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BIODIVERSITY VIEWPOINTS

The renowned cactus moth, *Cactoblastis cactorum*: its natural history and threat to native *Opuntia* floras in Mexico and the United States of America

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Abstract. The cactus moth, *Cactoblastis cactorum* (Berg) (Phycitidae) is native to South America. It was released as a biological control agent against alien *Opuntia*-cacti in Australia in the 1920s, then in southern Africa, and latterly on several islands, including those in the Caribbean. In 1989, the cactus moth was discovered in Florida, in the United States of America, where it is now threatening the survival of indigenous *Opuntia* species. In this paper we identify some of the attributes that have contributed to the success of *C. cactorum* as a weed biological control agent. Many of these same qualities account for the problems that *C. cactorum* has caused in Florida and predispose it as a major threat to the speciose, native *Opuntia*-floras of Central and North America. An estimated 79 platyopuntia (prickly pear) species are at risk: 51 species endemic to Mexico; nine species endemic to the United States; and 19 species common to both countries. Many cultivated and wild *Opuntia* species, that are used in various ways, are also vulnerable to attack by *C. cactorum*, including at least 25 species in Mexico and three species in the United States, particularly the widely exploited and culturally important cultivars of *O. ficus-indica*. Some control strategies are suggested that may minimize the risk and consequences of invasion by the cactus moth. The wider implications of this threat to the practice of weed biological control and to conservation are discussed.

Key words. Biological control, biological invasions, Cactaceae, Mexico, native opuntias, non-target effects, threatened floras, United States.

INTRODUCTION

Cactus species are among the most cosmopolitan and destructive of invasive, alien plants. They constitute a significant actual and potential threat to conservation and agricultural production in many parts of the world (Cronk & Fuller, 1995; Bright, 1998). The cactus moth, *Cactoblastis cactorum* (Berg) (Phycitidae), which is native to South America, has been used as a biological control agent against several invasive species of *Opuntia* cacti in Australia since the 1920s and in Africa south of the Sahara since the 1930s. The cactus moth was later imported to New Caledonia, Hawaii, Mauritius, the Caribbean Islands, the Cayman Islands, St Helena, Ascension Island and Pakistan (where establishment is uncertain). It was introduced to Kenya in 1966 but did not establish (Julien & Griffiths, 1998). Some of these introductions have provided textbook examples epitomizing the great success that can be achieved through the manipulation of plant-feeding insects as biological control agents (Dodd, 1940; Fullaway, 1954; Moran & Zimmermann, 1984; Julien & Griffiths, 1998).

The detrimental effects of introduced biological control agents on organisms other than the target pest have, rightly, been criticized and the safety of biological control as a practice has recently been questioned (Howarth, 1991; Miller & Aplet, 1993; Simberloff & Stiling, 1996; Thomas & Willis,

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1998; Lockwood, 1999; Stiling & Simberloff, 1999). Concerns about non-target effects in biological control were the subject of an international conference held under the auspices of the International Organization of Biological Control, in Montpellier, France, from 17–20 October 1999 (see Cory & Myers, 2000). Compared with biological control of insect pests, the practice of *weed* biological control has a very good safety record (McFadyen, 1998; McEvoy & Coombs, 1999). In his critique of the safety of biological control generally, Howarth (1991) notes that 'greater care and stricter guidelines (are) required for the introduction of herbivores (i.e. mainly plant-feeding insects) ...'. He advocates that 'The protocols for weed control need to be strengthened and applied to programs aimed at other pests'. Ehler (1999) notes that in weed biological control 'concern over nontarget effects is of prime importance'. Strict protocols and the meticulous screening of insects and pathogens have ensured that risks are minimal and that there have been few recorded deleterious effects as a result of the release of biological control agents against weeds.

