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The current status of research on *Solenopsis invicta* Buren (Hymenoptera: Formicidae) in Mainland China

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ABSTRACT. Since the Red Imported Fire Ant *Solenopsis invicta* was found in late 2004 in Mainland China, researchers have paid much attention to this new invasive species. Here we summarise a series of studies on this serious invasive pest, including research on reproductive biology and ecology, ecosystem impacts, quarantine techniques, potential distribution and risk of spread, besides monitoring and management techniques. To date, *S. invicta* has been found in five provinces in South China and has the potential to spread further north, not only by natural dispersal but also by human transportation. The total *S. invicta* population increases greatly in spring and autumn, and causes serious ecological impacts because of its high population density in South China. Besides quarantine techniques intended to prevent the fire ant from further dispersal, chemical control has been the main management method until a more effective biological control agent is found. In some areas control strategies have achieved promising results.

Keywords: Review, population ecology, biodiversity impact, quarantine techniques, management

INTRODUCTION

The Red Imported Fire Ant (RIFA), *Solenopsis invicta* Buren, is an important invasive species. In around the 1930s it was first introduced from South America into the United States (Vinson & Sorensen 1986), where it now inhabits more than 1.3 million km^2 and is responsible for many economic, agricultural and ecological problems (Williams *et al*. 2001). More recently, *S. invicta* was detected in Australia and New Zealand in 2001 (Moloney & Vanderwoude 2002; Bissmire 2006), Taiwan in 2003 (Zhang *et al*. 2007), and Mainland China in 2004 (Zeng *et al*. 2005b). In South China *S. invicta* has spread rapidly, and it is found in several provinces, Guangdong, Guangxi, Hunan, Fujian and Jiangxi, occupying at least 71 km^2 (Zhang *et al*. 2007).

Since its detection in Mainland China, there has been much research into all aspects of *S. invicta* biology, ecology, genetics and control. Here we summarise this research to provide a comprehensive overview of the status of *S. invicta* in China, and the prospects for its effective management.

Social form

Solenopsis invicta is a eusocial insect with two social types, monogyne (having a single queen within a colony) and polygyne (multiple queens) (Vinson 1997). These two social forms have distinct differences in their biology and dispersal abilities (Keller & Ross 1993; Kintz-Early *et al*. 2003). In the first study in Mainland China, Zeng *et al*. (2005a) investigated the distance between *S. invicta* nests, the number of queens in one nest, and defensive behaviour. They concluded that China predominantly had polygyne colonies, which possibly arose from monogyne colonies. Further detailed research in some localities (Shao *et al*. 2008) found that the ratio of polygynous to monogynous colonies was 4:1.

The origin of *S. invicta* in China

To obtain a full picture of the historical process of RIFA invasion, the occurrence within the population of variable genetic markers is helpful (Shoemaker *et al.* 2003). He *et al.* (2006) found that three haplotypes of mitochondrial cytochrome oxidase I (CO I) were present in 13 RIFA populations in recently invaded areas in Mainland China, all of which were known only from populations in Argentina (Shoemaker *et al*. 2003), suggesting introduction from South America (He *et al*. 2006; Xiong 2007). However, specimens from Wuchuan, Guangdong province, where *S. invicta* was first found, were reported to have a 100% homology with *S. invicta* in Florida, USA (Zeng *et al*. 2005b). Recently, Ascunce *et al.* (2011) and Yang *et al.* (2012) have suggested that the population of RIFA in China is from southern USA only, after testing genetic variation at a diverse set of molecular markers. These results indicate that unravelling the origin of RIFA in China is a complex process, and far more sampling is needed for comprehensive analysis.

Range expansion

Although it was first found in 2004, it has been speculated that *S. invicta* had already inhabited Mainland China for about ten years, and Shenzhen may have been the first place where RIFA occurred (Lu *et al.* 2008b); according to He *et al*. (2006) they probably invaded via Hong Kong, whereas Xiong (2007) argued that *S. invicta* arrived directly from the New World. It is clear that *S. invicta* has dispersed to new regions via both human transportation and self-dispersal (Zeng *et al*. 2005a). Long-distance dispersal occurred through the transportation of waste plastics, tires, turf, saplings and dairy cow fodder. More localised dispersal occurred not only via self-dispersal, by nuptial flights and rafting in floods, but also by manure transport (Lu *et al.* 2008a). Natural expansion has been found to occur at 188 m per year along a stream ecosystem (Xu *et al.* 2006b), and about 80 km per year via human-assisted transport (Lu *et al*. 2008a).

