Biocontrol Science and Technology

ISSN: 0958-3157 (Print) 1360-0478 (Online) Journal homepage: www.tandfonline.com/journals/cbst20

Biocontrol of thistle cholla cactus, *Cylindropuntia pallida*: a successful agent in Australia is incompatible with the invasive populations in South Africa

Wade Sexton, Phillippa Muskett, Andrew John McConnachie, Liberato Portillo, Ana Lilia Vigueras & I.D. Paterson

To cite this article: Wade Sexton, Phillippa Muskett, Andrew John McConnachie, Liberato Portillo, Ana Lilia Vigueras & I.D. Paterson (2025) Biocontrol of thistle cholla cactus, *Cylindropuntia pallida*: a successful agent in Australia is incompatible with the invasive populations in South Africa, Biocontrol Science and Technology, 35:10, 1073-1087, DOI: 10.1080/09583157.2025.2550439

To link to this article: https://doi.org/10.1080/09583157.2025.2550439

© 2025 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group

Published online: 15 Sep 2025.

Submit your article to this journal

Article views: 82

View related articles

View Crossmark data

Full Terms & Conditions of access and use can be found at https://www.tandfonline.com/action/journalInformation?journalCode=cbst20

BIOCONTROL SCIENCE AND TECHNOLOGY
2025, VOL. 35, NO. 10, 1073–1087
https://doi.org/10.1080/09583157.2025.2550439

Taylor & Francis
Taylor & Francis Group

REVIEW ARTICLE

OPEN ACCESS Check for updates

Biocontrol of thistle cholla cactus, *Cylindropuntia pallida*: a successful agent in Australia is incompatible with the invasive populations in South Africa

Wade Sexton [a], Phillippa Muskett [a], Andrew John McConnachie [b], Liberato Portillo [c], Ana Lilia Vigueras [c] and I.D. Paterson [a]

[a]Centre for Biological Control, Department of Zoology and Entomology, Rhodes University, Makhanda, South Africa; [b]Weed Research Unit, New South Wales Department of Primary Industries and Regional Development, Biosecurity and Food Safety, Orange, Australia; [c]Departamento de Botánica y Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias (CUCBA), Universidad de Guadalajara, Nextipac, Zapopan, Mexico

ABSTRACT

Cylindropuntia pallida F.M. Knuth (Cactaceae) is an invasive alien species in Australia and South Africa. Two lineages of the cochineal insect *Dactylopius tomentosus* Lamark were considered as potential biocontrol agents for *C. pallida* in South Africa. One lineage, referred to as 'californica var. parkeri', was collected off *Cylindropuntia bernardina* (Engelm. ex Parish) (= *Cylindropuntia californica* var. *parkeri* (J.M.Coult.) Pinkava) in Mexico, was exported into quarantine in Australia and subsequently released in that country. The second lineage was collected off *C. pallida* in Mexico and was imported into quarantine in South Africa and is referred to as the 'pallida' lineage. Compatibility of the cochineal lineages with invasive *C. pallida* from South Africa was tested by comparing fitness parameters when reared on either the South African *C. pallida* or control plants (either Australian *C. pallida* or Mexican *C. pallida*). Ten crawlers were inoculated onto each of the controls and the South African cladodes. Measurements were taken to assess fitness, which included female mass, settlement and female fecundity. The 'californica var. parkeri' lineage survived effectively on Australian plants but had significantly lower settlement rates, longer duration of development and produced smaller females on the South Africa *C. pallida*. The 'pallida' lineage had similar settlement, mass and fecundity on South African plants when compared to Mexican plants. The results indicate that the 'californica var. parkeri' lineage is incompatible with *C. pallida* plants in South Africa. The 'pallida' lineage is compatible with South African *C. pallida* and should be considered further as a potential agent.

ARTICLE HISTORY
Received 29 July 2024
Returned 29 July 2025
Accepted 17 August 2025

KEYWORDS
Thistle cholla; cochineal; invasive alien plant; biological control; genetic mismatch

CONTACT Wade Sexton wadesexton1@gmail.com Centre for Biological Control, Department of Zoology and Entomology, Rhodes University, Makhanda 6140, South Africa

© 2025 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group
This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives License (http://creativecommons.org/licenses/by-nc-nd/4.0/), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way. The terms on which this article has been published allow the posting of the Accepted Manuscript in a repository by the author(s) or with their consent.

Introduction

The use of different cochineal (Dactylopiidae) lineages as biocontrol agents against invasive alien cactus species has been well documented for over a century and has proved to be an extremely effective method of control, particularly in Australia and South Africa (Hosking et al., 1994; Jones et al., 2023; Paterson et al., 2021). Thirty-two cactus species have been targeted for biocontrol using cochineal and 19 have been effectively controlled across the globe using different cochineal lineages (Novoa et al., 2019; Winston et al., 2014). Therefore, for any new invasive cactus species, an investment in biocontrol should be strongly considered.

The host range of cochineal insects is restricted to the Cactaceae, with some species that are host specific to a cactus genus or a single cactus species (Paterson et al., 2021). For example, *Dactylopius opuntiae* (Cockerell) is restricted to the cactus genus *Opuntia* whereas *Dactylopius tomentosus* (Lamark) is restricted to *Cylindropuntia* (Githure et al., 1999; Mathenge et al., 2009a). Host-adapted lineages have evolved within single cochineal species (Jones et al., 2016; Van Steenderen et al., 2021). These lineages of cochineal exhibit no clear morphological differences, can interbreed with other lineages within the species, and can only be identified by their host range and/or genetic sequencing (Jones et al., 2015, 2016; Mallet, 2005; Mathenge et al., 2015; Van Steenderen et al., 2021).

Some lineages are damaging to particular cactus species, but are less effective on others, so it is essential that the correct lineage is released on the correct cactus species to achieve control (Van Steenderen et al., 2021). In South Africa, the use of the *D. opuntiae* 'ficus' and 'stricta' lineages on *Opuntia ficus-indica* (L.) Mill., and *Opuntia stricta* (Haw.) Haw. respectively, have been extremely successful in controlling these species, but using the incorrect lineage (i.e. the 'ficus' lineage on *O. stricta* or the 'stricta' lineage on *O. ficus-indica*) resulted in negligible damage (Githure et al., 1999; Volchansky et al., 1999). *Dactylopius tomentosus* also has intraspecific lineages that are host specific to different plant species within the *Cylindropuntia* (Jones et al., 2015, 2016; Mathenge et al., 2015; Paterson et al., 2021). The *D. tomentosus* 'cholla' lineage resulted in the control of *Cylindropuntia fulgida* var. *fulgida* (Engelm.) F.M. Knuth in South Africa (Klein et al., 2020). This lineage has continued to be an effective agent on *C. fulgida* var. *fulgida* in South Africa as well as *Cylindropuntia fulgida* var. *mammillata* (Schott ex Engelm.) in Australia and South Africa (Jones et al., 2023). Further to this, *Cylindropuntia imbricata* (Haw.) F.M. Knuth and *Cylindropuntia leptocaulis* (DC.) Knuth are both under effective control by the *D. tomentosus* 'imbricata' lineage (Paterson et al., 2021).

