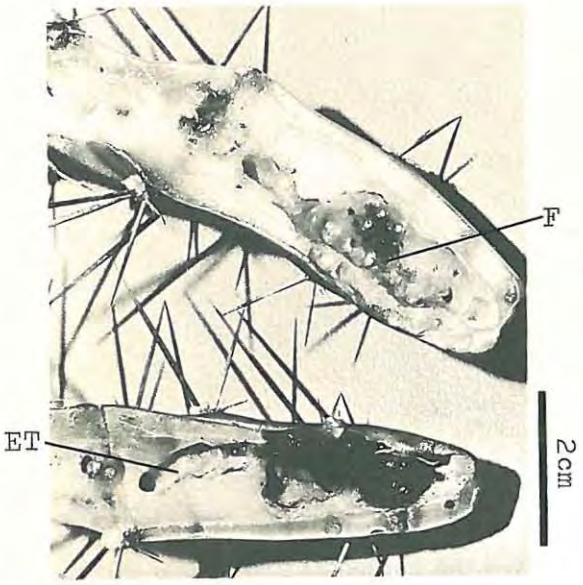

Fig. 7. Z. tapiacola tunnel in a bisected O. aurantiaca cladode. ET- escape tunnel; F- feeding area.

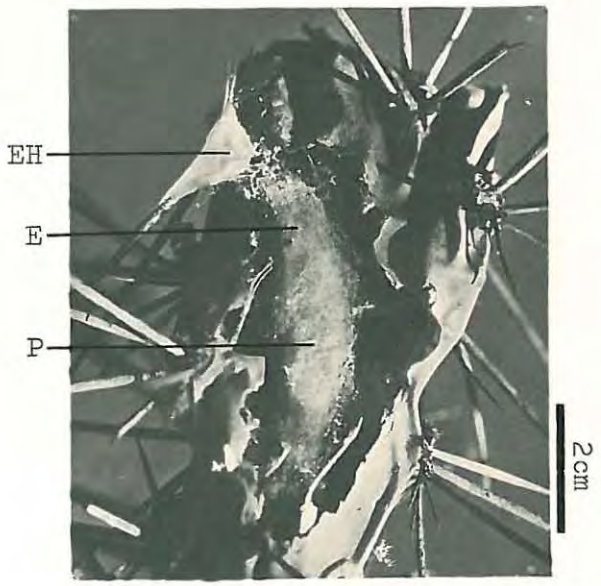

Fig. 8. O. aurantiaca husk opened to show a Z. tapiacola cocoon. EH- escape hole; E- emergence tunnel; P- pupa.

EGGS

The 0,9mm long eggs are initially cream coloured, ageing through brown to dark brown prior to hatching. They have a characteristic sculptured chorion (fig. 5). A system of ridges forms a network of triangles raised above triangular depressions with aeropyles at the intercese of the ridges. Each egg is pressed against and glued on a thorn so that the contact surface becomes concave to accomodate the curve of the thorn.

LARVAE

After an incubation period which always lasted ten days in the laboratory, the young larvae chew their way out of the egg. Each first instar larva (fig. 6) is approximately 1,9mm long at hatching and it has a white body with a black head. The larvae are very mobile and they wander about spinning a silk thread on which they can lower themselves if disturbed or exposed in an unsheltered area. The larvae have a negative phototactic response on the host plant which leads them to the lower shaded parts of the plant were they seek a suitable entry point for initial feeding and penetration of the cuticle. Table 1 shows that most Z. tapiacola entry sites on a cladode were situated on the shaded side whether the light was directed from above or below. In total dark with no shaded area, the larval entry points were distributed evenly around the whole cladode.

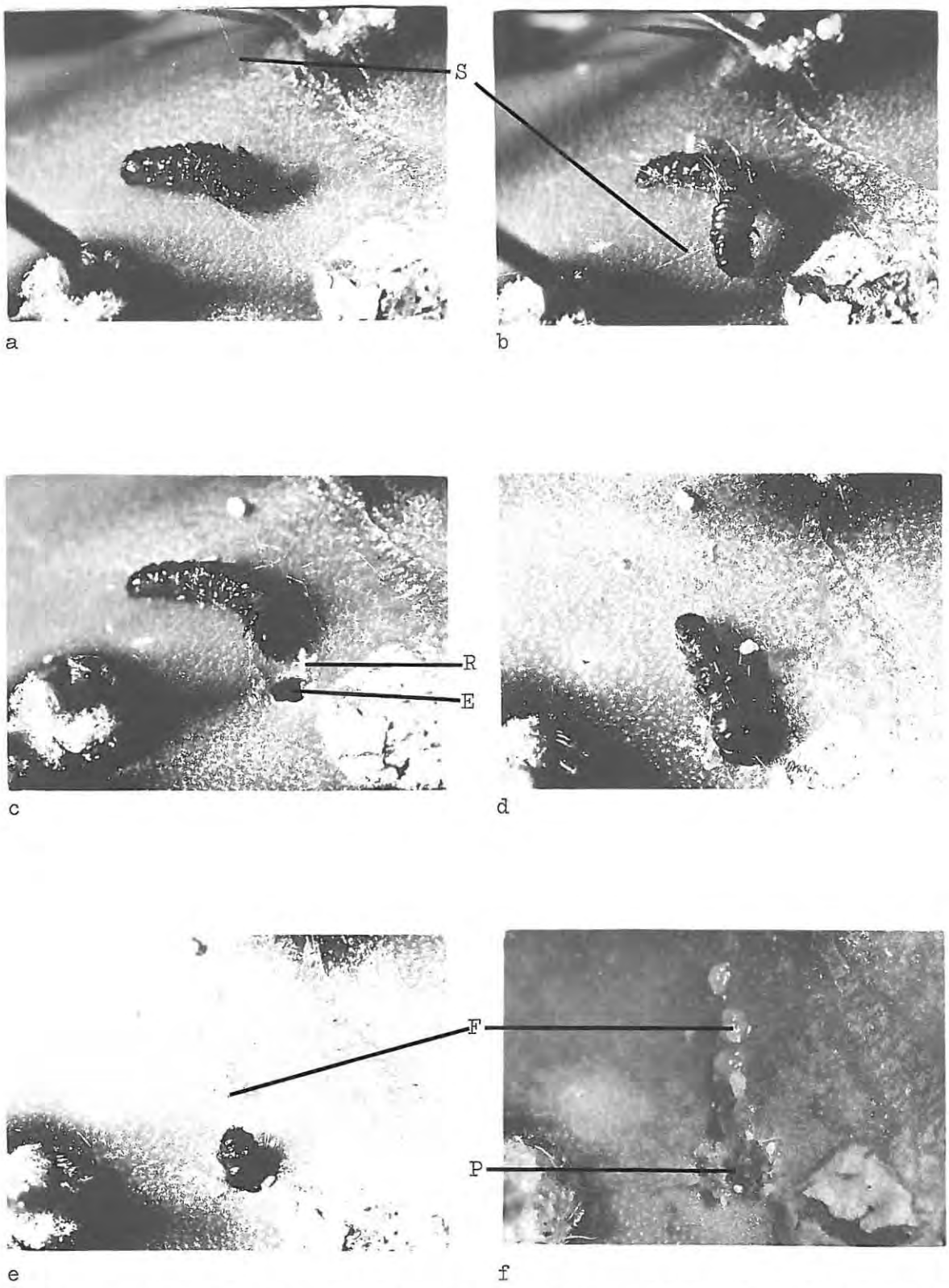

Fig. 9. The behavioural sequence followed by Z. tapiacola during entry into a host plant. The larva spins a 'silk-tent' (a) which it pushes against to pierce the cuticle with its mandibles (b). The larva withdraws from the tunnel to regurgitate ingested tissue (c) until its head and thorax are accommodated (d). Excavated tissue is then deposited as frass outside the tunnel (e & f). Finally the entrance is plugged with silk and frass (f). (x6). E- entrance; F- frass; P- plugged entrance hole; R- regurgitated tissue; S- silk.

Table 1. The number of Z. tapiacola entry points on upper and lower surfaces of O. aurantiaca cladodes with illumination from above and below or in total darkness.

CONDITION	NUMBER OF ENTRY POINTS LOWER SURFACE	UPPER SURFACE	TOTAL	χ^2	PROBABILITY
LIGHT ABOVE	89	40	129	18,612	P =<0,001 significant
LIGHT BELOW	36	66	102	8,8236	P =>0,001<0,01 significant
TOTAL DARK	89	71	160	2,025	P =>0,1<0,9 not significant

Having selected a suitable entry site the young larva spins a loose 'silk-tent' around itself (fig. 9a). An uneven area of the plant is always utilised because the 'tent' cannot be constructed on a flat surface. Observations of 250 larval penetrations showed that 63% entered the plant alongside an areole using the glochids and thorns as a support for the 'tent'; 30% spun silk across the depression at the internode of two adjoining cladodes and 7% entered the plant at rough, scar tissue. Figure 9a-f shows the sequence adopted by a Z. tapiacola larva penetrating a jointed cactus cladode at an areole. The larva spins a number of threads between the thorns and the cuticle, until it is enclosed in a loose silk mesh. At this stage the larva arches its body and pushes against the 'tent' (fig. 9b) using it as a brace to force its mandibles down into the cuticle. To facilitate penetration, the larva chews the cuticle exterior while pushing against the 'tent'. Often, initial attempts to colonise the cladode fail because

the 'tent' is not substantial enough and too little force is transferred to the mandibles. After several unsuccessful penetration attempts, the larva reinforces its 'tent' and tries again to pierce the cuticle. The process may be repeated 5 or 6 times, but if no success is achieved after two or three hours the larva vacates the 'tent' and begins anew elsewhere.

Once the mandibles pierce the cucicle of the host plant the larva chews deeper into the cladode. Initially the insect swallows masticated tissue until its foregut is full, it then withdraws from the tunnel and regurgitates the tissue on the plant surface, (fig. 9c) before tunnelling commences. In this way a hollow is excavated in the cladode which soon accommodates the head and thorax of the larva (fig. 9d). As the larva tunnels deeper into the plant, food is passed through the gut and deposited on the outside of the plant as frass (fig. 9e & f). After one to two hours the whole larva is able to withdraw into the newly excavated tunnel. Immediately, it turns around in the tunnel and plugs the entrance hole with a silk net intermeshed with frass (fig. 9f).

Feeding, and consequent widening of the tunnel, commences once the entrance hole has been sealed. Frass is deposited in the tunnel and is accumulated near the entrance point. As the larva ages, a verticle escape tunnel leading downwards is excavated away from the feeding site (fig. 7), so that by the third larval instar the escape tunnel usually traverses the cladode from the feeding site to its lowest extremity.

Zimmermann (1968) and Mann (1969) have noted in Argentina and Australia that Z. tapiacola larvae construct a silk 'escape' tube from the invaded cladode "several inches" into the ground. When the colonised cladode is disturbed and during periods of intense heat, the larva retreats into this ground tube.

As the larva develops, the feeding and frass deposition area is extended. The frass is further broken down by bacterial action after which it desiccates and shrinks, forming large hollow cavities in the drying husk. When the whole cladode has been ingested, and the frass has desiccated, all that remains is a hollow husk of cuticle, partially filled with dry frass, containing the larva which may or may not have completed its development. Some larvae colonise cladodes which are not large enough to support them for their complete development. In these cases the larvae can vacate the old destroyed cladode and wander some distance for three to five days in search of a new host, which is then colonised.

Z. tapiacola larvae moult five times and pass through six instars (see Appendix 1). Mann (1969) described the larvae as being varied in colour from dark red to purple red, light wine coloured, pink, yellow brown, light orange or light yellow. The larval colours in fact change predictably with age. The white first instar larva turns a pale pink and darkens to a deep red by the third instar. They remain dark red until the final instar when they become lighter and turn a pale yellow prior to pupation. The final instar larvae

attain a maximum length of approximately 25mm and by the time they are ready to pupate the occupied cladode is completely hollowed out and destroyed, so that the husk can serve as a pupation chamber. The larva will not pupate in a cladode that is only partially destroyed but will vacate it to pupate in the leaf litter or soil. The reason for this seems to be that any green tissue that remains in the cladodes after larval feeding is complete, is susceptable to bacterial infection and excessive rot which may be detrimental to the pupa.