General biology

Population and breeding peaks in China occur in spring and autumn (Xu *et al.* 2009d), and a strong sex-ratio bias when producing alates has been observed in south China (Ye *et al.* 2010). Colonies were inclined to produce more males, but the investment ratio between males and females had no significant difference, while the ratio of females to males changed seasonally (Ye *et al.* 2011a, b). Foraging activity of *S. invicta* has been found to have more than two peaks through the year (Li *et al.* 2008; Jiang *et al.* 2011) in south China, and daily foraging activity and number of foraging workers varies among seasons (Chen *et al.* 2010); however, nuptial flights can occur throughout the year (Xu *et al.* 2009b). Xu et al. (2009d) reported it was climate rather than habitat that had a major effect on colony dynamics.

Owing to its aggressive behaviour and venom, *S. invicta* can easily gain territory and occupy food resources (Tschinkel *et al.* 1995). When a mound is disturbed, RIFA immediately workers rush from their nest, and their numbers were found to peak in 60-90 seconds, and return inside within another 20-60 seconds (Xu *et al.* 2011). Mound size, colony structure, habitat, temperature, humidity, disturbance degree and pesticides have been found to affect aggressive activity (Gao 2007), but starvation has been found to have no effect (Cao *et al.* 2011).

The spatial distribution of mounds can reveal the activity and behaviour of *S. invicta*. Li *et al.* (2006) found that active mounds were distributed randomly in horizontal space, and active mounds newly founded by the nuptial flights of RIFA were also at random dispersion (Lu *et al.* 2007). However, the spatial distribution of RIFA mounds varies in different habitats. Taking newly invaded areas as an example, *S. invicta* mounds were dispersed quite widely in roadside verges, but randomly on lawns (Xu *et al.* 2010). Sun (2009) suggested the spatial distribution of active mounds was influenced by mound density, the mounds displaying aggregated distribution at high density and random distribution at low density.

The venom of RIFA, which is composed of 95% alkaloids (Obin & Vander Meer 1985), can provoke anaphylaxis in humans. The abundance and composition of alkaloids are correlated not only with worker size and age (Deslippe & Guo 2000), but also with caste (Ma *et al.* 2009). In China four main alkaloids have been found in the venom of workers, whereas only two, cis and trans-2-Methyl-6-n-undecenyl piperidine, have been detected in queens. The venom allergen Sol i 4 of RIFA was successfully cloned and expressed in *Escherichia coli*, and the recombinant protein produced a marked allergenic effect after in rabbits at low doses (Wang 2008, Han *et al*. 2009). These studies have set a firm basis for developing drugs to treat fire ant stings.

Ecological impacts

Solenopsis invicta has had a negative impact on biodiversity in its introduced ranges (Allen *et al.* 1994; Wojcik *et al.* 2001). Lin *et al.* (2006) indicated that 41 species on China's National List of Protected Wildlife are at risk from *S. invicta,* including 22 birds, one amphibian and 18 reptile species. Invasion by *S. invicta* has been found to reduce the diversity and abundance of invertebrate communities in the crowns of litchi trees, on the ground surface and in the soil (Xi *et al.* 2010a). RIFA significantly reduced the occurrence of both lepidopteran larvae and their natural enemies (including the mantids *Hierodula patellifera*, *Tenodera sinensis* and *Creobroter gemmata*, the reduviid bug *Isyndus reticulates*, the lacewing *Chrysopa sinica*, the parasitoid wasp *Anastatus japonicus*, and the spiders *Oxyopes sertatus*, *O. lineatipes*, *Runcinia albostriata* and *Philodromus cespitum*) in the litchi canopy and on ground vegetation (Xi *et al*. 2010a).

In wastelands and lawns, native ant abundance was clearly reduced with *S. invicta* invasion, and the richness of ant species was reduced by 33% and 46% respectively in two different studies (Shen *et al.* 2007; Wu *et al.* 2008). Invasive ants displace native ants by exploitation and aggressive interference (Porter & Savignano 1990). The influence of *S. invicta* was found to be greatest within 5 m of the mound at the early stage of invasion (Wu *et al.* 2009). Its impacts are also density-dependent, i.e. the larger the population, the greater the influence on native ant species, and the quicker ecological displacement occurs (Song *et al.* 2010).

