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

Lian-Sheng Zang,[1] Su Wang,[2,*] Fan Zhang,[2]
and Nicolas Desneux[3,*]

[1]Institute of Biological Control, Jilin Agricultural University, 130118 Changchun, China

[2]Institute of Plant and Environment Protection, Beijing Academy of Agriculture and Forestry Sciences, 100097 Beijing, China; email: wangsu@ipepbaafs.cn

[3]Université Côte d'Azur, INRAE, CNRS, UMR ISA, 06000 Nice, France;
email: nicolas.desneux@univ-cotedazur.fr

*Co-corresponding authors.

Keywords

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

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 in 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
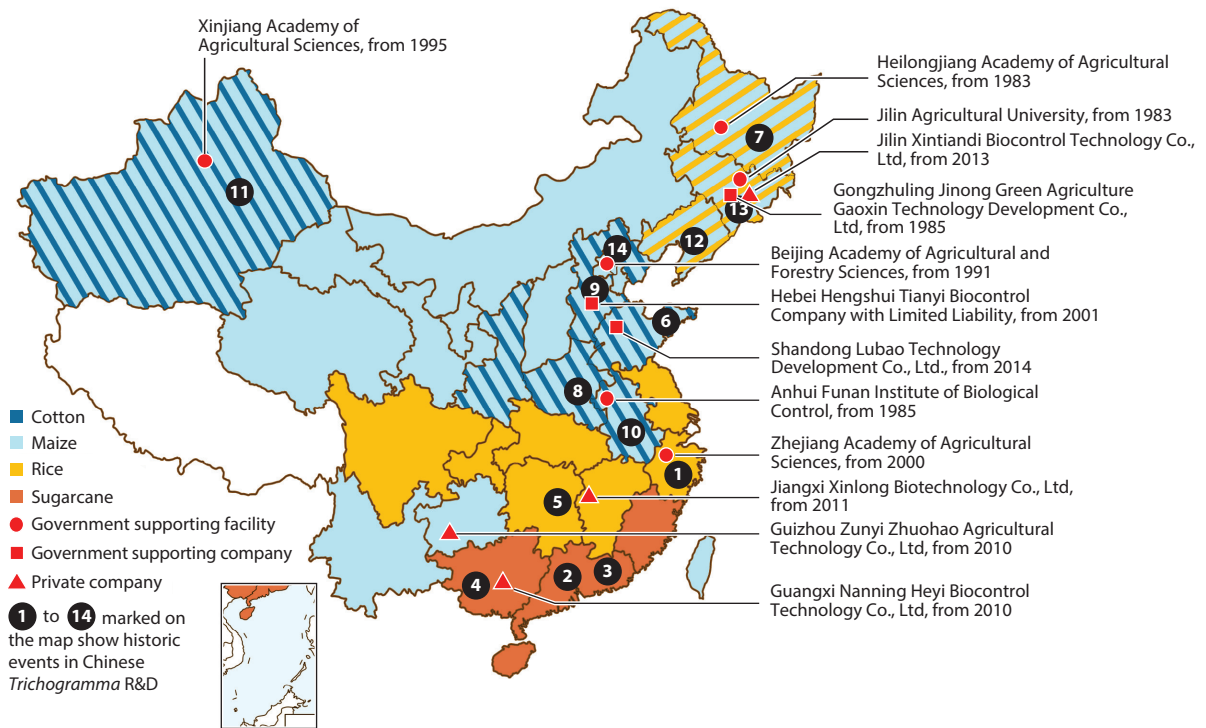
Figure 1

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).

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 key *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).

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

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

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).

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 and progeny survival rates in this host) (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 could perform better than southern ones on hosts native to the tropics (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), have 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 faces 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* 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 *Trichogramma* 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).