PUPA

Normally, the final instar larva chews an escape hole in the drying cuticle of the cladode. It then commences cocoon production which begins with the prepupa spinning a loose silk net to seal the escape hole. The prepupa then retreats one to two centimeters into the cladode where it spins a substantial pupation chamber which is connected to the escape hole by a flimsy silk guide tunnel constructed by the prepupa as it backs into the cladode (fig. 8). In the laboratory, the prepupa took from 36 to 48 hours to construct their cocoons, after which they pupated in the pupation chamber.

Eclosion of the imago took between 16 and 26 days (Mean 21 days) in the laboratory. Each emerging moth is directed to the escape hole in the husk cuticle by the guide tunnel. At the escape hole, it loosens the sealing silk threads with a wetting fluid, before it crawls out onto the husk and finds a thorn, or other protrusion, on which to spread and dry its wings. The mean developmental duration

from egg hatch to adult eclosion was 81 days for males and 95 days for females. This difference is not significant ($P = >0,2 < 0,4$).

2. THE HOST SPECIFICITY OF ZOPHODIA TAPIACOLA

Zwolfer & Harris (1971) list a number of methods to determine the host specificity of an insect. One of these is to conduct starvation and negative-oviposition tests on economic plants. They point out, however, that the artificial nature of the tests can easily lead to misinterpretation of the true facts. Consequently, economic plants that are eaten or used for egg deposition in confined cages are not necessarily suitable hosts because in the field there are many isolating mechanisms that restrict insects to particular plants (Huffaker, 1959; Harris, 1963). However, the tests are of value in that they show plant defences which repel insect attacks and also some of the plants that will not be utilised, even when the insect is starving. As not every economic plant can be screened, Harris and Zwolfer (1968) and Wapshere (1974) have outlined principles that should be followed when choosing plants for the tests.

Starvation and negative-oviposition tests were conducted on Z. tapiacola using two groups of plants; (i) members of the Cactaceae, because they are botanically related to O. aurantiaca, (ii) South African indigenous succulents, because they have never been exposed to Z. tapiacola, and there is always uncertainty about behaviour of phytophagous organisms faced with a new plant species (Wapshere, 1974). The tests were not extended to other plants or groups of plants for the following reasons. (a) Dodd (1940) reports that

Z. tapiacola never utilised beneficial non-cactaceous plants during host specificity tests in Australia. (b) Extensive surveys in South America have only recorded Z. tapiacola on a few low growing cacti (Mann, 1969; Zimmermann, 1972). (c) Almost without exception, cactus feeding insects do not feed on plants outside the Cactaceae and vice versa; this rule is especially true for the cactus phycitids (Mann, 1969).

2.1 Starvation tests

All starvation tests were conducted in the controlled environment room. For each test, ten newly hatched Z. tapiacola larvae (less than 5 hours old) were placed on actively growing potted plants possessing young flush and mature foliage. Every two days the plants were scrutinised for signs of feeding or successful colonisation. The results of the tests are summarized in Table 2.

Apart from slight 'nibbling' on three of the Euphorbia spp. there was no sustained feeding on these, or any of the other South African succulents, probably because, like other lepidopterous larvae (Schoonhoven, 1973), Z. tapiacola may have a variety of chemical and physical requirements which are only met by normally acceptable host plants, in this case certain species of cacti. Attempted feeding and different degrees of development occurred on nearly all the cacti presented during the tests. However, there were a few genera that Z. tapiacola never attempted to colonise (e.g. Epiphyllum spp., Pereskia spp.) and the only species

Table 2. Results of starvation tests on *Z. tapiacola*. The columns indicate; i. the plants tested; ii. their economic status (if any); iii. the number of replicates for each test; iv. the extent of colonisation and development on each plant (0 - No penetration or feeding attempted; X - No development; A - attempted feeding; B - larva penetrated into plant tissue; C - larva developed; D - larva pupated; E - adult emerged); v. Remarks.

i PLANT SPECIES	ii IMPORTANCE	iii NO. OF REPLI-CATES	iv COLONISATION & DEVELOPMENT	v REMARKS
CACTACEAE				
Opuntia aurantiaca Lindley	Weed	10	A B C D E	All mature cladodes acceptable for colonisation. Each larva destroyed a relatively large part of the plant during its development.
Opuntia rosea D.C.	Weed	10	A B C D E	
Opuntia imbricata (Harv.) D.C.	Weed	10	A B C D E	
Opuntia monocantha Haworth	Weed	10	A B C D E	
Opuntia microdasys (Lehmann) Pfeiffer	Weed	10	A B C D E	
Opuntia verschaffeltii Cels	Weed	10	A B C D E	
Opuntia cylindrica (Lamark) De Candolle	Weed	10	A B C D E	
Harrisia martinii (Labuoret) B. & R.	Weed	10	A B C D E	
Opuntia megacantha Salm Dyk	Weed	10	A B X	High gum content in mature cladodes prevented larvae from colonising and damaging these plants.
Opuntia tardospina Griffiths	Weed	10	A B X	
Opuntia maxima Mill. (Burbank Spineless Cactus)	Fodder	10	A B X	

Pereskia aculeata Mill	Weed	10	O	
Rhypsalidopsis rosea (Lagërheim) B. & R.	Ornamental	5	A B C	Larvae only able to develop up to third instar after which the thin stems of these species were not suitable for development.
Rhypsalis cassutha Gaertner	Ornamental	5	A B C	
Rhypsalis spp.(3)	Ornamental	5	A B C	
Schlumbergera sp.	Ornamental	5	A B C	
Trichocereus candicans (Gillies) B. & R.	Ornamental	5	A X	Fluid gum repelled larva.
Trichocereus spachianus (Lamaire) Riccobono	Ornamental	5	A	Desiccation of plant at wound prevented entry of larvae.
Trichocereus thelegonus (Weber) B. & R.	Ornamental	5	O	
Weberocereus sp.	Ornamental	1	A B C	Whole plant rotted before larvae developed.
Zygocactus truncatus (Haworth) Schumann	Ornamental	5	A B C	Stems too thin to support complete development.

AIZOACEAE

Carprobrotus edulis (L.) L. Bol.	Indigenous	10	O
Conophytum spp. (2)	Indigenous	10	O
Delosperma echinatum (Ait.) Schwant	Indigenous	10	O
Fenestraria spp. (3)	Indigenous	10	O
Glottiphyllum longum (Haw.) N.E. Br.	Indigenous	10	O
Lithops spp. (4)	Indigenous	10	O

Table 2. Continued...

PLANT SPECIES	IMPORTANCE	NO. OF REPLI-CATES	COLONISATION & DEVELOPMENT	REMARKS
Lemaireocereus pruinosus Otto	Ornamental	10	O	
Lobivia sp.	Ornamental	10	A B C	Young shoot colonised but not main plant.
Lophocereus schottii (Engelmann) B. & R.	Ornamental	10	O	
Malocarpus sp.	Ornamental			
Monvillia spegazzinii (Weber) B. & R.	Ornamental	5	A B C	Localised rotting prevented complete development.
Neomammilaria columbiana (Salm Syk) B. & R.	Ornamental	10	O	
Neomammilaria collinsii B. & R.	Ornamental	10	A B C	Plants rotted before larvae matured.
Neomammilaria galeotii (Scheidweiler) B. & R.	Ornamental	10	A B C	
Neomammilaria haageana (Pfeiffer) B. & R.	Ornamental	10	A B C	
Neomammilaria magnimamma (Haworth) B. & R.	Ornamental	10	O	
Neomammilaria pringlei (Coulter) B. & R.	Ornamental	10	O	
Neomammilaria spp. (4)	Ornamental	10	A B C	
Neopteria spp. (3)	Ornamental	10	O	
Pachycereus pecten-aboriginum (Engelmann) B. & R.	Ornamental	5	A B X	No larval development.

Astrophytum myriostigma Lemaire	Ornamental	3	A B C	Plant rotted before larva matured.
Astrophytum ornatum (D. C.) Weber	Ornamental	10	O	
Borzicactus sp.	Ornamental	10	A B X	
Cephalocereus palmeri Rose	Ornamental	5	A B X	Larva repelled by fluid gum exuded at wound in response to attack.
Cereus jamacaru De Candolle	Ornamental	5	A B X	
Cereus spp. (2)*	Ornamental	3	A B X	
Cleistocactus spp. (2)	Ornamental	5	O	Dense glochid concentration prevented larvae reaching plant cuticle.
Coryphanta spp. (2)	Ornamental	2	A B C D E	Only one individual reached maturity.
Dolicothele sp.	Ornamental	1	A B C	Plant rotted before larva matured.
Echinocactus grusonii Hildmann	Ornamental	10	O	
Epiphyllum sp.	Ornamental	10	O	
Echinopsis rhodotricha Schumann	Ornamental	10	O	
Erdisia sp.	Ornamental			
Esposta sp.	Ornamental	2	A B C	Plants rotted before larva matured.
Ferocactus flavovirens (Scheidweiler) B. & R.	Ornamental	1	A B C	
Ferocactus latispinus (Haworth) B. & R.	Ornamental	3	A B C	
Gymnocalcium sp.	Ornamental			
Hamatocactus setispinus (Engelmann)	Ornamental	10	O	

* Numbers in brackets represent the number of undetermined species tested in some genera.

Table 2. Continued...

PLANT SPECIES	IMPORTANCE	NO. OF REPLI-CATES	COLONISATION & DEVELOPMENT	REMARKS
Mesembryanthemum sp.	Indigenous	10	O	
Ophthalmophyllum sp.	Indigenous	10	O	
APOCYNACEAE				
Pachypodium bispinosum (L.f.) A.DC.	Indigenous	10	O	
Pachypodium succulentum A.DC.	Indigenous	10	O	
ASCLEPIADACEAE				
Caralluma keithii R.A. Dyar	Indigenous	10	O	
Stapelia spp. (2)	Indigenous	10	O	
COMPOSITAE				
Othonna carnosa (L.f.) Less.	Indigenous	10	O	
Senecio sp.	Indigenous	10	O	
CRASSULACEAE				
Bryophyllum tubiflorum Harv.	Weed	10	O	
Crassula lactea Soland.	Indigenous	10	O	

Crassula multicava Lam. et Versch.	Indigenous	10	0	
Crassula portulacea Lam.	Indigenous	10	0	
Crassula ? spatulata Thunb.	Indigenous	10	0	
Crassula ? tetragona L.	Indigenous	10	0	
Crassula spp. (6)	Indigenous	10	0	
Cotyledon orbiculata L.	Indigenous	10	0	
Kalanchoe ? hirta Harv.	Indigenous	10	0	
EUPHORBIACEAE				
Euphorbia gradidens Haw.	Indigenous	10	0	A few web tents spun using thorns of these species, but attempted entries were terminated after the cuticle had been pierced.
Euphorbia horrida Boiss.	Indigenous	10	0	
Euphorbia pugniformis Boiss.	Indigenous	10	0	
Euphorbia stellaspina Boj.	Indigenous	10	0	
Euphorbia spp. (3)	Indigenous	10	0	
LILIACEAE				
Aloe ? arborescens Mill.	Indigenous	10	0	
Aloe ferox Mill.	Indigenous	10	0	
Agave americana L.	Exotic	10	0	
Bulbine natalensis Bak.	Indigenous	10	0	
PORTULACACEAE				
Portulacaria afra Jacq.	Indigenous Fodder	10	0	Important grazing plant (Batten & Bokelmann, 1966).

that supported complete development were O. aurantiaca, O. rosea, O. imbricata, O. monocantha, O. microdasys and H. martinii. These six species are the same, or closely related, plants to those colonised by Z. tapiacola in Argentina and Australia. There were two larvae that completed their development on ornamental cacti, one on Coryphanta sp., and the other on Neomammilaria sp., however, both cases were exceptional.

