



Biology, History, Threat, Surveillance and Control of the Cactus Moth, *Cactoblastis cactorum*



Biology, History, Threat,
Surveillance and Control
of the Cactus Moth,
Cactoblastis cactorum

H. Zimmermann
S. Bloem
H. Klein



FAO



IAEA

Joint FAO/IAEA Programme of
Nuclear Techniques in Food and Agriculture

BIOLOGY, HISTORY, THREAT,
SURVEILLANCE AND CONTROL
OF THE CACTUS MOTH,
Cactoblastis cactorum

IAEA, VIENNA, 2004
IAEA/FAO-BSC/CM

Printed by the IAEA in Austria
June 2004
ISBN 92-0-108304-1

FOREWORD

Alien invasive insect pests are increasingly threatening agriculture and the environment. In the context of the rapidly growing international travel and trade, the potential for moving dangerous pest species to new geographic regions and locations has been drastically increasing. The United States Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS) reports that the expanding flow of passengers and cargo is far outpacing the inspection capabilities despite increases in funding, staffing and use of technology. The potential threat of bio-terrorism also adds to the complexities of excluding major foreign pest species.

Under the Convention of Biodiversity, the International Plant Protection Convention (IPPC) and other binding international treaties that also address alien invasive species, prevention of entry is recommended as a far more cost effective and environmentally desirable measure than other measures that have to be taken once introduction of an alien invasive species has occurred. As such, offshore pest risk mitigation at the point of origin is recommended as the most viable approach to pest prevention and exclusion. In this approach, identifying potential invasive pests that are high risk so that appropriate preventive and preparedness strategies can be developed is of paramount importance.

Unfortunately, safeguarding systems are often breached and major alien invasive pests continue to enter and spread, even in countries such as Australia, Chile, Japan, New Zealand and the USA, which are purported to have state-of-the-art quarantine systems in operation. Once the establishment of an alien invasive species has been detected, the above mentioned international conventions urge countries to give priority to eradication over containment or management measures. Of course the best opportunity for eradicating introductions of alien invasive species is in the early stages of invasion, when populations are small and localized. However, appropriate response strategies and tools are in many cases not available to eradicate outbreaks of invasive pest introductions, thus forcing countries to only employ containment or mitigation measures. Moreover, some of the existing eradication methods are somewhat controversial or at risk of being phased

out as a result of laws like the Food Protection Quality Act (FQPA) in the USA.

The Sterile Insect Technique (SIT), being environment-friendly and acting inversely density dependent and therefore optimally suited to deal with invasive pest populations up to the last individuals, is the ideal tool to complement efforts to eliminate beach-heads of alien insect invasions. Examples of successful integrated application of SIT in such a context include the eradication of the New World Screwworm from the Libyan Arab Jamahiriya, and of medfly in California and Florida. Australia has invested considerable efforts in developing the SIT for the Old World Screwworm to be able to address potential outbreaks of this pest insect, which would cause major economic damage to its livestock industry in case it became established. California has stand-by contracts in place for the provision of sterile flies of various *Anastrepha* fruit fly species, and New Zealand, being fruit fly-free, has considered a similar approach to be able to procure sterile flies in the case of fruit fly outbreaks.

Unfortunately, however, SIT methodologies have not been developed for many of the major potential invasive pest species for which it could play an important role in eradicating incipient outbreaks. Among the USDA-APHIS Exotic Pest Arthropod List for the USA, which highlights 100 high-risk pests, ca. fifty percent of this “worst of the worst” list are from the order Lepidoptera. Many of these Lepidoptera are a threat not only to the USA but also to many other regions of the world. Nevertheless, research to develop SIT for these high risk, exotic lepidopteran pests is lacking in most cases (gypsy moth and false codling moth being an exception). Cooperative efforts are needed to develop appropriate response strategies that would include eradication technologies in advance of invasive lepidopteran pest introductions.

One is the cactus moth, *Cactoblastis cactorum* (Pyralidae). Known as the best example of successful biological control of weeds in Australia and elsewhere, it was detected in Florida in 1989 and has been rapidly expanding its range along the Atlantic coast and the Gulf of Mexico. *C. cactorum* is now considered a serious threat to the high diversity of *Opuntia* species throughout the world, both native and cultivated. Its presence in the

Caribbean and its rapidly expanding range in the southeastern USA represents an imminent threat to areas in the southwestern USA, Mexico, and Central/South America where *Opuntia* cacti are regarded as extremely important plants, especially in arid and semi-arid regions. These plants play a role in subsistence and commercial agriculture, in maintaining ecological balance in these unique ecosystems, and in soil conservation. As a result of worldwide increases in *Opuntia* cultivation and increased reliance on *Opuntia* as a source of food and income from its products, the invasion by *C. cactorum* has the potential to impact thousands of subsistence farmers in Central and South America, the Mediterranean, North Africa and other countries. Furthermore, impacts on biodiversity and ecosystems where *Opuntia* are dominant components of the vegetation, including the centre of *Opuntia* radiation, Mexico, also loom large. The critical nature of this threat, and the timing and scale of the likely responses needed, require immediate action. Although the emphasis of an intervention campaign may initially focus on Mexico, Cuba, other Caribbean islands and the USA, this does not mean that the threat is less important in other countries. Any effective contingency/control programme will need to be approached on a regional or even interregional scale.

To raise awareness of this major environmental threat and of the potential effectiveness of SIT to help address the control of alien species, the FAO and IAEA hosted a planning and co-ordination meeting, that included representatives of some environmental organizations. The meeting participants assessed the role that SIT/F₁ Sterility could play in addressing the cactus moth invasion as a model for the invasive pests affecting not only agriculture but the environment. We foresee an increased role in the use of SIT for suppression of alien invasive species that will help FAO and IAEA Member States deal with the threat of outbreaks of such pests.

This publication on *Cactoblastis* was funded by the IAEA and summarizes the current knowledge on history, biology, threats, surveillance and control of this insect. It is part of a wider publicity campaign to draw attention to the threat of *Cactoblastis* to the *Opuntiae* of North America with emphasis on Mexico and the USA. This threat should not only be the concern of countries for which the risk is imminent but should constitute a global concern, as the social, environmental and economic effects of *C. cactorum* would be devastating in any country where *Opuntia* cacti are a significant resource.

The IAEA is grateful to H.G. Zimmermann (ARC-Plant Protection Research Institute, Pretoria, South Africa), S. Bloem (Centre for Biological Control, Florida A&M University, Tallahassee, Florida, USA) and H. Klein (ARC-Plant Protection Research Institute, Pretoria, South Africa) for drafting this publication. This work is unique and represents a major contribution to the cactus moth problem worldwide.

The IAEA also wishes to thank those who contributed to the preparation and review of this publication as follows: K. Bloem and S. Hight (USDA-ARS Tallahassee, Florida, USA), J. Carpenter (USDA-ARS Tifton, Georgia, USA), J. Hosking (Dept. Agriculture, NSW, Australia), J. Perea and M. Perez-Sandi y Cuen (SAGARPA-SENASICA-DGGSV, Mexico), and A.L. Alfaro (Mexico), as well as A. Madero for photographs of native Mexican cacti, B. Brobbelaar and F. Heystek (ARC-Plant Protection Research Institute, Pretoria, South Africa), J. Hoffmann (University of Cape Town, South Africa) and H. Robertson (South African Museum) for photographs of cactoblastics and its predators, and P. Stiling (University of South Florida, Tampa, Florida, USA) for a photograph of the semaphore cactus.

The IAEA officer responsible for the publication was W. Enkerlin of the Joint FAO/IAEA Programme of Nuclear Techniques in Food and Agriculture.

EDITORIAL NOTE

The use of particular designations of countries or territories does not imply any judgement by the publisher, the IAEA, as to the legal status of such countries or territories, of their authorities and institutions or of the delimitation of their boundaries.

The mention of names of specific companies or products (whether or not indicated as registered) does not imply any intention to infringe proprietary rights, nor should it be construed as an endorsement or recommendation on the part of the IAEA.

CONTENTS

INTRODUCTION	1
CHAPTER 1: Taxonomic status of <i>Cactoblastis cactorum</i>	3
The cactus-feeding Pyralidae	3
The genus <i>Cactoblastis</i>	3
<i>Cactoblastis cactorum</i> (cactoblastis)	3
CHAPTER 2: The biology of <i>Cactoblastis cactorum</i>	7
Life cycle	7
Duration of life stages	8
Fecundity	9
Damage to host plants	9
Oviposition behaviour	10
Dispersal ability and spread	10
CHAPTER 3: Host plants of <i>Cactoblastis cactorum</i>	11
Natural hosts in South America	11
Extended host ranges outside its natural distribution	11
Basis for host preference of <i>Cactoblastis</i>	12
CHAPTER 4: The history of <i>Cactoblastis cactorum</i> as a biological control agent	17
Deliberate distribution of <i>Cactoblastis cactorum</i> (cactoblastis) as a biological control agent	17
The inadvertent dispersal of <i>C. cactorum</i> to additional Caribbean Islands and North America	21

CHAPTER 5: <i>Cactoblastis cactorum</i> as a threat	24
Potential dispersal routes to Texas, adjacent States and Mexico	24
Threat to the United States and Mexico	24
Threat to other countries	26
CHAPTER 6: The surveillance and control of <i>Cactoblastis cactorum</i>	29
Prevention (inspections, phytosanitary methods, early detection, public vigilance)	29
Surveillance	29
Control	30
Research	35
CONCLUSIONS	36
REFERENCES	37

INTRODUCTION

Cactoblastis cactorum (cactoblastis) has become famous for its contribution to the spectacular control of various invasive *Opuntia* species, notably in Australia where it has cleared 25 million hectares of land invaded by *Opuntia stricta*. Today, the “Cactoblastis Memorial Hall” (Fig.1) and the “Cactoblastis Cairn” in Queensland are amongst the memorabilia celebrating these remarkable events. This success was replicated, to a lesser extent, in South Africa and more so in the Leeward Island group of the Caribbean Islands. What was not foreseen at that time was the natural, accidental and possibly deliberate spread of the insect throughout the Caribbean Islands, which would lead to its unexpected arrival in Florida around 1989.

The first alarm signals announcing this event came from Habeck & Bennett (1990) and Dickle (1991), and from Pemberton (1995). But it was not until the publications by Johnson & Stiling in 1996 and 1998, and of Zimmermann & Perez-Sandi in 1999, that the authorities recognized the imminent disaster in the event of the cactus moth’s arrival in Mexico (Fig. 2). A recurrence of the Australian experience in Mexico was unthinkable. Furthermore, the extremely rapid dispersal of *C. cactorum* along the Florida coast over the past ten years also brought home the necessity of halting the continued dispersal of the moth (Hight *et al.* 2002).

The first initiative came from concerned entomologists from the USDA-APHIS National Biological Control Institute and the Cactus and Succulent



FIG. 1. Boonarga Memorial Hall in Australia, in honour of *cactoblastis*.

FIG. 2. Native Mexican cacti.

Society of America, who co-funded the first workshop on cactoblastis in Tampa, Florida, in September 2000. Several specialists on cactoblastis and on the Cactaceae were invited, and their contributions were published in volume 84 no. 4 of *Florida Entomologist*, 2001. The questions that were raised and which were only partially answered were:

- How far is cactoblastis likely to expand its range?
- How will it affect natural stands of *Opuntia* spp. and other species of plants and animals that depend on this resource?
- How will it affect the agricultural and horticultural uses of prickly pear?
- How can it be controlled?
- How will this situation affect the science and application of classical biological control, particularly of weeds?

The first international involvement came when the International Atomic Energy Agency (IAEA) recognized the potential of the inherited (or F₁) sterility technique (Carpenter *et al.* 2001a) in halting the further spread of cactoblastis. They supported research, an international consultants meeting and several activities aimed at evaluating the feasibility of the F₁ sterility technique for this purpose. The Mexican Government (through SAGARPA and CONABIO), in collaboration with, and with support from IAEA and FAO, initiated a rigorous campaign to alert all stakeholders and phyto-

sanitary officers in Mexico to the dangers of the cactus moth and to the importance of early detection and control. These activities are most commendable and encouraging and it is hoped that further international support, co-funded by the USDA-APHIS and SAGARPA, will be forthcoming to carry this project forward.

Urgent research is needed to address gaps in our knowledge on cactoblastis, including the refinement of the application of the F₁ sterility technique, more accurate predictions of its potential impact on cultivated and native *Opuntia* species in Mexico and the USA, and of its expected rate of dispersal in North America. To this end, all knowledge concerning cactoblastis that is available elsewhere, e.g. in Australia, Argentina and South Africa, has to be drawn upon.

Currently, the sex pheromone of cactoblastis is being identified and will be used as a monitoring tool. In addition mass rearing methods are being refined in the USA and in South Africa. Lastly, the radiation biology for the cactus moth has been determined (Carpenter *et al.* 2001b). An SIT/F₁ sterility programme is being considered to prevent further geographical expansion of this moth, but the use of F₁ sterility is also being assessed as a tool to determine the eventual host and geographical range and to study the rate of spread of this invading insect.

CHAPTER 1

Taxonomic status of *Cactoblastis cactorum*

The cactus-feeding Pyralidae

The sub-family Phycitinae of the family Pyralidae has about twenty genera with no fewer than 58 species, which are associated exclusively with the Cactaceae. *Cactoblastis* is one of these genera. Except for the genus *Ozamia*, which is found in both Americas, all genera are geographically isolated, either in the north or in the south. *Cactoblastis* is a genus found only in South America and its equivalents in the north are the genera *Melitara* and *Olycella*, with similar feeding patterns and biologies except that the colour of their larvae is always grey-blue to blue (Fig. 3) in contrast to *Cactoblastis*, all of whose species have orange coloured larvae with black transverse bands (Fig. 4) (Mann 1970; Zimmermann & Granata 2002).



FIG. 3. Larvae of *Olycella* sp.



FIG. 4. *Cactoblastis cactorum* larva.

