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ECOLOGY AND MANAGEMENT OF *PARACOCCUS MARGINATUS* (PAPAYA MEALYBUG) (HEMIPTERA: PSEUDOCOCCIDAE) IN THE INDIAN SUBCONTINENT – ACHIEVEMENTS, AND LESSONS

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ABSTRACT

Paracoccus marginatus*, first described in 1992, is native to Mexico. Accidentally it started spreading in the Caribbean in 1995. About 2008, it was reported from the Indian subcontinent and several other countries in the South- and Southeast-Asia. This polyphagous insect infests plants belonging to *c*. 50 families. *Carica papaya* (Caricaceae, papaya) and *Manihot esculenta* (Euphorbiaceae, cassava) are the principal species attacked by *P. marginatus*. In 1999, classical biological-control (hereafter, management) efforts to manage this insect were implemented by the U.S. Department of Agriculture (USDA). *Carica papaya*, *M. esculenta*, and *Morus alba* (Moraceae, mulberry) were heavily infested and suffered severe economic loss. Locally available natural enemies when trialled as biological-management agents were ineffective. This outcome instigated scientists to seek a classical biological-management option by introducing exotic parasitoids. Five potential parasitoids, *Apoanagyrus* nr. *californicus, Pseudaphycus* sp., *Anagyrus loecki, Acerophagus papayae* and *Pseudleptomastix mexicana* (all Encyrtidae) were obtained from Mexico in 1999. In the Indian subcontinent, three parasitoids (*A. papayae*, *P. mexicana*, and *A. loecki*) were first released in Sri Lanka in 2009 and in Tamil Nadu, India in 2010. They established well in the field and in five months they regulated the population of *P. marginatus*. *Acerophagus papayae* was found playing a major role in managing populations of *P. marginatus.

Key words: papaya mealybug, biological control, Indian subcontinent, parasitoids

Paracoccus marginatus Williams and Granara de Willink (Hemiptera: Pseudococcidae) was first obtained from *Manihot esculenta* Crantz (Euphorbiaceae) in Mexico in 1955. However, it was formally described only in 1992 and redescribed by Miller and Miller in 2002 (Miller et al*.,* 2002). *Paracoccus marginatus* accidentally spread outside of Mexico *via* live-plant material trade. Damage incurred by *P. marginatus* was first observed on *Carica papaya* L. (Caricaceae) in St. Martin Island in the Caribbean in 1995, and by 2000, it had spread to 13 countries in the Caribbean, six countries in Central and South America, and Florida in the United States (Muniappan, 2009a; Myrick et al., 2014). *Paracoccus marginatus* started to spread to the West and Central Pacific Islands in 2002, South and Southeast Asia in 2008, West Africa in 2010, Middle East in 2011, and East Africa in 2015. The rapidly changing climate patterns are indicated as an acceleration factor in the spread of *P. marginatus* (Finch et al*.,* 2020). Further spread to Central and East Africa and widening of its territory in Central America and Asia is due to (a) suitability of climatic conditions and (b) available host plants grown as crop plants (Finch et al*.,* 2020). In India, it was first reported from Coimbatore in Tamil Nadu in July 2008 (Muniappan et al*.*, 2008, Muniappan, 2009b, 2011; Mani et al*.*, 2012a).

The spread of *P. marginatus* from Central America to about 50 countries within a decade (1994–2014) affirms *P. marginatus* as an invasive. However, *P. marginatus* is amenable to successful management with natural enemies- introduced either intentionally or fortuitously- which has proved an economically sustainable effort in protecting crops such as *C. papaya*, *M. esculenta*, and *M. alba*. In this manuscript, we refer to the ecology, spread, and aspects of management of populations of *P. marginatus* in the Indian subcontinent.

Bionomics and ecology

Mani et al. (2012a) indicate that *P. marginatus* can reproduce both sexually and parthenogenetically. However, Amarasekare et al. (2008a) and Seni and Sahoo (2014) indicate that parthenogenetic reproduction does not occur. Tropical wet and dry climate favours building-up of populations of *P. marginatus*. Although the lifecycle of *P. marginatus* has been studied in the laboratory, bionomics of *P. marginatus* get affected by host plants, temperature, and field conditions

