

Biological control of Cactaceae in South Africa

I.D. Paterson^{1*}, J.H. Hoffmann², H. Klein³, C.W. Mathenge⁴,
S. Nesoer³ & H.G. Zimmermann⁵

¹Department of Zoology and Entomology, Rhodes University, P.O. Box 94, Grahamstown, 6140 South Africa

²Zoology Department, University of Cape Town, Rondebosch, 7700 South Africa

³Agricultural Research Council-Plant Protection Research Institute, Private Bag X134, Queenswood, 0121 South Africa

⁴Centre for Plants and the Environment, University of Western Sydney (Hawkesbury Campus), Locked Bag 1797, Penrith South DC, NSW 1797 Australia

⁵Helmuth Zimmermann & Associates (Central), P.O. Box 974, Faerie Glen, 0043 South Africa

This review is a summary of developments that have contributed to the success of several biological control programmes against invasive cactus species (Cactaceae) that have been worked on in South Africa over the last 12 years. Six potential biological control agents have been identified for the control of *Pereskia aculeata* Mill. and molecular studies have identified the origin of the South African *P. aculeata* population. Host-specificity testing is now required for the three most promising of these agents. The successful biological control programme against *Opuntia stricta* (Haw.) Haw. has resulted in a change in management strategies against this weed in the Kruger National Park and the control of *O. stricta* is now almost entirely reliant on biological control. Taxonomic problems associated with the identification of *Cylindropuntia fulgida* var. *fulgida* (Engelm.) F.M.Knuth var. *fulgida* have been resolved and an appropriate cochineal insect (Hemiptera: Dactylopiidae) biotype has been released, resulting in substantial declines in *Cyl. fulgida* var. *fulgida* populations. A long-term monitoring programme has been initiated to evaluate the progress of this new cochineal insect biotype. The Harrisia mealybug, *Hypogeococcus pungens* Granara de Willink (Hemiptera: Pseudococcidae), which was originally released on *Harrisia martinii* (Labour.) Britton & Rose has been collected and redistributed onto *Cereus jamacaru* DC., where it reduces fruit production and leads to the death of both seedlings and large plants. Resolving taxonomic problems to ensure the correct identification of plant species and the most appropriate biological control biotypes have been key issues that have led to the successful control of several cactaceous weed species in South Africa.

Key words: cactaceous weeds, *Pereskia aculeata*, *Opuntia stricta*, *Cylindropuntia fulgida*, *Cereus jamacaru*, cochineal insects, biotypes.

INTRODUCTION

The first biological control agent deliberately introduced into South Africa against an invasive plant was the cochineal insect, *Dactylopius ceylonicus* (Green) (Hemiptera: Dactylopiidae), for the control of the weed, *Opuntia monacantha* Haw. (Cactaceae), in 1913 (Lounsbury 1915). The biological control programme was extremely successful, reducing the density of the weed to negligible levels (Zimmermann *et al.* 2009). Since this early success, a further 14 biological-control-agent entities (species or biotypes) have been released for the control of 15 cactaceous weed species in South Africa. The agents were originally released against eight target species (including *O. monacantha*) but subsequently became established on seven additional cactus species. Of the

Cactaceae that have biological control agents established on them, eight species (53 %) are considered to be under substantial biological control (*i.e.* other forms of management are still needed to supplement biological control, but far less, or less frequently than before), and four species (27 %) are considered to be under complete biological control (*i.e.* no other management interventions are necessary) (Klein 2011). Notable successes include the biological control of *Opuntia aurantiaca* Lindl. (Moran & Annecke 1979; Moran & Zimmermann 1991a), *Opuntia ficus-indica* (L.) Mill. (Annecke & Moran 1978; Zimmermann & Moran 1991), and *Opuntia stricta* (Haw.) Haw. (Hoffmann *et al.* 1999), which are considered to be under substantial control; and *Cylindropuntia leptocaulis* (DC.) F.M.Knuth (Moran & Zimmermann 1991b), *Cylindropuntia fulgida* (Engelm.)

*To whom correspondence should be addressed.
E-mail: i.paterson@ru.ac.za

F.M.Knuth var. *fulgida*, *Cereus jamacaru* DC. (Klein 1999), and *Harrisia martinii* (Labour.) Britton & Rose (Klein 1999), which are under complete control.

Factors that have contributed to the success of biological control of Cactaceae in South Africa include unusual aspects of the biology of the plants and of the cactophagous insects. The taxonomic isolation and characteristic morphology and anatomy of the Cactaceae have resulted in adaptations in their insect herbivores which in turn have resulted in almost no cactophagous insects being able to feed on any plant species outside of the family (Mann 1969; Moran 1980). Because there are no native Cactaceae in the Old World, with the possible exception of *Rhipsalis baccifera* (J.Müller) Stern, oligophagous cactophages can be used for biological control without risk to non-target native or commercial plants (but see below), thereby considerably broadening the pool of suitable agents that are available. The increasing commercial importance of some cactus species such as *O. ficus-indica*, *Opuntia robusta* Wendel and *Hylocereus* species (Cactaceae) in South Africa has hampered efforts to extend biological control of cactus weeds, especially for species in the genus *Opuntia*. This is not a new phenomenon. The introduction of *Cactoblastis cactorum* Berg. (Lepidoptera: Pyralidae: Phycitinae) into South Africa in 1933 was opposed initially on the grounds that the larvae would damage *Opuntia* plants which were providing fruit and fodder for commercial gain. It eventually took a parliamentary decision, in the early 1900s, to allow release of the moth on the grounds that the losses caused by *O. ficus-indica* far exceeded any gains that were derived from this and related cactus species (Annecke & Moran 1978; van Sittert 2002; Zimmermann *et al.* 2009). The success of *C. cactorum* in Australia helped sway opinion in favour of its release in South Africa (Petty 1948; Annecke & Moran 1978; Beinart 2003).

The historical successes of many biological control programmes around the world have benefited from collaboration in the transfer of successful agents between countries sharing common problems. This approach has been especially prominent between Australia and South Africa in the case of the biological control of Cactaceae (Moran & Zimmermann 1984; Zimmermann *et al.* 2009). Not only have these exchanges assisted in the control of already widespread cactus species in

South Africa (*e.g.* *O. aurantiaca* and *O. ficus-indica*), they have also facilitated the control of species that had not yet become problematic in South Africa by providing agents which had proved to be successful in Australia, *e.g.* *H. martinii* (Hoffmann 1995).

In this paper, the biological control programmes against weeds in the family Cactaceae that have been worked on since 1999 in South Africa are reviewed, including the selection of potential biological control agents for *Pereskia aculeata* Mill., recent research on *Cylindropuntia fulgida* var. *fulgida*, long-term post-release evaluations on *O. stricta*, and some observations on the biological control of *Cereus jamacaru*. Species of Cactaceae that have not been worked on in the past 12 years are not included as they were dealt with in previous reviews (Annecke & Moran 1978; Moran & Annecke 1979; Moran & Zimmermann 1991a,b; Zimmermann & Moran 1991; Klein 1999).

PERESKIA ACULEATA

Pereskia aculeata (Barbados gooseberry, pereskia) is a primitive creeping cactus with well developed leaves and woody stems and branches (Fig. 1). The plant is armed with paired, hooked thorns at the leaf-bases on the young, green shoots and clusters of long spines which develop progressively on older, woody stems (Henderson 1995). Flowers are creamy-white and have creamy-white stamen filaments in South Africa, and either creamy-white or purple stamen filaments in the native distribution (Leuenberger 1986; Paterson *et al.* 2009). The fruits are yellow and spiny when immature, but as the fruit ripens the spines are lost and the fruit changes to an orange colour (Leuenberger 1986).

Pereskia aculeata is native to parts of Central America and the Caribbean as well as to southeastern Brazil and northern Argentina (Leuenberger 1986). It was first recorded in South Africa in the Cape Town Botanical Gardens in 1858 (McGibbon 1858) and has become naturalized in areas around Cape Town and in Gauteng, Mpumalanga and Limpopo provinces. It has also naturalized along the eastern coast of the country in the Eastern Cape Province and KwaZulu-Natal Province, where it is particularly invasive and abundant in forests and coastal vegetation (Fig. 2) (Henderson 2001). The plant overgrows and kills indigenous coastal and forest flora, sometimes even causing large trees to collapse under the weight of the

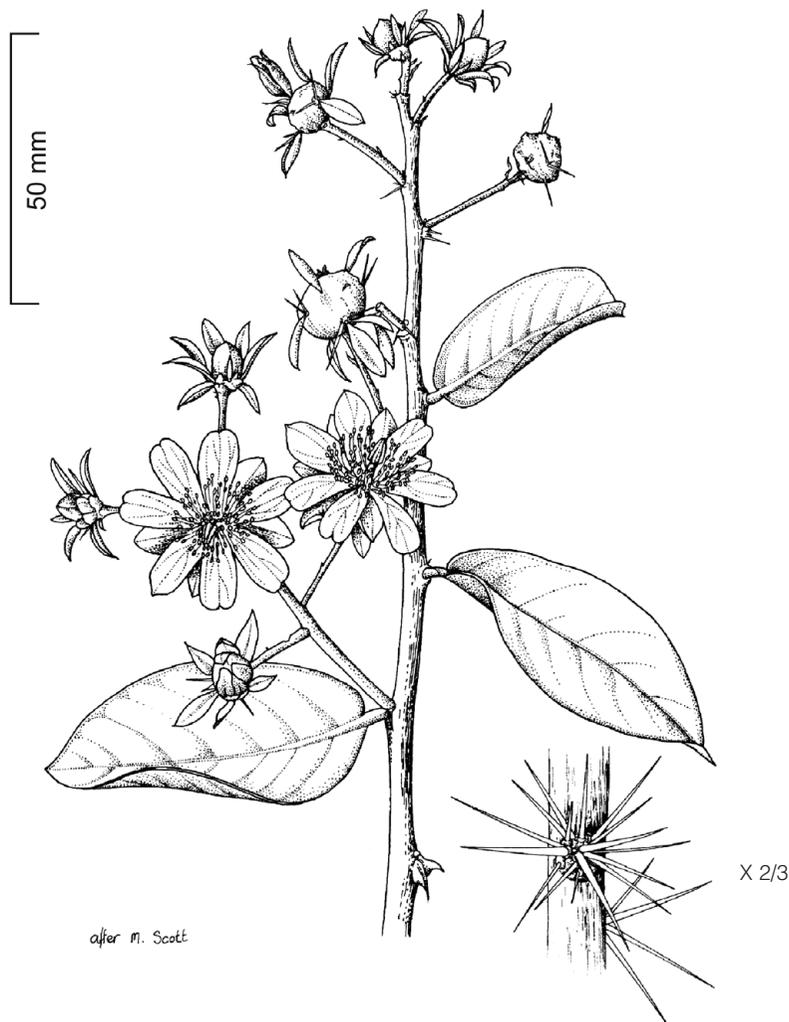


Fig. 1. *Pereskia aculeata*. (Drawn by G. Condy; first published in Henderson (1995), ARC-Plant Protection Research Institute, Pretoria.)

infestation (Moran & Zimmerman 1991b, Paterson *et al.* 2011). It was declared a weed in 1979, Proclamation R35 (1979), and under the Conservation of Agricultural Resources Act (Act 43 of 1983) (CARA 1983). It is also listed as an invasive alien plant in the draft regulations in terms of the National Environmental Management: Biodiversity Act (Anon. 2004).