However, there are two recent, much-publicized examples of undesirable non-target effects in weed biological control. First, the musk thistle weevil, *Rhinocyllus conicus*, which was introduced for the biological control of thistles in Canada in 1968, in Montana and Virginia in 1969, and in California in 1971 (see Zwölfer & Harris, 1984) is now attacking the seed-heads of native thistles over large areas in the West and Central United States (Turner, 1985; Turner *et al.*, 1987; Louda & Potvin, 1995; Guretzky & Louda, 1997; Louda *et al.*, 1997; Strong, 1997; Louda, 1998, 1999; Nechols, 1999). Secondly, the cactus moth, *C. cactorum*, has arrived in Florida, probably from the Caribbean, and is damaging native opuntias, including the critically endangered semaphore cactus, *O. spinosissima* (= *O. corallicola*) (Bennett & Habeck, 1995; Pemberton, 1995; Johnson & Stiling, 1996, 1998; Stiling & Simberloff, 1999; Stiling, 2000; Stiling *et al.*, 2000). This very well-known biological control agent has now, ironically, itself become a threat to conservation because of the danger it poses to indigenous and cultivated *Opuntia* cacti in the United States and Mexico.

The case of *C. cactorum* has excited recent comment and warnings about possible consequences from a number of authors (e.g. Simberloff & Stiling, 1996; Lockwood, 1999; Stiling & Simberloff, 1999; Zimmermann & Perez-Sandi y Cuen, 1999; Cory & Myers, 2000; Stiling, 2000; Strong & Pemberton, 2000). Besides the direct threat to conservation, the fear is that the invasion and possible impacts of *C. cactorum* in the Americas could be used by political lobbies as an argument to impose unrealistic constraints on the practice of biological control (Ehler, 1999; McEvoy & Coombs, 1999). In this paper we deal with the natural history of *C. cactorum* as a biological control agent and we detail the threat it poses to the native *Opuntia* floras of Mexico and the United States. In doing so, we attempt to place the case of *C. cactorum* and the conservation issues associated with it, in a wider historical and geographical context than has been done yet.

THE BIOLOGY AND CACTUS HOSTS OF *CACTOBLASTIS CACTORUM*

The biology of *C. cactorum* is well documented (Dodd, 1940; Pettey, 1948; Robertson, 1985, 1987; Robertson & Hoffmann, 1989). This cactus-feeding phycitid, in common with some other cactophagous moths (Moran, 1980), lays its eggs one on top of the other to form spine-like 'eggsticks'. An 'eggstick' comprises, on average, 60–100 eggs and each female usually lays a total of 200–300 eggs (Dodd, 1940; Pettey, 1948; Robertson, 1985). The neonate larvae, collectively, burrow and enter cactus cladodes through a single entry hole, thus probably overcoming the defensive gum-secretions of the host plant (Hoffmann & Zimmermann, 1989). The larvae feed gregariously within the cladodes for about 2 months in summer and about 4 months in winter, before exiting to pupate in leaf-litter or in the soil (Dodd, 1940; Pettey, 1948). In Australia and South Africa, where *C. cactorum* occurs in temperate latitudes, there are two (rarely three) generations per year (Pettey, 1948; Robertson, 1985). In the warmer tropical climate of the Caribbean and Florida there may be more generations each year.

Cactoblastis cactorum is native to Argentina, Paraguay, Uruguay and southern Brazil (Mann, 1969) and is one of four described cactophagous species in the genus. Unlike its congeners, which are host-specific (i.e. monophagous) and have limited geographical ranges, *C. cactorum* exploits several species of *Opuntia* cacti as hosts (i.e. it is oligophagous). It

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occurs over a wide range of climates in South America (Mann, 1969) and in its countries of introduction, notably in Australia (Dodd, 1940) and South Africa (Pettey, 1948). In its native lands, *C. cactorum* has been recorded feeding on almost all of the many *Opuntia* species in the platyopuntia group (prickly pears) (Dodd, 1940; Mann, 1969; Zimmermann *et al.*, 1979; McFadyen, 1985). However, in South America, it does not attack the platyopuntias *O. longispina* var. *corrugata*, *O. quimilo* or *O. sulphurea* (Zimmermann *et al.*, 1979; McFadyen, 1985), nor any other genera of Cactaceae, including those in the cylindropuntia group (chollas) (Zimmermann & Perez-Sandi y Cuen, 1999).

