Understanding the Ghost of Cactoblastis Past: Historical Clarifications on a Poster Child of Classical Biological Control

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Understanding the Ghost of *Cactoblastis* Past: Historical Clarifications on a Poster Child of Classical Biological Control

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*The applied ecological discipline of classical biological control (CBC) has a long history, bolstered by some spectacular successes in the management of pest insect and plant species. A major poster child of CBC is the control of prickly pear (*Opuntia *spp.) in Australia by the moth* Cactoblastis cactorum. *In this article we investigate the idiosyncrasies of this CBC program and relate it to contemporary CBC, highlighting the intensive rearing and spatially extensive distribution effort critical to the rapid success of this project. We also emphasize the importance of the sociopolitical and economic context of the* Opuntia *CBC program and its role in its success. We use these historical clarifications to temper the expectations of equivalent successes in future CBC projects.* Cactoblastis cactorum *has recently invaded North America, and its threat to native cacti is of concern. We examine the global use of this moth as a biocontrol agent to clarify the nature of the hazard that it may pose as an invader in North and Central America.*

Keywords: invasive species, biological control, Cactoblastis cactorum, Opuntia*, risk*

When release from natural enemies is the basis for invasiveness of an exotic species, biological control could be a valuable and potentially safe method of management of the invasive species. Classical biological control (CBC) is the method of introducing an herbivore that either specializes on the target invasive species or has a diet sufficiently narrow in breadth for it to have a significant impact on the target species without posing a significant risk to nontarget species. Perhaps the best-known successes of CBC are the control of cottony-cushion scale (*Icerya purchasi*) in California and the control of prickly pear (*Opuntia* spp.) in Queensland, Australia. It is therefore not surprising that these two cases serve as illustrative examples of CBC in many textbooks (DeBach 1974, Hajek 2004). Although these and other successes have been the subject of many papers and books, the idiosyncrasies that may have critically contributed to their success have seldom been highlighted.

Our aim is neither to denigrate nor to praise the practice of biological control. We believe it is a vital tool in the management of some invasive species, but one that can be significantly enhanced through a better understanding of the scientific reasons behind past successes and failures. Our objectives in this article are threefold. First, we wish to bring to light information that is seldom acknowledged (or simply not known) on the use of the *Cactoblastis cactorum* (*Cactoblastis* hereafter) in the control of *Opuntia* species in Australia. Having been based at Alan Fletcher Research Station (the former headquarters of the Commonwealth Prickly Pear Board), which was responsible for the successful management of *Opuntia* in Australia, we were able to delve into its archives to access this information. Second, we want to temper the expectations of people hoping to mimic *Cactoblastis*-like successes when funding or requesting biological control as a management option. We hope to encourage biocontrol practitioners to elucidate the reasons for successful CBC. Finally, we argue for caution in predicting the effects of *Cactoblastis* as a North American invasive species on the basis of its success as a biocontrol agent elsewhere, given the idiosyncrasies associated with its historical use as a biocontrol agent.

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A brief history of *Opuntia* in Australia

European settlement of Australia was accompanied by the introduction of hundreds of plant and animal species to support the settlers, including 29 different prickly pear species, 9 of which were to become invasive and pose significant economic and ecological threats (Walton 2005). The earliest records of the introduction of prickly pears go back to 1788, when the first British fleet arriving in Australia brought both the drooping prickly pear (*Opuntia vulgaris*) and the cochineal (*Dactylopius* spp.) to produce the red dye needed for the coats of soldiers (Mann 1970). The first records of an *Opuntia* pest species go back to 1839, when *Opuntia stricta* (= *Opuntia inermis*) was moved from Parramatta (near Sydney) to various parts of rural New South Wales and Queensland to be used as a hedge plant around homesteads. In 1870, the plant was found as far north as Rockhampton in Queensland, and by 1884, the problem of its spread was reported in the media. By 1900, some 4 million hectares (ha) of Queensland were infested by prickly pears. The use of the prickly pear as drought fodder further enhanced its rate of spread (Dodd 1940); by 1925, some 24 million ha of Queensland and New South Wales were infested (figure 1), with densities of up to 16,000 plants per ha and an estimated biomass of 250,000 kilograms (kg) per ha. The rate of spread over the previous 10 years was estimated to be about 320,000 ha per year (Walton 2005).

