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MINI REVIEW

Dactylopius opuntiae, a new prickly pear cactus pest in the Mediterranean: an overview

Gaetana Mazzeo*, Salvatore Nucifora, Agatino Russo & Pompeo Suma

Department of Agriculture, Food and Environment, University of Catania, Via S. Sofia 100, 95123 Catania, Italy

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Abstract

The Opuntia cochineal scale or false carmine cochineal scale, *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactylopiidae), is spreading rapidly in many countries, especially in the Mediterranean basin, where it has become a serious pest of prickly pear crops, *Opuntia ficus-indica* (L.) Miller (Cactaceae). This crop is an important food resource both for humans and livestock. The cochineal was originally used as a biological agent to control cactaceous weeds in many countries where Opuntiaceae had been introduced. Currently, in some countries where the prickly pear is no longer considered a weed but a productive crop, as in the Mediterranean area, *D. opuntiae* has changed its role from a highly prized biological control agent to the status of serious pest. This paper provides an overview of the current knowledge on *D. opuntiae* for farmers and stakeholders in order to indicate the most appropriate way to limit or counteract the spread of this pest especially in new cultivated areas.

Introduction

After the discovery of America, the Spanish conquistadors started to trade carmine, a precious dye extracted from the females of *Dactylopius coccus* Costa (Barbera & Inglese, 1993), and both the insect and its host plant, *Opuntia ficus-indica* (L.) Miller (Cactaceae), were introduced into the Mediterranean basin (Donkin, 1977). In fact, interactions between the insect and Cactaceae probably date back to the pre-Columbian era (Casas & Barbera, 2002; Chávez-Moreno et al., 2009). The Mediterranean climate was favorable to the host plant, but not for *D. coccus* survival. Despite attempts to rear the cochineal in greenhouses in Italy (Russo & Mazzeo, 1996; Mazzeo et al., 1998; Russo et al., 2001; Pellizzari et al., 2016), today, in the EU, carmine dye is only produced in the Canary Islands (Spain).

The prickly pear cactus acclimated along the Mediterranean coast and became integrated with the local flora (Donkin, 1977), to the extent that it was adopted as the emblem of Sicily (southern Italy), despite being an alien species (Mazzeo et al., 2017). In most Mediterranean countries, the plant is cultivated above all for its fruits and today it is farmed intensively in Italy (Sicily, in particular), Spain, Portugal, Morocco, Algeria, Tunisia, Egypt, Israel, Turkey, and Greece (Barbera et al., 1999; Sáenz, 2013; Ochoa & Barbera, 2017). Other Cactaceae also attracted the interest of colonizers, and were probably introduced, with other exotic plants and animal species, into Spain (Barbera et al., 1999), quickly spreading into new areas. Consequently, Cactaceae are currently found in other European countries, and in Africa, Asia, and Australia (Sáenz, 2013), becoming weeds in favorable conditions. To control these infesting plants biologically, the false carmine cochineal scale, *Dactylopius opuntiae* (Cockerell) (Hemiptera: Dactylopiidae), was introduced into Australia (Dodd, 1940), India, Sri Lanka (Pérez Guerra & Kosztarab, 1992), and South Africa (Pettey, 1950; Annecke et al., 1969), determining the actual worldwide distribution of the insect (Table 1; Moran & Zimmermann, 1984; García Morales et al., 2016).

Dactylopius opuntiae proved to be the most aggressive species in the genus *Dactylopius* (Klein, 2002; Paterson et al., 2011), and in certain newly cultivated areas in the Mediterranean basin (e.g., Israel, Spain, and Morocco), it has become a destructive pest of *O. ficus-indica* (Foldi, 2001; Spodek et al., 2014; Ben-Dov & Sánchez-Garcia, 2015; Bouharroud et al., 2016). In this area the risk of infestation is always high due to a variety of factors, such

*Correspondence: E-mail: gamazzeo@unict.it

Table 1 Distribution of *Dactylopius opuntiae*

Countries	References
Australia	De Lotto (1974a); Pérez Guerra & Kosztarab (1992)
Brazil	Kuwana, (1901); Pérez Guerra & Kosztarab (1992); Miller (1996); Lopes et al. (2009a)
Cape Verde	Van Harten et al. (1990)
France	Foldi (2001)
France, Réunion	Pérez Guerra & Kosztarab (1992); Miller (1996); Germain et al. (2014)
India	Mann (1969); De Lotto (1974a); Pérez Guerra & Kosztarab (1992); Miller (1996); Kumar (2015)
Israel	Spodek et al. (2014)
Jamaica	Cockerell (1897); Miller (1996); Pérez Guerra & Kosztarab (1992)
Kenya	De Lotto (1974a); Pérez Guerra & Kosztarab (1992); Miller (1996)
Lebanon	Moussa et al. (2017)
Madagascar	Mann (1969); Miller (1996)
Mauritius	Pérez Guerra & Kosztarab (1992); Miller (1996)
Mexico	Cockerell (1896); MacGregor & Sampedro (1984); Pérez Guerra & Kosztarab (1992); Miller (1996); Chávez-Moreno et al. (2011)
Morocco	Bouharroud et al. (2016)
Pakistan	Fernald (1903); Pérez Guerra & Kosztarab (1992); Miller (1996)
South Africa	Pettey (1947); De Lotto (1974a); Annecke et al. (1976); Pérez Guerra & Kosztarab (1992); Miller (1996)
Spain	Ben-Dov & Sánchez-Garcia (2015)
Sri Lanka	Mann (1969); De Lotto (1974a); Pérez Guerra & Kosztarab (1992); Miller (1996)
UK	Fernald (1903)
USA	Pérez Guerra & Kosztarab (1992); Gill (1993); Miller (1996)
USA, Hawaii	Miller (1996)
Zimbabwe	Pérez Guerra & Kosztarab (1992)