Following the introduction of the cactus moth to Australia, southern Africa and elsewhere, *C. cactorum* readily attacked a number of novel *Opuntia* hosts of North American origin. These include: *O. compressa*, *O. ficus-indica*, *O. lindheimeri* (= *O. engelamannii*), *O. megacantha*, *O. spinulifera*, *O. streptacantha*, the various subspecies of *O. stricta* (= *O. dillenii*), *O. tomentosa*, *O. triacantha*, *O. tuna* and *O. vulgaris* (Pettey, 1948; Fullaway, 1954; Mann, 1969; Annecke & Moran, 1978; Moran & Zimmermann, 1984; Julien & Griffiths, 1998). It occasionally attacks the North American cylindropuntia, *O. imbricata*, in South Africa, but never becomes abundant on this species. It now also attacks the six native *Opuntia* species found in Florida (Johnson & Stiling, 1996).

CACTOBLASTIS CACTORUM AS A BIOLOGICAL CONTROL AGENT

Cactoblastis cactorum was released in several countries as a biological control agent in spite of its oligophagous habit and ability to damage or kill numerous species of opuntias. In Australasia and in the Old World, where there are no native *Opuntia* species, nor other con-familial cactus species, the release of *C. cactorum* was rational and safe. Before its release in the 1930s in South Africa, the impact of *C. cactorum* on cultivated spineless varieties of the target weed species, *O. ficus-indica*, was anticipated, assessed and discounted (Pettey, 1948; Annecke & Moran, 1978).

The spectacular success of *C. cactorum* in the control of invasive, alien opuntias has been cited often in ecological and biological control literature (e.g. Debach, 1974). Although several agents were implicated in the biological control of pest prickly pears in Australia, the cactus moth was the most important. The original stock of *C. cactorum* that was destined for Australia was derived from last-instar larvae collected in 1925 in pads of *O. delaetiana* and *O. monacantha* from Argentina (Dodd, 1940). Adult females from this stock produced about 3000 eggs which were placed on *O. monacantha* pads in Wardian cages and shipped, via Cape Town, to Australia, a journey which took 10 weeks. Over the next 9 years the cactus moth was mass-reared and about 2750 million eggs were distributed on infestations of *O. stricta* (the main pest prickly pear in Queensland and New South Wales) (Dodd, 1940). The rapid spread and success of *C. cactorum* was attributed to this massive rearing and release effort.

Dodd (1940) reports that, at the start of the campaign in Australia, about 24 million hectares (60 million acres) was infested with prickly pear, of which half of this area was so densely infested 'that the land was useless from a productive viewpoint'. For several years, until 1933, the scale of the operation was 'vast' and the scenery changed rapidly 'from flourishing [prickly] pear to dead [prickly] pear ... to crops and fodder grasses'. 'The celerity with which the insect multiplied and spread from many release centres is illustrated by the situation along the Moonie River ... In August 1930, for 150 miles [240 km] along the river the pest [*O. stricta*] was in its full vigour, its continuity almost unbroken by cleared land; the pastoral properties had been overrun and mainly deserted, former large holdings having become mere names on a map; ...' '... in August 1932, 90% of the [prickly] pear had collapsed. The change in exactly two years was extraordinary.' 'Its [i.e. the cactus moth] progress has been spectacular; its achievements border on the miraculous ...'. 'The prickly pear territory has been transformed as though by magic from a wilderness to a scene of prosperous endeavour'; '... 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.' Dodd (1940) estimated that about 25 million *C. cactorum* larvae had been required to kill off one hectare of heavily infested *O. stricta* (i.e. about 10 million per acre).

Today, the '*Cactoblastis* Memorial Hall' and the '*Cactoblastis* Cairn' in Queensland, are among

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the memorabilia celebrating these events. Dodd's (1940) observations emphasize the astronomical numbers of insects involved and the extraordinary scale of the success. They also serve as an indication of the magnitude of the potential threat to native opuntia floras in North and Central America.