Various control methods were attempted, with results that ranged from ineffective (e.g., slashing, mulching, and burning) to effective but dangerous (e.g., chemical control involving the use of some 3 million kg of blends of arsenic pentoxide and sulfuric acid between 1912 and 1932; Melville 1935, Payne 1936). Resort to dangerous control measures reflected the desperation associated with having most of the arable land under invasion.

Biological control. Biological control efforts were initiated in 1899, and the first releases of a biological agent (*Dactylopius ceylonicus*) occurred in 1903. Unfortunately, these releases were made on *O. stricta,* when its actual host was *O. vulgaris,* and the cochineal failed to establish. Release on the correct host in 1914 resulted in substantial reductions in populations of *O. vulgaris* (Walton 2005). This success was followed by a well-funded program over a 15-year period (1920–1935) during which 150 insect species were identified from extensive travel and surveys across the native range of the prickly pears in 15 countries in North, Central, and South America as well as South Africa and Asian countries where prickly pears had established. Of those insect species, 52 were imported into Australia for host testing and 12 were successfully released for control of major prickly pear species. These insects included the moth borer (*Olycella* sp.), two species of plant suckers (*Chelinidea* spp.), the prickly pear red spider mite (*Tetranychus opuntiae*), and various cochineal species (*Dactylopius* spp.).

One of the most successful insect introductions was *Dactylopius tomentosus,* which was imported in 1921. In its 1929 report, the Prickly Pear Commission noted, "It is estimated that cochineal can be credited with a 50 percent control of prickly pear." This cochineal insect showed a preference for the younger leaves of common prickly pear. Its role, and the role of other biocontrol agents, in the reduction of prickly pears is often forgotten (Walton 2005).

In 1914, a *Cactoblastis* species was imported into Brisbane, but poor knowledge of the rearing requirements of this species resulted in failure to establish a colony (Mann 1970). It was not until 1925 that *C. cactorum* would be reimported and reared successfully. Much of the story of these importations and of the eventual success of *Cactoblastis* rearing efforts is well known and documented (see Mann 1970), but the following aspects are seldom acknowledged.

