APPLICATIONS OF F_1 STERILITY FOR RESEARCH AND MANAGEMENT OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

The unintentional arrival of the cactus moth, *Cactoblastis cactorum* (Berg), in Florida has raised concerns for the safety of native and rare *Opuntia* species in the Florida Keys and the potential spread of *C. cactorum* to the *Opuntia*-rich areas of the western United States and Mexico. In addition to threatening the biodiversity of these native ecosystems, such non-target effects would generate negative publicity that could heighten public concern over the use of exotic natural enemies and jeopardize future biological control programs against weeds. In this paper we discuss the use of inherited (F_1) sterility in Lepidoptera to study, predict, and manage the expanding populations of *C. cactorum*. Research areas in which the use of F_1 sterility would be most applicable include (1) elucidation of the host range of *C. cactorum* for key native *Opuntia* species from across the U.S., (2) prediction of the geographic range of *C. cactorum* in the U.S. and Mexico, and (3) delineation of the impact of native natural enemies on the spread of *C. cactorum*. The use of F_1 sterility for control of *C. cactorum* would be most appropriate for (1) eradication of *C. cactorum* from areas of new introductions, or from isolated and/or environmentally sensitive areas such as the Florida Keys, (2) establishment of a barrier by means of release of irradiated moths along the leading edge of the *C. cactorum* geographical range, and (3) provisioning sterile *C. cactorum* in the field as hosts for released natural enemies to increase their initial survival and establishment.

Key Words: cactus moth, sterile insect technique, biological control, inherited sterility

RESUMEN

La accidental introduccion de la palomilla del cactus, *Cactoblastis cactorum* (Berg), al estado de Florida ha incrementado la conciencia sobre la amenaza que esta introduccion causa a las especies nativas y poco comunes de cactus del genero *Opuntia* en los cayos de Florida y concientiza el peligro de esta invasion a las areas ricas en *Opuntia* en el oeste de los Estados Unidos y Mejico. Ademas de amenazar la biodiversidad en estos ecosistemas, la publicidad negativa sobre estos efectos no dirigidos tendra como consecuencia alarmar al publico sobre el use de enemigos naturales importados y afectara el progreso de futuros programas de control biologico de malezas. En este articulo discutimos el uso potencial de la esterilidad adquirida (o esterilidad F_1) en Lepidoptera para estudiar, predecir y manejar las poblaciones de *C. cactorum*. Algunas de las areas de investigacion donde la aplicacion de la esterilidad F_1 es mas apropiada incluyen (1) el estudio de el rango potencial de hospederos de *Opuntia* en los Estados Unidos, (2) predicciones sobre el potencial rango de expansion geografica de esta especie en Estados Unidos y Mejico y (3) el estudio del impacto de los enemigos naturales ya presentes en la expansion del rango de *C. cactorum*. El uso de la esterilidad F_1 para el control de esta especie seria apropiada en el caso de (1) erradicacion de la especie en areas de invasion reciente, en areas aisladas o en areas ecologicas en peligro como los cayos de Florida, (2) el establecimiento de una barrera para impedir la expansion de la especie a traves del uso de insectos irradiados liberados en el frente de invasion y (3) el uso de insectos irradiados en el campo como suplemento alimenticio para asegurar el establecimiento y supervivencia de enemigos naturales liberados para el control de *C. cactorum*.

The control of exotic *Opuntia* cacti (Caryophyllales: Cactaceae) in Australia by the cactus moth, *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) (Dodd 1940), has long been cited as one of the classic success stories in biological control (Sweetman 1936; Johnson & Stiling 1996). However, the recent unintentional arrival of *C. cactorum* in Florida from the Caribbean has raised concerns for the well being of native *Opuntia* in the southern United States and Mexico (Pemberton 1995; Johnson & Stiling 1998). In the United States, Pemberton (1995) estimated that *C. cactorum* should be able to reach Charleston, SC, San Antonio, TX, and the lower-altitude areas of New Mexico, Arizona and California north to Sacramento. Although specific interactions cannot be predicted at this time, establishment of *C. cactorum* in the southwestern U.S. and Mexico could have devastating effects on the landscape and biodiversity of these native desert ecosystems, and on the forage and vegetable *Opuntia* industries.