The genus *Cactoblastis*

There are five described species in the genus *Cactoblastis*: *C. cactorum*, *C. bucyrus*, *C. mundelli*, *C. doddi* and *C. ronnai*. All of these are confined to the southern part of South America, from southern Peru to Bolivia, Paraguay, Uruguay, Argentina and southern Brazil. The taxonomic status of *C. ronnai* is doubtful. The species can be distinguished by their genitalia, wing patterns and wing colouration (Heinrich 1939). With the exception of *C. cactorum*, which has a wide host range within the Opuntioidea, all the species have very restricted host ranges and limited distributions. Hosts include species in the genera *Cylindropuntia*, (for *C. mundelli*), *Cereus* (for *C. bucyrus*) and *Eriocereus* (for *C. cactorum* type F) (McFadyen 1985), a few species in *Opuntia* (for *C. doddi*) and many species of *Opuntia* (for *C. cactorum*).

Cactoblastis cactorum (cactoblastis)

Sub-specific differences

Recent surveys for cactus-feeding insects revealed the possible existence of five host-adapted biotypes, sub-species or even separate, independent species within *C. cactorum* (McFadyen 1985). These differences are based on host ranges and colour patterns of the mature larvae. DNA sequencing and detailed host range studies of all the taxa will be needed to determine the true status and relationship of all the described and proposed entities in the genus *Cactoblastis*.

Origin of the exported

Cactoblastis cactorum stock

Cactoblastis cactorum occurs naturally in the northern parts of Argentina, in Uruguay and Paraguay and in the southern parts of Brazil (Fig. 5) (Mann 1969). The cactoblastis stock introduced into Australia and South Africa, and from there to the Caribbean Islands (see Chapter 4), was collected from *Opuntia delaetiana* (now known as *O. paraguayensis*) (R. Kiesling pers. comm.) and from an *Opuntia* species of the “*monacantha*” group (Fig. 6) (McFadyen 1985). This specific entity is



FIG. 5. The native distribution of *C. cactorum* in South America.



FIG. 6. *Cactoblastis* on *Opuntia monacantha*, near Periapolis, Uruguay. All *Cactoblastis* populations outside Argentina originated from this region.

restricted to the genus *Opuntia* but has a wide host range within this genus in its native geographical range. It also readily accepts many *Opuntia* species from North America and was responsible for the spectacular control of several invading *Opuntia* species in different countries (Moran & Zimmermann 1984; Julien & Griffiths 1998). All populations outside Argentina originated from this one introduction to Australia in 1925, which comprised about 3,000 eggs. Previous and subsequent introductions of *Cactoblastis* spp. from

Argentina to Australia and South Africa failed to establish (McFadyen 1985).

The moth

The adult moths (Fig. 7) are inconspicuous, their forewings are brownish-grey with two wavy transverse bands. The wings are somewhat whiter towards the costal margin. The hind wings are pale-grey with a dark band along the margin. In contrast, moths of *Melitara* show considerably more white colouration in the forewing (Heinrich 1939). Moths have a wingspan of 27–40 mm when reared from optimal hosts but can be considerably smaller when reared from sub-optimal hosts or from small host plants constituting a limited food supply.

Females are generally larger than males, their wings are slightly darker and their palpi are more prominent than those of the males (Fig. 8). Microscope preparation of the genitalia can provide positive identification (Heinrich 1939).

The egg

The individual egg is cylindrical and flattened, about 0.9 mm wide and 0.4 mm long. It is initially cream coloured, and darkens to brown and later almost black, shortly before the larva emerges. The female stacks its eggs coin-like to form a chain or small stick (Fig. 9), resembling a cactus spine. The first egg in the egg stick is glued to a spine or directly on the cactus pad (cladode) with an amber-coloured substance presumably derived from the accessory glands. The positioning of eggs on top of one another is guided by setae that surround the ovipositor. The egg stick contains on average 70 to 90 eggs but seldom more than 105. An egg stick of 70 eggs has a length of about 2.4 cm. Short egg sticks



FIG. 7. Female (left) and male (right) adults of *Cactoblastis cactorum*.



FIG. 8. Wing pattern of *Cactoblastis cactorum* male (above) and female (below).



FIG. 9. An egg stick of *C. cactorum* being deposited.

are straight but the normal egg stick is slightly curved. It is pliable at first but becomes brittle when dry. Several environmental conditions and host plant characteristics also affect oviposition behaviour (Myers *et al.* 1981; Robertson 1987; Hoffmann & Zimmermann 1989; Stange *et al.* 1995).

The habit of ovipositing eggs in the form of a stick is also observed in the cactus-feeding genera *Melitara* and *Olycella*, both from North America. Their egg sticks can be distinguished from those of *Cacto-*



FIG. 10. First instar *Cactoblastis* larvae.



FIG. 11. Final instar *Cactoblastis* larvae.

blastis by their shorter length. The egg stick of *Melitara* contains between 30 and 40 eggs while those of *Olycella* are even shorter, with only 10 to 12 eggs or fewer.

The larva

First instar larvae (neonates) of *C. cactorum* (Fig. 10) are 2.5 mm long and are greenish-grey in colour. Later instars have a rich salmon, orange to red colour with blackish spots forming transverse bands (Fig. 11). These transverse bands in the final (sixth) instar are nearly always divided into four separate blocks or spots and are never fused in the mid-line, thus distinguishing it from other, related taxa in the genus (McFadyen 1985). Full-grown larvae are about 33 mm long before they pupate, but they can be considerably smaller when reared from small or sub-optimal hosts.

The pupa

Mature larvae spin a silky white cocoon in which they pupate, usually under debris, e.g. dry cladodes,



FIG. 12. Pupae: with soil particles adhering to cocoon, with clean cocoon, and without cocoon.

leaf litter, near or on the host plant. The cocoons are often covered with soil or plant particles, which makes them difficult to detect (Fig. 12).

To distinguish between the sexes, the pupae have to be studied from the venter (underside) (Fig. 13). Locate the first five visible spiracles on the side of

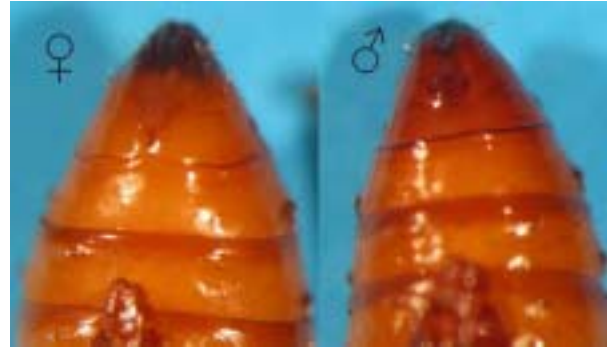


FIG. 13. Abdominal tip of female (left) and male pupa (right).

the abdomen. These are followed by a smaller non-functional spiracle on the next segment. In the female the segment with the non-functional spiracle has a slit-like genital scar. In the male the genital scar is located in the next segment between two raised bullae. The genital scars should not be confused with the anal scar, which is near the tip of the abdomen.

CHAPTER 2

The biology of *Cactoblastis cactorum*

Life cycle

The life cycle of *Cactoblastis cactorum* (cactoblastis) (Fig. 14) was described in detail by Dodd (1940), Pettey (1948) and Mann (1969). The moths emerge from their pupae in the early evening. There are usually slightly more males than females in a normal population, and the difference is more pronounced if the amount or quality of available food is unsuitable for the larvae. They mate early in the morning of the first or second day after emergence, and during the following night the females start laying eggs. The adult moths live about 9 days and do not feed. They rest during the day on the lower parts of plants and are reluctant to fly, even when disturbed. At night, the moths become active and the females are occasionally attracted to light.

Most eggs are deposited during the early evening. Female moths do not attach any eggs to spines that are too long for their ovipositors to reach. They lay their eggs mainly on the succulent segments on the lower parts of suitable host plants, but when suitable hosts are not available they will occasionally deposit egg sticks on unsuitable host plants or even objects

inside houses near prickly pear infestations. No eggs are deposited in the presence of artificial light.

The eggs usually hatch during the day, but will even hatch at night if it is warm enough. Larvae from the same egg stick are gregarious after hatching, sitting in a circle at the base of the spine to which their egg stick was attached while chewing a communal entrance hole into the cactus segment (Fig. 10, Chapter 1). This communal behaviour enables the tiny larvae to penetrate the tough epidermis of the cactus, and possibly overcome the mucilaginous sap exuded by the cladode. Larvae are often repelled by the sticky exudates and are forced to make another entrance elsewhere.

The larvae feed as a colony (Fig. 15) while tunneling through a cactus pad (cladode), consuming the interior except for the fibrous vascular tissues (Fig. 16). Faeces are discharged through the original entrance hole, and slimy green ooze is often noticeable on affected segments as well as on the ground. The larvae occasionally cluster on the outside of a segment to bask in the sun on cold days, or to shelter in the shade on hot days. Having consumed the contents of one cladode, the larvae either tunnel into an adjacent cladode, or the entire colony leaves the cladode, crawling over the plant surface before entering another pad.

When mature, the larvae vacate the cladode individually, drop to the ground and spin cocoons of white silk under or in rotting cactus pads on the ground, in crevices in the cactus stems, in the leaf litter or in

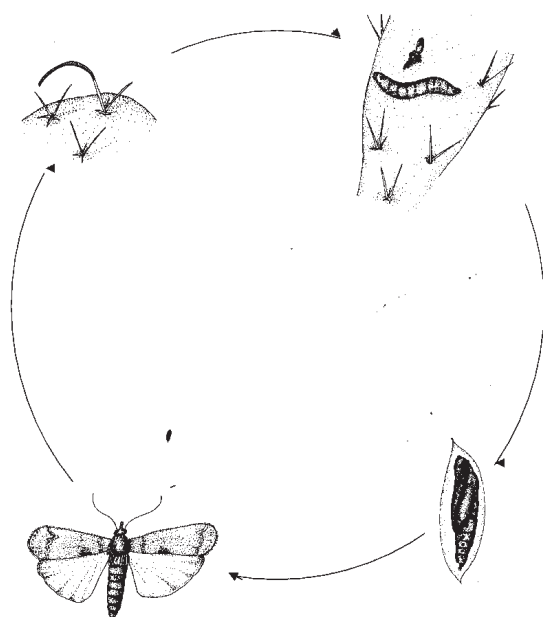


FIG. 14. Life cycle of *Cactoblastis cactorum*.



FIG. 15. Larvae feeding gregariously internally in cladodes.



FIG. 16. Cladode hollowed-out by larvae.

loose soil. They pupate inside these cocoons, and eventually emerge as adult moths.

Duration of life stages

Dodd (1940) described the duration of life stages in Australia, Pettey (1948) in South Africa, and Mann (1969) worldwide. In temperate regions, such as the moth's natural distribution in Argentina as well as most parts of South Africa and Australia where the moths have become established, cactoblastis has two distinct generations per year. In the warmer regions of South Africa, (e.g. Kruger National Park), Australia and Florida, a full or partial third generation occurs in autumn (J.E. Carpenter & S.D. Hight, unpublished data), and it is expected that in even warmer regions (e.g. Mexico) the generations might overlap and have no clear peaks. In the coolest parts of New South Wales, the life cycle occasionally occupies a full year.

In Australia and South Africa, the summer generation (Fig. 17) takes 4–5 months, with adults flying and laying eggs during September–November,

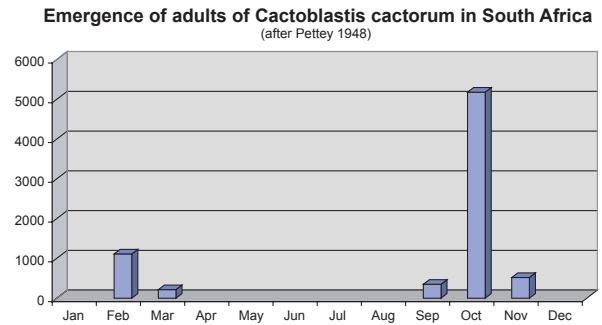


FIG. 17. Graph of Cactoblastis phenology in South Africa.

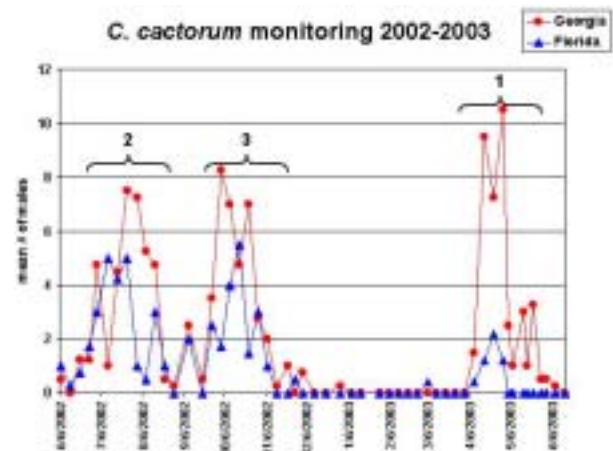


FIG. 18. Graph of Cactoblastis phenology in Florida and Georgia.

larvae hatching after about 40 days, developing for 50–60 days before pupating, and moths emerging after about 28 days during January–March. The winter generation takes about 8 months, with moths laying eggs during January–March, larvae hatching after about 50 days, developing for 130–180 days before pupating, and moths emerging after about 40–70 days during September–November. The average length of the cactoblastis life cycle in South Africa is 113–132 days in the summer generation, and 234–256 days in the winter generation. In Australia, it is 100–120 days in summer and 235–265 days in winter.

Two populations of cactoblastis that were studied at coastal locations in south Georgia and north Florida, USA, during 2002–2003, completed three non-overlapping generations per year (Fig. 18), with the spring adult flight lasting for about two months from early April to the end of May (#1, Fig. 18), the summer flight occurring between early July and

mid-August (#2, Fig. 18) and the fall flight occurring from mid-September to mid-November. (#3, Fig. 18) (J.E. Carpenter & S.D. Hight, unpublished data). Observations of laboratory colonies initiated from field collections in Georgia and Florida show the life cycle to be approximately 90 days from egg to adult (J.E. Carpenter, unpublished data).

Fecundity

The average number of eggs laid per female is around 88–97 (South Africa) or 99–125 (Australia) for the September–November moths (winter generation), and around 161–188 (South Africa) or 75–120 (Australia) for the January–March moths (summer generation) (Robertson 1989). Each egg stick contains on average 70 to 90 and sometimes up to 120 eggs, and a female can produce three or four egg sticks during her lifetime, usually about two egg sticks per night (Petty 1948; Mann 1969). The number of eggs produced per female varies considerably between seasons and geographical locality (Petty 1948).

