POTENTIAL AND RISKS OF BIOLOGICAL CONTROL OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE) IN NORTH AMERICA

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ABSTRACT

Cactoblastis cactorum Berg, an invasive moth and famous biological control of weeds agent, threatens numerous native and economic prickly pear cacti (*Opuntia*) in the United States and Mexico. Biological control of the moth, using a variety of approaches, is considered including: introduction of parasitoids and pathogens from the moth's native home in South America, introduction of parasitoids from related North American cactus moths (Pyralidae: Phycitnae), inundative releases of parasitoids known to attack the moth in Florida, and inundative releases of mass reared generalists parasitoids. The primary risk of employing biological control is the reduction of the many North American cactus moths, some of which probably regulate native *Opuntia* that can be weedy. The various biocontrol approaches are ranked according to their relative risk to the native cactus moths. The introduction of South American parasitoids or pathogens specific to the genus *Cactoblastis* (if they exist) may be the least risky approach. The introduction of South American parasitoids that can attack many cactus moths is the most risky approach because it could result in persistent "control" of these non-target native insects. Biological control probably can reduce the abundance of *C. cactorum* populations but is unlikely to prevent the spread of the moth. The relative benefits and risks of biological control need to be carefully assessed prior to any operational biological control programs. It will be difficult to reach agreement on acceptable levels of risk, if the likely benefits can't be predicted. Other management options need to be considered.

Key Words: *Opuntia*, biological control risk, cactus moths, host specificity, parasitoids, insect pathogens

RESUMEN

Cactoblastis cactorum Berg, una polilla famosa como agente de control biológico de malezas, amenaza numerosas especies nativas y económicas de cactos del género *Opuntia* en los Estados Unidos de América y en México. Se considera en este trabajo el control biológico de la polilla, utilizando diversas alternativas: la introducción de parasitoides y patógenos de Sud América, el área nativa de la polilla; la introducción de parasitoides de polillas de cactos de Norte América (Pyralidae: Phycitinae); liberaciones inundativas de parasitoides que atacan a *C. cactorum* en la Florida, y liberaciones inundativas de parasitoides generalistas criados en forma masiva. El principal riesgo de la utilización del control biológico es el empobrecimiento de las muchas especies de polillas de cactos de Norte América, algunas de las cuales probablemente regulan *Opuntia* nativas que podrían ser malezas. Las distintas alternativas del control biológico son ordenadas de acuerdo al riesgo relativo hacia las polillas de cactos nativas. La introducción de parasitoides y patógenos específicos del género *Cactoblastis* (si existieran) en Sud América, sería la alternativa menos riesgosa. La introducción de parasitoides sudamericanos que ataquen muchas polillas de cactos es la alternativa más riesgosa porque podría resultar en el "control" permanente de estos insectos que no son objetos del control biológico. El control biológico probablemente pueda reducir la abundancia de las poblaciones de *C. cactorum* pero es poco probable que pueda prevenir la dispersión de la polilla. Los beneficios relativos y riesgos del control biológico necesitan ser cuidadosamente evaluados antes del comienzo de los programas de control. Será tal vez difícil lograr acuerdos sobre los niveles de riesgo aceptables si los beneficios esperados no pueden ser estimados. Otras opciones de manejo necesitan ser consideradas.

Cactoblastis cactorum Berg has successfully controlled pest prickly pear cacti (*Opuntia* species) in Australia (Dodd 1940) and in many other places in the world (Moran & Zimmermann 1984). The moth was introduced to Nevis in the Caribbean in 1957 to control native *Opuntia* species that were weeds of pasture (Simmons & Bennett 1966). In 1989, *C. cactorum* was found in Florida (Habeck & Bennett 1990). The insect may have spread on its own from other places in the

Caribbean (Johnson & Stiling 1996) or may have been accidentally introduced by the nursery industry (Pemberton 1995). Since that time the moth has spread throughout the Florida peninsula where it attacks five of the six *Opuntia* species native to the state, including the endangered *Opuntia spinosissima* Miller (see Stiling & Moon this volume). There is considerable concern that the moth will continue to spread and attack additional *Opuntia* species. There are many native *Opuntia* in the southwestern U.S. and Mexico that could be harmed by the moth (Strong & Pemberton 2000; Zimmermann et al. 2000). An estimated 79 *Opuntia* species native to Mexico and the United States are at risk (Zimmermann et al. 2000). In addition, as many as 25 *Opuntia* species in Mexico and three species in the United States are used by people as food, animal fodder, and as the host of the cochineal dye producing scale (Zimmermann et al. 2000).

Currently in Florida the primary host plant of *C. cactorum* is *O. stricta* (Haworth) Haworth which is distributed around the Gulf of Mexico from Florida to Texas and Mexico. It appears likely that the moth will spread from Florida to Texas using this plant. If *C. cactorum* reaches Texas and Mexico, many other *Opuntia* species could become hosts and the moth could continue its spread via these new hosts. This would also bring the moth into contact with endangered *Opuntia* species that could be harmed. The ability of *C. cactorum* to quickly and completely control many exotic weedy *Opuntia* in disparate parts of the world, and also native weedy *Opuntia* species in the Caribbean, suggest that the moth could be particularly dangerous in North America.