No satisfactory method of chemical control has been reported for *C. cactorum* (Habeck & Bennett 1990) and because many of the *Opuntia* species in the U.S. are associated with sensitive ecological areas, widespread use of pesticides has not been recommended. For example, in the Florida Keys *Opuntia* cacti occur together with rare and endangered fauna such as the Schaus swallowtail (*Papilio aristodemus ponceanus* Schaus, Papilionidae), Florida leafwing (*Anaea floridalis* Johnson & Comstock, Nymphalidae) and Bartram's scrub-hairstreak (*Strymon acis* (Drury), Lycaenidae) butterflies (Habeck & Bennett 1990), and the Gerstaeckeria cactus weevil (*Gerstaeckeria fasciata* Pierce, Cryptorhynchinae) (O'Brien, Florida A&M Univ., pers. comm.). In addition to environmental considerations, the economics of treating large tracts of coastal and desert land with pesticides would be prohibitive. The use of systemic insecticides injected into cactus stems was investigated by Pretorius et al. (1986) as a means of protecting ornamental cacti and small populations of endangered cacti, but these insecticides provided inadequate control. In addition, the use of insect pathogens does not appear to hold much promise. Vail et al. (1984) conducted bioassays to determine the susceptibility of *C. cactorum* to the nuclear polyhedrosis virus (AcMNPV) isolated from *Autographa californica* Speyer (Lepidoptera: Noctuidae) and found that *C. cactorum* was only moderately susceptible to the virus.

Classical biological control is another tactic that could be used against *C. cactorum*. In its native habitat in South America several natural enemies have been identified, including *Apanteles alexanderi* Brethes (Hymenoptera: Braconidae), *Phyticiplex doddi* (Cushman) and *P. eremnus* (Porter) (Hymenpotera: Ichneumonidae), *Brachymeria cactoblastis* Blanchard (Hymenoptera: Chalcididae), and *Epicoronimyia mundelli* (Blanchard) (Diptera: Tachinidae) (Habeck & Bennett 1990). However, the host range of these natural enemies and any potential non-target effects should be scrutinized carefully before approval for their release in the U.S. is granted. There are a number of native moth species closely related to *C. cactorum* that attack native *Opuntia* in the U.S. These species are under good biological control by a complex of native natural enemies. It is possible that the introduction of exotic parasitoids or other natural enemies might disrupt this equilibrium and cause secondary pest problems. Similarly, inundative releases of parasitoids, such as *Trichogramma* egg parasitoids (Hymenoptera: Trichogrammatidae), could have adverse non-target effects on desirable Lepidoptera (Habeck & Bennett 1990).

Three genetic control methods have been developed and field-tested against Lepidoptera. These are the sterile insect technique (SIT), inherited sterility (also known as inherited partial sterility or F_1 sterility), and backcross sterility (LaChance 1985). In SIT and F_1 sterility, mass production and release of large numbers of genetically altered (sterilized or partially sterilized) insects are used to insure that when matings occur in the field a significant proportion of these involve a sterile released insect. These methods are unparalleled in their specificity and safety because only the target species is affected. 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 may allow the dose of radiation to be adjusted so that treated females are completely sterile and males are partially sterile. Second, when partially sterile males are outcrossed with wild fertile females the radiation-induced deleterious effects are inherited by the F_1 generation. As a result, egg hatch is reduced and the (F_1) offspring produced are both highly sterile and predominately male. The lower dose of radiation used in this technique increases the quality and competitiveness of the released moths (North 1975). In addition, 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). Not only is there a magnification of the sterility effect, but the production of F_1 sterile offspring enhances the buildup of native natural enemies that attack the insect pest (Carpenter et al. 1996).

The production of sterile progeny allows developmental and behavioral observations to be made under actual field conditions without the concern of establishing a breeding population. These observations allow for confirmation of oviposition behaviors and host associations, field-testing of larval feeding preferences, and studies of larval development and survival on related plants that are of concern. Also, both the impact that native natural enemies might have over an expanded geographic range of *C. cactorum* and the ability of *C. cactorum* to survive and overwinter under various climatic conditions can be studied with the use of F_1 sterility. While the control potential of releasing partially sterile insects is well documented (Carpenter et al. 1987a, b, c; Carpenter & Gross 1993; Bloem et al. 1999a, b), the latter applications of F_1 sterility are benefits of this technique that to date have not been utilized. In this paper we discuss the application of F_1 sterility to study and manage expanding populations of *C. cactorum*. Research areas in which the use of

F_1 sterility would be most applicable include (1) elucidation of the potential host range of *C. cactorum* for key native *Opuntia* species from across the U.S., (2) prediction of the geographic range of *C. cactorum* in the U.S. and Mexico, and (3) delineation of the impact of native natural enemies on the spread of *C. cactorum*. The most appropriate uses of F_1 sterility as a control tactic against *C. cactorum* include (1) eradication of *C. cactorum* from areas of new introductions, or from isolated and/or environmentally sensitive areas such as the Florida Keys, (2) establishment of a barrier by means of release of irradiated moths along the leading edge of the *C. cactorum* geographical range, and (3) provisioning sterile *C. cactorum* in the field as hosts for released natural enemies to increase their initial survival and establishment.

