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BIOLOGICAL CONTROL WITH *TRICHOGRAMMA*: Advances, Successes, and Potential of Their Use

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ABSTRACT

Major contributions to the release of *Trichogramma* for biological control of lepidopterous pests have been made in the past 20 years. Most trials have used only five species of *Trichogramma* against two pests; *Ostrinia* in corn is considered the most universally feasible. All *Trichogramma* programs must address the following four aspects to be successful commercially. Selection of the appropriate population is based on inter- and intraspecific variation, as well as on current definitions of parasitoid quality. Mass rearing is comprised of both host and parasitoid components, although major emphasis is now on developing artificial systems. Effective distribution of *Trichogramma* requires supportive extension and advanced technology. Strategies for use in the field vary according to the approach desired (inundative or inoculative), the timing, frequency and rate of release, and the multiple factors that affect release, such as the weather, crop, host, predation, pesticides, and dispersal. The past difficulty in assessing the efficacy of *Trichogramma* should be improved with new guidelines for standardizing terminology and measurements.

HISTORICAL PERSPECTIVE

The release of *Trichogramma* for biological control of lepidopterous pests has been considered for more than 100 years, although the mass rearing of these hymenopterous parasitoids was not proposed in North America until the 1920s. Flanders' work (49) inspired activity during the 1930s, but this activity quickly dissipated in the West with the rise of chemical insecticides. It was left primarily to scientists in the former USSR (from 1937) and China (from 1949)

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to develop *Trichogramma* as biological-control agents (12, 100). In the 1960s, the Europeans and Americans revitalized research on *Trichogramma*; in the 1970s, they began mass-rearing and release (14, 62, 65, 70, 118, 127, 193).

It has been almost 20 years since an exhaustive review of inundative releases has been conducted (180). Although the genus *Trichogramma* is not the only group to be used with this approach, much of our understanding of inundative release comes from studies with these minute egg parasitoids. At the same time as Stinner's review (180), a compendium of international research was published (158) that marked the beginning of an exchange of information among scientists in North America, Europe, the former USSR, and China. This exchange resulted in an explosion of research that continues today. International symposia with published proceedings have been conducted every four years since 1982 (74, 199, 206), and informal sessions have been held at the last three International Congresses of Entomology. In addition, there have been eight international symposia on quality control (16). Wajnberg & Hassan (205) summarized current knowledge in a recent publication.

This review critically analyzes and ties together the studies from the mid-1970s. Because *Trichogramma* can be considered the *Drosophila* of the parasitoid world, the genus has generated a large volume of information. Emphasis here is on how we have used this basic information to implement successful field programs.

SCOPE OF USE

Most *Trichogramma* releases have been conducted in the past 20 years; trials before 1975 were aimed at control of lepidopterous pests in sugarcane and corn. Between 1975 and 1985, pests of cotton, sugarbeet, vineyards, cabbage, plum, apple, forests, tomato, and rice were also targeted. Since 1985, numerous crops have been investigated, and the list is growing (65). Most research—and the most consistent success—has been in corn. Inconsistent results have been found in crops such as cotton and rice, for which, despite intensive research, the use of insecticides to control multiple pest problems reduces the action of *Trichogramma* (65, 88, 101).

Today, inundative releases for control of lepidopterous pests are being investigated in more than 50 countries and are reported to be used commercially on more than 32 million ha each year (65). This hectarage is inflated, as some areas in the former USSR receive repeated applications (48). *Trichogramma* are considered commercially efficient in the former USSR and China and compete successfully with insecticides for commercial control of corn borer in Europe, although some of the costs are subsidized (127). Eastern bloc countries and some Asian and South American countries have a longer history, whereas Australia and countries in North and Central America have only recently begun to investigate the potential of *Trichogramma* (38, 54, 170). In North America, their niche is in organically grown crops and in areas where pesticide resistance has developed.

Despite the plethora of crops and countries where inundative releases have been made, surprisingly few pest and *Trichogramma* species have been studied. Most trials have been initiated against the key pests, *Ostrinia* spp. and *Helicoverpa zea,* with infrequent releases against various pyralids, tortricids, noctuids, oleuthrids, and pierids, in decreasing order (Table 1). Even in the former USSR, *Trichogramma* are used to control only about seven pest species (59). Most trials have used five species of *Trichogramma,* in decreasing order: *evanescens*, *dendrolimi*, *pretiosum*, *brassicae* (=*maidis*), and *nubilale*. An additional ten species have been used infrequently (Table 1). In general, the first three species have dominated the studies because of their plasticity in habitat and host selection (101).

Most papers address specific research questions, although several describe commercial successes (Table 1). To reach successful commercial application, all *Trichogramma* programs must address four issues: selection of the appropriate population to release, a system for mass rearing, distribution of the parasitoid, and a strategy for field release.

SELECTION OF PARASITOIDS TO RELEASE

Interspecific and Intraspecific Variation

The selection of the most appropriate parasitoid for release starts with the best species. This process is difficult, because there is considerable interspecific variation in the more than 145 species known, and the taxonomy of the genus is poorly understood (147). Members of the genus are polyphagous egg parasitoids on ten orders of insects, including Lepidoptera, Coleoptera, Diptera, Heteroptera, Hymenoptera, and Neuroptera. As more species are discovered, however, increasing specialization is recognized (147). Recent molecular studies may help clarify the taxonomy of this genus (149, 163, 194).

The local species is generally selected for release on the ecological basis that it is better adapted to the proposed climate, habitat, and host conditions (66, 197). For example, at least six species of *Trichogramma* have been used around the world to control *Ostrinia* spp. In their native regions, the most common are *T. nubilale* and *T. pretiosum* in the United States, *T. ostriniae* and *T. dendrolimi* in China, and *T. evanescens* and *T. brassicae* (=*maidis*) in Europe (Table 1). Use of the local species is the basis of inundative theory and is only contraindicated when there is no native species or when preintroductory screening suggests otherwise (66). Different species of *Trichogramma* compete with each other (140, 182, 197). In diverse habitats, this competition

Table 1 Field strategies for inundative release of *Trichogramma* species against lepidopeterous pests on various crops

