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Biological Control with *Trichogramma* in China: History, Present Status and Perspectives

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Abstract

Trichogramma species make up one of the most commonly used groups of natural enemies for biological control programs worldwide. Given the major successes in using *Trichogramma* to control economically important lepidopterous pests on agricultural crops in China, the biology and ecology of these wasps have been intensively studied to identify traits that contribute to successful biological control. Since the 1960s, improved mass production of *Trichogramma* and better augmentative release methods to suppress agricultural pests have been achieved. We review the history of research and development; current knowledge on biodiversity and bio-ecology of the species used; and achievements in mass-rearing methods, release strategies, and current large-scale applications in China. In addition, we discuss potential issues and challenges for *Trichogramma* research and applications in the future.

1. INTRODUCTION

Factitious host: alternative host species enabling production of large numbers of parasitoids under laboratory conditions, notably for mass rearing in biological control

Mass rearing: industrialized rearing process that is largely mechanized and/or automated, enabling production of large quantities of insects, e.g., *Trichogramma*, in a cost-effective way

Biological control methods have been utilized worldwide for more than a century, providing sustainable control of multiple major agricultural pests (33). Egg parasitoids in the genus *Trichogramma* have been used successfully in various parts of the world, mostly through inundative releases (81). While the use of *Trichogramma* has been at low levels in some places (e.g., <3% of maize has been protected by *Trichogramma* since the early 2000s in Europe) (21; N. Desneux, personal observation), in the past decades, research and industrial-scale developments in China have achieved effective wide-scale use (35, 36, 116, 138). In northeastern China, the area of maize relying on *Trichogramma* releases for control of corn borers jumped from 600,000 to 5,500,000 ha during 2005–2015, accounting for 35% of the area under corn cultivation in this most important corn production region in China (35, 138). The use of *Trichogramma* is well industrialized across the country and relies on mechanized processes, complex technology to manipulate diapause, optimal use of factitious hosts, genetic tools, and novel application methods (48, 84, 121, 138, 140). In this article, we review practical achievements and knowledge gained through development of *Trichogramma*-based biological control programs in China. In reviewing the topic, we highlight the factors that enabled successful wide-scale use of *Trichogramma*, which we believe may prompt more implementation in developing countries and renewed interest about *Trichogramma*-based methods in industrialized countries.

2. HISTORY OF RESEARCH AND DEVELOPMENT

Seminal studies on *Trichogramma* in China started in the late 1930s (134); entomologists of the Insect Bureau of Zhejiang Province studied the bio-ecology of parasitoids of eggs of *Dendrolimus punctatus* on pine trees and *Chilo venosatus* on sugarcane. Possible applications for sugarcane borer control were first tested in 1936 in Guangdong Province (109). However, economic and political constraints during the 1930s and 1940s (notably the war against Japanese invasion from 1931–1945 and the civil war from 1945–1949) strongly limited research into developing *Trichogramma* as biological control agents.

The end of the civil war in 1949 enabled a resumption of research and development (R&D) with *Trichogramma*, notably for control of sugarcane borers in Guangdong and Guangxi Provinces. A mass-rearing method relying on *Samia cynthia ricini* as a factitious host was developed during the 1950s and 1960s (58, 73) and enabled the establishment of the first mass-rearing facility in Guangdong in 1958 (134). During that time, the focus was primarily on optimizing mass-rearing methods, and various factitious hosts were soon identified, e.g., *Antheraea pernyi* eggs for *Trichogramma dendrolimi* and *Trichogramma chilonis* and *Corcyra cephalonica* eggs for *Trichogramma japonicum* (73). Inundative releases of *T. chilonis* against sugarcane borers began with only 600 ha treated but increased to 50,000 ha treated/year in the early 1970s in Guangdong and Guangxi owing to facilities for these releases being established at various levels (e.g., county and village). Simultaneous to the development of biological control against sugarcane borers, R&D was implemented and facilities were created targeting corn borers in northern and southern China, as well as targeting *Helicoverpa armigera* in cotton in Xinjiang (73) (**Figure 1**). Limited governmental support slowed further developments in the early 1980s (scientists focused mostly on mass-rearing optimization), and *T. dendrolimi*–protected maize area peaked at 530,000 ha/year in the early 1990s.

Effective industrialization of *Trichogramma* started by the late 1990s, with more candidates identified, more factories built, and routine support from central and local Chinese authorities (27 *Trichogramma* projects have been funded since the 1990s) (125). Funds were largely directed to mass production in northeast China (a major maize area); US$10.3 million were provided to the Jilin Academy of Agricultural Sciences in 1999 to build a factory with the aim of protecting