Identifying damaging cochineal lineages that are compatible with the target weed is therefore an important step in many cactus biocontrol projects (Paterson et al., 2021). Fitness measurements, such as survival, female weight, days to emergence of offspring and number of progeny, are good indicators of a cochineal biocontrol agent's compatibility (Czypionka & Hill, 2007; Grevstad, 1999; Mathenge et al., 2009a). These measurements can give a better understanding of whether a potential agent will be effective against the target plant if it were released. Mathenge et al. (2009b) showed that female weight is correlated with the number of offspring, whereby the higher the weight of a female, the more progeny will be produced. Female weight can therefore be used as a proxy for the number of progeny.

Cylindropuntia pallida (Rose) F.M. Knuth (Cactaceae) commonly known as the thistle cholla is invasive to many arid areas around the world, including Australia and South Africa (Al-Robai et al., 2018; Paterson et al., 2019, 2021; Verloove et al., 2017). The spines can injure livestock and wildlife, and are a contaminant in wool production (Al-Robai et al., 2018). *Cylindropuntia pallida* infestations also restrict human and animal movement, reducing access to grazing, shade, and water sources (Deltoro et al., 2013), and are considered a threat to indigenous biodiversity. In South Africa, *C. pallida* was initially controlled using herbicides, which reduced plant populations but did not provide a permanent solution because complete eradication was not feasible and regrowth after herbicide treatments was a reoccurring problem (Mokotjomela et al., 2024; Paterson et al., 2021). Given the success of cochineal in the past on *Cylindropuntia* species, biocontrol is considered the best option for its management (Paterson et al., 2021).

A lineage of cochineal called *Dactylopius tomentosus* 'californica var. parkeri' was collected from Baja California, Mexico, from the cactus species *Cylindropuntia bernardina* Engelm. ex Parish (=*Cylindropuntia californica* var. parkeri (J.M. Coult.) Pinkava) to control invasive populations of *C. pallida* in Australia (Paterson et al., 2021). Since cochineal lineages are by convention referred to by the host plant they are collected off, the cochineal released in Australia is referred to as the 'californica var. parkeri' lineage as that was the name of the host plant. Testing conducted under quarantine conditions in Australia showed that it was a suitably host specific and damaging agent for *C. pallida* in Australia (Paterson et al., 2021). This resulted in the agent's release, and initial results show that it has successfully reduced *C. pallida* infestations in Australia (Unpublished data. A.J. McConnachie). The success of the agent in Australia, and the success of sharing agents between the countries in the past, suggested that *D. tomentosus* 'californica var. parkeri' would be a suitable agent for consideration in South Africa (Paterson et al., 2021). *Dactylopius tomentosus* 'californica var. parkeri' was imported into quarantine in South Africa to assess its compatibility with South African *C. pallida* plants. Early signs of poor survival of the 'californica var. parkeri' lineage on South African *C. pallida* during rearing indicated that it might not be suitable as an agent. Therefore, a second cochineal lineage collected off *C. pallida* in its native range of Hidalgo, Mexico, was brought into quarantine in South Africa and referred to as *D. tomentosus* 'pallida'.

The aim of this study was to determine the suitability of the two lineages of cochineal on South African *C. pallida*. This included the successful agent used in Australia, *D. tomentosus* 'californica var, parkeri', and the new potential agent collected off the same species as the target weed in the indigenous distribution, *D. tomentosus* 'pallida'. If either are compatible with South African *C. pallida*, they will be subjected to host-specificity testing and considered for release on *C. pallida* in South Africa.

Methods and materials

Collection of cochineal and cladodes

Dactylopius tomentosus 'californica var. parkeri' was collected at a mass-rearing facility in Lightning Ridge in Australia (29°26'12″S, 147°58'54″E), where the agent is mass-reared

on *C. pallida*. *Dactylopius tomentosus* 'pallida' was collected off *C. pallida* plants in its native distribution: Hidalgo, Mexico (19°52'23″N, 98°48'31″W). The two cochineal lineages were then imported into the Centre for Biological Control Quarantine Facility, at Rhodes University, Eastern Cape, South Africa ('pallida' = Permit number: P0116839, 'californica var. parkeri' = Permit number: P0109765). All predators found in the cultures were removed. Cochineal-free cladodes of *C. pallida* were collected from the invasive distribution in Cumborah, Australia (29°38'6″S, 147°40'40″ E) as a positive control for the 'californica var. parkeri' lineage. The same was done for the 'pallida' lineage collected in Hidalgo, Mexico, at the same site where the cochineal was sourced (19°52'23″N, 98° 48'31″W). South African *C. pallida* cladodes were collected in Cradock, Eastern Cape (32°09'51″S, 25°37'09″ E).

Experimental set-up

For each cochineal lineage ('californica var. parkeri' and 'pallida'), 10 newly emerged crawlers were inoculated onto a single South African *C. pallida* cladode and 10 crawlers were placed onto the respective control cladodes (either Australian or Mexican cladodes). Crawlers were removed from their respective cultures using a fine paintbrush and placed in a Petri dish, counted under a microscope, and then transferred carefully onto each cladode. The cladodes were separated in closed containers with a mesh covered hole in the lid for ventilation while ensuring that the crawlers could not escape. This was replicated 5 times for the 'californica var. parkeri' lineage and 10 times for the 'pallida' lineage.

Two separate experiments were conducted, one comparing the 'californica var. parkeri' cochineal on South African and Australian cladodes, and the other comparing the 'pallida' cochineal on South African and Mexican cladodes. Having two cochineal lineages within the same facility at the same time was not possible due to the potential for cross-contamination through interbreeding. The two experiments were therefore undertaken at different times and the data are analysed separately for this reason. The quarantine facility was maintained at 25°C with a 14:10 day: night cycle.

Measurements

Settlement

The proportion of crawlers that settled on each replicate was recorded as an indicator of insect survival. Measurements were taken after 2 weeks because this is the period when crawlers have either settled on the plant or died (Mathenge et al., 2015). Settlement was recorded by counting the number of crawlers that had started producing wax (Mathenge et al., 2009a). If a crawler did not produce wax 2 weeks after inoculation it was presumed to be dead.

