Chapter 4

Egg Parasites (*Trichogramma* spp.) for Control of Sugar Cane Moth Borers

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1. Introduction

The family Trichogrammatidae (Hymenoptera: Chalcidoidea) is a natural group of egg parasites with few genera. Many of its species are cosmopolitan and the commonest, *Trichogramma* spp. (Fig. 1), which attack Lepidoptera, are prevalent as parasites of sugar cane moth borers (Eucosmidae and Pyralidae). Members of the Scelionidae (Hymenoptera: Proctotrupoidea) also parasitize the eggs of sugar cane moth borers, but their role is usually secondary to that of *Trichogramma*.

The importance of egg parasites in the natural control of sugar cane moth borers has long been recognized, and formerly any that hatched from borer eggs collected by field gangs (a classical method of borer control) were returned to the field (Bodkin, 1914; Dash, 1917; Quelch, 1914). From this to rearing parasites for liberation was a small step. With improved techniques for rearing *Trichogramma*, liberations took place on an ever-increasing scale, reaching their peak against *Diatraea* spp. in the Americas. The rationale of mass release was that at certain seasons (usually winter or harvest) the natural parasite population declines to a greater extent than the host population, and the host-parasite balance is only slowly re-established; liberations during this critical period, by supplementing the natural *Trichogramma* population, might hasten the restoration of the balance. Mass release of *Trichogramma* has been the subject of considerable controversy but, although largely discarded in the Americas, is still continued in India and the

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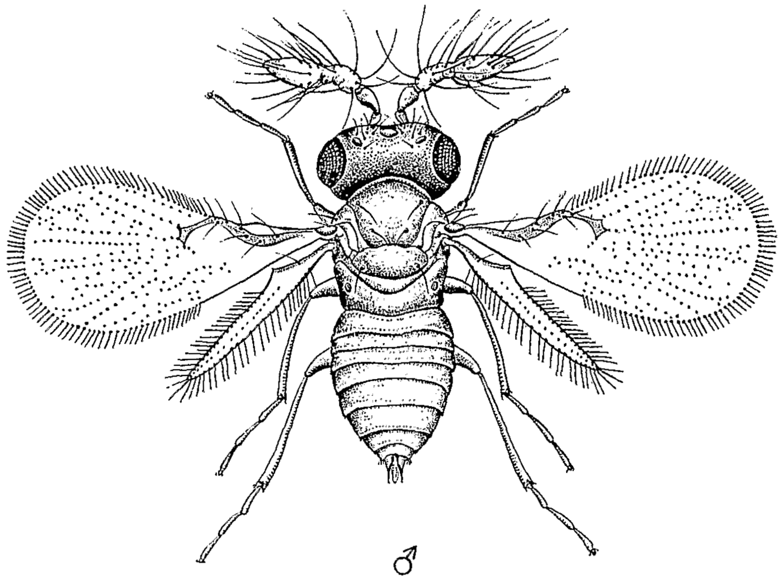

Fig. 1. *Trichogramma australicum* Gir., adult male, ×120.

Far East. Introduction of foreign species or races has until recently been of secondary consideration.

A full assessment of the part *Trichogramma* plays in the regulation of borer populations can be made only from data on borer mortality at all stages of development over a number of generations. Such data are not available. To determine whether liberation of *Trichogramma* is an effective means of borer control is a more limited objective, demanding an understanding of the biology and ecology of the parasite and careful assessment of results in the field.

2. Taxonomy and Distribution

The taxonomy of the genus *Trichogramma* used to be based solely on morphological characters such as the number and form of the wing cilia, and length of the fringes (Girault, 1912; Kryger, 1919). The existence of intermediate types and morphologically inseparable races more or less adapted to particular hosts and environments (Bare, 1935; Flanders, 1930*d*; Marchal, 1927; Moutia and Courtois, 1952; Peterson, 1930) led to much confusion but a complete revision of the genus has been made possible by the development of biological techniques (Quednau, 1956; Flanders and Quednau, 1960). The progeny of field-collected specimens are studied on several hosts under defined rearing conditions to determine fecundity, oviposition habits and rates of development. Further characters

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TABLE 1

THE DISTRIBUTION OF *TRICHOGRAMMA* SPECIES ON SUGAR CANE MOTH BORERS

Trichogramma australicum Gir.	China (as *T. evanescens* Westw.)	S.E. Flanders (1965 *in litt.*) after Box (1953)
	Formosa	Box (1953)
	Java	Box (1953)
	Madagascar	Box (1953)
	Mauritius	Box (1953)
	Philippines (introduced)	Estioko (1961)
T. japonicum Ashm.	Formosa	Box (1953)
	Philippines (introduced)	Estioko (1961)
T. nanum (Zehnt.)	Formosa	Box (1953)
	India	Box (1953)
	Java	Box (1953)
	Malaya	Box (1953)
	Philippines	Box (1953)
T. sp. ? *nanum*	Mauritius	Box (1953)
T. fasciatum Perk.	Caribbean islands	S.E. Flanders (1965 *in litt.*)
	North, South and Central America	S.E. Flanders (1965 *in litt.*)
T. perkinsi Gir.	Colombia	S.E. Flanders (1965 *in litt.*)

of systematic value are the colour of the adult reared at constant temperatures, and host and habitat (host-plant) preferences of the gravid female (Flanders, 1960; Quednau, 1960, 1961). At least six species of *Trichogramma* are morphologically distinct, but there are many others identifiable biologically (Flanders, 1960). Some of the groups formerly known as races have been or will be raised to specific status. The term 'race' in the literature on *Trichogramma* has no precise meaning.