as rising temperatures (changing climate), which play an important role in the increasing desertification. In fact, several researchers have reported that all climate models predict that the Mediterranean area will become drier and hotter (Zdruli, 2011), and these climatic changes will affect all components of the European agricultural ecosystem (Iannetta, 2007). Global warming plays an important role in the development and survival of all insect species, indirectly affecting the trophic relations (host plants and natural enemies) (Stange & Ayres, 2010). It is thus likely that a pest such as *D. opuntiae* poses a serious threat for the prickly pear cultivation in those Mediterranean countries that have not yet been infested (e.g., Italy).

This paper presents an overview of the taxonomy, biology, distribution, and host plants of *D. opuntiae*, and its role as either a pest or a biological control agent. The entity of the damage caused and the control strategies currently available are also reported.

Dactylopius species

All known species of the family Dactylopiidae have females characterized by a purple-red colorful oval-shaped body, covered with a cotton-type white wax (Claps & De Haro, 2001; Torres & Giorgi, 2018), produced in the form of filaments that become denser as the individuals mature. This waxy covering is a mechanical barrier that protects the body of the cochineal from heat, cold, and predators (Torres & Giorgi, 2018). Adult females are sessile, and live in colonies of up to a few thousand individuals of mixed age (Moran et al., 1987), forming conspicuous clusters of white wax all over the plant. Adult females produce red glucosidal hydroxyanthrapurin (carminic acid) which occurs naturally within their body depending on the species; for example, it reaches 18–26% of the body weight in *D. coccus* and 6–8% in the other species of the same genus (Claps & De Haro, 2001; Ochoa et al., 2015).

The family Dactylopiidae includes only the genus *Dactylopius* (Williams & Ben-Dov, 2015) which is native to the Americas as are its host plants (Chávez-Moreno et al., 2009). Originally, there were nine recognized species belonging to the genus (De Lotto, 1974b). Two additional species *Dactylopius bassii* (Targioni Tozzetti) and *Dactylopius gracilipilus* Van Dam & May (Ben-Dov & Marotta, 2001; Van Dam & May, 2012) were considered valid, though there is still an open debate on the latter one (Torres & Giorgi, 2018). Still, the official databases currently report 11 valid species (García Morales et al., 2016).

According to Pérez Guerra & Kosztarab (1992), who conducted the first phylogenetic analysis based on morphological characters, all the species of this genus derived from a common ancestor, with *D. coccus* being the most ancient species. Other phylogenetic analyses, based not only on morphology but also on distribution areas, considered *D. coccus* to be closely related to *Dactylopius austrinus* De Lotto, *Dactylopius ceylonicus* (Green), and other South American species, and less closely to *Dactylopius confusus* (Cockerell), *D. opuntiae*, and *Dactylopius tomentosus* (Lamark), which are found in North America (Rodríguez et al., 2001). More recent studies, based on the molecular analyses of several populations of five *Dactylopius* species, clearly separated *D. tomentosus* from *D. coccus* and considered *D. ceylonicus*, *D. confusus*, and *D. opuntiae* to be closely related (Ramírez-Puebla et al., 2010).

From a morphological point of view, all *Dactylopius* species are characterized by the presence of truncate dorsal setae and clusters of quinquelocular pores associated with tubular ducts on the body of the females (first and second instars and adults), and by the absence, in all instars, of microducts and a cellular anal ring bearing setae (De Lotto, 1974a; Pérez Guerra & Kosztarab, 1992; García Morales et al., 2016). Large, truncate, and rounded setae (longer than the width at the base) and the numerous narrow ventral pores on the last three body segments differentiate *D. opuntiae* from all its congeners (Pérez Guerra, 1991).

Dactylopius opuntiae was first described as *Coccus cacti opuntiae* by Cockerell who collected the 'grana silvestre' from cactus plants in Mexico (Cockerell, 1896). Later it was considered as a synonym of *D. tomentosus* (Cockerell, 1898, 1899) and, according to De Lotto (1974b), it became common practice 'to call *opuntiae* a wild cochineal insect morphologically well distinct from *tomentosus*, the status and identity of which have never been settled'. In fact, the cochineal was identified on the basis of its external appearance and very often workers referred to the same species by different names, or used the same name for different species (De Lotto, 1974b). In 1929, the species was classified as *D. opuntiae* (Cockerell, 1929).