Z. tapiacola was not able to colonise young flush growth of any of the cacti, including the acceptable hosts. The reason for this failure was that the water retention mechanism of the flush was destroyed when the cuticle was pierced by the attacking larva. As a result, rapid desiccation occurred which caused the tissues around the wound to shrink and form a hard callous. The young larvae either were trapped in the hardened tissue and died, or they were forced out of their tunnel and subsequently left the plant.

The majority of the cactus species presented to Z. tapiacola in the tests supported some degree of larval development, although they were not successfully colonised for a number of reasons, some of which were noted and listed below.

(i) The glochids of the Cleistocactus spp. are very dense and they seemed to form an impenetrable mesh which prevented Z. tapiacola from achieving the plant cuticle.

(ii) The narrow stemmed cacti (e.g. Rhypsalis spp.

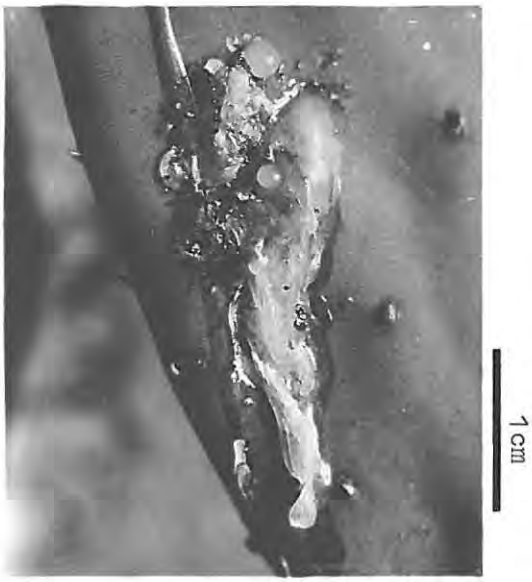

Fig. 10. Gum exuded by spineless cactus as a result of continued colonisation attempts by Z. tapiacola.

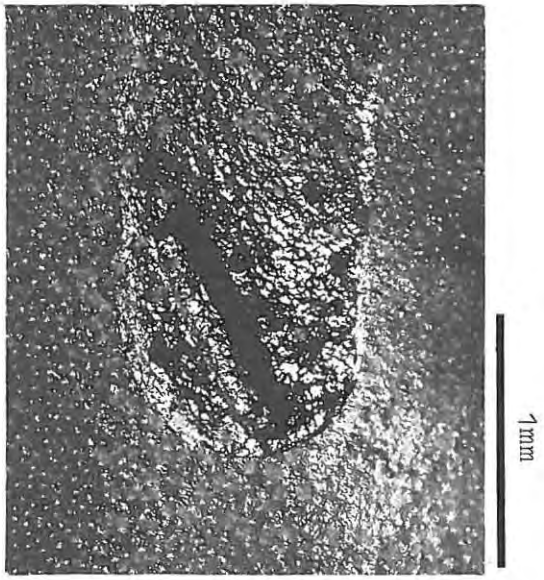

Fig. 11. A first instar Z. tapiacola encapsulated by spineless cactus gum exuded in response to damage by the larva.

Fig. 12. Mature spineless cactus forming new cladodes after numerous Z. tapiacola larval colonisation attempts which resulted in large amounts of exuded gum.

Rhypsalidopsis spp., Schlumbergera spp. and Zygocactus spp.) were colonised by the small first, second and even third instar larvae. However, the stems were too narrow for the tunnels of large, older individuals which consequently vacated the plants.

(iii) Many cactus species (e.g. Neomammilaria spp., Astrophytum spp. Ferocactus spp.) are very susceptable to bacterial infection so that when they were colonised by Z. tapiacola, rot usually set in, which brought about complete collapse of the plant before the larva matured.

(iv) The economically most important cactus, O. maxima, along with the closely related O. megacantha and O. tardospina, as well as the Cereus spp., all resisted Z. tapiacola larval colonisation by exuding a sticky mucilage at the site of attack (fig. 10). One to three days after the larvae had been released onto O. maxima plants, gum appeared and oozed through the damaged cuticle where the larvae had attempted entry. The gum filled the newly excavated tunnels and forced the larvae out. Sometimes, the larvae were caught up by the sticky substance and being unable to escape they eventually died in the hardened gum (fig. 11). Usually, however, the larvae were driven from their tunnels, whereupon they vacated the plant, or occassionally tried unsuccessfully to penetrate the same plant elsewhere. Although larvae were able to excavate small tunnels into the spineless cactus plants, the cladodes were not detectably affected by the slight damage and subsequent gum production. Even cladodes that had been attacked continuously by numerous larvae (more than 100) developed normally and gave rise to new shoots (fig. 12).

2.2. Negative-oviposition tests

The offspring of the most oligophagous insects will not survive unless the females place their eggs in situations suitable for the development of the F_1 generation. As a result, ovipositional behaviour in these insects has evolved a complex pattern which is dependant for its release on the reception of suitable stimuli, usually provided by acceptable host plants (Dethier, 1959; Gupta & Thorsteinson, 1960; Thorsteinson, 1960; Beck, 1965; Stadler, 1974). The degree of restriction to particular plants does not seem to be absolute and observations on various host specific Lepidoptera species by Dethier (1959) have shown that females do not always choose the correct host plants, but eggs may also be deposited on a variety of biotic and abiotic substrates. However, the eggs that are not laid on or near the correct host plants appear to be placed at random and not exclusively in particular alternative situations. Wiklund (1974) sites examples of species that will not oviposit on plants which are nutritionally suitable for larval development. Ovipositional specificity in many species must therefore be the key factor determining the spectrum of plants colonised. Consequently, a potential biological control insect which feeds on beneficial plants during starvation tests might be shown to be safe by determining whether or not the adult will oviposit on those species in the field. Attempts were therefore made to try and determine which plants are choosen by Z. tapiacola for egg deposition in the hope that its host range may be further substantiated.

Ovipositional choice tests were attempted under controlled laboratory conditions where adult females were confined in perspex cages with nylon gauze lids. Further tests were conducted in a 3 x 3 x 2 meter nylon gauze field cage. During tests, Z. tapiacola adults were presented with O. aurantiaca and other Cactaceae, as well as representatives from the Euphorbiaceae, Liliaceae, Aizoaceae and Portulacaceae. In both cage situations, females deposited eggs equally frequently on all the plants, on the gauze sides and lids and on any small projection. The results suggest that either Z. tapiacola lays its eggs haphazardly throughout its habitat or alternatively, the confines of the test cages caused the moths to behave atypically forcing them to oviposit on normally unacceptable substrates. Zwolfer and Harris (1971) pointed out that in many attempts to determine the ovipositional specificity of Lepidoptera, the confining nature of test cages has led to completely artificial results. Z. tapiacola, which has solitary feeding larvae living in small host plants, may be expected to have a dispersal mechanism built into its ovipositional behaviour pattern so that it spreads its eggs around, because each plant can only support a limited number of larvae. As a result, there may be some essential activity by the moth between each egg deposition and this activity, such as a period of flight, might be necessary to initiate the next egg deposition. The confines of the test cages would seriously affect such a behavioural response and lead to artificial oviposition. Whatever the explanation, no preference for any particular plant type could be detected and

ovipositional choice tests were discontinued.

Although no distinction was made about the ovipositional specificity of Z. tapiacola, when the moths laid on jointed cactus cladodes lying on the floor of the cages, they always deposited most of their eggs on the thorns situated on the lower surfaces of the cladodes (Table 3). This trend was the same both in dim light and in total dark ($P => 0,1 < 0,9$) and did not appear to be a phototactic response. Also, the moths seldom laid eggs on cladodes which were suspended in mid air by threads from the ceiling of the cages. Less than 10% of the total eggs laid by ten females were deposited on hanging cladodes, most being placed on the cage walls. These observations suggest that there may be a behavioural response by Z. tapiacola females to place their eggs in sheltered situations, a feature which may limit them to small, low-growing thorny plants in the field. If this conclusion is correct and is not an artifact of the caged conditions, then ovipositional behaviour may be a major factor limiting Z. tapiacola to small O. aurantiaca type plants in the field.

Table 3. The number of eggs laid by Z. tapiacola on the thorns of the lower and upper surfaces of O. aurantiaca cladodes lying on the cage floors in dim light and in total dark.

	LIGHT CONDITION	
SURFACE	DIM	DARK
UPPER	121	210
LOWER	301	435
NUMBER OF FEMALES	12	20

3. THE EFFECTS OF ZOPHODIA TAPIACOLA ON OPUNTIA MAXIMA

Defensive gum secretions initiated by insect damage to Opuntia spp. has been documented previously by Pettey (1947) who noted that C. cactorum was not able to colonise O. tardospina because the first instar larvae were repelled from the plants by a mucilagenous sap secreted at the entry wound. The same secretions in mature O. megacantha and O. maxima occassionally forced C. cactorum larvae to vacate their feeding sites. He also observed that the eggs of the cerambycid borer, Lagochirus fernestus, which were oviposited in grooves excavated by the adults in O. megacantha and O. maxima, were often encapsulated in mucilagenous sap which hardened and suffocated them before they could hatch. Gum production is probably the most important feature preventing Z. tapiacola from colonising O. maxima. Consequently, after the mechanism had been detected during starvation tests, further tests were conducted to determine the efficiency of its defensive value.

3.1 The gum secreting O. maxima cultivars

The species, O. maxima, embraces a wide range of spineless cactus varieties or cutivars, of which five or six are grown extensively for fodder in the drier areas of the country. One of these cultivars, Chico, showed during the starvation tests that it is able to resist Z. tapiacola colonisation attempts in the laboratory by secreting defensive gum. However, because the five other varieties, Castillo, Fusicaulis,

Monterey, Morado and Robusta are also of economic importance and because Z. tapiacola may attempt to colonise all six varieties in the field, further tests were conducted to establish whether the defensive gum is effective in the field and whether it is found in all the economically beneficial spineless cacti.

First instar Z. tapiacola were released onto established spineless cactus plants growing in a cultivated patch. Each plant was caged with twenty individuals and after ten days the number of attempted entries was noted (Table 4).

Table 4. The number of attempted and successful entries by Z. tapiacola first instar larvae on caged plants of different O. maxima cultivars in the field.

CULTIVAR	No. OF PLANTS	LARVAE/ PLANT	TOTAL No. LARVAE	ATTEMPTED ENTRIES	SUCCESSFUL COLONISATIONS
Castillo	12	20	240	10	0
Chico	12	20	240	9	0
Fusicaulis	12	20	240	30	0
Monterey	11	20	220	12	0
Morado	12	20	240	14	0
Robusta	12	20	240	7	0
TOTALS	71		1420	82	0

A successful entry is one in which the larva can penetrate the plant cuticle and excavate a tunnel which will accomodate it during its development. Out of 1420 first instar Z. tapiacola larvae released onto 71 plants, made up of six O. maxima varieties, none were able to colonise any

of the plants and all were repelled by secreted gum. Gum secretion in response to wounding by Z. tapiacola is therefore characteristic of the six most important cultivars of O. maxima, and it may be universal throughout all the varieties, including the less important ones.

The 82 attempted entries recorded above, represent less than 6% of the total number of larvae released. The tough cuticle of O. maxima, and the inability of Z. tapiacola larvae to penetrate it, probably accounts for the low percentage attack. The plant cuticle as a defense mechanism is discussed later (Chapter 3.4).