Female fecundity

Females that produced eggs and/or crawlers before 90 days were considered to have reproduced (Mathenge et al., 2009a). Females that had not produced offspring by this time either failed to develop to sexual maturity or had not mated. Only females that had reproduced were included in this fitness metric. Females that did reproduce were removed by gently rolling the side of a pin against the female's body under the wax,

so that the female was detached from the cladode. Using a small pin was necessary because the female's mouthparts were embedded into the cladode and a pin gave just enough force to gently remove them from the cladode. Once removed from the cladode, each female was dewaxed gently with a pin, and the female and the eggs in the wax were placed in separate containers. The wax needed to be removed so that the weights of females could be accurately measured, and the few eggs that were produced before the wax was removed were counted and included in the progeny count for each female. Once females start producing eggs they will continue after being dewaxed, so the majority of the eggs produced were after dewaxing had taken place. After 30 days, the number of progeny produced per female was counted, which was the sum of both the number of eggs and crawlers per reproducing female. This time period was chosen to give the females time to produce all the eggs possible (Mathenge et al., 2015).

Female mass

Mass was recorded on a Disney fine balance with accuracy to the nearest 0.01 mg. Females that produced progeny were weighed the day that the first crawlers were seen, while those that did not produce crawlers by 90 days were weighed at that time. These females may have failed to reach sexual maturity or may not have been mated because no males were present in the replicate. Female mass did not include the wax, which was removed for both reproducing and non-reproducing females. The mass (mg) of females for each lineage was compared between those that developed on the South African cladodes and the respective controls.

Days to development of offspring

Days to development of offspring was measured as the time crawlers were first seen emerging from the wax of an individual female (Mathenge et al., 2009a, 2015). Therefore, days to development of offspring was recorded from only mated females and not non-mated females. All females that did not reproduce were removed after 90 days.

Statistical analyses

Insect performance metrics were analysed using a series of general linear models (GLM) and generalised linear mixed models (GLMM), whereby the GLMMs were used to account for non-independence of data points, where necessary (Bolker et al., 2009). For both lineages of cochineal, the proportion of crawlers that settled after two weeks was modelled as a function of the origin of the cladodes that were tested (Australia/Mexico vs South Africa), which was specified as a categorical predictor variable. The model was specified assuming a binomial error distribution with a logit link function, and accounting for unequal variance between females from the same replicate using a random intercept term (Bolker et al., 2009).

Female fecundity was modelled as a function of the origin of the cladodes tested, which was specified as a categorical predictor variable. For both the 'californica var. parkeri' and 'pallida' lineages, the GLM was specified assuming a negative binomial error distribution with a log link function (Bolker et al., 2009). Female body mass (mg) was modelled as a function of the origin of the cladodes that were tested (Australia/Mexico vs South Africa). We assessed whether female body mass differed between the two cochineal

lineages ('pallida' and 'californica var. parkeri') and from which country each lineage was sourced (Australia/Mexico vs South Africa), using a Gaussian error distribution and an identity link function. For the 'californica var. parkeri' lineage, we relaxed the assumption of equal variance between countries to account for unequal variance.

To assess whether there was a correlation between female body mass (mg) and the number of progeny produced, a negative binomial GLM was specified, with female body mass specified as a continuous predictor. Originally, this model was specified as a GLMM with a random intercept term to account for repeated measurements taken from the same replicate (Bolker et al., 2009). However, the final model was simplified to a GLM due to singularity issues with the GLMM, whereby the within-replicate variation was not sufficient to warrant inclusion in the final model specification (Baars & Neser, 1999). Female mass was log-transformed prior to model fitting to stabilise its variance.

Days to development of offspring was modelled as a function of the origin of the cladodes that were tested. For both the 'californica var. parkeri' and 'pallida' lineages, the GLM was specified assuming a Poisson error distribution with a log link function, and accounting for non-independence between females from the same replicate using a random intercept term (Bolker et al., 2009). Hypothesis testing was performed for each measurement using a likelihood ratio test. For the survival and female mass GLM, a Wald's test, with robust standard errors was used to account for unequal variances between females ($P < 0.05$) (Hothorn & Zeileis, 2015).

All statistical analyses were done in R version 4.3.3 (R Core Team, 2023). All values presented in the manuscript are mean ± 1 standard error, unless stated otherwise.

Results

Settlement

For the 'californica var. parkeri' lineage, there was a statistically significant difference in crawler settlement on the South African cladodes (14 ± 6%; $n = 5$) compared with those on the Australian cladodes (42 ± 9%; $n = 5$) ($\chi^2 = 4.82$, df = 1, $P = 0.028$) (Figure 1a). For the 'pallida' lineage, there was no evidence of a statistically significant difference in crawler settlement on the South African cladodes (40 ± 8%; $n = 10$) compared with those on the Mexican cladodes (48 ± 4%; $n = 10$) ($\chi^2 = 0.62$; df = 1; $P = 0.433$) (Figure 1b).

Female mass

For the 'californica var. parkeri' lineage on Australian cladodes, 19 females reached maturity in total, and there were mature females in each of the five replicates. On the South African cladodes, only three females reached maturity, all three were in a single replicate. There was a statistically significant difference in female mass on the South African cladodes (0.60 ± 0.32 mg; $n = 3$) in one replicate compared with those on the Australian cladodes (3.39 ± 0.57 mg; $n = 19$) in all five replicates ($\chi^2 = 3.67$, df = 1, $P = 0.055$) (Figure 2a). There was evidence for a statistically significant correlation between the number of progeny and female mass per female across both lineages of cochineal for both the South African cladodes and their respective control cladodes

