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The performance of *Dactylopius opuntiae* as a biological control agent on two invasive *Opuntia* cactus species in South Africa

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ABSTRACT

Many biological control projects targeting weeds in the Cactaceae have been noteworthy successes. Recently, populations of a prickly pear, *Opuntia humifusa*, have spread across South Africa, endangering both grazing lands and natural biodiversity. A biotype of the cochineal insect, *Dactylopius opuntiae* 'stricta', which has been successfully used in South Africa to control *Opuntia stricta,* has been observed to use *O. humifusa* as a host. However, it does not appear to effectively control *O. humifusa* infestations. To investigate the possible reasons for this, we tested two hypotheses: firstly, that *O. humifusa* is a sub-optimal host of *D. opuntiae* 'stricta' compared to *O. stricta;* and, secondly, that the underground tubers characteristic of *O. humifusa* enable it to regenerate after sustaining cochineal damage. We compared the survival, fecundity and development of *D. opuntiae* on the two host plant species under controlled conditions. Host plant had no significant effect on the survival rates and development of the insects. In addition, *O. stricta* plants generated more new growth after sustaining damage from *D. opuntiae* than *O. humifusa* under the same conditions. These results show that *O. humifusa* and *O. stricta* are equally suitable hosts for *D. opuntiae* 'stricta' and that the underground tubers of *O. humifusa* do not increase its resistance to *D. opuntiae* damage. Further ecological observations may elucidate other possible reasons for the failure of cochineal insects to control invasive *O. humifusa* populations in South Africa.

1. Introduction

With one possible exception, all cactus species are native to the New World and do not occur naturally anywhere else. They are well adapted to living in xeric areas, are tolerant of temperature extremes and outcompete most other plant species in disturbed habitats. These traits allow them to flourish in a wide range of environments, including areas where they do not occur naturally (Rebman and Pinkava, 2001; Zimmermann et al., 2009). As a result, many species of Cactaceae (at least 49, according to Zimmermann et al., 2009) have become widespread invasive aliens and some prickly pears (*Opuntia* spp.) were amongst the earliest recorded plants to spread outside their natural ranges (von Humboldt, 1850; Casas and Barbera, 2002; Davis, 2009).

Opuntia humifusa (Raf.) Raf. is one of several cactus species that have proliferated in recent years in South Africa and it is now formally classified as an invasive plant species (National Environmental Management Act, No. 10 of 2004. Alien and Invasive Species List, 2014). This species originates from the central and eastern USA and is a small shrub-like prickly pear that grows up to 30 cm tall and has yellow flowers, circular grey-green cladodes and underground tubers (Britton and Rose, 1937; Henderson, 2001). The first record of *O. humifusa* in the South Africa was in 1980 near the border between Limpopo and Mpumalanga Provinces (L. Henderson, Southern African Plant Invaders Atlas, 2015). It has since been recorded more than 100 times and occurs in every province of South Africa (Fig. 1A). Although its presence is acknowledged, no research has been published on it in South Africa to date (except a mention in Henderson, 1999) and it has not been targeted by any national management plans. Given the history of other invasive *Opuntia* species in South Africa (Hoffmann et al., 1999; Richardson and van Wilgen, 2004; de Lange and van Wilgen, 2010), the recent increase in the spread of *O. humifusa* across the country (Fig. 1B) is of concern and methods for controlling *O. humifusa* are needed.

Although no formal biological control project has been initiated against *O. humifusa* in South Africa, the history of the plant in Australia indicates that biological control could be used to great effect. Dodd (1940) and Mann (1970) recorded the presence of a small population of *Opuntia opuntia* (L.) H. Karst (a synonym of *O. humifusa* according to Britton and Rose, 1937) in New South Wales, Australia. However, by 1988 this population had not spread, and it was thought to be under the biological control of *Cactoblastis cactorum* (Bergroth) (Hosking et al., 1988). *Opuntia humifusa* is not, at present, listed as a weed by the Australian Government (Department of the Environment, 2015),

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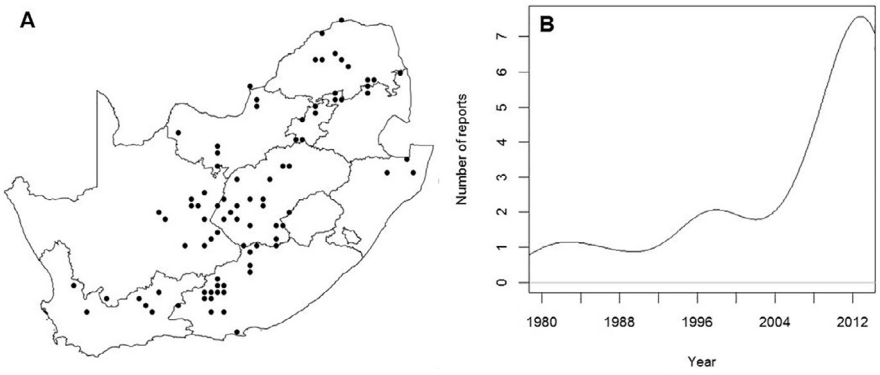

Fig. 1. Map showing the distribution of *O. humifusa* populations in South Africa (A; L. Henderson, SAPIA, 2015), and the frequency of *O. humifusa* records for each year from 1980 to 2014 (B).

suggesting that it is of little significance, presumably because it is controlled by the insects used against other prickly pear species.