Over the years, the false carmine cochineal has played an important role as a biological control agent of cactus plants such as *Opuntia stricta* (Haw.) Haw. and *O. ficus-indica* which became weeds after the uncontrolled introduction by humans in Australia and South Africa, respectively (Dodd, 1940; Annecke & Moran, 1978; Zimmermann & Moran, 1982, 1991; Moran & Zimmermann, 1984, 1985; Hosking et al., 1994; Chávez-Moreno et al., 2009).

For a long time, it was thought that the stocks of cochineal insects introduced into Australia and South Africa came from the same area in North America (Volchansky et al., 1999). Comparative biological studies on populations from the two continents found two biotypes: one biotype predominant in Australia and associated with *O. stricta* and other low-growing *Opuntia* species (this biotype is normally referred to as 'stricta'), and another biotype predominant in South Africa on *O. ficus-indica* and other similar species with erect habit (named 'ficus') (Githure et al., 1999; Volchansky et al., 1999). Subsequent studies showed the inability of the biotype 'stricta' to survive on *O. ficus-indica* and other spineless cultivars. This is important for the biological control of the infestation of *O. stricta* in areas where the prickly pear is grown (Githure et al., 1999; Volchansky et al., 1999). However, the two biotypes are able to cross mate and the hybrids lose their host plant specificity (Hoffmann et al., 2002), representing a potential risk in biological control programs. More recent studies carried out in Mexico (Chávez-Moreno et al., 2011) with a large number of scale insect specimens collected from many Opuntiaceae identified another *D. opuntiae*, named biotype 1, which morphologically was more similar to *Dactylopius salmianus* De Lotto. This biotype is less aggressive than *D. opuntiae* and grows mainly on cladodes and fruits of the host plants (Chávez-Moreno et al., 2011). Morphological and molecular studies conducted in 2013 on the natural populations of *D. opuntiae* in northeastern Brazil showed that it was the only cochineal species present in all samples, and its populations showed a low genetic variability, thus demonstrating a high degree of relatedness (Da Silva et al., 2013).

Biology

The development of *D. opuntiae* is similar to that of other species of the genus, with two nymphal instars before adult females, and two nymphal instars, prepupa, and pupa before adult males (Moran & Cobby, 1979; Pérez Guerra & Kosztarab, 1992; Vanegas-Rico, 2009). Several studies have been conducted on its biology in South, Central, and North America (Mann, 1969; Romero López et al., 2006; Vanegas-Rico, 2009; Palafox-Luna et al., 2018), South Africa (Pettey, 1947, 1950; Foxcroft & Hoffmann, 2000), and Australia (Mann, 1969), and the life cycle has been studied both in the laboratory and in the open field. In laboratory observations, the complete biological cycle lasted 77 and 43 days for females and males, respectively, with a 1:1 sex ratio (Flores-Hernández et al., 2006; Romero López et al., 2006). In greenhouse conditions, an offspring sex ratio of 3.7:1 (females: males) was found (Palafox-Luna et al., 2018).

In the field, the life cycle of females lasted 40–180 days overall, depending on the period of the year and climatic conditions, whereas males usually complete their life cycle in 35–52 days (Mann, 1969; Ochoa et al., 2015). The optimum temperature for *D. opuntiae* development was 30 °C. At 35 °C, males do not emerge from the cocoon, adult females cannot lay eggs, and the survival of crawlers is negatively affected, although they can live for 24 h at 45 °C (Karny, 1972). Overall, adult lifespan is 4.2 and 38.4 days for males and females, respectively (Flores-Hernández et al., 2006). The species usually reproduces bisexually, although, under particular circumstances (e.g., high temperature), it tends to reproduce by parthenogenesis, with a lower progeny production (Mann, 1969; Flores-Hernández et al., 2006; Romero López et al., 2006; Ochoa et al., 2015). Other field studies conducted in the Americas and Australia have shown that the species produces 4–5 generations per year, five in the warmest areas (Mann, 1969).

The ovoviviparous females lay the eggs one at a time beneath their body; the eggs start hatching within 0.25–6 h (Mann, 1969), although Palafox-Luna et al. (2018) claim that the incubation period is difficult to assess. As in other Dactylopiidae, female and male crawlers are nearly indistinguishable (Mann, 1969; Moran & Cobby, 1979; Pérez Guerra & Kosztarab, 1992) although, according to Moran et al. (1982), male crawlers of *D. austrinus* have shorter and fewer filaments than female crawlers. After a phase of active dispersal (24–48 h), they settle down in the cladodes, often close to the mother (Mann, 1969) or on other plants that they reach passively carried by air currents aided by the long wax filaments that cover their body (Foxcroft & Hoffmann, 2000). The colonies are usually established at the joints of the cladode-trunk, flower-cladode, or fruit-cladode (Chávez-Moreno et al., 2011) tending to prefer areas less exposed to direct sunlight (Mann, 1969), with some preferences depending on the host species. For example, Mann (1969) observed how in Australia *D. opuntiae* mainly infests the basal stems of *O. stricta* and the main stems of *Opuntia tomentosa* Salm-Dyck.