Crop	Target genera	*Trichogramma* species	Releases			
			Number	Intervals (days)	Timing predictor	Total rate (thousands)/ha
Corn	*Ostrinia*	*brassicae*	2 – 4	7	Degree-day, pheromone	196 – 200 wasps
		brassicae	1 – 3	7 – 10	Light trap	300 wasps
		brassicae	1 – 2	7 – 14	Light trap	150 – 300 wasps
		brassicae	4 – 9	—	Pheromone, light trap	450 – 2,800 wasps
		brassicae	3	7 – 10	Light trap	150 – 300 wasps
		brassicae	2 – 3	8 – 9	Pheromone	200 wasps
		nubilale	22	3 – 4	Plant development	56.5 females
		nubilale	1 – 3	7 – 8	Degree-day, light trap	681 – 4,400 wasps
		nubilale	1 – 3	7 – 8	Light trap, degree-day	4,400 wasps
		nubilale	3	7 – 8	Egg-laying	3,195 females
		nubilale	11	1 – 2	—	48.4 wasps
		ostriniae	4 – 5	1 – 5	Egg-laying	91 – 420 wasps
		ostriniae	1 – 2	—	Egg-laying	75 – 120 wasps
		ostriniae	1 – 2	—	Egg-laying	225 – 600 wasps
		evanescens	2 – 5	8 – 21	Egg-laying	600 – 2,000 eggs
		evanescens	3 – 4	7 – 10	Egg-laying	90 – 180 wasps
		evanescens	1 – 3	10 – 15	Light trap	76 – 1,200 wasps
		evanescens	1 – 4	—	Egg-laying	100 – 2,400 wasps
	Cnephasia	*evanescens*	1	—	Egg-laying	108 – 900 wasps
	Ostrinia	*pretiosum*	11	1 – 2	—	550 wasps[e]
	Helicoverpa	*pretiosum*	11 – 18	2 – 3	Light trap	13,750 – 22,500 wasps
Cotton	*Helicoverpa*	*confusum*	—	—	—	300 – 600 wasps
		pretiosum	3	7	Plant development	62.5 wasps
		pretiosum	7 – 18	2 – 4, 7	Degree-day, pheromone	46 – 956 wasps
		pretiosum	14	1 – 12	Date	760 wasps
	Helicoverpa	*pretiosum*	—	7	—	100 – 200 wasps
Sugarcane	*Chilo*	*evanescens*	1 – 6	10 – 30	Egg-laying	375 – 4,500 wasps
		Multiple species	—	—	—	—
	Tetramoera, Chilotraea	Multiple species	8	2 – 7	Egg-laying	100 wasps
	Diatraea	*chilonis*	6	10–15	Pheromone	900 wasps
Spruce	*Choristoneura*	*minutum*	1–2	6–10	Pheromone, degree-days	600 – 30,900 females
Pine	*Dendrolimus*	*dendrolimi*	4 – 5	5 – 7	Egg-laying	1,050 wasps
Forests	*Dendrolimus*	15 species	2 – 3	5 – 7	Egg-laying	200 – 750 wasps
Oak	*Lampronadata*	*dendrolimi*	6	5	Egg-laying	30,000 wasps
Apple	*Cydia*	*dendrolimi*	4–6	10–15	Pheromone	1,000 – 4,700 wasps
	Adoxophyes	*embryophagum*	4 – 6	10–15	Pheromone	1,000 – 4,700 wasps
Fruit	*Adoxophyes, Grapholitha*	*dendrolimi*	3 – 5	5	Egg-laying	1,800 – 2,300 wasps
Citrus	*Cryptophlebia*	*toidea cryptophlebiae*	29 – 33	7	Plant development	2,300 – 3,800 females[f]
Pomegranate	*Deudorix*	*chilonis pomegra*	1–4	30	—	7,020 wasps[g]
Tomato	*Helicoverpa*	*pretiosum*	6 – 10	3 – 4	Crop planting	430 – 795 wasps
	Trichoplusia	*pretiosum*	6–10	3 – 4	Crop planting	430 – 795 wasps
	Manduca	*pretiosum*	6 – 10	3 – 4	Crop planting	430 – 795 wasps
	Helicoverpa	*ivelae*	13	7	Plant development	1,300 wasps
Pepper	*Ostrinia*	*nubilale*	20	1	Plant development	225 – 450 females
	Ostrinia	*brassicae*	6 – 12	3 – 19	—	9,000 – 48,000 wasps
Grape	*Eupoecilia*	*cacociae*	1	3	Pheromone	2,200 wasps
	Lobesia	*dendrolimi*	1	3	Pheromone	2,200 wasps
		embryophagum	1	3	Pheromone	2,200 wasps
Peanut	*Cadra*	*pretiosum*	9 – 14	2 – 7	Date	5.8 – 35 wasps[h]
	Plodia	*pretiosum*	9 – 14	2 – 7	Date	5.8 – 35 wasps[h]
Sugarbeet	*Autographa, Agrostisbuesi, Mamestra*	*dendrolimi, brassiecae, evanescens*	2 – 3	30 – 50	Pheromone	120 black egg
Cabbage	*Mamestra, Pieris, Plutella*	*evanescens*	3	10 – 12	Pheromone	120 black eggs
Brussel sprouts	*Mamestra*	*brassicae*	7	14	Egg-laying	1,400 – 3,150 wasps
Cocoa	*Conopomorpha*	*'toidea bactrae fumata*	12 – 90	1 – 7	—	13,000 – 31,000 wasps[d]
Rice	*Cnaphalocrocis*	*japonicum*	4 – 9	7 – 10	Adult emergence	400 – 900 wasps

[a] Increase in egg parasitism calculated as percentage in treatment areas minus percentage in the control areas, percentage reduction calculated as values in the control areas minus values in the treated areas divided by values in the control areas.

[b] No control plots cited.

[c] Reduction in larval numbers and damage compared in parasitoid- vs insecticide-treated plots.

[d] Releases made year-round.

[e] Number per plot, plot size not specified.

[f] Number per tree per hectare.

[g] Number per tree.

[h] Number per m^3.

[i] Potential for using *Trichogramma:* 0 = no potential; 1 = possible potential with better understanding of system; 2 = biologically feasible; 3 = economically feasible; 4 = being used commercially.

% egg parasitism increase[a]	Reduction (%)[a]		Rearing host	Notes	Potential[i]	Reference
	Target larvae	Damage				
57 – 86	—	45 – 87	*Ephestia*	Adults fed honey	2	214
75 – 93[b]	—	70 – 82	*Ephestia*		3	14
60 – 70	—	47 – 72	*Ephestia*	Staggered emergence	3	21
15	—	—	*Ephestia*		0	111
—	—	38 – 94	*Sitotroga*		4	155
62[b]	—	—	*Ephestia*		2	38
40	—	—	*Ostrinia*	Staggered emergence	2	81
0 – 63	50 – 100	0 – 31	*Ostrinia*	Staggered emergence	2	153
57	97	93	*Ostrinia*	Sentinel eggs	2	153
57	92 – 97	31	*Ostrinia*	Sentinel eggs	2	109
20	—	—	*Ostrinia*	Staggered emergence; sentinel eggs	2	152
39 – 87	44 – 75	42 – 57	*Dendrolimus*, silkworm spp.		3	154
≤90[b]	99	—	—		4	207
60 – 70[b]	—	90[b]	—		4	207
45 – 74	12 – 68	19 – 71	*Sitotroga*		1	185
—	65 – 93	—	*Sitotroga*	Staggered emergence	3	62
—	39 – 100	—	*Sitotroga*		2	69
—	8 – 90	18 – 97	*Ephestia*	Staggered emergence	2	124
11 – 71	—	—	*Sitotroga*	Staggered emergence	2	200
0	—	—	*Sitotroga*		0	109
—	12 – 74	—	*Sitotroga*		1	122
28 – 68[b]	11 – 81[c]	—	*Corcyra*		4	219
2 – 18	—	—	*Sitotroga*	Aerial release	0	78
0 – 76	7 – 27	0 – 31	*Sitotroga*	Aerial release	0	88,90
40	—	—	—		2	116
49	—	—	—		0	187
10 – 55	—	28 – 66	*Ephestia*, *Sitotroga*		2	44
32 – 67[c]	—	0 – 21[c]	—		3	220
73	94	—	*Corcyra*		4	2
87 – 91	—	67[c]	*Philosamia*, *Antheraea*		3	106
0.7 – 83	0 – 82	0 – 56	*Sitotroga*	Sentinel eggs; aerial release	2	173
80 – 96[b]	98[b]	—	*Antheraea*		3	72
45 – 90[b]	98 – 99[b]	—	*Corcyra*		4	181
29[c]	71[c]	—	*Antheraea*		4	46
—	—	42 – 63	*Sitotroga*	Staggered emergence	1	67
—	—	12 – 88	*Sitotroga*	Staggered emergence	1	67
64 – 82	60[c]	45 – 58[c]	*Antheraea*		4	46
15 – 45	54 – 60	49 – 61	*Cryptophlebia*	Sentinel eggs	3	128
49 – 86[b]	—	—	*Corcyra*	Sentinel eggs	2	156
31 – 74	—	0 – 83	*Trichoplusia*		1	134
3 – 47	—	0 – 38	*Trichoplusia*		1	134
18 – 68	—	0 – 87	*Trichoplusia*		1	134
—	—	55 – 98	*Sitotroga*		2	114
47 – 74	—	—	*Ostrinia*	Sentinel eggs	2	34
44	—	79	*Ephestia*	Sentinel eggs	2	112
—	—	4 – 61	*Sitotroga*	Staggered emergence	0	36
—	—	4 – 29	*Sitotroga*	Staggered emergence	0	36
—	—	10 – 35	*Sitotroga*	Staggered emergence	0	36
—	13 – 42	4 – 23	*Cadra*		2	30
—	6 – 21	5 – 19	*Cadra*		1	30
77 – 92[b]	—	80 – 92[b]	*Ephestia*		4	38
17 – 32[b]	—	—	*Ephestia*		4	38
7 – 47	0 – 48	17 – 21	*Sitotroga*		0	142
33 – 44	—	25 – 36	*Corcyra*		2	104
7 – 31	—	0 – 59	*Corcyra*	Adults fed honey	2	13