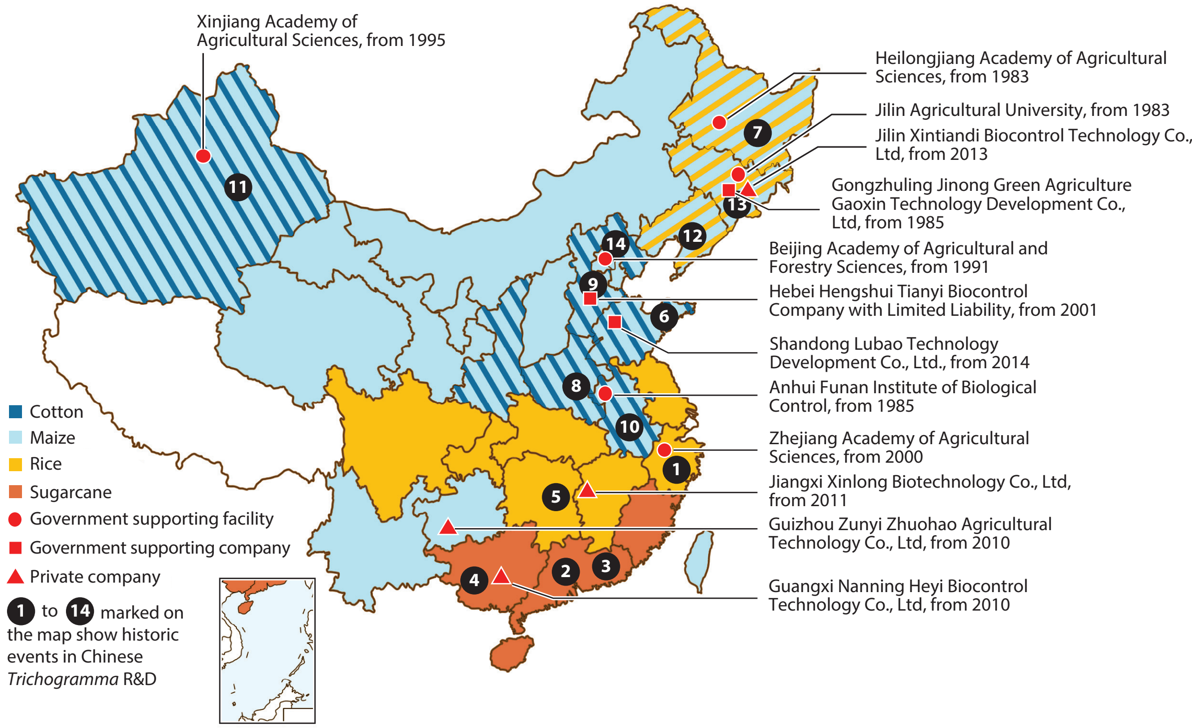

Figure 1

Distribution of *Trichogramma* facilities in China; details are provided with arrows for those still operating, and numbers indicate locations of historic facilities no longer operating (96, 134, 138). The different colors in each of the provinces indicate the main crop(s) in which *Trichogramma* are released. Red circles, squares, and triangles indicate facility type. (*Location 1*) In 1930–1937, the Insect Bureau of Zhejiang Province evaluated the biological and ecological characteristics of *Trichogramma* wasps. (*Location 2*) In 1958, South China Agricultural University established the first *Trichogramma* mass-rearing station. (*Location 3*) In 1961, the Guangdong Committee on Science and Technology evaluated the field applications of *Trichogramma* wasps in Guangdong province. (*Location 4*) In 1954–1955, the Guangxi Academy of Agricultural Sciences started to manage sugarcane borer and *Ostrinia furnacalis* with mass-reared *Trichogramma*. (*Location 5*) In 1955–1956, the Hunan Academy of Agricultural Sciences started to control *Chilo suppressalis*. (*Location 6*) In 1957–1960, the Shandong Academy of Agricultural Sciences started to control *O. furnacalis*. (*Location 7*) In 1961, the Heilongjiang Academy of Agricultural Sciences started to control *O. furnacalis*. (*Location 8*) In 1961, the Henan Academy of Agricultural Sciences started to control *O. furnacalis*. (*Location 9*) In 1964, the Hebei Academy of Agricultural Sciences started to control *O. furnacalis*. (*Location 10*) In 1966, the Anhui Agricultural Technology Extension Station started to control *O. furnacalis*. (*Location 11*) In 1961, the Xinjiang Academy of Agricultural Sciences started to control *Helicoverpa armigera*. (*Location 12*) In 1972, the Liaoniang Academy of Agricultural Sciences started to control *O. furnacalis*. (*Location 13*) In 1974, the Jilin Academy of Agricultural Sciences started to control *O. furnacalis*, and in 2014, it started to control *C. suppressalis*. (*Location 14*) In 1977, the Beijing Miyun Plant Protection Station and Beijing Academy of Agricultural and Forestry Sciences started to control *O. furnacalis*.

1,333,000 ha of maize yearly (¥ values have been converted to US$ throughout, using ¥7:US$1 as the exchange rate between the two currencies). The National Development and Reform Commission allocated US$5.7 million to build another facility at the Hebei Academy of Agricultural Sciences. By 2012, in Jilin province, the yearly budget allocated to protect 2,000,000 ha of maize through *T. dendrolimi* mass production was US$11.4 million. A reduction of funds allocated to *Trichogramma*-based biological control programs targeting maize induced a shift from maize to rice in terms of *Trichogramma* usage and associated R&D. Since 2018, decreasing governmental support toward maize has to some extent been compensated for by increasing involvement of private companies in *Trichogramma* production (e.g., in Jilin province) (L.S. Zang, unpublished observations).

Superparasitism: parasitism in which a given host is parasitized more than once by a single species of parasitoid

3. BIODIVERSITY

There are approximately 620 species described worldwide in the order of Trichogrammatidae, with 219 recorded in China (**Supplemental Table 1**) (72, 94). In the framework of the development of *Trichogramma* parasitoid as key biological control tools in China, Pang & Chen (70) described taxonomic characteristics of major *Trichogramma* species, including *T. chilonis*, *T. dendrolimi*, and *T. japonicum*. They identified six new species, *Trichogramma closterae*, *Trichogramma sericini*, *Trichogramma ivelae*, *Trichogramma lingulatum*, *Trichogramma ostriniae*, and *Trichogramma leucaniae*, and provided first records of *Trichogramma euproctidis* and *Trichogramma raoi* presence in China. Extensive surveys have been running since the late 1990s in Hebei, Shandong, Henan, Fujian, Hainan, and Xinjiang (51, 87, 146) aiming to detect candidates matching the various crops and ecozones targeted in China. These surveys identified 24 species as potential biological control agents (96), and 10 of these were further developed for field applications (**Supplemental Table 2**), including *T. dendrolimi* (maize, rice, cotton), *T. japonicum* (rice), *T. chilonis* (sugarcane, rice, cotton), *T. ostriniae* (maize), and *T. leucaniae* (soybean); together, the 24 species can target over 120 pests in China (50, 94). Characterizing wild *Trichogramma* species helps identify species for use in new biological control programs (e.g., against new invasive pests), as well as for use in biological control conservation programs. For example, up to 40% parasitism by local *Trichogramma* species has been observed on *Argyroploce schistaceana* (in Yunnan) and *H. armigera* (in northern China) in sugarcane and cotton fields, respectively (47, 52).

Multiple molecular-based identification methods (based on RAPD-PCR, PCR-RFLP, or species-specific PCR primers) have been developed in China, enabling rapid and reliable *Trichogramma* identification, notably when using mtDNA or rDNA-ITS2 (24, 25, 48). More recently, identifications have been carried out using high-resolution melt analysis (based on real-time PCR), a low-cost and relatively easy genetic typing technology (129), and Chinese resources have been redirected toward molecular-based characterization methods over regular morphologically based taxonomy methods. However, relying mostly on molecular methods might indirectly slow down the identification of new wild species as biological control candidates (as fewer resources are allocated to explore wild *Trichogramma* diversity and describe new species).