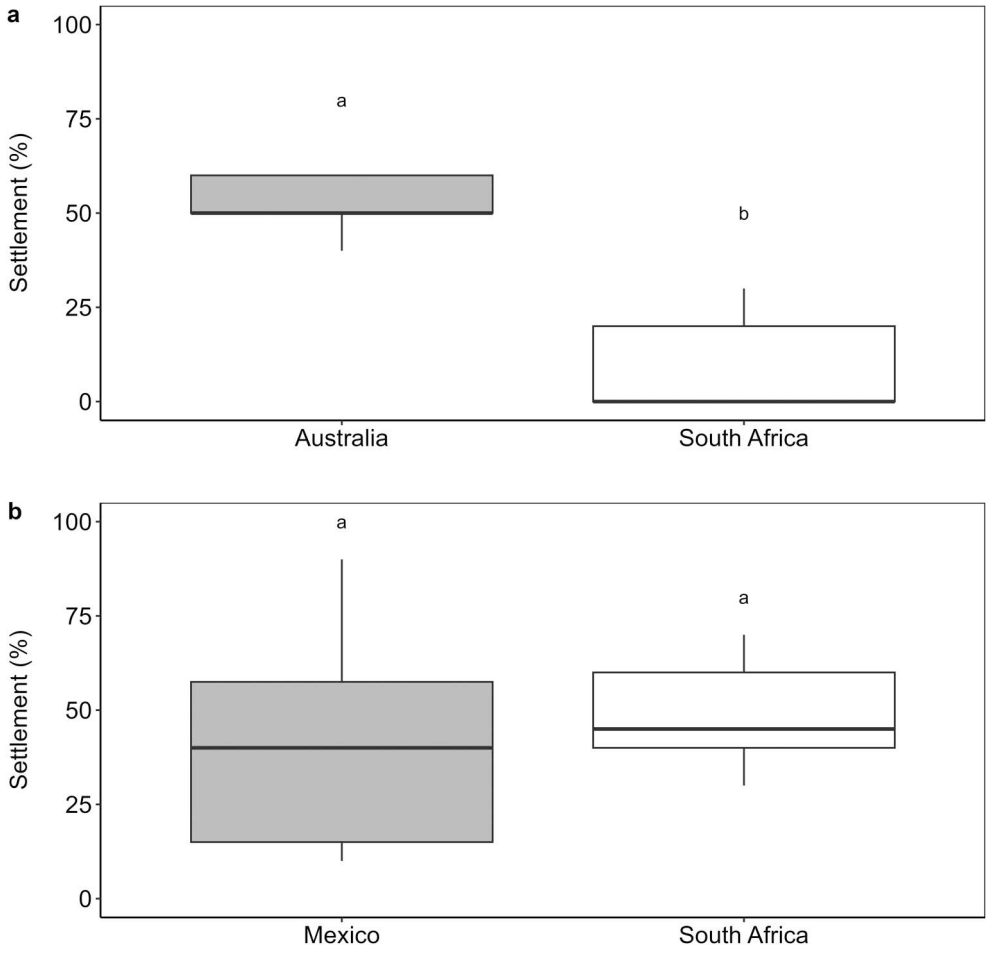

Figure 1. (a) Mean (±SE) settlement percentage of crawlers of *Dactylopius tomentosus* 'californica var. parkeri' on Australian and South African *Cylindropuntia pallida* and (b) *D. tomentosus 'pallida'* lineage on Mexican and South African *C. pallida*. Different small case letters indicate significant difference between groups ($p < 0.05$).

($\chi^2 = 73.6$, df = 1, $P < 0.001$) (Figure 3). The beta coefficient was 0.45 which tells us that as the log of female weight increases by 1 unit, the number of progeny produced increases by 56.8% on average. For the 'pallida' lineage on Mexican cladodes, 28 females reached maturity in all replicates. On the South African cladodes, a total of 34 females reached maturity in all replicates. There was no statistically significant difference in female mass on the South African cladodes (3.64 ± 0.41 mg; $n = 34$) when compared with those on the Mexican cladodes (3.94 ± 0.49 mg; $n = 28$) ($\chi^2 = 0.23$ df = 1, $P = 0.63$) (Figure 2b).

Female fecundity

For the 'californica var. parkeri' lineage, there was no statistically significant difference between the number of progeny produced per female on the South African cladodes

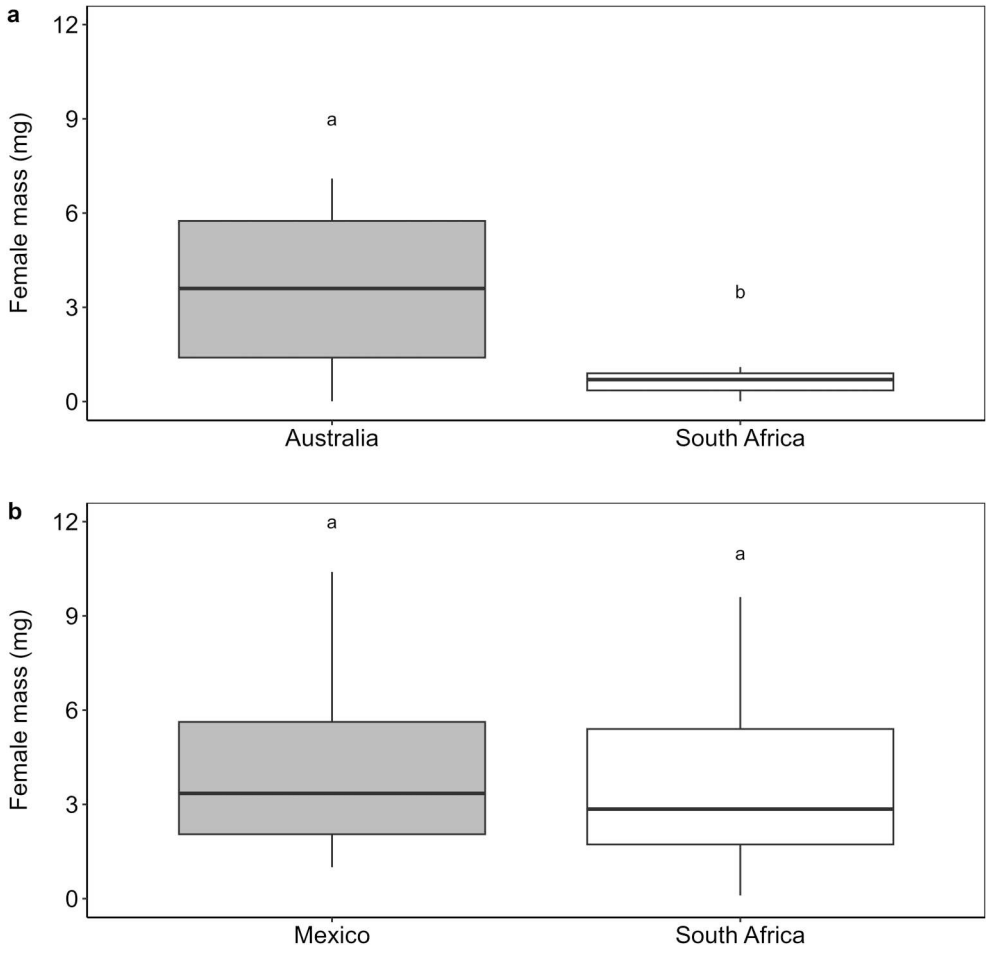

Figure 2. (a) Mean (±SE) female mass (mg) of *Dactylopius tomentosus* 'californica var. parkeri' on Australian and South African *Cylindropuntia pallida* and (b) *D. tomentosus* 'pallida' on Mexican and South African *C. pallida*. Different small case letters indicate significant difference between groups ($p < 0.05$).