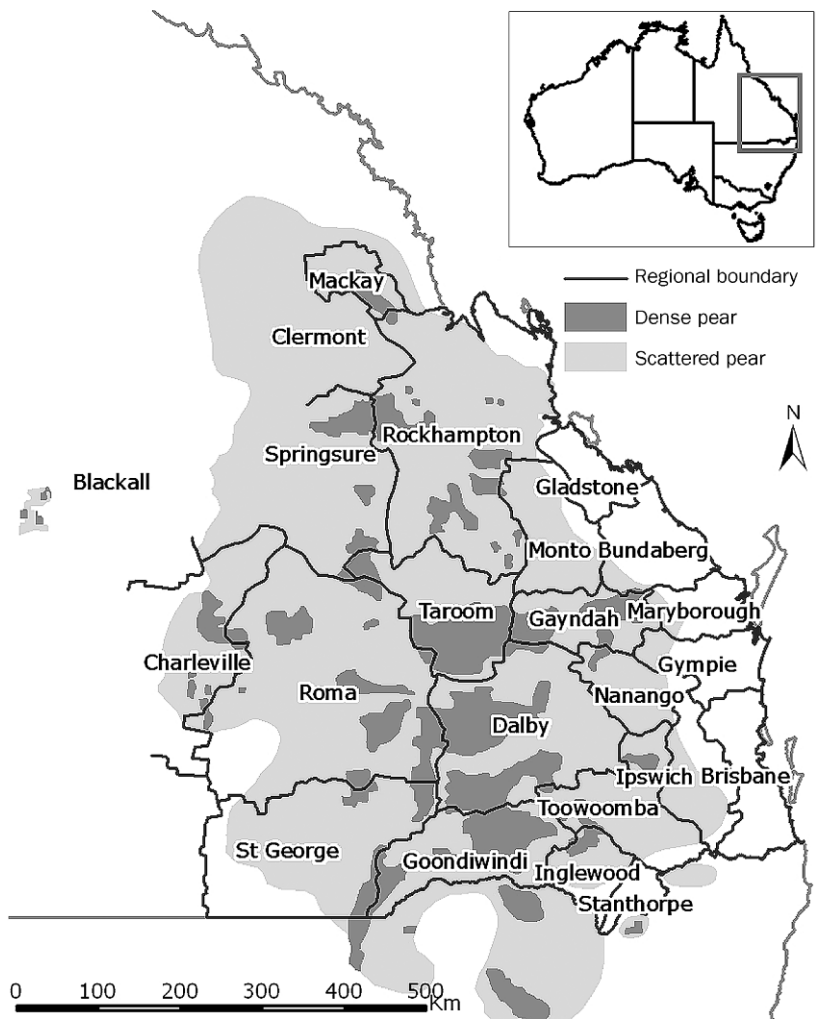

Figure 1. Spatial extent of the* Opuntia *infestation in Australia in 1924. District boundaries are indicated. Redrawn from Mann (1970).

Spatial extent, method of release, and time taken to affect *Opuntia* populations. After mass rearing in four dedicated facilities, a large workforce (> 200 workers) delivered a coordinated program releasing almost two billion egg sticks (each egg stick containing 50 to 100 eggs) in a four-year period across the entire range of the *Opuntia* invasion (table 1; Power et al. 1928, 1929, 1930). These numbers do not include the release of 10,196,150 egg sticks across 19 locations in Queensland and New South Wales between 1927 and 1928, and another 179,395,650 egg sticks between 1931 and March 1933 (Mann 1970). The release information for individual districts for the 1930s dates was not detailed in the archives, but we presume that this was as spatially extensive as that detailed in table 1. In addition, some restricted releases occurred in subsequent years, with 1,350,000 egg sticks released in 1934–1935 and 480,000 in 1935–1936 (Melville 1935, Payne 1936), in response to *Opuntia* regrowth after the initial impacts of *Cactoblastis.*

The release efforts detailed above were only those undertaken by the officers of the Commonwealth Prickly Pear Board and by state government officials. Landholders who made an application for this agent were also supplied with some 1,292,882,500 egg sticks of *C. cactorum,* and approximately 692,700,000 egg sticks were distributed from motor vehicles to control roadside infestations and infestations on Crown (public) lands (Power et al. 1930, Mann 1970). One can only imagine the number of unrecorded redistributions and releases that were made in addition to those accounted for by the Commonwealth Prickly Pear Board.

The method of release is a part of what made this effort unique. Egg sticks were collected from colonies and pasted on a square piece of paper or on short wax quills, which were then pinned on pear plants (Power et al. 1930, Mann 1970) to ensure that the agents found the plants. This is unlike many modern efforts, which typically involve the release of adults; the endogenous dispersal drive of adults of many insect species (den Boer 1990) means that there is an increased chance that they may fly away from a potential host patch and may not encounter another suitable one. The method of releasing a large number of eggs directly onto plants also meant that when adults emerged, mate finding (a vital part of establishing local populations) was significantly enhanced, and the likelihood of Allee effects was low.

Ecologically, successful biocontrol agents are hypothesized to be *r* strategists, capable of rapid reproduction and strong dispersal mechanisms (Waage 1991). In the case of *Cactoblastis,* these traits were engineered through arguably the most efficient and intentional human-aided dispersal and spread of a species thus far. It is unlikely that such an intensive rearing and spatially extensive release effort has since been undertaken for any other weed biocontrol agent. This is perhaps most starkly reflected in the time taken for biological control to produce drastic reductions in pear populations. Even by 1928, two years after the first release efforts, some large infestations of prickly pear (ranging from 600 to 2000 acres, or about 240 to 810 ha) had been completely destroyed (Power et al. 1928). By 1936, the annual report of the Prickly Pear Land Commission declared, "The prickly pear menace has been overcome and the devastation it wrought a short ten years ago is now becoming merely a memory," and the *Cactoblastis* Memorial Hall at Boonarga was built on a site that had once been covered with a dense infestation of *O. stricta* (Payne 1936).