Several factors hinder the development of the cochineal, leading to high mortality (Mann, 1969). Among these, temperature can directly influence the development of younger instars: Flores-Hernández et al. (2006) reported that only 67% of the females and 65% of the males reach the adult stage when exposed to high temperatures. Also the mechanical action of rain can have a negative impact on the survival of the younger instars (Moran et al., 1987), and resistance factors of the host plants can be crucial in containing the cochineal proliferation.

Histological analysis has shown that after the insect's stiletto-shaped mouthparts have penetrated the phloem of a vascular bundle, the tissues die and are filled with a pink substance. It is thought that the scale insect produces toxic substances that spread systemically inside the plant which reacts by producing a necrosis of tissues around the stylets (Mann, 1969). The thickness of the epidermis and cuticle are also important resistance factors of *Opuntia* spp. to the cochineal (Da Silva et al., 2010). In addition, the layer of calcium oxalate present in the epidermal tissue walls (Trachtenberg & Mayer, 1982) hinders the insertion of the stylets into the host plant tissues (Ruiz et al., 2002).

Dactylopius opuntiae has been reported on several species of Opuntiaceae, whose systematics is exceedingly complex. Here, we refer to the taxonomic classification provided by Samah & Valadez-Moctezuma (2014) and to The Plant List (2013) for the accepted Latin names of the host plant species (Table 2).

Dactylopius opuntiae as biological control agent

In South Africa, before biological control programs were started, prickly pear infested over 900 000 ha of grazing land with variable densities (Zimmermann & Moran, 1991). In 1932, *D. opuntiae* was introduced as a possible biological control agent of the cactus, along with three other insect species, that is *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae), *Lagocheirus funestus* (Thomson) (Coleoptera: Cerambycidae), and *Metamasius spinolae* Gyllenhal (Coleoptera: Curculionidae) (Annecke & Moran, 1978). The scale insect cleaned 75% of the infested areas, including those with the highest levels of opuntia infestation (Annecke & Moran, 1978). Aside from a few exceptions, within 12–18 months of its introduction into an area, the cochineal caused large defoliation killing the smaller plants (Pettey, 1947). Subsequently, about 90% of the original 900 000 ha returned to sheep-rearing, also due, to a lesser extent, to *C. cactorum* (Annecke & Moran, 1978; Zimmermann & Moran, 1991). However, there are still dense populations of prickly pear, in cold and rainy areas, which are less favorable to the development of *D. opuntiae* (Zimmermann et al., 1986).

Inside the Kruger National Park, subsequent introductions of *D. opuntiae*, carried out in the mid 1990s, failed to control *O. stricta* (Lotter & Hofmann, 1998; Hoffmann et al., 1999), thus confirming the importance of matching particular biotypes of biocontrol agents and host plants for weed control (Volchansky et al., 1999). A new strain of the cochineal was then introduced from *O. stricta* collected in Australia in 1997 with encouraging results (Lotter & Hofmann, 1998; Hoffmann et al., 1999). More recently, the genotype of *D. opuntiae* which effectively controlled *O. stricta* in South Africa, was introduced in Kenya, into the OI Jogi Natural reserve, resulting in the reduction in flowering and fruiting, and leading to the death of the plants (Shackleton et al., 2017). De Souza & Hoffmann (2015) assessed the performance of *D. opuntiae* in controlling *Opuntia monacantha* Haw., showing that it was less efficient than the congeneric *D. ceylonicus* which provides complete biological control of this cactus species.

Table 2 Species of plants on which *Dactylopius opuntiae* have been recorded

Plant species	References
Opuntia engelmannii Salm-Dyck ex Engelm.	De Lotto (1974b); Chávez-Moreno et al. (2011)
Opuntia engelmannii subsp. *lindheimeri* (Engelm.) U. Guzmán & Mandujano)	Moran & Zimmermann (1991) (as *Opuntia lindheimeri* Engelm.)
Opuntia ficus-indica (L.) Mill.	Pettey (1947, 1950); De Lotto (1974b); Moran & Zimmermann (1991) (as *Opuntia vulgaris* Mill.); Romero López et al. (2006) (as *Opuntia megacantha* Salm-Dyck); Chávez-Moreno et al. (2011); Spodek et al. (2014); Bouharroud et al. (2016)
Opuntia fuliginosa Griffiths	Chávez-Moreno et al. (2011)
Opuntia humifusa (Raf.) Raf.	Hall (1922); Pérez Guerra & Kosztarab (1992)
Opuntia hyptiacantha F.A.C. Weber	Chávez-Moreno et al. (2011)
Opuntia leucotricha DC.	Chávez-Moreno et al. (2011)
Opuntia littoralis (Engelm.) Cockerell	Pérez Guerra & Kosztarab (1992)
Opuntia maxima Mill.	Ben-Dov & Sánchez-Garcia (2015)
Opuntia × *occidentalis* Engelm. & J.M. Bigelow (pro sp.)	Pérez Guerra & Kosztarab (1992)
Opuntia robusta J.C. Wendl.	Chávez-Moreno et al. (2011)
Opuntia streptacantha Lem.	De Lotto (1974b); Chávez-Moreno et al. (2011)
Opuntia stricta (Haw.) Haw.	Pérez Guerra & Kosztarab (1992)
Opuntia tomentosa Salm-Dyck	De Lotto (1974a); MacGregor & Sampedro (1984); Chávez-Moreno et al. (2011)
Opuntia tuna (L.) Mill.	Pérez Guerra & Kosztarab (1992)
Tacinga palmadora (Britton & Rose) N.P. Taylor & Stuppy	Pérez Guerra & Kosztarab (1992)