Mechanical and herbicidal control methods are not effective against *P. aculeata* and have deleterious effects on non-target plants because *P. aculeata* usually grows intertwined with native vegetation. Mechanical control is ineffective because any small piece of the plant that is overlooked can

regenerate. Herbicides are not translocated within the plant's tissues so all parts of the plant must be sprayed for effective control (Klein 1999). Biological control is therefore the only economically viable and sustainable method to control *P. aculeata* (Moran & Zimmermann 1991b).

The disjunct native distribution of *P. aculeata* was seen as a possible constraint to the biological control programme because insects or pathogens may have developed close associations with different *P. aculeata* populations (Paterson *et al.* 2009). This could result in some insects and pathogens being more damaging on plants from certain populations (Kniskern & Rausher 2001). *Pereskia aculeata* is

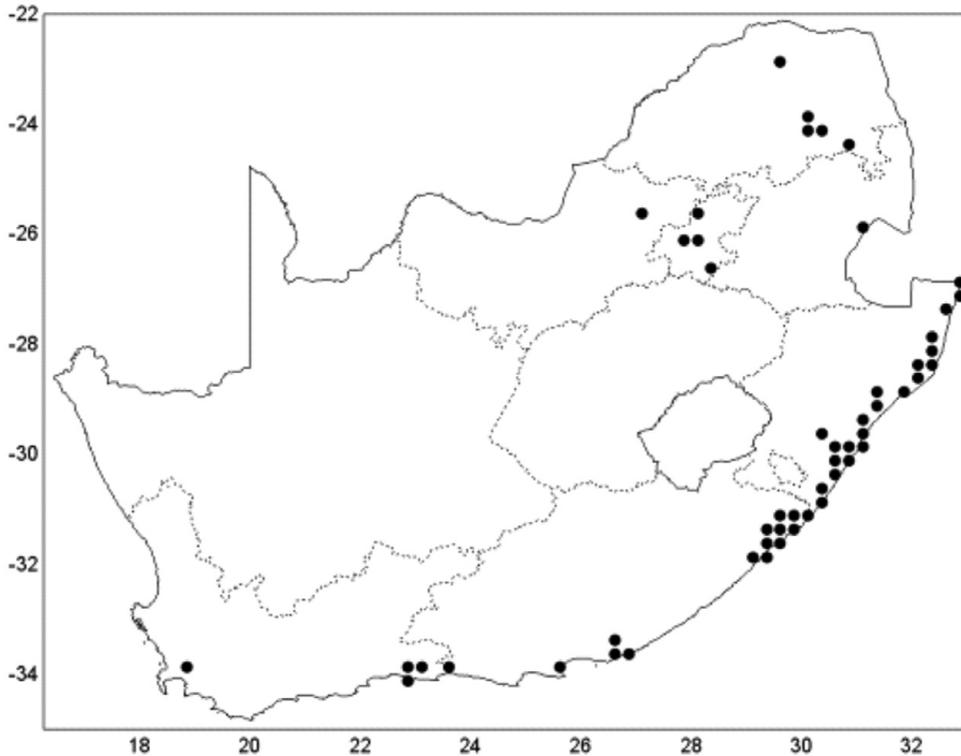


Fig. 2. Distribution of *Pereskia aculeata* in South Africa. (Drawn by L. Henderson; data source: SAPIA database, ARC-Plant Protection Research Institute, Pretoria.)

a polymorphic species that includes a number of different wild and garden varieties, and plants from the northern and southern regions within its native distribution are morphologically distinct (Leuenberger 1986). Plants from the South African populations exhibit a mixture of morphological characters from both regions of the native distribution making it difficult to determine the origin of the South African plants. A recent genetic study indicated that the South African *P. aculeata* population matched the population in Rio de Janeiro Province in southern Brazil most closely, making this region the most appropriate in which to commence surveys for biological control agents in terms of genotype matching (Paterson *et al.* 2009).

Current biological control of *Pereskia aculeata*

The only biological control agent released for the control of *P. aculeata* is *Phenrica guerini* Bechyné (Coleoptera: Chrysomelidae) which was released in small numbers (from 36 to about 100 beetles per release) at ten sites in KwaZulu-Natal Province and at two sites in Eastern Cape Province between

1991 and 1997 (Klein 1999). Establishment was recorded at only two of the original release sites (30°24'S 33°41'E; 33°36'S 26°53'E) and no reduction in *P. aculeata* density was apparent at either site. Recent releases of higher numbers have resulted in the establishment of *P. guerini* at Wewe Dam (29°32'27"S 31°08'06"E) in KwaZulu-Natal Province and the high levels of damage at this site suggest that the potential impact of *P. guerini* may have been underestimated (D. Conlong, pers. comm.).

Surveys for new potential biological control agents

Pereskia aculeata has been surveyed for potential biological control agents in southern Brazil, northern Argentina, Venezuela and Dominican Republic during eight field trips between 1984 and 2007. Many of these field trips were brief and in some cases *P. aculeata* was only examined on an opportunistic basis while surveying for insects on various other South American plant species that are problematic in South Africa. Forty-three insect species

were recorded on *P. aculeata* during these field trips (I.D. Paterson, unpubl.). Six of these species are discussed below based on the fact that they were either commonly encountered or may hold some promise as potential biological control agents. Specimens are housed at the South African National Collection, Agricultural Research Council-Plant Protection Research Institute (ARC-PPRI), Pretoria, and referred to by Rhodes University (RH) or National Collection (Ac) accession numbers. A leaf-tying moth, *Loxomorpha cambogialis* (Guenée) (formerly under *Epipagis*) (Lepidoptera: Pyralidae), which was rejected due to its broad host range, is not included because it was dealt with in a previous review (Klein 1999).

Maracayia chlorisalis (Walker) (Lepidoptera: Crambidae) (RH 745, RH 746, RH 774) is considered a promising agent due to the mode of damage and the effect this has on plants in its country of origin. Eggs are deposited on young shoots and the larvae bore into and mine the cortex, pushing excreta through holes to the outside (Klein 1999). The damage sometimes results in shoot death and induces the development of secondary shoots from below the mine. Preliminary host-specificity testing and the known host range of *M. chlorisalis* suggest that it will be restricted to a few genera in the Cactaceae and the moth is therefore likely to be safe for release in South Africa.

However, *M. chlorisalis* is considered a pest on *Hylocereus undatus* Britton & Rose in the State of Puebla, Mexico (CESAVEP 2006) and was also recorded on *Hylocereus ocamponis* (Salm-Dyck) Britton & Rose in Columbia (Zenner de Polania 1990). The fruits of *Hylocereus*, commonly referred to as pitahaya or dragon fruit, are widely consumed in Asia and in some South and Central American countries, and are rapidly becoming popular in the European market (Nerd *et al.* 2002; Le Bellec *et al.* 2006). It is traditionally grown in South-East Asia and Central America, and is now considered a promising new crop species elsewhere. It is cultivated extensively in Israel and on a smaller scale in Australia and on Réunion Island (Van Wyk 2005; Le Bellec *et al.* 2006). Pitahaya is a new crop species grown on a small scale in South Africa (J. Husselman, Institute for Tropical and Subtropical Crops, ARC, pers. comm.). Thus, the introduction of *M. chlorisalis* could cause a conflict of interest between biological control practitioners and pitahaya farmers. Although the pitahaya industry in South Africa is very small at present there is a great deal of poten-

tial for production in South Africa and neighbouring countries. The possible negative impact of *M. chlorisalis* on South African pitahaya production should not be ignored, but, currently, the benefits of control of *P. aculeata* outweigh the benefits of pitahaya production. *Maracayia chlorisalis* should therefore be considered for release provided host-specificity tests confirm that the insect's host range is restricted to the Cactaceae.

An undescribed moth species, *cf. Porphyrosela* sp. (Lepidoptera: Gracillariidae: Lithocolletinae) (RH 747, RH 748), is another potential agent for use in South Africa. It mines the leaves of *P. aculeata*, feeding between the epidermal layers of the leaf blade and pupating within the mine. Members of the Lithocolletinae are usually host specific or live on a suite of closely related plants (Holloway *et al.* 1987) but observations in the native range suggest that this species feeds on *Talinum paniculatum* Gaertner (Portulacaceae) and *Anredera cordifolia* (Ten.) Steenis (Basellaceae). Leaf-mining species are not usually considered effective biological control agents (Harris 1973; Goeden 1983) and it is possible that damage to the leaves of the plant without destroying the growing tips would have little negative effect on overall plant growth. Although observations in the native range suggests that this species may have a broad host range and inflict little damage, further research is warranted. If *cf. Porphyrosela* sp. proves to be suitably host specific for release in South Africa it could contribute to control in conjunction with other agents.