DISPERSAL AND SPREAD OF *CACTOBLASTIS CACTORUM*

An understanding of the biology of natural, unaided dispersal in *C. cactorum* is obviously crucial in the debate about how the cactus moth came to be in Florida, in anticipating and assessing the threat of its further invasion onto native cacti in the United States, Mexico and the rest of Central America, and in devising strategies that minimize this risk. Unfortunately, evidence from the literature is mostly anecdotal and circumstantial and it is difficult to gain a clear impression of how far the cactus moth is able to disperse unaided and how quickly the species is able to spread once a new area is invaded.

Cactoblastis cactorum has not spread naturally from its native range in Argentina, Paraguay, Uruguay and southern Brazil to the large cultivated stands of *O. ficus-indica* in the state of Pernambuco in central Brazil (Arruda *et al.*, 1999), in spite of the presence of available hosts and of suitable climates *en route*. Within Argentina, it has not spread to cultivated *O. ficus-indica* plants in the valleys in the foothills of the Andes. The Andean mountain chain may have prevented the cactus moth from spreading to Chile, although suitable native *Opuntia* host-species and abundant commercial plantings of opuntias are present there (Marticorena & Quezada, 1985; Hoffmann, 1989). Physical barriers also may have prevented the spread of *C. cactorum* onto suitable cactus hosts in Central and North America.

In Australia, the unaided spread of *C. cactorum* on *O. stricta* was relatively slow (Dodd, 1940; Pettey, 1948). Larvae are able to move short distances from one host plant to another, but these trivial movements must be almost irrelevant in the context of the overall spread of the species. Where suitable hosts are densely abundant the adults seldom range far, but as food plants decrease in density the moths travel more widely (Dodd, 1940; Pettey, 1948; Robertson, 1985). There is a record of individual females flying as far as 24 km (15 miles) to oviposit (Dodd, 1940). In Australia, the cactus moth spread unaided, from the release points, for about 16–24 km (10–15 miles) in dense *O. stricta* infestations in 2.5 years (Dodd, 1940).

In South Africa, the unaided rate of spread of the cactus moth through infestations of the larger, tree-like prickly pear, *O. ficus-indica*, was less, at about 3–6 km in 2.5 years (Pettey, 1948). *C. cactorum* was introduced into South Africa nearly 70 years ago and is well established on several species of opuntias. However, it has failed, on its own, to colonize some isolated infestations and plantings of *O. ficus-indica*, although this host plant is very widely distributed in South Africa (Henderson, 1995). It also failed to spread naturally to a large (≈19 000 hectare) infestation of *O. stricta* in the Kruger National Park. This is surprising because the host plant, *O. ficus-indica*, was present in 1932 at high densities in the Eastern Cape Province (where *C. cactorum* has been established in large numbers since the late 1930s), and was contiguous in scattered infestations across the centre of the country, almost to the borders of the Kruger National Park (see distribution map in Pettey, 1948).

CACTOBLASTIS CACTORUM IN THE CARIBBEAN AND FLORIDA

The decision in 1957 to release *C. cactorum* to control native opuntias on islands in the Caribbean (Simmonds & Bennett, 1966) was not contested at the time. Only recently, after the moth was discovered in Florida, was this biological control programme in the Caribbean questioned. Certainly, such an introduction would not be sanctioned nowadays because of the risk of attack by *C. cactorum* on non-target native opuntias and because biological control of native plants that are pests is now considered to be unwise. Julien & Griffiths (1998) record that *C. cactorum* was introduced into the Caribbean for the control of *O. dillenii* (= *O. stricta*) (Cayman Islands, Nevis, Puerto Rico and associated islands), *O. lindheimeri* (Antigua and Nevis), *O. triacantha* (Antigua, Montserrat, Nevis, Puerto Rico and associated islands) and *Opuntia* species (St Kitts, U.S. Virgin Islands and Puerto Rico) (and see Moran & Zimmermann, 1984). The cactus moth was also found by one of us (HGZ) on at least one non-target species, *O. repens*, in Puerto Rico as long ago as 1974.