Subsequently, Rule & Hoffmann (2018) investigated the effectiveness of the 'stricta' biotype of *D. opuntiae* as a biological control agent for both *Opuntia humifusa* (Raf.) Raf. and *O. stricta*. After a semi-field experiment, *D. opuntiae* was able to develop equally on both host plants. This would seem to indicate that the different efficacy levels in controlling the two host species could be attributed to the overall size of the plants which enables them to compensate more easily for cochineal damage.

To promote a quicker spread of the scale insect, the dispersal capability of *D. opuntiae* away from the first areas of inoculum was assessed (Foxcroft & Hoffmann, 2000). To maximize the antagonistic action of the cochineal, the colonies needed to be inoculated at no more than 10 m in between, as the spread of cochineal is primarily anemophilous (Gonzàlez, 2001). The efficacy of *D. opuntiae* is often limited by predator coccinellids (Geyer, 1946, 1947; Pettey, 1947; Annecke et al., 1969) and to a greater extent by rain (Dodd, 1940; Zimmermann et al., 1986; Moran & Hoffmann, 1987; Moran et al., 1987). A good approach is thus to infest as many plants as possible during dry periods (Foxcroft & Hoffmann, 2000).

In South Africa, the reduction in the role of the prickly pear (*O. ficus-indica*) as a weed, and its increased use for human consumption, for forage, and as a host plant for the rearing of *D. coccus*, has radically changed the public's perception of this plant and the role of *D. opuntiae* as a biological control agent (Zimmermann & Moran, 1991).

Dactylopius opuntiae as pest

Dactylopius opuntiae is a sap-sucking insect that can have a strong negative impact on both the production of prickly pear fruit for fresh consumption and on cladodes as fodder for livestock feed (MacGregor & Sampedro, 1984). The cochineal species tends to form variably sized colonies on cladodes, which in some cases are totally covered by the insect (Mena & Rosas, 2004; Cruz-Rodríguez et al., 2016). As a consequence, the fruits drop and cladodes dry out and fall off (Mann, 1969). The infested plant first shows chlorotic yellowish areas and necrosis on the cladodes, then it dries (Warumby et al., 2005; Santos et al., 2006b) within about a year, though the woody stems of the plant can survive for another 6 months (Klein, 2002). In specialized crops, farmers consider the control of *D. opuntiae* of primary importance because the trophic activity weakens the plants, favoring the attack of pathogens which can lead to their death (Batista-Lopes et al., 2010). Moreover, the high population level of *D. opuntiae* on *O. ficus-indica* profoundly modifies the endophytic fungal community of the host plant (Freire et al., 2015).

In northeastern Brazil, where *D. opuntiae* was imported from Mexico to produce the dye, the production of forage cactus has been severely hit (Almeida et al., 2011). In other Brazilian states (i.e., Pernambuco, Paraíba, and Ceará), *D. opuntiae* has infested over 100 000 ha, causing more than 100 million US dollars of annual damage with serious socio-economic consequences for farming communities in which milk production is linked to the cultivation of the prickly pear (Chiacchio, 2008; Lopes et al., 2009a). In Morocco, since its first detection at the end of 2014, the cochineal spread rapidly and caused serious damage leading the local authorities to adopt an emergency intervention, uprooting and incinerating more than 400 ha of plantations in the Doukkala region (Ochoa & Barbera, 2017).

Integrated pest management

The extensive damage that the insect causes requires an integrated pest management (IPM) approach that also takes into account the direct effects on biodiversity that could be affected by the introduction of alien organisms (Santos et al., 2006a). This approach consists of several techniques based on mechanical, physical, biological, chemical, and other methods (Cavalcanti et al., 2001; Santos et al., 2006a; Lopes et al., 2007) which can be combined in various ways in order to achieve the best results in controlling the pest.

Mechanical and physical methods

Mechanical methods could be crucial in those areas where the first sign of cochineal infestation is detected, especially when inspections in the field are regularly carried out. The method mainly consists of the mechanical harvesting or cleaning of the infested cladods or plants which can be destroyed (e.g., by burning) or stored for subsequent use as food for cattle. Considering that often the highly infested cladodes fall onto the ground, due to abscission, infested parts which could spread the infestation need to be collected and destroyed as soon as possible after their first detection. Unfortunately, this effective mechanical intervention is applicable when only a few plants are infested, as it is expensive and time-consuming (Santos et al., 2006a; Torres & Giorgi, 2018).