could lead to the elimination of local species or strains when non-native species are released (71a). A survey of local species should be conducted before parasitoids are released, because natural levels of parasitism, although sometimes negligible, can be as high as 40–100% (116, 204a). The recent move by national agencies in some countries to restrict the importation of organisms for biological control makes it important that effective native species be identified, especially during the first screening.

Once the species has been selected, the population (= strain) to release must be determined. *Trichogramma* display both interspecific and intraspecific variations in biology and behavior that are strongly influenced by environmental factors. These variations complicate the selection process further, and numerous studies have focused on phenotypic differences among strains (interpopulations). These populations have been compared in terms of development, fecundity, egg absorption, sex ratio, longevity, host age selection, oviposition, host preference, and activity (137, 145, 174, 189), as well as in terms of their response to environmental conditions (135, 138, 144, 176). A few studies have also addressed the occurrence of thelytokous (100% female offspring) or deuterotokous (almost all female offspring) populations and their fitness or fecundity relative to the more common arrenotokous (sex ratio of offspring, 50–75% female) strains (179, 209). The ultimate choice of strain will depend on how it ranks in terms of those biological attributes considered advantageous for the environment into which it will be released and the type of release to be conducted (e.g. inundative or inoculative).

The final aspect of selection is that of founding populations, i.e. where and how many collections (both individuals and populations) are needed to initiate a vigorous colony. This field is one of the least studied, because it is based on the population genetics, and almost nothing is known about the genetics of *Trichogramma*. A few studies have examined the genetic variability of traits, including fecundity (150), reactive distance (32), walking behavior (105, 204a), and sex allocation (203, 205a), but the genetic base for biological differences among or within populations (intrapopulations) has been rarely examined (204). Traditional wisdom, based on balanced gene systems in diploid organisms, suggests that a minimum of 500–1000 individuals should be used to found a population with high levels of heterozygosity (192); this approach has been taken in the former USSR (59). *Trichogramma* are haplodiploid organisms (most females arise from fertilized diploid eggs, and most males from unfertilized haploid eggs), however, and are characterized by high rates of sib-mating [an estimated 55–64% in the field (84)] and naturally low heterozygosity (163). This feature suggests that the degree of heterozygosity normally required to maintain a vigorous colony of a *Trichogramma* species might be less than expected and that healthy colonies may be founded with fewer than 500 individuals. Considerable work is needed to develop an understanding of if and how *Trichogramma* maintain sufficient levels of variation under conditions of small population size.

Parasitoid Quality

Variation within populations allows the selection of high-quality parasitoids. Populations for inundative release are often selected on the basis that those with high fecundity, emergence, sex ratio (percentage of female offspring), longevity, host preference for the target species, host-searching activity, and tolerance to local weather conditions will be best. A population with these characteristics is defined as a parasitoid of "high quality," because these traits are assumed to be ecologically important for these parasitoids when released inundatively. For those used in inoculative releases, such characteristics as development rate, oogenesis, and competitive ability are also important. Unfortunately, one strain is seldom superior in all attributes, and it is often unclear whether high-quality strains in the laboratory are synonymous with effective parasitoids in the field. In addition, some of those attributes that make the parasitoid effective in the field may not be advantageous in mass rearing (e.g. those that prefer the target species may be more difficult or impossible to rear on a factitious host), and trade-offs must be made in terms of the desired traits (192).

Numerous authors have examined individual components of quality, including fecundity (8, 39, 161, 204a, 217), development rate (8, 35, 61, 160, 174, 204a), oogenesis (182), emergence (39, 175, 204a), sex ratio (10, 145, 202), longevity (9, 10, 35, 39, 174, 175, 204a), host acceptance and preference (8, 64, 65, 137, 141, 189), host searching and activity (85, 183), and the effect of the environment (144, 165). Attempts to link these qualities have been rare, and the current recommendation is to measure a few individual variables (93). A few studies have attempted to combine these traits into a single predictive value (18, 36a, 47, 161). Only locomotion (walking), however, has been shown to be a good predictor of field efficacy in *Trichogramma* to date (18, 151, 197, 204a).

One of the more controversial measures of parasitoid quality has been size. Individuals of a *Trichogramma* species will vary in size according to the host egg in which they are reared (8, 26, 39). Body size in *Trichogramma*, as measured by hind tibial or wing length, has been generally shown to be positively correlated with biological characteristics, such as fecundity, longevity, rate of search, and flight (8, 17). To some extent, this relationship appears to depend on the physiologic state of the parasitoid. The correlation is stronger for adults that are fed honey than for those that are not (9), for those that are presented with large host eggs than for those presented with small ones (26), and for those that are reared on small host eggs than for those reared on large ones (83). In the last case, although increasing parasitoid size from larger host eggs resulted in higher levels of fecundity, the variation among individuals was so high that the authors considered size an unreliable measure of parasitoid quality. Pavlik (146) has recently found that the length of the hind tibia is a poor predictor of quality. Size therefore seems to be an uncertain predictor of quality, although further studies are warranted because it is so easy to measure.

There is a strong need to establish measurable parameters that assess parasitoid quality accurately and to standardize them internationally for the commercial use of *Trichogramma* (66). The current recommendation of the International Organization for Biological Control working group on Quality Control of Mass Reared Arthropods (IOBC-QC) is to conduct an intensive preliminary screening of candidate strains and species for all possible biological and behavioral traits (17, 93). This screening is considered important, because these populations will form the basis of the rearing and release program and should be selected carefully. The subsequent assessments of quality that must be made throughout the rearing and distribution processes should be less intensive and more focused on attributes that can be measured quickly (17). (See section on Parasitoid Rearing.)