3.2 The efficiency of defensive gum in O. maxima

Although O. maxima and O. megacantha repel solitary feeding Z. tapiacola larvae, they are both successfully colonised by the immature stages of the pyralid moth, Cactoblastis cactorum Salm Dyk. C. cactorum lays 'sticks' of up to 150 eggs (Dodd, 1940) and the hatching larvae all aggregate at the base of a thorn, usually near the one on which the eggs were laid. The size of the group depends on the number of eggs, but there are usually 70 to 90 individuals which pierce the cuticle and enter the plant at the same place. Consequently, the group is able to penetrate the plant tissue more rapidly than the relatively slow-feeding, solitary individuals of Z. tapiacola. The speed at which C. cactorum tunnels into the plant is quicker than the plant can respond by secreting gum and therefore the larvae are not forced out

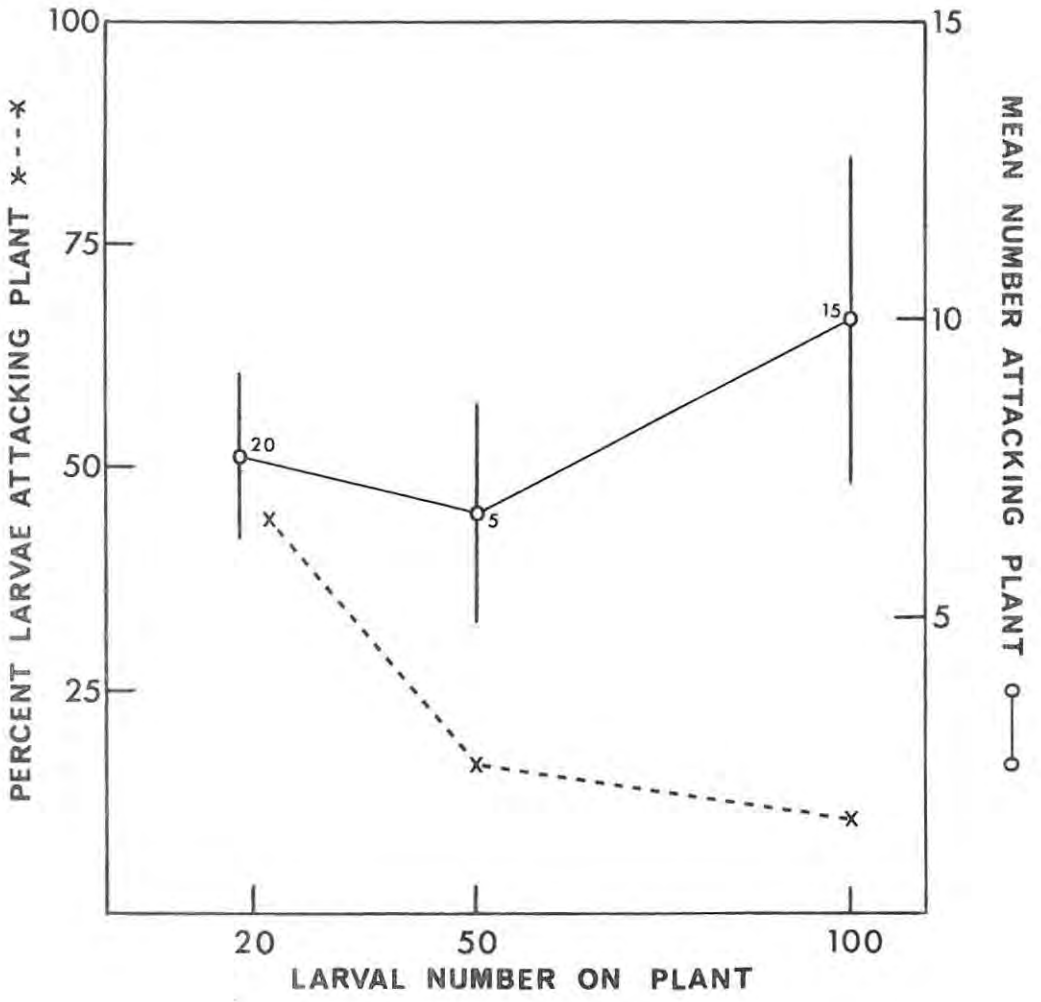

Fig. 13. The percentage and number (mean +1 S.E.) of Z. tapiacola attacking O. maxima when 20, 50 and 100 larvae were released on individual forty centimeter tall plants. Number of replicates is represented next to each point.

of their tunnel. The gregarious habit allows C. cactorum to colonise plants which it would not be able to if it was a solitary feeder like Z. tapiacola.

The impact of large groups of Z. tapiacola larvae on spineless cactus was determined by releasing groups of first instar larvae onto 30 to 40cm tall potted O. maxima plants in the laboratory, after which their progress was recorded. The mean number of larvae attempting to enter each plant was practically the same when 20, 50 and 100 larvae were released on the plants and the percentage attempted colonisations was inversely related to the number of individuals released on the plants (fig. 13). These trends suggest that there were a limited number of suitable entry points (e.g. thorn bases and internodes of cladodes) at which Z. tapiacola could penetrate the cuticle and once these were occupied, the remaining larvae could not attempt entry. However, of major importance is the fact that none of the attempted penetrations was ever successful because the larvae were repelled by the defensive gum secretions characteristic of O. maxima. Also, Z. tapiacola did not aggregate when present in large numbers and never adopted a gregarious habit which may otherwise have enabled then to have entered and successfully colonised the spineless cacti.

3.3 The source of gum in O. maxima

Gums and mucilages are loosely defined terms applied to the polysaccharides produced by plants. Mucilages differ from

Fig. 14. Four different sources of polysaccharides which contribute to gum exudates from flowering plants.

gums in that they are usually less complex, they are maintained within the plant and they are produced as a result of normal metabolism. Gums on the other hand are more chemically complex and are exuded from the plant as a result of injury. The function and origin of gums in plants is not clearly understood (Smith & Montgomery, 1959; Aspinall, 1969) however, the source of gum exuded at the wounds of injured plants appears to originate via one or more of four basic pathways (fig. 14)(Haberlandt, 1928; Fritsch & Salisbury, 1946; Esau, 1964; Fahn, 1967; McLean & Ivimey-Cook, 1967).

The four pathways are as follows; (i) many plants, including the Opuntia spp. and most other cacti, have mucilagenous cells scattered throughout their ground tissue (Boodle & Fritsch, 1908; Metcalfe & Chalk, 1950). The formation and function of these cells is not clearly understood, (Scott & Bystrom, 1970) but when they are ruptured they may discharge their contents and contribute to the exuded gum. (ii) When the cells of plants are damaged, they undergo an enzymatic breakdown which converts all the contents into an amorphous polysaccharide. This process is known as gummosis and it may contribute to the gum. (iii) The cell walls of plant cells are generally very mucilagenous and this mucilage may be released when the cells are broken down after damage. Mucilage from this source will mix with the products of gummosis and may be exuded from the plant. (iv) Finally, some plants, including the Opuntia spp. and other cacti (Stewart, 1919; Archibald, 1936), have gum canals, or resevoirs,

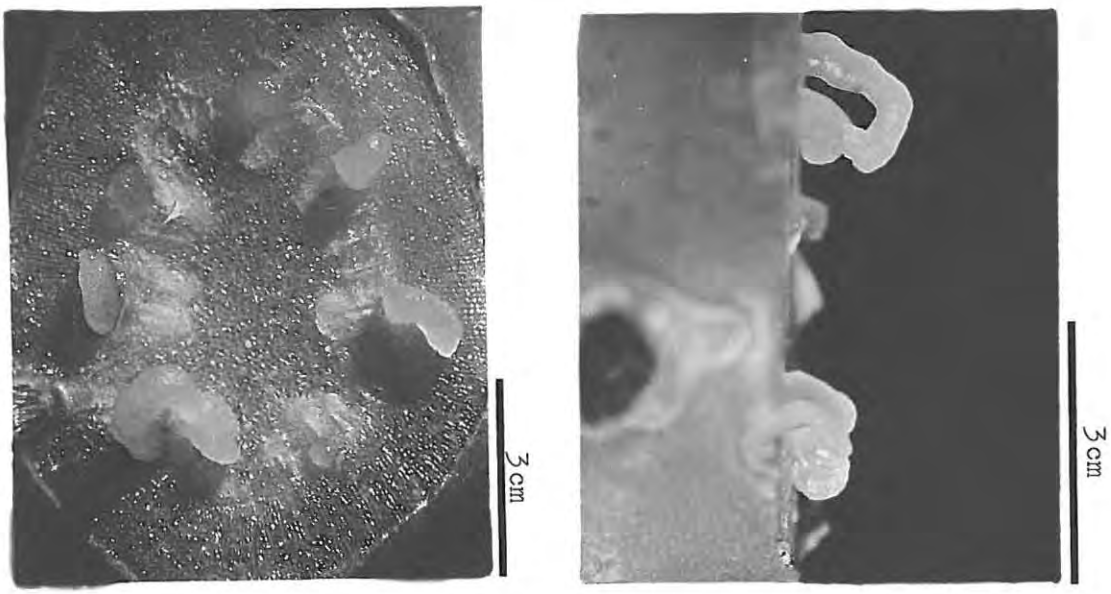

Fig. 15. Cut surface in frontal view (A) and side view (B) of O. maxima showing gum forced out of the gum canals by internal pressure.

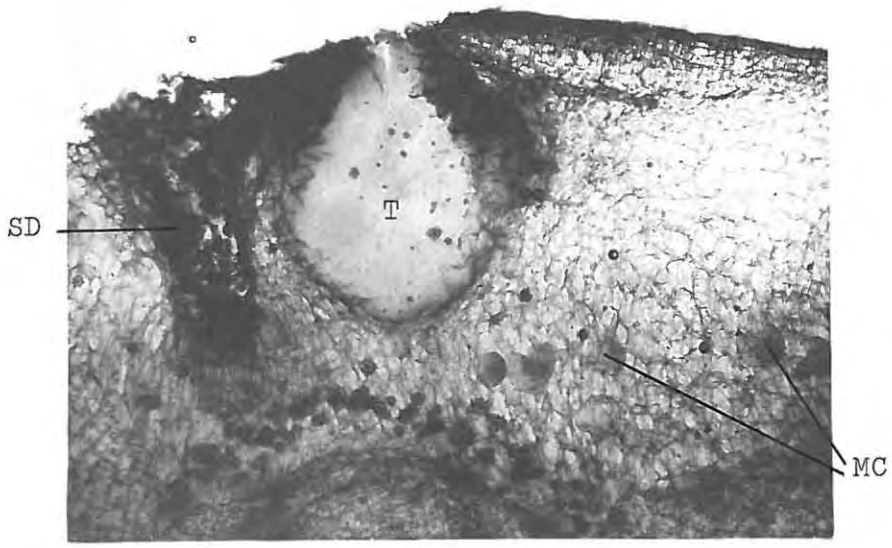

Fig. 16. A hand section through O. maxima tissue at the site of a Z. tapiacola tunnel excavated alongside scar damage (x10). MC- mucilage cells; SD- scar damage; T- tunnel.

which are elongated pockets filled with gum and are usually orientated with the long axis of the stem and associated with the vascular tissue. Gum-canals are formed naturally in some plant species, including the cacti, while in others they develop as a result of physiological, chemical or disease damage to the plants tissues. Wounding of the plant results in the gum, which is under pressure in the canals, being exuded (fig. 15).

Any, or all, of the above pathways could be responsible for the gum produced by O. maxima when damaged by Z. tapiacola. However, there is substantial evidence which suggests that only the gum-canals (i.e. pathway 4) contribute significantly to the exudate. Firstly, microscopic sections of O. maxima and O. aurantiaca stained with thioin (Scott & Bystrom, 1970) show that there are approximately equal concentrations of mucilagenous cells in both cacti. If these cells were responsible for the production of repelling gum in O. maxima, while not doing so in O. aurantiaca, then there would have been a proliferation of them at the site of damage in O. maxima and not in O. aurantiaca. Sections through Z. tapiacola excavations in O. maxima (fig. 16) show that there is no such proliferation and that the amount of gum produced (figs 10 & 12) could not have originated from the few ruptured mucilagenous cells in the vicinity of the wound. Gummosis is not likely to contribute much to the exudate because all the damaged cells are ingested by the larva and their contents are not therefore available for enzymatic

Table 5. The cross sectional areas of gum canals in O. maxima and O. aurantiaca. Means were derived by sectioning five young flush, five mature and five old woody cladodes for both species, and measuring the four largest canals in each.