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

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 1/10 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 2a**). 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 2b**).
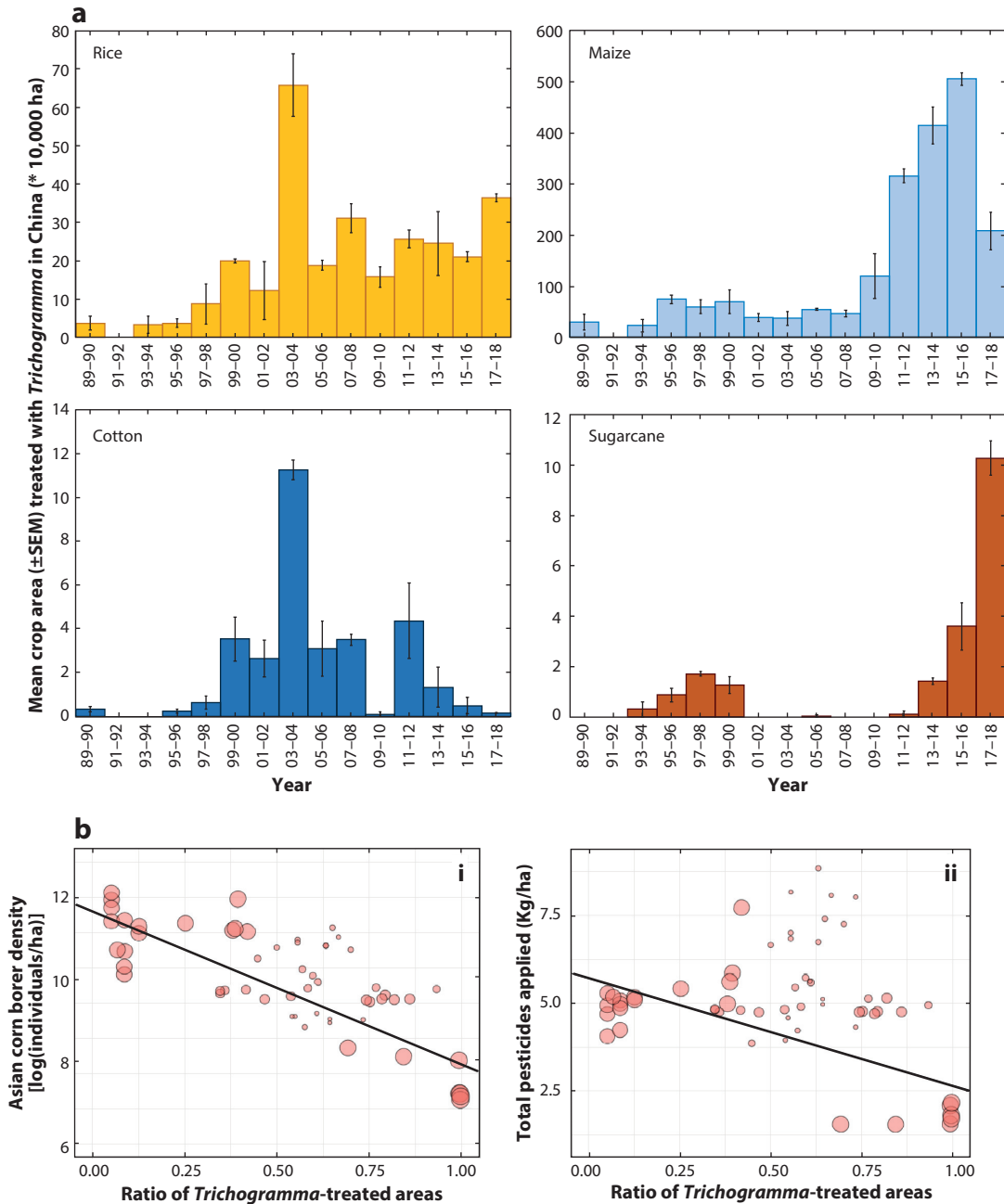
Figure 2

(*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 2a**), 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 **2a**), 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 crossroads 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

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

LITERATURE CITED

1. Babendreier D, Bigler FSK. 2003. Non-target host acceptance and parasitism by *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) in the laboratory. *Biol. Control* 26:128–38

2. Babendreier D, Wan M, Tang R, Gu R, Tambo J, et al. 2019. Impact assessment of biological control-based integrated pest management in rice and maize in the greater Mekong subregion. *Insects* 10:226

3. Bai Q, Tian JC, Lu YH, Zang LS, Lv ZX. 2017. Olfaction responses of three *Trichogramma* species to sex pheromone of *Chilo suppressalis* and *Cnaphalocrocis medinalis*. *Chin. J. Biol. Control* 33:584–89

4. Bai SX, Wang ZY, He KL, Wen LP, Zhou DR. 2004. Olfactory responses of *Trichogramma ostriniae* Pang et Chen to kairomones from eggs and different stages of female adults of *Ostrinia furnacalis* (Guenée). *Acta Entomol. Sin.* 47:48–54

5. Biondi A, Guedes RNC, Wan FH, Desneux N. 2018. Ecology, worldwide spread and management of the invasive South American tomato pinworm, *Tuta absoluta*: past, present and future. *Annu. Rev. Entomol.* 63:239–58

6. Chen HY, Wang SY, Chen CF. 2000. Quality control of *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) mass reared with rice moth *Corcyra cephalonica* eggs. *Nat. Enem. Insects* 22:145–50

7. Chen KW, Zhou J, Gong J, He YR, Huang SS. 2006. Effects of high temperature on laboratory *Trichogramma ostriniae* population. *Chin. J. Appl. Ecol.* 17:1250–53

8. Chen RZ, Klein MG, Sheng CF, Li QY, Li Y, et al. 2014. Mating disruption or mass trapping, compared with chemical insecticides, for suppression of *Chilo suppressalis* (Lepidoptera: Crambidae) in northeastern China. *J. Econ. Entomol.* 107:1828–38

9. Chen RZ, Li XY, Shi ZF, Fan LL, Zheng HB, Sun GZ. 2007. Preliminary study on biology characteristic and control effect on *Ostrinia furnalis* Guence of *Trichogramma dendrolimi* carrying *Bacillus thuringiensis*. *J. Jilin Agr. Univ.* 29:259–61

10. Chen RZ, Zheng HB, Shi ZF, Huang Y, Fang LL, Ma JY. 2007. Controlling *Chilo suppressalis* with *Trichogramma chilonis* carrying *Bacillus thuringiensis*. *J. Jilin Agr. Sci.* 32:39–40

11. Cheng Y, Han LL, Yu HC, Wang H, Yang X, et al. 2016. Using sex pheromones in combination with *Trichogramma* spp. and a chemical insecticide to control the soybean pod borer, *Leguminivora glycinivorella* (Mats.) Obraztsov. *Chin. J. Appl. Entomol.* 53:752–58

12. Chicu BB, Gorban VP, Greenberg SM. 2015. Methods and technical facilities for *Trichogramma* release. In *Biological Control of Pests Using Trichogramma: Current Status and Perspectives*, ed. SB Vinson, SM Greenberg, TX Liu, A Rao, LF Volosciuk, pp. 338–46. Yangling: Northwest A&F Univ. Press

13. Davies AP, Zalucki MP. 2008. Collection of *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae) from tropical northern Australia: a survey of egg parasitoids for potential pest insect biological control in regions of proposed agricultural expansion. *Aust. J. Entomol.* 47:160–67