Damage to host plants

The feeding larvae cause physical damage by hollowing out and destroying the young cladodes that have not become woody. The larval damage enables microbial pathogens to enter the plant, leading to secondary infections, which can cause the death of the entire plant (Starmer *et al.* 1987).

Small cactus species or small individuals of larger species may die in cases of severe attacks (Fig. 19), but the cactus moth seldom destroys the older, woody parts of the larger, tree-like cactus species such as *Opuntia ficus-indica* (Fig. 20). In Australia, where the major pest species were low-growing, shrub-like cacti such as *Opuntia stricta*, the original stands were killed to ground level or, in the case of resistant types, all growth except for the tough basal stems was destroyed within a short time, causing a sharp decline in the numbers of cactoblastis. Although the stumps did survive, cactoblastis also soon recovered and caused the virtual complete control of the major pest plants (Dodd 1940).

In South Africa, where the cactus tree, *O. ficus-indica*, is the most important pest species, the surviving woody stems or trunks invariably re-grow after the young segments have been destroyed (Fig. 21). Therefore, the cactus moth plays only a



FIG. 19. *Cactoblastis* is able to kill small cactus plants.



FIG. 20. The woody trunks of larger plants are seldom killed.



FIG. 21. A large specimen of *Opuntia ficus-indica* in South Africa regrowing after attack by *Cactoblastis*.

lesser role in the biological control of invasive cacti in South Africa, and its value lies in finding and killing small, isolated cactus plants. Even the smaller *O. stricta* plants are rarely killed by *cactoblastis* in South Africa, although they constantly lose their terminal segments (Petty 1948; Hoffmann *et al.* 1998a).

Oviposition behaviour

The *cactoblastis* moth has the ability to locate small, isolated host plants. When the host plant density is high, moths disperse very little, but as their food plants become sparse, they fly further to lay eggs.

In Australia, *cactoblastis* tends to lay most of its eggs near the emergence site, preferably on the young, succulent, terminal cladodes with well developed spines. Often the number of eggs

deposited on one plant exceeds the number of larvae that can feed on the plant, even though there is no shortage of suitable host plants in the area. This causes many larvae to starve, and confirms that moths do not disperse readily while the host plant population is dense (Dodd 1940).

Dispersal ability and spread

The fact that the females have undeveloped mouthparts and therefore cannot take in any food, probably explains why they deposit their eggs over a short period of time and do not fly far. The moths fly close to the ground, with a jerky, erratic flight pattern, which is not typical of long flyers. The furthest that a female has been known to disperse is 24 km (Dodd 1940).

In Australia, the population dispersed only 16–24 km within 2½ years (Dodd 1940), and in South Africa it dispersed 3–6 km in 2½ years (Petty 1948). In South Africa, *cactoblastis* failed during 15 years of careful monitoring to disperse to large host populations as little as 40–60 km away. It did not reach a large (19,000 ha) infestation of *O. stricta* in Kruger National Park in the 70 years since release, even though suitable host plants occurred in scattered infestations from the Eastern Cape, where it was released, almost to the border of the Park. Some large commercial plantations in South Africa are still free of *cactoblastis*.

Cactoblastis in its native range has failed to reach large cultivations in Pernambuco, Brazil and in the Pre-Andean valleys in Argentina, despite the presence of available hosts and of suitable climates *en route*. Neither has it crossed the Andean mountain chain to Chile (Zimmermann *et al.* 2000a) (Fig. 5, Chapter 1).

Recent re-examination of *cactoblastis* dispersal rates in Florida, USA, suggest that the moth is dispersing over a distance of about 50–75 km per year (see Stiling 2002 based on data reported in Johnson & Stiling 1998 and Hight *et al.* 2002). Clearly, additional work on *cactoblastis* dispersal in Florida is warranted because of the need to predict when the moth will make its appearance in the *opuntia*-rich regions of the southwestern USA and Mexico.

CHAPTER 3

Host plants of *Cactoblastis cactorum*

Although some information exists on the natural and adopted hosts of *Cactoblastis cactorum* (cactoblastis) within the cactus genus *Platyopuntia*, this is not sufficient to allow reliable predictions to be made on its potential host range in North America and on the factors that determine its host selection and acceptance. This chapter intends, firstly, to summarize the present knowledge about the known host plants of cactoblastis and, secondly, to predict its potential host range outside its natural distribution. In order to improve the assumptions made regarding host selection and acceptance, further research is needed.

The taxonomy of the *Platyopuntia* remains highly confusing, and the classifications of Benson (1982) and Anderson (2001) have been used here. Certain taxonomists regard *Platyopuntia* and *Cylindropuntia* as sub-genera of *Opuntia*, while others regard them as independent genera. Here, the classification of *Consolea* as a sub-genus of *Opuntia* is followed (Benson 1982). Species names for Argentinian species have been provided by R. Kiesling (pers. comm.).

Natural hosts in South America

Of the five described species within the genus *Cactoblastis*, *C. cactorum* has by far the widest host range within the *Platyopuntia* and this explains in part why this particular species has been so successful as a biological control agent of *Opuntia* invaders (Moran & Zimmermann 1984, 1985). With only a few exceptions, it has been collected from all *Opuntia* (*Platyopuntia*) spp. within its wider geographical range in Argentina, Uruguay, Paraguay and southern Brazil (Mann 1969; Zimmermann *et al.* 1979). It has not been collected from the large tree cactus, *O. quimilo* (Fig. 22) (except on small plants of this species) nor on *O. longispina*. Other widely distributed *Opuntia* species in Argentina and Bolivia, e.g. *O. sulphurea* and *O. pampeana*, are not attacked because they grow in the dry northwestern Andes, outside the natural distribution of *C. cactorum*. These cactus species are the primary hosts of the sibling species, *C. doddi*. *Cactoblastis cactorum* is therefore clearly oligophagous (accepting a number of host species).

Extended host ranges outside its natural distribution

The introduction of cactoblastis into many countries (see Chapter 4) has provided opportunities to study the extended host ranges of this insect within the full geographical range of the genus *Platyopuntia*. In Australia and South Africa, cactoblastis successfully controlled or damaged several alien *Opuntia* species of North American origin, e.g. *O. stricta*, *O. streptacantha*, *O. ficus-indica*, *O. humifusa* (Fig. 23) etc., which are all “new-association” hosts (hosts to which the insect has not been exposed in its native range) (Hosking *et al.* 1988; Moran &



FIG. 22. *Opuntia quimilo*, one of the few species of *Platyopuntia* that are not attacked by *Cactoblastis* in its native range.



FIG. 23. *Opuntia humifusa*, a “new-association” host of *C. cactorum*.

Zimmermann 1984). For a full account of its natural and new-association hosts, see Table I.

The introduction of cactoblastis into the Caribbean Islands and its recent arrival in Florida (see Chapter 4) also constitutes new-association feeding, but differs from Australia and South Africa in so far as the attack is on native *Opuntia* species, which are also subject to feeding by locally co-evolved species. Some native *Opuntia* became problematic because of overgrazing and other human-induced activities, which was the main reason why cactoblastis was introduced into the Caribbean in the first place. The extent to which cactoblastis attacks these native species in the Caribbean Islands may reveal much information on its potential impact in Mexico and the USA, but this has not been adequately studied, except for a brief report by Simmonds & Bennett (1966) from the Leeward Islands.

In Florida, USA, there are six native *Opuntia* spp. (Benson 1982). Three species are widespread: *Opuntia stricta* (varieties *stricta* and *dillenii*), *O. humifusa* (var. *humifusa* — the Eastern prickly pear) and *O. pusilla*. Three additional species are considered rare in the Florida Keys: *O. corallicola* (sometimes placed in the genus *Consolea* and now considered a synonym of *O. spinosissima* — the semaphore cactus), *O. cubensis* and *O. triacantha*. In addition, four naturalized species are also common in Florida: *O. ficus-indica*, *O. monacantha* (= *O. vulgaris*), *O. leucotricha* and *O. cochenillifera* (formerly in *Nopalea*). It has now been confirmed that all opuntia present in Florida are attacked by cactoblastis (S.D. Hight pers. comm.), although Johnson & Stiling (1998, 1996) did not observe any damage on *O. pusilla*.

Basis for host preference of cactoblastis

In South Africa, Hawaii and Australia, cactoblastis causes considerable damage to the smaller *Opuntia* species. The damage is much less in the tree-cacti, *O. ficus-indica*, *O. streptacantha*, *O. megacantha* and *O. rubusta* (spineless cultivars), and only after repeated attacks over several seasons can large plants be killed (Annecke & Moran 1978; Annecke et al. 1976) (Figs 19, 20 and 21, Chapter 2).

Large, unprotected cactus orchards have been destroyed by cactoblastis, but mostly only in combination with attacks by cochineal (*Dactylopius opuntiae*) (Mann 1969; Fullaway 1954; Annecke & Moran 1978). The thick, woody stems of all tree-like cactus are more resistant to larval attack and larvae will only feed on a woody stem if no other succulent cladodes are available. Several authors have commented on the high mortalities of first instar larvae, caused by excessive gum (mucilage) exudate when cladodes are penetrated, and this appears to be particularly common in large *Opuntia* species (Fig. 24) (Moran 1980; Robertson & Hoffmann 1998; Zimmermann & Granata 2002).

Amongst the shrub-type *Opuntia* host species, including *O. stricta*, *O. monacantha*, *O. engelmannii*, *O. triacantha*, *O. tuna*, *O. humifusa* and *O. cubensis* (see Table I), most are extensively damaged by cactoblastis, and the history of the biological control of some of these species is well known (Bennett et al. 1982; Julien & Griffiths 1999). However, in this category of species we also find some that are less susceptible to cactoblastis in the field, including *O. engelmannii* (*O. lindheimeri*) and *O. spinulifera* in South Africa, as well as *O. microdasys* and *O. polyacantha* (or near *polyacantha*).



FIG. 24. Mucilage exudate killing a first instar Cactoblastis larva.

When female cactoblastis moths in South Africa were provided with a choice of three species as oviposition sites, namely *O. stricta*, *O. microdasys* and an unidentified *Opuntia* sp., egg sticks were only deposited on *O. stricta* (Fig. 25). This agrees with the fact that cactoblastis has never been observed feeding on naturalized *O. microdasys* populations in South Africa. However, when egg sticks were placed on leaf pads of the non-preferred species, the larvae developed normally and caused damage to the plants (Fig. 26). Johnson & Stiling (1996) conducted host choice experiments using four native *Opuntia* species of Florida to determine if any one species was preferred by cactoblastis. They found that ovipositing females showed no host preference while larvae preferred *O. corallicola* over the other *Opuntia* species tested. The ovipositional behaviour of the cactoblastis females appears to form the basis for the apparent host specificity in these cases.

Under caged conditions, *C. cactorum* will feed and develop on other, normally unsuitable cactus hosts, and mature larvae can even be forced to feed and mature to some extent on peaches, melons and tomatoes, although this has never been observed under natural conditions (Dodd 1940).

Cactoblastis larvae collected and reared from *O. taylori* in Santo Domingo were consistently small and the adults that emerged were difficult to reconcile with this species. This may be because of the sub-optimally small host plant, which offers considerably less resources for the larvae to feed on. However, when eggs obtained from this population were transferred to *O. ficus-indica*, the larvae and adults reared were of normal size again.

Cactoblastis develops normally on many other small *Opuntia* species, e.g. *O. aurantiaca* (Fig. 27), *O. discolor*, *O. salmiana*, and others. The size of the host plant does not seem to be a limiting factor for host acceptance.

In South Africa, larval damage caused by cactoblastis is occasionally observed on *Opuntia* (*Cylindropuntia*) *imbricata* (Fig. 28), *O.* (*Cylindropuntia*) *exaltata* and *O.* (*Cylindropuntia*) *fulgida*, commonly known in Mexico as the chollas, but only when these are growing in association with *Platyopuntia* species infested with cactoblastis. This appears to be a spillover effect only, as the damage to chollas is



FIG. 25. Cactoblastis eggs were laid on *Opuntia stricta* (centre), but not on *O. microdasys* (left) or unidentified *Opuntia* sp. (right).



FIG. 26. Larvae were able to survive on the same unidentified *Opuntia* sp.



FIG. 27. Cactoblastis on *O. aurantiaca*.

minimal; apparently, cactoblastis populations cannot sustain themselves on these hosts under natural conditions. However, this needs further investigation to fully ascertain the potential impact on cladodes in North America.



FIG. 28. *Cactoblastis* damage on *Opuntia* (*Cylindropuntia*) *imbricata*.

The reason why *O. quimilo* in Argentina is not accepted as a host is unknown and needs investigation. In addition, the apparent resistance of *O. cochenillifera* to attack by cactoblastis in the Caribbean Islands, even though the species is readily attacked in Florida (S.D. Hight, pers. comm.), needs further attention.

Despite the observed attack by cactoblastis of all the native *Opuntia* species in Florida, not all *Opuntia* species in Mexico and the USA will be suitable hosts to cactoblastis. Further research and surveys on the host preferences and the mechanisms of host selection will enable a more careful prediction of the real threat to the native *Opuntia* flora.

Table I. The impact of *Cactoblastis cactorum* on *Opuntia* species outside its natural distribution in South America

<i>Opuntia</i> host or weed, and country of observation	Country of origin of cactus species	Impact of <i>Cactoblastis cactorum</i> on species	Reference
Large tree-like species			
<i>O. ficus-indica</i> (all varieties) Australia, South Africa, Hawaii (= <i>O. megacantha</i>)	Mexico	Substantial impact and control, and highly effective on small plants. General pest on cultivated orchards.	Annecke, D.P. & V.C. Moran 1978, Fullaway, D.T. 1954, Hosking et al. 1988, Julien, M.H. & M.W. Griffiths 1998, Pettey, F.W. 1948
<i>O. (Nopalea) cochenillifera</i> South Africa, USA	Mexico	Attacked in Florida.	S.D. Hight, pers. comm.
<i>O. tomentosa</i> Australia, South Africa	Mexico	Insignificant impact.	Julien, M.H. & M.W. Griffiths 1998, Mann, J. 1970
<i>O. streptacantha</i> Australia	Mexico	Substantial impact and highly effective in the control of small plants.	Dodd, A.P. 1940, Mann, J. 1970
<i>O. robusta</i> (all Burbank varieties) South Africa	Mexico USA	Significant impact and highly damaging to small plants. A pest on cultivated spineless varieties.	Annecke, D.P. & V.C. Moran 1978
Shrub-like species			
<i>O. elatior</i> Australia	Central America, Caribbean, Venezuela	Present but impact unknown.	Hosking et al. 1988

Table I. The impact of *Cactoblastis cactorum* on *Opuntia* species outside its natural distribution in South America (cont.)