4. BIO-ECOLOGY

By the 1970s, studies in China had already focused on *Trichogramma* bio-ecology, but research expanded strongly through support from the Chinese government in the 1980s (29, 30, 61, 74). While most efforts focused on applied aspects for supporting *Trichogramma* development as biological control tools, some scientists studied key traits of Chinese species (host location, fecundity, thelytokous parthenogenesis, and superparasitism). The increased basic knowledge of *Trichogramma* bio-ecology provided useful information for improving utilization of major *Trichogramma* species in mass rearing and release programs in China.

4.1. Host Location

Egg parasitoids respond to semiochemicals from the host plants, host adults, and host-associated products to locate eggs (22), and at least 13 sensilla types (on antennae, eyes, mouthparts, wings, legs, and external genitalia) have been described in *Trichogramma* females (143). Long-range location of hosts is primarily based on plant volatiles for most species, e.g., mungbean for *T. ostriniae* (117) and masson pine for *T. dendrolimi* (112), and such odors stimulate female parasitism activity (149). Colors can be used for short-range foraging; for example, *T. ostriniae* showed host egg color preference in which yellow > white > green > black (60). Stimuli from other host life stages play roles in short-range host location and for actual parasitism; *T. japonicum* and *T. ostriniae* use sex pheromones from adults to locate *Chilo suppressalis* and *Ostrinia furnacalis* eggs, respectively (3, 4), and abdominal scales of hosts (*H. armigera*, *O. furnacalis*, and *Plutella xylostella*) can act as kairomones (86, 114). Associative learning of odor(s) during oviposition increased speed of host location and reduced handling time (42).

Thelytoky: parthenogenesis in which females are produced by unfertilized eggs via various mechanisms, e.g., owing to *Wolbachia* in *Trichogramma* parasitoids

Multiparasitism: parasitism in which a given host is parasitized by more than one species of parasitoid

4.2. Fecundity

Trichogramma parasitoids are haplo-diploid, with diploid females derived from fertilized eggs and haploid males from unfertilized eggs, and the female adult wasps possess the ability to exert control on the sex of their progeny at oviposition (via muscle contraction involved in releasing sperm and inducing visible abdominal movements during oviposition) (30). Most Chinese studies have focused on evaluating parasitoid fecundity as affected by host egg characteristics (being generalists, *Trichogramma* show adaptive strategies to cope with different host species). Host eggs often vary in size and chorion thickness (30, 38, 142), which could impact parasitoid fecundity (e.g., increased oviposition duration); for example, *Trichogramma confusum* fecundity on *C. cephalonica* and *A. pernyi* eggs (egg chorion thickness of 4.2 and 48.0 μm, respectively) is 147 and 47, respectively (142). Host egg size affects sex allocation by females at oviposition and modulates production of offspring; for example, *T. dendrolimi* can oviposit, on average, 1, 19, and 77 eggs in *C. cephalonica* (egg length 0.5 mm), *D. punctatus* (egg length 1.5 mm), and *A. pernyi* eggs (egg length 3.0 mm), respectively (30).

4.3. *Wolbachia*-Induced Parthenogenesis

Wolbachia is an endobacteria that can induce thelytoky in parasitoids (37). It is widely distributed in *Trichogramma* species in China, e.g., in various *T. chilonis*, *T. dendrolimi*, *Trichogramma evanescens*, and *T. ostriniae* populations (85, 97, 103, 147). Following seminal work documenting effective transmission between *Trichogramma* species through microinjection (27), Chinese scientists demonstrated possible horizontal transmission via multiparasitism of a *Wolbachia*-bearing species together with *Wolbachia*-free species (68). Studies demonstrated that, despite *Wolbachia* enabling an increase in female ratio of offspring, the endobacterium negatively affects parasitoid fitness through decreased fecundity, longevity, and offspring survival, as well as through altered behavioral patterns (54, 69, 126). These results highlighted the need to discard *Wolbachia*-contaminated *Trichogramma* strains when developing industrial biological control approaches.

4.4. Superparasitism and Multiparasitism

Superparasitism and multiparasitism occur when females parasitize an already-parasitized host (38, 46, 92, 93). In *Trichogramma*, this happens mostly in naive females, and oviposition-experienced individuals usually avoid self- and conspecific superparasitism, as well as multiparasitism (29, 98). The impact of such experience could be modulated by host egg availability and competitor species; experienced *T. chilonis* engaged in more superparasitism than multiparasitism (with *Trichogramma bactrae*) when females were provided only with parasitized host eggs (98). The impact on parasitoid fitness has been extensively documented for parasitoid species used in China; negative effects on progeny include slower development (with an extreme superparasitism rate causing development failure) (29); reduced size, longevity, fecundity, and diapause rate; and increased sex ratio (44, 53, 144, 145). Studies on mass rearing identified factors that could be manipulated to lower superparasitism, such as female:host egg ratio and exposure time (29); the optimal ratio of *T. chilonis* and *T. japonicum* female:*C. cephalonia* eggs ranged from 1:20 to 1:10 for a 24-h exposure time (29, 53). By contrast, the optimal ratio was much higher (2:1–3:1) for *T. dendrolimi* on *A. pernyi* eggs (36).

Host suitability: capacity a parasitoid species to successfully develop offspring when parasitizing a given host species

5. APPLIED RESEARCH

The development of *Trichogramma*-based biological control programs prompted thorough evaluation of characteristics linked to efficacy of key candidate species (e.g., *T. dendrolimi*, *T. japonicum*, *T. ostriniae*, and *T. chilonis*) and the feasibility of using them widely (138). Work has focused on assessing pest and factitious host suitability, adult dispersal, and variability among parasitoid strains (20, 34, 36, 90, 91). By contrast, no studies have addressed potential risk(s) associated with annual mass releases of *Trichogramma* across the country, despite potential concerns raised elsewhere (67); for example, *Trichogramma pretiosum* superseded native *Trichogramma* species in many habitats after its initial release in Australia (13). *Trichogramma* parasitoids have been considered safe owing to a lack of negative effects in European field studies (1, 41), as well as because field-collected native species are used for biocontrol programs. Despite this, risk assessment studies should ideally be undertaken to ensure that *Trichogramma* do not induce long-term disturbance in nontarget habitats commonly bordering fields (e.g., woodlands and wild brush lands).