In South Africa, the introduction of a cochineal biotype, the so called 'stricta' biotype of *Dactylopius opuntiae* (Cockerell), has successfully controlled populations of another invasive prickly pear, *Opuntia stricta* (Haworth) Haworth (Githure et al., 1999; Hoffmann et al., 1999; Volchansky et al., 1999; Klein, 2011; Paterson et al., 2011). *Opuntia stricta* is larger than *O. humifusa,* growing up to two metres tall, with lighter green, flattened, oblong cladodes and yellow flowers (Britton and Rose, 1937; Henderson, 2001). *Dactylopius opunitae* 'stricta' is also commonly found in association with *O. humifusa* (H.G. Zimmermann pers. obs.). While there are reports of considerable die back being caused by *D. opuntiae* on *O. humifusa*, there are also indications that the insect is less damaging than on its normal host, *O. stricta* (H.G. Zimmermann, pers. obs.) based on observations that *O. stricta* succumbs to cochineal damage in a shorter time than *O. humifusa* in areas where the two plant species co-occur.

Two hypotheses that might explain the discrepancy in responses of *O. stricta* and *O. humifusa* to attack by *D. opuntiae* are: (i) O. *humifusa* is a sub-optimal host for *D. opuntiae*, such that the development of *D. opuntiae* is inhibited on *O. humifusa* compared to *O. stricta*; and (ii) the underground tubers that characterise *O. humifusa* plants are inaccessible to *D. opuntiae* and serve as storage organs which are able to produce new aerial cladodes and replace those destroyed by *D. opuntiae*. To test these hypotheses, comparisons were made of the development of *D. opuntiae* on *O. stricta* and *O. humifusa* and of the ability of the two plant species to regrow after exposure to high levels of damage by the insects.

2. Material and methods

2.1. Sample collection

Thirty-three *O. stricta* and seventy-four *O. humifusa* plants were collected from field populations northeast of Clanwilliam in the Western Cape, South Africa (32° 4.291′S 19° 4.641′E for *O. humifusa* and 32° 1.097′S 19° 3.488′E for *O. stricta*) in February 2015. The plants were returned to the University of Cape Town (UCT) where they were potted and grown in glasshouses until the beginning of the experiments in August 2015. Prior to potting, all plants were washed to remove any cochineal. They were then inspected weekly and any residual cochineal were removed to ensure that none were present on the plants prior to the experiment. While they were growing in the glasshouses, the plants were watered once a week and no additional nutrients or fertiliser were provided.

The *D. opuntiae* used for the experiment were derived from a colony housed at UCT, originally imported to South Africa from Australia in 1987 for biological control of *O. stricta*. The colony consisted of the distinct 'stricta' biotype which is normally associated with *O. stricta* but which is also associated with *O. humifusa* in South Africa. Prior to the experiment, the colony was housed on *O. stricta* in a controlled environment room at 28 ± 2 °C and 40 ± 10% relative humidity with 12 h of light and 12 h of dark.

2.2. Host suitability

Ten *O. stricta* and ten *O. humifusa* plants were selected for the host suitability experiment. The cochineal from the colony were allowed to reach maturity and mate on their host *O. stricta* plant. Once they had started to produce crawlers, mature females were removed from the plants. The wax covering was removed from each female and she was placed in a vial where she continued to produce crawlers. Crawlers produced by eighteen females were used to inoculate the experimental plants. One at a time, crawlers that were < 24 h old were picked up with a fine paint brush, removed from the vials and examined at 25× magnification under a dissecting microscope (WILD Heerbrugg, Gais, Switzerland) to confirm that they were alive and intact. Each crawler was then placed on one of the potted plants until 30 crawlers were placed on each of the ten *O. stricta* and ten *O. humifusa* plants.

The inoculated plants were housed in a controlled environment room for the duration of the experiment (40 days). The environment was maintained under the same conditions as for the cochineal colony described in 2.2., as these conditions are optimal for the development of *D. opuntiae* (Hoffmann et al., 2002).

The position of each crawler that had settled (i.e. that had started to produce a wax coat) was marked with a felt-tip marker pen on the surface of the plant. The plants were then monitored each day until the cochineal females reached maturity and began to reproduce. The first crawlers were produced 32 days after inoculation. Once one female on the plant had started to produce crawlers, the number of marked females on each plant was recorded. This number was divided by the total number of marked insects on the plant to calculate the sex ratio. Males were not counted directly because they are smaller and harder to identify than females, and sometimes develop in undetectable positions beneath the wax coat of a female (Hoffmann et al., 2002). On the day on which they started to produce crawlers, each female was removed from the plant. The waxy coat was removed from the female and the mass was recorded to the nearest 0.1 mg on a GH-202 balance (A&D, San Jose, USA). The number of crawlers already produced by the female was recorded.

After being de-waxed and weighed, each female was placed in the well of a microtitre tray and the wells were covered with adhesive tape. A small hole was made in the tape to allow aeration, and the females were left to produce crawlers in the well. After they had stopped producing crawlers (after 10–15 days), the adhesive tape was removed from the wells and the number of crawlers produced by each female was counted. Crawler counts were performed on a sub sample of 81 of the 190 females that reached maturity and were removed from the plants.