(88 ± 38; $n = 3$) in one replicate compared with that on the Australian cladodes (121 ± 16; $n = 19$) in all five replicates ($\chi^2 = 0.46$, df = 1, $P = 0.497$) (Figure 4a). For the 'pallida' lineage, there was no statistically significant difference in the number of progeny produced per female on the South African cladodes (96 ± 16; $n = 8$) in five replicates compared with that on the Mexican cladodes (65 ± 17; $n = 2$) in 2 replicates ($\chi^2 = 1.49$, df = 1, $P = 0.222$) (Figure 4b).

Days to emergence of offspring

For the 'californica var. parkeri' lineage, there was no statistically significant difference between the days to emergence of offspring per female on the South African cladodes (61 ± 0; $n = 3$) compared with that on the Australian cladodes (59.9 ± 0.06; $n = 19$) ($\chi^2 = 0.05$, df = 1, $P = 0.818$). For the 'pallida' lineage, there was no statistically significant difference between the days to emergence on the South African cladodes

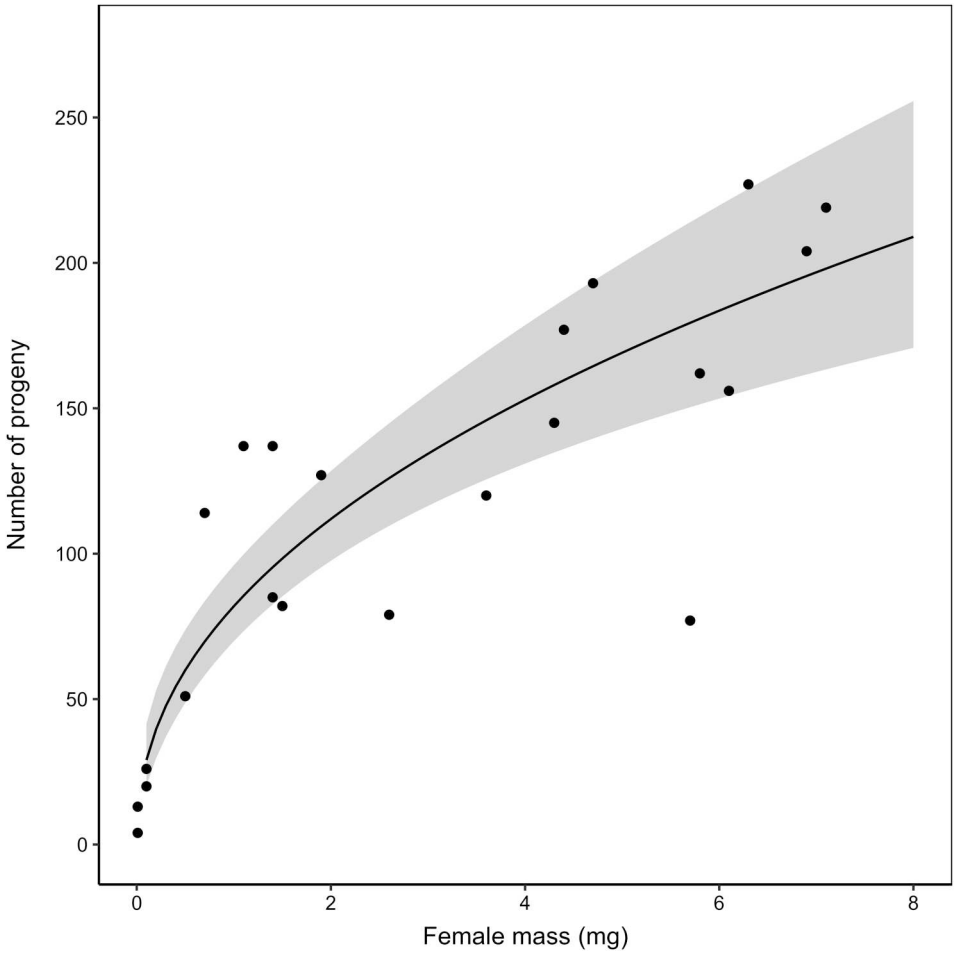

Figure 3. Correlation between number of progeny produced per female and the female mass (mg) for the 'californica var. parkeri' lineage. Black line represents the mean expected number of progeny per female and the shaded area represents the 95% confidence interval of the mean.

(92.5 ± 2.6; $n = 8$) and that on the Mexican cladodes (87.5 ± 3.5; $n = 2$) ($\chi^2 = 0.44$, df = 1, $P = 0.509$).

Discussion

Despite being an effective agent against *C. pallida* in Australia, *D. tomentosus* 'californica var. parkeri' is unlikely to be successful in South Africa. The 'californica var. parkeri' lineage had significantly higher settlement and female weight on the Australian *C. pallida* cladodes than on the South African cladodes, under the same conditions. Survival was very low on South African plants indicating that the agent would most likely be ineffective in controlling *C. pallida* in South Africa. These data indicate that there must be some genetic difference between the plants in South Africa and those in Australia that influences the survival of the 'californica var. parkeri' cochineal, despite the plants being considered the same species.