The composition of the existing ant community may also influence invasibility, but this has been little studied to date. In China there is evidence that pygidial gland secretions of *Tapinoma melanocephalum*, a worldwide invasive ant believed to come from Africa or Asia (Wheeler 1960; Wetterer 2009), provide defence against *S. invicta* (Li *et al.* 2008a); *T. melanocephalum* also has different food preferences to *S. invicta* (Zheng & Zhang 2010). In general, to date the relative influence of habitat and species composition has not been differentiated. Lu *et al.* (2012) indicated that the small impact of RIFA on the richness of native ants in litchi orchards may be due to high tree density; so far it is not recorded from dense-canopy forest in China. It may be that keeping or restoring the complexity and diversity of ecosystems, and protecting native ant communities, are important means to limit the impact of the fire ants.

Plant seeds are an important food source for *S. invicta* (Wilson & Olive 1969). One study in southern China found 12% of refuse in their middens to be seeds (Xu *et al.* 2009e). RIFA workers prefer to move and scarify elaiosome-bearing seeds (Zettler *et al.* 2001); after this process the germination rates of *Sesamum indicum* (Sesame), *Ageratum conyzoides* (Goatweed) and *Pennisetum purpureum* (Napier Grass) seed were only 37%, 44% and 50% respectively (Huang *et al.* 2010b). Furthermore, spatial distribution of *A. conyzoides* was influenced by the fire ants: as the density of *A. conyzoides* was significantly higher in the presence of *S. invicta*, we can conclude that the Goatweed benefited from the association (Huang *et al*. 2010b).

RIFA also affect invaded ecosystems by altering relationships among native organisms. RIFA can displace native ants by disrupting the mutualisms between native ants and aphids (Huang *et al.* 2010a). Fire ants can take honeydew produced by the aphid *Monellia caryella* as a source of carbohydrate food, and attack the predators of aphids (Tedders *et al.* 1990; Eubanks 2001). Such food-for-protection mutualisms play an important role in the success of fire ant (*S. invicta*) invasion (Wilder *et al.* 2011). Huang *et al*. (2010a) observed that the abundance of the ladybird *Menochilus sexmaculatus*, which preys on aphids, was reduced by over 90% in the presence of RIFA under laboratory conditions, and the ladybird larvae rarely survived. This is similar to the findings of Kaplan & Eubanks (2002) in American cotton fields. Zhou *et al.* (2012) found *S. invicta* had a strong attraction to the honeydew of the mealybug *Phenacoccus solenopsis*, a new invader in southern China (Wu & Zhang 2009). If the mutualism between *S. invicta* and *P. solenopsis* exists widely, like that between *S. invicta* and *Dysmicoccus morrisoni* (Tedders *et al.* 1990), it may become a big problem in agroecosystems.

Solenopsis invicta also altered the content of organic matter, causing alkali-hydrolysable nitrogen and available phosphorus to decrease, and available potassium and soil acidity to rise, in infested areas in southern China (Xi *et al.* 2010b). These changes in the physical and chemical properties of soil caused by fire ants are likely to exert a great influence on the soil-organism community.

Although RIFA has a serious impact on China ecosystems, its potential beneficial effects, in biological control of other pests, have been explored (Morrill 1977; Sterling 1978; Reilly & Sterling 1983; Lee *et al.* 1990; Zappalà *et al.* 2007). Cao *et al.* (2012) evaluated the possibility of using fire ants as a biological control agent on pupae of the fruitfly *Bactrocera dorsalis*. Fire ant workers preferred to prey on 6^{th}-day *B. dorsalis* pupae, and the predation rate on pupae 4 cm deep in the soil could be as high as 70%.

Quarantine

It is believed that *S. invicta* first reached Mainland China because traditional quarantine management for imported goods was not adequate for current requirements (Huang & Sun 2006). Clearly China requires updated and improved quarantine procedures, not only giving more attention to high-risk goods, but also undertaking proactive surveillance at ports of entry (Zhang *et al.* 2007). The importation of logs, waste paper, and wood packing materials are the perceived modes of greatest risk to the accidental introduction of *S. invicta* into China. Goods originating in USA, Germany and the UK have been found to harbour most *S. invicta* at Chinese ports (Ma *et al.* 2010). It is suggested that Germany and the UK are merely transit stations of the goods, because these countries do not have this species.