In addition to the ecological damage caused by the moth, public confidence in biological control practice is being injured because of the moth's damage and threat to native *Opuntia*. Unfortunately, this situation is occurring when biological control, a critical tool in the fight against the many invasive species, is needed more than ever before.

The possible use of biological control against *C. cactorum* in North America was first raised by Bennett and Habeck (1992). Biological control has controlled many insects, including Lepidoptera that feed within plants. For example, the European pine shoot borer, *Rhyacionia buoliana* (Denis & Schiffermuller), and the European corn borer, *Ostrinia nubialis* (Hübner), have been successfully reduced using biological control (Kogan et al. 1999; Dahlsten and Mills 1999). In this paper, we will consider the possibilities of various biological control approaches that might be useful to reduce existing populations of the moth in Florida and adjacent Georgia, and perhaps limit its spread. The possible benefits and perceived risks of each approach will be discussed. We do not wish to advocate the use of biological control for *C. cactorum* in North America, but we think it is important to explore the potential use and implications of various biological control options.

Materials and Methods

Searches of the literature were made to detect the known parasitoids and diseases of *Cactoblastis* species and other species of cactus moths (Pyralidae: Phycitinae). Compilations of these organisms were created in different categories related to various biological control options. Other literature, primarily parasitoid catalogues, were searched to detect records of other host insects of these natural enemies, to help judge their host specificity. Criteria related to the potential benefit and risk of different biological control approaches were developed and then used to rank these approaches.

Results and Discussion

Biological control using parasitoids of *Cactoblastis cactorum* from its native range in South America

The 8-9 parasitoids associated with the cactus moth in South America are shown in Table 1. These include one braconid larval parasitoid, one chalcidid pupal parasitoid, 5-6 ichneumonid wasps and one tachinid fly. Apparently no egg parasitoids are known. The chalcidid wasp, *Brachymeria cactoblastidis* Blanchard, is suspected of being a hyperparasitoid (Zimmermann et al. 1979). The braconid wasp, *Apanteles alexanderi* Brethes, has been recorded to cause more than 30% parasitism of the larvae and the ichneumonid, *Temelucha* sp., was recorded to cause 5-30% parasitism of the larvae (Zimmermmann et al. 1979). Parasitism rates of the other parasitoids were not recorded, but two of the ichneumonid wasps are rare. *Apanteles alexanderi* attacks other cactus moths and at least three other genera of Lepidoptera, and probably others (DeSantis 1967; Mann 1969). The *Temelucha* sp. and the tachinid, *Epicoronimyia mundelli* (Blanchard), are known to use other genera of cactus moths (Mann 1969; Blanchard 1975; Zimmermann et al. 1979). No information about other potential hosts of the remaining parasitoids, the four ichneumonid wasps, was found, but this is probably due to a lack of knowledge rather than a true absence of other hosts.

Some of these wasps appear to have the potential to reduce *C. cactorum* populations (e.g., *A. alexanderi* and *Temelucha* sp.). If used in the United States, they probably would be able to orient to the plants and locate *C. cactoblastis* inside the pads where they feed. It is, however, unlikely that any of these parasitoids are monophagous, so their introduction for *C. cactorum* control could result in use of and harm to non-target Lepidoptera in North America, especially native cac-

TABLE 1. KNOWN PARASITOIDS OF *CACTOBLASTIS* IN THEIR NATIVE SOUTH AMERICA.

Parasitoid species	*Cactoblastis* species	Other hosts	Stage attacked	Degree of attack of *Cactoblastis*	Reference	Presumed specificity
Hymenoptera						
Braconidae						
Apanteles alexanderi Brethes	*C. cactorum* Berg		Larvae		Parker et al. 1953	broad
	C. cactorum Berg *C. doddi* Heinrich	*Tucumania tapiacola* Dyar *Salambona analamprella* (Dyar)		Not mentioned	Mann 1969	
	Cactoblastis spp.			>30%	Zimmermann et al. 1979	
	C. cactorum?				Bennett & Habeck 1992	
		Salambona analamprella *Tucumania tapiacola* *Plutella maculipennis* Curt. *Eulia loxonephes* Meyr. *Eulia* sp. *Argyrotaenia sphaleropa* (Meyr.) Lepidoptera sp.			DeSantis 1967	
Chalcididae						
Brachymeria (*Pseudobrachymeria*) *cactoblastidis* Blanchard	*C. doddi* Heinrich		Pupae		Mann 1969	
	Cactoblastis spp.		Pupae prob. hyperparasitoid		Zimmermann et al. 1979	
	C. cactorum?				Bennett & Habeck 1992	
Brachymeria sp.	*C. cactorum*		Pupae?		Thompson 1943	
Ichneumonidae						
Chromocryptus doddi (Cushman)	*Cactoblastis* spp.		?	Rare	Zimmermann et al. 1979	?
Cryptus sp.	*C. cactorum*		?		Mann 1969	?
Phyticiplex doddi (Cushman) (Probably a synonym of *Chromocryptus doddi*)	*C. cactorum*		?		Bennett & Habeck 1992	?
Phyticiplex eremnus (Porter)	*C. cactorum*		?		Bennett & Habeck 1992	?
Podogaster cactorum (Cushman)	*C. cactorum*		?		DeSantis 1967	?
	Cactoblastis spp.			Rare	Zimmermann et al. 1979	
Podogaster sp.	C. cactorum				Mann 1969	?