5.1. Host Suitability

Accurately estimating host suitability is key for successful biological control programs, both for mass rearing and efficacy (33, 81), and many studies have evaluated the suitability of agricultural pests and factitious hosts for *Trichogramma* (19, 34, 127, 137, 138).

Eggs of the rice pest *C. suppressalis* proved suitable for *T. dendrolimi*, *T. japonicum*, and *T. chilonis* but not for *T. ostriniae* (which had low parasitism rates and rates of progeny survival) (137). *T. ostriniae* exhibited its best performance on eggs of the maize pest *O. furnacalis*. Interestingly, this host is actually suboptimal for *T. dendrolimi* (116, 145), but its suitability can be enhanced via prior parasitism by irradiated *T. ostriniae* females, with emergence jumping from 6.5% to 72% in individuals that were previously stung by infertile females (152), suggesting that *T. dendrolimi* larvae are not limited by host resources, but instead probably by maladapted venom injected by females during oviposition.

Trichogramma females usually prefer parasitizing young host eggs, reducing competition with host embryos (34, 56); for example, parasitism by *T. leucaniae*, *T. chilonis*, *T. japonicum*, and *T. dendrolimi* showed a negative relationship with egg age of *Leguminivora glycinivorella* and *C. suppressalis* (83, 137). However, exceptions exist; for example, *T. leucaniae* showed high fitness independently of *L. glycinivorella* egg age (83), and females could distinguish unfertilized from fertilized eggs, showing preference for and higher performance on the latter (19, 46, 127). Such preference could disappear when females parasitize highly suitable hosts (e.g., *T. ostriniae* on *O. furnacalis* eggs) (46) or be reversed under artificial conditions (e.g., the preference of *T. dendrolimi* for manually extracted *A. pernyi* unfertilized eggs) (111).

5.2. Dispersal Ability

Dispersal ability could modulate a biological control agent's effectiveness (33), and most Chinese studies on this topic are linked to application-related requirements. Active migration after release occurs over short distances (modulated by parasitoid preference for particular habitats), and wind has been reported to be a key driver for *Trichogramma* dispersal (e.g., up to 400 m downwind versus 40 m under regular conditions), although upwind dispersal can occur (41, 150). Dispersal of *T. chilonis* in cotton fields is increased with wind speed, with dispersal being dictated by wind direction at the time of take-off (107), and a breeze enables *T. japonicum* to spread up to 16 m on the day of release in rice paddies (91). Wind speed–modulated *T. dendrolimi* dispersal only occurs during daytime (150), and temperature limits dispersal when it is <20°C or >34°C (90). Besides abiotic factors, habitat complexity could affect *Trichogramma* dispersal; for example, sesame planted in rice field ridges promoted *T. japonicum* dispersal of up to 25 m from sesame flower location (88), presumably owing to improved sugar food resources (89).

5.3. Impact of Abiotic Factors

Abiotic factors impact *Trichogramma*, with temperature and humidity being major influential factors on, notably, longevity, development speed, survival, and fecundity (7, 56, 76, 78, 133). A relative humidity of 75% is optimal for development of many species, and temperatures <15°C or >31°C impair survival and/or parasitism performance (7, 76, 78, 133). Heat stress is particularly detrimental (116), although various strains are adapted to harsh climates (28). Assessment of *Trichogramma* strain effectiveness at various temperatures is needed, as field-based biological control programs often differ in rearing conditions (28). In addition, climate change may affect *Trichogramma* effectiveness; parasitism by various *Trichogramma* spp. in maize, rice, and cotton showed negative relationships with daily extreme high temperatures (119). Interestingly, plant and/or habitat complexity may mitigate negative abiotic effects (148, 149), notably through providing shelter or extra resources; for example, *T. dendrolimi* survival was higher in alfalfa-covered areas than in those covered by weeds (16).

5.4. Variability Among Strains

In general, populations of a given species were better adapted to climatic conditions from their collection area (28). Northern *T. dendrolimi* strains showed higher reproduction and survival than southern strains after months of cold storage (79), as well as higher sensitivity to low-temperature diapause induction (55, 136). Southern strains are better able to cope with high temperatures; for example, fitness of southern *T. japonicum* strains is twice that of northern strains under high temperatures (32–36°C) (90), and more adults of southern strains can fly at 34°C (57% versus 20%). However, exceptions occur; for example, northern strains performed better than southern ones on tropical hosts (e.g., *T. dendrolimi* northern strains performed better than southern ones on *C. cephalonica*) (20). Differences occur both in morphological characteristics [e.g., northern *T. dendrolimi* showed longer flagellum setae than did southern individuals (124)] and at the genetic level [mitochondrial DNA COII sequence differences were reported among geographically distinct populations in *T. dendrolimi* and *T. ostriniae* (48, 131)].

6. MASS-REARING SYSTEMS

Mass-rearing systems are crucial for cost efficiency and to enable large-scale use through inundative releases (36, 138). Several stages of the rearing process, e.g., cleaning and drying of host eggs, preparation of egg cards, parasitoid inoculation, and selection–collection of parasitized host eggs (59, 84, 95), has been mechanized and/or automated, and cost efficiency depends on the possibility of using low-cost factitious hosts for rearing the selected *Trichogramma* species. Four key factitious hosts, *A. pernyi*, *C. cephalonica*, *S. cynthia ricini*, and *Sitotroga cerealella*, have been studied in this framework, and *Trichogramma* mass-rearing methods differ mainly in parasitoid female:host egg ratios and cold storage and diapause conditions for short- and long-term storage, respectively (18, 53, 139).