<i>Opuntia</i> host or weed, and country of observation	Country of origin of cactus species	Impact of <i>Cactoblastis cactorum</i> on species	Reference
<i>O. cardiosperma</i> (= <i>O. paraguayensis</i>) Australia	Argentina, Uruguay, Paraguay	Present but impact unknown.	Hosking et al. 1988
<i>O. dillenii</i> Caribbean Islands	Caribbean Islands	Significant impact on species in Cuba and elsewhere.	Cock, M.J.W. 1985, Hernandez, L.R. & T.C. Emmel 1993, Julien, M.H. & M.W. Griffiths 1998, Simmonds, F.J. & F.D. Bennett 1966
<i>O. leucotricha</i> USA	Mexico	Attacked in Florida.	S.D. Hight, pers. comm.
* <i>O. monacantha</i> Australia, South Africa, Florida	South America	Moderate to significant impact.	Barbera et al. 1995, Julien, M.H. & M.W. Griffiths 1998, Moran, V.C. & H.G. Zimmermann 1991, S.D. Hight, pers. comm.
<i>O. triacantha</i> Caribbean Islands, Mauritius, Florida Keys	Caribbean Islands, Florida Keys	Significant impact.	Bennett, F.D. & D.H. Habeck 1995, Garcia-Tuduri, et al. 1971, Greathead, D.J. 1971, Julien, M.H. & M.W. Griffiths 1998
<i>O. tuna</i> Mauritius	Caribbean Islands	Significant impact.	Greathead, D.J. 1971, Julien, M.H. & M.W. Griffiths 1998
<i>O. stricta</i> var. <i>stricta</i> and var. <i>dillenii</i> Australia, South Africa, south-east USA, Caribbean Islands	South-east USA, south-east Mexico, Caribbean Islands	Spectacular impact in Australia and less so in South Africa. Significant impact in Florida and Caribbean Islands.	Dodd, A.P. 1940, Hoffmann et al. 1999, Mann, J. 1970, Simmonds, F.J. & F.D. Bennett 1966
<i>O. lindheimeri</i> (?) (= <i>O. engelmannii</i> ?) Antigua, Nevis	Caribbean Islands	Unknown.	Simmonds, F.J. & F.D. Bennett 1966
<i>O. antillana</i> Caribbean Islands	Caribbean Islands	Host of <i>Cactoblastis</i> . Impact unknown.	Garcia-Tuduri, J et al. 1971
<i>O. moniliformis</i> Desecho island near Puerto Rico	Desecho, Haiti and Dominican Republic	Host of <i>Cactoblastis</i> . Impact unknown.	Garcia-Tuduri et al. 1971
<i>O. rubescens</i> Puerto Rico	Puerto Rico	Host of <i>Cactoblastis</i> . Impact unknown.	Garcia-Tuduri et al. 1971
<i>O. engelmannii</i> (= <i>O. lindheimeri</i> ?) South Africa, West Indies	USA	Moderate impact.	Brutsch, M.O. & H.G. Zimmermann 1995, 1971, Bennett, F.D. Moran, V.C. & H.G. Zimmermann. 1984
<i>O. tardospina</i> (= <i>O. engelmannii</i> ?) South Africa	USA	Limited impact.	Moran, V.C. & H.G. Zimmermann 1991, Pettey, F.W. 1948
<i>O. humifusa</i> Florida, South Africa	Florida	Significant impact.	Johnson, D.M. & P.D. Stiling 1996, Johnson, D.M. & P.D. Stiling 1998, S.D. Hight, pers. comm.
<i>O. pusilla</i> Florida	Florida	Limited(?) impact.	S.D. Hight pers. comm.

Table I. The impact of *Cactoblastis cactorum* on *Opuntia* species outside its natural distribution in South America (cont.)

<i>Opuntia</i> host or weed, and country of observation	Country of origin of cactus species	Impact of <i>Cactoblastis cactorum</i> on species	Reference
<i>O. corallicola</i> Florida Keys	Florida Keys	Significant impact and endangering the species.	Johnson, D.M. & P.D. Stiling 1996, Johnson, D.M. & P.D. Stiling 1998, Stiling, P. & D. Simberloff 1999
<i>O. cubensis</i> Florida Keys	Florida Keys	Significant impact.	Johnson, D.M. & P.D. Stiling 1996, Johnson, D.M. & P.D. Stiling 1998
<i>Opuntia</i> sp. Asuncion	Unknown	Reasonable impact. Limited data available.	Julien, M.H. & M.W. Griffiths 1998
<i>Opuntia</i> sp. St. Helena	Unknown	Substantial impact. Limited data available.	Julien, M.H. & M.W. Griffiths 1998
Small low-growing species			
* <i>O. aurantiaca</i> South Africa, Australia	Argentina Uruguay	Moderate to significant impact, more so on large plants.	Mann, J. 1970, Moran, V.C. & D.P. Annecke 1979, Moran, V.C. & H.G. Zimmermann 1991
* <i>O. salmiana</i> South Africa	Argentina	Moderate impact, more so on larger plants.	H.G. Zimmermann, pers. comm.
<i>O. repens</i> Puerto Rico	Puerto Rico	Significant impact.	Garcia-Tuduri et al. 1971
<i>O. curassavica</i> (?) Antigua, Nevis	Antigua, Nevis	Significant impact. Confusing data.	Bennett, F.D. & D.H. Habeck 1995, Simmonds, F.J. & F.D. Bennett 1966
<i>O. taylori</i> Haiti, Santo Domingo	Haiti, Santo Domingo	Wide spread but impact unknown.	M. Perez Sandi, pers. comm.

* *Opuntia* species which are natural hosts of *C. cactorum* in South America.

CHAPTER 4

The history of *Cactoblastis cactorum* as a biological control agent

Deliberate distribution of *Cactoblastis cactorum* (cactoblastis) as a biological control agent

Cactoblastis cactorum as a biocontrol agent (Fig. 29) (Julien & Griffiths 1998)

- 1926: Introduced from Argentina to Australia
- 1933: From Australia to South Africa
- 1933: From Australia to New Caledonia
- 1950: From Australia to Hawaii
- 1950: From South Africa to Mauritius
- 1957: From South Africa to Nevis
- 1960: From Nevis to Antigua
- 1960: From Nevis to Montserrat
- 1966: From Antigua to Kenya, establishment unconfirmed
- 1970: From Nevis & Antigua to Cayman Islands
- 1971: From Nevis & Antigua to St. Helena
- 1973: From St. Helena to Ascension Island
- 1994: From Australia to Pakistan, establishment unconfirmed
- ?: South Africa to Israel, not established

Australia

Before the biological control campaign was initiated in Australia (see Dodd 1940; McFadyen 1985), about 25 million ha of land in Queensland and New South Wales were infested with prickly pear (*Opuntia stricta*). Half of this infestation was so dense that the land was useless from a productive viewpoint (Fig. 30). A Commonwealth Prickly Pear Board was appointed in 1920, which sent entomologists to America to study the natural enemies of

prickly pears and to create facilities to breed them in Australia.

The third introduction of cactoblastis, in 1925, was the only one that became established, after two previous attempts had failed. At Concordia in the province of Entre Rios, Argentina, fully-grown larvae were collected from *O. delaetiana* and another *O. monacantha*-related species, which are now lumped into *Opuntia paraguayensis*. Their



FIG. 29. Official distribution of *Cactoblastis* for biological control.



FIG. 30. Dense infestation of prickly pear (*Opuntia stricta*) in Queensland before the biological control.

offspring, 30–50 egg sticks with 3,000 eggs, were dispatched by ship from Buenos Aires in March 1925. In Cape Town, *en route* to Australia, a small back-up colony of larvae was removed and retained in South Africa, but these were never released.

About 2,750 larvae arrived in Australia in May 1925, and were reared in cages for two generations (one year), by which time the number had multiplied to 2,540,000. The first releases were made in February–March 1926. The moths were mass reared in cages for 18 months only, producing about 10 million eggs, and thereafter egg sticks for mass distribution could be collected in the field. Until 1930, a total of 30 million–40 million egg sticks (2,750 million eggs) were released throughout the prickly pear territory. About 25 million larvae were necessary to kill off 1 ha heavily infested with *Opuntia stricta*.

By 1930, all the original prickly pear stands had been killed to ground level or, in the case of resistant types, all growth except the tough trunks had been destroyed (Figs 31 & 32). The cactoblastis population subsequently declined drastically. During 1932–1933, the cactus plants produced abundant re-growth, followed by a rapid recovery of the cactoblastis population during 1933–1935. By 1935–1940, cactoblastis had virtually brought the major pest pears under complete control, and there has never been any need for redistribution of the insect.

Dodd (1940) reports that “...The most optimistic scientific opinion could not have foreseen the extent and completeness of the destruction. The spectacle of mile after mile of heavy prickly pear growth collapsing *en masse* and disappearing in the short

space of a few years did not appear to fall within the bounds of possibility.”

Fifty years later, in 1980, the situation was still unchanged, with cactoblastis exerting control over prickly pear except for the coastal areas and some areas in the southwest of Queensland (White 1980).

Several factors affected the success of cactoblastis in Australia. Cactus plants growing under conditions of water or nutrient stress, particularly *Opuntia inermis* (= *O. stricta* var. *dillenii*), are reported to have thick mucilaginous segments, which suppresses the development of the cactoblastis population in certain areas, e.g. the coastal areas of Queensland. Larvae hatching on woody cactus segments also have difficulty penetrating the plant tissue. High temperatures are regarded as being of major importance in reducing the fecundity of the summer generation of cactoblastis (White 1980; Hosking *et al.* 1994).

South Africa

The exact extent of the pest prickly pear (*Opuntia ficus-indica*) in South Africa before the biological control campaign is unknown, but by 1942, some 900,000 ha were affected by the weed (Figs 33 & 34) (Petty 1948) in the (then) Cape Province alone.

Petty (1948) relates how, in the early 1930s, a consignment of 112,600 cactoblastis egg sticks was brought to South Africa from Australia. Following additional specificity testing and mass rearing at three breeding stations in the Karoo and the (then) eastern Cape Province, the first small release was made in November 1933 on *Opuntia ficus-indica*. Mass rearing continued for seven years, and once



FIG. 31. Prickly pear in Queensland collapsing due to feeding by Cactoblastis larvae.



FIG. 32. The same area as in Fig. 31, cleared of prickly pear.

the insects had become established, egg sticks were also collected in the field. Until April 1941, a total of almost 580 million cactoblastis egg sticks, either lab reared or collected from the field, were distributed in the eastern Cape Province.

The insects attained peak populations, accompanied with considerable damage to the target weed, followed by slumps in the insect population and the subsequent re-growth of prickly pear. The damage caused by cactoblastis in South Africa was not as great or as extensive as that in Australia, and the

insect has never completely “cleared half a hectare of the weed”. However, it extensively destroys most young plants up to 30 cm high and causes most of the larger plants to lose the two or three terminal segments of all branches up to about 2 m high. This results in extensive thinning out of dense cactus stands, and significantly retards the spread of the weed by reducing its fruiting capacity and killing the seedlings (Fig. 35).

From about 10 years after the first releases, the cactoblastis populations in the pest pear areas have



FIGs 33 & 34. Dense infestations of the tree-pear, Opuntia ficus-indica, in the Eastern Cape, South Africa, in 1939, before the biological control campaign.



FIG. 35. The same area as in Fig. 34, cleared of O. ficus-indica by Cactoblastis and cochineal, in 1957.

always been low. Although this is usually sufficient to prevent the spread of the cactus by attacking isolated small plants or the succulent terminal segments of the lower branches of scattered large plants, they do not cause appreciable damage to large plants. In all inland areas, cactoblastis has now been largely replaced as the primary biological control agent by the cochineal, *Dactylopius opuntiae* (Pettey 1948; Robertson 1985).

Control of *Opuntia stricta* by cactoblastis in South Africa: As already mentioned, in the first 70 years since its release, cactoblastis failed to reach a 19,000 ha infestation of the low-growing *Opuntia stricta* in Kruger National Park (KNP) (Fig. 36), even though its normal host plant (*O. ficus-indica*) was contiguous in scattered infestations from the Eastern Cape almost to the border of KNP.

Eventually cactoblastis was released in KNP in 1987 and became well established. In both dense and sparse cactus infestations, larval feeding has

resulted in the fragmentation of large plants (Fig. 37), but the fragments take root and produce new plants. The few large plants have now been replaced by many smaller plants, which first have to reach a certain size (about 28 cladodes) before they will produce any fruit. This has resulted in an overall reduction in the levels of fruit production, but the spectacular biocontrol of *O. stricta* by cactoblastis that was reached in Australia has not been repeated in South Africa. (Hoffmann *et al.* 1997). The effect of cactoblastis on *O. stricta* in Florida is very similar to that in KNP (see Chapter 5).

Factors affecting effectivity of cactoblastis in South Africa: The difference in performance of cactoblastis between Australia and South Africa can be partially explained by imperfect adaptation of cactoblastis to the woody cactus tree, *O. ficus-indica*. The larvae do not readily kill hosts that comprise more than about 14 cladodes (Zimmermann & Malan 1981). On the other hand, overall mortality of cactoblastis caused by natural



FIG. 36. *Opuntia stricta* in Kruger National Park, South Africa, before control.



FIG. 37. *Opuntia stricta* in KNP, killed by Cactoblastis.

enemies in all the life stages was shown to be greater than mortality from host plant incompatibility (Robertson 1985, 1988).

Cactoblastis developed best in non-mountainous areas or in valleys with deep fertile soil, where the cactus plants were more succulent and were growing intermingled with bush. The cactoblastis population growth was slowest in the highest or coldest parts of the Karoo, and on the highest slopes of mountains with least exposure to the winter sun. As in Australia, cactus plants growing in shallow, nutrient-poor soil have thicker cuticles and secrete more mucilage, which causes high larval mortality. The newly-hatched cactoblastis larvae survive better in terminal segments, which secrete less mucilage and whose cuticles are thinner than those of the older segments (Petty 1948).