(Amarasekare et al., 2008a, b). An adult female is 2-3.5 mm long, soft, slightly flat, and elongate. On maturation, it secretes sticky, elastic, white, waxy filaments from the abdominal glands and develops a protective ovisac. One female lays 230-400 eggs (Amarasekare et al., 2008a; Mahalingam et al., 2010). The ovisac is 3-4 times the body length and usually is wrapped in the whitish waxy filaments (Pantoja et al., 2007). Eggs are greenish-yellow. Hatching usually occurs in 7-14 days. During unfavorable conditions, *P. marginatus* also shows 'population reverse metamorphosis,' where the adult females start preserving eggs within waxy wraps and could choose non-living substrates to preserve the egg mass as cottony, fluffy caskets (Krishnan et al., 2016). No sexual dimorphism is apparent between female and male instars. Females undergo three instars and males undergo four instars. The duration of development of instars is reported differently in various studies for males and females (Nisha and Kennedy 2017; Munwar et al., 2016; Laneesha, 2016).

Lifecycle duration varies at different temperatures (Amarasekare et al., 2008b; Munwar et al., 2016; Laneesha, 2016). In general, the developmental time for the 1st instar is *c*. 6 d, 2nd 6-10 d, 3rd 2-4 d (for both males and females), and the 4th 3-5 d for males at 25°C and 65% RH. The development time of different instars was 1st instar 4-5 d, 2nd 4-5 d, and 3rd 5-6 d. for females raised and verified on *Hibiscus rosa-sinensis* L. (Malvaceae), *Acalypha wilkesiana* Müll. Arg. (Euphorbiaceae), *Plumeria rubra* L. (Apocynaceae), and *Parthenium hysterophorus* L. (Asteraceae) (Amarasekare et al., 2008a). The total time to complete development by a female is 24-25 d and a male is 27-30 d (Amarasekare et al., 2008a). In general, *P. marginatus* has ~11 generations/y and takes 30- 40 d to complete one generation (Seni and Sahoo, 2014). In tropical conditions (e.g., Coimbatore, Tamil Nadu), it completes 15 generations/ year (CABI, 2021). The optimal temperature for its development is 28-32°C, and temperatures lower than 13°C and higher than 35°C disrupts the biology of *P. marginatus* and are not favourable for the development of eggs and survival of different lifestages of *P. marginatus* (Laneesha, 2016; Amarasekare et al., 2008b; CABI, 2021).

Paracoccus marginatus inflicts significant economic damage to both *M. esculenta* and *C. papaya*, the loss ranging from 10 to 60%, depending on the crop (Myrick et al., 2014), and the shortest female developmental time is ~19 days on *C. papaya*, whereas, on *M. esculenta,* the longest developmental period is ~33 days (Maharani et al., 2016). The developmental time of *P. marginatus* varies in different studies despite trials made on relatively similar temperature and humidity levels (~25°C and ~65 RH), which could be attributed to the nutritional factors of the host plant (Kumar et al., 2014). In the Indian subcontinent, the biology of *P. marginatus* was studied at various laboratories trialling on *C. papaya*, *M. esculenta, M. alba*, *Jatropha* sp. (Euphorbiaceae), *Solanum melongena* L. and *Solanum tuberosum* L. (both Solanaceae), and species of *Hibiscus* and *Gossypium* (both Malvaceae) (Seni and Sahoo, 2014; Kumar et al., 2014; Sharma et al., 2013; Nisha and Kennedy, 2017; Munwar et al., 2016). In India, *P. hysterophorus* was the most preferred alternate host of *P. marginatus* in and around *C. papaya* fields (Rasheed et al., 2017).

Many formicids (*e.g.*, *Solenopsis geminata* (F.), *Tapinoma melanocephalum* (F.), *Monomorium indicum* Forel) (Hymenoptera) play a major role in distributing *P. marginatus*. These formicids also protect populations of *P. marginatus* from predators and parasitoids. Eight species of Formicinae, Myrmicinae, Dolichoderinae were associated with *P. marginatus* in India, of which *S. geminata* was the most common (Gowda et al., 2014).

Host plants, damage and spread

Paracoccus marginatus is an intensely polyphagous insect. It attacks vegetables, fruits, ornamental plants, and nuisance plants belonging to about 50 plant families including the Fabaceae, Solanaceae, Asteraceae, Apocynaceae, Euphorbiaceae, and Malvaceae (García Morales et al., 2016; accessed on 12 June 2021). *Paracoccus marginatus* is associated with 158 plant taxa including *C. papaya, M. esculenta, Jatropha* sp., *Acalypha indica* L. (Euphorbiaceae), *Cassia sericea, Vachellia* sp. (Fabaceae), *P. hysterophorus*, *Annona squamosa* L. (Annonaceae), *Gossypium* spp., *H. rosa-sinensis*, *Ipomea* sp. (Convolvulaceae), and *S. melongena* (Muniappan, 2011; García Morales et al., 2016).