PRODUCTION SYSTEM FOR MASS REARING

Once a parasitoid colony has been selected, the next step is to rear large numbers for release. This process has been accomplished in various ways during the past 70 years and has been the focus of considerable attention (14, 42, 49, 59, 62, 95, 100, 117, 119, 129, 201, 204a). Mass production of *Trichogramma* is a growing field, and many facilities have been established or expanded in the past five years (127).

Two types of rearing systems have evolved: those with short-term high daily output and those with long-term low daily output (17, 127). A range in production from 4 to 1000 million parasitoids/day has been found, depending on the mode of output; short-term output usually has the higher values (95, 100, 119, 129). Consistent levels of output of 100 million female parasitoids/week, although rarely specified, are not uncommon for the larger facilities (127).

Major commercial facilities are currently found in Europe (France, The Netherlands, Switzerland, Germany), the United States, Canada, and Mexico, as well as in large-scale, government-supported facilities in China, the former USSR, and Brazil (127). Numerous other smaller facilities can be found throughout the world (South and Central America, Australia, southern and eastern Europe, South Africa, India, and southern Asia) with various forms of government, private, and cooperative support (11, 45, 54, 127, 169, 170). Most of the larger facilities produce parasitoids on a year-long basis, whereas the smaller facilities produce parasitoids for local periodic releases (127). Many of these facilities sell wholesale to international suppliers; Hunter (73) recently published a list that shows 78 suppliers of *Trichogramma* in North America.

Production companies are understandably hesitant to discuss their internal processes and standards (192). Leppla & Fisher (98) thought that it was important for industrial producers of beneficial insects to standardize their rearing of *Trichogramma.* They designated three essential areas that are being adopted currently by the industry: product, process, and production control. Aspects of process and production will probably remain somewhat guarded, as these deal with relationships between inputs and outputs within the facility. Examples of these aspects include weights or volumes of eggs produced for given amounts of grain used, for production box/unit, or for adult hosts; daily or total capacities of individual host or parasitoid production units; and costs per unit (66, 95, 117, 197). Product control is related to parasitoid quality and is discussed in the section on Parasitoid Rearing. In addition to these production lines, facilities must also consider internal economic aspects, such as initial capital costs, reusable components, automation, and space, as well as the health and safety issues of cleanliness and potential for allergies (G. Eden, Eden Consulting, Guelph, Ontario, Canada).

There are generally only two biological components in a mass rearing facility: the rearing host and the parasitoid. Most larger facilities have these compartmentalized into smaller units for host production and parasitization [most in the West are modeled after the boxes of Morrison & King (119)]; these units are then replicated in the facility according to the desired level of output. A common factor in almost all facilities is that they allocate at least two thirds their space and energy for the production of the rearing host(s) and the remainder for the parasitoid (17, 127).

Rearing Host

Two major biological aspects of host rearing are the species to use (including artificial host eggs) and whether the eggs can be stored to extend the production period of the facility. To date, the consequential choice in host rearing has been limited to species that produce either small or large eggs.

Flanders (49) originally proposed a small host egg, the Angoumois grain moth, *Sitotroga cerealella*, and producers in slightly more than half the countries today use this species (Table 1). Several countries, including France and Canada, have switched to the Mediterranean flour moth, *Ephestia kuehniella*, because of better production from the rearing medium, ease in mechanization, and improved sanitation conditions. The third small egg species, the rice meal moth, *Corcyra cephalonica*, is used in various Asian countries because of its local availability. No trials have compared parasitoids reared from *Corcyra* with other small egg species. Repeated studies have shown, however, that

Trichogramma emerging from either *Ephestia* or *Sitotroga* are equivalent in the field. Somewhat better performance has been noted in the laboratory by parasitoids from *Ephestia,* possibly because of their slightly larger size (15, 22, 39, 68, 124).

Approximately four large host egg species of Lepidoptera have been used to rear *Trichogramma;* three of these species are from China. The silkworm hosts are considered commercially viable because their eggs are readily available as a by-product of silk production (100), whereas *Ostrinia nubilale* has been used primarily for research (34, 81, 109, 152, 153). When reared on these large host eggs, *Trichogramma* wasps may be of much better quality (e.g. larger size and higher percentage of females) than when reared on small host eggs. Thus, facilities can continuously produce either large numbers of small (low-quality) parasitoids or low numbers of large (high-quality) parasitoids. The feasibility of using species that lay large host eggs in commercial production has not yet been compared with that of species that lay small host eggs, despite the potential for increased parasitoid quality.

A relatively recent development in *Trichogramma* rearing is in vitro production on artificial host media (57). This area has been researched in China since 1975 (100, 102). Two approaches have been taken. In the first approach, the natural insect egg hemolymph is partially replaced with egg yolk and milk solids (197). In the second approach, a completely artificial diet is created from biochemical analysis of the insect and its egg (123, 213). Eighteen species of *Trichogramma* have now been reared from egg to adult in various forms of artificial media (57). The closest system to commercial production is that developed for *T. dendrolimi* in China on the basis of insect hemolymph (57, 204a). This diet has been packaged in plastic host egg-cards (produced at 1200 egg-cards per hour), and the resultant parasitoids have been used on more than 1300 ha with parasitism equal to parasitoids from natural host eggs (41, 204a). The development of completely artificial hosts is an important goal and, when realized, will lead to major reductions in the size of facilities, the cost of the product, and changes in the strategy for implementation in the field.

An essential part of producing the rearing host is some means of storing the eggs to ensure a continuous supply; sterilization and cool temperatures are the most common features. Sterilization increases the storage and flexibility of unparasitized small host eggs (e.g. by preventing emergence of cannabalistic larvae) and is achieved by either cold storage or freezing for short periods of time or by irradiation using ultraviolet or gamma sources (14, 29, 41a, 55, 197). Bigler (14) reported a maximum storage of four weeks for irradiated *Ephestia* eggs held at 2°C and 90% RH, and Vieira & Tavares (196) recently suggested that eggs still can produce high-quality parasitoids after storage at 0.7°C and 60% RH in the dark for up to 3.5 months. A more promising approach to long-term storage is liquid nitrogen for all types of host eggs.

High-quality parasitoids have been produced both in China, where eggs of both silkworm and *Corcyra* have been stored from 8 to 30 months in liquid nitrogen and have produced high-quality parasitoids, and in the United States, where eggs of *Sitotroga* have been stored for 21 days (199).

Parasitoid Rearing

To ensure high product quality and to avoid contamination, facilities usually rear only a few parasitoid strains or species at any given time (59). Improved techniques for identifying different populations rapidly by using DNA markers are being developed, and their integration into facilities may help screen for such rearing problems (163, 194).

The ratio of the number of parasitoids to host eggs in the parasitization units is also important. High ratios may lead to superparasitism, high numbers of male progeny, and poor product quality, whereas low ratios may result in poor parasitization and inefficient use of host eggs (40, 164, 205a). The acceptance and allocation of offspring in host eggs by *Trichogramma* are influenced by the density of the host (87, 92, 139, 157), and parasitoid fecundity or clutch size is adjusted according to host availability relative to abundance (10, 50, 179), host egg size (167), and spacing between eggs (166). Ratios of females to small host eggs of 1:10 are often used to maintain parasitism of 70–80% and sex ratios of 50–80% females in rearing facilities.