Whereas low temperatures (of up to -10°C for a short duration) have never been recorded to kill cactoblastis larvae or eggs in South Africa, moths do not lay eggs during nights when the temperatures are below 12°C , and low night temperatures during the winter generation are regarded as the most important factor limiting fecundity in this country. The longer development times during the winter generation increase the vulnerability of the larval and pupal stages to predation and parasitism. On the other hand, exposure of larvae to sand or gravel at high temperatures (of 40°C or more) is a common cause for deaths in South Africa (Petty 1948).

Islands in the Caribbean and other countries

In 1950, cactoblastis was brought from Australia to Hawaii (Fullaway 1954) to control *Opuntia ficus-indica*, and from South Africa to Mauritius (Greathead 1971) to control *O. tuna* and *O. monacantha*. In both cases, biocontrol was effective (Julien & Griffiths 1998).

In 1957, cactoblastis was shipped from South Africa by British entomologists and released on the island of Nevis, in the Leeward Islands group of the Caribbean Islands (Simmonds & Bennett 1966). The aim was to control a complex of native cacti, dominated by *Opuntia triacantha*, which were replacing grasses in over-grazed rangeland (Fig. 38). Cactoblastis gave very effective control of the indigenous cacti (Simmonds & Bennett 1966). In hindsight, this introduction appears unwise. The internationally accepted protocols currently

regulating biological control of weeds would not have approved the release of cactoblastis on an island with indigenous *Opuntia* species, and in the vicinity of the centre of origin of so many more *Opuntia* species. However, at that time biodiversity was not held in as much esteem as it is today, and nobody then contested the release (Zimmermann *et al.* 2000).

Following the successful control on Nevis, cactoblastis was sent from there to the surrounding islands of Montserrat and Antigua in 1960, and to Grand Cayman in 1970. On these islands, it also controlled native *Opuntia* species (Simmonds & Bennett 1966). Cactoblastis was also shipped from Nevis to St. Helena Island in 1971, and from there to Ascension Island in 1973. Attempts to establish cactoblastis in Kenya, Pakistan and Israel have failed (Julien & Griffiths 1998).

The inadvertent dispersal of *C. cactorum* to additional Caribbean Islands and North America

The Caribbean Islands

From Nevis, cactoblastis spread to nearby St. Kitts (Simmonds & Bennett 1966) and the U.S. Virgin Islands, and was recorded from Puerto Rico in the Greater Antilles in 1963 (Fig. 39) (Garcia-Tuduri *et al.* 1971). From there, it dispersed to many regions of the Caribbean, including Haiti, the Dominican Republic, the Bahamas and Cuba, where it attacked both weedy and non-weedy, native *Opuntia* species.



FIG. 38. Cactoblastis was taken to the Caribbean Islands to control abnormally dense growth of native cacti.



FIG. 39. The present distribution of *Cactoblastis* in the Caribbean area. Red dots denote official biocontrol projects, and red circles indicate inadvertent dispersal.

Florida, USA

Habeck & Bennett (1990) were the first to report the discovery of *cactoblastis* in the Florida Keys — one adult female collected in a mercury vapour lamp — in October 1989 (#1, Fig. 40). In addition, larval *cactoblastis* were collected from infested *O. stricta* in 1989 (#2, Fig. 40) and again in May 1990 (#3, Fig. 40) (Dickle 1991). Between May 1990 and October 1991 collections of *cactoblastis* were made at several locations along both Florida coasts that went as far north as Brevard County (#4, Fig. 40) to the east and Manatee County (#5, Fig. 40) to the west, approximately 330 and 370 km north, respectively, from the initial detection site in the Florida Keys. By 1999, *cactoblastis* had been reported from Cumberland Island (#6, Fig. 40) on the southern coast of Georgia. More recently, Hight *et al.* (2002) found *cactoblastis* as far north as Folly Island (#7, Fig. 40) near Charleston, South Carolina and as far west as St. George Island (#8, Fig. 40), Franklin County, Florida. In addition, several previously unreported inland infestations were also reported by Hight *et al.* (2002) in Orange and Osceola Counties (#9, Fig. 40) halfway “up” the Florida peninsula. The 2003 westward limit of *cactoblastis* is currently at Santa Rosa Island (#10, Fig. 40), Escambia County, Florida (S.D. Hight, pers. comm.).

Although the method by which *cactoblastis* reached Florida is unknown, several authors have suggested natural spread through “island hopping” from the Caribbean as a plausible hypothesis (Habeck &



FIG. 40. Map of south-eastern USA, showing recorded sightings of *Cactoblastis*.

Bennett 1990, Johnson & Stiling 1996). Weather events in the Caribbean, particularly during the summer hurricane season (June–November), may have played a part in its dispersal and should be kept in mind as infestations along the Gulf Coast are tracked (Stiling 2002). Pemberton (1995) reported U.S. interceptions of *cactoblastis* in nursery stock from the Caribbean as early as 1981 and suggests that the moth may have entered the USA as an unintended introduction in shipments of ornamental plants (most likely on pads of *O. stricta* from the Dominican Republic). Heppner (2000) reported an interdiction of *cactoblastis* in a shipment of cactus plants from Miami to a Wal-Mart store near Pensacola, Santa Rosa County, Florida, in June 2000, some 200 km west of the current leading edge of the infestation, as well as an interception of infested plants in baggage at the Dallas International Airport in Texas. Regardless of its mode of entry into the USA, clearly the inadvertent transport of *cactoblastis* by humans is a real concern.

It is difficult to accurately assess the true rate of spread of *cactoblastis* in Florida. As suggested by Stiling (2002), one of the confounding factors is that the moth may have been present in the Florida Keys as early as 1985 and remained undetected until 1989. He cites as evidence a letter written to the Florida Division of Plant Industry in 1990 that describes the level of damage by *cactoblastis* in the Florida Keys as “widespread and severe ... with cacti being reduced to rotting masses”. Stiling (2002) further states that in Australia and South

Africa it took several years for *Opuntia* stands to collapse in this manner (Dodd 1940; Pettey 1948). Even though initial records suggest that dispersal from the Florida Keys to Brevard County occurred much faster than had been reported for cactoblastis in other parts of the world, once better records of colonization were collected it appeared that the moth was dispersing over a distance of about 50–75 km per year (Stiling 2002 based on data reported in Johnson & Stiling 1998 and Hight *et al.* 2002). Clearly, additional work on cactoblastis dispersal in Florida is warranted because of the need to predict when the moth will make its appearance in the opuntia-rich regions of the southwestern United States and Mexico.

The arrival of cactoblastis in Florida was viewed with grave concern by many authors because of its potential adverse impact on native opuntia occurring in the state, including the rare *O. corallicola* (= *O. spinosissima* – the semaphore cactus) (Stiling *et al.* 2000) (Fig. 41), *O. cubensis* and *O. triacantha*. All opuntia present in Florida are attacked by cactoblastis, and infestations can be severe (Fig. 42), with thirty egg-sticks collected from a single plant in a 24-hour period (on *O. ficus-indica* at Alligator Point, FL, July 2003, K.A. Bloem, pers. comm.).



FIG. 41 The rare semaphore cactus (*Opuntia corallicola*), which is threatened by *Cactoblastis*.



FIG. 42. *Opuntia stricta* plant severely attacked by *Cactoblastis* in Florida.

CHAPTER 5

Cactoblastis cactorum as a threat

Considering the presence of cactoblastis on most islands of the Greater Antilles in the Caribbean, as well as in Florida, Georgia and South Carolina (USA), it is inevitable that this voracious cactus-feeding insect will also find its way to Texas, adjacent U.S. States and Mexico.

Potential dispersal routes to Texas, adjacent States and Mexico

A general listing of potential dispersal routes north and west into other U.S. States and Mexico (Fig. 43) includes:

- continued unaided westward movement of cactoblastis via the Gulf Coast along the “opuntia bridge”
- transportation north and west facilitated through weather events
- movement of infested nursery plants
- intentional (non-approved) movement by landowners or homeowners
- accidental transport of insects in man-made vehicles.

If the mean low temperatures of known cactoblastis habitats in South America are compared with various North American localities, indications are that the moth would probably be able to survive as far north as Charleston (South Carolina), San Antonio (Texas) and Sacramento (California) (Pemberton 1995). Indeed, cactoblastis is already



FIG. 43. Possible entry routes of cactoblastis into Mexico.

established at Folly Island off the Atlantic Coast near Charleston, South Carolina (Hight *et al.* 2002). Studies in Florida are underway to determine the lowest and highest temperatures at which cactoblastis is able to reproduce successfully. Another technique, suggested by Carpenter *et al.* (2001a), is to release reproductively inactivated cactoblastis in various regions of the USA and Mexico to study its host range under field conditions without concern of establishing a breeding population. The results of both these studies should be useful to predict the true geographic limits for cactoblastis in the USA and Mexico.

Soberón *et al.* (2001) present bio-climatological data to determine the possible distribution and spread of cactoblastis through Mexico. Based upon these data and the presence of favourable hosts, they conclude that the most likely routes of invasion into Mexico are from Florida along the Gulf Coast States into Texas and from there into northern Mexico. In addition, dispersal of cactoblastis from Cuba, Haiti and the Dominican Republic to Mexico across the Yucatán channel or via Guatemala, aided by weather events, is a distinct possibility (see also Zimmermann *et al.* 2000b).

Threat to the USA and Mexico

Although it is not yet clear which cactus species cactoblastis will attack, establishment of *C. cactorum* in the south-western USA and Mexico could have devastating effects on the landscape and biodiversity of native desert ecosystems, and on the forage and vegetable opuntia industries in these areas. For example, even in Florida where cactus is a minor component of the native flora, there are three species of *Opuntia* (*O. corallicola*, *O. triacantha*, and *O. cubensis*) that are limited to local populations in the Florida Keys. *O. triacantha* and *O. cubensis* are considered rare, and *O. corallicola* is under review for addition to the Federal Endangered Species List (Johnson & Stiling 1998; but see Hight *et al.* 2002). All are being impacted by cactoblastis. The Florida opuntia habitats are also shared by rare and endangered fauna such as the Gersteckeria weevil (C.W. O'Brien, pers. comm.), Schaus swallowtail, and Florida leaf-wing and Bartram's hair-streak butterflies (Habeck & Bennett 1990). *Opuntia*

species also serve as nurse plants, nesting habitats and a food source for many mammals, birds and insects. The endangered San Salvador island rock iguana on Green Cay in the Bahamas is being threatened because cactoblastis has almost completely destroyed the cacti that serve as its primary food source (Cyril *et al.* 2000). Similarly, cactoblastis has almost eliminated cactus plants from the preserve on the Florida Atlantic University's Boca Raton campus on the eastern edge of the Florida Everglades that serve as an important food for the threatened gopher tortoise (Pierce 1995). Interactions such as these are expected to be an increasingly greater cause for concern as the moth moves westward.

Of the *Opuntia* species outside of the natural distribution of cactoblastis that are known to be attacked by this insect (Table I, Chapter 3), nine species are native to the USA and five are native to Mexico. In total there are 46 native *Opuntia* species in the USA (U.S. Department of Agriculture 1982). One of these is a federally protected endangered species (*O. basilaris* var. *kernii* and var. *treleasei*, which only occurs near Bakersfield, California) and twelve others are under review for protected status (U.S. Department of the Interior 1993a, b). The species diversity of *Opuntia* increases significantly in Texas and even more so in Mexico. Furthermore, there is a continuous distribution of potentially acceptable host species of *Opuntia* (an "opuntia bridge") from Florida across the southern USA to the Pacific Coast (Mahr 2001). Although the dominant species of *Opuntia* present in the desert south-west are still being tested for their suitability as hosts of cactoblastis, most prickly pear species are thought to be at risk.

Soberón *et al.* (2001), Perez-Sandi (2001) and Viguera & Portillo (2001) discuss the importance of opuntia products in Mexico, both from ecological and economic standpoints. Ecologically, opuntias are dominant components of the natural Mexican flora, especially in the Chihuahuan and Sonoran Deserts (Fig. 44). Mexico has one of the highest species diversities of opuntia, and populations cover three million hectares of land area. Opuntia cacti constitute the most important plant group in maintaining the ecological balance in large extensions of the Mexican territory. Currently, 104 species of *Opuntia* are recognized in Mexico, 38 of which are endemic. They also contribute significantly to soil stability and regeneration and are a



FIG. 44. *Opuntias* are dominant ecological components of the natural Mexican flora in the Sonoran Desert.

major positive force in the fight against desertification. In addition, they constitute an important dietary staple for a number of species of mammals (including deer, rodents, javelinas and coyotes) and provide nesting sites for many insects and birds.

Economically, opuntias in Mexico are an extremely important agricultural resource and are used in the production of fresh juice, jam and alcoholic beverages. Many thousands of jobs are generated by cultivation of opuntia (Fig. 45) and the manufacture of its sub-products in Mexico. For example, fruit production (Fig. 46) occurs in 15 States, utilizes 50,000 ha and involves 120,000 growers, while vegetable production (Fig. 47) involves 14 States, 10,000 ha and 90,000 growers. Production values for these commodities amount to \$80 million per year, with an export value of \$30 million. As a forage crop, 3 million ha grow wild and 150,000 ha are under regular cultivation. Mexico also has an important dye industry that utilizes opuntias as



FIG. 45. In Mexico, 10,000 ha are planted with opuntias for vegetable production.



FIG. 46. *Opuntia* fruit production involves 120,000 growers in Mexico.



FIG. 47. The young *Opuntia* pads (nopalitos) are an important vegetable in Mexico.

hosts for the dye-producing cochineal insect, *Dactylopius coccus* (Fig. 48). *Opuntia* is used as the main food for cattle in poorer areas, and as emergency fodder during periods of prolonged drought in the richer, more developed areas of Mexico. Additionally, opuntias are used as an energy source (as firewood and in the production of ethanol and bio-gas), to manufacture soap, fertilizer and adhesives, and as fencing, hedges and ornamental plants.



FIG. 48. *Opuntias* are the host plants of *Dactylopius coccus*, from which a valuable carmine dye is extracted.