***Cactoblastis* versus contemporary classical biological control.** Although the success of *Opuntia* management can be attributed to biological control, it appears to be more a case of atypical biological control than of CBC. A relative assessment of contemporary rearing and release practices in CBC may shed light on the validity of this claim. Even though some release densities may be as high as those in the *Cactoblastis* example, we very much doubt that the sustained rearing and release efforts that almost certainly led to the successful management of *Opuntia* are mimicked in contemporary cases.

To illustrate this point, we present the case of *Lantana camara* L., a modern-day equivalent of *Opuntia* in Australia that infests a comparable area. *Lantana camara* was introduced as an ornamental plant in the 1840s; it has since escaped

Table 1. Number of egg sticks of* Cactoblastis cactorum *released by the Commonwealth Prickly Pear Board from 1927 through 1930 across districts infested with* Opuntia *species.

District	Egg sticks released 1927–1929	Egg sticks released 1930	Area of district (km²)
Inglewood	5,263,800	57,063,800	5862
Goondiwindi	6,928,130	222,913,130	13,385
St. George	6,705,000	52,650,000	31,130
Charleville	8,122,000	80,194,000	40,762
Roma	36,993,700	277,065,700	52,377
Dalby	39,265,630	231,903,130	36,417
Toowoomba	7,860,000	247,980,500	8309
Ipswich	1,501,000	57,223,600	1207
Brisbane	2,215,000	14,872,500	5871
Nanango	2,000,000	12,100,000	14,771
Gympie	1,005,070	2,005,070	7465
Taroom	11,940,000	85,972,000	18,642
Blackall	3,160,520	4,910,520	16,393
Springsure	13,282,825	47,782,825	56,055
Rockhampton	15,000,000	125,800,500	62,352
Gayndah and Monto	14,824,830	101,924,830	24,944
Maryborough	1,394,890	10,594,890	5488
Bundaberg	100,000	3,800,000	6332
Clermont	11,268,950	26,763,950	30,078
Mackay	31,773,000	35,979,060	10,003
Gladstone	0	500,000	5875
Total	220,604,345	1,700,000,005	453,718

Source: Power et al. 1928, 1929, 1930.

and covers more than 4 million ha along eastern Australia. Biological control efforts began in Australia in 1914, and 30 insect and fungal agents have been introduced against *L. camara* since then (Julien and Griffiths 1998), of which 16 have established at last count (Day et al. 2003). Two of the most recent agents released (representing some of the largest release numbers for this weed's agents) include a leaf-sucking mirid, *Falconia intermedia,* and a stem-sucking membracid, *Aconophora compressa.* The rearing and release efforts of these species present a stark contrast to the *Cactoblastis* example (tables 1, 2). This might in part explain the moderate success in controlling *L. camara* with biological control.

This discrepancy may simply reflect how easy *Cactoblastis* was to rear or, conversely, how difficult the *Lantana* agents were to rear. However, even in releases of chrysomelid beetles that are easy to rear and have been extensively used as weed biocontrol agents, the release numbers are orders of magnitude below those of *Cactoblastis.* For example, an effort targeting *Lythrum salicaria* in Illinois involved the intensive rearing and extensive statewide distribution of *Galarucella* species, including the release of some three million beetles between 1995 and 2005 (Susan Post, Illinois Natural History Survey, Champaign, IL, personal communication, 7 August 2007). This is similar to releases of the tropical chrysomelid *Zygogramma bicolorata* targeting *Parthenium hysterophorus* (Kunjithapatham Dhileepan, Alan Fletcher Research Station, Biosecurity Queensland, Australia, personal communication, 6 August 2007). However, the spatial extent of these releases was typically a small subset of the overall range of infestation of the weed.

Perhaps the rearing and release efforts are substantially better in the case of similar extensive programs against aquatic weeds in South Africa (Zimmermann et al. 2004a), but such information is seldom published. Even in these cases, one suspects that the spatial extent of the *Cactoblastis* release effort may have been difficult to match.

Table 2. Rearing and release efforts of two recent biocontrol agents for* Lantana camara *in Queensland and New South Wales, Australia.