Once uniform parasitism of the host eggs has been achieved through manipulation of lighting and temperature (119), their emergence must be programmed. Programming can be as simple as allowing the parasitoids to complete development at a specified temperature and photoperiod (114) or it may involve more complex manipulation of environmental conditions to achieve synchronization, long-term storage and delayed emergence. In general, storage at low temperatures (6–12°C) during the pupal stage is considered best for *Trichogramma* (76, 218), although such storage has never extended much longer than two weeks without losses in parasitoid quality (196). Those species that are more cold hardy [e.g. *T. brassicae* (=*maidis*), *ostriniae, evanescens,* and *dendrolimi*] and/or undergo diapause (initiated by temperature and photoperiod effects on the maternal generation and developing larvae, as well as possible host egg effects) can tolerate longer storage (24, 94, 218). The specific conditions that promote parasitoid storage and diapause are being pursued actively to allow rearing facilities to economize and maintain the genetic quality of their stock better (195, 198). Other factors that may affect the spread of emergence include superparasitism and intrinsic competition (40).

The maintenance of parasitoid quality is critical to the reputation of a production facility, and the quality may be compromised after rearing *Trichogramma* for many generations under uniform conditions and on an atypical host. Two important changes can occur: loss of tolerance to natural physical extremes and loss of preference for the target host. The first change has been rarely studied, although rearing the parasitoid under fluctuating temperatures has been recommended to maintain tolerance. Unfortunately, this recommendation is difficult to implement in a commercial rearing facility (17, 201).

The loss of preference for the target host is a controversial area, because this effect has been demonstrated for some *Trichogramma* species (59, 125, 188) but not for others (25, 80, 145, 215). Approaches taken to counter this effect include the setting of maximum limits for the number of generations that can be reared in the facility, periodically switching the parasitoids to different hosts, or both. The first approach is used in France, where 100 female *T. brassicae* are collected annually and maintained in isofemale lines for three generations and then mixed together for a maximum of 20–25 generations (52). In Switzerland, *T. brassicae* is reared for a maximum of six generations on *Ephestia;* if kept longer, it is switched to the target host (14). This switching to the target or any factitious host is also recommended in Germany, Australia, and the former USSR (59, 64, 169, 188), although parasitization problems can occur in the initial generation (25).

Laing & Bigler (93) and Gusev & Lebedev (59) recommend the use of standardized biological and behavioral tests to monitor quality in rearing facilities. Recent work with molecular markers may help identify genetic shifts in populations (163, 168, 174). Whether quality changes occur in continuous rearing must be determined to support recommendations for rejuvenating commercial cultures routinely.

DISTRIBUTION OF *TRICHOGRAMMA*

Although stringent controls may ensure that parasitized host eggs leave a production system in good condition, they do not guarantee that the eggs will be released this way (192). With the exception of the work by Bouse & Morrison (27), no attention has been given to the distribution (formulation, packaging, storage, and transport) of *Trichogramma* to the field. This problem exists because the rearing process and the field trials often are separated not only by time and distance but also by the persons involved. Conversely, many trials are small scale and local and are rarely repeated experimentally. Unfortunately, lack of attention to proper delivery of the product can negate all other efforts.

Several field studies cite transport and subsequent parasitoid problems as the cause of poor success (173, 185). Most shipping problems occur during hot conditions or when the rearing facilities are a considerable distance from the release sites (>200 km). Both these situations jeopordize survival or the programming of parasitoid emergence. Bouse & Morrison (27) developed an insulated, thermocouple-regulated box for shipping parasitized eggs to the field. Research is needed, however, to compare the different modes of transport (various ground routes vs air) and to determine the advantage that insulation, ventilation, or air circulation in the containers might provide. We also need to apply what we know about temperature and storing *Trichogramma* to problems during shipping.

Problems seen in the field are not surprising. Material often is packaged and shipped without detailed instructions regarding what it is and how it should be handled. Standard measures of ensuring product quality to the user must be implemented. Laing & Bigler (93) have proposed the use of labels for each shipment to guarantee biological data as well as the number of viable female parasitoids/unit. Individual countries are now setting legal requirements for such labels in the registration of these new pest control products.

Laing & Bigler (93) also have recommended that users take subsamples of parasitoid material to test its quality before release. This step is feasible when those who receive the material in the field (e.g. researchers) understand the technical and biological details of such tests. In a commercial operation (e.g. growers), however, this level of expertise may not always be available. Once in the field, there is often no extension support for the grower, and it may not be possible to keep parasitized eggs under acceptable conditions for long-term storage. Hassan (in 169) emphasized the extreme importance of cooperative extension in the successful implementation of a *Trichogramma* program. In Europe, extension agents monitor corn fields and distribute parasitoids to farmers only after the first moths are collected. Standardized procedures need to be established, and *Trichogramma* releases need to be integrated into all aspects of the farming system, with the support of consultants, users, and the public; these steps are lacking currently.

Smith (172) has presented the various methods of releasing *Trichogramma*. Almost all studies have used ground releases, usually from point sources in research trials or from commercial application where labor costs are low. Point sources have been containerized to reduce the effect of predation and inclement weather (19, 67, 153). Large-scale broadcast release from the ground has been developed only in the former USSR and the United States. These two countries, with Canada and China, are also the only ones to have released parasitized eggs in broadcast aerial applications from aircraft or helicopters, either alone or with extenders of grass seed, water, and sawdust (27, 59, 173). A new ultraviolet motorplane, which can treat at rates of 30 ha/h (195), has recently been described for use in France. In addition, a new liquid application system is currently being developed in the United States (S. Penn, Beneficial Insectary, Oak Run, California). Different modes of release technology that direct the material to the targeted location better, such as small, remote-controlled model airplanes, mechanized ground applicators, and global positioning systems, merit continued investigation. This has been a neglected area, and each crop/ pest system will have different requirements.

STRATEGIES IN THE FIELD

Approaches for Release

After large numbers of parasitoids have been reared and distributed to the field, they are ready for release. *Trichogramma* have been used in all three biological control approaches: introduction, inoculation, and inundation. Inundative releases achieve an immediate, nonsustaining reduction in the host population. In inoculative releases, however, it is the progeny of parasitoids released at the beginning of the season that have a later effect on the host population. Inundative releases have predominated in the West (14, 62, 88, 89, 90, 173), whereas countries in Asia and parts of the former USSR have put emphasis on inoculation and occasional introductions (201, 208). Warmer climates favor multivoltine pests and inoculative releases, because the parasitoids can multiply during a long growing season. Inundative releases, which are timed specifically to the ovipositional period of the pest, are more appropriate in northern climates with uni- or bivoltine host species. Several countries use both strategies through the repeated annual applications of *Trichogramma* (44, 101, 201). In China, a slight modification of the inoculative approach has been used; *Trichogramma* are released in vegetable gardens adjacent to the target crop in ratios ranging from 1:5 to 1:14 (release garden:target crop) (208). Introductions of new species have occurred in India (156), North America, and Russia (12).