Similar to other Coccoidea, feeding action of *P. marginatus* inflicts a low level mechanical damage to plant tissue than that inflicted by chewing and biting insects, such as the Coleoptera and Lepidoptera. However, due to their salivary chemistry, they alter the physiology of the host plant and drain cell sap from plant tissue, thus stressing the plant and consequently affecting its fitness, and ultimately affecting plant growth (Huang et al., 2012). As a sap sucker, *P. marginatus* consumes phloem sap and exudates copious honey dew. Deposition of honey dew on plant parts induce

the growth of sooty mould (species of *Cladosporium*, Capnodiales: Davidiellaceae; *Alternaria*, Pleosporales: Pleosporaceae) the spread of which interferes with light radiation and air movement to and from leaves reducing photosynthetic efficiency (Williams and Granara de Willink, 1992; Muniappan, 2011) (Fig. 1). Physical expressions of the physiological stress caused by *P. marginatus* include distortion, stunting, wilting, dieback of stems, twisting, yellowing, curling, distortion of leaves, leaf drop, and premature fruit drop (CABI, 2021; Muniappan, 2011). Fruit tissues of *C. papaya* infested by *P. marginatus* become hard in texture and bitter in taste. In the Indian subcontinent, *P. marginatus* affects multiple economically important plants such as *C. papaya*, *Hibiscus cannabinus* L. (Malvaceae), *Jatropha curcas* L., *M. esculenta*, *M. alba*, *Psidium guajava* L.) (Myrtaceae), *Punica granatum* L. (Lythraceae), *S. melongena*, *S. tuberosum,* and *Tectona grandis* L. f. (Verbenaceae) (Regupathy and Ayyasamy, 2010; Mahalingam et al., 2010; Kumar et al., 2014; Prasad et al., 2012; Shekhar et al., 2011). More than 50 plants host *P. marginatus* in Tamil Nadu (Regupathy and Ayyasamy, 2010; Sakthivel et al., 2012).

Paracoccus marginatus is now present in 53 countries **(**García Morales et al., 2016). It first started to spread in Dominican Republic in the 1990s, and by 2000, it had spread to Antigua, Belize, the British Virgin Islands, Costa Rica, Guatemala, Mexico, Nevis, Puerto Rico, St. Barthélémy, St. Kitts, St. Martin, and the US Virgin Islands and also to the USA (Florida). In the next 10 years, it spread into the Bahamas and Guam in 2002, Palau in 2003, Hawaii in 2004, Northern Mariana Islands in 2005, and most of Asia and Africa as follows: India, Sri Lanka, Philippines in 2008, Thailand, Cambodia, Togo, Benin, Ghana, Maldives, Malaysia, Bangladesh in 2009, Jamaica in 2010, Taiwan, Oman in 2011, China, Mauritius in 2014, Tanzania, Mozambique in 2015, Israel, Gabon, Kenya in 2016, South Sudan in 2020, (Meyerdirk et al., 2004; Muniappan et al., 2006, 2011; Muniappan, 2008, 2009a, b; Goergen et al., 2011; Mastoi et al., 2011; Germain et al., 2010; Chen et al., 2011; Ahmed et al., 2015; Mendel et al., 2016; Macharia et al., 2017; Gama et al., 2020) and Uganda in February 2021 (Richard Molo, personal communication, email, 1 February 2021).

Spread and management in the Indian subcontinent

In the Indian subcontinent, it was first reported in Coimbatore (Tamil Nadu) in 2008 (Muniappan et al., 2008). Between 2009 and 2012, it spread to Kerala (Krishnakumar and Rajan, 2009; Sakthivel et al., 2012), Andhra Pradesh (Rasheed et al., 2017), Karnataka (Gowda et al., 2014), West Bengal (Lalitha et al., 2015), Assam (Sarma, 2013) and Gujarat (Dhobi et al., 2014), Rajasthan (Mani et al., 2012b). It concurrently spread to countries in the neighbourhood: Sri Lanka (Galanihe et al., 2010) in 2008, Bangladesh (Muniappan, 2009b) in 2009, Pakistan (Munwar et al., 2016) in 2015, and the Maldives (Muniappan et al., 2011) in 2009 (Fig. 2). It was recorded in Nepal in 2014 (R. Muniappan, personal observations).