	Falconia intermedia (introduced in 2000)		*Aconophora compressa* (introduced in 1995)	
Year	Queensland	New South Wales	Queensland	New South Wales
1995	–	–	2800	0
1996	–	–	10,140	0
1997	–	–	3290	0
1998	–	–	250	4000
1999	–	–	31,682	20,700
2000	12,399	4580	34,694	11,974
2001	9000	2000	10,106	6300
2002	22,555	3500	0	0
2003	83,550	39,900	0	0
2004	48,800	0	0	0
2005	5600	0	0	0
Total	181,904	49,980	92,962	42,974

Source: Michael Day, Biosecurity Queensland, Brisbane, Australia, personal communication, 7 August 2007.

Economic and sociopolitical factors. Perhaps the best predictor of success for a biological control program is the level of financial investment in it. The prickly pear problem in Australia was so significant that involvement by Prime Minister William Hughes preceded the establishment of the Commonwealth Prickly Pear Board in 1919. This board was a cooperative effort funded by the Commonwealth of Australia and the state governments of Queensland and New South Wales. This level of cross-government cooperation was rare in Australia's early political history. The board operated from 1920 to 1939. Initial funding was £8000 (Australian currency is used throughout this article) per annum for five years. During its 19 years of existence, the total cost of the board's activities was £168,000. Queensland spent an additional £65,000 and New South Wales £6400 to spread the biocontrol agents, for a total of approximately £240,000 spent on prickly pear control (Walton 2005). The cost of this program was equivalent to more than $700 million in today's dollars, a staggering sum, with the equivalent of $210 million (30 percent of the total program) spent on distribution of agents. The resulting benefits appeared to justify the expense. The capital value of the lands returned to productivity within five years of the release of the biocontrol agents was estimated at £10 million, or 42 times the cost of the program (Walton 2005). The gross primary production in the area (Darling Downs, Queensland) is $1.4 billion per annum in today's dollars, and benefit–cost estimates of the prickly pear biological control program have shown significant benefits over the long term (benefit–cost ratio 312.3:1; Page and Lacey 2006).

Although significant sums of money have since been invested in the biological control of weeds, they are insignificant in comparison with the costs of the prickly pear control program. For example, the annual investment in *all* weed biological control in Australia between 1980 and 2000 was approximately $4.3 million in 2004 dollars (Page and Lacey 2006), and the extensive *Parthenium hysterophorus* CBC program cost $9 million over 25 years (Walton 2005).

Cactoblastis as a biocontrol agent in South Africa and the Caribbean

In South Africa, the initial target for *Cactoblastis* was *Opuntia ficus-indica,* which occupied some 900,000 ha in the Cape Province alone in 1942 (Zimmermann and Moran 1991, Zimmermann et al. 2004b). An intense *Cactoblastis* rearing program released some 580 million egg sticks between 1933 and 1941 (Petty 1948, Zimmermann et al. 2004b). However, the "damage caused [to *Opuntia*] by *Cactoblastis* in South Africa was not as great or as extensive as that in Australia," although it did significantly retard "the spread of the weed by reducing its fruiting capacity and

killing the seedlings" (Zimmermann et al. 2004b). This diminished impact may in part be due to a substantially greater predation rate (from baboons, rodents, and insects) in South Africa (Petty 1948, Zimmermann et al. 2000, 2004b) than in Australia, where both the moth and the prickly pear had few natural enemies. Better control of *O. ficus-indica* was provided by *Dactylopius opuntiae.* Despite the *Cactoblastis* release effort in Eastern Cape Province, large nearby populations of *O. stricta* (the target for *Cactoblastis* in Australia) in Kruger National Park were not colonized by *Cactoblastis* for more than 70 years. In 1988, limited numbers of *Cactoblastis* (60 egg sticks) were released into a 19,000-ha cactus infestation (Hoffmann et al. 1998a). This established *Cactoblastis* populations, but the impacts on *O. stricta* populations were limited, and other methods of control were required to bring weed populations under control (Hoffmann et al. 1998a, 1998b). These results from South Africa suggest that *C. cactorum* may exhibit subspecific variation in host range.