The different approaches to the use of *Trichogramma* have resulted in two different perspectives: the inundative approach, which tends to view the parasitoid as a fast-acting replacement for chemical insecticides, and the inoculative/ introduction approach, which sees the parasitoid as one aspect of integrated pest management. Considerably less experimental research has gone into inoculative releases than into inundative releases because of the ecological complexity involved and lack of funding. This situation is unfortunate, because the few integrated studies with *Trichogramma* and microbials, such as *Bacillus thuringiensis* (Bt), *Nosema,* and *Beauvaria,* have been positive (54, 121, 173, 201, 212). Several authors suggest that releases of more than one species of *Trichogramma* will improve efficacy (38, 67, 169), and some countries have combined *Trichogramma* releases with those of other parasitoids (e.g. *Habrobracon*) to provide acceptable levels of control for pests in cotton, tomato, and pine (201, 212). In Colombia, releases that integrate *Trichogramma* with both Bt and *Apanteles* or *Telenomus* have reduced the use of insecticide by 50% on tomato and cassava (121).

Trichogramma releases may have an immediate effect not only on the target pest, but possibly on other insect populations as well (197). Direct effects may be seen on nontarget Lepidoptera in the crop and surrounding area, and indirect effects may be seen on the natural enemy complexes associated with them (71a). Only one published work has addressed this area. Lopez & Morrison (108) showed that predators of *Helicoverpa* in cotton where *Trichogramma* wasps were released were unaffected compared with insecticide plots. Little research has been conducted in this area, because agricultural systems tend to be self-contained and are already disturbed monocultures of low natural diversity. Boreal forests are much less disturbed; in Canada, work in the area is currently under way to assess the effect of *T. minutum* releases on nontarget Lepidoptera, as well as native larval and pupal parasitoids of the target pest (RS Bourchier & SM Smith, unpublished data). The effects on nontargets will become increasingly important, not only because of the worldwide interest in biodiversity but because producers are now being asked to address this aspect before *Trichogramma* can be registered.

Timing, Frequency, and Rates of Release

The timing, frequency, and rates of release all depend on the approach taken. With inoculative releases, relatively few parasitoids are required very early in the season, possibly independent of the ovipositional period of the pest. In contrast, inundative releases require large numbers to be synchronized closely with the start of oviposition of a uni- or bivoltine pest (172). The earlier oviposition can be predicted, the better for the rearing facility and the field program. If large numbers of parasitoids are needed in a short time, then some facilities may require several weeks' or months' notice.

Different methods, including calendar date, plant development, pheromone or light traps, egg-laying, and developmental degree-days, have been used to synchronize inundative releases with the start of host oviposition (Table 1). Plant development is the least accurate method, unless it is linked to pest phenology (34, 81). Although currently too variable to be used alone, the degree-days method (211) allows the greatest forecasting (approximately one month); this method is potentially the most valuable (122, 153, 173, 214). Light traps (14, 21, 111, 122, 155) and, where available, pheromone traps (38, 62, 89, 90, 111, 173) appear to be the best predictors, because they collect adult moths before oviposition starts (especially pheromone traps). Studies that compare trap catch, oviposition, and efficacy have shown consistently that the best results are achieved when the *Trichogramma* are released a few days before, rather than at the start of, oviposition (62, 63, 81, 173).

Synchronization with the host also means that programming of parasitoid emergence must be considered. Although most facilities ship parasitoid material ready to emerge, and the majority of releases have used material emerging within hours of release, this is not always the case. Some key strategies mix different stages of *Trichogramma* development, thereby staggering emergence, particularly if only one or a few releases can be made (Table 1; 14, 21, 62, 67, 71, 81, 152, 153, 173). This approach ensures that there are always some females actively searching throughout host oviposition (177). In practice, this approach is limited if the released eggs are exposed to predation or extreme temperatures.

The first release is usually aimed at just before host oviposition, not only to achieve high levels of parasitism but also to enable released material to multiply in the natural host eggs. Such an approach ensures that a continuous supply of superior-quality parasitoids is produced from the target pest in the field (14, 96, 176). This field multiplication reduces the need for many releases and is the basis for some of the more successful programs (14, 62, 67, 173). The release of unparasitized factitious host eggs concurrently with *Trichogramma* has also been proposed to provide for self-multiplication when the target pest is low (91).

The goal of most release programs is to maintain a level of more than 80% parasitism on freshly laid host eggs (91). When single releases and field multiplication do not achieve this goal, then multiple releases at various frequencies are used. Few studies have actually compared different frequencies of similar final release rates (155), although most use multiple releases (Table 1). The interval between releases is variable but averages 5–7 days (Table 1; 59). This interval often is based on unpublished studies of parasitoid longevity (67, 81, 173) rather than on direct measures of survival in the field.

Similarly, the actual rates of release vary considerably, even for the same pest, crop, and country (Table 1). For example, the total rates of release for *T. brassicae* (=*maidis*) alone, which is reared from small host eggs against *Ostrinia* in Europe, range from 150,000 to 2.8 million wasps/ha. Rates in the several millions of wasps/ha are generally cited in arboreal situations, such as forestry (72, 173), and in fruit or nut orchards (46, 67, 128, 156), whereas those in agricultural crops, such as corn, cotton, and tomato, range from 500 to more than 1 million wasps/ha, with averages of 200,000–600,000 wasps/ha (Table 1; 59). This range is probably related to the range in dimensional volume of the crop. China often reports lower rates than other countries, possibly because of the frequent use of large host eggs (207).

Much of the confusion in application rates results from the inconsistency with which they are reported. The rearing host often is not identified, and numbers may be cited per release rather than the total number per hectare. In addition, some individuals refer to numbers of host eggs, whereas others refer to numbers of parasitized (black) eggs, wasps/parasitoids, or females per hectare. To compare these values, assumptions must be made regarding parasitoid size and quality, parasitism rates (usually 60–70%), emergence rates (usually

80–90%), and sex ratio (usually 50–70%). This lack of uniformity makes it difficult to compare studies and provide specific information on which rate should be used.

The reason why different rates of application are selected is not usually given, although an expected ratio of female wasps:hosts on the order of 1:2 or 1:10 for egg masses and 1:20 for eggs and the volume of the crop are often starting points (4, 12, 81, 152). More emphasis has been placed on establishing the correct spacing of points for given release rates or their vertical location within the crop (1, 81, 171, 214). Higher rates generally result in better parasitism. This is not always the case, however, as many factors influence the outcome of the release.

Factors That Affect Release

Weather, the crop, host, predation, use of pesticides, and parasitoid quality all influence the release and disappearance rate (4) of *Trichogramma*. Weather is probably the most pervasive, in that it is a complex of meterologic variables that affect the development, emergence, survival, activity, and fecundity of *Trichogramma*. The most influential components are temperature and humidity; in the extreme, both these components have been linked to poor field results (89, 90, 111, 154, Hassan in 169, 173, 176, 214). Parasitoid development is directly related to temperature; thus, extremes in the field disrupt not only survival and performance but also the programming of emergence. From laboratory work, most species apparently perform best (in terms of activity and fecundity) at 20–29°C and 40–60% RH, with lower thresholds of 9°C and 25% RH and higher thresholds of 36°C and 70% RH (35, 51, 92, 107, 137, 144, 204a). Rare field studies suggest that *Trichogramma* avoid dew (85), extreme temperature (85, 92, 204a), areas of bright light intensity (72, 92, 176, 204a), heavy rain (92), and winds greater than 1.1 km/h (72, 85). Thus, if inclement weather cannot be avoided, the rate and frequency of release must be adjusted upward, with specific regard to changes in the pattern and extent of emergence.