An unidentified species of Tenthredinidae (Hymenoptera) was found at coastal sites in Santa Catarina Province, Brazil (26°46'00"S 48°38'27"W; 26°47'26"S 48°35'16"W; 26°55'07"S 48°38'33"W). The larvae are large, solitary, external leaf feeders and the final-instar larva migrates to the base of the plant to pupate in the soil. Although this species has only been found in one localized area, the climatic conditions there were found to match those where *P. aculeata* is invasive in South Africa. This species should be identified, if possible, prior to host-specificity testing to reveal any available host-range records, and because similar-looking larvae have been observed feeding on *Talinum paniculatum* Gaertner (Portulacaceae) in a nearby region in South America (Misiones, Argentina).

A leaf-galling wasp, *Bruchophagus* sp. (Hymenoptera: Eurytomidae) (AcSN 2784, RH 749, RH 750), was found in Rio de Janeiro and Santa Catarina provinces, Brazil, and in Misiones Province, Argen-

lina. Each wasp larva forms a button gall up to about 5 mm in diameter causing a raised area on the surface of the leaf. A yellow necrosis is sometimes associated with the galls, presumably as the galls age. Even at sites where *Bruchophagus* sp. was found to be reasonably common, such as north of Rio de Janeiro (22°56'29"S 42°39'57"W) and near Itajaí in Santa Catarina Province (26°55'07"S 48°38'32"W), the plants appeared to be unaffected by the galls. The majority of the galls seen were green, so photosynthesis does not appear to be immediately disrupted by the galling action and *Bruchophagus* sp. by itself is unlikely to be adequately damaging for biological control.

Weevil larvae (Coleoptera: Curculionidae) were found mining the stems of *P. aculeata* at two coastal sites in Santa Catarina Province, Brazil (26°45'43"S 48°38'49"W; 26°47'19"S 48°35'14"W). The larvae have not been reared to the adult stage to allow identification and nothing is known about the potential host range of the species. It is possible that more than one species of curculionid was responsible for the damage. Because of the mode of damage and the past success of Curculionidae as biological control agents, identification of the species should be considered a priority.

Galled fruits were found at four sites near Foz do Iguazu in Misiones Province, Argentina (25°41'29"S 54°26'13"W; 25°35'18"S 54°31'08"W; 25°36'24"S 54°29'39"W; 25°40'33"S 54°26'47"W). Affected fruits were enlarged and did not ripen to the orange colour of an undamaged fruit, remaining green and developing a woody exterior and apparently remaining on the plant for an extended period. Hymenopterous larvae found in the fruits, at the first of the four listed sites, were tentatively assumed to be responsible for the galling. The galled fruits did not contain seeds. Seeds of *P. aculeata* are viable in South Africa (Campbell 1988) and are spread by birds and bats that consume the fruits, enhancing the need for a seed-feeding agent such as this. Maintaining a culture of this species in quarantine may be difficult as a supply of young, actively growing fruits will most likely be needed for oviposition.

Future research into the biological control of *P. aculeata*

The most promising of the potential agents, based on damage done to the plant in the region of origin, are *M. chlorisalis*, the tenthredinid and the curculionid stem borers. These species should

be considered priority species and collected in southern Brazil, preferably in Rio de Janeiro Province, for further study.

Further intensive general surveys for new potential agents are also needed, especially in areas that have not yet been visited. If no suitable natural enemies are found in the southern regions of the plant's native distribution, then surveys should be conducted in the northern region of the native distribution where plants are less closely aligned with the South African populations (Paterson *et al.* 2009). Natural enemies found in the northern region of the native distribution could possibly form new host-plant associations and perhaps, therefore, according to the theory of Hokkanen & Pimentel (1984, 1989), might be more damaging than agents that are taxonomically closer to the South African *P. aculeata* populations.

Extensive surveys for *M. chlorisalis* on wild and cultivated pitahaya species and other species of Cactoideae in southern and eastern Brazil are necessary to determine its natural host range and to determine whether *M. chlorisalis* is likely to be a threat to South African pitahaya farmers. It is possible that there are different forms of *M. chlorisalis* and that the form present in southeastern Brazil differs from the form which is reported as a crop pest in Central America.

The recent observations of extensive damage by *P. guerini* at the Wewe Dam site in KwaZulu-Natal, suggests that this species may still have a role to play as a biological control agent, and that releases of *P. guerini* should continue and post-release evaluations should commence.

OPUNTIA STRICTA

Two previous reviews of the biological control of *O. stricta* in South Africa (Moran & Zimmermann 1991b; Hoffmann *et al.* 1999) described the formative stages of a programme that has since become highly successful. The two agents deployed, the cactus moth *C. cactorum* and, especially, the cochineal insect *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactylopiidae), continue to suppress *O. stricta* populations. *Opuntia stricta* is currently considered under substantial control (Klein 2011).

An ongoing monitoring programme at research sites in the Kruger National Park (25°01'S 31°35'E) has shown that the biomass of *O. stricta* (measured as cladodes/m²) declined by approximately 90 % within six years of the 'stricta' biotype of *D. opun-*

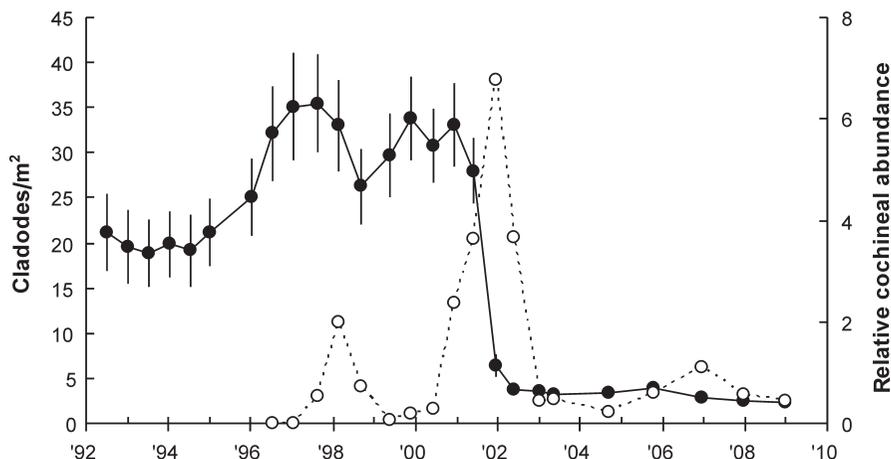


Fig. 3. Biomass of *Opuntia stricta* (shown as mean \pm S.E. cladodes/m²; ●) in an area of Kruger National Park over a 17-year period. Open circles show the relative abundance of the cochineal insect, *Dactylopius opuntiae*, since its introduction during 1997.

tiae being released and that the cactus has remained at low levels ever since (Fig. 3). The period between release of cochineal insects and the abrupt decrease in biomass of the cactus could have been much shorter were it not for a period of high rainfall and flooding in the region during the late 1990s. Heavy rain destroys cochineal insects by dislodging the immobile females and nymphs from the host plant (Moran & Hoffmann 1987; Moran *et al.* 1987), causing their populations to dwindle, and allows recovery of the host plants, which flourish while ample moisture is available and damaging insects are scarce. This pattern was apparent between 1998 and 2000 (Fig. 3) when, after an initial escalation in cochineal insect populations and signs of a drop in cactus biomass in 1997, the relative abundance of the cochineal insects declined and the biomass of cactus increased. A period of low rainfall during the early part of the 21st century once again favoured the cochineal and a rapid increase in abundance of the insects was accompanied by a sharp decline in the cactus (Fig. 3). Since 2002 the biomass of cactus has remained at low levels and insecticidal-exclusion experiments have confirmed that both *C. cactorum* and *D. opuntiae* are responsible for keeping the weed in check (J.H. Hoffmann *et al.*, unpubl.).

Besides reducing the standing biomass of *O. stricta*, the insects have also brought about a substantial decline in the mean size of the *O. stricta* plants in the thickets, from *c.* 11 cladodes per plant before 2003 to *c.* 2 cladodes per plant since then (J.H. Hoffmann *et al.*, unpubl.). This has happened

because nearly all plants of fruit-bearing size (*i.e.* >27 cladodes) (Hoffmann *et al.* 1998a,b; Lotter & Hoffmann 1998) have been destroyed and practically no fruits have been produced in the research plots since 2005 (J.H. Hoffmann *et al.*, unpubl.). The lack of fruits has put a stop to the long range dispersal potential of *O. stricta*, thereby curbing expansion of the weed into surrounding unaffected areas.

The success of the biological control programme against *O. stricta* has brought about a substantial decrease in the use of herbicides that otherwise would have had to be used to contain the problem. Limitations on the natural dispersal of *D. opuntiae* (Foxcroft & Hoffmann 2000) have been overcome by instituting a manual distribution campaign in Kruger National Park. The team of labourers that was previously employed to apply herbicides is now responsible for rearing *D. opuntiae* in a specially-constructed facility from where consignments of the insects are deployed, both within the park and on surrounding properties (Foxcroft & Hoffmann 2000). The whole management programme against *O. stricta* in Kruger National Park has focused on maximizing the use of biological control and is now almost entirely reliant on *C. cactorum* and *D. opuntiae* (Lotter & Hoffmann 1998; Foxcroft *et al.* 2004, 2007a,b; Foxcroft & Freitag-Ronaldson 2007; Foxcroft & Rejmanek 2007).

Biotypes of cochineal insects and hybridization

The introduction of a distinct biotype of *D. opuntiae* onto *O. stricta* in South Africa has opened

Table 1. Release sites of the 'cholla' biotype of the cochineal insect, *Dactylopius tomentosus*, against *Cylindropuntia fulgida* var. *fulgida* in South Africa.