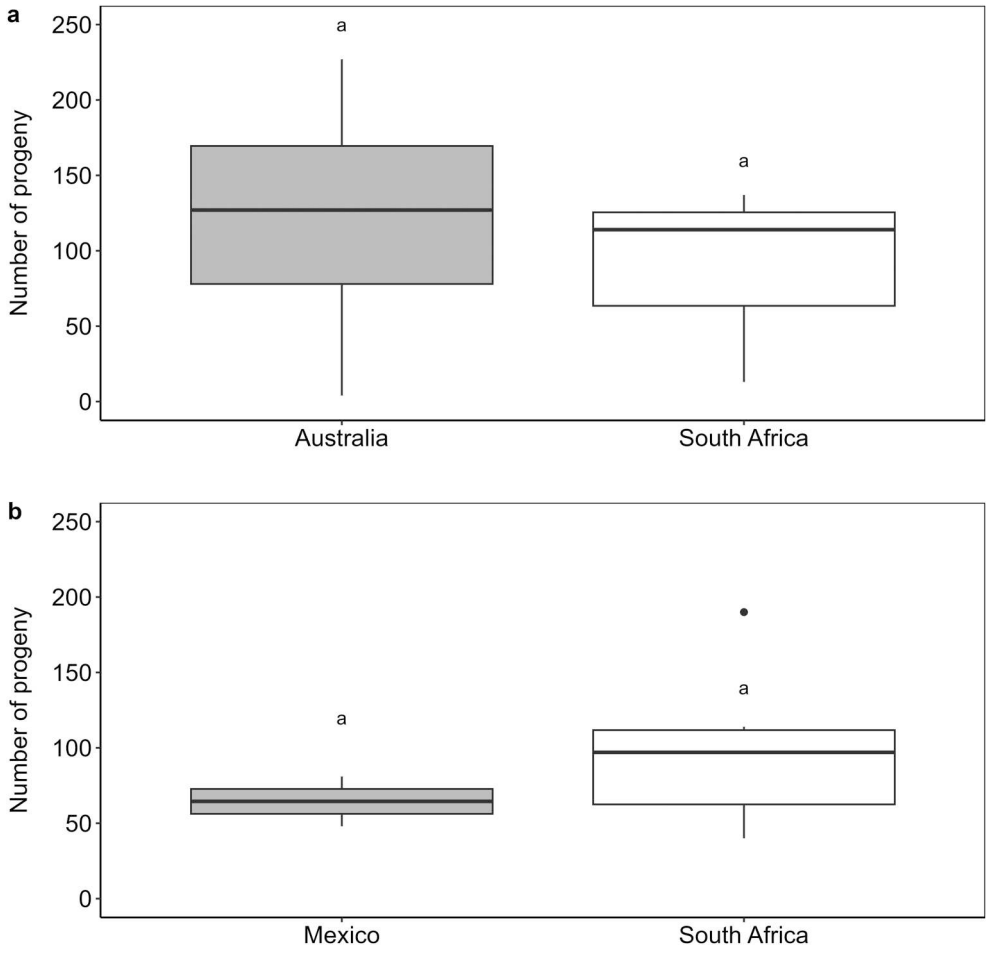

Figure 4. (a) Mean (±S.E) progeny that was produced by *Dactylopius tomentosus* 'californica var. parkeri' females on Australian and South African *Cylindropuntia pallida* and (b) *D. tomentosus* 'pallida' females on Mexican and South African *C. pallida*.

The differences in host suitability recorded in this study may have resulted from local adaptations of cochineal lineages to certain host plant genotypes in the indigenous distribution (Kawecki & Ebert, 2004). Local adaptations in the field of biocontrol can lead to an agent-plant mismatch (Harms et al., 2020). An example of an agent-plant mismatch is the biocontrol agent *Hydrellia pakistanae* Deonier (Diptera: Ephydridae), a shore fly used for the biocontrol of *Hydrilla verticulata* (L. f.) Royle (Hydrocharitaceae), a submerged aquatic weed, in the USA (Center et al., 1997). The agent was able to establish populations in only southern USA and was not effective and had poor establishment in the northern areas of the USA (Center et al., 1997). Studies showed that this was because a dioecious genotype occurred in the southern areas, and a monoecious genotype occurred in the northern areas, and the agent was not able to effectively attack the monoecious plants (Center et al., 1997). A similar issue was seen with the release of *Floracarus perrepae* Knihinicki & Boczek (Acariformes: Eriophyidae), a leaf-galling mite on

Lygodium microphyllum (Cav.) (Lygodiaceae), an invasive climbing fern in Florida, USA (Boughton & Pemberton, 2011; Goolsby et al., 2006). Distinct haplotypes of the plant and mite occurred in certain areas of the indigenous distribution and mites collected from the plant genotype matching the weed population were more damaging to the target weed populations (Goolsby et al., 2006). Although the difference in host plant suitability elucidated in this study is likely due to local adaptations developed in the source populations of the plants in the indigenous distribution, it is also possible that the Australian *C. pallida* plants developed local adaptations that favour the 'californica var. parkeri' lineage since the introduction of the plants to Australia (Thomas et al., 2010).

Although the origins of *C. pallida* are not fully understood, it is thought to be a hybrid of *C. imbricata* and *Cylindropuntia tunicata* (Lehm.) F.M. Knuth (Johnson et al., 2009; Laguna et al., 2013). Hybrids are known to have increased genetic variability within their native distribution, and given that introduced populations are likely not to have been sourced from the same population in a given area (Harms et al., 2020), there is a greater chance that invasive populations will be different from each other. Hybridisation can complicate the search for a biocontrol agent because natural enemies may have very different impacts on hybrids than on parent plant species, or on other hybrids at different stages of introgression (Ellstrand & Schierenbeck, 2000; Fritz et al., 1999). One example of hybridisation complicating effective biocontrol is *Lantana camara* L. (Verbenaceae) (Baars & Neser, 1999; Urban et al., 2011; Vardien et al., 2012). Biocontrol research on *L. camara* in South Africa dates back to as early as 1961 and since then 26 biocontrol agents have been released, but success has been variable because the invasive populations are composed of multiple hybrids and ornamental varieties (Urban et al., 2011; Zachariades, 2021; Zalucki et al., 2007). The impacts of biocontrol agents differ on each of the hybrids and varieties, resulting in overall reduced levels of control (Urban et al., 2011). Each hybrid of *L. camara* should therefore be considered a different species of target weed for the purpose of biocontrol because each of them needs a different biocontrol agent, similarly to the two varieties of invasive *C. pallida* (Australian and South African) which require different lineages of cochineal.

For other invasive cactus species, agents have been shared between Australia and South Africa with both countries having success in reducing cactus invasions (Paterson et al., 2011). *Cylindropuntia imbricata* was controlled in both countries using the *D. tomentosus* 'imbricata' lineage and *C. fulgida* var. *fulgida* and *C. fulgida* var. *mamillata* are both controlled using the *D. tomentosus* 'cholla' lineage (Paterson et al., 2021). Several *Opuntia* species such as *O. stricta* and *O. ficus-indica* are controlled with the *D. opuntiae* 'stricta' and 'ficus' lineages (Paterson et al., 2021). Sharing agents between countries has been extremely valuable and cost effective, and should still be continued in the future given the success in the past. However, the results of our study indicate that factors such as local adaptation and genetic mismatches between the agent and the target weed genotype need to be taken into consideration, even if the target weeds are thought to be the same species and are morphologically identical. An agent in one country might not always be suitable for another, as is the case for *C. pallida*.

The 'californica var. parkeri' lineage is unsuitable for *C. pallida* in South Africa, but the 'pallida' lineage could be a promising biocontrol agent. The 'pallida' lineage performed just as well on the South African plants as the 'californica var. parkeri' lineage did on the Australian plants. Therefore, if there are similarities in these fitness parameters, we

could expect the 'pallida' lineage to be similarly damaging on *C. pallida* in South Africa as the 'californica var. parkeri' lineage is on *C. pallida* in Australia. Therefore, the 'pallida' lineage is a more suitable option for the biocontrol of *C. pallida* in South Africa than the 'californica var. parkeri' lineage. Host-specificity testing of the 'pallida' lineage has commenced, and if it proves to be suitably host specific, an application for release will be submitted to the relevant authorities in South Africa.