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OPUNTIA stricta var. *dillenii* was an important weed problem in Cuba in the early 1970s but, in contrast to the situation elsewhere in the Caribbean, a decision was taken not to import *C. cactorum*. In spite of this, the cactus moth was discovered on *O. stricta* var. *dillenii* in Cuba in 1974 and gave good control of the infestations (E.P. Montesbravo, personal communication). *C. cactorum* was subsequently recorded from the Isle of Pines (Bibijagua Beach) in 1992 (Hernández & Emmel, 1993). The origin of these *C. cactorum* populations is unknown and there have been no studies to determine the effects of the cactus moth on native, Cuban *Opuntia* species (E.P. Montesbravo, personal communication).

Over the years, the cactus moth has 'dispersed' to many islands in the Caribbean Basin such as Hispaniola and the Bahamas (Habeck & Bennett, 1990). The latter authors as well as Johnson & Stiling (1996) assumed that the moth had spread naturally among the Caribbean Islands and eventually dispersed of its own accord from there to Florida in the United States of America. The supposition that the 'moths dispersed on their own' to Florida 'which is just 90 miles (144 km) from Cuba' (Stiling, 2000) is problematic because *C. cactorum* is abundant only in the dry south-eastern part of Cuba, around Guantanamo (E.P. Montesbravo, personal communication), about 800 km on a direct line from the Florida Keys. Pemberton (1995) also speculated that the moth might have dispersed repeatedly between islands in the Caribbean as it is reputed to have done in Hawaii (Tuduri *et al.*, 1971). Although the moths are strong flyers, there is no direct evidence of natural, unaided inter-island dispersal in the Caribbean (Simmonds & Bennett, 1966). Certainly, *C. cactorum* was frequently transported between islands by man, for example from the Caribbean to the U.S. Virgin Islands (Simmonds & Bennett, 1966).

Recent studies by Pemberton (1995, 1996) provide evidence that *C. cactorum* could have been introduced to Florida through shipments of cactus plants that were colonized by larvae of the cactus moth and that were imported from the Dominican Republic to Florida by the plant-nursery trade. *C. cactorum* has colonized several native and introduced *Opuntia* species in Puerto Rico, Antigua, Nevis, St Kitts, Montserrat, Cuba, Hispaniola, Bahamas and the Dominican Republic (Habeck & Bennett, 1990; Bennett & Habeck, 1995; Julien & Griffiths, 1998). Shipments of any of these cactus species from any of these islands may have been the original source of the infestation by *C. cactorum* of the *Opuntia*-cacti in Florida. From 1981 to 1986 there were 13 interceptions of *C. cactorum* larvae at Miami ports and larvae were found inside *Opuntia* cladodes originating from a Dominican Republic supplier owned by a Florida nursery (Pemberton, 1995, 1996). Of the more than 300 000 *Opuntia* plants entering Miami from the Dominican Republic annually during the 1980s, most arrived in marine shipments (Pemberton, 1995, 1996) and illegal introductions by cactus collectors were also probably very frequent.

Following the introduction of the cactus moth into Florida, Johnson & Stiling (1998) estimated an initial northward 'migration' of *C. cactorum* from the lower Florida Keys at 256 km per year, decreasing to 40 km per year thereafter. They estimated that the moth had 'dispersed' 360 miles (576 km) northwards through Florida, from 1989 to 1991. They noted that the rate of spread depended on host plant availability and abundance. In 1999, the cactus moth was reported on Sapelo Island, Georgia (Stiling, 2000), which is about 650 km north of Miami.