Release dates	Localities
Dec. 2003, Oct. 2008, Sept. 2009	Five release sites on the farm 'Kleinplaas' on road between Douglas and Campbell, Northern Cape: 28°55'12"S; 23°45'06"E ; 28°55'15"S; 23°45'09"E; 28°55'15"S; 23°45'09"E; 28°53'52"S; 23°42'51"E; 28°53'26"S; 23°42'34"E
18 Nov. 2008	Island in Limpopo River course, ±4 km WNW of Musina, Limpopo Province 22°12'39.64"S; 29°56'54.91"E

opportunities for there to be cross breeding between this and the already-long-established but different biotype on *O. ficus-indica*. In using the two biotypes, consideration needs to be given as to what might happen when the host plants occur sympatrically and the insects are free to interbreed. Laboratory studies showed that the two biotypes interbreed freely and produce viable progeny that develop equally well on either of their parental host plant species (Hoffmann *et al.* 2002).

The production of a more-generalist lineage of cochineal could be advantageous for biological control because the insects would have a larger pool of plants on which to develop, enhancing chances of successful host-plant location by the passively-dispersed crawlers and boosting the overall populations of *D. opuntiae*. This potential advantage is negated because the F₂ and subsequent generations produce progeny which revert to being host specific and at least half of the crawlers that are produced occur on plants on which they cannot develop (Hoffmann *et al.* 2002; Hoffmann 2004).

Hybridization has happened under field conditions with an outcome that was not anticipated and, under some circumstances, with possible negative consequences for the use of *D. opuntiae* as a biological control agent (Hoffmann 2004). In at least one area where the 'stricta' biotype of *D. opuntiae* was introduced onto *O. stricta* plants interspersed with *O. ficus-indica*, 'ficus' biotype males have crossed with 'stricta' biotype females but not the converse (Hoffmann 2004). Such crossings result in a disproportionate number of crawlers with 'ficus' traits hatching on *O. stricta* and not surviving because they are on an unsuitable host. While the consequences of these asymmetrical crosses have not yet been investigated, it is envisaged that the performance of *D. opuntiae* as a biological control agent should not be affected on

O. ficus-indica but could be curtailed, or even lost altogether, on *O. stricta* populations that are in close proximity to *O. ficus-indica* (Hoffmann 2004). Every effort is currently being made to keep the two biotypes apart and to use only one biotype where *O. ficus-indica* and *O. stricta* occur together.

CYLINDROPUNTIA FULGIDA VAR. FULGIDA

Cylindropuntia fulgida (Engelm.) F.M.Knuth var. *fulgida* is an upright, much-branched cactus (Fig. 4), the terminal segments of which are easily dislodged. Its cylindrical stem segments are covered in dense clusters of elongate yellow spines, each enclosed in a detachable sheath (Anderson 2001). The flowers are pink to magenta with recurved petals. Fruits remain attached to the plant and new flowers develop from the areoles of the fruit, giving rise to chains of fruit (Benson 1982). The species occurs naturally in the Sonoran Desert of Arizona, and Sonora, Sinaloa and northern Baja California, Mexico. It is commonly known as the chain-fruit cholla or jumping cholla (Anderson 2001) – the latter refers to the ease with which its terminal segments are able to attach themselves to animals or humans that brush past the plant.

Chain-fruit cholla was imported into South Africa, probably as an ornamental, at least as early as the 1940s (De Beer 1986). It is now encroaching upon natural pastoral land and conservation areas in the warm, arid parts of the country, reducing the value and productivity of infested areas (Moran & Zimmermann 1991b) and causing harm, even death, to domestic animals, small antelope and other small mammals and birds. Infestations are localized around Douglas in the Northern Cape Province (Moran & Zimmermann 1991b), as well as on both the South African and Zimbabwean sides of the Limpopo River near Musina in the Limpopo Province (Table 1). Infestations have also been reported from the Western Cape,

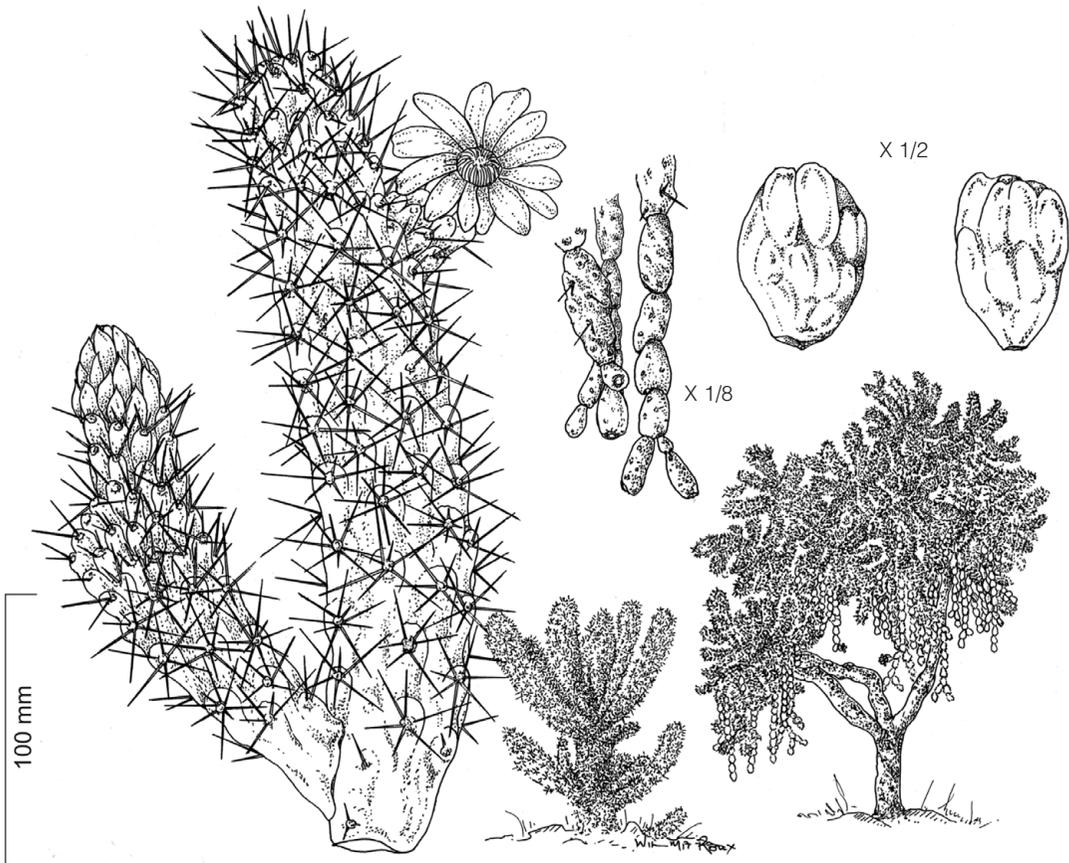


Fig. 4. *Cylindropuntia fulgida*. (Drawn by W. Roux; first published in Henderson (1995), and modified in Henderson & Zimmermann (2003), ARC-Plant Protection Research Institute, Pretoria.)

North West and Free State provinces of South Africa (Henderson & Zimmermann 2003) (Fig. 5), although some of these records might mistakenly be of the closely related *Cyl. tunicata* (Lehmann) F.M.Knuth or *Cyl. rosea* (DC.) Backeb.

Herbicidal control subsidized by the Department of Agriculture, first using picloram and later MSMA, has been in practice since the late 1970s without much success. The costs involved are prohibitive, particularly for the low-value land on which many of the infestations occur. The *Working for Water* Programme of the Department of Water Affairs is currently employing people for mechanical and chemical management of the infestations as part of a public works programme. Large parts of the infestation east of Musina have been controlled through this initiative (H. Klein, unpubl.).

Taxonomy of *Cylindropuntia fulgida* var. *fulgida* and of its associated cochineal insects

In common with many other cactus biological control projects, taxonomic confusion has impeded exploration for and the success of natural enemies used against *Cyl. fulgida* (Moran & Zimmermann 1984), which for many years was incorrectly identified in South Africa as *Cyl. rosea* (= *Cyl. pallida* (Rose) Knuth) (Wells *et al.* 1986), and earlier as *Cyl. tunicata* (M.J. Wells, unpubl.). Because of previous successes in South Africa and elsewhere, biological control using cochineal insects, *Dactylopius* species, was also the preferred control option against chain-fruit cholla (Moran 1981; Moran & Zimmermann 1984, 1991a; Hosking *et al.* 1988; Zimmermann & Moran 1991; Hoffmann *et al.* 1999). *Dactylopius tomentosus* (Lamarck), which was known to attack *Cylindro-*

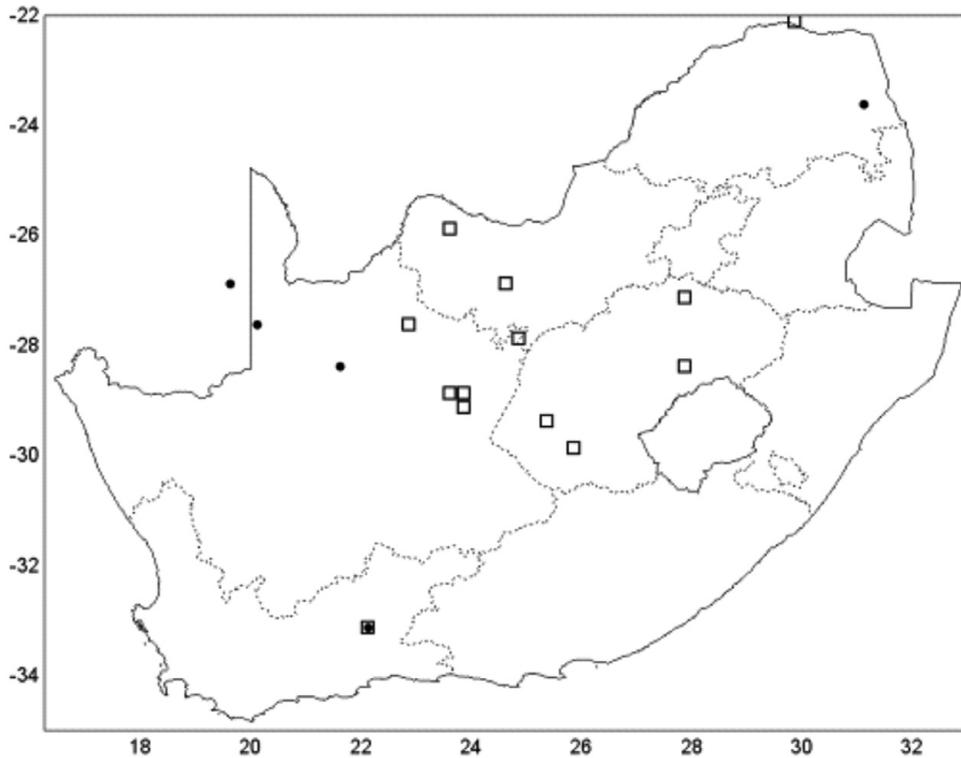


Fig. 5. Distribution of *Cylindropuntia fulgida* in South Africa. □, *Cyl. f. var. fulgida*; •, *Cyl. f. var. mamillata*. (Drawn by L. Henderson; data source: SAPIA database, ARC-Plant Protection Research Institute, Pretoria.)