Many of the cactus species that are most important commercially are known hosts of cactoblastis. Among these, *Opuntia ficus-indica*, *O. streptacantha* and *O. megacantha* — grown for forage, fruit and vegetable —, and *O. engelmannii* (= *O. lindheimeri*), *O. stricta* and *O. robusta* — used for forage —, are hosts of cactoblastis. However, the acceptability and suitability of many other economically important *Opuntia* species to cactoblastis attack are not yet known. These include four opuntias used for forage and vegetable (*O. amyclaea*, *O. hyptiacantha*, *O. leucotricha* and *O. tapona*), and six species used for forage (*O. azurea*, *O. cantabrigiensis*, *O. durangensis*, *O. phaeacantha*, *O. rastrera* and *O. macrocentra*). Host specificity studies (see Chapter 6) that include as many of these species as possible are urgently needed.

Threat to other countries

In addition to the USA and Mexico, many other countries around the world make use of naturally occurring or introduced species of *Opuntia* to produce various products destined for local use or

consumption, or for export. Table II and III below summarize currently known data from these countries. Countries listed in Table II do not yet have cactoblastis present, while countries listed in Table III are attempting to bolster production of cactus products while dealing with the presence of cactoblastis. These tables are updated from the original tables prepared as part of the working

material for the consultants meeting entitled “Mitigating the Threat of *Cactoblastis cactorum* to International Agriculture and Ecological Systems and Biodiversity” organized by the Technical Co-Operation Department of the International Atomic Energy Agency and the Joint FAO/IAEA Division of Nuclear Applications in Food and Agriculture held in Vienna, Austria, in July 2002 (IAEA 2002).

Table II. Countries utilizing *Opuntia* species: *Cactoblastis* absent

Country	Species	Estimated area cultivated (ha)	Products	Remarks
Brazil (except southern areas)	<i>O. ficus-indica</i> , <i>O. robusta</i>	400,000	fodder & fruit	expanding plantations
Chile	<i>O. ficus-indica</i>	2,000	cochineal dye & fruit	fruit destined for export; high income from cochineal dye
Peru	<i>O. ficus-indica</i>	70,000	cochineal dye, fodder & fruit	75% of world's cochineal production
Bolivia	<i>O. ficus-indica</i>	1,000	cochineal dye, fodder & fruit	becoming increasingly important
Italy	<i>O. ficus-indica</i>	30,000	fruit, fodder, pharmaceutical	major industry in Sicily
Spain	<i>O. ficus-indica</i>	1,000	fruit	mainly non-commercial
Canary Islands	<i>O. ficus-indica</i>	1,000	cochineal dye & fruit	high income from cochineal dye
Israel	<i>O. ficus-indica</i>	300	fruit	intensive production 11 months of the year
Egypt, Portugal, Turkey, Jordan, Pakistan, India, China	<i>O. ficus-indica</i>	unknown	fodder & fruit	production in its infancy
Tunisia	<i>O. ficus-indica</i>	600,000	fodder & fruit	becoming increasingly important
Other North African countries	<i>O. ficus-indica</i>	120,000	fodder & fruit	increasing in importance in Morocco and Algeria
Ethiopia (Fig. 49)	<i>O. ficus-indica</i>	31,000 cultivated, 300,000 naturalized	fodder & fruit	increasingly important for food security
Eritrea, Yemen	<i>O. ficus-indica</i>	unknown	fodder & fruit	becoming increasingly important

Table III. Countries utilizing *Opuntia* species: Cactoblastis present

Country	Cactoblastis as a problem in <i>Opuntia</i> cultivation
Argentina	Despite the presence of a large complex of co-evolved natural enemies, cactoblastis remains a serious pest in opuntia plantations destined for fodder and fruit production. Insecticides are the preferred method of control. Peasant farmers increasingly rely on <i>O. ficus-indica</i> as a source of fruit and they rarely have the means to control cactoblastis.
Australia	Cultivation of useful <i>Opuntia</i> species is discouraged for fear of a conflict of interest with the biocontrol efforts against opuntia. Only recently has some cultivation been initiated. The present status of cactoblastis is unknown, but is expected to be similar to its status in South Africa.
Cuba	Cactus pear as a source of fruit is limited to isolated plants in home gardens. However, Cuba is initiating a project to increase cultivation and uses of cactus pear. Cactoblastis may become a limiting factor as it is already present in the eastern part of the island.
Dominican Republic and other Caribbean Islands including Bahamas, Haiti, and Puerto Rico	Cactoblastis is present and infesting ornamental cacti destined for horticultural export from the Dominican Republic (see Pemberton 1995). Many rural households on most of the drier Caribbean Islands cultivate small areas of <i>O. ficus-indica</i> and these are severely damaged by cactoblastis.
Namibia	<i>C. cactorum</i> is present in areas of <i>O. ficus-indica</i> cultivation. However, there are also infestations of <i>O. stricta</i> that require control by cactoblastis.
South Africa	Although not a limiting factor, cactoblastis is regarded as a serious pest in plantations of <i>O. ficus-indica</i> and <i>O. robusta</i> (Fig. 50). Control methods (chemical & mechanical) are necessary to protect plants and to maintain production of fruit and fodder. Cactus pear is becoming more important to subsistence farmers who do not have the means to control cactoblastis.
Botswana	Becoming increasingly important as a source of fruit and fodder in the Kalahari desert. Cactoblastis is already infesting some of these cultivations.



FIG. 49. Cactoblastis has not yet reached Ethiopia, where *Opuntia ficus-indica* is utilized as fodder and for its fruit.



FIG. 50. In South Africa, *Opuntia robusta* is cultivated as fodder despite the presence of cactoblastis.

CHAPTER 6

The surveillance and control of *Cactoblastis cactorum*

Prevention (inspections, phytosanitary methods, early detection, public vigilance)

The best chance of preventing a pest from becoming established is early detection. Early detection allows for eradication efforts to be conducted while an infestation is still small and unstable. It also allows for simple management practices, such as removal and destruction of infested pads and of egg sticks, to be used effectively. Presently visual inspections for damage or the use of sterile virgin female baited traps are the most effective tools for detecting new infestations. Early detection also depends heavily on a thorough awareness of the problem. One of the first lines of defence is the education of agricultural inspectors, border guards, park rangers, ranchers, *Opuntia* growers, nurserymen, homeowners, teachers, students and the general public as to the seriousness of the threat and how to identify it, coupled with an increased level of inspection and heightened vigilance at all ports of entry (including airports and borders). As stated in the introduction, the primary objective of this publication is to help in the education and awareness process.

Mexican authorities are diligently working on the development of action plans to prevent the entry of cactoblastis into Mexico. Some of the components of these action plans include conducting risk assessment studies, implementing a vigorous public awareness campaign, training phytosanitary and customs staff as well as growers in the identification of cactoblastis life stages and in the detection of damaged plants, establishment of an expert advisory group that includes both national and international scientists, and increased surveillance at possible points of entry and in areas determined to be “high risk” (such as Tamaulipas, Nuevo León, Veracruz, Yucatán and Campeche). Most importantly, Mexico has recently issued a Federal Phytosanitary Law through which the Mexican government can enforce quarantine actions and emergency eradication campaigns in cases of a cactoblastis outbreak.

Surveillance

Most distribution records for cactoblastis from the USA have emerged from surveys of larval feeding damage and the presence of egg sticks on infested plants. Although it may be difficult to locate egg sticks on plants in areas where population densities are low, larval damage is relatively easy to identify. Gregarious larvae bore into the cactus pads and hollow them from the inside. Frass (faeces) and plant mucilage oozing from larval entry holes (Fig. 51), collapsed cactus pads, as well as whitish papery-looking cladodes, are characteristic of cactoblastis infestations (see Chapter 2 for more photographs).

Sticky traps baited with virgin females have also been used in areas with low population densities in Florida and Georgia to attract male cactoblastis, as an indication of the presence and abundance of



FIG. 51. Frass and mucilage oozing from a cactoblastis-infested cactus cladode.

cactoblastis throughout the year (Hight *et al.* 2002). Sticky traps are baited with newly emerged (0–24 h) virgin female cactoblastis. Small screen cages are used to confine the females and these are provisioned with a small square of host plant material and a moistened cotton plug. At this time, the best monitoring tool appears to be a Pherocon 1-C sticky trap (Fig. 52) baited with four virgin females and placed 2.0 m aboveground near cactus. Traps were effective at detecting cactoblastis at sites where no larval feeding damage was evident. Trapping data revealed that cactoblastis have non-overlapping generations with distinct periods of adult flight activity, followed by periods of larval development during which no adults are flying (see Chapter 2).

Because of concerns over the use of fertile females in these traps to attract males in areas that currently are not infested with cactoblastis, Bloem *et al.* (2003) conducted experiments to determine whether irradiated (and fully sterile) virgin females are as effective at luring males into traps as are



FIG. 52. Pherocon 1-C sticky trap baited with four virgin females used to determine the presence of Cactoblastis.

fertile unirradiated females. Results indicated there was no significant difference in male capture in traps baited with virgin females treated either as mature pupae or as newly emerged adults with 200 Gy¹ of gamma radiation versus traps baited with fertile females. The efficiency of the virgin female baited traps relative to the absolute population number of cactoblastis present in a given area remains to be determined. A sticky trap baited with synthetic female calling pheromone would be a significant positive addition to a cactoblastis monitoring programme, especially for surveys beyond the leading edge of moth infestation. Efforts to identify the female sex pheromone for cactoblastis are currently under way at a USDA laboratory in Miami, Florida (N. Epsky, pers. comm.).

Control

The control of cactoblastis infestations in cactus pear orchards has been in practice in South Africa since the late 1950s when it became evident that the cultivation of this commercial plant was not possible without protecting it against the cactus moth and the cochineal, *D. opuntiae*. Several publications dealing with this issue were published (Burger 1972; Annecke *et al.* 1976; Pretorius *et al.* 1986; Pretorius & Van Ark 1992). Control of cactoblastis is usually part of an integrated control approach, which is often primarily directed at the control of the cochineal, *D. opuntiae*. Therefore insecticides that are effective against both pest species are preferable. The options for biological control are limited (Pemberton & Cordo 2001a) although a considerable knowledge of potential natural enemies within the native range of cactoblastis and in Australia and South Africa exists (Dodd 1940; Robertson & Hoffmann 1989).

The choice of control measures against cactoblastis is influenced by several circumstances, namely:

- The value of the orchard or crop. Expensive and rigorous chemical control is affordable in cases where the value of the crop is high and where no insect damage is tolerated.
- Persistent contact insecticides are the key to successful control of cactoblastis, but zero

¹ Gy (Gray) = 1 J/kg (energy absorption).

residue tolerance on fruit often precludes the use of such insecticides.

- It is not economical to protect low-value cactus pear orchards, e.g. those used for drought emergency fodder, with expensive insecticides. Management practices and sanitation are more often used, sometimes in combination with less expensive insecticides.
- Cactoblastis can only be controlled in wild opuntia populations provided that the area is confined to a few hectares. Therefore, the practicality of protecting native *Opuntia* species that are widely distributed is very limited.
- Biological control cannot be considered in countries like South Africa or Australia, which still need cactoblastis as a biocontrol agent of invasive cactus species. The use of host-specific parasitoids and microorganisms offers the best possibilities in North America, but the chances of finding suitable agents are remote.

Management practices

In temperate regions, such as the Eastern Cape Province (South Africa) and Queensland (Australia), cactoblastis has two well-defined periods when egg sticks are deposited: during spring and again late summer/early autumn (Fig. 17, Chapter 2). In these regions the egg sticks are removed from orchards during the peak egg-laying periods, and two surveys about two weeks apart are usually sufficient to remove a large proportion of each generation's egg stick production.

In more tropical regions, the generations overlap considerably and there may even be a third generation present (Fig. 18, Chapter 2). Oviposition in these areas is protracted over a considerable period and makes the collecting of egg sticks impractical as a control method. The preferred method is to scout for infested cladodes and to remove these from the orchards by pruning (Fig. 53) (pruning is a common practice to shape and rejuvenate the trees). Infested cladodes are destroyed collectively by any method available, which may include chemical spraying, burning, burying or shredding for use as fodder. Large commercial orchards in South Africa use about 6 persons per 100 ha, part time, for cactoblastis control.



FIG. 53. Removing cladodes infested with Cactoblastis.

The large *O. robusta*-based spineless plantations, which are exclusively used for fodder in South Africa, are more resistant to cochineal damage than *O. ficus-indica*, and cactoblastis is a more serious pest which is capable of destroying entire orchards (Fig. 54) (Anneck *et al.* 1976). In these plantations, management methods are the most economical methods of control.



FIG. 54. Cactoblastis is the major pest in plantations of spineless *Opuntia robusta*-based plants used for fodder.

Chemical control

Chemical control (Fig. 55) can be aimed at killing the neonate (first instar) larvae on contact before they penetrate the cladodes (Fig. 10, Chapter 1). The timing of application is therefore critical, and best results are achieved in temperate regions where the egg-laying period is synchronized (see above) (Pretorius & Van Ark 1992). This method would not be as effective where the oviposition period is protracted.

Most contact insecticides that are effective against Lepidoptera and have a long residual activity will be suitable (Leibee & Osborne 2001). Some farmers prefer to inject these insecticides into the cavities where cactoblastis larvae feed, especially when cover sprays are not recommended, e.g. when approaching the fruit harvesting period. The use of new-generation systemic insecticides could be considered, although the high dilution factor in succulents requires high dosages, which may render this approach too expensive (Pretorius *et al.* 1986). No systemic insecticide has yet been shown to be effective against either cochineal or cactoblastis. Insecticides presently registered for use against cactoblastis in South Africa include carbaryl, deltamethrin, methidathion and tralomethrin (Nel *et al.* 2002). Most insecticides used for the control of cactus pests in South Africa are effective against both cactoblastis and cochineal.

Integrated control

Control of cactoblastis is best achieved by combining both the above methods. The approach followed depends on the value of the orchard, on



FIG. 55. Chemical treatment of cactus pear plantation against both cactoblastis and cochineal.

insect damage threshold levels and on fruit residue tolerances. A combination of common pruning activities with cactoblastis removal and control is often sufficient to keep damage below the economic threshold. The most common problem encountered is that control of cactoblastis is not systematically included in routine farming operations. Once the infestation levels of cactoblastis (and cochineal) have reached certain thresholds it becomes difficult, very expensive and uneconomical to rescue the orchard.