6.1. Factitious Host Eggs

The most successful mass-rearing methods have been developed using host species showing large size eggs. The method using *S. cynthia ricini* eggs (developed in 1952) (58) was superseded in the 1960s by one relying on *A. pernyi* eggs (110). *A. pernyi* is reared on oak trees in northeastern forests (as opposed to *S. cynthia ricini*, which is produced indoors), and yields are higher, up to 260 and 60 *Trichogramma* produced per *A. pernyi* and *S. cynthia ricini* egg, respectively (116). In addition, *A. pernyi* cocoons harvested in fall can be shipped easily and cold stored at −5°C for up to 5 months (138). Using this host has enabled the two leading facilities from Jilin province to produce 400 billion *T. dendrolimi* per year for a cost of US$11.4 million (mean production being 40 billion parasitoids/year in other Chinese facilities) (36, 138). However, mass rearing of *Trichogramma* using *A. pernyi*–based methods face some challenges. When too many parasitoids develop in a single host egg, adults show reduced body size, fitness, and longevity and increased sex ratio (29, 53, 57, 144, 145). Thus, researchers have aimed to identify the optimal parasitoid female:host egg ratios, as well as optimal exposure time. In addition, only *T. dendrolimi* and *T. chilonis* have been mass reared at a commercial scale using this host (32, 138). Interestingly, many other species can reach adulthood inside *A. pernyi* eggs (e.g., *T. ostriniae* and *T. leucaniae*), but they cannot emerge, failing to break through the egg chorion (32, 38, 46). Recently, multiparasitism with *T. dendrolimi* and *T. chilonis* enabled emergence of *T. ostriniae* and *T. leucaniae*, respectively (38, 46), the two latter species using holes made by *T. dendrolimi* and *T. chilonis*; this may open a way to use multiparasitism for mass rearing of high-potential species. Host suitability of *A. pernyi* increases as it is used as the rearing host for more generations; over four generations of rearing, *T. leucaniae* parasitism and emergence rates jumped from 40% and 57% to 87% and 93%, respectively (123).

Small lepidopteran eggs are also used worldwide for *Trichogramma* mass rearing (81). They differ from *A. pernyi* eggs in size and shell thickness; they are useful for rearing species showing a weak ovipositor and/or mouthparts, i.e., species that cannot be reared on large eggs (36, 38, 46). *C. cephalonica* and *S. cerealella* are highly suitable for mass rearing key species such as *T. japonicum* and *T. ostriniae*, respectively (6, 39, 138); the drawback is their high cost for mass rearing, as well as for *Trichogramma* rearing. While *C. cephalonica* was used during the early stage of *Trichogramma* development in China (116), *S. cerealella* was introduced later from Europe (in 2000) to aid in developing mass rearing of economically important species such as *T. ostriniae* (100% of the production). Mass rearing of *C. cephalonica* was developed and optimized from the late 1970s onward (similar methods being implemented on *S. cerealella* after its introduction in China) and included an automatic medium blender and machines for moth and egg collection, egg cleaning, UV-based sterilization, and card production (75, 116). Advances in diet recipes, standardized production, and quality controls were achieved in the 1980s, as well as increasing use of sophisticated machines, further optimizing the entire process (6, 15, 36). Such R&D enables high productivity; for example, 2 billion *T. japonicum* are produced yearly in Jilin production facilities (for a cost of US$0.43 million) (L.S. Zang, unpublished observations).

In addition to lepidopteran eggs, artificial eggs have been developed in China for *Trichogramma* mass rearing. Early studies suggested that insect hemolymph, animal serum, and egg yolk were key components for developing artificial media (120), and an effective artificial egg system was developed for rearing *T. dendrolimi* and *T. chilonis* (31). It relied on concentrated and dried *A. pernyi* tissues, oviposition stimulants, tricosane, and polyvinyl alcohol hydrophilic colloid; using artificial eggs produced 90% parasitism and 75% emergence (31, 141). Fully mechanized production was achieved with mass rearing of *Trichogramm*a in vitro for large-scale biological control (23) in two distinct production lines located in north and south China. However, despite its full mechanization and the possibility of producing parasitoids throughout the year (via long-term storage of artificial media) (57), this method did not prove cost effective (i.e., versus the large egg–based method), and the production lines were discontinued in the early 2000s. Recent research has focused on reducing the costs (replacing insect hemolymph with trehalose) (62) and on possibly adapting this method for *T. ostriniae* mass rearing (49).

Inundative release: release(s) of large numbers of natural enemies to provide biological control of a targeted agricultural or forest pest

6.2. Storage Methods

Relying on cold conditions proved possible only for short-term storage, and duration depended on the factitious host used. Prepupal parasitoids developing in *C. cephalonica* eggs could be stored at 4–10°C for 10–15 days without impairing key biological traits (emergence rate and parasitism capacity) (18). Longer-term cold storage induces negative effects owing to reduced moisture content, dry matter, and pH in host eggs (118). Nonetheless, cold storage of *Trichogramma* developing in *A. pernyi* eggs proved possible for up to 40 days without negative impacts when stored at 2–7°C (43).

Beyond regular cold storage, diapause induction is key for efficient long-term storage of mass-reared *Trichogramma* (139, 140). Diapause occurs at prepupal stages and is regulated by particular temperature and photoperiodic conditions. *T. dendrolimi* can enter diapause both through a two-step temperature change (e.g., 40 h at 26°C followed by 31 d at 10°C) or continuous low temperature (66, 139, 151) and enables storage for up to 4 months without impairing *Trichogramma* traits (151). Host species also affect diapause induction with high diapause rates (up to 98%) in *T. japonicum*, *T. ostriniae*, and *T. dendrolimi* when reared on *S. cerealella* eggs, but these rates are much lower in individuals raised on *C. cephalonica* (13–34%) (45). Diapause rates vary among geographically distinct *Trichogramma* populations (136), so optimal conditions should be identified for each strain.

7. RELEASE STRATEGIES

7.1. Inundative Releases

The inundative release method has been rapidly adopted over the course of *Trichogramma* program development in China; large numbers of parasitoids are released, essentially acting as a biopesticide spray (36). Large-scale inundative release–based biological control programs have been used successfully against the Asian corn borer (ACB) *O. furnacalis*, notably using *T. dendrolimi* in northeastern China. The method is adjusted according to the number of ACB generations occurring in the region. Regions with one generation of ACB receive 225,000 wasps/ha, spread over 15 release sites spaced 20 m apart (112,500 wasps/release, with 5–7 day intervals from one release to the next) (138). The two-generation regions receive 225,000 wasps/ha in the first generation and 75,000–150,000 wasps/ha in the second generation (116). Such inundative releases are possible due to the low cost of *A. pernyi*–based *Trichogramma* production (US$5.8/ha) (138). The method has been continuously optimized, e.g., through developing egg cards and mixing different parasitoid developmental stages, to increase the time span of *Trichogramma* presence during the ACB oviposition period (138).