14. Desneux N, Decourtye A, Delpuech JM. 2007. The sublethal effects of pesticides on beneficial arthropods. *Annu. Rev. Entomol.* 52:81–106

15. Di N, Wei YL, Wang S, Guo XJ, Zhang F. 2018. Optimization of artificial rearing technology for *Corcyra cephalonica* Stainton. *Chin. J. Biol. Control* 34:831–37

16. Dong J, Xu CX, Wu XY, Zhang QW, Jin XH, et al. 2006. The adult longevity of *Trichogramma dendrolimi* Matsumura under field conditions and its influencing factors. *Acta Entomol. Sin.* 49:969–75

17. **Du WM, Lin Y, Zang LS, Zhang C, Liu XJ, Ruan CC. 2016. Interspecific interference of *Trichogramma japonicum* with other two *Trichogramma* species on eggs of the rice stripped stem borer, *Chilo suppressalis* (Walker). *J. Environ. Entomol.* 38:488–93**

18. Du WM, Qu SX, Hu XX, Shao XW, Zang LS, Ruan CC. 2015. Effect of different cold-storage conditions on quality of *Trichogramma japonicum* Ashmead. *J. Environ. Entomol.* 37:1247–51

19. **Du WM, Xu J, Hou YY, Lin Y, Zang LS, et al. 2018. *Trichogramma* parasitoids can distinguish between fertilized and unfertilized host eggs. *J. Pest Sci.* 91:771–80**

20. Du WM, Zhang LL, Zhang JJ, Qi YH, Ruan CC. 2016. Functional response and numerical response of two geographic populations of *Trichogramma dendrolimi* to the eggs of rice moth, *Corcyra cephalonica*. *Sci. Agr. Sin.* 49:4669–76

21. Food Agric. Org. U. N. 2020. *FAOSTAT*. Stat. Database, Food Agric. Org. U. N., Rome. **http://www.fao.org/faostat**

22. Fatouros NE, Dicke M, Mumm R, Meiners T, Hilker M. 2008. Foraging behavior of egg parasitoids exploiting chemical information. *Behav. Ecol.* 19:677–89

23. Feng JG, Tao X, Zhang AS, Zhang CW. 1997. Study on using artificial eggs of *Trichogramma chilonis* to control *Helicoverpa armigera*. *Chin. J. Biol. Control* 13:6–9

24. Fu HB, Cong B, Du XZ. 2006. Application of mitochondrial cytochrome oxidase II (mtDNA CO II) to molecular identification of *Trichogramma* spp. *Sci. Agr. Sin.* 39:1927–33

25. Geng JH, Li ZX, Shen ZR. 2004. Application of species-specific primers to molecular identification of three important *Trichogramma* species (Hymenoptera: Trichogrammatidae) in China. *Acta Entomol. Sin.* 47:639–44

26. Gibson GAP. 2019. Institute of Biological Control, Jilin Agricultural University, Changchun, China. *Hamuli* 10:2–3

27. Grenier S, Pitureau B, Heddi A, Lassabliere F, Jager C, et al. 1998. Successful horizontal transfer of *Wolbachia* symbionts between *Trichogramma* wasps. *Proc. R. Soc. B* 265:1441–45

28. Guo L, Jiao XG, Song K, Babendreier D, Zhang F, Hou ML. 2017. Thermal tolerance of potential *Trichogramma* strains for mass-production and paddy field release in the Greater Mekong Subregion. *Biocontrol* 62:731–40

29. Guo M. 1992. Study on parasitising behaviour of *Trichogramma*. I. Superparasitism and progeny allocation. *Nat. Enem. Insects* 14:6–12

30. Guo M, Zhang J. 1993. Study of parasitizing behavior of *Trichogramma*. IV. Progeny number allocation and sex allocation. *Nat. Enem. Insects* 15:51–59

31. Han SC, Chen QX, Li LY. 1994. A study on the oviposition synergists for in vitro rearing *Trichogramma* spp. *Entomol. Sin.* 1:333–38

32. Hassan SA, Liscsinszky H, Zhang G. 2004. The oak-silkworm egg *Antheraea pernyi* (Lepidoptera: Anthelidae) as a mass-rearing host for parasitoids of the genus *Trichogramma* (Hymenoptera: Trichogrammatidae). *Biocontrol Sci. Technol.* 14:269–79

33. **Heimpel GE, Mills N. 2017. *Biological Control: Ecology and Applications*. Cambridge, UK: Cambridge Univ. Press**

34. Hou YY, Yang XB, Zang LS, Zhang C, Monticelli L, Desneux N. 2018. Effect of oriental armyworm *Mythimna separata* egg age on the parasitism and host suitability for five *Trichogramma* species. *J. Pest Sci.* 91:1181–89

17. Identified the optimal ratio for ensuring efficacy of mixed-species releases against *Chilo suppressalis* in rice.

19. *Trichogramma* parasitoids distinguish fertilized host eggs from and prefer them over unfertilized ones.