Opuntia triacantha (Spanish lady cactus) had been a major cause for concern as a weed in pastureland on Nevis and other Leeward Islands (West Indies). Nevis is a small island (93 square kilometers [km^2]), with a productive coastal plain approximately 1 km wide. The success of biological control in reducing populations of *O. stricta* in Australia made it an appealing prospect for controlling *O. triacantha* in Nevis (Simmonds and Bennett 1966). *Cactoblastis* and two *Dactylopius* species were released in Nevis from material obtained from South Africa, but only *Cactoblastis* established and had a significant impact: "It was difficult to find clumps more than one foot in height and most clumps [had] been reduced to the point where only six or eight single rooted cladodes remained" (Simmonds and Bennett 1966). Unfortunately, there are few published data on the size of the *O. triacantha* infestations before and after biological control. In the absence of such data, it is difficult to critically evaluate the true impact of *Cactoblastis* on the basis of comments indicating that "the biological control programme was successful, and the degree of control compares favourably to the classic success obtained by the introduction of *Cactoblastis* into Australia" (Simmonds and Bennett 1966). The reported success on Nevis prompted releases on other Leeward Islands, with good effect, but again, the role of *Cactoblastis* in controlling *O. triacantha* on these islands is difficult to evaluate because information on release numbers, the spatial extent of the releases, and the area of *Opuntia* before and after initiation of biological control is not published (Simmonds and Bennett 1966).

Cactoblastis as an invasive species in North America

The detection of *Cactoblastis* in North America, its potential to spread, and the impact on natural and cultivated *Opuntia* species are a significant cause for concern (Stiling 2002). This has prompted investigations of the direct effects (based on the physiological and ecological host range of *Cactoblastis*) and indirect effects (on *Opuntia*-dependent species) of *Cactoblastis* invasion (e.g., Johnson and Stiling 1996, Vigueras and Portillo 2001, Stiling 2002, Stiling et al. 2004). Certainly *Opuntia* species that are already rare and threatened in North America (e.g., *O. triacantha, Opuntia corallicola* [semaphore cactus]) are likely to be threatened by the invasion of *Cactoblastis,* because of direct herbivory, pathogenic decay facilitated by wounds created during larval feeding (Starmer et al. 1988), and other indirect effects (Stiling et al. 2004).

Inferring the risks of *Cactoblastis* invasion on the basis of its success as a biocontrol agent

To estimate the threats posed by *Cactoblastis* in North America on the basis of a direct comparison with its effects in the biological control of *O. triacantha* in Nevis, *O. ficus-indica* in South Africa, and *O. stricta* in Australia would not be entirely appropriate. Because of differences in the area of infestation, the relative density of the release of *Cactoblastis,* the habitat context (small island, large island, or continent), and the *Opuntia* species targeted, inferences about any of these scenarios based on the others are limited and require qualification.

One common feature of situations in which *Cactoblastis* has moderate to high impacts on *Opuntia* species appears to be high release densities. Currently, pasture is about 3 percent of the area of Nevis (*www.cia.gov/library/publications/the-world-factbook/geos/sc.html*). Assuming that when biological control was undertaken in the 1950s, the area of pasture was twice this size (6 km^2), and that *O. triacantha* covered all the land under pasture, the release of 5200 *Cactoblastis* (egg sticks and small larvae) (Simmonds and Bennett 1966) equates to a potential density of 867 egg sticks per km^2 of *Opuntia* infestation. Releases in South Africa had a potential density of 64,444 egg sticks per km^2 of *Opuntia* infestation. The density of the *Cactoblastis* releases in Australia (total from 1927–1930) was 7320 ± 2589 egg sticks per km^2 of *O. stricta* infestation (mean ± standard error, assuming that the entire district was covered with *Opuntia;* range 85 to 48,653 egg sticks per km^2; $n = 21$ districts; table 1). This estimate does not include subsequent releases totaling 2,177,004,300 egg sticks, whose spatial distribution is not evident from the archives (potential density = 9071 egg sticks per km^2, calculated over the entire *Opuntia* distribution in Australia). Information on the spatial extent of releases vis-à-vis the distribution of the *Opuntia* species in South Africa and the Caribbean is not available for comparison with the Australian efforts. Release density alone, however, may not be an adequate predictor of risk. Although *Cactoblastis* was not sufficient to control *O. stricta* in Kruger National Park, populations that established from a release of 60 egg sticks did have a measurable impact on cactus populations (Hoffmann et al. 1998a, 1998b).