7.2. Mixed-Species Releases

Mixed-species release: method enabling release of different and complementary species together to increase cost-effectiveness of biological control

Agricultural drones: unmanned aerial vehicles used to help optimize agriculture field task operations, such as spraying pesticides and monitoring or releasing parasitoids

Releasing different species together has been explored to increase the cost effectiveness of biological control. *T. japonicum* is the major parasitoid of *C. suppressalis* on rice in northeastern China, and *T. dendrolimi* is also an effective parasitoid to a lesser extent (127, 137). As the cost of rearing *T. dendrolimi* is only 1/75 of that of rearing *T. japonicum* (which relies on *C. cephalonica* eggs), a mixed-species release method was developed (*T. dendrolimi* reared on *A. pernyi* + *T. japonicum* reared on *C. cephalonica*). The optimal ratio between the two *Trichogramma* species was identified, and the mixed-species release proved both efficient against the pest and much cheaper than *T. japonicum* alone (17, 138).

7.3. Release Tools

Traditional egg cards used for *Trichogramma* releases have major limitations: They are not rain-, enemy-, and sunshine-proof (12, 36), and various capsules have been developed according to crop characteristics and/or environmental conditions. Ball-, bag (triangle)-, and box (square)-shaped capsules are currently used for *Trichogramma* releases in China. The box-shaped capsule was designed based on maize leaf structure and is used for packing *Trichogramma*-parasitized *A. pernyi* eggs provided for ACB control (138). For rice paddy fields, ball-shaped capsules made from biodegradable materials were designed to provide an automatic floating position, enabling parasitoid exit holes to remain above the water surface (26).

Trichogramma manual release proved increasingly expensive and not practical during agricultural peak activity. Unmanned aerial vehicles, such as agricultural drones (ADs), are being deployed in China. These are suitable for complex farmlands with numerous separate plots and small farms (102), and ADs specifically fitted to the needs of *Trichogramma* releases are being developed; for example, AD systems using hex-rotors have been developed in parallel to the design of a specific *Trichogramma* delivery device (121). Such ADs weigh 9 kg when loaded, fly for 20 min at 36 km/h, are Global Positioning System (GPS)-assisted, and can treat 15 ha of rice per flight. In addition, ADs may help expand *Trichogramma* usage; for example, *Trichogramma pintoi* controlled mangrove pests (92% parasitism) successfully during a 500-ha trial relying on a system combining ADs, spherical biological containers, and corresponding dispensers (64).

8. USE OF *TRICHOGRAMMA* IN INTEGRATED PEST MANAGEMENT PROGRAMS

Trichogramma-based methods are a cornerstone of pest management in various regions of China (notably on maize), and multiple studies have evaluated the possibility of including them in integrated pest management (IPM) packages. Studies have focused on possible compatibility with pesticides, entomopathogens, and sex pheromone–based mating disruption methods.

8.1. Pesticides

Insecticides and fungicides proved lethal to key *Trichogramma* species used in China, with the adult stage being the most susceptible (115, 130). Chemical insecticides such as beta-cypermethrin, chlorfenapyr, cypermethrin, and fipronil, together with the biopesticides avermectin and spinosad, were lethal to *T. chilonis*, *T. japonicum*, and *T. ostriniae* (99, 104, 115). By contrast, azadirachtin, *Bacillus thuringiensis* (*Bt*), chlorfluazuron, and tebufenozide appeared to be safer for *Trichogramma* species (99, 115). Insecticides could also impair parasitoid effectiveness through sublethal effects (14); for example, *T. chilonis* fecundity and longevity are reduced by exposure to sublethal concentrations of acetamiprid, avermectin, fipronil, and spinosad (99, 104), and sex pheromone communication and mating behavior are affected by LC_{20} of spinosad and beta-cypermethrin, respectively (100, 101). In contrast, no sublethal effects have been reported following exposure to indoxacarb, *Bt*, beta-cypermethrin, chlorfenapyr, chlorfluazuron, and tebufenozide, and hormesis can even occur, e.g., increased fecundity after exposure to low concentrations of chlorfluazuron and tebufenozide (99, 104). Given the potential hazards posed by pesticides for *Trichogramma* (including biopesticides, e.g., spinosad) (99), their combined use in IPM should be carefully considered.

8.2. Entomopathogens

The use of *Trichogramma* coupled with entomopathogens such as *Bt*, cytoplasmic polyhedrosis virus (CPV), and *Beauveria bassiana* has been suggested to improve IPM (81). Entomopathogens did not impact *Trichogramma* life history traits (9, 65) and proved effective in reaching pests when carried by *Trichogramma* (71, 108). Efficacy of control of ACB and *C. suppressalis* with *Bt*-carrying *T. dendrolimi* and *T. chilonis*, respectively, increased by 10–15% when compared to parasitoids alone (9, 10), and releases of *B. bassiana*–carrying *T. dendrolimi* reduced ACB damage on maize by a further 28% compared to the parasitoid alone (128). Two field trials showed a 23% increase in *D. punctatus* control when *T. dendrolimi* was carrying *D. punctatus wenshansis*–CPV (71).

8.3. Sex Pheromones

Sex pheromone–based mating disruption has been widely used for IPM in China (8), either jointly with *Trichogramma* to maximize control of a pest or in parallel, targeting pest(s) not attacked by released parasitoids. Since *Trichogramma* females preferentially parasitize fertilized host eggs (19, 127), reduction of fertilized host eggs via mating disruption was thought to increase parasitoid effectiveness because relatively more parasitoids would search for attack on these host eggs. However, enhancement of pest control is usually low; for example, control of the soybean pod borer *L. glycinivorella* increased by only 16% when mating disruption was combined with *T. chilonis* release (11). In addition, negative effects occurred; mating disruption reduced parasitism of *C. suppressalis* by *T. japonicum* by up to 50%, and distracted *T. dendrolimi* and *T. ostriniae* from parasitism activity as they aggregated near dispensers in the field (82).