puntia species (Mann 1969), was present in South Africa, having been introduced during 1969 via Australia, and released in 1970 for the successful control of *Cyl. imbricata* (Haw.) F.M.Knuth (Moran & Zimmermann 1991b). Attempts were made to use these populations of *D. tomentosus* (i.e. those of the identical provenance, originating from Australia, and already present in South Africa) against *Cyl. fulgida* var. *fulgida* near Douglas in the Northern Cape during the 1970s. The insects survived and even killed some small plants, but they were ineffective against the large plants (Moran & Zimmermann 1991b) and the infestations of the weed persisted and increased.

During 2000, attempts were made to obtain other provenances of the agent and a consignment of *D. tomentosus* was collected in Mexico from *Cyl. rosea*, which was the species presumed to be problematic in South Africa at the time. This release also did not succeed, creating some doubts about the correctness of the identity of the weed (Mathenge *et al.* 2009b). Consultation and exchange of material with cactus taxonomists from

Mexico and the U.S.A. culminated in the conclusion that the problem cactus in South Africa was indeed *Cyl. fulgida* var. *fulgida*. The initial taxonomic confusion seems to have arisen because some of the plants around Douglas were uncharacteristically small and lacked the chain-fruits, which are so characteristic of *Cyl. fulgida* var. *fulgida*. However, the discovery of plants bearing chains of fruits and floral structures characteristic of *Cyl. fulgida* var. *fulgida* on the Zimbabwean side of the Limpopo River gave the vital clue that led to resolution of the dilemma: in Zimbabwe the cactus was not subject to any form of control and the plants there were reaching their full size and state of maturity, bearing chain fruits, unlike the populations of plants near Douglas where chemical control operations were continually destroying the largest plants in the population and where no chain-fruits were being produced. Furthermore, the subsequent discovery of old photographs from the Douglas area, prior to the start of the chemical control campaign, revealed that large plants with typical chains of fruits had occurred in

the area, confirming the identity of the problem cactus as *Cyl. fulgida* var. *fulgida* (Henderson & Zimmermann 2003).

Once the identity of the target weed had been definitively resolved, further shipments of *D. tomentosus* were obtained from Mexico during 2001. These collections purposefully included populations from several *Cylindropuntia* species, based on the recent discovery that the cochineal insect, *D. opuntiae*, comprised at least two biotypes (Volchansky *et al.* 1999; Githure *et al.* 1999), implying that *D. tomentosus* might also have distinct biotypes on the range of host plants with which it is associated. Cochineal insects were collected from *Cyl. fulgida* var. *fulgida* between Sonoyta and Puerto Penasco (31°12'N 112°27.5'W), from *Cyl. fulgida* var. *mamillata* (Schott ex Engelm.) Backeb. at Hermosillo, in the Sonoran Desert (29°3'N 110°58'W), and, fortuitously, also from the morphologically similar *Cyl. cholla* (F.A.C. Weber) F.M. Knuth (chain-link cholla) collected near Loreto (23°44'N 110°06'W), and at the CIBNOR research station near La Paz (24°10'10"N 110°17'43"W), both in Baja California Sur.

In South Africa, the biology and host specificity of these provenances of *D. tomentosus* were investigated (Mathenge *et al.* 2009a,b) revealing that *D. tomentosus* had some unique characteristics, e.g. due to a prolonged egg stage, the life cycle of the females is of 63 days duration which is about 17 days longer than that of its congeners. Host-specificity trials confirmed that the different provenances of *D. tomentosus* behaved as distinct biotypes (Mathenge *et al.* 2009b; 2010b). Surprisingly, development of the 'cholla' biotype (the population of *D. tomentosus* collected from *Cyl. cholla* in Baja California Sur) was faster than that of any of the other populations collected from *Cyl. fulgida* var. *fulgida*, their crawlers settled and survived more successfully, reached maturity more rapidly, and the resultant females were larger and produced more progeny (Mathenge *et al.* 2009b). Thus the 'cholla' biotype became the agent of choice for release against *Cyl. fulgida* var. *fulgida* in South Africa (Mathenge *et al.* 2009b).

Laboratory hybridization trials between the 'cholla' biotype and the 'imbricata' biotype of *D. tomentosus* revealed that the two biotypes were still reproductively compatible, and that hybrid offspring were less host specific than either of the parental lines (Mathenge *et al.* 2010a), which could be beneficial to biological control. However, since

the effects of hybridization on later generations and the influences of the environment on the insects were not tested, it was recommended that the new 'cholla' biotype only be released on *Cyl. fulgida* var. *fulgida* in areas that are free from cochineal-infested *Cyl. imbricata* plants, pending further studies in the field.

Investigations using molecular techniques demonstrated that the *D. tomentosus* populations collected from *Cyl. fulgida* var. *fulgida*, *Cyl. fulgida* var. *mamillata* and *Cyl. imbricata* had closer phylogenetic relationships with each other than with populations from *Cyl. cholla* (Mathenge 2010; Mathenge *et al.* in prep.). The largest genetic divergence was recorded in populations of *D. tomentosus* from *Cyl. rosea* suggesting that the 'rosea' biotype may justify a different taxonomic status, such as a host race or sibling species, and explains why this provenance had failed earlier on in the programme.

Impact of the cochineal insects on *Cyl. fulgida* var. *fulgida*

The 'cholla' biotype of *D. tomentosus* was released on a large infestation of *Cyl. fulgida* var. *fulgida* on the farm Kleinplaas near Douglas, Northern Province (Table 1) but was less damaging to the weed than had been expected. Suspicions that the insect culture might have inadvertently been contaminated with the biotype from *Cyl. imbricata* during mass-rearing prompted acquisition of new shipments of the insects for release. During September 2007 two populations of *D. tomentosus* were collected from *Cyl. cholla* growing at the two Baja California Sur sites in Mexico. In South Africa the colony was cleared of predators, parasitoids and contaminants under quarantine conditions at Rietondale, Pretoria, and mass-reared for release during 2008 at the localities listed in Table 1.

Four months after the release near Musina, all of the inoculated plants were heavily colonized with cochineal insects, cladodes were falling from the plants, small plants were dying and the insects had dispersed up to 5 m from the release sites. By November 2009, a year after release, many plants were dead, and it was difficult to find plants in the area that were not heavily colonized by cochineal insects. By June 2010, the cochineal insects had dispersed throughout the 87-ha infestation, the majority of small plants were dead, and only a few large cactus plants with woody stems still survived,

although most of their cladodes had detached and died. Heavy summer rains at the time washed the cochineal insects from the exposed sides of the surviving plants but a substantial portion of the cochineal population survived on the underside and protected parts of the stems and cladodes.

As a result of the unexpectedly rapid proliferation of the cochineal insects at Musina, the opportunity was missed to monitor the earliest stages in the establishment, including population growth and dispersal of the insect, and to measure the early effects on the target weed. Long-term monitoring of the fate of later releases in the Northern Cape, where the cactus is evenly distributed, is planned.

A visit to Douglas in the Northern Cape during July 2010 showed that the damage from cochineal insects was less marked than it had been at Musina. There was considerable new growth on many of the large, woody-stemmed cactus plants but practically all the small plants and detached segments were dead or dying. The new growth on all monitored plants was already infested with cochineal insects (H. Klein, unpubl.). The superior performance of the cochineal insects at Musina compared to Douglas is probably related to Musina's higher winter temperatures and lower rainfall, both of which are known to favour cochineal insect development (Zimmermann & Moran 1982; Moran & Hoffmann 1987; Moran *et al.* 1987).

During March 2009, the *Working for Water* clearing team at Musina was advised about the *Cyl. fulgida* var. *fulgida* infestations and they agreed to harvest cactus cladodes colonized by the cochineal insects and to redistribute them, instead of applying herbicides. *Cylindropuntia fulgida* var. *fulgida* is now considered under complete control (Klein 2011).

CEREUS JAMACARU

The initiation of biological control against the columnar cactus, *Cereus jamacaru*, commonly known as queen of the night cactus (Fig. 6), was reviewed by Moran and Zimmermann (1991b) and by Klein (1999). This project is the secondary consequence of the release of two agents, the mealybug, *Hypogeococcus pungens* Granara de Willink (Hemiptera: Pseudococcidae), referred to in earlier literature as *H. festerianus* (Lizer e Trelles), and the stem borer *Nealcidion cereicola* (Fisher)

(formerly under *Alcidion*) (Coleoptera: Cerambycidae), against another cactus, *Harrisia martinii* in the same subfamily, Cactoideae. As expected, both of these agents readily accepted *Ce. jamacaru* as a host.

Nealcidion cereicola has become established at only a few sites, but is very damaging where populations reach high levels. By weakening the structural tissues of the cactus, they cause large stem sections to break off, or the entire plant to collapse.