The female *P. marginatus* is wingless and has limited capability to move. However, air current, rain, irrigation, birds, clothing, and farm equipment assist in the short-

Fig. 1. Infestation by *P. marginatus* on *C. papaya* a: fruits (bar=6 cms) and b: leaves (bar= 10 cms)

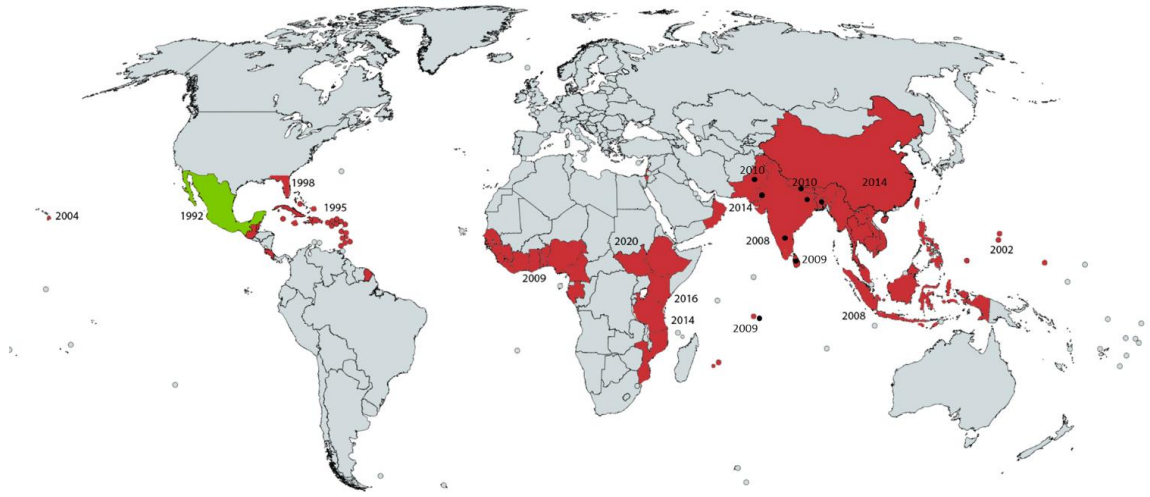

Fig. 2. Global distribution of *P. marginatus*. Green — epicentre of possible origin of *P. marginatus*; red — spread of *Paracoccus marginatus*. Black spots — *P. marginatus* incidence in the Indian subcontinent

distance movement of somewhat agile immatures. Other factors responsible for the dispersal of the insect are the movement of plant material, including fruits and vegetables, and the presence of alternative host plants that allow *P. marginatus* to thrive. Some species of the Formicidae are indicated to act as herders enabling the movement of the immatures of *P. marginatus* (Mani et al., 2012a; Tanwar et al., 2010). Strategies to keep the population of *P. marginatus* in control include managing the populations of the associated Formicidae that are attracted to the honeydew secreted and discharged by *P. marginatus*. Additionally, periodical scouting for and monitoring the presence of *P. marginatus* populations, pruning infested branches and burning them, removal and burning of plant residues, removal of alternate host plants, isolation of infested fields, and sanitization of farm equipment before moving them to uninfested fields also contribute to better manage *P. marginatus* populations (Tanwar et al., 2010).

Commonly used systemic organophosphate and contact insecticides are useful in managing dense populations; however, because *P. marginatus* populations are occur embedded in waxy wraps, several applications of the insecticides would become necessary to manage *P. marginatus* (Mani et al., 2012a; Ayyasamy and Regupathy, 2010). Amutha and Banu (2011) indicated that entomopathogenic fungi (EPF), *Verticillium lecanii* R. Zare & W. Gams (Hypocreales: Cordycipitaceae), *Beauveria bassiana* (Bals.-Criv.) Vuill. (Hypocreales: Cordycipitaceae), and *Metarhizium anisopliae* (Metchnik.) Sorok. (Hypocreales: Clavicipitaceae) caused 40-50% mortality of *P. marginatus* in laboratory and greenhouse conditions. A species of *Paecilomyces* (Eurotiales: Trichocomaceae) is one other EPF considered useful in managing *P. marginatus* populations (Ayyasamy and Regupathy, 2010). Other commonly used biopesticides, such as neem products, can also be effective in managing populations (Amutha and Banu, 2011). However, the above strategies can only be useful to a limited extent, due to its special bionomics, waxy coating, and feeding behaviour.