As the bottom component in the tritrophic interaction and the principal factor in habitat location, the crop is another important variable for *Trichogramma*, as it has both physical and chemical effects. Different levels of parasitism can be found on the same host in different crops (3, 86, 113, 133), and *Trichogramma* are much more habitat-specific than host-specific (85, 132, 183). Because *Trichogramma* are thought to search for host eggs randomly, parasitism is directly proportional to the size of the plant (1), its surface area (5, 21, 34, 81, 112), and the complexity (number of planes and angles) of the plant (5, 85) and its leaf surfaces (82, 183, 186). From the chemical perspective, the plant provides volatile cues (synomones) that, although not specific or long range (132), arrest and stimulate searching and parasitism in *Trichogramma* (3, 130, 133). These factors all influence the rate of release necessary and the resulting expected level of parasitism. Andow & Prokrym (4) suggest that the rate of release should be standardized by always expressing it in terms of the surface area of the plant (e.g. numbers/m^2).

The abundance and location of the host also influence *Trichogramma* releases. Parasitism tends to be higher in areas that have more hosts (11, 86, 171), although some releases have not shown this response (36, 216). *Trichogramma* generally demonstrate either independent or Type 2 functional responses to host density (87, 157, 176), with better parasitism seen in hosts that lay eggs in clusters rather than singly (193). Most species use kairomones to locate hosts from varying distances and sizes and shapes of the eggs on closer [e.g. 1.8 mm (136)] examination. In addition to plant cues, sex pheromones (99, 131), chemicals on the wing scales of the host moths (58, 178), and chemicals on the surface of the host eggs (46) all delay flight initiation, suppress positive phototaxis, intensify searching, increase retention time, and decrease speed of movement (131). Releasing kairomones with *Trichogramma* has given both positive (in cotton; 58) and negative (in spruce forests; 77) results. Conditioning the parasitoid during mass rearing to the kairomone of the target host, however, also has been positive, although this method has been tried only to a limited extent (58, 204a).

If emergence of *Trichogramma* is delayed in the field, then high losses may occur through predation. Depending on the diversity and location of the crop system, major predators include *Geocoris, Nabis, Orius, Hippodamia, Coleomegilla, Chrysopa*, ants, spiders, and small vertebrates. Predation of released material can be significant, with losses up to 50% in corn (21, 214) and 91–98% in cotton (79). Studies suggest that anthocorid predators are more likely to accept unparasitized host eggs than those that contain pupae of *Trichogramma,* although younger stages of *Trichogramma* are equally susceptible (31, 159). It is difficult to predict which predators will be the most significant in a system, as this aspect depends extensively on the climate, structure of the plant community, and cultural practices. Attempts to reduce predation have been made by using specialized wax capsules for release points (197). The effect of predation on the efficacy of *Trichogramma* releases merits increased focus, as it significantly influences cost and success of releases.

Pesticides also have been shown to reduce the effect of *Trichogramma* significantly (89, 90, 103, 115, 169). Many studies have compared the relative toxicity of pesticides, including insecticides, fungicides, and herbicides, to *Trichogramma* in screening trials (28, 53, 100, 120). In general, parasitoids are affected more by insecticides than by the other two groups, with the greatest mortality of adult *Trichogramma* seen 5–10 days after the use of selective pesticides, 15 days after moderately toxic pesticides, and 20–30 days after toxic pesticides (33, 59, 75, 216). *Bacillus thuringiensis* does not appear to affect parasitism when fed to adult wasps but can reduce parasitism when applied to the surface of host eggs (162, 184). Immature stages within the parasitized host eggs are generally unaffected, especially by selective pesticides, whereas adults are extremely sensitive (92, 102, 184, 201). Voegelé (197) has suggested that the sensitivity of *Trichogramma* to toxic pesticides may extend up to 1 km from the application site. With a few exceptions (204a), the use of *Trichogramma* in the same crop system as toxic pesticides must be carefully planned, as the two are generally incompatible.

Parasitoid quality is the final component that affects releases. Quality (longevity, fecundity, and searching capacity) can be increased two to ten times by providing a food source to adult wasps (9, 97, 176, 201, 215). In the field, this food source may be obtained from host feeding, nectar (6, 210), and plant fluids of damaged leaves (85). Although we know little about plants as nurseries or refugia for *Trichogramma*, several countries use plantings of nectariferous plants successfully, either in the fields or in adjacent areas (101, 201). If these plants are not widely available, one way of improving parasitoid quality is to supply a sugar source (e.g. honey or molasses) with the parasitoids on release (214). This approach has also been proposed in rearing facilities, although neither approach has been undertaken commercially.

The selection for increased parasitoid quality, such as fecundity and tolerance to environmental extremes and pesticide residues, is important to the success of releases; yet, little research has been done in this area. Lopez & Morrison (107) found that continuous rearing under variable temperatures and light regimes did not produce more heat-resistant parasitoids; however, selection studies to improve tolerance to heat and activity in uniparental populations of *T. pretiosum* (7), fecundity in *T. brassicae* (148), and parasitism at 15°C in *T. minutum* (Tocheva & Smith, unpublished data) have all been positive. Work is needed to identify which traits have sufficient genetic variation to be selected for; how quickly selection can occur; how long it can last without selection pressure; and whether selection of one trait is linked to another, which would affect overall parasitoid quality.

The dispersal or movement of *Trichogramma* is important to releases from two aspects: uniformity of parasitism within a crop and reduction caused by dispersal outside the crop. These tiny wasps actually have two modes of dispersing: either on their own or through phoresy on adult moths. The latter has been largely undocumented; thus, little is known of its effect on releases. The former has been intensively studied, although only from the perspective of parasitism so that little is known about movement related to food, mates, or refugia (51, 85). Greenhouse studies suggest that there may be an early migratory phase for *T. evanescens;* on emergence, it responds to light by flying upward instead of searching for hosts (178).

The ability of *Trichogramma* to disperse on its own appears to be high within single plants but low between plants (81, 85, 171, 204a, 216), which suggests that the parasitoids avoid open areas where they lose their ability for directed flight. Most studies show that parasitism decreases with distance from the release point (18, 154, 204a, 216) with distances of 4–50 m. Upwind dispersal is usually impossible (85); thus, most studies find significantly greater parasitism downwind (20, 72, 171, 216). Although significant losses of 60–75% by parasitoids dispersing out of fields have been cited (5, 18), this occurrence generally is not considered a major factor. Vertical movement within the plant usually is related to the location of host eggs and the release point (1, 11, 126, 171, 204a). These studies suggest that few release points are necessary in crops with continuous foliage (9 points/ha); in those systems with individual plants, however, more information is needed to assess the relationship between distance of opening and disruption in movement within and outside the crop.