PLANT STAGE	CANAL CROSS SECTIONAL AREA mm^2		NO. OF TIMES O. MAXIMA > O. AURANTIACA
	O. MAXIMA	O. AURANTIACA	
FLUSH (still bearing fleshy leaves)	0,30	0,03	10
MATURE (fully grown, less than two years old)	2,43	0,11	22
OLD (woody, hard, basal cladodes. More than two years old)	7,07	0,41	17,3

breakdown and mucilage formation. Further, gummosis is a universal phenomenon throughout the plant kingdom, probably occuring equally in both O. aurantiaca and O. maxima. It is therefore unreasonable to assume that the process may be responsible for producing repelling gum in one and not the other.

The only remaining source of exudate in O. maxima is from the gum canals. Gum canals occur in O. maxima and O. aurantiaca but the number per cladode in both species varies considerably. In large O. maxima pads counts of between 20 and 40 canals per cladode have been made, while O. aurantiaca has between 5 and 15 canals in each of its smaller cladodes. Gum canals are differentiated early in the development of the flush and they are readily discernable in sections of young cladodes. The canal size seems to be the critical factor as to whether gum will be exuded or not. Measurements of canals in O. maxima and O. aurantiaca (Table 5) show that the canals get broader as the plants age, however, in O. aurantiaca the gum canals never reach the same dimensions as those in O. maxima. Mature O. maxima has large canals which always exude enough gum to repel Z. tapiacola attacks. O. maxima flush and mature O. aurantiaca, on the other hand, only occassionally repel Z. tapiacola, probably because they have small canals which do not store enough gum to form an exudate. (Only twice during hundreds of observations over two years has Z. tapiacola been seen to be repelled by gum in O. aurantiaca).

The penetrating larva does not have to actually rupture one of the canals in O. maxima to initiate exudation. As soon as the cuticle of an O. maxima plant is pierced, a low pressure area is created in the tissues. Immediately, gum starts flowing from the high pressure canals through the intercellular spaces to the wound. Consequently, the larvae are always repelled even when they excavate their tunnel some distance away from the closest gum canal. The delay of one to three days between the larva piercing the cuticle and the appearance of gum might be explained by the delay for gum to force its way through the intercellular spaces.

3.4 Cactus cuticle as a barrier to Z. tapiacola larvae

The toughness of plant cuticles has been implicated in preventing or reducing insect feeding (Tanton, 1962; Agarwal, 1969; Feeny, 1970; Southwood, 1973). The cactus feeding pyralid borers may also be affected by cuticular toughness because Pettey (1947) noted that C. cactorum colonised young O. megacantha cladodes more successfully than they did older ones. Also, Mann (1969) recorded that while rearing Z. tapiacola prior to its release in Australia, the first instar larvae had to be provided with young joints of O. aurantiaca as they were unable to penetrate the older ones. These observations were extended during this investigation.

The number of larvae penetrating jointed cactus was recorded by releasing sixty first instar Z. tapiacola onto fifty O. aurantiaca cladodes of differing cuticular thickness.

(Abercrombie et al, 1966 defined the cuticle as the superficial, non-cellular layer which forms a continuous covering over the aerial parts of the plant). All the cladodes were in contact with each other so that the larvae could choose those cladodes prefered for colonisation. Ten days after release, the number of larvae in each cladode was recorded and the cuticular thickness near the penetration site was measured. Thickness was measured by stripping $1cm^2$ sections of cuticle from the plants. Any green tissue attached to the sample was scraped off lightly with a sharp blade before measurements were made using a Mercer 95011 411 micrometer accurate to $2\mu m$. The mean of three to five measurements on each block of cuticle was taken. The relative toughness of the same or similar blocks was measured using a penetrometer which recorded the mg pressure needed to pierce the cuticle with a flat-tipped 'minuten' pin of 0,254mm diameter (Moran & Buchan, 1975).

Most of the larvae (77%) penetrated cladodes with a cuticle that was less than 0,1mm thick, while no larvae penetrated cladodes with a cuticular thickness of 0,15mm (Table 6). Cuticular thickness seems therefore to limit young Z. tapiacola larvae to particular cladodes. Consequently, the thickness and toughness (= penetrability) of O. maxima and O. aurantiaca cuticle was measured and compared with respect to their vunerability to Z. tapiacola larvae.

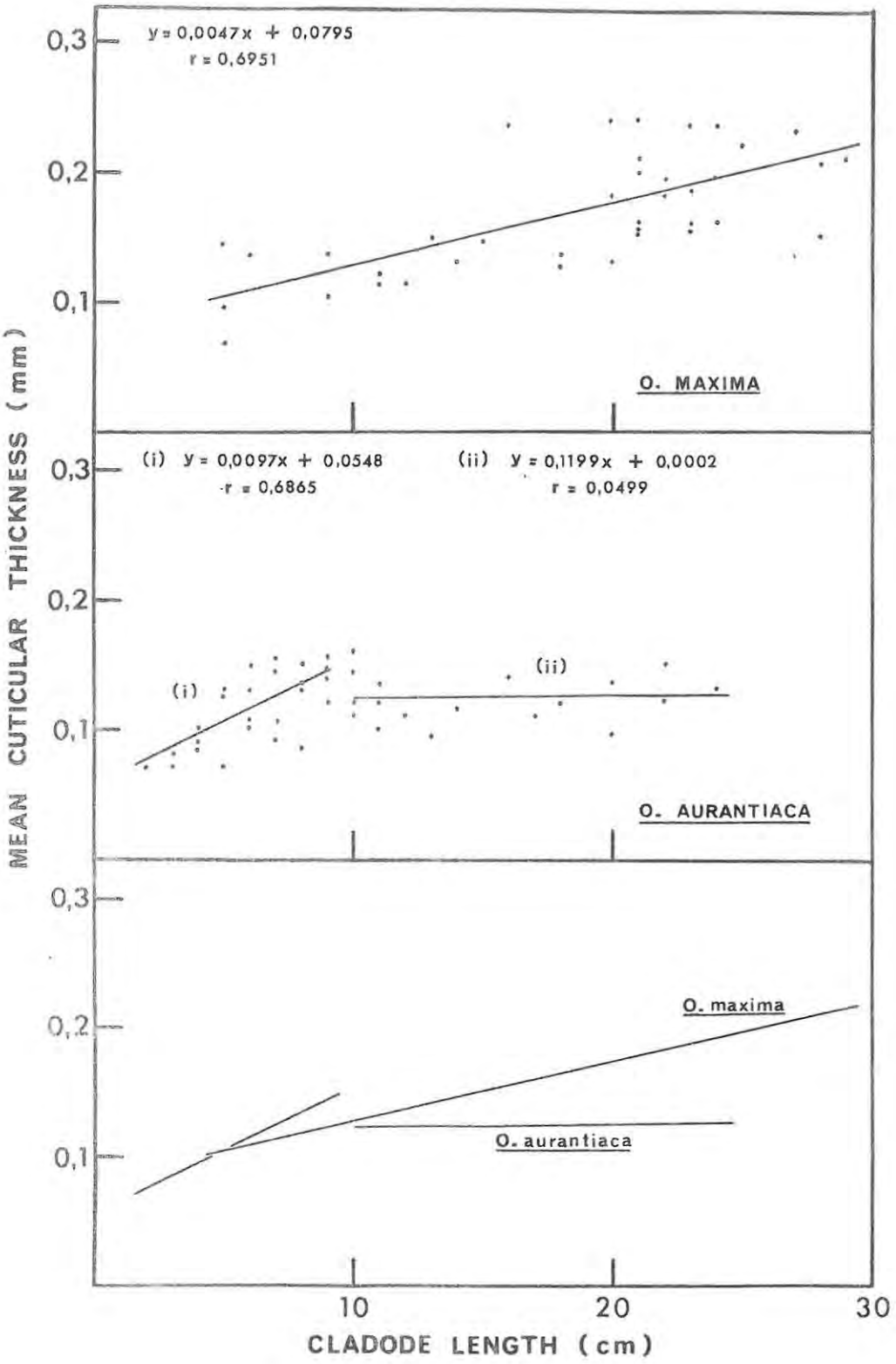

Fig. 17. Variation in cuticular thickness with cladode age (= length; see text) for O. maxima and O. aurantiaca. Each point represents the mean of three to five measurements.

Table 6. Z. tapiacola larval numbers colonising O. aurantiaca cladodes of different cuticular thickness. The numbers of cladodes in each group are in parentheses. Penetrations at aereoles, intenodes and damaged areas were noted.

CUTICLE THICKNESS mm	COLONISATIONS AT AREOLE	AT INTERNODE	AT DAMAGE	TOTAL
0,09 (8)	13	1	0	14
0,10 (5)	12	5	1	18
0,11 (10)	5	3	1	9
0,12 (6)	3	3	0	6
0,13 (12)	1	4	2	7
0,14 (6)	1	1	0	2
0,15 (3)	0	0	0	0
TOTAL (50)	35	17	4	56

In plants generally, the cuticle thickens with age (Martin & Juniper, 1970) and this trend was quantified specifically for O. aurantiaca and O. maxima. The mean cuticular thickness of different length cladodes was measured and the results are plotted in fig. 17. Cladode length was used as a measure of age because the lengths of Opuntia spp. cladodes grown under the same conditions are proportional to their age until they are fully grown. The regressions show that the thickness of the cuticle of both species increase significantly with age ($P = <0,05$). However, the cuticle in mature O. maxima (i.e. with cladodes greater than 25cm long) achieves a greater thickness than that in mature O. aurantiaca (i.e. with cladodes greater than 10cm). Although O. aurantiaca

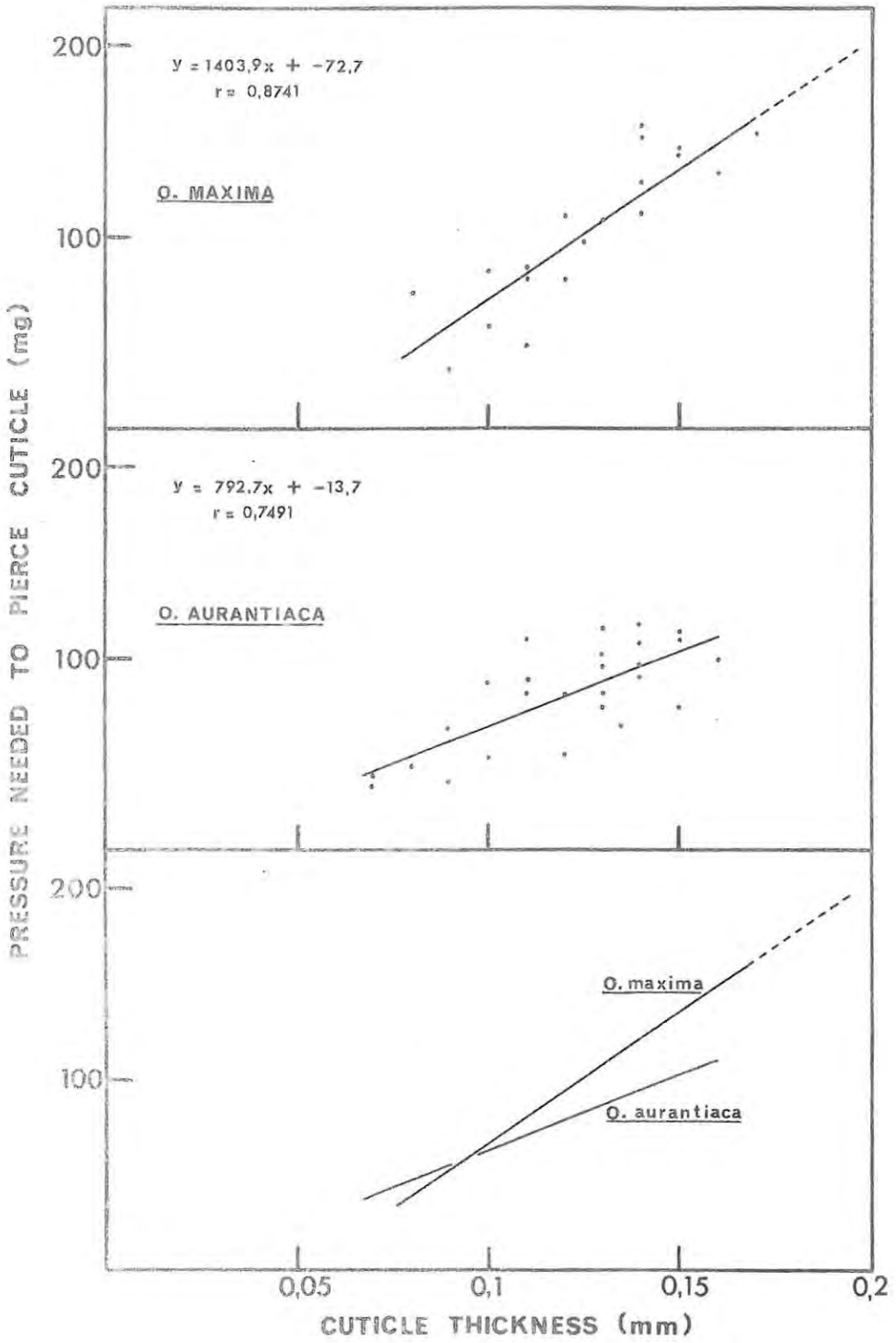

Fig. 18. Relative cuticular hardness plotted against cuticular thickness for O. maxima and O. aurantiaca.