33. The most comprehensive and up-to-date reference on biological control in general.

35. **Huang NX, Jaworski CC, Desneux N, Zhang F, Yang PY, Wang S. 2020. Long-term, large-scale releases of *Trichogramma* promotes pesticide decrease in northeastern China. *Entomol. Gen.* In press**

36. Huang SS, Zang LS, Ruan CC. 2013. *Parasitic Ecology and Industrial Production of Trichogramma*. Beijing: Science

37. Huigens ME, Luck RF, Klaassen RHG, Maas MFPM, Timmermans MJTN, Stouthamer R. 2000. Infectious parthenogenesis. *Nature* 405:178–79

38. Iqbal A, Chen YM, Hou YY, Zhang LS, Desneux N, et al. 2019. Factitious host species impact on the outcome of multiparasitism between egg parasitoids. *J. Pest Sci.* 92:1261–69

39. Jia NX, Huang YG, Li QZ, Li Y. 2002. Studies on reproducing *Trichogramma* by using *Sitotroga cerealella* Oliver eggs. *J. Jilin Agr. Univ.* 24:58–60

40. Kereman Yue CY, Zhang XP, Alimu M, Zhao M, et al. 2009. Study on *Trichogramma dendrolimi* Matsumura to control *Neoris haraldi* Schawerda. *Chin. J. Biol. Control* 25:12–14

41. Kuske S, Widmer F, Edwards PJ, Turling TCJ, Babendreier D, Bigler F. 2003. Dispersal and persistence of mass released *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae) in non-target habitats. *Biol. Control* 27:181–93

42. Li B, Liu X. 2002. Effects of learning on host-location and host-acceptance in *Trichogramma evanescens* (Hym. Trichogrammatidae). *Nat. Enem. Insects* 24:154–58

43. Li LJ, Lu X, Zhang GH, Liu HW, Ding Y, Wang YZ. 2008. Studies on storing of the factory product of *Trichogramma chilonis* in low temperature. *J. Jilin Agr. Sci.* 33:27–29

44. Li LY, Zhu D. 1995. Intraspecific variation and the role of superparasitism in diapause induction of *Trichogramma evanescens* Westwood. *Entomol. Sin.* 2:337–44

45. Li LY, Zhu D, Chen Q, Zhang M, Shliachtich VA, Greenberg SM. 1992. *Trichogramma* spp. diapause induced by low temperature relation to hosts. *Nat. Enem. Insects* 14:117–25

46. **Li TH, Tian CY, Zang LS, Hou YY, Ruan CC, et al. 2019. Multiparasitism with *Trichogramma dendrolimi* on egg of Chinese oak silkworm, *Antheraea pernyi*, enhances emergence of *Trichogramma ostriniae*. *J. Pest Sci.* 92:707–13**

47. Li WF, Zhang RY, Pu CH, Yin J, Luo ZM, et al. 2019. Natural enemies of sugarcane pests and their roles in natural control in Yunnan, China. *Pak. J. Zool.* 51:1953–58

48. Li ZX, Shen ZR. 2002. Application of rDNA-ITS2 sequences to the molecular identification of *Trichogramma* spp. *Acta Entomol. Sin.* 45:559–66

49. Lian YG, Wang SQ, Bai SX, Kang ZJ, Wang ZY. 2009. The effect of artificial host egg contents and attractants on egg surface on rearing of *Trichogramma ostriniae*. *Chin. Bull. Entomol.* 46:551–56

50. Lin NQ. 1994. *Systematic Studies of Chinese Trichogrammatidae (Hymenoptera: Chalcidoidea)*. Fuzhou, Chin.: Fujian Sci. Technol. Publ. House

51. Lin X, Lin NQ. 2011. The keys to the known genera of Trichogrammatidae and Mymaridae from Hebei, Shandong and Henan provinces in China (Hymenoptera: Chalcidoidea). *Wuyi Sci. J.* 27:29–33

52. **Liu B, Yang L, Yang F, Wang Q, Yang YZ, et al. 2016. Landscape diversity enhances parasitism of cotton bollworm (*Helicoverpa armigera*) eggs by *Trichogramma chilonis* in cotton. *Biol. Control* 93:15–23**

53. Liu H, Fang X, Liu J, Huang SS, Ouyang G. 2017. Superparasitism of *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae) by different inoculation proportion and its influences on offspring. *Chin. Plant Prot.* 37:5–10

54. Liu QQ, Zhang TS, Li CX, Gu JW, Hou JB, Dong H. 2018. Decision-making in a bisexual line and a thelytokous *Wolbachia*-infected line of *Trichogramma dendrolimi* Matsumura (Hymenoptera: Trichogrammatidae) regarding behavior toward their hosts. *Pest Manag. Sci.* 74:1720–27

55. Liu SS, Shi ZH, Shao MJ, He JH. 1994. Comparative studies on the biological characteristics of geographic populations of *Trichogramma dendrolimi* in China. V. Response to diapause induction. *Chin. J. Biol. Control* 10:145–50

56. Liu SS, Zhang GM, Zhang F. 1998. Factors influencing parasitism of *Trichogramma dendrolimi* on eggs of the Asian corn borer, *Ostrinia furnacalis*. *Biocontrol* 43:273–87

57. Liu ZC, Liu JF, Yang WH, Wang CX. 1995. Study on special procedures for prolonged cold storage of key material to make artificial eggs from *Antheraea* pupal holotissues. *Chin. J. Biol. Control* 11:52–53

35. Long-term wide-scale inundative releases of *Trichogramma* in maize enabled promotion of insecticide decrease at the province scale.

46. Developed a multiparasitism-based method to rear particular *Trichogramma* species on the factitious host *Antheraea pernyi*.

52. Demonstrated the relationship between landscape variables and the biological control service provided by *Trichogramma* in Chinese farmlands.