By contrast, *H. pungens* has been actively redistributed throughout the range of *Ce. jamacaru* in South Africa (Fig. 7). In most parts of the country, this agent keeps *Ce. jamacaru* under effective control, and all other control measures have been discontinued. When the mealybug becomes established on a cactus plant, the insects congregate in any area of the plant which is actively growing, where they cause abnormal growth, especially on the stem tips, which become swollen and spiny. These lumps apparently result from the proliferation of thin, twisted shoots with shortened internodes and closely-spaced spines. Each infested plant dies eventually: young plants succumb before having reached flowering age, whereas plants that only become infested when they are several metres tall, may take up to four years to die. However, even on such large plants, fruit production is markedly reduced almost from the time that the insects become established, since the mealybugs aggregate on the developing flowers. Generally, one large specimen of *C. jamacaru*, infested with *H. pungens*, is sufficient to ensure that all seedlings germinating in the area become infested and die (H. Klein, pers. obs.). No formal quantitative post-release evaluations have been undertaken on this biological control project but the weed is considered under complete control (Klein 2011).

In KwaZulu-Natal Province, the cactus has been reported to tolerate *H. pungens* damage better than in the rest of the country (R. Brudvig, pers. comm.). It is not clear whether this is a result of the subtropical climate or a combination of other factors, including parasitism and predation. Predation of *H. pungens* by coccinellid beetles such as *Chilocorus* species and parasitism by the encyrtid wasp, *Homalotylus flaminus* (Dalman) (Hymenoptera: Encyrtidae), have been observed in South Africa (Danninger 2002), but their impact has not been quantified. *Cereus jamacaru* plants growing in KwaZulu-Natal might differ taxonomically from those in other parts of the country;

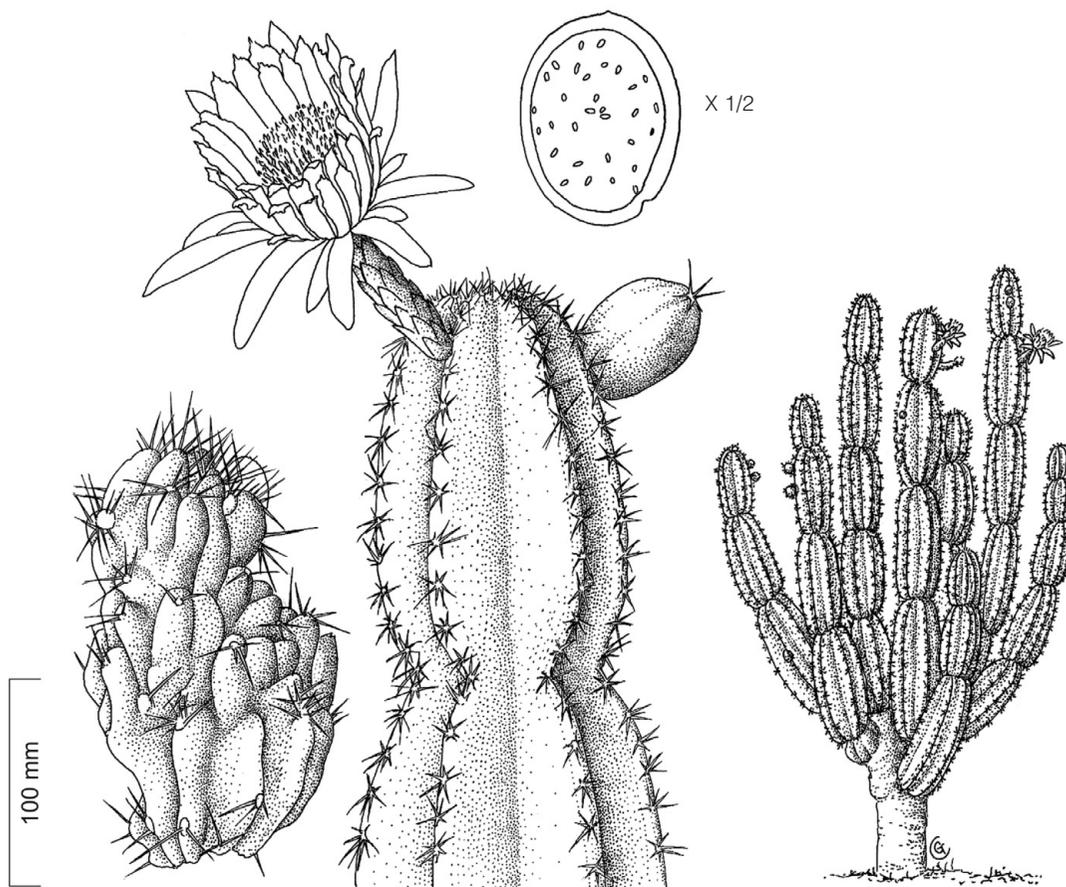


Fig. 6. *Cereus jamacaru*. (Drawn by G. Condy; first published in Henderson (1995), ARC-Plant Protection Research Institute, Pretoria.)

for example, it is suspected that *Ce. hildmannianus* K. Schum. (= *Ce. uruguayanus* Ritter ex Kiesling) might be present in South Africa. However, since *H. pungens* (as *H. festerianus*) is known to feed widely within the subfamily Cactoideae (McFadyen & Tomley 1981), this is unlikely to be a limiting factor in the biological control of *C. jamacaru*.

CONCLUSIONS

In retrospect, after a century of biological control projects against cactus weeds in South Africa – from the successful control of *O. monacantha* in 1913 (Lounsbury 1915) until the equally successful control of *Cyl. fulgida* var. *fulgida* in 2010, it is possible to identify three distinct stages in cactus biological control which in aggregate have resulted in relatively high levels of success when compared to

biological control projects against other plant families in South Africa.

The earliest cactus biological control projects involved no research by South Africans. Instead, the first project exploited the inadvertent control of a cactus by a mistakenly introduced cochineal insect species to India in 1795 (Zimmermann *et al.* 2009), and several subsequent projects benefited from this precedent in India, and from subsequent research and implementation of biological control carried out in Australia. The second stage, however, did include several South African initiatives, beginning with the introduction of a weevil, *Metamasius spinolae* (Gyllenhal) (Coleoptera: Curculionidae), for the biological control of *O. ficus-indica* in 1948 (Annecke & Moran 1978).

Contrary to the prediction by Moran & Zimmermann (1985) that 'there seems to be little chance of

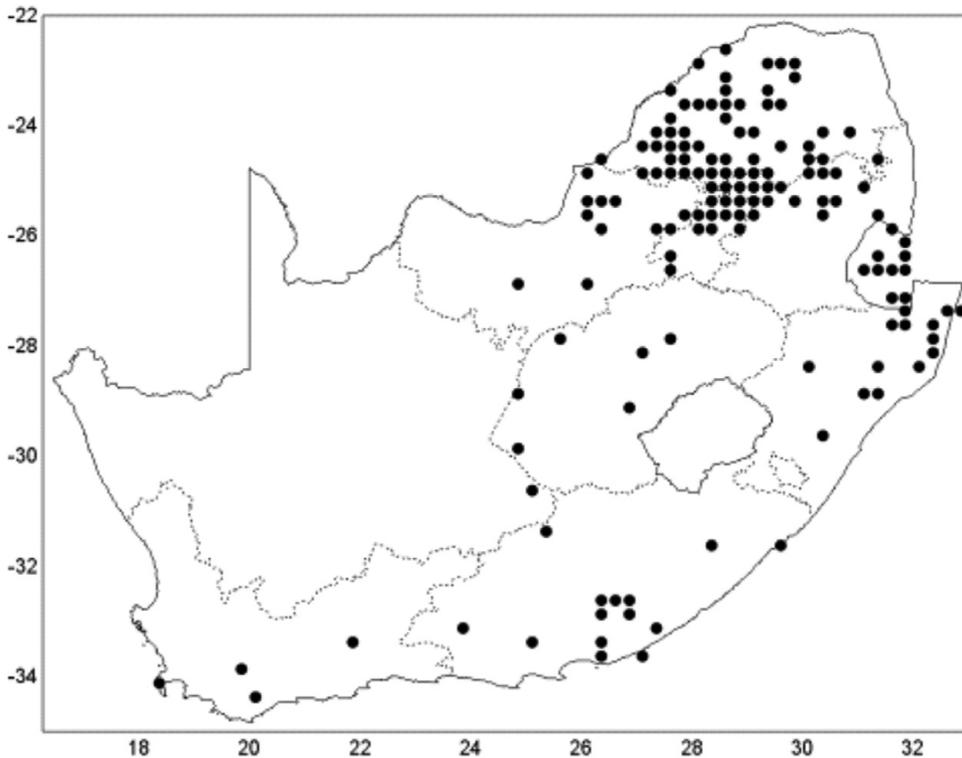


Fig. 7. Distribution of *Cereus jamacaru* in South Africa. (Drawn by L. Henderson; data source: SAPIA database, ARC-Plant Protection Research Institute, Pretoria.)

finding new dactylopiid species in the Americas, [and that] the emphasis in the biological control of cacti should shift to the use of pathogens in combination with plant-sucking bugs', the third stage, spanning the period from 1999 to 2010, involved almost exclusively the use of new cochineal insect biotypes of two *Dactylopius* species that provided excellent control of two cactus weeds, *O. stricta* and *Cyl. fulgida* var. *fulgida*, respectively. With the exception of *P. aculeata*, the future of cactus biological control in South Africa is likely to rely further on host-adapted cochineal biotypes for the control of incipient cactus weeds such as *Opuntia humifusa* (Rafinesque) Rafinesque, *Cyl. rosea*, *Cyl. tunicata* and *Opuntia engelmannii* Salm-Dyck ex Engelm. Another emerging cactus weed in South Africa, *O. salmiana* J.Parm ex Pfeiff., could possibly be controlled using its own monophagous cochineal insect, *Dactylopius salmianus* De Lotto (De Lotto 1974).

The relatively depauperate fauna of phytopagous insects associated with *P. aculeata* contrasts with the 150–160 phytopagous insect species associated

with the more than 175 succulent cacti surveyed so far (Mann 1969; Zimmermann *et al.* 1979). The paucity of species on *P. aculeata* is unexpected given that the host plants are woody scrambling shrubs that have true leaves and seemingly offer many niches and an abundant resource for leaf-feeding and stem- or twig-boring insects. The situation calls for further exploration and study.