Besides visual inspection, baiting was the most labour-efficient method of fire ant detection, but different techniques were required for specific goods (Huang *et al.* 2009b). A combination of sausage bait and visual inspection was found an efficient method for detecting presence on flower seedlings, while honey trapping was better for *Pennisetum purpureum* grass (Huang *et al.* 2009b). For bait, Zhang *et al.* (2007) suggested that a mixture of fish peptone and peanut oil exerts a strong attraction to fire ants, and is thus appropriate for use in quarantine. A bait-based monitoring method was developed to assess the presence of *S. invicta* in marine cargo containers (Fang *et al.* 2011). Future surveillance techniques should not be restricted to the detection of individual ants; Chen (2009) proposed detecting the Cytb gene to identify the presence of *S. invicta* in situations when morphological identification is difficult.

Many studies have investigated methods to kill *S. invicta* within freight. Applying methyl bromide at a rate of 32 g/m^3 for 4 hours, 29 g/m^3 for 6 hours, or 26 g/m^3 for 8 hour could effectively kill all *S. invicta* in full containers (Zhou *et al.* 2011). Beta-cypermethrin, deltamethrin, fenvalerate and abamectin could eradicate all fire ants in flower seedlings, without negative effects on the flowers (Zhan *et al.* 2005). Liquid nitrogen can be used as a quarantine treatment for *P. purpureum* grass without any negative impact on the animals that feed on it (Huang *et al.* 2009a). Li (2009) indicated a one-in-30,000-part dilution of 40% chlorpyrifos and 2.0% abamectin killed all fire ant workers in turf. These two pesticides can be used for turf quarantine before turf is planted in parks and playgrounds.

Potential distribution in China

Temperature and rainfall are key factors determining the geographical distribution and expansion of *S. invicta* (Korzukhin *et al.* 2001; Morrison *et al.* 2004). An extreme low-temperature isotherm of -17.8^{o}C has been used to estimate the limit of fire ant distribution (Killion & Grant 1995). In China, all models have indicated that all areas south of the Yangtze River are suitable habitats for *S. invicta*. However, the potential northern boundary of natural expansion for fire ants is much less clear (Xue *et al.* 2005;

Zhou 2005; Chen *et al.* 2006; Du *et al.* 2007). Xue *et al*. (2005) argued that the northern limit of RIFA invasion would be to the south of Shandong, Tianjin, Hebei and Shanxi Provinces. However, Xiong (2007) suggested that Jiangsu Province is the transitional zone between suitable and unsuitable areas, and both Du *et al*. (2007) and Shen *et al.* (2008) indicated that the northern limit is in the north of Anhui and Jiangsu Provinces.

The temperature limits and drought tolerance of *S. invicta* may be modified by pre-acclimation (Xu *et al.* 2009a, 2009c) which will ultimately increase its potential range. Meanwhile Korzukhin *et al*. (2001) predicted that the RIFA-inhabitable area in the eastern USA will expand over the next century because of climate change. Yu *et al.* (2011) indicated that the warming trend has been significant in the past 20 years throughout China. *Solenopsis invicta* will also potentially invade further north in China as temperature rises, but more work must be undertaken in this field to make reliable predictions.

Risk assessment

In China *S. invicta* is considered a high-risk pest (Zheng & Zhao 2005; Huang & Huang 2010). Because of the diversity of ecosystems and climates, the invasion risk and severity vary among provinces. For example, *S. invicta* is considered a pest of high risk in Guangxi and Fujian Provinces (Hu 2008; Deng 2011) but of lower risk in Jiangsu Province because of abiotic unsuitability (Xiong 2007).

MANAGEMENT

Survey and monitoring methods for the occurrence of RIFA include public questionnaires, visual assessments, disturbing nest mounds, and sampling by means of traps and baits (Zeng *et al.* 2005a). The use of baits has proven to be the most reliable method (Huang *et al.* 2007a), and baits containing lipids work best (Xu *et al.* 2006a). In particular, *S. invicta* is readily attracted to sausage meat (Zhong *et al.* 2009). The preferred practice is a bait mixture, especially sausage and honey or pilchard and honey, which can also be used to investigate native ant communities (Song *et al.* 2007). Trials of bait traps have shown that a trap composed of a 30 ml plastic vial and a 5 mm-thick sausage works efficiently for fire ant field investigations (Huang *et al.* 2007a).