Biological control methods

Natural enemies. The carminic acid produced by the cochineal is toxic to other insects (Eisner et al., 1980) and only some natural enemies are able to overcome this protection system (Gilreath & Smith, 1988; Eisner et al., 1994; Cruz-Rodríguez et al., 2016). Several species of predators (insects and spiders) have been recorded in association with the cochineal (Torres & Giorgi, 2018) and some are able to control it. The following beetle species (Coleoptera) have been recorded: *Hyperaspis trifurcata* Schaeffer, *Chilocorus cacti* (L.), *Coccidophilus citricola* Brèthes, *Zagreus bimaculosus* Mulsant, *Exochomus flavipes* (Thunberg), *Exochomus flaviventris* Mader, and *Cryptolaemus montrouzieri* Mulsant (Coccinellidae) and *Cybocephalus* sp. (Nitidulidae) (Pettey, 1950; Annecke et al., 1969; Karny, 1972; Vanegas-Rico et al., 2010b; Lima et al., 2011; Ramírez et al., 2011).

Hyperaspis trifurcata has been shown to be one of the most abundant, frequent, and, in some cases, most effective species (Cruz-Rodríguez et al., 2016; Protasov et al., 2017) and is thus judged as a valuable biological control agent for *D. opuntiae* in agroecosystems. This ladybird is an active predator, and each female is able to consume more than 5 400 nymphs during its lifespan, enhancing its developmental rate proportionally to the increase in prey density (Vanegas-Rico, 2015; Vanegas-Rico et al., 2016).

The beetles *C. citricola*, *Z. bimaculosus*, *Exochomus* sp., and *Cybocephalus* sp. have been found in colonies of *D. opuntiae* in Brazil (Lima et al., 2011) but particular attention is currently given to the native *Z. bimaculosus*, which preys upon both *D. echinocacti* and *D. opuntiae* (Torres & Giorgi, 2018). On the other hand, *E. flavipes*, *E. flaviventris*, and *C. montrouzieri* have been shown to successfully control the cochineal in South Africa (Pettey, 1950; Annecke et al., 1969; Karny, 1972). In the laboratory, *C. montrouzieri* successfully developed and preyed on *D. opuntiae* and could be a potential biocontrol agent against the cochineal. However, in the field its efficacy is hindered by high temperatures and by other environmental factors (Torres & Giorgi, 2018). In northern Israel, inundative releases of *C. montrouzieri* (about 100 000 individuals) were unsuccessful in managing the early outbreak of the wild cochineal (Protasov et al., 2017) although along the coast, local acclimated populations of this beetle began to reduce the cochineal populations (Mendel et al., 2018). In Morocco, the release of 30 *C. montrouzieri* adults per m^2 of ground surface, significantly reduced the cochineal population by 92% within 77 days after their release into areas where the minimum temperature exceeds 5 °C (Bouharroud et al., 2018).

Other groups of insects feed mainly on the nymphs of the cochineal, such as *Leucopis bellula* Williston (Diptera: Chamaemyiidae) and *Sympherobius barberi* Banks (Neuroptera: Hemerobiidae) (Pacheco Rueda et al., 2011; Vanegas-Rico, 2015; Cruz-Rodríguez et al., 2016), whereas *Laetilia coccidivora* (Comstock) (Lepidoptera: Pyralidae) and *Eosalpingogaster cochenillivora* (Guerin-Meneville) (Diptera: Syrphidae) were observed feeding on adults (Eisner et al., 1980; Esparza-Gómez et al., 2008a,b; Mengual & Thompson, 2011; Flores et al., 2013). In Mexican organic prickly pear cultivations, *L. coccidivora* together with *H. trifurcata* were the most effective predators of *D. opuntiae* (Cruz-Rodríguez et al., 2016).

Subsequently in 2017, in prickly pear crops in Mexico, *L. bellula* and *S. barberi* were found to be the most numerous predators (70% of the total number) with populations well synchronized with that of their prey (Vanegas-Rico et al., 2017). On the other hand, ants (Hymenoptera: Formicidae) play a dual role. For example, species such as *Pheidole* sp., *Solenopsis germinata* (Fabricius), and *Solenopsis xyloni* McCook have been observed to prey on *L. bellula*, *L. coccidivora*, and *S. barberi*, limiting their effectiveness as biological control agents of *D. opuntiae*. At the same time, *S. xyloni* feed on second instars of the cochineal, whereas *Pheidole* sp. attacks *D. opuntiae* males (Vanegas-Rico et al., 2010a).