The taxonomic complexities and inconsistencies within in the family Cactaceae (Hunt 2006) have been a long-standing source of confusion for entomologists who study cactophagous insect species associated with very specific cactus taxa. For example *Acanthocereus tetragonus* (L.) Humik. (Cactaceae), which is naturalized in South Africa, and has the tendency to be invasive, is recorded as one of six species in the genus by Anderson (2001), while Hunt (2006) lists only one species in the genus *Acanthocereus*. There are several cases where the biological control of problematic cactus species has been impeded by an inadequate understanding of the taxonomy of the group under investigation (Moran *et al.* 1976). The work of the International

Cactaceae Systematics Group of the International Organization for Succulent Plant Studies, and the availability of modern molecular taxonomic techniques, is making substantial contributions towards a new practical classification of the Cactaceae and is resulting in improved nomenclatural consistency and reliability. This will be advantageous to future biological control projects against cactus weeds, in particular.

Extensive infestations of dominantly *Opuntia* species are becoming increasingly problematic in other African countries. These include *O. stricta* var. *stricta* and var. *dillenii* in Madagascar, Namibia, Kenya, Ethiopia, Yemen and Saudi Arabia, and *O. elatior* Mill. Gard. in Kenya. There is no doubt that the South African experiences with host-specific cochineal insect biotypes will be the foundation of successful biological control in these countries, should they opt for biological control. Recent experiences in research and implementation of biological control could be of particular and immediate benefit to South Africa's immediate

neighbours, Zimbabwe and Namibia, which share many of the same problems of invasive cactus species and where many of the biological control agents that have been used could be effective.

ACKNOWLEDGEMENTS

The authors thank J. Hosking (NSW Department of Agriculture, Australia) for information regarding cactus invaders in Australia, the Biological Control Implementation Officers and other WfW staff for providing data on releases and observations of biological control agents; B. Mashope (SANBI), L. Pretorius (ARC-PPRI) and A. van den Berg (ARC-PPRI) for technical assistance; D.C. Thomas (Department of Entomology, Plant Pathology and Weed Science, New Mexico State University, U.S.A.) for assistance with rearing and transporting insects. South African National Parks is thanked for supporting the *O. stricta* programme. Funding for these projects was provided by the *Working for Water* Programme of the South African Department of Water Affairs.

REFERENCES

- ANDERSON, E.F. 2001. *The Cactus Family*. Timber Press, Portland, Oregon, U.S.A.
- ANNECKE, D.P. & MORAN, V.C. 1978. Critical reviews of biological pest control in South Africa 2. Prickly pear, *Opuntia ficus-indica* (L) Miller. *Journal of the Entomological Society of South Africa* **41**: 161–188.
- ANON. 2004. National Environmental Management: Biodiversity Act 10 of 2004. Government Printer, Pretoria, South Africa.
- BEINART, W. 2003. Prickly pear in the Cape: useful plants and invaders in the livestock economy 1890–1930. In: *The Rise of Conservation in South Africa*. 266–303. Oxford University Press, Oxford, U.K.
- BENSON, L. 1982. *The Cacti of the United States and Canada*. Stanford University Press, Stanford, California, U.S.A.
- CAMPBELL, P.L. 1988. Seed germination of *Harrisia martinii* and *Pereskia aculeata* with reference to their potential spread in Natal. *Applied Plant Science* **2**: 60–63.
- CESAVEP – Comité estatal de sanidad vegetal de Puebla. 2006. *Recomendaciones para el manejo integrado de la mancha del tallo y vaina ocasionado por Alternaria sp.* 1st Edition. OPF-RE-09. Secretaría de Agricultura, Ganadería, Desarrollo rural, Pesca y Alimentación (SAGARPA).
- CARA – CONSERVATION OF AGRICULTURAL RESOURCES ACT. 1983. Act 43 of 1983. Amendment No. R 280 (30 March 2001). Government Gazette, Republic of South Africa, Pretoria, Vol. 429, No. 22166.
- DANNINGER, E. 2002. A preliminary survey of the predators and parasitoids of the cactus mealybug *Hypogeococcus pungens* in South Africa. Unpublished report, ARC-PPRI, Pretoria, South Africa.
- DE BEER, H. 1986. Rosea cactus. *Farming in South Africa. Weeds A13*. Department of Agriculture and Water Supply, Pretoria.
- DE LOTTO, G. 1974. On the status and identity of the cochineal insects (Homoptera: Coccoidea: Dactylopiidae). *Journal of the Entomological Society of Southern Africa* **37**: 167–193.
- FOXCROFT, L.C. & FREITAG-RONALDSON, S. 2007. Seven decades of institutional learning: managing alien plant invasions in the Kruger National Park, South Africa. *Oryx* **41**: 160–167.
- FOXCROFT, L.C. & HOFFMANN, J.H. 2000. Dispersal of *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactylopiidae), a biological control agent of *Opuntia stricta* (Haw.) Haw (Cactaceae) in the Kruger National Park, South Africa. *Koedoe* **43**: 1–5.
- FOXCROFT, L.C. & REJMANEK, M. 2007. What helps *Opuntia stricta* invade Kruger National Park, South Africa: baboons or elephants? *Applied Vegetation Science* **10**: 265–270.
- FOXCROFT, L.C., HOFFMANN, J.H., VILJOEN, J.J. & KOTZE, J.J. 2007a. Environmental factors influencing the distribution of *Opuntia stricta*, an invasive alien plant in the Kruger National Park, South Africa. *South African Journal of Botany* **73**: 109–112.
- FOXCROFT, L.C., HOFFMANN, J.H., VILJOEN, J.J. & KOTZE, J.J. 2007b. Factors influencing the distribution of *Cactoblastis cactorum*, a biological control agent of *Opuntia stricta* in Kruger National Park, South Africa. *South African Journal of Botany* **73**: 113–117.
- FOXCROFT, L.C., ROUGET, M., RICHARDSON, D.M. & MACFADYEN, S. 2004. Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park,

- South Africa: environmental determinants and propagule pressure. *Diversity and Distributions* **10**: 427–437.
- GITHURE, C.W., ZIMMERMANN, H.G. & HOFFMANN, J.H. 1999. Host specificity of biotypes of *Dactylopius opuntiae* (Cockerell) (Homoptera: Dactylopiidae): prospects for biological control of *Opuntia stricta* (Haworth) Haworth (Cactaceae) in Africa. *African Entomology* **7**: 43–48.
- GOEDEN, R.D. 1983. Critique and revision of Harris' scoring system for selection of insect agents in biological control of weeds. *Protection Ecology* **5**: 287–301.
- HARRIS, P. 1973. The selection of effective agents for the biological control of weeds. *Canadian Entomologist* **105**: 1495–1503.
- HENDERSON, L. 1995. *Plant Invaders of Southern Africa*. Plant Protection Research Institute Handbook No. 5. Agricultural Research Council, Pretoria, South Africa.
- HENDERSON, L. 2001. *Alien Weeds and Invasive Plants: A Complete Guide to Declared Weeds and Invaders in South Africa*. Plant Protection Research Institute Handbook No. 12. Agricultural Research Council, Pretoria, South Africa.
- HENDERSON, L. & ZIMMERMANN, H.G. 2003. Chainfruit cholla (*Opuntia fulgida* Engelm.) misidentified as rosea cactus (*Opuntia rosea* DC.) in South Africa. *South African Journal of Plant and Soil* **20**: 46–47.
- HOFFMANN, J.H. 1995. Biological control of weeds: the way forward, a South African perspective. In: Stirton, C.H. (Ed.) *British Crop Protection Council Symposium Proceedings No. 64: Weeds in a Changing World*. 77–89. British Crop Protection Council, Farnham, U.K.
- HOFFMANN, J.H. 2004. Biotypes, hybrids and biocontrol: lessons from cochineal insects on *Opuntia* weeds. In: Cullen, J.M., Briese, D.T., Kritikos, D.J., Lonsdale, W.M., Morin, L. & Scott, J.K. (Eds) *Proceedings of the XI International Symposium on Biological Control of Weeds*. 283–286. CSIRO Entomology, Canberra, Australia.
- HOFFMANN, J.H., IMPSON, F.A.C. & VOLCHANSKY, C.R. 2002. Biological control of cactus weeds: implications of hybridisation between control agent biotypes. *Journal of Applied Ecology* **39**: 900–908.
- HOFFMANN, J.H., MORAN, V.C. & ZELLER, D.A. 1998a. Evaluation of *Cactoblastis cactorum* (Lepidoptera: Phycitidae) as a biological control agent of *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa. *Biological Control* **12**: 20–24.
- HOFFMANN, J.H., MORAN, V.C. & ZELLER, D.A. 1998b. Long-term population studies and the development of an integrated management programme for control of *Opuntia stricta* in Kruger National Park, South Africa. *Journal of Applied Ecology* **35**: 156–160.
- HOFFMANN, J.H., MORAN, V.C. & ZIMMERMANN, H.G. 1999. Integrated management of *Opuntia stricta* (Haworth) Haworth (Cactaceae) in South Africa: an enhanced role for two, renowned, insect agents. In: Olckers, T. & Hill, M.P. (Eds) *Biological Control of Weeds in South Africa (1990–1998)*. *African Entomology Memoir* **1**: 15–20.
- HOKKANEN, H.M.T. & PIMENTEL, D. 1984. New approach for selecting biological control agents. *Canadian Entomologist* **116**: 1109–1121.
- HOKKANEN, H.M.T. & PIMENTEL, D. 1989. New associations in biological control: theory and practice. *Canadian Entomologist* **121**: 829–840.
- HOLLOWAY, J.D., BRADLEY, J.D. & CARTER, D.J. 1987. Lepidoptera: In: Betts, C.R. (Ed.) *Guides to Insects of Importance to Man*. 262. CABI, Wallingford, U.K.
- HOSKING, J.R., MCFADYEN, R.E. & MURRAY, N.D. 1988. Distribution and biological control of cactus species in eastern Australia. *Plant Protection Quarterly* **3**: 115–123.
- HUNT, D. (Ed.). 2006. *The New Cactus Lexicon*. DH Books, The Manse, England.
- KLEIN, H. 1999. Biological control of three cactaceous weeds, *Pereskia aculeata* Miller, *Harrisia martinii* (Labouret) Britton and *Cereus jamacaru* De Candolle in South Africa. In: Olckers, T. & Hill, M.P. (Eds). *Biological Control of Weeds in South Africa (1990–1998)*. *African Entomology Memoir* **1**: 3–14.
- KLEIN, H. 2011. A catalogue of the insects, mites and pathogens that have been used or rejected, or are under consideration, for the biological control of invasive alien plants in South Africa. *African Entomology* **19**: 515–549.
- KNISKERN, J. & RAUSHER, M.D. 2001. Two modes of host–enemy coevolution. *Population Ecology* **43**: 3–14.
- LE BELLEC, F., VAILLANT, F. & IMBERT, E. 2006. Pitahaya (*Hylocereus* spp.): a new fruit crop, a market with a future. *Fruits* **61**: 237–249.
- LEUENBERGER, B.E. 1986. *Pereskia* (Cactaceae). *Memoirs of the New York Botanical Garden* **41**: 1–141.
- LOTTER, W.D. & HOFFMANN, J.H. 1998. An integrated management plan for the control of *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa. *Koedoe* **41**: 63–68.
- LOUNSBURY, C.P. 1915. Plant killing insects: the Indian cochineal. *Agricultural Journal of South Africa* **1**: 537–543.
- MANN, J. 1969. Cactus feeding insects and mites. *Bulletin of the United States National Museums* **256**: 1–158.
- MATHENGE, C.W. 2010. The biology and host specificity of *Dactylopius tomentosus*: prospects for biological control of *Cylindropuntia fulgida* var. *fulgida* in South Africa. Ph.D. thesis, University of Western Sydney, Sydney, Australia.
- MATHENGE, C.W., HOLFORD, P., HOFFMANN, J.H., SPOONER-HART, R., BEATTIE, G.A.C. & ZIMMERMANN, H.G. 2009a. The biology of *Dactylopius tomentosus* (Hemiptera: Dactylopiidae). *Bulletin of Entomological Research* **99**: 551–559.
- MATHENGE, C.W., HOLFORD, P., HOFFMANN, J.H., ZIMMERMANN, H.G., SPOONER-HART, R. & BEATTIE, G.A.C. 2009b. Distinguishing suitable biotypes of *Dactylopius tomentosus* (Hemiptera: Dactylopiidae) for biological control of *Cylindropuntia fulgida* var. *fulgida* (Caryophyllales: Cactaceae) in South Africa. *Bulletin of Entomological Research* **99**: 619–627.
- MATHENGE, C.W., HOLFORD, P., HOFFMANN, J.H., ZIMMERMANN, H.G., SPOONER-HART, R. & BEATTIE, G.A.C. 2010a. Hybridization between *Dactylopius tomentosus* (Hemiptera: Dactylopiidae) biotypes and its effects on host specificity. *Bulletin of Entomological Research* **100**: 331–338.
- MATHENGE, C.W., HOLFORD, P., HOFFMANN, J.H., ZIMMERMANN, H.G., SPOONER-HART, R. &