58. Liu ZC, Pu ZL. 1960. Suppression sugarcane borer by using *Trichogramma evanescens* Westw. *Chin. Bull. Entomol.* 3:77–79

59. Liu ZC, Yang HW, Wang CX, Liu JF, Liang YF, Zeng JC. 1991. A machine for obtaining clean infertile eggs of oak silkworm used in *Trichogramma* production. *Chin. J. Biol. Control* 7:38–40

60. Lobdell CE, Yong TH, Hoffmann MP. 2005. Host color preferences and short-range searching behavior of the egg parasitoid *Trichogramma ostriniae*. *Entomol. Exp. Appl.* 116:127–34

61. Lu WQ, Lang S. 1979. Oviposition behaviour of Trichogrammatid wasps. *Acta Entomol. Sin.* 22:361–63

62. **Lü X, Han SC, Li LY, Grenier S, De Clercq P. 2013. The potential of trehalose to replace insect hemolymph in artificial media for *Trichogramma dendrolimi* (Hymenoptera: Trichogrammatidae). *Insect Sci.* 20:629–36**

63. Lu YH, Wu KM, Jiang YY, Guo YY, Desneux N. 2012. Widespread adoption of Bt cotton and insecticide decrease promotes biocontrol services. *Nature* 487:362–65

64. Luo J, Chang MS, Li DW, Mou XW, Cheng HY, et al. 2018. Technique on control of mangrove pests by spreading *Trichogramma* using UAV. *Guangxi For. Sci.* 47:473–75

65. Luo K, Zhang GR, Gu DX, Pang Y. 2005. Effect of *Spodoptera exigua* multicapsid nucleopolyhedrovirus on *Trichogramma confusum*: comparison of population parameters and PCR detection. *Acta Entomol. Sin.* 48:57–60

66. Ma CS, Chen YW. 2005. Effects of alternating temperature and time on diapause of *Trichogramma dendrolimi*. *Acta Phytophyl. Sin.* 32:174–78

67. Orr DB, Garcia-Salazar C, Landis DA. 2000. *Trichogramma* non-target impacts: a method for biological control risk assessment. In *Nontarget Effects of Biological Control*, ed. PA Follet, JJ Duan, pp. 111–25. Berlin: Springer

68. Pan XH, He YR. 2011. Horizontal transfer of *Wolbachi*a between *Trichogramma pretiosum* and *T. confusum*. *Acta Agr. Boreali-occidentalis Sin*. 20:186–88

69. Pan XH, He YR, Chen KW, Pan F, Pan M. 2007. Effect of *Wolbachia* infection on longevity, fecundity and olfactory response of *Trichogramma confusum* (Hymenoptera: Trichogrammatidae). *Acta Entomol. Sin.* 50:207–14

70. Pang XF, Chen TL. 1974. *Trichogramma* of China (Hymenoptera: Trichogrammatidae). *Acta Entomol. Sin.* 17:441–54

71. Peng HY, Chen XW, Jiang Y, Shen RJ, Zhou XM, Hu ZH. 1998. Controlling *Dendrolimus punctatus* with *Trichogramma dendrolimi* carrying *Dendrolimus punctatus wenshansis* cytoplasmic polyhedrosis virus. *Chin. J. Biol. Control* 14:111–14

72. Pinto JD, Stouthamer R. 1994. Systematics of the Trichogrammatidae with emphasis on *Trichogramma*. In *Biological Control with Egg Trichogramma*, ed. E Wajnberg, SA Hassan, pp. 1–36. Wallingford, UK: CAB Int.

73. Pu ZL. 1984. *Principles and Methods of Pest Biological Control*. Beijing: Science

74. Qian YQ, Cao RL, Li GZ. 1984. Biology of *Trichogramma ostriniae* and evaluation of its effectiveness in controlling corn borer on spring corn. *Acta Entomol. Sin.* 27:287–93

75. Qiu SB, Tian YQ, Zhou WR, Yu JJ, Wang CX, Wang ZG. 1980. Improved technique for mass rearing rice moth. *Acta Phytophyl. Sin.* 7:153–58

76. Ruan CC, Guo RT, Hu XX, Du WM, Zang LS, Zhang JJ. 2018. Effect of temperature on development and parasitizing capacity of *Trichogramma japonicum* reared on the eggs of rice moth (*Corcyra cephalonica*). *Chin. J. Rice Sci.* 32:398–404

77. Shi Z, Chen H, Qin Z, Guo Q, Bi D, et al. 2018. Population dynamics of borers and its control effect evaluation by using *Trichogramma chilonis* Ishii in Chongzuo cane area. *Chin. J. Biol. Control* 34:656–62

78. Shi ZH, Liu SS. 1993. The influence of temperature and humidity on the population increase of *Trichogramma dendrolimi*. *Acta Ecol. Sin.* 13:328–33

79. Shi ZH, Liu SS, Xu WL, He JH. 1993. Comparative studies on the biological characteristics of geographic/host populations of *Trichogramma dendrolimi* in China. III. Response to temperature and humidity. *Chin. J. Biol. Control* 9:97–101

80. Silver A. 2019. China seeks predator to stop voracious caterpillar. *Nature* 570:286–87

81. Smith SM. 1996. Biological control with *Trichogramma*: advances, success, and potential of their use. *Annu. Rev. Entomol.* 41:375–406

82. Song J, Huang J, Wang LY, Li YX. 2017. Effects of sex pheromone of *Chilo suppressalis* on parasitic ability of *Trichogramma japonicum* and parasitization efficiency in field. *Chin. J. Biol. Control* 33:481–86

83. Song LW, Wen XY, Zang LS, Ruan CC, Shi SS, et al. 2015. Parasitism and suitability of different egg ages of the soybean pod borer, *Leguminivora glycinivorella*, for three indigenous *Trichogramma* species. *J. Econ. Entomol.* 108:933–39