Several studies have assessed the efficacy of microbiological agents in controlling the pest insect. The use of microbials can be adversely affected by environmental factors including high temperatures, low relative humidity, direct sunlight, and ultraviolet light (Reis et al., 2005). The fungus *Empusa lecanii* Zimm. in South Africa was found to infect nymphs and young females of *D. opuntiae* during winter with over 80% of the hosts parasitized in some years (Pettey, 1950). In Brazil, other species of fungi, that is, *Beauveria bassiana* (Bals.-Criv.) Vuill. and *Metarhizium anisopliae* (Metschn.) Sorokin, gave promising results although overexposure to sunlight can greatly reduce their persistence in the environment and in turn their use in IPM programs (Santos et al., 2011). In laboratory experiments, *B. bassiana* conidia protected in oily formulations containing photo protectors were tested with satisfactory results on first instars of the cochineal (Santos et al., 2011).

Fusarium spp. have also been studied as biological control agents of Hemiptera (Teetor-Barsch & Roberts, 1983). The *Fusarium incarnatum-equiseti* species complex has been used in Brazil to control *D. opuntiae* alone (Carneiro-Leão et al., 2017) or in combination with natural extracts of *Ricinus communis* L. and *Poincianella pyramidalis* (Tul.) L.P. Queiroz with promising results (Santos et al., 2016). A key point for the use of this fungus in IPM is the molecular characterization of the genetic profiles of strains of *F. incarnatum-equiseti*, given the considerable differences in the effectiveness as control agents among biotypes collected in the field (Tiago et al., 2016; Carneiro-Leão et al., 2017). The use of *Fusarium* isolates obtained from *D. opuntiae* collected in the field and combined with 5% aqueous extract of *R. communis* stood out as the most promising for the control of *D. opuntiae* (Santos et al., 2016).

Natural extracts. In addition to aqueous and hydroethanolic extracts of *R. communis* and *P. pyramidalis*, several other plant extracts have been tested for the control of *D. opuntiae*. Neem (*Azadirachta indica* A. Juss.) and cassava (*Manihota esculenta* Crantz) starch (i.e., the liquid waste generated in the pressing process), tested in greenhouses, have been shown to reduce the infestation rate of *D. opuntiae* on prickly pear, although the industrial preparation made with cassava did not produce good results probably due to the time gap between its extraction and the application in the field (Borges et al., 2013b).

In Mexico, extracts of *Mentha piperita* L. (Lamiaceae), *Mentha spicata* (= *viridis*) L., *Tagetes erecta* L., *Tagetes lucida* Cav. (= *Tagetes florida* Sweet), and *Dysphania ambrosioides* (L.) Mosyakin & Clemants (= *Chenopodium ambrosioides* L.) mixed with different emulsifiers (i.e., Tween20, SLS20, Citrim, Panodan) caused body dehydration, obstruction of spiracles, and asphyxia on second instars, thus affecting adult female survival and other reproductive parameters (Vigueras et al., 2009). The essential oils of *Ocimum basilicum* L., *M. spicata*, *Cymbopogon winterianus* (Jowitt ex Bor), and *Lippia graveolens* Kunth were found to be toxic for first instars (Soassuna et al., 2008; Vázquez-García et al., 2011), and some terpenoids (e.g., eugenol, 1-8 cineol, and menthol) successfully led to the reduction in *D. opuntiae* crawlers fixed to healthy *Opuntia* cladodes (Pérez-Ramirez et al., 2014).

An orange oil (sodium tetraborohydrate decahydrate) and the monoterpene D-limonene, obtained from citrus juice, were tested against *D. opuntiae* (Lopes et al., 2009b). The former caused the death of nymphs and adults within 48 h after treatment and no side effects on the ladybugs *Cycloneda sanguinea* (L.) and *Scymnus intrusus* Casey were observed, whereas a dose of 0.7% negatively affected the survival of the syrphid larvae (*Baccha* sp.) (Lopes et al., 2009b). In Morocco, D-limonene at 120 and 150 ppm showed the most toxic effect against adult females of *D. opuntiae*, although chlorotic damage to the cladodes was also observed (Bouharroud et al., 2018). It is interesting that the aqueous extract of *D. opuntiae* hemolymph was found to repel crawler fixation – this has good potential as a control measure due to its availability for farmers and the simple preparation procedure (Pérez-Ramirez et al., 2014).

Plant clones resistant to *Dactylopius*

In Brazil, the absence of efficient control methods has led to the selection of resistant varieties of *Opuntia* to feed livestock, with numerous experiments in the laboratory and in the field (Santos et al., 2006b; Da Silva et al., 2009; Vasconcelos et al., 2009; Lopes et al., 2010; Borges et al., 2013a). In laboratory tests, some clones, especially ‘Orelha de Elefante Mexicana’ and ‘Miúda’, have shown an immunity-type resistance to the carmine cochineal as there was no insect infestation (Da Silva et al., 2009; Vasconcelos et al., 2009; Borges et al., 2013a).