The broad differences in the estimated rates of spread of the cactus moth in Australia (Dodd, 1940) and South Africa (Pettey, 1948) compared with Florida (Johnson & Stiling, 1998) are difficult to reconcile. In Australia the slow natural dispersal of *C. cactorum* was purposely enhanced by redistributions of the eggs and inadvertently supplemented through the behaviour of the cactus moth itself. Female moths (but not males) are attracted to light and were transported in vehicles and trains: '... electric lights in passing trains have proved attractive; moths have been found resting in railway carriages a long distance from the locality where they had entered on the previous night' (Dodd, 1940). It is possible that the relatively rapid spread of the cactus moth reported in Florida was also partly the result of inadvertent transport on trains, cars and aeroplanes. Perhaps the lower densities of hosts in Florida induced far more rapid and widespread natural dispersal of the cactus moth than was the case in Australia and South Africa, where there were very high host-plant densities. However, it is also possible that *C. cactorum* invaded the Florida Keys of its own accord and that, at about the same time, the

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species was imported inadvertently to the Miami area in shipments of cacti from the Caribbean. Multiple introductions, both natural and human-assisted, together with intrastate movement of infected nursery plants, rather than natural dispersal entirely, could provide a plausible explanation for the rapid spread of the cactus moth in Florida.

THE THREAT TO *OPUNTIA* SPECIES IN MEXICO AND THE UNITED STATES

Regardless of how *C. cactorum* arrived in Florida, it is almost inevitable that the moth will spread to other parts of North America and to Mexico and Central America either unaided or through the assistance of human activity. Dispersal of *C. cactorum* from Cuba to Mexico across the Yucatan Channel is a distinct possibility. However, its presence has not yet been detected in the Yucatan Province, or elsewhere in Mexico, even though cactus growers and agricultural officials have been widely consulted and alerted to the danger (Zimmermann & Perez-Sandi y Cuen, 1999). Natural spread on suitable hosts (such as *O. stricta*) that grow along the Gulf of Mexico from Florida to Mexico (Benson, 1982) is a likely avenue of dispersal. Otherwise it could move as larvae in horticultural-cactus freight or inadvertently as adults in craft via road, sea or air (see Bright, 1998). Indeed, a consignment of plants infested with *C. cactorum* was intercepted on a flight from (or via) Mexico to Miami in 1992 (Pemberton, 1995).

If the cactus moth invades the southern United States and Mexico the effects may be severe. Several studies in Australia and South Africa have shown that *C. cactorum* can kill individual plants and whole populations of small- to medium-sized *Opuntia* species (Dodd, 1940; Pettey, 1948; Zimmermann & Malan, 1981; Hoffmann *et al.*, 1998a, 1998b). Individual plants of the larger, woody, tree-like opuntias are not killed by *C. cactorum*. However, several authors (e.g. Pettey, 1948; Zimmermann & Malan, 1981; Johnson & Stiling, 1998) have noted that the new growth of mature plants is particularly susceptible to *C. cactorum* damage and that population reductions of the larger species of opuntias can be expected through the destruction of juvenile plants.

In the southern United States, besides the numerous varieties of *O. ficus-indica* that are cultivated for fodder and fruit, wild populations of *O. lindheimeri* and *O. robusta* are also utilized extensively for fodder (Felker, 1995). In Mexico, cacti have been of special importance since ancient times and have featured in the history, economy and cultural life of the country (Hoffmann, 1983). Opuntias were cultivated for food in the valleys of Tehuacan in the State of Puebla since at least 6500 BC (Smith, 1967). Wild prickly pears, which occur at a density of about 200 plants per hectare over 300 000 km^2 in Mexico, rival corn and agave (*Agave tequilana*) in importance (Pimienta-Barrios *et al.*, 1999). Besides their use as fodder, wild and cultivated opuntias are used widely for fruit and the tender young cladodes are harvested as a vegetable (Pimienta, 1994). A large industry is based on opuntia by-products including juices, jams, confectioneries, pharmaceuticals and cosmetics (Pimienta, 1994). Cultivars of *O. ficus-indica* serve as host plants for rearing the cochineal insect, *Dactylopius coccus* (Homoptera), which is the basis of a carmine-dye industry that has been in practice from ancient times (Sáenz-Hernández, 1995). Prickly pear opuntias are so important in the life and culture of Mexico that they are depicted in the National flag and on the modern-day Mexican coat-of-arms.