TABLE 1. (CONTINUED) KNOWN PARASITOIDS OF *CACTOBLASTIS* IN THEIR NATIVE SOUTH AMERICA.

Parasitoid species	*Cactoblastis* species	Other hosts	Stage attacked	Degree of attack of *Cactoblastis*	Reference	Presumed specificity
Temelucha sp. (*Temelucha* = *Cremastus*)	*Cactoblastis* spp.	*Salambona analamprella* *Tucumania* spp.		5-30% Rare 5-30%	Zimmermann et al. 1979	?
Diptera						
Tachinidae						
Epicoronimyia mundelli (Blanchard)	*C. doddi*	*Tucumania tapiacola* Dyar			Mann 1969	?
					Blanchard 1975	
	C. cactorum?				Zimmermann et al. 1979	

tus moths. Careful host specificity research might identify some of these parasitoids with narrow enough host ranges to minimize potential non-target risks. Such parasitoids could be a viable control option. Parasitoids probably could be obtained from climatic areas of South America that are similar to Florida, which would increase the probability of establishment and control.

Biological control using insect pathogens

Two types of diseases, an entomopathogenic fungus and a protozoan, have been recorded to infect *Cactoblastis* species (Table 2). The fungus *Beauveria* sp. caused high death rates of larvae in many places in Australia (Dodd 1940), but *Beauveria* probably *bassiana* (Balsamo) Vuillemin caused only low levels of infection in larvae and pupae in South Africa (Pettey 1948). This fungus is a cosmopolitan disease with a broad host range. It has been isolated from more than 200 hosts, including spiders (Feng et al. 1994). *Beauveria bassiana* has been used in biological control of grasshoppers, scarab beetles and other insects (Hajek & Butler 2000). It might be possible to use the fungus in an inundative biological control of *C. cactorum* in limited situations such as where the moth threatens the few remaining plants of *Opuntia spinossisma* in the Florida Keys. The control obtained would be dependent on local weather conditions and perhaps broader climatic conditions as suggested by the differing levels of infection of *C. cactorum* in Australia and South Africa. Control at best would be temporary.

Many pathogens such as *B. bassiana* have wide host ranges, but fungal pathogens with narrower host ranges are known. One such fungus, *Entomophaga maimaiga* Humber, Shimazu & Soper, is successfully controlling the gypsy moth, *Lymantria dispar* L., in the U.S. (Hajek et al. 1990). No such fungal pathogens are known from *C. cactorum* but none has been sought. Exploration for pathogens of the moth could be productive. Demonstrating the safety of such pathogens probably would be difficult because the laboratory host ranges and field host ranges are different and host acceptance is not always determined by phylogenetic position of the host insect (Hajek & Butler 2000).

Two *Nosema* were described from *Cactoblastis* species in South Africa (Fantham 1939). One of these, *N. cactoblastis* Fantham, was described causing up to 100% infection of winter broods of larvae in some South African localities (Pettey 1948). This microsporidium was thought to be the cause of the lack of control of pest *Opuntia* by *C. cactorum* in these areas. Surveys for these *Nosema* spp. were recently made in South Africa and Argentina, where they may have originated (Pemberton & Cordo 2001, this volume). Considerations for their use against *C. cactorum* in

TABLE 2. KNOWN DISEASES OF *CACTOBLASTIS*.

Agent	Host	Stage attacked	Degree of attack	Place of attack	Reference	Presumed specificity
Fungi						
Beauveria sp.	*C. cactorum*	Larvae, winter generation	High death rate in many places	Australia	Dodd 1940	Broad
Beauveria prob. *bassiana* (Bals.) Vuill.	*C. cactorum*	Larvae and pupae	3.3 (summer) to 5.2% (winter)	South Africa	Pettey 1948	Broad
Microsporidia						
Nosema cactoblastis Fantham	*C. cactorum*	All stages	0-100% winter; 0-18.7% summer	South Africa	Fantham 1939 Pettey 1948	Narrow
Nosema cactorum Fantham	*Cactoblastis* sp.	All stages		South Africa	Fantham 1939 Pettey 1948	Narrow
Nosema sp. or spp.	C. cactorum	All stages, detected in larvae	0 to 5.8% summer	Argentina	Pemberton & Cordo 2001	?

North America are discussed in that paper. *Nosema*, like other pathogens, usually have their greatest impact at high host population levels. This characteristic might limit their impact on *C. cactorum* if they were introduced against the moth in North America.

Bacillus thuringensis Berliner and its products are commonly used in biological control programs against pest Lepidoptera (Beegle & Yamamoto 1992). *Cactoblastis cactorum* larvae could probably be killed by the disease and its products, but they would be unlikely to contact it because they feed entirely within the pads of their prickly pear hosts.