Biological control

Any introduced parasitoid to be released in South Africa for classical biological pest control needs to be screened against some key introduced biocontrol agents of weeds, such as cactoblastis. Should the parasitoids reduce the efficacy of these introduced phytophages, it might result in a population increase of the weeds that they control. Similarly, the native and potentially aggressive *Opuntia* species in Florida are being kept in check by their own natural enemies, some of which are pyralid moths closely related to cactoblastis. If non-specific parasitoids or diseases were to be introduced from outside Florida to control cactoblastis, these might also affect the native pyralids, resulting in unnatural population increases and invasions by the native *Opuntia* species (Pemberton & Cordo 2001a). The host specificity of any biological control agent to be considered for introduction to Florida in an attempt to control cactoblastis is therefore crucial. Any risks of non-target effects will have to be evaluated carefully against the threat of the insect to native and commercial *Opuntia* species.

Pemberton & Cordo (2001a, 2001b) have reviewed the known parasitoids (nine species) and diseases of cactoblastis in Argentina, as well as of the cactus-feeding pyralids of North America. They discussed the options and risks associated with using these and other established stenophagous parasitoids and diseases for classical biological control of cactoblastis in Florida, providing seven possible approaches and ranking them according to relative risks to non-target species. The classical introduction from South America of parasitoids specific to the genus *Cactoblastis* is the preferred option, followed by inundative releases of cactus moth parasitoids that have moved over to *C. cactorum* from related, native, cactus-feeding pyralids in Florida, e.g. from the genus *Melitara*. The inundative release of other, less specific parasitoids

that are known to attack cactoblastis and which are already in Florida is a less preferred option.

However, it appears that the currently known parasitoids of cactoblastis in South America are unlikely to be limited to the genus *Cactoblastis*, which precludes the use of the first and preferred option. In order to address this uncertainty, more research on the full complex of natural enemies associated with the genus *Cactoblastis* in Argentina, combined with life table studies that will identify key species, is urgently needed. Life table studies carried out on cactoblastis in South Africa (Robertson 1988; Robertson & Hoffmann 1989) identified only two parasitoids, which had only an insignificant effect on populations. The most important components of mortality were general predators (Fig. 56) (mainly ants) and weather related factors. Baboons and monkeys also excavate the larvae and pupae from the cladodes (Fig. 57) (Hoffmann *et al.* 1998a & b).

Most fungi that kill insects have wide host ranges or are used in broad-spectrum biopesticides, which may be useful under certain conditions to control cactoblastis. No fungal pathogens are known from cactoblastis in South America, and exploration for such pathogens could be productive (Pemberton & Cordo 2001b). More promising are the protozoans in the genus *Nosema*, which appear to be host-specific. Two species are known from cactoblastis, including *N. cactoblastis* from South Africa. Considerations for their use against cactoblastis in North America were discussed by Pemberton & Cordo (2001b) after surveys had been made in South Africa and Argentina.

It is important to consider carefully the capabilities of classical biological control in reducing the threat of cactoblastis to North America. At this stage, the main aim is to stop the further spread of the insect westward and, if at all possible, to eradicate populations from the leading edge and to push them back. Classical biological control may thus not be the best approach, except where only a general reduction of cactoblastis populations is needed.

Sterile insect technique (SIT)

Autocidal pest suppression using the SIT is unique in that it involves the release of mass reared and reproductively inactivated insects to control populations of the same species. A major benefit of the SIT is that there are no non-target effects.



FIG. 56. These hemipterans (*Nysius* sp.) preying upon the eggs of *Cactoblastis* in South Africa are probably non-specific.



FIG. 57. Baboons excavate *cactoblastis* larvae from *O. stricta* in South Africa.

Historically, SIT programmes have been successful against a number of pest insects including the screwworm fly (*Cochliomyia hominivorax*), the Mediterranean fruit fly (*Ceratitis capitata*) and the

codling moth (*Cydia pomonella*). However, SIT programmes for Lepidoptera (moths) tend to be more problematic because these insects are more expensive to rear, are more radio-resistant than Diptera (flies), and the increased amount of radiation required to completely sterilize Lepidoptera often affects their competitiveness and performance in the field.

An effective approach to reduce the negative effects of radio-resistance in Lepidoptera has been the use of inherited or F_1 sterility (Bloem & Carpenter 2001). Like SIT, F_1 sterility involves the mass rearing and release of insects to ensure that when matings occur in the field, a significant proportion of these involve a treated, released insect. F_1 sterility takes advantage of two unique genetic phenomena in Lepidoptera. First, lepidopteran females generally are much more sensitive to radiation than are males of the same species. This allows the dose of radiation to be chosen such that the irradiated females are completely sterile and the irradiated males are partially sterile. Second, when these partially sterile males mate with feral, fertile females, the radiation-induced deleterious effects are inherited by the offspring (F_1 generation). As a result, egg hatch in the F_1 generation is reduced and the resulting offspring are more sterile than the irradiated parent and, in most cases, predominately male. The lower dose of radiation used in F_1 sterility increases the quality and competitiveness of the irradiated released insects (North 1975). Because F_1 sterile progeny are produced in the field, the release of partially sterile insects offers greater suppressive potential than the release of fully sterile insects (LaChance 1985).

Carpenter *et al.* (2001a) were the first to suggest the use of SIT/ F_1 sterility to study, predict and manage the expanding populations of cactoblastis in the USA. Carpenter *et al.* (2001b) provide data on the response of cactoblastis to increasing doses of gamma radiation and the documentation of inherited sterility in this species. SIT/ F_1 sterility could have several applications for suppression of cactoblastis populations. It could provide a way to protect rare cacti from attack (such as those present in the Florida Keys), it could be available as an eradication tool against new infestations of cactoblastis beyond the leading edge of the current infestation, provided that infestations are detected early in the colonization process, and it could be used to erect a barrier to prevent or slow the expansion of the geographical range of cactoblastis (Carpenter

et al. 2001a). As stated by Stiling (2002), the use of SIT/ F_1 sterility for cactoblastis “offers perhaps the only realistic chance of drawing a line in the sand, literally, in Florida, and trying to prevent further spread of cactoblastis into the USA southwest and Mexico”.

The implementation of SIT/ F_1 sterility requires the ability to mass rear the target insect. Efforts are currently under way in South Africa to mass rear cactoblastis in outdoor cages (Fig. 58) for shipment to the USA in support of an SIT/ F_1 sterility programme. Significant progress has been made in South Africa and the USA in developing an efficient artificial diet rearing system (Fig. 59) for this species. Moreover, radiation biology studies have



FIG. 58. Rearing Cactoblastis in outdoor cages in South Africa in support of the F_1 sterility programme.



FIG. 59. Rearing Cactoblastis on artificial medium in South Africa.

confirmed the potential to apply F₁ sterility to this pest (Carpenter et al. 2001 b).

Research

Current and future research efforts in the USA include the continuation of studies that examine the rate of spread and the colonization dynamics of cactoblastis into un-infested areas both north and west of the leading edge of the infestation. Field and laboratory studies have been initiated to determine which species of *Opuntia* and which plant size (if

any) is first chosen for colonization, as well as the impact that colonization has on different species of *Opuntia*. Further optimization of the trapping system, including trap calibration studies using release-recapture of cactoblastis in the USA and South Africa, examination of the effect of trap colour as a short-range visual cue, and field testing of different pheromone fractions and blends are also planned. Finally, evaluation of the effectiveness of sterile males to suppress known populations of cactoblastis in field-cages has shown the feasibility of using the SIT against this pest.

CONCLUSIONS

The cactus moth, *Cactoblastis cactorum*, has become a textbook example epitomizing the great success that can be achieved through the manipulation of plant-feeding insects as biological control agents of alien invasive plants (Dodd 1940; Pettey 1948). *A worm that turned* is the title of a recent popular article that describes the threat of the same “miracle” insect when its host plants suddenly are not weeds anymore, but cacti of great economic, ecological and aesthetic value (Stiling 2000). The arrival of cactoblastis on the shores of North America, whether by natural dispersal or unintentional introductions by humans, also epitomizes a consequence of globalization. The next destination for cactoblastis may be North Africa, Peru, Ethiopia or northeastern Brazil. The efforts in dealing with the threat of cactoblastis to the USA and Mexico thus have much wider implications and should be viewed in this context.

Probably the most uncertain aspect when estimating the true threat of cactoblastis is its potential impact on the native *Opuntia* flora of North America. There is sufficient evidence that predicts the worst, but there are also indications that preclude a repeat of the Australian experience. Although much can be learned from impacts of cactoblastis on the 25 new-association *Opuntia* species, the prediction based on observations is too uncertain when considering the approximately 200 species threatened. Clear host preferences are detectable but the basis of host-plant selection and host-plant acceptance needs urgent attention. Although cactoblastis has a wide climatic tolerance in Argentina, Australia and South Africa, climate will certainly limit its spread into the northern USA (Monro 1975; Murray 1982). Some areas in Mexico may also be immune to invasions, but these areas will be small and limited to mountains or desert pockets.

Several aspects of the biology and morphology of cactoblastis lend themselves to easy identification and control. The damage caused by the larvae is easily detectable, and in contrast with the adult moth, which is cryptic and nocturnal, the larvae and egg sticks are easily identified. With the necessary training and alertness programmes in place it should not be difficult to locate early infestations of cactoblastis outside its present distribution in North

America. In temperate regions, which will include most parts of Mexico, the insect should have two well-defined generations. This will facilitate more effective chemical and integrated control. Furthermore, the pupae are easily sorted by gender, and the irradiation of adult moths even to the point of 100% sterility did not appear to affect their fitness (Carpenter et al. 2001b). Mass rearing the cactus moth appears feasible, and good progress has been made towards synthesizing the female pheromone that is a necessary tool in the monitoring programme. The prospects of effective control and even eradication of cactoblastis are favourable, provided new infestations can be identified at an early stage of invasion.

An outstanding issue concerns reasons for the fast rate of dispersal of cactoblastis along the Atlantic and Gulf coasts of the USA (Hight et al. 2002; Stiling 2002). These rates are considerably faster than the observations on spread during the biological control campaigns in Australia and South Africa during the thirties and forties (Zimmermann et al. 2001). Research on dispersal of cactoblastis, which will provide some indication of the chances of its arrival by natural spread to Mexico, is crucial for fine-tuning the population suppression campaign against the insect.

Each of the control methods that have been proposed has its limitations. Although biological control may not be the answer during this early phase of the project, its value as a self-perpetuating control option is undisputable where cactoblastis has established on *Opuntia* spp. in native habitats covering millions of hectares. Even the risks of using less host-specific natural enemies may have to be weighed up against the consequences of not using them. Research into the various options of biological control as described by Pemberton & Cordo (2001a) is a worthwhile investment. New-generation insecticides are also available, and these should be screened for the control of cactoblastis. At this stage the emphasis of control will be on eradication or containment (Carpenter et al. 2001a) and hence the importance of having effective chemical control methods in place and investing in fine-tuning the F₁ sterility technique.

REFERENCES

- Anderson, E.F. 2001. *The cactus family*. Timber Press, Portland, Oregon.
- Anneck, D.P., W.A. Burger & H. Coetzee 1976. Pest status of *Cactoblastis cactorum* (Berg) (Lepidoptera: Phycitidae) and *Dactylopius opuntiae* (Cockerell) (Coccoidea: Dactylopiidae) in spineless opuntia plantations in South Africa. *Journal of the Entomological Society of Southern Africa* 39: 111-116.
- Anneck, 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.
- Barbera, G., P. Inglese & E. Pimienta-Barrios (Eds) & E. de J. Arias-Jiménez (Coord.) 1995. *Agroecology, cultivation and uses of cactus pear*. FAO Plant Production and Protection Paper No. 132.
- Bennett, F.D. 1971. Some recent successes in the field of biological control in the West Indies. *Revista Peruana de Entomologia* 14: 369-373.
- Bennett, F.D., M.J.W. Cock, I.W. Hughes, F.J.S. Simmonds, & M. Yaseen [M.J.W. Cock (ed.)] 1985. *A review of biological control of pests in the Commonwealth Caribbean and Bermuda up to 1982*. Commonwealth Inst. Biol. Contr. Tech. Com. 9. 218 p.
- Bennett, F.D. & D.H. Habeck 1995. *Cactoblastis cactorum*: A successful weed control agent in the Caribbean, now a pest in Florida? *Proceedings of the VIIIth International Symposium on Biological Control of Weeds, Canterbury, New Zealand*, 21-26.
- Benson, L. 1982. *The cacti of the United States and Canada*. Stanford University Press, Stanford, California.
- Bloem, S. & J.E. Carpenter 2001. Evaluation of population suppression by irradiated Lepidoptera and their progeny. *Florida Entomologist* 84: 165-171.
- Bloem, S., J.E. Carpenter & K.A. Bloem 2003. Performance of sterile *Cactoblastis cactorum* (Lepidoptera: Pyralidae) females in luring males to traps. *Florida Entomologist* 86: 395-399.
- Brutsch, M.O. & H.G. Zimmermann 1995. Control and utilization of wild Opuntias. In: Barbera, G., Inglese, P. & Pimienta-Barrios, E. (Eds) *Agroecology, cultivation and uses of cactus pear*. FAO, Rome. 155-166.
- Burger, W.A. 1972. Control of cactoblastis and cochineal. *Farming in South Africa* 459: 1-4.
- Carpenter, J.E., K.A. Bloem & S. Bloem 2001a. Applications of F₁ sterility for research and management of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). *Florida Entomologist* 84(4): 531-536.
- Carpenter, J.E., S. Bloem & K.A. Bloem 2001b. Inherited sterility in *Cactoblastis cactorum* (Lepidoptera: Pyralidae). *Florida Entomologist* 84(4): 537-542.
- Cock, M.J.W. (ed.) 1985. *A review of biological control of pests in the Commonwealth Caribbean and Bermuda up to 1982*. Technical Communication no. 9. Commonwealth Institute of Biological Control. 1-218.
- Cyril, S., W.K. Hayes & R.L. Carter 2000. *Reproductive ecology, spatial relationships, and diet of the endangered San Salvador island rock iguana *Cyclura rileyi rileyi**. Department of Natural Sciences Loma Linda University. Abstract presented at the Society for the Study of Amphibians and Reptiles annual meeting, La Paz, Mexico.
- Dickle, T.S. 1991. *Cactoblastis cactorum* in Florida (Lepidoptera: Pyralidae: Phycitinae). *Tropical Lepidoptera* 2: 117-118.
- Dodd, A.P. 1940. *The biological campaign against prickly pear*. Commonwealth Prickly Pear Board, Brisbane, 1-177.
- Fullaway, D.T. 1954. Biological control of cactus in Hawaii. *Journal of Economic Entomology* 47: 696-700.
- Garcia-Tuduri, J, L.F. Martorell & S. Medina Guad 1971. Geographical distribution and host plant list of the cactus moth, *Cactoblastis cactorum* (Berg) in Puerto Rico and the United States Virgin Islands. *Journal of the Agricultural University of Puerto Rico* 55: 130-134.
- Greathead, D.J. 1971. *A review of biological control in the Ethiopian region*. Technical Communication No. 5, Commonwealth Institute of Biological Control, Commonwealth Agricultural Bureaux, Slough. 1-162.
- Habeck, D.H. & F.D. Bennet 1990. *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae), a phycitine new to Florida. *Entomology Circular* 333, 4 pp.