Acknowledgements

Thanks are given to Edgar Roldan and his students from the Colegio del Estado de Hildago for providing transport and guiding us to sites in Hidalgo, Mexico. Thanks are also extended to all the landowners who allowed the collection of cladodes. Thanks are also given to Guy Sutton for his help with the statistics in this study. This work was funded by the South African Working for Water (WfW) Programme of the Department of Forestry, Fisheries and the Environment: Natural Resource Management Programmes (DFFE: NRMP). Funding was also provided by the South African Research Chairs Initiative of the Department of Science and Technology (DST) and the National Research Foundation (NRF) of South Africa (84643, Martin P. Hill). Any opinion, finding, conclusion or recommendation expressed in this material is that of the authors, and the funding agencies do not accept any liability in this regard.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by Department of Forestry, Fisheries and the Environment; National Research Foundation: [Grant Number 84643]; South African Research Chairs Initiative of the Department of Science and Technology.

Author contribution statement

Conceptualisation: W.T. Sexton, I.D. Paterson, P.C. Muskett, A.J. McConnachie, L. Portillo, and A.L. Vigueras; methodology: W.T. Sexton, I.D. Paterson, P.C. Muskett experiment: W.T. Sexton, and P.C. Muskett; formal analyses: W.T. Sexton; writing: W.T. Sexton; review and editing: I.D. Paterson and P.C. Muskett.

ORCID

Wade Sexton http://orcid.org/0000-0002-5807-661X
Phillippa Muskett http://orcid.org/0000-0002-6663-7499
Andrew John McConnachie http://orcid.org/0000-0002-2947-4408
Liberato Portillo http://orcid.org/0000-0002-7282-6982
Ana Lilia Vigueras http://orcid.org/0000-0001-5376-8417
I.D. Paterson http://orcid.org/0000-0002-0406-7945

References

Al-Robai, S. A., Howladar, S. M., Mohamed, H. A., & Ahmed, A. A. (2018). *Cylindropuntia rosea* (DC.) Backeb, (Cactaceae): a new generic alien record in the flora of Saudi Arabia. *Journal of Asia-Pacific Biodiversity*, *11*(2), 320–323. https://doi.org/10.1016/j.japb.2018.04.001

Baars, J. R., & Neser, S. (1999). Past and present initiatives on the biological control of *Lantana camara* (Verbenaceae) in South Africa. *African Entomology Memoir*, *1*(1), 21–33.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Boughton, A. J., & Pemberton, R. W. (2011). Limited field establishment of a weed biocontrol agent, *Floracarus perrepae* (Acariformes: Eriophyidae), against old world climbing fern in Florida – A possible role of mite resistant plant genotypes. *Environmental Entomology*, *40*(6), 1448–1457. https://doi.org/10.1603/EN11030

Center, T. D., Grodowitz, M. J., Cofrancesco, A. F., Jubinsky, G., Snoddy, E., & Freedman, J. E. (1997). Establishment of *Hydrellia pakistanae* (Diptera: Ephydridae) for the biological control of the submersed aquatic plant *Hydrilla verticillata* (Hydrocharitaceae) in the Southeastern United States. *Biological Control*, *8*(1), 65–73. https://doi.org/10.1006/bcon.1996.0491

Czypionka, K., & Hill, M. P. (2007). The relationship between female pupal mass and fecundity of *Gratiana spadicea* (Klug, 1829) (Coleoptera: Chrysomelidae). *African Entomology*, *15*(2), 380–382. https://doi.org/10.4001/1021-3589-15.2.380

Deltoro, V., Ballester, G., Benavent, J., Perez Botella, J., Pérez-Rovira, P., Gómez-Serrano, M., & Jiménez, J. (2013). The practicalities of eradicating an extremely invasive cactus: Hudson pear *Cylindropuntia rosea* in the Valencia region (East Spain). *Aliens*, *33*(1), 23–27.

Ellstrand, N. C., & Schierenbeck, K. A. (2000). Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences*, *97*(13), 7043–7050. https://doi.org/10.1073/pnas.97.13.7043

Fritz, R. S., Moulia, C., & Newcombe, G. (1999). Resistance of hybrid plants and animals to herbivores, pathogens, and parasites. *Annual Review of Ecology and Systematics*, *30*(1), 565–591. https://doi.org/10.1146/annurev.ecolsys.30.1.565

Githure, C. W., Zimmermann, H. G., & Hoffmann, J. H. (1999). Host specificity of biotypes of *Dactylopius opuntiae* (Cockerell) (Hemiptera: Oactylopiidae): Prospects for biological control of *Opuntia stricta* (Haworth) Haworth (Cactaceae) in Africa. *African Entomology*, *7*(1), 43–48.

Goolsby, J. A., De Barro, P. J., Makinson, J. R., Pemberton, R. W., Hartley, D. M., & Frohlich, D. R. (2006). Matching the origin of an invasive weed for selection of a herbivore haplotype for a biological control programme. *Molecular Ecology*, *15*(1), 287–297. https://doi.org/10.1111/j.1365-294X.2005.02788.x

Grevstad, F. S. (1999). Factors influencing the chance of population establishment: Implications for release strategies in biocontrol. *Ecological Applications*, *9*(4), 1439–1447. https://doi.org/10.1890/1051-0761(1999)009[1439:FITCOP]2.0.CO;2

Harms, N. E., Cronin, J. T., Diaz, R., & Winston, R. L. (2020). A review of the causes and consequences of geographical variability in weed biological control successes. *Biological Control*, *151*, 104398. https://doi.org/10.1016/j.biocontrol.2020.104398

Hosking, J. R., Sullivan, P. R., & Welsby, S. M. (1994). Biological control of *Opuntia stricta* (Haw.) Haw. var. *stricta* using *Dactylopius opuntiae* (Cockerell) in an area of New South Wales, Australia, where *Cactoblastis cactorum* (Berg) is not a successful biological control agent. *Agriculture, Ecosystems & Environment*, *48*(3), 241–255. https://doi.org/10.1016/0167-8809(94)90106-6

Hothorn, T., & Zeileis, A. (2015). Partykit: A modular toolkit for recursive partitioning in R. *The Journal of Machine Learning Research*, *16*(1), 3905–3909.

Johnson, S. B., Hosking, J. R., Chinnock, R. J., & Holtkamp, R. H. (2009). The biology of Australian Weeds 53: *Cylindropuntia rosea* (DC.) Backeb. and *Cylindropuntia tunicata* (Lehm.) F.M. Knuth. *Plant Protection Quarterly*, *24*(2), 42–49.