Hence, classical biological control plays a major role in managing *P. marginatus* in the regions where it has invaded. The predatory *Spalgis epius* Westw. (Lepidoptera: Lycaenidae), *Cryptolaemus montrouzieri* Muls., *Scymnus taiwanus* Ohta, *Cheilomenus sexmaculatus* F., *Coccinella transversalis* F., *Chilocorus nigrita* F., *Anegleis cardoni* Weis., *Brumoides suturalis* F., *Nephus quadrimaculatus* Herbs. (all Coleoptera: Coccinellidae), *Chrysoperla carnea* Steph. (Neuroptera: Chrysopidae), *Ischiodon scutellaris* F. (Diptera: Syrphidae), and *Phintella vittata* Koch (Araneae: Salticidae) (Mani et al., 2012a; Fazlullah et al., 2017; Thangamalar et al., 2010) are considered useful in regulating *P. marginatus* populations.

In Mexico, *P. marginatus* populations remain under control due to parasitoids. However, after its spread to the Caribbean and USA, it caused significant yield losses to *C. papaya* and other horticultural crops, such as *Mangifera indica* L. (Anacardiaceae), *Annona reticulata* L. (Annonaceae), and *P. guajava*. In 1999, the US Department of Agriculture (USDA) Agricultural Research Service (ARS) collected the parasitoids, *Apoanagyrus* nr. *californicus* Comp., *Anagyrus loecki*

Noyes*, Acerophagus papayae* Noyes and Sch.*,* species of *Pseudaphycus,* and *Pseudleptomastix mexicana* Noyes and Sch. (all Hymenoptera: Encyrtidae) to manage *P. marginatus* populations in Mexico. Of these, *A. papayae, P. mexicana,* and *A. loecki* were recognized effective and the Animal and Plant Health Inspection Service (APHIS, USDA) initiated a biological control program to rear them in partnership with the Puerto Rican Department of Agriculture for distribution to countries in need (Myrick et al., 2014; Meyerdirk, 1999; 2000). *Acerophagus papayae, P. mexicana,* and *A. loecki* have been released in the Dominican Republic, Puerto Rico, and Florida (USA), and this programme developed by the USDA-APHIS has been successfully implemented in Florida, the Caribbean Islands, tropical South American countries, Guam, Palau, the Hawaiian Islands, and Tinian in the Mariana Islands. Also, in Indonesia, Thailand, Cambodia, Vietnam, the Philippines, and Malaysia *P. marginatus* is controlled due to the fortuitous introduction of these parasitoids. The classical biocontrol strategy has been implemented in India and Sri Lanka in the Indian subcontinent (Muniappan, 2009b). The selected parasitoids are host specific and attack the immatures only. Gravid parasitoids usually insert one egg and the emergent parasitoid larva occurring within an immature of *P. marginatus* kills it (Shylesha et al., 2010).

Achievements and lessons

When populations of *P. marginatus* were first noted in the Indian subcontinent in 2008, several pesticides were applied to manage it. Between 60 and 80% yield loss in *C. papaya* and almost 100% loss in *M. alba* were recorded in Karnataka in January 2009 (Mahalingam et al., 2010). *Acerophagus papayae, P. mexicana,* and *A. loecki* were brought to India from USDA-APHIS, Puerto Rico Centre. About 3,500 individuals of *A. papayae*, 1,500 of *P. mexicana,* and 500 of *A. loecki* were received by the National Bureau of Agriculturally Important Insects, Bangalore in July-October, 2010 (Mani et al., 2012a). All of these were initially reared in the laboratory; however, later, *A. papayae* was reared on a large scale and released into fields in different Indian states. For example, by October 2010, *A. papayae* was released on *C. papaya*, species of *Morus*, species of *Jatropha*, and species of *Plumeria* in Tamil Nadu and Karnataka (Shylesha et al., 2010; Mani et al., 2012a). *Acerophagus papayae* was observed in fields as early as 20 d after release and high numbers were observed in the field after 40 d of release and within three months 80-90% reduction of the population of *P. marginatus* eventuated, and the new shoots of infested plants were not infested by *P. marginatus*. Subsequently, a release rate of 1,000-1,500/ acre was recommended for *C. papaya* orchards (Mani et al., 2012a).