cladodes grow up to more than 30cm under certain conditions, their cuticle does not thicken significantly ($P => 0,80$) above that of 10cm cladodes.

The penetrability, or toughness, of both O. aurantiaca and O. maxima cuticle was also measured and fig. 18 shows that the penetrability of cuticle is proportional to its thickness. As a result, O. maxima develops not only a thicker cuticle than O. aurantiaca, but as it thickens it becomes tougher so that in mature cladodes it serves as an effective barrier to Z. tapiacola. Consequently, the percentage larvae that enter O. aurantiaca and O. maxima when placed on flush growth is much higher than when they are placed on mature growth, especially on O. maxima (Table 7).

Table 7. The percentage penetration of cuticle by first instar Z. tapiacola larvae on flush and mature O. aurantiaca and O. maxima.

PLANT	STAGE	NUMBER OF LARVAE ON PLANTS	NUMBER PENETRATING CUTICLE	PERCENTAGE PENETRATION
O. aurantiaca	FLUSH	120	103	85,8
O. maxima	FLUSH	156	126	80,8
O. aurantiaca	MATURE	640	467	73,0
O. maxima	MATURE	1570	224	14,3

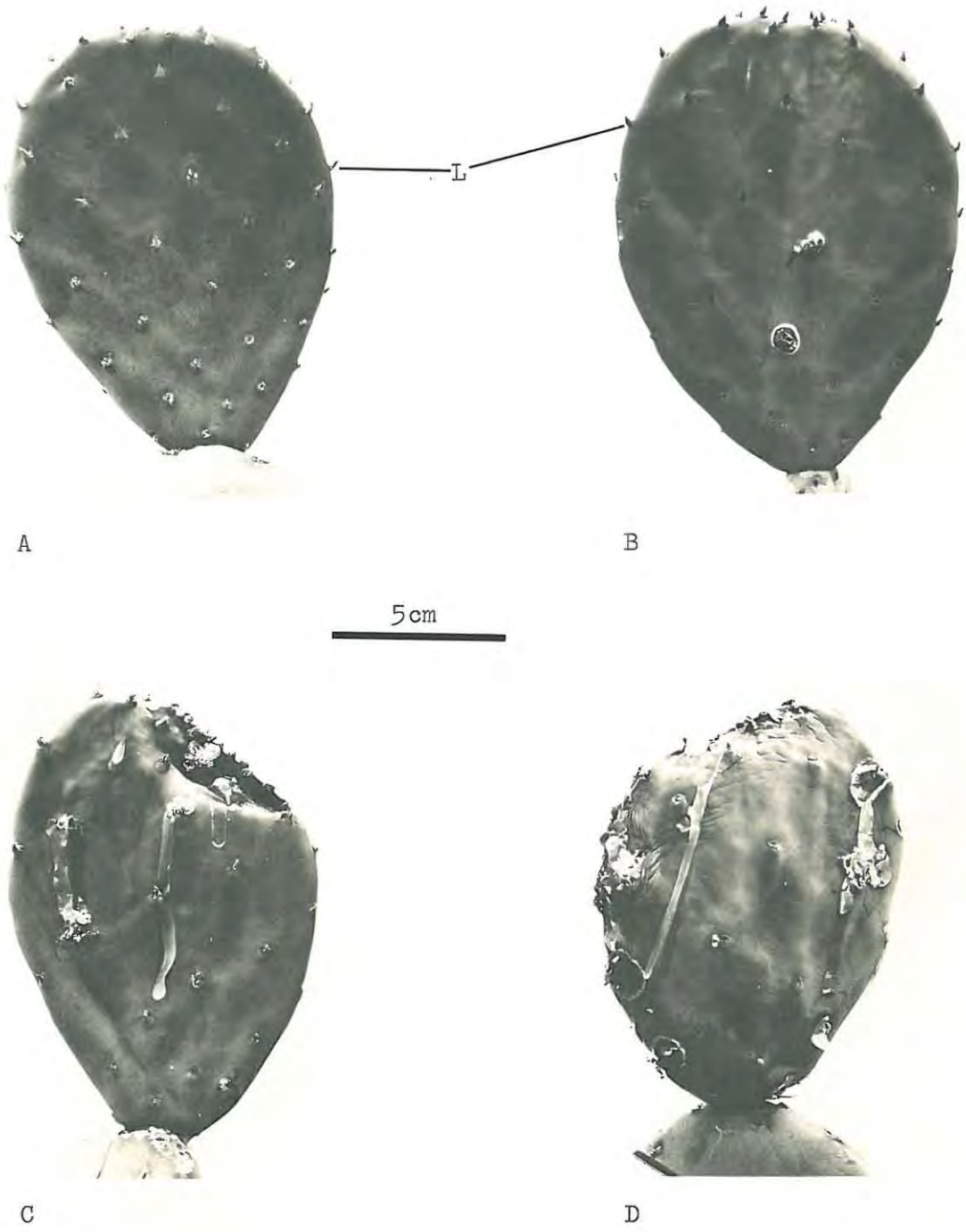

Fig. 19. O. maxima flush cladodes damaged during attempted colonisations by Z. tapiacola first instar larvae. (A) Healthy flush cladode bearing small fleshy leaves (L). (B) Flush with two attempted colonisations resulting in localised desiccation but little damage. (C) Destroyed growing point and limited gum production. (D) Whole flush cladode desiccating 24h prior to dropping from the plant.

3.5 Z. tapiacola attacks on O. maxima flush

Small flush cladodes which still bear fleshy leaves typical of young Opuntia growth, are very susceptible to Z. tapiacola larvae because they have a soft easily penetrated cuticle. Further they only develop the ability to repel Z. tapiacola attacks with gum exudates when they reach a length of 15 to 20cm and their gum canals have increased in volume. However, larval colonisation of flush is abortive because the attack initiates rapid desiccation which results in the formation of hard impenetrable callouses in the tissues around the wounds. As a result, Z. tapiacola attacks, although never successful, may initiate damage to the spineless cactus flush and the degree of damage can be divided into three classes (fig. 19A-D);

(i) Localised desiccation at the site of an attack away from the growing point which imparts no real damage to the cladode and it continues to develop normally (fig. 19B)

(ii) The growing area may be permanently damaged so that the cladode cannot develop further and it remains stunted on the plant (fig. 19C).

(iii) Excessive desiccation from a large number of attacks causes complete collapse and subsequent shedding of the cladode from the plant (fig. 19D).

The degree of damage inflicted on an O. maxima flush cladode is dependent on the size of the cladode and the number of larvae attempting to colonise it. In each of 34 experiments, a number of larvae were placed on a flush cladode of known

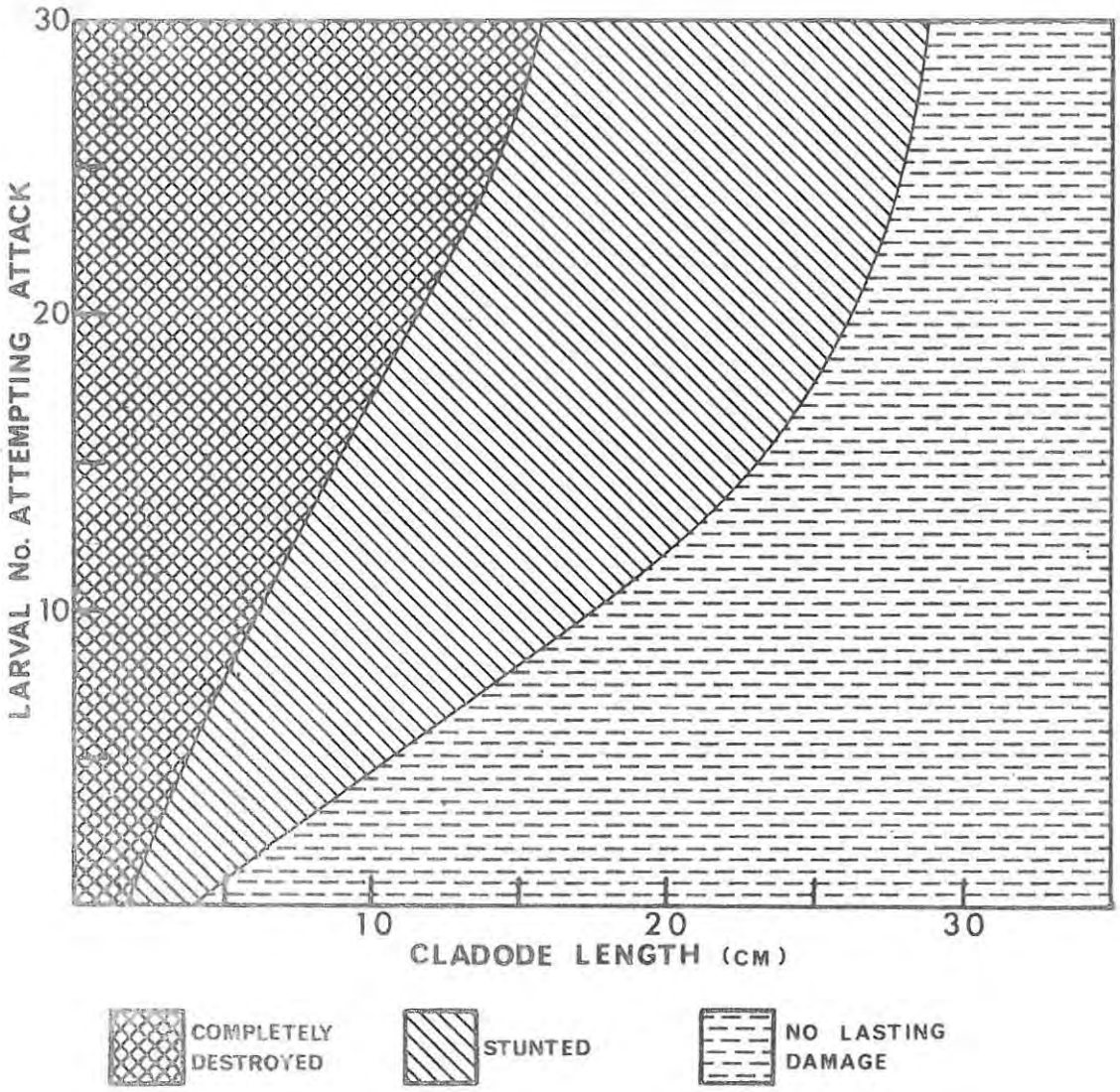

Fig. 20. Diagramatic representation of the degree of damage inflicted on different sized O. maxima flush cladodes by varying numbers of Z. tapiacola larvae.

length. The degree of damage resulting from the attacks of these larvae was recorded and used to construct fig. 20 which indicates the degree of damage that might be expected from differing numbers of larvae on a flush cladode. Small cladodes are more susceptable to Z. tapiacola attacks and one larva will inevitably bring about the collapse of a cladode less than 3cm long. As the cladodes increase in size, more larvae are needed to bring about complete destruction. Similarly, the chances of the growing point being damaged are lower in large cladodes. Therefore, as the cladodes get larger the Z. tapiacola attempted colonisations become less damaging until in cladodes greater than 20 to 25 cm the gum canals become active and attacking larvae are repelled by gum. In spite of their ability to damage flush, Z. tapiacola larvae never successfully colonised the flush points and they cannot utilise them to make their way into the mature cladodes on the plant.