Biological control using parasitoids known to attack *Cactoblastis cactorum* in Florida

An alternative to importing exotic parasitoids for *C. cactorum* control could be to employ the parasitoids already known to attack the moth in Florida (Table 3). Only three species, two chalcidoid pupal parasitoids and one trichogrammatid egg parasitoid, are known (Bennett & Habeck 1992). One of the chalcidoids, *Brachymeria ovata* Say, attacked 55% of *C. cactorum* pupae at one site. The other chalcidoid, *B. pedalis* Cresson, was reared from a single pupa. The host range of *B. ovata* is very wide; it has been reared from diverse butterflies and moths (Peck 1963). *Brachymeria pedalis* may be limited to cactus moths (Thompson 1943; Krombein et al. 1979; Mann 1969). This parasitoid probably moved to *C. cactorum* from *Melitara prodenialis* Walker, a native cactus moth host of the parasitoid (Krombien et al. 1979) which attacks platyopuntias (prickly pears) in Florida. The egg parasitoid, an unidentified *Trichogramma*, was recorded to attack two egg sticks. Since this species was not determined, its other hosts are unknown, but most *Trichogramma* species have broad host ranges (Pinto & Stouthamer 1994).

All three of these parasitoids could be collected, reared to increase their numbers, and then released against *C. cactorum* in the field. The *Brachymeria* spp. might be reared on easily cultured Lepidoptera such as the pyralid flour moths, *Plodia* and *Ephestia* spp., if they proved to be acceptable hosts. It also might be feasible to mass rear the *Trichogramma* sp. on other more easily grown moth eggs and then release on particular *C. cactorum* populations. These might be employed against *C. cactorum* attacking vulnerable *Opuntia* such as *O. spinossisima* in the Florida Keys, or *O. stricta,* at the leading edge of the moth's populations in northern Florida and southern Georgia. The suitability of these parasitoids for this approach is unknown. Inundative releases of *Trichogramma* could have an adverse impact on non-target Lepidoptera, especially rare butterflies such as those in the Florida Keys (Bennett & Habeck 1992). Inundative releases of *Brachymeria pedalis* could also depress *Melitara prodenialis* populations and perhaps other cactus moths, but should impact no other species. *B. ovata* releases could potentially affect a wide array of Lepidoptera.

The relative lack of parasitoids attacking *C. cactorum* in Florida, which could be used in this approach, may reflect the limited knowledge of its natural enemies in Florida and also the relatively short time that the moth has been in the state. Increased research may reveal additional parasitoids that could be employed in this approach.

Biological control using cosmopolitan generalist parasitoids known to attack *Cactoblastis cactorum*

Perhaps more suitable for the inundative biological control approach are two generalist parasitoids known to attack *C. cactorum* (Table 4). A braconid wasp, *Bracon hebetor* Say, parasitized up to 25% of the larvae in South Africa (Pettey 1948) and *Trichogramma minutum* Riley parasitized up to 32% of the moth's eggs in Australia (Dodd 1940). These attack rates were naturally occurring. Higher rates of attack might be obtained with inundative releases into *C. cactorum* populations. Both parasitoids already occur in North America, and *T. minutum* has been used previously in inundative biological control of many pest insects (Li 1994), including the sugarcane borer *Diatraea saccharalis* (Fab.) in Florida (Wilson 1941). *Trichogramma minutum* is easily reared on a variety of insect eggs and is also available commercially. *Bracon hebetor* could be mass reared on some of its known hosts that are easily raised, including *Galleria mellonella* (L.), *Plodia interpunctella* (Hübner) and *Sitotroga cerealella* (Olivier).

These parasitoids, like those already recorded to attack the cactus moth in Florida, could be released into *C. cactorum* populations that threaten rare cacti, and populations at the leading edge of the moth's expansion. These parasitoid species would attack non-target insects. *Bracon hebetor* parasitizes at least three families of moths (Krombein et al. 1979) but prefers concealed hosts like most *Bracon* species (Askew 1971). *Trichogramma minutum* is known to attack insects in many different orders (Clausen 1940). The release of this parasitoid should not be made in areas where rare butterflies or moths occur. *Trichogramma* species are usually habitat specialists and many have poor dispersal abilities (Orr et al. 2000). Both control of *C. cactorum* and impacts on non-target species brought by these wasps would probably be temporary because neither wasp may persist in the environment. Periodic releases would be necessary for ongoing control of *C. cactoblastis.*

Biological control of *Cactoblastis cactorum* with parasitoids of related North American cactus moths

The 14 parasitoids listed in Table 5 are reported to parasitize seven cactus moth species in

TABLE 3. PARASITOIDS KNOWN TO ATTACK *CACTOBLASTIS CACTORUM* IN FLORIDA.