By November 2010, in Coimbatore, due to the spread of *A. papayae,* the population of *P. marginatus* decreased to 2-3% and farmers discontinued spraying pesticides to regulate populations of *P. marginatus*. Mass rearing of *A. papayae* occurred at Research Institutes, Krishi Vigyan Kendras, and colleges. Although *A. papayae, P. mexicana,* and *A. loecki* were released in India and Sri Lanka, *A. papayae* played a key role in managing *P. marginatus* and an immediate positive feedback was received from farmers wherever *A. papayae* was released (Sakthivel, 2013; C A Mahalingam, Tamil Nadu Agricultural University, Coimbatore and E I Jonathan, Centre for Plant Protection Studies; personal communication, email, 10 November 2011). However, in a recent article, Vennila et al. (2021) (page 1310) have incorrectly referred to this parasitoid as '*Anagyrus papaya'*.

In Sri Lanka, *P. marginatus* was reported in 2008. It caused damage to *C. papaya* in the Colombo and Gampha districts. About 2,000 individuals of *A. loecki,* 3,000 of *P. mexicana,* and 5,000 of *A. papayae,* were released in October 2009. In three months, *A. papayae* was established in all the released sites, and populations of *P. marginatus* were reduced by 90-100% by December 2009 (Mani et al., 2012a; Muthulingam and Vinobaba, 2021). *Acerophagus papayae* was fortuitously introduced to Bangladesh and a hyperparasitic species of *Chartocerus* (Hymenoptera: Signiphoridae) was also collected on *P. marginatus* (Muniappan, 2014). In 2017, *A. papayae* was reported from Pakistan (Fazlullah et al., 2017).

'In the Indian subcontinent, the parasitoids A. papayae, P. mexicana, and A. loecki were first introduced in Sri Lanka in 2009 and in India in 2010 after approval from the Plant Protection Advisor, Government of India. The parasitoids were mass produced in 57 locations in Tamil Nadu and released into fields at various locations within Tamil Nadu (Myrick et al., 2014). Approximately 500 parasitoids of each species were released in heavily infested areas. These parasitoids swiftly established on *P. marginatus* on *C. papaya* and other crops, such as *M. alba, M. esculenta,* and species of *Jatropha*. *Acerophagus papayae* played a major role in managing *P. marginatus* by establishing and managing populations of *P. marginatus* swiftly at the released sites. The total cost of accomplishing this

project in India was approximately $200,000 in 2010 and $100,000/year for the next three years (Shylesha et al., 2010; USAID, 2012; Myrick et al., 2014). Total benefit in five years (2010-2015) in India ranged from $524 million to $1.34 billion (Myrick et al., 2014). There are not many invasive species that have been managed in short time as *P. marginatus* was. This is a success story in terms of coordinated and rapidly implemented classical biological control. Major lessons we could learn from the successful management of *P. marginatus* include quick identification of the problem, coordination between different national and international agencies, introduction and multiplication of parasitoids, and dissemination of information to extension agents and farmers.

The spread of *P. marginatus* took about 10 years from Caribbean countries to Asia and similarly, it took almost 10 years to move from West Africa to East Africa. Finch et al. (2020) indicated the potential spread of *P. marginatus* into novel areas in Central and East Africa, and further expansion of *P. marginatus* in Central America and Asia. However, it should be realized that movement of parasitoids and fortuitous establishment not only managed the populations of *P. marginatus* but also slowed the movement and spread of *P. marginatus*.

CONCLUSIONS

Paracoccus marginatus has caused severe damage to *C. papaya*, *M. alba, M. esculenta,* and species of *Jatropha* in the Indian subcontinent, since its rapid spread in the late 2000s. In laboratory conditions, variation in time occurs the lifecycle and it appears that the host plants play a key role in regulating the bionomics of *P. marginatus*. The developmental period is the longest on *M. esculenta* (~33 d) as against on *C. papaya* (~19 d). However, *M. esculenta* appears as a preferred host plant further to *C. papaya*. *Paracoccus marginatus* has been successfully managed by implementing classical biological control measures and fortuitous introductions in all of the countries where it had invaded. Management of *P. marginatus* can be cited as a highly successful example of classical biological control. This strategy became effective in its non-native regions because it was timely and several organizations worked together, with extensive cooperation among scientists, government agencies, and farmers. In India and Sri Lanka, the collaboration enabled the management of *P. marginatus* on papaya and other plants, and hence, farmers and consumers are immensely benefited.

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