84. Song RC, Chi YM, Wang HP, Lu GY, Wang QX, Zhang QB. 1994. A study on setting equipment of manufactured reproduction of *Trichogramma*. *Trans. CSAE* 10:48–52

85. Song Y, Shen ZR, Wang Z, Li ZY. 2010. Distribution and genetic stability of *Wolbachia* in populations of *Trichogramma chilonis*. *J. Environ. Entomol.* 32:188–93

86. Tao S, Wan F, Tong Z, Zhao K. 2000. Allelochemicals for egg parasitoids, *Trichogramma chilonis* and *T. dendrolimi*: resources and activity bioassay. *Sci. Agr. Sin.* 33:59–66

87. Tian HX, Lin NQ. 2009. The genus *Trichogrammatoidea* Girault from Hainan, with description of a new species (Hymenoptera, Trichogrammatidae). *Acta Zootaxon. Sin.* 34:360–66

88. Tian JC, Wang GS, Zheng XS, Lv ZX. 2018. The effect of sesame flowers on the fecundity and dispersal ability of *Trichogramma japonicum*. *Chin. J. Biol. Control* 34:807–12

89. Tian JC, Wang GW, Romeis J, Zheng XS, Xu HX, et al. 2016. Different performance of two *Trichogramma* (Hymenoptera: Trichogrammatidae) species feeding on sugars. *Environ. Entomol.* 45:1316–21

90. Tian JC, Wang ZC, Wang GR, Zheng XS, Zang LS, Lü ZX. 2017. Evaluation of fecundity, flight ability and insecticide tolerance of southern and northern *Trichogramma japonicum* populations. *Chin. J. Biol. Control* 33:32–38

91. Tian JC, Wang ZC, Wang GR, Zheng XS, Zang LS, Lv ZX. 2017. Assessment of the flight ability of four *Trichogramma* species and the dispersal of *T. japonicum* in rice field. *Chin. J. Biol. Control* 33:26–31

92. Van Alphen JJM, Visser ME. 1990. Superparasitism as an adaptative strategy for parasitoids. *Annu. Rev. Entomol.* 35:59–79

93. Van Dijken MJ, Waage JK. 1987. Self and conspecific superparasitism by the egg parasitoid *Trichogramma evanescens*. *Entomol. Exp. Appl.* 43:183–92

94. Vinson SB, Greenberg SM, Liu TX, Rao A, Volosciuk LF. 2015. *Biological Control of Pests Using Trichogramma: Current Status and Perspectives*. Yangling: Northwest A&F Univ. Press

95. Wang CL, Mao G, Gao Y, Li LJ, Cui DJ. 1999. An instrument for selecting healthy parasitized host eggs. *Chin. J. Biol. Control* 15:139–40

96. Wang CL, Zhang J, Huo ST, Zhou YN, Feng JG, et al. 1998. Study, reproduction and utilization of *Trichogramma*. In *Biological Control in China*, ed. JZ Bao, DX Gu, pp. 67–123. Taiyuan, Chin.: Shanxi Sci. Technol. Press

97. Wang CM, Cong B, Cui BY, Dai QH, Zhang ZL. 2006. A comparative study on the bionomics of gamogenesis and thelytoky lines of *Trichogramma dendrolimi*. *Chin. J. Biol. Control* 22:96–100

98. Wang D, Lu L, He Y, Shi Q, Tu C, Gu J. 2016. Mate choice and host discrimination behaviour of the parasitoid *Trichogramma chilonis*. *Bull. Entomol. Res.* 106:530–37

99. Wang DS, He YR, Guo XL, Luo YL. 2012. Acute toxicities and sublethal effects of some conventional insecticides on *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae). *J. Econ. Entomol.* 105:1157–63

100. Wang DS, Lu LH, He YR. 2017. Effects of two conventional insecticides on male-specific sex pheromone discrimination and mate choice in *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae). *Environ. Entomol.* 46:328–34

101. Wang DS, Lu LH, He YR. 2018. Effects of insecticides on sex pheromone communication and mating behavior in *Trichogramma chilonis*. *J. Pest Sci.* 91:65–78

102. Wang G, Lan Y, Qi H, Chen P, Hewitt A, Han Y. 2018. Field evaluation of an unmanned aerial vehicle (UAV) sprayer: effect of spray volume on deposition and the control of pests and disease in wheat. *Pest Manag. Sci.* 75:1546–55

103. Wang JL, Zhang J, Yang CC. 1990. Experiment on parthenogensis of *Trichogramma ostriniae*. *J. Shenyang Agr. Univ.* 20:91–92

104. Wang K, Wang S, Song LF, Zhang F, Li YD. 2014. Sublethal effects of acetamiprid and beta-cypermethrin on reproduction of *Trichogramma chilonis*. *J. Environ. Entomol.* 36:933–38

105. Wang L, Feng H, Guo W, Zhang H, Yang L, Yu J. 2011. Dynamic state of *Laspeyresia pomonella* and release techniques of *Trichogramma* in orchards. X*injiang Agr. Sci.* 48:261–65

106. Wang L, Zhao X, Zhou C, Yan F, Li Q, et al. 2010. Studies on the effect of controlling the sunflower moth by the *Trichogramma*. *Heilongjiang Agr. Sci.* 7:69–71

107. Wang LH, Zhang QW, Yang SX, Cai QN, Zhang F. 1998. Effect of wind on dispersal direction of *Trichogramma chilonis* in cotton field. *Acta Entomol. Sin.* 41:76–81