Parasitoid species	Other hosts[1]	Stage attacked	Degree of attack in *C. cactorum*	Reference	Presumed specificity
Hymenoptera					
Chalcididae					
Brachymeria ovata Say	Diverse butterflies and moths	Pupae	To 55%	Bennett & Habeck 1992 Peck 1963	Broad
B. (*Pseudobrachymeria*) *pedalis* Cresson	Other specialised phycitid moths attacking cacti	Pupae	One pupa in 1991	Bennett & Habeck 1992	Moderately narrow?
	Melitara prodenialis Walker			Krombein et al. 1979	
	M. dentata (Grote)			Mann 1969	
	Olycella junctolineella (Hulst)			Mann 1969	
	Alberada parabates (Dyar)			Mann 1969	
	Ozamia fuscomaculella clarefacta (Dyar)			Mann 1969	
Trichogrammatidae					
Trichogramma sp.	Yes, unknown	Egg	Two egg sticks	Bennett & Habeck 1992	Broad

[1]Recorded host not necessarily in Florida.

TABLE 4. COSMOPOLITAN GENERALIST PARASITOIDS KNOWN TO ATTACK *CACTOBLASTIS* THAT ARE KNOWN TO OCCUR IN NORTH AMERICA.

Parasitoid species	Other hosts	Stage attacked	Degree of attack in *C. cactorum*	Place of attack	Reference	Presumed specificity
Hymenoptera						
Braconidae						
Bracon hebetor Say	*Heliothis obsoleta* (Noctuiidae), *Ephestia*, *Galleria*, *Plodia*, *Vitula* (Pyralidae: Phycitinae), *Sitotroga* (Gelechiidae)	Larvae	To 25%	South Africa	Pettey 1948 Krombein et al. 1979	Broad
Trichogrammatidae						
Trichogramma minutum Riley	Many species	Egg	To 32%	Australia	Dodd 1940	Broad

three genera in the tribe Phycitinae (Pyralidae). These moths include three *Melitara*, three *Olycella* and one *Ozamia* species. All feed within the pads of prickly pear cacti. The 14 parasitoids include: one chalcid pupal parasitoid, five ichneumonid parasitoids (four attack larvae and one species is an egg-larval parasitoid), five braconid wasp larval parasitoids, and three tachinid flies that attack both larvae and pupae. *Brachymeria pedalis* (Chalcididae), *Temelucha sinuatus* Cushman (Ichneumonidae), and *Apanteles etiellae* Vierek (Braconidae) appear to be specialists of cactus moths, whereas the other parasitoids appear to be generalists. The degree of attack of these parasitoids on their native hosts is unknown to us, so it is difficult to sense how much parasitism they might induce in *C. cactorum*. The ability of these parasitoids to attack *C. cactorum* is also unknown, except for *Brachymeria pedalis* that attacks the moth in Florida (Bennett & Habeck 1992). However, *C. cactorum* probably would be a suitable host for most of these parasitoids.

Releases of specialist parasitoids of *Melitara prodenialis* into *C. cactorum* populations could be effective because the moths are closely related, use *Opuntia* species, and are partly sympatric, so occupy areas of climatic similarity. Introduction of any of the ten North American cactus moth parasitoids, distributed beyond the current distribution of *C. cactorum*, would be classical introductions to Florida. These parasitoids are mostly from western cactus moths and may be less suitable for *C. cactorum* control in Florida and Georgia because they may be unable to survive and develop effective populations in this humid region.

Potential risks of biological control of *Cactoblastis cactorum* in North America

The potential risks associated with biological control of *C. cactorum* in North America are both direct and indirect. The direct risk is the reduction of populations of non-target insects by parasitoids employed against the moth. The insects most likely to be harmed by the introduction of "specialist" parasitoids from the native South America range of *C. cactorum* are related cactus moths in North America (Table 6). The level of risk will depend on the level of specialization. There are at least 16 species of cactus moths (Pyralidae: Phycitinae) in eight genera that occur in the U.S., Mexico and the West Indies (Heinrich 1939). In addition, in the same geographic areas there are at least seven species of specialist cactus feeding moths in seven genera in four other families: the Pyraustidae (*Megastes*, *Noctuelia*, and *Mimorista*), Gelechiidae (*Metapleura* and *Aerotypia*), Tineidae (*Dyotopasta*), and Gracillariidae (*Maramara*) (Mann 1969). It is probable that the highest risk of specialist parasitoids from *C. cactorum* in its native range would be to cactus moths most similar to *C. cactorum* and which co-

TABLE 5. PARASITOIDS OF RELATED CACTUS MOTHS (PYRALIDAE: PHYCITINAE) WHICH MAY HAVE POTENTIAL AS CONTROL AGENTS OF *CACTOBLASTIS CACTORUM*.