Jones, P. K., Day, M. D., McConnachie, A. J., Holtkamp, R. H., Conroy, J., Pidgeon, G., Clark, E., Clark, P., Fletcher, A., & Savage, M. (2023). The successful biological control of *Cylindropuntia fulgida* var. *mamillata* (A. Schott ex Englem.) Backeb. (Cactaceae) (coral or boxing glove cactus) at two field sites in Queensland, Australia. *Biological Control*, *182*, 105235. https://doi.org/10.1016/j.biocontrol.2023.105235

Jones, P. K., Holtkamp, R. H., & Day, M. D. (2016). The host range of four new biotypes of *Dactylopius tomentosus* (Hemiptera: Dactylopiidae) from southern USA and their potential as biological control agents of *Cylindropuntia* spp. (Cactaceae) in Australia: Part II. *Biocontrol Science and Technology*, *26*(8), 1033–1047. https://doi.org/10.1080/09583157.2016.1182620

Jones, P. K., Holtkamp, R. H., Palmer, W. A., & Day, M. D. (2015). The host range of three biotypes of *Dactylopius tomentosus* (Lamarck) (Hemiptera: Dactylopiidae) and their potential as biological control agents of *Cylindropuntia* spp. (Cactaceae) in Australia. *Biocontrol Science and Technology*, *25*(6), 613–628. https://doi.org/10.1080/09583157.2014.999747

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, *7*(12), 1225–1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Klein, H., Zimmermann, H. G., & Xivuri, T. (2020). Exceptional biological control of two varieties of *Cylindropuntia fulgida* (Cactaceae) in South Africa using a recently-identified different biotype of the cochineal insect, *Dactylopius tomentosus* (Dactylopiidae). *Biological Control*, *149*, 104314. https://doi.org/10.1016/j.biocontrol.2020.104314

Laguna, E., Deltoro, V. I., Ferrer, P. P., Novoa, A., & Guillot, D. (2013). About the binomen *Cylindropuntia rosea* (Cactaceae) and its invasive individuals recorded in the Valencian Community (Spain). *Bouteloua*, *16*(1), 40–51.

Mallet, J. (2005). Hybridization as an invasion of the genome. *Trends in Ecology & Evolution*, *20*(5), 229–237. https://doi.org/10.1016/j.tree.2005.02.010

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*(6), 551–559. https://doi.org/10.1017/S0007485308006597

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*(6), 619–627. https://doi.org/10.1017/S0007485309006671

Mathenge, C. W., Riegler, M., Beattie, G. A. C., Spooner-Hart, R. N., & Holford, P. (2015). Genetic variation amongst biotypes of *Dactylopius tomentosus*. *Insect Science*, *22*(3), 360–374. https://doi.org/10.1111/1744-7917.12120

Mokotjomela, T. M., Nelufule, T., Scott, Z., Vukeya, L. R., Xivuri, T., Matsokane, K., Mweli, N., Magqabi, F. L., & Jaca, T. (2024). The invasion threat of the emerging alien cactus *Cylindropuntia pallida* (Rosa), F.M. Knuth in South Africa and the potential for control using herbicides. *Environmental Monitoring and Assessment*, *196*(7), 673. https://doi.org/10.1007/s10661-024-12821-w

Novoa, A., Brundu, G., Day, M. D., Deltoro, V., Essl, F., Foxcroft, L. C., Fried, G., Kaplan, H., Kumschick, S., Lloyd, S., Marchante, E., Marchante, H., Paterson, I. D., Pyšek, P., Richardson, D. M., Witt, A., Zimmermann, H. G., & Wilson, J. R. U. (2019). Global actions for managing cactus invasions. *Plants*, *8*(10), 421. https://doi.org/10.3390/plants8100421

Paterson, I. D., Hoffmann, J. H., Klein, H., Neser, S., Mathenge, C. W., & Zimmermann, H. G. (2011). Biological control of cactaceae in South Africa. *African Entomology*, *19*(2), 230–246. https://doi.org/10.4001/003.019.0221

Paterson, I. D., Klein, H., Muskett, P. C., Griffith, T. C., Mayonde, S., Mofokeng, K., Mnqeta, Z., & Venter, N. (2021). Biological control of Cactaceae in South Africa. *African Entomology*, *29*(3), 713–734.

Paterson, I. D., Manheimmer, C. A., & Zimmermann, H. G. (2019). Prospects for biological control of cactus weeds in Namibia. *Biocontrol Science and Technology*, *29*(4), 393–399. https://doi.org/10.1080/09583157.2018.1562040

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Thomas, H. Q., Zalom, F. G., & Roush, R. T. (2010). Laboratory and field evidence of post-release changes to the ecological host range of *Diorhabda elongata*: Has this improved biological

control efficacy? *Biological Control*, *53*(3), 353–359. https://doi.org/10.1016/j.biocontrol.2010.02.011

Urban, A. J., Simelane, D. O., Retief, E., Heystek, F., Williams, H. E., & Madire, L. G. (2011). The invasive '*Lantana camara* L.' hybrid complex (Verbenaceae): a review of research into its identity and biological control in South Africa. *African Entomology*, *19*(2), 315–348. https://doi.org/10.4001/003.019.0225

Van Steenderen, C. J. M., Paterson, I. D., Edwards, S., & Day, M. D. (2021). Addressing the red flags in cochineal identification: The use of molecular techniques to identify cochineal insects that are used as biological control agents for invasive alien cacti. *Biological Control*, *152*, 104426. https://doi.org/10.1016/j.biocontrol.2020.104426

Vardien, W., Richardson, D. M., Foxcroft, L. C., Thompson, G. D., Wilson, J. R. U., & Le Roux, J. J. (2012). Invasion dynamics of *Lantana camara* L. (sensu lato) in South Africa. *South African Journal of Botany*, *81*, 81–94. https://doi.org/10.1016/j.sajb.2012.06.002

Verloove, F., Ojeda-Land, E., Smith, G. F., Guiggi, A., Reyes-Betancort, J. A., Samarín, C., Hernández, A. G., & Barone, R. (2017). New records of naturalised and invasive cacti (Cactaceae) from Gran Canaria and Tenerife, Canary Islands, Spain. *Bradleya*, *2017*(35), 58–79. https://doi.org/10.25223/brad.n35.2017.a6

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*(1), 85–91. https://doi.org/10.1046/j.1365-2664.1999.00381.x

Winston, R., Schwarzländer, M., Hinz, H. L., Day, M. D., Cock, M. J., & Julien, M. (2014). *Biological control of weeds: A world catalogue of agents and their target weeds*. USDA Forest Service, Forest Health Technology Enterprise Team.

Zachariades, C. (2021). A catalogue of natural enemies of invasive alien plants in South Africa: Classical biological control agents considered, released and established, exotic natural enemies present in the field, and bioherbicides. *African Entomology*, *29*(3), 1077–1142.

Zalucki, M. P., Day, M. D., & Playford, J. (2007). Will biological control of *Lantana camara* ever succeed? Patterns, processes & prospects. *Biological Control*, *42*(3), 251–261. https://doi.org/10.1016/j.biocontrol.2007.06.002