108. Wang P, Li MJ, Bai QR, Ali A, Desneux N, et al. 2020. Performance of *Trichogramma japonicum* Ashmead as vector of *Beauveria bassiana* for parasitizing eggs of the rice striped stem borer, *Chilo suppressalis*. *Entomol. Gen.* In press

109. Wang SM, Zhou Y. 1995. *History of Modern Chinese Entomology*. Xian, Chin.: Shaanxi Sci. Technol. Press

110. Wang SQ. 2001. Research progress in *Trichogramma* mass rearing by using artificial host eggs. *Plant Prot. Technol. Extens.* 21:40–41

111. Wang Y, Hou Y, Yang X, Wang S, Dai HJ, Zang LS. 2020. Manually-extracted unfertilized eggs of Chinese oak silkworm, *Antheraea pernyi*, enhance mass production of *Trichogramma* parasitoids. *Entomol. Gen.* In press

112. Wang Y, Xiao TG, He Z, Ge F. 2008. Effects of masson pine volatiles on olfactory and parasitic behavior of *Trichogramma dendrolimi*. *Chin. Bull. Entomol.* 45:944–49

113. Wang Z, Qian H, Dong H, Wang ZY, Cong B. 2008. Studies on the damage degree and yield loss by Asian corn borer. *Plant Prot.* 34:112–15

114. Wang Z, Zhou D, Hassan SA. 1996. Effect of hexane extract of European corn borer female moth scale on host-seeking behavior of *Trichogramma ostriniae*. *Acta Phytophyl. Sin.* 23:373–74

115. Wang ZC, Tian JC, Wang GR, Zheng XS, Zang LS, et al. 2016. Safety assessment of pesticides targeted at non-Lepidopteran rice pests to *Trichogramma japonicum* (Hymenoptera: Trichogrammatidae). *Chin. J. Biol. Control* 32:19–24

116. Wang ZY, He KL, Zhang F, Lu X, Babendreier D. 2014. Mass-rearing and release of *Trichogramma* for biological control of insect pests of corn in China. *Biol. Control* 68:136–144

117. Wang ZY, Zhou DR. 2000. Effects of mungbean leaf water extracts on parasitism of *Trichogramma ostriniae*. *Acta Phytophyl. Sin.* 27:190–91

118. Wu H, Huang YC, Guo JX, Liu JB, Lai XS, et al. 2018. Effect of cold storage of *Corcyra cephalonica* eggs on the fitness for *Trichogramma chilonis*. *Biol. Control* 124:40–45

119. **Wu LH, Hoffmann AA, Thompson LJ. 2016. Potential impact of climate change on parasitism efficiency of egg parasitoids: a meta-analysis of *Trichogramma* under variable climate conditions. *Agr. Ecosyst. Environ.* 231:143–55**

120. Xie ZN, Wu PY, Deng XL. 1982. Research of artificial diet of *Trichogramma*. 1. Amino acid analysis of hemolymph of *Philosamia cynthia ricini* larvae and pupae. *Nat. Enem. Insects* 4:5–11

121. Xu D, Bai Y, Gong X, Xu Z. 2016. Design of *Trichogramma* delivering system based on hex-rotor UAV. *Trans. Chin. Soc. Agr. Mach.* 47:1–7

122. Xu JJ, Guo WC, Yao J, Turxun Wang ZP, et al. 2004. Study on using mass-release *Trichogramma chilonis* to control *Helicoverpa armigera* in cotton field in Xinjiang. *Xinjiang Agric. Sci.* 41:378–80

123. Xu W, Wen XW, Hou YY, Desneux N, Ali A, Zang LS. 2020. Suitability of Chinese oak silkworm eggs for the multigenerational rearing of the parasitoid *Trichogramma leucaniae*. *PLOS ONE* 15(4):e0231098

124. Xu ZH, He JH. 1994. Comparative studies on the morphology of geographic/host populations of *Trichogramma drendrolimi* in China. *Chin. J. Biol. Control* 10:2–4

125. Yang HW. 2015. Review in utilization of insect natural enemies during the period from 1985 to 2015 in China. Part 1. *Chin. J. Biol. Control* 31:603–12

126. Yang KD, Zhang HY, Qian HT, Dong H, Zhang Y, Cong B. 2008. Effect of *Wolbachia* infection on fecundity, developmental duration and survival of *Trichogramma dendrolimi*. *Chin. J. Biol. Control* 24:210–14

127. Yang X, Qu YL, Wu ZY, Lin Y, Ruan CC, et al. 2016. Parasitism and suitability of fertilized and nonfertilized eggs of the rice striped stem borer, *Chilo suppressalis* (Lepidoptera: Crambidae), for *Trichogramma* parasitoids. *J. Econ. Entomol.* 109:1524–28

128. **Yang Z, Lu Y, Mao G, Zhao Y, Zhang Q, et al. 2020. Use of *Trichogramma* phoretic *Beauveria bassiana* in control of Asian corn borer in field. *Chin. J. Biol. Control* 36:52–57**

129. Yu C. 2017. *Identification of* Trichogramma *Species by HRM Technique and Field Application Technology Research of* Trichogramma dendrolimi. Shenyang, Chin.: Shenyang Agr. Univ.