Applications of F_1 Sterility for Research

Elucidation of the Potential Host Range of *C. cactorum* for Key Native *Opuntia* Species

The larvae of *C. cactorum* are widely polyphagous, feeding on nearly all species of *Opuntia* cactus tested to date (Sweetman 1936; Johnson & Stiling 1996). As such, it is expected that *C. cactorum* will readily attack most *Opuntia* spp. in the U.S. and Mexico. However, the degree to which the moth impacts specific *Opuntia* species varies both in its native habitat and in the places where it has been used as a biological control agent (Mann 1969; Moran 1984; McFadyen 1985). For example, *C. cactorum* control of *O. stricta* (Haw.) Haworth in Australia was enormously successful but its control of *O. ficus-indica* (L.) Miller in South Africa was only moderately successful. Therefore, key *Opuntia* species that represent a cross section of subgenera from different geographical and ecological areas within the predicted geographical range of *C. cactorum* should be tested for their acceptability and suitability as hosts. The host range of *C. cactorum* on Florida *Opuntia* spp. has already been tested (Johnson & Stiling 1996). Although selected *Opuntia* species could be collected and shipped to the *C. cactorum* endemic area for the host-range testing, it would be more desirable and informative if the host-range testing could be accomplished within the natural environment of each candidate species or species complex. Using F_1 sterility, it would be possible to study oviposition behaviors, host associations, and larval feeding preferences under actual field conditions. Transport of fertile *C. cactorum* into these environments would be unthinkable. However, it might be possible to develop acceptable protocols that would allow for the transport of sterile moths or moths carrying F_1 sterility. In this way, there would be no risk associated with any potential escape of *C. cactorum* because the irradiated moths could only produce sterile progeny and, therefore, no reproducing colony could be established. The use of F_1 sterility for these assays should be appropriate because similar studies on different lepidopterans revealed no interactions between radiation treatment and the ability to survive on different hosts/diets and in different environmental conditions (Carpenter et al. 1985, 1987b; Carpenter & Wiseman 1992a, b).

Prediction of the Potential Geographic Range of *C. cactorum*

The geographic range that could be achieved by *C. cactorum* in the U.S. is unknown. Pemberton (1995) compared mean low temperatures for some of its known South American habitats with various North American localities and estimated that *C. cactorum* may colonize as far north as Charleston, SC, San Antonio, TX, and the lower altitude areas of New Mexico, Arizona and California north to Sacramento. Observations on *C. cactorum* distribution in South Africa suggest that the geographical range in the U.S. may be even greater than the estimates by Pemberton (Zimmermann, Plant Protection Research Institute, South Africa, pers. comm.). It is likely that the geographic range of *C. cactorum* in the U.S. will be limited by environmental factors such as temperature and photoperiod rather than by host availability. *Opuntia* spp. have a broad range extending from Massachusetts to Minnesota, south to Florida, and west to California. *Opuntia* spp. are tolerant of temperatures as low as -30°C and as high as 45°C. Because developmental studies of *C. cactorum* at different temperatures have not been reported, the temperature thresholds for survival and development of the different life stages of *C. cactorum* should be determined. Also, the ability of low temperature and short day length to induce diapause in *C. cactorum* should be studied. Diapause in the family Pyralidae has been studied in depth for several pest species (Teetes et al. 1969; Chippendale & Reddy 1974; Bell & Bowley 1980; Rojas et al. 1989). In these pyralids, as well as others, diapause is induced in the mature larvae. Both temperature and photoperiod influence diapause induction, but temperature is the most critical factor (Chippendale & Reddy 1974).

The influence of temperature and photoperiod on diapause induction of *C. cactorum* could be studied in any laboratory equipped with environmental chambers. However, exact environmental conditions experienced under field conditions cannot be simulated. The ability of *C. cactorum* to overwinter under different environmental extremes would be determined best by onsite field studies. Cages erected over cacti infested with *C. cactorum* larvae could be used to capture moths from the emerging spring generation. As discussed in the previous section, use of fertile *C. cactorum* for these studies would not be acceptable. However, sterile larvae from irradiated parents can be used without the risk of establishing a breeding colony of *C. cactorum* outside the infested area. F_1 sterile larvae would be suitable test subjects for these assays because Carpenter & Gross (1989) found no interactions between F_1 sterility and diapause in *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae). Data from these studies will be useful in determining the geographic range of *C. cactorum* and in calculating the possible number of annual generations at different locations.