9. FIELD APPLICATIONS

9.1. Maize

ACB is a key maize pest in China, causing up to 30% yield loss due to grain damage when no management is implemented (113). Achievements made in R&D during the 1980s enabled the protection of 0.5 million maize ha/year using *T. dendrolimi*, and governmental investments since 2000 (US$140 million) enabled 5,500,000ha of maize to be protected with *Trichogramma* in 2015 (**Figure 2*a***). Inundative releases of *T. dendrolimi* resulted in over 70% of ACB eggs being parasitized in the first generation, and effective pest control was accomplished (138). Plant protection stations in each province place orders for *Trichogramma* from companies or institutes according to extension plans, and parasitoids are distributed to farmers (through county-level stations). Release timing is determined by ACB monitoring, pupation of overwintered larvae, and detection of adult emergence using sex pheromone traps. Such long-term, large-scale *Trichogramma* releases promoted a decrease in pesticide use while securing or enhancing corn yields, e.g., in Jilin (35) (**Figure 2*b***).

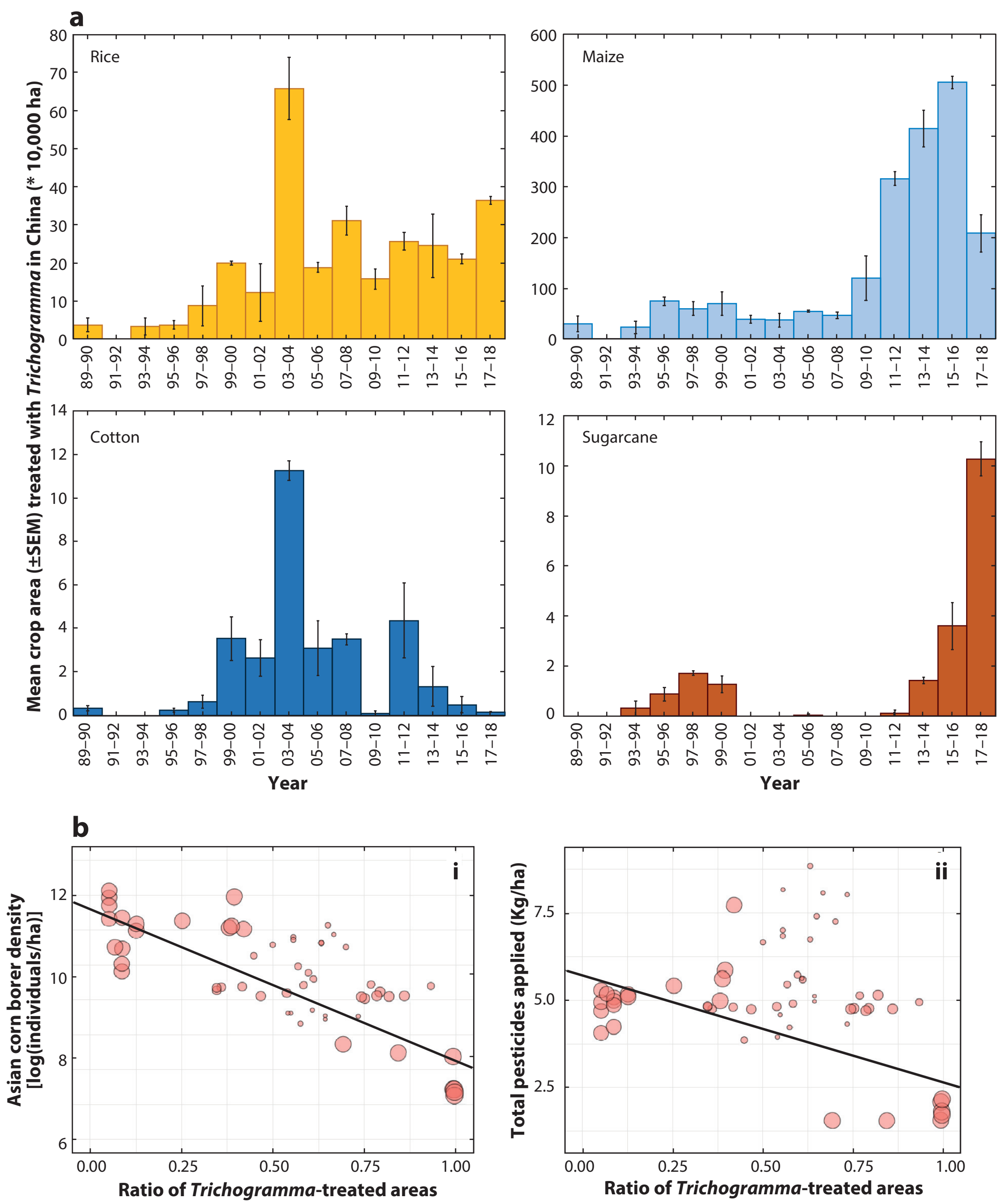

Figure 2

(*a*) Records of inundative *Trichogramma* releases in China from 1989 to 2018 (Ministry of Agriculture of the People's Republic of China). Shown are the two-year mean surfaces in ha (±SEM) where *Trichogramma* were released in four main crops: rice, maize, cotton, and sugarcane. Usage of *Trichogramma* in rice had boomed in 2003–2004 in Hunan and Hubei Provinces (over 410,000 ha) owing to additional funding provided by the local governments. (*b*) Relationships between the ratio of *Trichogramma*-treated maize areas per county in Jilin Province and (*i*) maize corn borer densities in maize fields in the province ($R^2 = 0.69$) and (*ii*) pesticide applications ($R^2 = 0.42$). Each dot shows the data from one county, and different dot sizes indicate weight of each datum according to the maize surface in the respective county (with seven counties surveyed per year during 2000–2015). Panel adapted with permission from Reference 35.