4. THE IMPACT OF *ZOPHODIA TAPIACOLA* ON *OPUNTIA AURANTIACA*

Huffaker (1962) stated that,"an insect must be capable of decisive destruction of its plant host for it to be useful as a weed control agent." He also pointed out that it is not possible to "assess the importance of a regulating factor simply by measuring the level of impact, independent of density, at a given time; the importance lies in whether or not the factor is geared to increase in density of the population." Wilson (1964) on the other hand says that under some conditions an insect that only inflicts a small amount of damage to a plant may cause it to succumb to plant competitors and that, because of the multitude of factors involved, it is difficult to estimate the effectiveness of phytophagous insects in regulating plant abundance. Andres & Goeden (1971) stated, "Theoretically any organism that is potentially destructive to a weed might find use as a weed control agent."

It seems, therefore, that it is impossible to predict prior to release whether or not a damaging insect will significantly surpress a weed and the only real test is to release the insect. However, if an insect can be shown to be considerably damaging before release, this argues in favour of its introduction, and at least gives some indication of whether it will be more or less successful than other associated enemies (Harris, 1972). Initially, therefore, the impact that *Z. tapiacola* has on jointed cactus was quantified by measuring the weight of fresh cactus that had to be supplied to individual larvae for them to be able to complete their development.

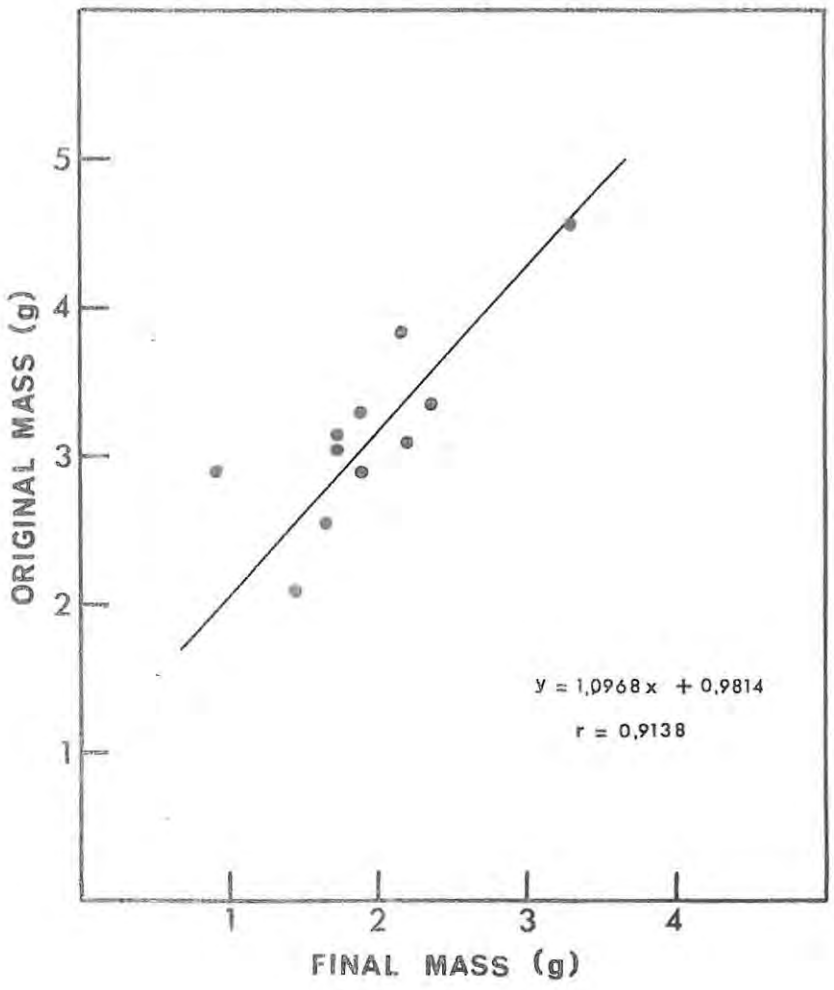

Fig. 21. Weight loss from O. aurantiaca over 90 days in the controlled environment room. The regression was used to convert the mass of cactus not destroyed by Z. tapiacola to its original mass.

The food requirements of Z. tapiacola larvae were measured by isolating forty larvae in dishes with individual jointed cactus cladodes of known mass. Fifteen dishes had small cladodes (ranging from 2 - 5g) 15 had medium size cladodes (12 - 16g) and the remaining 10 had large cladodes (+50g)(Only 10 cladodes in excess of 50g were observed because individual joints of this size class are scarce). As each joint was destroyed it was replaced with a fresh one of known mass, so that the larvae had a continual supply of food and the total weight of fresh cactus destroyed by each individual was recorded. In some cases, the medium sized cladodes were not completely destroyed and green living tissue remained after the larva had pupated. The remaining tissue was weighed and its original mass at the start of the experiment was extrapolated from fig. 21. The original mass of undamaged tissue was then subtracted from the total mass supplied which gave the total mass destroyed by the larvae. The mass of cactus destroyed when larvae invade large (+50g) cladodes could not be calculated because each larva destroyed only a small proportion of the cladode. However, the developmental duration of larvae in large cladodes was recorded and compared to that in medium and small cladodes.

The mean mass of O. aurantiaca destroyed by Z. tapiacola larvae during their development was 15,3g.(minimum, 9,4g; maximum, 28,7g) (Table 8). There was no significant variation ($P => 0,1 < 0,9$) between the mass destroyed by larvae of both sexes and the mass destroyed in different cladode size classes

Table 8. The developmental duration and mass of O. aurantiaca destroyed by individual Z. tapiacola larvae in the controlled environment room. Gaps in the table represent larvae that died before reaching maturity. * represent larvae that pupated, but no adult emerged. Numbers in brackets are the mass of living cactus remaining after the larva had pupated.

LARVAL NUMBER	DEVELOPMENTAL DURATION days	SEX	FRESH CLADODE MASS SUPPLIED 1	2	3	4	5	TOTAL FRESH CLADODE MASS DESTROYED	
1									
2	*	*	2,6	3,7	4,4			10,7	
3	95	F	2,2	2,9	2,9	4,7	4,6	17,3	
4	86	M	2,4	3,8	2,2	4,5	4,9	17,8	
5	102	F	4,4	4,3	2,9	4,8		16,4	
6	99	F	2,5	3,0	3,4	4,0	4,1	17,0	
7	80	M	3,0	4,2	2,9	3,5		13,6	
8	*	*	2,7	3,5	4,3			10,5	
9	74	F	3,3	2,6	3,5			9,4	
10	107	M	4,0	2,2	2,7	4,7		13,6	
11	*	*	3,0	2,2	3,7	2,5	4,3	15,7	
12									
13	100	F	4,5	4,8	4,8			14,1	
14	98	F	2,7	4,0	6,0	4,7		17,4	
15									
								MEAN = 14,47	SMALL SIZE CLASS CLADODES 2 - 5g
16	*	*	13,3	10,0				23,3	
17	74	M	13,7					13,7	
18									
19	105	F	15,1	11,5(3,3)				21,8	
20	83	M	12,6					12,6	
21	77	M	15,6(2,9)					11,3	
22	*	*	14,1					14,1	
23	76	M	12,4(0,7)					10,6	
24	74	F	13,5					13,5	
25	88	M	12,3	15,4(3,9)				22,2	
26	118	F	13,7	15,4				28,7	
27	76	M	15,7(,3)					13,3	
28	75	M	13,7(1,1)					11,4	
29	74	M	11,2					11,2	
30	87	F	13,7					13,7	
								MEAN = 16,15	MEDIUM SIZE CLASS CLADODES 12 - 16g

did not differ significantly ($P = <0,8>0,6$). However, the four larvae (Numbers 16,19,22 and 24) that destroyed the most cactus all came from the medium size group. The mass destroyed by each larva (23,3g; 21,8g; 22,2g; 28,7g) was far in excess of the mean (15,3g) utilised by all the other larvae. These four larvae invaded a medium sized cladode in the penultimate instar and as a result all had more tissue than they needed to complete their development. Apparently final instar larvae in this situation eat larger amounts, apparently in an effort to destroy all the tissue in the cladode. Only completely destroyed cladodes are suitable for pupation because green tissue in the damaged husk is susceptable to bacterial rot which may affect the pupa. Larvae supplied with small cladodes did not show obvious 'force-feeding' because they never had more than 5g excess tissue, even when the final instars colonised new small cladodes. Although it could not be measured, in large cladodes (+50g), there is evidence to suggest that 'force-feeding' does occur.

The average development duration of ten Z. tapiacola larvae in large cladodes was 100 days (minimum, 83; maximum, 117). This was not significantly different ($P = <0,6>0,4$) from the average development time of 88 days for larvae in small and medium sized cladodes. However, a regression constructed from the data in Table 8 shows that there is a positive correlation between the mass of cactus destroyed by Z. tapiacola and its developmental duration (fig. 22). Consequently, the amount of cactus destroyed by larvae in

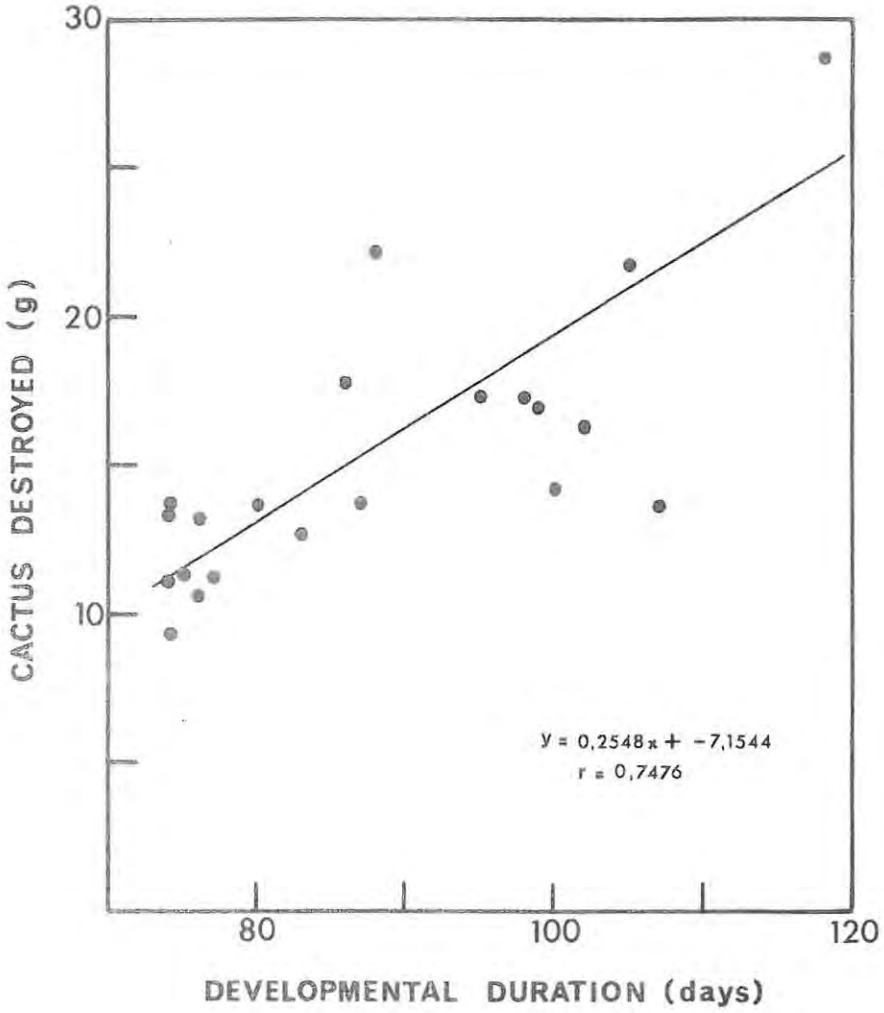

Fig. 22. The mass of O. aurantiaca destroyed by Z. tapiacola larvae with different developmental durations.

large cladodes is probably greater because developmental duration tends to be longer in large cladodes.