Efficacy of Releases

Various simulation approaches have been used to improve the efficacy of *Trichogramma* releases during the past 30 years. Most of these approaches have dealt with the timing or the number of parasitoids needed to achieve host reduction, in terms of host density (56, 91), parasitoid searching area (81), disappearance rate (5), and the population dynamics of the pest (177). Two other models have been developed to predict damaging host populations (211) and searching efficiency and parasitism relative to the field (37). The models that deal with application rates and timing suggest the following: 1. more than 80% parasitism is necessary to reduce pest populations (56, 91); 2. the rate of release will increase proportionally with leaf surface area and disappearance rate (5); and 3. the rate can be cut in half if the emergence of parasitoids is staggered (177). Field studies have verified most of these predictions. Simulation models warrant considerably more development, as all have increased our understanding and pointed to areas that need research emphasis.

One of the difficulties in assessing the efficacy of *Trichogramma* releases, as with application rates, is the variability with which they are reported (Table 1). Some studies cite only parasitism, others cite larval populations, others cite infestation level, and others cite weight or volume of produce. On top of this, some reports deal only with changes in these levels between control and treated areas, increases in parasitism and product, or reductions in pest, infestation, or damage. A particular problem in some studies is the reference to plots treated with insecticides as "control" plots. In other studies, true, untreated controls are never used (38, 46, 181, 207, 220). An additional complication occurs when the target host lays eggs in clusters (e.g. *Ostrinia, Choristoneura,* and

Dendrolimus), with reports of parasitism without reference to the cluster. Bin & Vinson (23) present a strong case for unifying the terminology in reporting such parasitism.

Most studies assess efficacy by measuring egg parasitism, usually of eggs laid by the target host in the field (Table 1). Unless these collections are made at the end of oviposition after sufficient time for all the parasitized eggs to be identified (e.g. turn black), however, this approach may underestimate parasitism (190). One way to solve this problem is to place sentinel eggs (e.g. factitious or target host eggs on cards) of known age in the field for a specific length of time (109, 152, 153, 173, 176). This approach provides a measure of daily parasitism, although recent work suggests that it also may underestimate parasitism, especially if the sentinel eggs are differentially attractive compared with the natural host eggs (37, 109). This problem points to the necessity of adjusting for this difference before final assessment.

Another fairly consistent measure of efficacy is reduction in pest damage (Table 1), as this has direct value for the grower. The least common assessment is the number of larvae/unit, possibly because of the labor required to sample (14, 21). Bigler et al (20) recently reported that comparing larval attack on treated and untreated corn underestimates real efficiency. Another less common means of evaluating the effectiveness of *Trichogramma* releases is M, an index of population trends from life tables (101, 143).

A relationship exists among egg parasitism, larval populations, and damage; however, this relationship has been rarely examined. Van Hamburg & Hassell (191) suggested that egg parasitoids were unlikely to reduce larval populations if mortality after the egg stage was density dependent. On the basis of analyzing the transformed results from 26 studies that report changes in both parasitism (%) and larval reduction (%) (Table 1), there does appear to be a loose but positive relationship between these two values ($R^2 = 0.54$; $p < 0.0001$). Although these data were collected from very different situations, they suggest that increases in egg parasitism by *Trichogramma* generally result in proportional reductions in larvae. Future studies must examine the relationships among release rates, parasitism, larval reduction, and damage reduction specifically to document the efficacy of this approach.

Trichogramma can be an effective form of pest control when compared with more traditional approaches in many parts of the world. Parasitoid releases in China, Switzerland, Canada, and the former USSR have all shown consistent levels of 60–80% parasitism, with reductions in damage of 77–92% on such crops as sugarcane, wheat, corn, and cole (101). In many cases, this level of control has been cost competitive, as it has either completely eliminated or reduced the use of insecticides and increased crop values three to eight times (101). The cost to buy or produce *Trichogramma* varies, but current retail figures in the West are approximately $0.30 US/1000 females or $200 US/million females (G. Eden, Eden Consulting). *Trichogramma* releases often cost more (e.g. up to 60%) than insecticides for the same level of control or are less effective for the same cost (21, 46, 72, 90, 128, 201). Several combined reasons can explain why *Trichogramma* is considered cost-effective, including lower threshold levels (e.g. *Helicoverpa* on cotton in the USSR vs the United States), a reduction in levels of residue or costs for insecticides, and promotion of increased natural enemy complexes that provide integrated control. As with most classical biocontrol work, the cost:benefit ratio of using *Trichogramma* can be very high. In the former USSR, the ratio has been estimated at 1:8; in three counties in China, it has been estimated at 1:25 (101).

FUTURE PROSPECTS AND NEEDS

The use of *Trichogramma* has made significant strides during the past 20 years, and this bodes well for the next decades. As with Bt and chemical insecticides, significant commercial achievements have been made with *Trichogramma* wherever major research emphasis has been placed (e.g. corn borer control). These achievements suggest that we have every chance of succeeding in those other host/parasitoid systems that remain unexplored. The taxonomy of this genera is now being worked out. This work is essential, for it is the basis on which other studies are built. Although considerable information is available on phenotypic variation, more work needs to be addressed to its genotypic base to determine whether the selection of a superstrain is possible. Similarly, although we have produced a large amount of data on parasitoid biology and behavior, we now need to condense these data into some coherent, standardized concept of parasitoid quality with appropriate means of prediction. Rearing facilities are now commercialized on a large scale, but there remains a need to examine different rearing hosts and artificial diets in automated systems to make major advancements.

One of the most important areas in the future will be the development of extension support to deliver the product to the user and allow them to get into the field in a form that can have an effect. Information regarding where, when, and how to release in different grower situations should be included with the product. This package, which will provide a service rather than a product alone, could come from either the producers, government extension, or private consulting. Best results with *Trichogramma* in the past have been based on trained personnel who provide this combination of biology and economic decision-making.

Stinner (180) concluded his review with an emphasis on integrating *Trichogramma* with other control options. The situation is no different today, except that we have more information on how to achieve this integration. All too often in the past, the genus *Trichogramma* has been approached as a replacement for chemical insecticides. Inoculative releases, in combination with selective insecticides (chemical or biological), other parasitoids, and nectariferous plants, such as refugia, need to be developed. Although release of *Trichogramma* is currently one of the most benign approaches to pest control, more attention must be paid to the population dynamics of the pest, the other natural mortality factors at work, and the native complex of natural enemies, in particular native *Trichogramma* species. This approach will ensure a better understanding of the effect of release on biodiversity and provide a minimally disruptive approach to pest management.

Finally, perhaps the greatest need is that of setting guidelines and standardizing terminology and measurements; this includes issues of taxonomy, quality control, and assessments of efficacy. Quality standards, such as seven-day fecundity and locomotion tests that are currently being set by the IOBC-QC, should be implemented with a view to incorporating new tests (e.g. DNA fingerprinting) as they arise (93). Researchers should ensure a minimal amount of information reported for all field studies, including the mode of release (ground, aerial, point with spacing); crop size (height or surface area); parasitoid programming (emergence pattern) and activity (longevity estimates); timing (first release relative to host), frequency (intervals), and rate of release (in number of females/ha); and assessment. In terms of assessment, untreated control plots, quantified absolute estimates of both final egg or egg mass parasitism (depending on target host) from natural hosts, and damage to the crop are recommended. All these types of data will help regulatory bodies produce sensible guidelines for registration, thus promoting rather than hindering the development of biological control agents such as *Trichogramma*.

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