- BEATTIE, G.A.C. 2010b. Determination of biotypes of *Dactylopius tomentosus* (Hemiptera: Dactylopiidae) and insights into the taxonomic relationships of their hosts, *Cylindropuntia* spp. *Bulletin of Entomological Research* **100**: 347–358.
- McGIBBON, J. 1858. *Catalogue of Plants in the Botanical Garden, Cape Town, Cape of Good Hope*. Saul Solomon, Cape Town, South Africa.
- McFADYEN, R.E. & TOMLEY, A.J. 1981. Biological control of *Harrisia* cactus, *Eriocereus martinii*, in Queensland by the mealybug *Hypogeococcus festerianus*. In: Delfosse, E.S. (Ed.) *Proceedings of the Fifth International Symposium on Biological Control of Weeds*. 589–594. CSIRO, Canberra, Australia.
- MORAN, V.C. 1980. Interactions between phytophagous insects and their *Opuntia* hosts. *Ecological Entomology* **5**: 153–164.
- MORAN, V.C. 1981. Belated kudos for cochineal insects. *Bulletin of the Royal Entomological Society of London* **5**: 54–57.
- MORAN, V.C. & ANNECKE, D.P. 1979. Critical reviews of biological pest control in South Africa. 3. The jointed cactus, *Opuntia aurantiaca* Lindley. *Journal of the Entomological Society of Southern Africa* **42**: 299–329.
- MORAN, V.C. & HOFFMANN, J.H. 1987. The effects of simulated and natural rainfall on cochineal insects (Homoptera: Dactylopiidae): colony distribution and survival on cactus cladodes. *Ecological Entomology* **12**: 61–68.
- MORAN, V.C. & ZIMMERMANN, H.G. 1984. The biological control of cactus weeds: achievements and prospects. *Biocontrol News and Information* **5**: 297–320.
- MORAN, V.C. & ZIMMERMANN, H.G. 1985. The biological control of Cactaceae: success ratings and the contribution of individual agent species. In: Delfosse, E.S. (Ed.) *Proceedings of the VI International Symposium Biological Control of Weeds*. 69–75. Agriculture Canada, Ottawa.
- MORAN, V.C. & ZIMMERMANN, H.G. 1991a. Biological control of jointed cactus, *Opuntia aurantiaca* (Cactaceae), in South Africa. *Agriculture, Ecosystems and Environment* **37**: 5–27.
- MORAN, V.C. & ZIMMERMANN, H.G. 1991b. Biological control of cactus weeds of minor importance in South Africa. *Agriculture, Ecosystems and Environment* **37**: 37–55.
- MORAN, V.C., HOFFMANN, J.H. & BASSON, N.C.J. 1987. The effects of simulated rainfall on cochineal insects (Homoptera: Dactylopiidae): colony composition and survival on cactus cladodes. *Ecological Entomology* **12**: 51–60.
- MORAN, V.C., ZIMMERMANN, H.G. & ANNECKE, D.P. 1976. The identity and distribution of *Opuntia aurantiaca* Lindley. *Taxon* **25**: 281–287.
- NERD, A., TEL-ZUR, N. & MIZRAHI, Y. 2002. Fruits of vine and columnar cacti. In: Nobel, P.S. (Ed.) *Cacti: Biology and Uses*. University of California Press, Berkeley, U.S.A.
- PATERSON, I.D., COETZEE, J.A., HILL, M.P. & DOWNIE, D.A. 2011. A pre-release assessment of the relationship between the invasive alien plant, *Pereskia aculeata* Miller (Cactaceae), and native plant biodiversity in South Africa. *Biological Control* (in press). DOI: 10.1016/j.biocontrol.2010.12.002.
- PATERSON, I.D., DOWNIE, D.A. & HILL, M.P. 2009. Using molecular methods to determine the origin of weed populations of *Pereskia aculeata* in South Africa and its relevance to biological control. *Biological Control* **48**: 84–91.
- PETTEY, F.W. 1948. The biological control of prickly pears in South Africa. *Science Bulletin, Department of Agriculture and Forestry of the Union of South Africa*. **271**: 1–163.
- PROCLAMATION R. 35. 1979. In terms of the Weed Act, 1937 (Act 42 of 1937). The declaration of certain plants to be weeds. Government Gazette, Republic of South Africa, Pretoria, Vol. 165, No. 6323.
- VAN SITTERT, L. 2002. Our irrepressible fellow colonists: the biological invasion of prickly pear (*Opuntia ficus-indica*) in the Eastern Cape Colony c. 1870–1910. In: Dovers, R.W., Edgecombe, R. & Guest, B. (Eds) 139–159. *South Africa's Environmental History: Cases and Comparisons*. Ohio University Press, Ohio, U.S.A., and David Philip, Cape Town, South Africa.
- VAN WYK, B.E. 2005. *Food Plants of the World: Identification, Culinary Uses and Nutritional Value*. Briza, Pretoria, South Africa.
- VOLCHANSKY, C.R., HOFFMANN, J.H. & ZIMMERMANN, H.G. 1999. Host-plant affinities of two biotypes of *Dactylopius opuntiae* (Homoptera: Dactylopiidae): enhanced prospects for biological control of *Opuntia stricta* (Cactaceae) in South Africa. *Journal of Applied Ecology* **36**: 85–91.
- WELLS, M.J., BALSINHAS, A.A., JOFFE, H., ENGELBRECHT, V.M., HARDING, G.B. & STIRTON, C.H. 1986. A catalogue of problem plants in southern Africa. *Memoirs of the Botanical Survey of South Africa* **53**: 1–658.
- ZENNER DE POLANIA, I. 1990. Biología y manejo de una nueva plaga en el cultivo de pitaya. *ICAINFORMA: Colombia. Enero-Febrero-Marzo 1990*: 5–8.
- ZIMMERMANN, H.G. & MORAN, V.C. 1982. Ecology and management of cactus weeds in South Africa. *South African Journal of Science* **78**: 314–320.
- ZIMMERMANN, H.G. & MORAN, V.C. 1991. Biological control of prickly pear, *Opuntia ficus-indica* (Cactaceae), in South Africa. *Agriculture, Ecosystems and Environment* **37**: 29–35.
- ZIMMERMANN, H.G., ERB, H.E. & McFADYEN, R.E. 1979. Annotated list of some cactus-feeding insects in South America. *Acta Zoologica Lilloana* **3**: 101–112.
- ZIMMERMANN, H.G., MORAN, V.C. & HOFFMANN, J.H. 2009. Invasive cactus species (Cactaceae). In: Muniappan, R., Reddy, G.V.P. & Raman, A. (Eds) *Biological Control of Tropical Weeds using Arthropods*. 108–129. Cambridge University Press, Cambridge, U.K.