It seems likely that the platyopuntias (prickly pears) will be most at risk and few of the species in North and Central America will be immune. There are an estimated 51 species of platyopuntias endemic to Mexico, nine species endemic to the United States, and 19 species common to both countries, i.e. a total of 79 species that are vulnerable (Bravo-Hollis, 1978; Benson, 1982; Scheinvar, 1999; Zimmermann & Perez-Sandi y Cuen, 1999). It is possible that the list of vulnerable species could extend to some cylindropuntias (chollas) and to some 10 species in the genus previously known as *Nopalea* (now *Opuntia*). This supposition is based on the fact that, in South Africa, *C. cactorum* occasionally attacks *O. imbricata* (a cylindropuntia) and is able to develop on *N. (Opuntia) cochenillifera*.

In Mexico, several cultivated species of platyopuntias are likely to be attacked by *C. cactorum*. These include *O. albicarpa*, *O. amyclaea*, *O. cochinillifera*, *O. robusta* var. *larreyi*, *O. streptacantha* and particularly the many cultivars of *O. ficus-indica* that are grown over a total of about 60 000 hectares (Scheinvar, 1995; Pimienta-Barrios *et al.*, 1999). Also at risk in Mexico are at least 18 other species

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of uncultivated, native opuntias. These wild prickly pears are utilized for forage (and other purposes) or are being considered for cultivation, and include *O. hyptiacantha*, *O. joconostle*, *O. lindheimeri*, *O. megacantha*, *O. mutudae*, *O. robusta* var. *robusta*, *O. sorea* and *O. tomentosa* (Pimienta, 1994; Flores-Valdez & Aranda Osorio, 1997; Ochoa de Cornelli, 1997).

The precedent of the cactus moth as a biological control agent in Australia, and elsewhere, where huge areas of suitable opuntias were destroyed, suggests that the threat of *C. cactorum* invasions should be taken very seriously.

CONTROL OF *CACTOBLASTIS CACTORUM*

Given the necessary expertise, funding and resolve, it is possible to envisage the control or even the eventual eradication of *C. cactorum* in Florida and, if necessary, elsewhere in Central and North America. No such programme has yet been mounted, although studies on control of the cactus moth in Florida have been initiated by Johnson & Stiling (1996, 1998).

There are a number of research areas related to the biology, invasive potential and possible impact of the cactus moth that need attention, including: (i) a detailed study of its taxonomy (see McFadyen, 1985); (ii) the pattern and extent of its invasion in Florida; (iii) its natural dispersal abilities and potential for spread by deliberate and inadvertent human interventions — aspects which have obvious implications for management of the threat; (iv) its climatic tolerances; (v) factors affecting its survival, fecundity and success in the field in South America and in Florida and the Caribbean — in this respect, it would be important to determine the role of native Floridian parasites, predators and diseases in suppressing populations of *C. cactorum*, and to compare this information with the extensive data on the subject published by Australian and South African entomologists (e.g. Dodd, 1940; Pettey, 1948; Robertson, 1985; Robertson & Hoffmann, 1989); (vi) the actual and potential impacts of the cactus moth on individuals and populations of vulnerable host plants in Mexico and the United States; and (vii) the possible effects of *C. cactorum* invasions on the native cactophagous faunas (particularly con-familial phycitid moth species) in Mexico and the United States.

In South Africa, *C. cactorum* is readily controlled in cultivated stands of *O. ficus-indica* by removing the conspicuous eggsticks from the plants during the two oviposition-periods for *C. cactorum*, namely in February–March and in September–October (Annecke *et al.*, 1976). Whether *C. cactorum* in tropical climates will display two such well-synchronized generations per year is unknown. It may be necessary in Florida to collect the eggsticks over a longer period. Whatever the case, eggstick collections should be followed by removal of all cladodes, or portions thereof, that have larval colonies. Applications of persistent contact insecticides will kill the eggs and hatching larvae and may be an effective adjunct against *C. cactorum*, particularly in cultivated plantations. Other methods, such as sterile male techniques or pheromone trapping, are also worth consideration.