Delineation of the Potential Impact of Native Natural Enemies on the Expansion of *C. cactorum*

The first record of *C. cactorum* in the continental United States was from the Florida Keys (Big Pine Key) in October 1989 (Habeck & Bennett 1990). *Cactoblastis cactorum* currently has a known geographical distribution limited to the coastal areas of Georgia and Florida, with the most northerly west coast record of *C. cactorum* at Cedar Key in Levy County, September 2000 (Stiling, University of South Florida, pers. obs.). The biotic and abiotic factors that influenced the expansion of the geographical range of *C. cactorum* during the past decade are unknown. However, because *C. cactorum* is an exotic species, the ability of native parasitoids and predators to attack *C. cactorum* may be crucial in moderating an expanding population. A knowledge of the natural enemy complex that could attack *C. cactorum* beyond the leading edge of its expansion would be valuable in predicting the rate at which *C. cactorum* would colonize new areas. This knowledge also would allow pest control specialists to consider whether or not an effort to use classical biological control against *C. cactorum* would be warranted. The interaction between *C. cactorum* and native natural enemies may be determined through surveys within the areas now colonized by *C. cactorum*. Methods for these surveys would include collecting egg sticks, larvae and pupae of feral *C. cactorum*, and placing sentinel egg sticks, larvae and pupae at field sites (Kring et al. 1992). The sentinel forms could be observed for predation while in the field, or they could be retrieved and observed in the laboratory for emerging parasitoids. Unfortunately, neither of these methods would be available in areas beyond the leading edge of *C. cactorum* expansion. No feral *C. cactorum* would be present beyond the leading edge and the use of sentinels would create the risk that escaped cactus moths would establish a breeding population in a previously uninfested area. However, this risk would be eliminated if irradiated *C. cactorum* and their sterile progeny were used as sentinels for surveys of potential natural enemies. In fact, irradiated *C. cactorum* and their sterile progeny could be used both in these uninfested areas (Carpenter et al. 1996; Greany & Carpenter 1999) and in infested areas where the goal would be to prevent further contribution to the feral pest population (Carpenter et al. 1996; Proshold et al. 1998; Mitchell et al. 1999).

Applications of F_1 Sterility for Control

F_1 sterility in *C. cactorum* could have several applications for control of *C. cactorum*. First, F_1 sterility could provide a tactic to protect rare *Opuntia* cacti in the Florida Keys. Through the release of irradiated moths, a zone of protection could be constructed around the area endemic for the cacti by excluding or eradicating of *C. cactorum* from this area. Another application would be as an available control/eradication tactic to be used against new introductions of *C. cactorum* (e.g., in Mexico or beyond the leading edge of the *C. cactorum*-infested area in the U.S.). As soon as an infestation is detected, irradiated moths could be released into the area surrounding the site where *C. cactorum* has been detected. After adequate assessment, it might be desirable to develop a partnership with a country in the Caribbean or with South Africa in which native *C. cactorum* could be collected/reared, irradiated and shipped to areas with new *C. cactorum* infestations. Such an arrangement would be similar to that of the sterile insect release programs for the Mediterranean fruit fly in which sterile flies are produced in other countries (i.e., Guatemala, Mexico) and released in Florida and California. F_1 sterility also may be used to erect a barrier to prevent the expansion of the *C. cactorum* geographical range. Surveys indicate that the current distribution of *C. cactorum* is mostly limited to within 40 km of the Atlantic and Gulf coastlines. By releasing irradiated moths along the coastal region, it may be possible to create a barrier that would impede the advance of *C. cactorum*. It may also be possible to slowly move the barrier into the infested area and, thereby, reduce the current distribution of *C. cactorum*. Finally, F_1 sterility could be used to provision *C. cactorum* as supplemental hosts in the field to increase the initial survival and establishment of released natural enemies. If the decision is made to use classical or augmentative biological control against *C. cactorum*, a low population of *C. cactorum* may impede the establishment or efficacy of the natural enemy. By releasing irradiated moths or their sterile progeny, it might be possible to enhance the activities of the natural enemies without contributing to the feral population of *C. cactorum* (Carpenter et al. 1996; Proshold et al. 1998; Mitchell et al. 1999).

Summary

Methods are needed for the containment, control and eradication of *C. cactorum*. The use of insecticides to control *C. cactorum* should be con-

sidered with much skepticism because of environmental and economic concerns. A classical biological control approach should also be considered with caution because of the need to thoroughly evaluate the safety of such releases, because its effectiveness is unknown, and because it would not prevent the spread of the moth. The use of F_1 sterility, however, would be species specific and environmentally friendly. F_1 sterility offers the potential to control the moth along the leading edge to limit geographical range expansion and the potential to develop an abatement program in environmentally sensitive areas (e.g., to protect rare and endangered *Opuntia* spp.). In addition, the use of F_1 sterility may also provide a framework for approaching future introductions of other exotic, invasive lepidopteran species, and may provide new risk management tools for assessing the safety of exotic lepidopterans being considered as biological control agents against invasive weeds.

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