Chemical control

According to Mena & Rosas (2004), cochineal should be chemically controlled when 30% of the plants have more than 10 colonies. In Mexico, pest control is essentially chemical and is based on the use of malathion, methyl parathion, chlorpyrifos (Aguilar, 2000; Badii & Flores, 2001; Cruz-Rodríguez et al., 2016), and trichlorfon (Badii & Flores, 2001). In South Africa, cypermethrin, carbaryl, and chlorpyrifos have been used; a mixture of cypermethrin and chlorpyrifos or chlorpyrifos alone led to satisfactory control of *D. opuntiae* (and *C. cactorum*), whereas carbaryl had little effect (Pretorius & van Ark, 1992). Mineral oil yielded between 93–97% (Brito et al., 2008) and 100% mortality (Borges et al., 2013b), also when mixed with 2% salt (Araújo De Lacerda et al., 2011). Laboratory tests evaluated the efficacy of biodegradable products (e.g., Rome and Peak Plus) (Palacios-Mendoza et al., 2004), and some authors suggested the use of detergents in the case of strong infestations, with doses ranging from 1 to 5% (Santos et al., 2006a; Carvalho & Lopes, 2007; Borges et al., 2013b).

Chemical control has been seriously hampered by the absence of insecticides registered for prickly pear, as was the case in Brazil until 2016 (Santos et al., 2016). The increasing problem has led the Brazilian Ministry of Agriculture, Livestock and Supply to give a special permission for the use of thiamethoxam, imidacloprid (both neonicotinoids), λ-cyalothrin, and bifenthrin (both pyrethroids) (Torres & Giorgi, 2018).

Conclusions

In areas where prickly pear is cultivated for human consumption or for cattle feed, nearby farmers regard the species as a pest and its control is considered a priority (Cruz-Rodríguez et al., 2016). In the Mediterranean basin, the harmfulness of *D. opuntiae* is expected to grow because of the changing weather conditions and rising temperature, which have a direct impact on the environment, in particular by the increase in drought and desertification. Under such conditions, prickly pear represents a feasible alternative to other crops. This is the case for Italy, where 90% of the cactus fruit production comes from Sicily with a cultivated surface of over 15 000 ha of which 3 500 ha are covered by specialized cultivation (Ochoa & Barbera, 2017). New prickly pear plantations are emerging in other Mediterranean countries, such as Morocco, where the agricultural policy is currently aimed at a production of 1.94 million metric tons by 2020 (Bouharroud et al., 2016) and each year, more than 4 000 ha are planted in the center and south of the country (Ochoa & Barbera, 2017). The environmental conditions and the availability of the host plants also seem to be favorable for the survival and development of the false carmine cochineal, which has become highly noxious to the prickly pear cultivation. The recent rapid infestation in Israel and Morocco requires control measures (Bouharroud et al., 2016, 2018; Protasov et al., 2017; Mendel et al., 2018).

The spread of *D. opuntiae* in Mediterranean countries has opened up a debate on the most effective strategies for controlling the pest. Currently, the control of *D. opuntiae* relies mostly on chemical and biological methods. Mechanical methods can be applied when there are only a few plants infested (Santos et al., 2006a; Torres & Giorgi, 2018). The biological control agents *H. trifurcata* and *C. montrouzieri* are currently considered to be the most promising candidates and they have been introduced in many countries newly infested by *D. opuntiae*, although sometimes with controversial results, as in Israel (Protasov et al., 2017; Bouharroud et al., 2018; Mendel et al., 2018).

The introduction of natural enemies from other countries is not always easy because they are considered as 'alien' organisms, and this process is often regulated by strict laws and the introduction of exotic entomophagous insects is regulated (e.g., in Italy). Therefore, the efficacy of authochtonous antagonists in newly invaded areas is considered the first step in any IPM program.

As reported by Cruz-Rodríguez et al. (2016), biological control based only on the use of the 'strongest' agents is not necessarily able to limit cochineal populations in the long term. The protection of indigenous natural enemies and the preservation of the ecological infrastructure represents the basis for a management strategy that could prevent the cochineal from reaching the pest status. Several plant extracts (e.g., neem, orange oil, D-limonene) have shown promising control of *D. opuntiae.* In semi-arid regions, a higher yield could be obtained using resistant cultivars of *Opuntia* and adopting suitable agronomic practices (spacing, fertilization, irrigation, weed control; Torres & Giorgi, 2018).

The most used chemical pesticides in the world (e.g., neonicotinoids, organophosphates, carbamate, pyrethroids) pose the risks of environmental pollution and are expensive. Other substances (e.g., mineral oil, vegetal oil, neutral detergents) are effective in controlling the cochineal and simultaneously preserve lady beetles and syrphid larvae in treated fields (Torres & Giorgi, 2018). Within each country, the use of insecticides on crops is regulated and sometimes the most effective ones are not admitted for use on prickly pear, as in the case of Brazil. In Italy, only a few insecticides are registered for use on prickly pear crops, and only paraffinic oils can be used against cochineals (SIAN, 2017).

Today, the ease with which goods and people move around the globe greatly favors the spread of scale insects, which may go unnoticed because of their morphological and biological features (Franco et al., 2011; Mazzeo et al., 2014). Closer surveillance by customs officers is therefore necessary, with controls taylored to detect cochineal specimens or obvious signs of their presence on the plant. A monitoring plan and a widespread information campaign are required to plan effective strategies for managing the problem.

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