As a supplement to these suggested control strategies, research should re-start on the possible biological control of *C. cactorum*. Some preliminary investigations have been performed in this respect (R.W. Pemberton, personal communication). In South America, native populations of *C. cactorum* are attacked by at least five parasitoid species of which *Apantales alexanderi* (Braconidae) is the most common (Mann, 1969; Zimmermann *et al.*, 1979). Pathogens (e.g. *Nosema* species) also attack *C. cactorum* (Pettey, 1948) Whether any of these potential biological control agents will prove to be specific to *C. cactorum* remains to be established. One, *A. alexanderi*, is a generalist and the risks of non-target damage to the native phycitid and pyralid moth faunas of the United States may eventually disqualify biological control of *C. cactorum* as a viable strategy.

Early detection of invasions by the cactus moth will be crucial for successful control. Concerted, international preventative strategies, including awareness programmes to alert politicians, educators, cactus-collectors, researchers and nursery-people to the dangers posed by *C. cactorum* to conservation in Mexico and the United States would seem to be important. A review of national and international phytosanitary procedures as they apply to this particular problem may also be appropriate.

DISCUSSION

The extraordinary history of *C. cactorum* as a biological control agent against alien prickly pears

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in Australia and elsewhere has been used in this paper to stress the potential of the cactus moth as a pest of native opuntias in North and Central America. It would not be wise, however, to extrapolate directly from these experiences to predict disaster for indigenous opuntias in Mexico and the United States. The impact of the cactus moth could be dramatic in dense growths or in cultivated stands of opuntias in these countries, and it is disconcerting that *C. cactorum* is a major pest of cultivated cactus pears in Argentina, where the cactus moth occurs naturally. However, what may eventuate, should the cactus moth invade Mexico and the southern United States, will, of course, be governed by the local climate, parasites, predators and diseases, host-plant characteristics and many biotic and abiotic influences on the cactus moth itself, including the vagaries of its natural- or human-aided dispersal. The cactus moth did not become established after its introduction into Pakistan and Kenya, so it may take particularly suitable conditions to allow its invasion and spread in new areas. It will probably prove as difficult to predict the effects of a *C. cactorum* invasion into Mexico and the southern United States as it has always been to anticipate success or failure for biological control agents that were purposely released against weeds.

The presence of *C. cactorum* in Florida, and the consequent risks to native opuntia floras elsewhere in the United States and in Central America, has tarnished the safety record of weed biological control. The case of *C. cactorum* will continue to stimulate criticism and debate on the non-target effects of biological control. These discussions could result in reforms and new protocols that lead to increased safety in biological control generally. However, the indirect danger to conservation is that the spread of the cactus moth to Central and North America may result in negative sentiment in lay, scientific and political communities and the imposition of unrealistic constraints ('revenge effects') on the practice of weed biological control (McEvoy & Coombs, 1999). These authors advocate 'treating new control organisms as "guilty until proven innocent": presume(ing) each new control organism species is unnecessary, unsafe and ineffective until it is shown, beyond a reasonable doubt, to be necessary, safe and effective'. The concern is that countries that have not yet adopted biological control as a management option may be constrained from doing so for fear of causing undesirable side-effects in their own regions. Reluctance to use biological control could have substantial consequences in countries where invasions by alien plants impinge directly on the lives of people and where there are no alternative solutions to alleviate the problems.

Although the emphasis in this paper has been on the threat of *C. cactorum* to native opuntias in Mexico and the United States, there may be wider implications. Cacti (mainly cultivars of *O. ficus-indica*) are increasingly grown as 'wonder-plants' in many parts of the world, including North Africa, the Mediterranean countries, the Middle East, India and China. Cultivated opuntias in these countries are susceptible to invasion by *C. cactorum* (through the inadvertent importation of pads colonized by larvae of the cactus moth, as has been discussed in this paper). Should this happen, biological control of the cactus moth, using suitably specific parasitoids and/or diseases as agents, may be feasible and relatively uncomplicated by non-target effects. In other countries, where the cactus moth is used successfully as a biological control agent for the management of alien cacti, the emphasis may be on ways and means to keep out these agents. The story of *C. cactorum* and its role in conservation may have only just begun.

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