Globally, control treatments for *S. invicta* include chemical, biological and physical control, with chemicals the most common method (Williams *et al.* 2001). Chemical applications mainly include individual mound treatment and toxic bait. In China, control efficacy of numerous active constituents, namely flursulamid, spinosad, fipronil, sulfluramid, pyriproxyfen, N-butyl perfluoro octane sulfonamide bait, abamectin and chlorpyrifos, have been evaluated both in the laboratory and in the field (Jiang 2008). Shen *et al.* (2008) revealed that the half-life of flursulamid in soil was less than 10 days, suggesting it can be used as an environmental-friendly chemical control method. Spinosad is also a suitable insecticide for use against RIFA because of its remarkable transferring activity within a colony; 54 mg/kg of spinosad caused mortality of 65% within 8 days (Zeng *et al.* 2006). A study on α-terthienyl, a photo-activated chemical, found knock-down rates of RIFA treated with 100 μg ml^{-1} to be over 90% when the treated workers were exposed to Ultraviolet Radiation A for 90 minutes (Liu *et al.* 2011). Pesticides derived from plants were also studied for controlling fire ants in China. *Capsicum annuum* (Sweet Pepper) oil strongly repelled *S. invicta* workers, showing >90% repellency at a concentration of 1000 μl/ml under laboratory conditions (Wang *et al.* 2012a). Zhong *et al.* (2008) reported that an ethanol extract of the shrub *Lantana camara* had a toxic effect on *S. invicta*. In one indoor experiment, 100% of fire ant workers were killed within five days. Another study found *Derris hancei* root powder mixture eliminated 95% of fire ant nests within 21 days (Tian *et al.* 2010).

Toxic bait can be an effective control measure for fire ants (Lofgren & Weidhaas 1972), but moist conditions and rainfall can decrease the efficacy of baits (Kafle *et al.* 2009). The humid and rainy spring in southern China adds to the difficulties of using baits to control fire ants. Wang et al. (2012b) indicated that moist soil conditions can enhance the toxicity of fipronil powder against *S. invicta.* In addition, the mortality rate of workers was significantly higher when the relative soil water content was 90% than when it was 10% or 50%. Further studies could focus on combined effects of powder and fungi in moist conditions to improve the control effect on fire ant in rainy season.

Some work has also been done on the pesticide susceptibility of different RIFA castes and the mode of action of pesticides against them (e.g. Miao *et al.* 2009). Insensitivity of larval ants to insecticides has been attributed to the strong activity of metabolic enzymes in larvae (Yan *et al.* 2011).

The absence of native natural enemies partly contributes to the success of *S. invicta* in newly invaded areas (Yang *et al.* 2010). Studies on biological control of fire ants have been ongoing for many years in the USA, and current research focuses on phorid flies and microsporidia, which are specific natural enemies of RIFA in South America (Williams *et al.* 2003; Williams & DeShazo 2004). Many Chinese native soil fungi have been evaluated for *S. invicta* control in the laboratory. A local strain of the widespread *Paecilomyces lilacinus* was isolated from fire ant workers collected from Guangdong province, and resulted in the death of 71% of *S. invicta* workers within 15 days of treatment, at 1×10^8 conidia/ml (Liu *et al.* 2010). Li *et al.* (2007) investigated the virulence of five strains of another fungus, *Matarhizium anisopliae*, and found three of these could cause 90% RIFA mortality. The toxicity of four strains of *Beauveria bassiana* were evaluated, and an engineered strain had higher virulence on RIFA workers than other strains; however, taking both the time and concentration effect into consideration, the strain 5974 provided by the US Department of Agriculture was found the most promising strain for further study to control *S. invicta* (Yang *et al.* 2009). Studies on *B. bassiana* pathogenesis showed that most conidia were deposited on RIFA intersegmental membranes, setae, cuticle cavities and rugose regions of the cuticle and tibiae, and the first penetration of germinated conidia occurred at 18 h after inoculation (Wang *et al.* 2010). After infection, the *B. bassiana* caused the protein content in different developmental stages of *S. invicta* to decline sharply, while the activities of superoxide dismutase, catalase peroxidase, carboxylesterase, and acetylcholinesterase in infected workers also decreased. Fan *et al.* (2012) presented a method to increase the virulence of *B. bassiana* towards fire ants by expressing fire ant pyrokinin beta-neuropeptide in workers. The strain of *B. bassiana* was six times more virulent than before and had no virulence towards the non-target insects tested. This research provided a good basis for enhancing the efficiency of controlling the species using entomopathogenic fungi.