- 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 no. 3053*, vol. 86: 331-413.
- Heppner, J.B. 2000. Tropical cactus borer, *Cactoblastis cactorum*, intercepted in west Florida (Lepidoptera: Pyralidae: Phycitinae). *Lepidoptera News* 2: 20-22.
- Hernandez, L.R. & T.C. Emmel 1993. *Cactoblastis cactorum* in Cuba (Lepidoptera: Pyralidae: Phycitinae). *Tropical Lepidoptera* 4: 45-46.
- Hight, S.D., J.E. Carpenter, K.A. Bloem, S. Bloem, R.W. Pemberton & P. Stiling 2002. Expanding geographical range of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America. *Florida Entomologist* 85: 527-529.
- Hoffmann, J.H., V.C. Moran & D.A. Zeller 1998a. Evaluation of *Cactoblastis cactorum* (Lepidoptera: Phycitidae) as a biological control agent of *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa. *Biological Control* 12: 20-24.
- Hoffmann, J.H., V.C. Moran & D.A. Zeller 1998b. Exploiting a partially successful biocontrol agent for integrated control of a weed: *Cactoblastis cactorum* (Lepidoptera: Phycitidae) on *Opuntia stricta* (Cactaceae) in South Africa. *Journal of Applied Ecology* 35: 156-160.
- Hoffmann, J.H. & H.G. Zimmermann 1989. Ovipositional and feeding habits in cactophagous pyralids: prediction for biological control of cactus weeds. *Proceedings of the VIIth Symposium on Biological Control of Weeds, MAF, Rome*, 395-399.
- Hoffmann, J.H., V.C. Moran & H.G. Zimmermann 1999. Integrated management of *Opuntia stricta* (Haworth) Haworth (Cactaceae) in South Africa: an enhanced role for two, renowned, insect agents. In: *Biological Control of Weeds in South Africa (1990-1999)*. *African Entomology, Memoir No. 1*. 15-20.
- Hosking, J.R., R.E. McFadyen & N.D. Murray 1988. Distribution and biological control of cactus species in eastern Australia. *Plant Protection Quarterly* 3: 115-123
- Hosking, J.R., P.R. Sullivan & S.M. Welsby 1994. Biological control of *Opuntia stricta* (Haw.) Haw. var. *stricta* using *Dactylopius opuntiae* (Cockerell) in an area of New South Wales, Australia, where *Cactoblastis cactorum* (Berg) is not a successful biological control agent. *Agriculture, Ecosystems and Environment* 48: 241-255.
- Hosking, J.R., R.E. McFadyen & N.D. Murray 1988. Distribution and biological control of cactus species in eastern Australia. *Plant Protection Quarterly* 3: 115-123.
- International Atomic Energy Agency (IAEA) 2002. Mitigating the Threat of *Cactoblastis cactorum* to International Agriculture and Ecological Systems and Biodiversity. Report of a Consultants Group Meeting organized by the Technical Co-operation Department of the IAEA and the Joint FAO/IAEA Division of Nuclear Applications in Food and Agriculture, Vienna, Austria, July 2002, pp. 45.
- Johnson, D.M. & P.D. Stiling 1996. Host specificity of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an exotic *Opuntia*-feeding moth, in Florida. *Environmental Entomology* 25: 743-748.
- Johnson, D.M. & P.D. Stiling 1998. Distribution and dispersal of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), an exotic *Opuntia*-feeding moth, in Florida. *Florida Entomologist* 81: 12-22.
- Julien, M.H. & M.W. Griffiths (eds.) 1998. *Biological control of weeds. A world catalogue of agents and their target weeds, 4th Edition*. CABI Publishing, Wallingford, 1-233.
- LaChance, L.E. 1985. *Genetic methods for the control of Lepidopteran species: Status and potential*. United States Department of Agriculture/Agricultural Research Service, Washington, DC.
- Leibee, G.L. & L.S. Osborne 2001. Chemical control of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). *Florida Entomologist* 84(4): 510-512.
- Mahr, D.L. 2001. *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America: A workshop of assessment and planning. *Florida Entomologist* 84(4): 465-473.
- Mann, J. 1969. Cactus-feeding insects and mites. *Smithsonian Institution Bulletin* 256, Washington D.D. 1-158.
- Mann, J. 1970. *Cacti naturalized in Australia and their control*. Department of Lands, Queensland, Australia. 1-129.
- McFadyen, R.E. 1985. Larval characteristics of *Cactoblastis* spp. (Lepidoptera: Pyralidae) and the selection of species for biological control of prickly pears (*Opuntia* spp.) *Bulletin of Entomological Research* 75: 159-168.
- Moran, V.C. 1980. Interactions between phytophagous insects and their *Opuntia* hosts. *Ecological Entomology* 5: 153-164.

- 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. & H.G. Zimmermann 1984. The biological control of cactus weeds: Achievements and prospects. *Biocontrol News & Information* 5: 297-320.
- Moran, V.C. & H.G. Zimmermann 1984. The biological control of Cactaceae: Success ratings and the contribution of individual agents. *Proceedings of the VI International Symposium on Biological Control of Weeds, Vancouver, Canada*, 69-75.
- Moran, V.C. & H.G. Zimmermann 1991. Biological control of cactus weeds of minor importance in South Africa. *Agriculture, Ecosystems and Environment* 37: 37-55.
- Monro, J.M. 1975. Environmental variation and the efficiency of biological control – *Cactoblastis* in the southern hemisphere. Managing Terrestrial Ecosystems. In: J. Kikkawa & H.A. Nix (Eds.) *Proceedings of the Ecological Society of Australia* 9: 204-212.
- Murray, N.D. 1982. Ecology and evolution of the *Opuntia-Cactoblastis* ecosystem in Australia. In: J.S.F. Baker & W.T. Starmer (Eds.). *Ecological genetics and evolution*. Academic Press, Sydney, pp. 17-30.
- Myers, J.H., J. Monro & N. Murray 1981. Egg clumping, host plant selection and population regulation in *Cactoblastis cactorum* (Lepidoptera). *Oecologia* 51: 7-13.
- Nel, A., M. Krause & N. Khelawanlall 2002. *A guide for the control of plant pests*. Dept. of Agriculture, Republic of South Africa. 1-231.
- North, D.T. 1975. Inherited sterility in Lepidoptera. *Annual Review of Entomology* 20: 167-182.
- Pemberton, R.W. 1995. *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in the United States. An immigrant biological control agent or an introduction of the nursery trade? *American Entomologist* 41: 230-232.
- Pemberton, R.W. & H. Cordo 2001a. Potential and risk of biological control of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America. *Florida Entomologist* 84(4): 513-526.
- Pemberton, R.W. & H. Cordo 2001b. *Nosema* (Microsporidia: Nosematidae) species as potential biological control agents of *Cactoblastis cactorum* (Lepidoptera: Pyralidae): Surveys for the microsporidia in Argentina and in South Africa. *Florida Entomologist* 84(4): 527-530.
- Perez-Sandi y Cuen, M. 2001. Addressing the threat of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), to *Opuntia* in Mexico. *Florida Entomologist* 84(4): 499-502.
- Pettey, F.W. 1948. The biological control of prickly pear in South Africa. *Science Bulletin*, Department of Agriculture of the Union of South Africa 271: 1-163.
- Pierce, R.K. 1995. Infestation of *Opuntia* by the Phycitid moths *Melitara prodenialis* and *Cactoblastis cactorum*. Master's Thesis, The Department of Biological Sciences, Florida Atlantic University, Boca Raton, FL.
- Pretorius, M.W. & H. Van Ark 1992. Further insecticide trials for the control of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) as well as *Dactylopius opuntiae* (Homoptera: Dactylopiidae) on spineless cactus. *Phytophylactica* 24: 229-233.
- Pretorius, M.W., H. Van Ark & C. Smit 1986. Insecticide trials for the control of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) on spineless cactus. *Phytophylactica* 18: 121-125.
- Rebman, J.P. & D.J. Pinkava 2001. *Opuntia* cacti of North America – an overview. *Florida Entomologist* 84: 474-483.
- Robertson, H.G. 1987. Oviposition site selection in *Cactoblastis cactorum* (Lepidoptera): Constraints and compromises. *Oecologia* 73: 601-608.
- Robertson, H.G. 1988. Spatial and temporal patterns of predation by ants on eggs of *Cactoblastis cactorum*. *Ecological Entomology* 13: 207-214.
- Robertson, H.G. 1989. Seasonal temperature effects on fecundity of *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae): Differences between South Africa and Australia. *Journal of the Entomological Society of Australia (N.S.W.)* 52: 71-80.
- Robertson, H.G. & J.H. Hoffmann 1989. Mortalities and life-tables of *Cactoblastis cactorum* (Berg) (Lepidoptera, Pyralidae) compared on two host plant species. *Bulletin of Entomological Research* 70: 7-17.

- Robertson, H.G. 1985. The ecology of *Cactoblastis cactorum* (Berg) (Lepidoptera: Phycitidae) in relation to its effectiveness as a biological control agent of prickly pear and jointed cactus in South Africa. Ph.D. Thesis, Rhodes University, Grahamstown, South Africa.
- Simmonds, F.J. & F.D. Bennett 1966. Biological control of *Opuntia* spp. by *Cactoblastis cactorum* in the Leeward Islands (West Indies). *Entomophaga* 11: 183-189.
- Stange, G., J. Monro, S. Stowe & C.B. Osmond 1995. The CO₂ sense of the moth *Cactoblastis cactorum* and its probable role in the biological control of the CAM plant *Opuntia stricta*. *Oecologia* 102: 341-352.
- Starmer, W.T., V. Aberdeen & M.A. LaChance. 1987. The yeast community associated with decaying *Opuntia stricta* (Haworth) in Florida with regard to the moth, *Cactoblastis cactorum* (Berg). *Florida Scientist* 51:7-11.
- Stiling, P. 2000. A worm that turned. *Natural History* 109(5): 40-43.
- Stiling, P. 2002. Potential non-target effects of a biological control agent, prickly pear moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae), in North America, and possible management actions. *Biological Invasions* 4: 273-281.
- Stiling, P., A. Rossi & D. Gordon 2000. The difficulties of single factor thinking in restoration: replanting a rare cactus in the Florida Keys. *Biological Conservation* 94: 327-333.
- Stiling, P. & D. Simberloff 1999. The frequency and strength of non-target effects of invertebrate biological control agents of plant pests and weeds. In: P.A. Follet and J.J. Duan (Eds.). *Non-target effects of biological control*. Kluwer Academic Press: 31-43.
- Soberón, J., J. Golubov & J. Sarukhan 2001. The importance of *Opuntia* in Mexico and routes of invasion and impact of *Cactoblastis cactorum* (Lepidoptera: Pyralidae). *Florida Entomologist* 84(4): 486-492.
- U.S. Department of Agriculture, Soil Conservation Service 1982. *National list of plant names*. United States Department of Agriculture Technical Publication 159.
- U.S. Department of the Interior, Fish and Wildlife Service 1993a. *Endangered and threatened wildlife and plants*. Title 50 Code of Federal Regulations 17.11 and 17.12.
- U.S. Department of the Interior, Fish and Wildlife Service 1993b. *Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species*. Federal Regulation 58: 51144-51190.
- Vigueras, A.L. & L. Portillo 2001. Uses of *Opuntia* species and the potential impact of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in Mexico. *Florida Entomologist* 84(4): 493-498.
- White, G.G. 1980. Current status of prickly pear control by *Cactoblastis cactorum* in Queensland. *Proceedings of the V International Symposium for Biological Control of Weeds*. Brisbane, Australia. 609-616.
- Zimmermann, H.G. & G. Granata 2002. Insect pests and diseases. In: P.S. Nobel (Ed.) *Cacti, Biology and Uses*. University of California Press. 235-254.
- Zimmermann, H.G. & D.E. Malan 1981. The role of imported natural enemies in suppressing regrowth of prickly pear, *Opuntia ficus-indica*, in South Africa. *Proceedings of the V International Symposium for Biological Control of Weeds*. Brisbane, Australia. pp. 375-381.
- Zimmermann, H.G., R.E. McFadyen & H.E. Erb 1979. Annotated list of some cactus-feeding insects of South America. *Acta Zoologica Lilloana* 32: 101-112.
- Zimmermann, H.G. & V.C. Moran 1982. Ecology and management of cactus weeds in South Africa. *South African Journal of Science* 78: 314-320.
- Zimmermann, H.G. & V.C. Moran 1991. Biological control of prickly pear, *Opuntia ficus-indica* (Cactaceae), in South Africa. *Agriculture, Ecosystems and Environment* 37: 29-35.
- Zimmermann, H.G. & M. Perez-Sandi y Cuen 1999. A new insect pest on Opuntiae in wait for Mexico. *Memorias VIII Congreso Nacional y VI Congreso Internacional sobre Conocimiento y Aprovechamiento del Nopal*. University of San Luis Potosi, Mexico. 99. 333-341.
- Zimmermann, H.G., V.C. Moran & J.H. Hoffmann 2000a. The renowned cactus moth, *Cactoblastis cactorum*: its natural history and threat to native *Opuntia* floras in Mexico and the United States of America. *Diversity and Distributions* 6:259-269.
- Zimmermann, H.G., M. Perez-Sandi y Cuen, J. Golubov, J. Soberón M & J. Sarukhan K. 2000b. *Cactoblastis cactorum*, una nueva plaga de muy alto riesgo para las opuntias de Mexico. *Biodiversitas* 33: 2-13.