9.2. Rice

C. suppressalis is the major rice pest targeted by *Trichogramma* in China. Biological control has been developed continuously since the 1980s (**Figure 2*a***), relying mainly on *T. japonicum*. The application was not cost-effective when small host eggs were used for mass rearing (138). The area of *Trichogramma*-treated rice has been increasing slowly and steadily; the sudden boom in 2003–2004 occurred due to temporary additional funding provided by some local governments to expand use of *Trichogramma* in regions of rice cultivation, particularly in Hunan Province. Since 2014, effort has been made to improve the system with newly designed ball-shaped release capsules and mixed-species releases. The program entails three timed releases of 150,000 parasitoids/ha (120,000 *T. dendrolimi* and 30,000 *T. japonicum*) spread across 45 sites (at 5–7-d intervals) and enables >80% parasitism (138). As its cost is only US$32/ha, this method has been increasingly used; for example, usage of *Trichogramma* in rice has increased from 1,300 to 73,300 ha in only 5 years (2014–2019) in Jilin.

9.3. Sugarcane

Sugarcane is a major crop in southern China (1,200,000 ha/year), and sugarcane borers such as *Chilo infuscatellus*, *Chilo sacchariphagus*, and *A. schistaceana* (132) have been targeted by *T. chilonis* inundative release since the 1960s (47). While *Trichogramma*-based management implementation in sugarcane struggled for decades, *T. chilonis* has been increasingly released since 2015 (notably in Guangxi), covering approximately 100,000 ha each year. The program involves 5–6 releases of 75,000 parasitoids/ha per release in a year, depending on the abundance of borers, and prevents approximately 20% of yield losses (77).

9.4. Other Crops

Methods of utilizing *Trichogramma* have been developed targeting pests in other agroecosystems, but most have not been implemented for field-level biocontrol. For example, *Trichogramma*-based biological control was suggested for managing *Homoeosoma nebulella* on sunflower (*T. dendrolimi* showed 62% parasitism) (106), *Cydia pomonella* and *Grapholitha molesta* in apple orchards (105), and *Neoris haraldi* on poplar (40). The use of *T. chilonis* against *H. armigera* in cotton never took off beyond Xinjiang province (122) (**Figures 1** and **2*a***), largely due to wide adoption of *Bt* cotton elsewhere (63). Nonetheless, *T. dendrolimi* has been used for *D. punctatus* control in pine forests (220,000 ha during 1970–1994), and entomopathogen-carrying methods are currently being developed (71).

10. CONCLUSION AND FUTURE OUTLOOK

Major achievements in *Trichogramma* R&D in China (32, 138) have established the country as a world leader in *Trichogramma*-based biological control programs, with successive governmental incentives and continuous improvement of the methodology. Achievements have included benefits for neighboring countries (e.g., Uzbekistan, Mongolia), with training programs being provided in Vietnam and production facilities and biological control programs established for rice and maize in Myanmar and Laos (2, 116). North Korea has also benefited from transfer of the relevant knowledge from China, including adaptations enabling it to bypass a lack of electricity supply in some areas (135).

Pitfalls and problems remain and warrant more research in the future. To date, only five *Trichogramma* species have been utilized for releases against pests. More screening should be undertaken targeting other major or invasive pests, e.g., *Spodoptera frugiperda* (80) and *Tuta absoluta* (5). In addition, the best factitious host species currently used (*A. pernyi*) enables mass rearing only of *T. dendrolimi* and *T. chilonis*. Recent research on multiparasitism for rearing other *Trichogramma* species will require further work to be practically employed in mass rearing. *A. pernyi* production depends on oak trees from northeastern China and thus raises concerns regarding impact on natural resources and possible limitations in production. Finally, the risk posed to biodiversity by release of billions of *Trichogramma* annually needs to be addressed.

The Chinese authorities aim to increase food safety, notably by reducing pesticide residues in agricultural products, and *Trichogramma* are being promoted for use in more crops (e.g., high-value greenhouse crops). Their use satisfies societal desires for more sustainable agriculture and safer food products. Still, key governmental decisions about *Bt* crops may change drastically the status of *Trichogramma* utilization, and the use of these parasitoids may be at a crossroad in the country. While the situation is clear and stable for cotton (>95% *Bt* cotton) (63) and rice (*Trichogramma* usage is growing through governmental support), the method widely used in maize is threatened by possible wide adoption of *Bt* maize in the near future. Therefore, *Trichogramma*-based biological control methods in China will require continuous development to maintain competitiveness versus other protection methods, notably by expanding their usage (e.g., more targeted pests and crops covered, notably high-value greenhouse crops). Furthermore, *Trichogramma* should be increasingly integrated with other pest management methods, e.g., potentially remaining a part of *Bt* resistance management plans in the event of widespread adoption of *Bt* maize in China.

SUMMARY POINTS

1. China has developed and industrialized a mass-rearing method for cost-effective production of *Trichogramma* parasitoids. The system is based on the use of large host eggs (*A. pernyi*), and one production line can produce 200 billion parasitoids per year. The other key mass-rearing method developed in China relies on small host eggs (*C. cephalonica*) and enables production of 2 billion *T. japonicum* per production line.
2. A mixed-species release method has been developed that combines *T. dendrolimi* (reared on the most cost-effective host, *A. pernyi*) with *T. japonicum* (reared on a much less cost-effective host, *C. cephalonica*) at an optimal ratio. This method decreases the cost of *Trichogramma*-based rice pest control without compromising biological control efficacy.
3. Long-term wide-scale inundative releases of *T. dendrolimi* in maize fields (2000–2015) have enabled a reduction in pesticide use while securing corn production, and in regions where only few destructive pests occur in each crop, e.g., maize and rice in northeastern China, the releases have resulted in complete removal of insecticide spray.
4. These achievements have provided benefits to neighboring countries via collaborative initiatives (notably North Korea, Mongolia, and Uzbekistan, including via adaptations fitted to specific situations in collaborating countries). Training programs have been implemented for extension services in Vietnam, and production facilities have been established in Myanmar and Laos for promoting biological control of rice and maize pests.
5. *Trichogramma*-based biological control has been proven cost effective in China and widely implemented in maize crops and may potentially be developed for use against major invasive pests in China, notably *S. frugiperda* on maize (as the method is well

implemented already and would likely need minimal additional R&D) and *T. absoluta* on tomato (a high-value crop on which *Trichogramma* use is efficient pending cost-effective production).

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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