130. Yu RX, Yu WH, Wu CX, Wu SG, Chen LP, et al. 2009. Effects of different pesticides on adults, larvae, eggs, and pupae of *Trichogramma nubilale*. *Agrochemicals* 48:588–90

131. Yuan J, Wang ZY, He KL, Bai SX, Li J. 2011. Sequence analysis of mtDNA gene and genetic differentiation in geographic populations of *Trichogramma ostriniae*. *Chin. J. Biol. Control* 27:16–21

132. Yuan X, Li D, Zhao Y, Feng X, Zuo C, Li S. 2014. Investigation report on effect of large-area release *Trichogramma* to control sugarcane borers in Guangxi in 2013. *Chin. J. Biol. Control* 30:630–34

133. Yuan XH, Song LW, Zhang JJ, Zang LS, Zhu L, et al. 2012. Performance of four Chinese *Trichogramma* species as biocontrol agents of the rice striped stem borer, *Chilo suppressalis*, under various temperature and humidity regimes. *J. Pest Sci.* 85:497–504

134. Zhan GX, Liang GW. 1999. Research and application of *Trichogramma* in China. *Acta Agr. Jiangxi* 11:39–46

135. Zhang F, Babendreier D, Wang ZY, Il KS, Zheng L, et al. 2010. Mass releases of *Trichogramma ostriniae* increase maize production in DPR Korea. *J. Appl. Entomol.* 134:481–90

136. Zhang JJ, Desneux N, Benelli G, Zang LS, Du WM, Ruan CC. 2017. Geographic variation of diapause induction rates in *Trichogramma drendrolimi* (Hymenoptera: Trichogrammatidae) in China. *J. Econ. Entomol.* 110:386–91

137. Zhang JJ, Ren BZ, Yuan XH, Zang LS, Ruan CC, et al. 2014. Effects of host-egg ages on host selection and suitability of four Chinese *Trichogramma* species, egg parasitoids of the rice striped stem borer, *Chilo suppressalis*. *Biocontrol* 59:159–66

138. Zhang JJ, Ruan CC, Zang LS, Shao XW, Shi SS. 2015. Technological improvements for mass production of *Trichogramma* and current status of their applications for biological control on agricultural pests in China. *Chin. J. Biol. Control* 31:638–46

139. Zhang JJ, Zhang X, Du WM, Ruan CC, Zang LS, Ren BZ. 2018. Effects of inducing initial stage, temperature and period on diapause induction and diapause termination of *Trichogramma dendrolimi*. *J. Plant Prot.* 45:1308–13

140. Zhang JJ, Zhang X, Zang LS, Du WM, Hou YY, et al. 2018. Advantages of diapause in *Trichogramma dendrolimi* mass production on eggs of the Chinese silkworm, *Antheraea pernyi*. *Pest Manag. Sci.* 74:959–65

141. Zhang LW. 1993. Attractive material for the oviposition of *Trichogramma dendrolimi* on artificial "eggs." *Nat. Enem. Insects* 15:101–5

142. Zhang M. 1999. The influence of the thickness of host eggs chorion on the longevity and fecundity of *Trichogramma confusum*. *Nat. Enem. Insects* 21:150–51

143. Zhang S, Zhang Z, Kong X, Wang H, Zhou G, Yu J. 2012. External morphology of *Trichogramma dendrolimi* Matsumura (Hymenoptera: Trichogrammatidae) organ and ultrastructure of the sensilla. *Microsc. Res. Technol.* 75:1513–21

144. Zhang YF, Cai H, Zhang F, Li YX. 2010. Effects of *Ostrinia furnacalis* egg age on interspecific competition between *Trichogramma ostriniae* and *Trichogramma dendrolimi*. *J. Nanjing Agr. Univ.* 33:75–80

145. Zhang YF, Song QT, Zhang F, Li YX. 2010. Comparison of superparasitism and suitability to superparasitism between *Trichogramma ostriniae* and *T. dendrolimi*. *Chin. J. Biol. Control* 26:377–84

146. Zhang ZQ, Guo JZ, Wang HQ, Hu HY. 2010. Analysis on biodiversity of Trichogrammatidae in northern regions of Xinjiang. *Xinjiang Agr. Sci.* 47:1152–56

147. Zhong M, Shen ZR. 2004. Infection of the endosymbiont *Wolbachia* in population of *Trichogramma evanescens* in China. *Acta Entomol. Sin.* 47:732–37

148. Zhou DR, Song YY, He KL, Wang ZY, Zheng L, Zhang GY. 1997. Study on the preference habitat of *Trichogramma ostriniae* I. Natural population distribution and dynamics of the parasitoid in different habitats. *Chin. J. Biol. Control* 13:1–5

149. Zhou DR, Song YY, Wang ZY, He KL, Zheng L, Zhang GY. 1997. Study on the preference habitat of *Trichogramma ostriniae* II. Effect of summer corn interplanted with creeping type mungbean on the parasitic rate. *Chin. J. Biol. Control* 13:49–52

140. *Trichogramma* produced with diapause technology are more efficient than those stored at low temperatures in field assays.

150. Zhou JC, Dong QJ, Zhang TS, Duan LJ, Ning SF, et al. 2019. Effect of wind time on the dispersal capacity of *Trichogramma dendrolimi* Matsumura (Hymenoptera Trichogrammatidae). *J. Asia-Pacific Entomol.* 22:742–49

151. Zhou SX, Lu X, Zhang GH, Li LJ, Ding Y. 2014. Research on the induction and termination of diapause in *Trichogramma dendrolimi*. *Chin. J. Appl. Entomol.* 51:45–52

152. Zhu P, Zhang YF, Song QT, Zhang F, Li YX. 2014. The suitability of *Ostrinia furnacalis* (Lepidoptera: Crambidae) eggs for *Trichogramma dendrolimi* (Hymenoptera: Trichogrammatidae) can be changed by *T. ostriniae*. *Appl. Entomol. Zool.* 49:265–72