Parasitoid species	Cactus moth hosts (Pyralidae: Phycitinae)	Other hosts	Stage attacked	Degree of attack	Reference	Presumed specificity
Hymenoptera						
Chalcididae						
Brachymeria (*Pseudobrachymeria*) *pedalis* Cresson	*Melitara prodenialis* Walker *M. dentata* (Grote) *Olycella junctolineella* (Hulst) *Ozamia fuscomaculella* (Dyar) = *O. odiosella* *Alberada parabates*		Pupae	?	Mann 1969	
Ichneumonidae						
Temelucha sinuatus Cushman) (*Temelucha* = *Cremastus*)	*Melitara prodenialis* Walker *M. dentata* (as *M. doddalis*) *Cactobrosis strigalis* (Barnes & McD.), *Rumatha glaucatella* (Hulst)		Larvae	?	Mann 1969 Krombein et al.1979	Relatively narrow?
T. facilis (Cresson)	*M. denata* (as *M. doddalis*)	*Crambus*, *Hellula*, *Ostrina* (Pyralidae), *Isophrictis* (Gelechiidae)	Larvae	?	Mann 1969 Krombein et al. 1979	Broad
Temelucha sp.	*Cahela ponderosella* Barnes & McD.		Larvae	?	Mann 1969	?
Trichomma prob. *maceratum* (Cresson)	*M. dentata*	*Etiella*, *Pima* (Pyralidae), *Barbara* (Torticidae)	Larvae	?	Mann 1969 Krombein et al. 1979	Broad
Chelonus electus (Cresson) (= *C. texanus*)	*M. dentata* (as *M. doddalis*) *Ozamia fuscomaculella* = *O. odiosella*, *Alberada parabates*	*Heliothis* (Noctuidae); *Laphygma*, *Prodenia*, *Ephestia*, *Loxostege* (Pyralidae)	Egg (emerges from larva)	?	Mann 1969 Muesebeck et al. 1951	Broad
Mesostenus gracilis Cresson	*Ozamia fuscomaculella* = *O. odiosella*	*Anagasta*, *Cadra*, *Ephestia*, *Euzophera*, *Homeosoma*, *Laetilia* (Pyralidae)	?	?	Krombein et al. 1979	Broad
Braconidae						
Apanteles etiellae Vierek	*Melitara prodenialis* *Cahela ponderosella* *Olycella*	*Eteiella*, *Cansarsia*, *Elasmopalpus*, *Psorosina*, *Ufa* (Pyralidae)	Larvae	?	Mann 1969 Krombein et al. 1979	Broad
A. megathymi Riley	*Olycella nephelepasa* (Dyar)	*Megathymus* (Hesperiidae)	Larvae	?	Mann 1969 Krombein et al. 1979	Broad
Apanteles sp.	*Olycella junctolineella* (Hulst)		Larvae	?	Mann 1969	?
A. mimoristae Muesebeck	*Olycella junctolineella*	*Mimorista*, *Hymenia* (Pyralidae: Pyraustinae)	Larvae	?	Krombein et al. 1979	Broad

TABLE 5. (CONTINUED) PARASITOIDS OF RELATED CACTUS MOTHS (PYRALIDAE: PHYCITINAE) WHICH MAY HAVE POTENTIAL AS CONTROL AGENTS OF *CACTOBLASTIS CACTORUM*.

Parasitoid species	Cactus moth hosts (Pyralidae: Phycitinae)	Other hosts	Stage attacked	Degree of attack	Reference	Presumed specificity
Bracon hebetor Say	*Melitara* sp., Texas (In cages)	*Anagasta*, *Cadra*, *Ephestia*, *Galleria*, *Laetilia*, *Moodna*, *Plodia*, *Vitula* (Pyralidae); *Phothorimaea*, *Sitotroga* (Gelechiidae)	Larvae	?	Dodd 1940 Muesebeck et al. 1951 Krombein et al. 1979	Broad
	M. dentata (as *M. doddalis*)				Mann 1969	
	Ozamia fuscomaculella = *O. odiosella*				Mann 1969	
Heterospilus melanocephalus Rohwer	*Olycella junctolineella*	*Noctuelia* (Pyralidae: Pyraustinae)	?	?	Muesebeck et al. 1951	?
Diptera						
Tachinidae						
Phorocera texana Aldrich & Webber	*Melitara prodenialis* *M. dentata* *Olycella junctolineella* *Olycella nephelepasa*	Hymenoptera: Diprionidae, Tenthridindae; diverse Lepidoptera	Larvae, pupae	?	Mann 1969 Arnaud 1978	Broad
Phorocera comstocki Williston	*M. dentata*	Hymenoptera: Diprionidae Lepidoptera: Cossidae, Megathymidae, Pyralidae—Ostrina	Larvae, pupae	?	Mann 1969 Arnaud 1978	Broad
Lespesia aletiae Riley	*Olycella junctolineella*	Coccinellidae (*Epilachna*), diverse Lepidoptera	Larvae, Pupae	?	Mann 1969 Arnaud 1978	Broad
Lespesia sp.	*Melitara prodenialis*	diverse Lepidoptera	Probably larvae, pupae	?	Mann 1969 Arnaud 1978	Broad

TABLE 6. CACTUS MOTHS (PYRALIDAE: PHYCITINAE) IN U.S., MEXICO, AND THE WEST INDIES THAT FEED IN *OPUNTIA* AND COULD BECOME NON-TARGETS OF A BIOLOGICAL CONTROL EFFORT AGAINST *CACTOBLASTIS CACTORUM*.[1]