Determining the relative contribution of natural dispersal rates and human movement of cacti (e.g., through the nursery trade) is key to understanding the risks of *Cactoblastis* as an invader. The hypothesized spread rate of *Cactoblastis* in North America (160 km per year; Hight et al. 2002, Solis et

al. 2004) is far greater than natural dispersal rates recorded in North America and other parts of the world, which suggests that human-aided dispersal plays an important role in the spread of this species (Johnson and Stiling 1998, Zimmermann et al. 2000). In South Africa, it was not until biocontrol practitioners moved *Cactoblastis* egg sticks into Kruger National Park that some level of control of *O. stricta* was effected (Hoffmann et al. 1998a, 1998b). Although *Cactoblastis*'s spread was rapid on the Caribbean island of Antigua, its distribution was patchy eight years after release (Simmonds and Bennett 1966). Meaningful inference of *Cactoblastis* dispersal rates in Australia is confounded by the spatially extensive release strategy (table 1). Perhaps ongoing molecular phylogeography studies (e.g., Simonsen et al. 2006) will reveal more about *Cactoblastis*'s dispersal mechanisms and the factors influencing and limiting its spread.

In all of the regions where significant populations of *Opuntia* species were successfully managed with biocontrol, *Cactoblastis* was not the sole agent of control. This fact is significant but often inadequately acknowledged. Cochineal species (*Dactylopius* spp.) were as important as *Cactoblastis* in suppressing *Opuntia* and preventing populations from becoming weedy in these situations (Zimmermann et al. 2004b, Walton 2005). The paucity of information on the impacts of cochineal species limits our ability to evaluate and understand the relative roles of different herbivore species in bringing weedy *Opuntia* species under control.

The invasion of *Cactoblastis* into the southern United States and Central America is a source of concern, given the diversity, endemism, and economic significance of various cactus species in this region (Zimmermann et al. 2000, Vigueras and Portillo 2001, Stiling 2002). Because *Cactoblastis* can feed on a wide range of hosts, it may pose a greater risk of invasion where prickly pear diversity is high—reservoir populations could become established in good or poor seasons, and those could prove difficult to control. Although this threat must be taken seriously, focusing only on the historic impacts of the biological control programs in Australia, South Africa, and the Caribbean, without considering the idiosyncratic features that contributed to *Cactoblastis*'s success as a biocontrol agent, could lead to exaggeration of the nature of the hazard. As stressed by Zimmermann and colleagues (2000), the true nature of the risk will "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 natural- or human-aided dispersal," and by how these factors influence the strength of the interactions between the moth and *Opuntia* populations.

Conclusions

Our objective has not been to deny the value of biological control as a tool in the management of invasive species, but rather to highlight the often overlooked facts and nuances associated with *Cactoblastis,* a poster child of classical biological weed control. We inferred that the spatial extent and density of the egg releases played a significant role in the establishment of the moth and in the dramatic rate of control of *Opuntia* in Australia; however, the continued and persistent control of *Opuntia* to this day is in apparent concordance with the more typical predator–prey cycles expected in CBC. Whether *Cactoblastis* would have been as successful in Australia without inundative releases is unfortunately not an empirically testable hypothesis, but we are exploring this question theoretically by building on preexisting *Cactoblastis–Opuntia* interaction models (Caughley and Lawton 1981).

Some of the features of the Australian *Opuntia* biological control program that contributed to its success—the length of the program, interstate cooperation, and financial input—are only rarely found in other biological control programs. Without these features, future *Cactoblastis*-like successes may be difficult to achieve. If the value of weed biological control is to be understood from iconic case studies, we should perhaps look to CBC successes such as rubber vine in Queensland and water hyacinth in Papua New Guinea and Africa (Walton 2005). Even in these examples, we recommend exploring the factors that contribute to success in each project before making generalizations, as each project is likely to have its own idiosyncrasies.

We hope that the historical details help clarify the ghost of *Cactoblastis* past that often serves as a benchmark to promote, to judge, and more recently, to haunt the discipline of weed biological control.

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