The sensitivity of newly-mated RIFA queens to the entomopathogenic nematodes *Steinernema carpocapsae* (strain Aii) and *S. scapterisci* was also evaluated. The mortality of queens was nearly 100% after six days, when 19,400 juvenile nematodes were added per individual queen in a petri dish (Zhang *et al.* 2010); however, the presence of workers greatly reduced this efficacy, and mortality of queens infected after six days ranged from 90% to 37% when the queen was accompanied by 6 to 100 workers respectively (Zhang *et al.* 2010). This result is consistent with the observations of Drees *et al.* (1992), showing the RIFA workers can protect the colony from nematodes.

To understand their ability to find fire ant prey, the ultrastructure of the antennal sensilla on female decapitating phorid flies was investigated, in nine species collected from North America and Brazil: *Pseudacteon crawfordi*, *P. cultellatus*, *P. curvatus*, *P. litoralis*, *P. obtusus*, *P. pradei*, *P. solenopsidi*, *P. tricuspis* and *P. wasmanni* (Li 2010). This was the first time the location of the antennal sensilla had been observed, in all species except *P. tricuspis* (Chen & Fadamiro 2007). All sensilla, including the sensilla trichodea, sensilla basiconica, sensilla coeloconica and sensilla chaetica, were located on the flagellum of the adult antenna of *Pseudacteon* spp. Sensilla trichodea and sensilla basiconica were shared by all species. *Pseudacteon curvatus* and *P. solenopsidi* did not have sensilla coeloconica, and sensilla chaetica were found in only four species: *P. cultellatus*, *P. obtusus*, *P. pradei* and *P. solenopsis*. Sharma *et al.* (2011) reported that *P. tricuspis* located fire ants by their alarm pheromones. The study by Li (2010) will be useful in understanding the host location mechanisms of decapitating phorid fly species.

A two-step method has generally been employed to deal with *S. invicta*: first baits were broadcasted in a large area, then contact insecticides were used to deal with the remnants of ant mounds individually (Drees *et al.* 2000). Huang *et al.* (2007b) developed the following method for controlling RIFA in a given area. Applying toxic baits in a large area, they meanwhile treated ant nests seen, first using contact insecticides, then employing chemicals in blocks where the fire ants were still serious. This method was employed twice in one year in an industrial district of Shenzhen, and the number of active mounds, and quantity of workers, were reduced by 94% and 97% respectively. Huang *et al.* (2009a) suggested that post-treatment assessments for fire ant insecticides in infested areas should include the number of active mounds, the number of workers and the colony social structure after pesticide application.

The US Department of Agriculture's Agricultural Research Service also recently initiated an integrated pest management (IPM) project against RIFA, using chemical baits in conjunction with biological agents on a large scale; such IPM projects can reduce the amount of pesticides needed and thus reduce damage to the environment (Vogt *et al.* 2003; Williams & DeShazo 2004).

SUMMARY

In conclusion, the Red Imported Fire Ant has been studied extensively in China over the last several years. Current distribution and occurrence status of *S. invicta* in China have been explored. Besides its dispersal trends, the abundance patterns and aspects of the biology of *S. invicta* have also been investigated, which have showed its high densities and serious impacts on ecosystems. Researchers have made great efforts to study control techniques for RIFA, though quarantine technologies were considered paramount to prevent further dispersal. The Government's stricter quarantine strategies are intended to control the dispersal of RIFA and the invasion of other exotic ants like the Argentine Ant *Linepithema humile*. Chemical control is the main management method until more effective biological control agents are found. Considering its extensive occurrence and the apparent impossibility of eradication, effective biological control agents are needed for future management, along with the application of comprehensive IPM measures.

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