Moth species	Host plant in *Opuntia* subgenus	Gregarious or solitary larvae	Feeding site	Region of occurrence	Size of geographic range	Warm or cold area
Alberada bidentella (Dyar)	Cylindropuntia prob.	Solitary	Stems	Western US	Large	Warm
A. holochlora (Dyar)	Cylindropuntia prob.	Solitary	Stems	Texas	Small	Warm?
Alberada parabates (Dyar)	Cylindropuntia	Solitary	Stems	W US-Mex	Large	Warm
Cahela ponderosella Barnes & McDunnough	Cylindropuntia	Solitary	Stems	W US-Mex	Large	Warm
Melitara dentata (Grote)	Platyopuntia	Gregarious	Pads	W US	Large	Warm-Cold
M. prodenialis Walker	Platyopuntia	Gregarious	Pads	FL to TX	Large	Warm-Cold
Olyca phryganoides Walker	Platyopuntia	Solitary	Pads?	Hispaniola	Small?	Warm
Olycella junctolineella (Hulst)	Platyopuntia	Gregarious-Solitary	Pads	W US-Mex	Small	Warm
O. nephelepasa (Dyar)	Platyopuntia	Gregarious-Solitary	Pads	W US-Mex	Large	Warm-Cold
O. subumbrella (Dyar)	Platyopuntia	Gregarious-Solitary	Pads	W US-Mex	Large	Warm-Cold
Ozamia odiosella = *O. fuscomaculella* (Wright)	Platyopuntia	Solitary	Fruit	W US-Mex	Large	Warm
Ozamia lucidalis (Walker)	Platyopuntia	Solitary	Fruit	FL-W Indies	Large	Warm
O. thalassophila Dyar	Cylindropuntia	Solitary	Fruit	CA	Small?	Warm
Rumatha bihinda (Dyar)	Cylindropuntia	Solitary	Stems	W US	Large	Warm
R. glaucatella (Hulst)	Cylindropuntia	Solitary	Stems	Texas	?	Warm
R. polingella (Dyar)	Cylindropuntia	Solitary	Stems	Arizona	Small	Warm

[1]Extracted from Heinrich, 1939.

occur with it in North America. *Melitara prodenialis*, with gregarious larvae in pads of the same hosts, and an overlapping geographic range, would be the most vulnerable cactus moth. It occurs from Florida to Texas, and introduced parasitoids which adopt the moth could move via this new host from Florida to Texas, where many other pad feeding cactus moths in the genera *Melitara, Olycella, Megastes, Mimorista and Mermara* occur**.** Cactus moths less likely to be attacked by introduced South American parasitoids are probably those most dissimilar to *C. cactorum.* These would be species that are not gregarious (*Olycella* and *Ozamia*), which attack flower buds and fruits instead of pads (*Ozamia, Noctuelia*), which use cylindropuntias (the chollas) instead of platyopuntias (*Alberada* and *Cahela*) or other genera of cacti (*Yosemitia*). Cactus moths that have many host plants and large geographic ranges would probably also be at less risk. Cactus moths that occur in cold areas, where *C. cactorum* and its introduced parasitoids are unlikely to colonize, should experience the least risk.

The risks associated with the introduction of parasitoids of native cactus moths from the western United States would be somewhat greater than that of specialist parasitoids introduced from *C. cactorum* in South America, because they would come from genera other than *Cactoblastis.* As such, they would likely have broader host ranges and be more likely to attack non-target moths.

The risks associated with inundative releases of parasitoids already associated with *C. cactorum* in Florida should be relatively minor because neither the geographic range nor the host range would be likely to increase. Large numbers of parasitoids could temporarily suppress host populations of insects in the area of release. The risk of inundative releases of cosmopolitan generalist parasitoids, such as *Trichogramma minutum* and *Bracon brevicornis*, could be the temporary suppression of many non-target insects in the area of release. Because these parasitoids are already in Florida, no increase in their geographic ranges would occur. A similar degree of risk would be associated with the use of generalists pathogens such *Beauveria bassiana.*

The risks involved with the use of the *Nosema* species could be very limited if they prove to be the narrow specialists that they are suspected to be, particularly if they have transovarial transmission and kill larvae within the pads where they feed. If they are not species or genus level specialists the risk will be commensurate with their host breadth.

The indirect risks of biological control relate to the potential effects caused by reducing populations of non-target insects, particularly effects to their host plants. The main effect could be increased populations of some *Opuntia* species due to the reduction of the cactus moths that help regulate their populations. This increase could allow some prickly pear cacti to become artificially abundant, enabling them to displace other species and to dominate natural communities. These plants could also become troublesome on rangeland where some *Opuntia* already tend to be weedy. Prickly pear cacti, including the Florida native *O. stricta*, are some of the worst weeds in the Old World, which has no native *Opuntia*. This is thought to occur, at least in part, because of the lack of regulating natural enemies (Moran and Zimmermann 1984). An additional indirect effect could be to negate the successful biological control of weedy *Opuntia* by *C. cactorum* in the Caribbean if introduced parasitoids spread to that region (Bennett & Habeck 1992). Finally, it is also possible that the introduction of parasitoids from South America that attack native cactus moths could result in competition with native parasitoids that lowers the overall level of control they provide. This might actually result in increased damage by native moth species to native cacti (e.g., Ferguson & Stiling 1996).