The conclusions from these results are that Z. tapiacola needs approximately 15g of jointed cactus for normal development. When the larvae invade small cladodes, they change from one to the other destroying more than one in order to reach maturity. In larger cladodes, they destroy at least 15g, although they may destroy much more when the tissue is available.

DISCUSSION

> "The critical phase of biological control work against weeds is the selection of species that will not harm other plants or at least useful plants. All other considerations are subordinate and a suitable insect species for introduction into a country against a weed is one that is safe to introduce, irrespective of its other characteristics." (Huffaker, 1959, quoting J.R. Williams).

The very few cases where introduced biological control insects have become pests on beneficial plants have generally only occurred when inadequate tests have been conducted prior to release, and they do not represent examples of insect species adapting biologically to invade new plants (Huffaker, 1957; 1959; Wapshere, 1974). An example of this is the lantana lacebug, Teleonemia scrupulosa Stäl., which attacked the cultivated crop, Sesamum indicum L., when the insect was introduced into Uganda as a biocontrol agent of Lantana Camara L. (Greathead, 1971). In some cases economic considerations have favoured release of the insect although its potential to invade and damage beneficial plants was expected. For example, the spineless cacti have been damaged by C. cactorum since the moth was introduced into South Africa (Pettey, 1947). The real danger involved, therefore, when introducing an insect into a new country is not that it may adapt itself to existence on beneficial plants in the new habitat, but rather, that the insect is inadequately screened so that it is considered safe for release although it possesses the ability to colonise and damage beneficial plants. Consequently, when all reasonable precautions have been taken and an insect has been shown to

be restricted to weed plants, it can be released with the assurance that it will not become a pest.

Co-evolution of plants and insects has led to the development of chemical and physical defense mechanisms in plants, some of which have been 'exploited' in a variety of ways by the insects and used to their own advantage (Southwood, 1973). As a result, both secondary plant substances and physical properties acting as attractants or repellants, determine which plants will be selected by an insect and whether or not it will support development of that insect (Snelling, 1941; Dethier, 1954; Painter, 1958; Thorsteinson, 1960. Fraenkel, 1959, 1969; Kennedy, 1965; Jeremy, 1966; Agarwal, 1969; Dethier & Schoonhoven, 1969; De Wilde & Schoonhoven, 1969; Bernays & Chapman, 1970; Schoonhoven, 1973). One of the most meaningful approaches to the investigation of an insect's host specificity is to examine its broad biology so that the specific attractants and repellents that affect it may be determined (Harris & Zwolfer, 1968). Unfortunately, such a comprehensive study requires a great deal of time and the urgency of most weed control programmes does not allow this approach to be taken. However, some of the physical requirements (which are generally easier to detect than chemical ones) that affect host selection in Z. tapiacola have been noted, and although secondary plant substances almost certainly also determine which plants Z. tapiacola will be able to colonise, they were not investigated.

The pre-release studies comprising this investigation were directed mainly at the association of Z. tapiacola with cactaceous plants because previous evidence clearly shows that the moth cannot colonise plants outside the family Cactaceae (Dodd, 1940; Mann, 1969; Zimmermann, 1972). The cacti can be divided into three economic groups in South Africa. (i) Cultivated fodder plants (e.g. O. maxima). (ii) Proclaimed weeds (e.g. O. aurantiaca, O. megacantha, O. tardospina). (iii) The so called 'ornamental' cacti that are grown for their decorative value (e.g. Neomammilaria spp., Cereus spp. Eiphyllum spp.). Z. tapiacola larvae attack representatives from all three groups but only certain of the weeds serve as suitable hosts. In spite of the potential destruction of ornamental cacti, there are three reasons why the moth's specificity does not need further investigation or justify postponment of its release. Firstly, ornamental cacti can easily be protected with insecticides. Secondly, the incidence of attempted colonisations in ornamental plants should be low because as Huffaker (1962) has pointed out, insects that cannot breed and subsist on a plant species will seldom inflict much damage on that species. Thirdly, and most important, the direct and indirect economic importance of O. aurantiaca is far greater than any or all of the ornamental species, and any agent that may affect some control over the weed must be used, irrespective of the damage it may bring about on the exotic decorative plants. However, growers of these plants should be warned of the potential threat to their collections when the moth is released.

Most of the study was therefore directed at the two economically important groups of cacti, the fodder plants and the weeds. Of all South African weeds, O. aurantiaca is the most damaging and is the primary target of this biological control campaign. However, four other South African weeds, O. rosea, O. imbricata, O. megacantha and H. martinii, although not treated specifically in this study, serve as suitable hosts for Z. tapiacola and may be damaged by the insect if it is released. On the other hand, the fodder cactus, O. maxima, and the weeds, O. megacantha and O. tardospina, are never colonised by Z. tapiacola in the laboratory because the plants have a high concentration of gum which is exuded by the damaged tissues, where larvae begin to tunnel into the plants. This gum defence mechanism is always effective in preventing Z. tapiacola from colonising O. maxima, however, other features of the spineless cacti also seem to make them unsuitable hosts for the moth. Firstly, the tough cuticle of mature growth forms a barrier which prevents most Z. tapiacola first instar larvae from ever reaching the internal plant tissues. Further, the moths seem to lay most of their eggs on the thorns of their host plant, while most hatching larvae are dependent on thorns around which they construct a 'silk-tent', essential for penetration of the cuticle. The general lack of thorns on O. maxima may, as a rule, render these plants unsuitable for ovipositing females and, at the same time, reduce the number of suitable sites at which first instar larvae may attempt to penetrate into the plant. Z. tapiacola is not expected

to cause much damage to the soft-cuticled, flush of O. maxima because the larvae that hatch from the few eggs that may be laid on these plants, have a negative phototaxis which should cause them to move down the plants and away from the growing points. Consequently, there should never be any damage to O. maxima by Z. tapiacola, even when the plants are at their most vulnerable stage.

Throughout this investigation, no major factor has been forseen that might critically hinder the progress of Z. tapiacola in the field, although various spiders and a braconid parasitoid, Bracon hebetor Say (see Appendix 11), on occassions accounted for considerable mortality in the rearing cages. Pettey (1947) noted that spiders and Microbracon habetor (sic.)(= B. hebetor) were responsible for a small percentage of C. cactorum killed in the field. Pettey presents no reasons to validate his conclusions about the affect of spiders, but he notes that the parasitoid cannot survive throughout the year only on C. cactorum, because it needs some alternative lepidopterous hosts, one of which might be Heliothis obsoleta on lucerne. Consequently, C. cactorum colonies are only parasitised by B. hebetor in the vicinity of cultivated lands and hopefully, for the same reasons, Z. tapiacola will not be heavily parasitised in the field.

Z. tapiacola is not expected to provide a totally effective and permanent solution to the jointed cactus problem,

in South Africa. However, certain features of its biology suggest that the moth will exercise some degree of control and that it should intergrate well with the presently active control agents (Table 9). The herbicide spray programme selectively destroys large O. aurantiaca bushes and their underground tubers while the small plants and tubers remain undetected and undamaged. Large bushes are also destroyed by both C. cactorum and D. austrinus. The latter also destroys small plants, especially when the insect is abundant in heavily infested areas. However, as a rule, neither insect seems to destroy the underground tuber. Consequently, the three control agents generally only destroy the aerial parts and tubers of large plants, while the small plants and their tubers are not significantly damaged and they remain as a constant resevoir for regrowth of the weed. Z. tapiacola is known to colonise preferentially small O. aurantiaca plants and to destroy the underground tuber of the plants it attacks

Table 9. The stages of O. aurantiaca destroyed by current control agents in South Africa. The expected impact of Z. tapiacola is presented.
+ = destroyed; - = not affected.

CONTROL AGENT	STAGE OF O. AURANTIACA DESTROYED		
	SMALL PLANTS	LARGE PLANTS	UNDERGROUND TUBER
TORDON HERBICIDE	-	+	+
C. CACTORUM	-	+	-
D. AUSTRINUS	+	+	-
Z. TAPIACOLA (Expected)	+	-	+

in South America. Consequently, when released in South Africa it is expected to show the same trend, so that it should destroy the two stages of jointed cactus that are at present least affected. Not only would this increase the pressure being exerted on the weed, but it also suggests that Z. tapiacola will intergrate with the other control agents, and will not be detrimentally affected by or have to compete directly with them.

As a result of this investigation, application will be made for permission to release Z. tapiacola in South Africa. It will then be necessary to monitor its progress in the field to determine what affect it has on the weed.

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Appendix I.

Summarized details of the development of Zophodia tapiacola immature stages in Opuntia aurantiaca., in the controlled environment room (see fig. 1).

INSTAR	HEAD WIDTH mm.			DURATION days.		
	MEAN	MIN.	MAX.	MEAN	MIN.	MAX.
LARVAL 1	0,312	0,312	0,312	3,4	3	4
LARVAL 2	0,467	0,429	0,507	5	5	5
LARVAL 3	0,687	0,624	0,858	5,8	5	8
LARVAL 4	0,998	0,819	1,170	8,1	6	12
LARVAL 5	1,416	1,209	1,638	10	7	14
LARVAL 6	1,816	1,716	1,911	13,1	10	18
PREPUPA	1,816	1,716	1,911	2	2	2
PUPA	-	-	-	20,6	16	26

The head widths were measured every two days. Larvae were removed from their tunnels and cooled. When they became inactive, their head width was measured using a Wild microscope ocular micrometer. The measured larvae were then replaced in their tunnels where they commenced feeding.

Appendix II.

Preliminary observations on the life cycle of Bracon hebetor Say* (Braconidae : Hymenoptera) on Zophodia tapiacola in the laboratory.

Mating of adult B. hebetor was never observed although both sexes were obtained. The females only oviposit on penultimate and final instar larvae and prepupae, ignoring first to fourth instar larvae and pupae. When presented with a suitable host the parasite approaches and stings it before rapidly retreating from the host. Occassionally the larva manages to swing round and regurgitate on the parasite so that it has to clean itself for sometime after its retreat. B. hebetor females confronted with prepupae in already partially constructed cocoons chew their way into the cocoon through the silk to paralyse their host. The paralysed larva becomes inactive within 2 to 15 minutes.

When the host is immobile and the parasite has cleaned itself, it again advances and over a one to two hour period it lays up to twenty 3mm long, curved, elyptical eggs on the cuticle of the larva. After two days, (under controlled environment room conditions) the eggs hatch and the small pink, apodous, ectoparasitic larvae commence feeding. The larvae grow for four days to 3mm in length after which they pupate

* Determined by Mr. G. Prinsloo, Plant Protection Research Institute, Department of Agricultural Technical Services, Pretoria, South Africa.

in a substantial cocoon constructed on or near their now desiccated host. Pupation lasts ten days before the adults emerge and chew their way out of the cocoon.