The criteria used to consider and rank the risk to non-target insects by different biological control approaches for *C. cactorum* control are shown in Table 7. These criteria relate in various ways to estimating the degree of use of non-target insects. Table 8 shows the rankings of the various approaches from the least to most risky. Both the criteria and the resulting rankings are not absolute, but are attempts to further compare and contrast relative risks. Both the least risky and most risky approaches in our scheme involve the importation of agents from the moth's native range. The least risky approach is the introduction of coevolved specialist parasitoids to the genus *Cactoblastis.* The most risky approach is the introduction of stenophagous agents from the moth and its relatives in South America, as they would likely have the greatest and most persistent effects on native, non-target cactus moths. The degree of host specificity of prospective biological control agents is the key aspect in our ranking.

Risks can be minimized or avoided by careful host specificity research on parasitoids considered

TABLE 7. CRITERIA TO CONSIDER AND RANK THE RISK TO NON-TARGET SPECIES OF BIOLOGICAL CONTROL APPROACHES FOR *CACTOBASTIS CACTORUM*.

Degree of host specificity of agent
If new hosts will be exposed
Relative number of new hosts that could be adopted
If the agent's geographical range will increase
Likely persistence of non-target use
If rare species will be exposed
Size of the treatment area

TABLE 8. BIOLOGICAL CONTROL APPROACHES FOR *CACTOBLASTIS CACTORUM* RANKED BY RELATIVE RISK TO NON-TARGET SPECIES (RANKED FROM LEAST TO MOST RISKY).

1. Classical introductions from South America of parasitoids specific to the genus *Cactoblastis*
2. Inundative releases of cactus moth parasitoids from Florida in Florida
3. Inundative releases of parasitoids that attack *C. cactorum* in Florida
4. Inundative releases of generalist parasitoids known to attack *C. cactorum* that also occur in Florida
5. Classical introductions of western cactus moth parasitoids that attack gregarious larvae
6. Classical introductions of other western cactus moth parasitoids
7. Classical introductions of stenophagous *Cactoblastis* parasitoids from South America

for introduction for biological control of *C. cactorum* in North America. However, it appears that the currently known parasitoids of *C. cactorum* are unlikely to be limited to the genus *Cactoblastis*, the level of specificity needed to avoid use of non-target insects. This may preclude their use as biological control agents of *C. cactorum* in North America. The relative risks and benefits of any such introduction would have to be carefully evaluated.

CONCLUSIONS

While it appears that the threat is substantial, the assumption that *C. cactorum* will devastate native North American *Opuntia,* as it did to exotic weedy *Opuntia* for which it was employed in Australia and elsewhere in the world, may be usefully questioned. Native *Opuntia* are different than the exotic weedy *Opuntia* in several important respects. Native *Opuntia* usually occur at lower densities and have complexes of specialist herbivores. These herbivores might effectively compete with *C. cactorum* and the predators and parasitoids of these native herbivores could limit the moth. The native herbivores might also reduce the suitability of the *Opuntia* plants as food for *C. cactorum.* However, the fact that *C. cactorum* did devastate native weedy *O. stricta* and other native *Opuntia* on Nevis (Simmonds & Bennett 1966) suggests that the threat is real. *Cactoblastis cactorum* was introduced to Nevis Island in the Caribbean more than 40 years ago to control weedy native *Opuntia* in a part of the world where the cactus family is an indigenous and diverse part of the flora (Britton & Rose 1937). Prior use of *C. cactorum* was against weedy exotic *Opuntia* in parts of the world without native cacti (Moran & Zimmermann 1984). The project in Nevis did not consider the conservation aspects of introducing the moth to the Caribbean (Fred Bennett, pers. comm.). Biological control practices during that era did not usually consider possible conservation consequences of introductions.

The use of biological control to try to correct, what might be seen in hindsight, a biological control error might seem appropriate. But it is important to carefully consider the actual capability of biological control to reduce the *C. cactorum* threat in North America. If the primary goal is to stop the spread of the moth, biological control is probably not the best tool. Inundative release approaches, as discussed above, might be both difficult and expensive to apply. The populations of the moth occur mostly along coastal Florida and Georgia. Their *Opuntia* host populations are scattered at various densities in complexes of natural vegetation. This situation is quite different from the homogeneous row crop environments where inundative biological control has been successful. The identification of a sex pheromone from *C. cactorum*, that could be combined with an insecticide to trap and kill the moth, might do a better job of stopping its spread. Biological control may, however, be able to reduce existing populations of the moth. The possibility of controlling *C. cactorum* must be carefully weighed against the direct and indirect risks of the approach. Although parasitoids may be able to reduce populations of the moth, they probably will produce some degree of non-target effects. The use of host-specific biological control agents is the best solution since they would pose the least risk. *Nosema cactoblastis* might be such an agent and it may be useful to control the moth.

Whether or not the risks of biological control are acceptable will depend on the level of the *C. cactorum* threat to native and economic *Opuntia* as it continues to spread and the degree to which introduced biological control agents might disrupt native *Opuntia* ecosystems. In light of our inability to predict the benefits of a given biological control agent, it might prove difficult to reach agreement about what level of risk is acceptable.

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