The species of *Trichogramma* attacking sugar cane moth borers are in urgent need of revision. Already the species generally known as *T. minutum* Ril. has been identified as *T. fasciatum* Perk. in the Americas and *T. nanum* (Zehnt.) in India; the true *T. minutum* never occurs in conjunction with sugar cane, and *T. evanescens* may be entirely European (S. E. Flanders, 1965 and 1967 *in litt.*). Table 1 gives a provisional list of the cane field species and their distribution. Two of these, *T. japonicum* Ashm. and *T. nanum* (Zehnt.), have good structural characters, but the remainder can be separated only biologically (S. E. Flanders, 1965 *in litt.*). Elsewhere in the text specific names follow the usage of the author concerned.

3. Biology

Life history

The development of all *Trichogramma* spp. is very similar. The egg (0.1 mm in length) is inserted into the host and doubles its size before hatching. The larva, which is reduced to a digestive sac provided with two crochets (mandibles) framing the mouth, feeds in the vitelline mass or embryo of the host, in the latter instance the embryo being destroyed by a process of lysis. There are three larval instars, all sacciform. These are followed by a prepupa, when the adult characters form, and a pupa. At the beginning of the third larval instar, the host egg turns black due to the deposition of black granules at the inner surface of the chorion (Fig. 2), an invaluable diagnostic character for parasitized eggs (Brenière, 1965*b*; Flanders, 1937; Krishnamurti, 1938; Marchal, 1936; Moutia and Courtois, 1952). The development time for *T. australicum* on *Corcyra cephalonica* Staint. at 28°C is as follows (Brenière, 1965*b*):

Egg	24 hours
1st larval instar	21 hours
2nd larval instar	27 hours
3rd larval instar	48 hours
Prepupa	24 hours
Pupa	48 hours
Total	8 days

Development times at 30°C and 80% r.h. on *Ephestia kuhniella* Zell. are, for *T. minutum*, 6 days 4 hours, for *T. fasciatum*, 6 days 6 hours, and for *T. australicum*, 6 days 6 hours (Quednau, 1960). The adult emerges through a circular hole eaten through the chorion of the host egg.

Mating, which is very rapid, is not obligatory. Facultative parthenogenesis is general, being arrhenotokous in *T. australicum*, *T. evanescens*, *T. japonicum* and *T. minutum*, and either arrhenotokous or thelytokous in *T. fasciatum* (Marchal, 1936; Peterson, 1930; Quednau, 1960). The sex ratio, although variable, is usually of the order of two females to one male; females always predominate (Quednau, 1956).

Under laboratory conditions, the preoviposition period does not exceed 24 hours (Quednau, 1960), and *T. australicum* can lay in the first hour after eclosion (Brenière, unpubl. data). In the absence of host eggs, the female can refrain from oviposition even until death, but the life span is shorter (Lund, 1938; Salt, 1936).

Fecundity varies between 20 and 120 eggs per female according to the species, the host, and the longevity of the adult. Longevity is related to food supply (sugar and water) (Nayaranan and Mookherjee, 1955), availability of host eggs, temperature, humidity, and the activity of the female (Lund, 1938; Quednau, 1957).

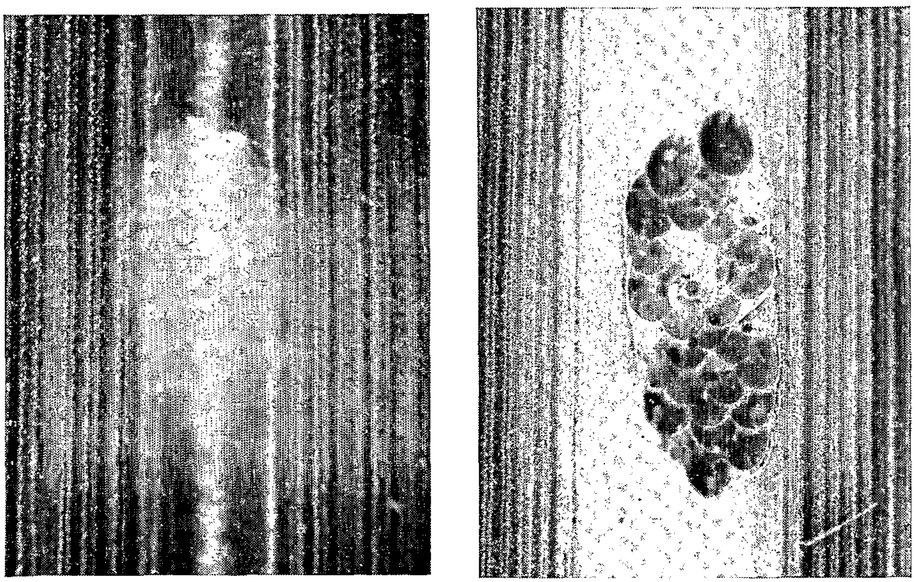

Fig. 2. Egg clusters of *Diatraea saccharalis* (F.) when freshly laid, *left*, and parasitized by *Trichogramma*, *right*. The parasitized eggs are black and some show the round emergence holes of the parasites. × 12.

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Under identical conditions with *Corcyra cephalonica* as host, the fecundity of *T. australicum* was 43, *T. fasciatum* 67, and *T. minutum* 76 (Brenière, 1965*d*).

The oviposition habit varies with species (Quednau, 1960). While *T. fasciatum* lays most of its eggs in the first 24 hours, *T. minutum* spreads them over 2–3 days, and *T. australicum* over 10–12 days.

Effects of physical factors

Temperature

Between certain upper and lower limits the rate of development increases with temperature, but the exact response varies with species (Quednau, 1957; Schepetilnikova, 1939). At the lower limits there is some resistance to cold, and diapause may occur, the threshold temperature being 15°C and 4°C for *T. minutum* and *T. cacaeciae* March., respectively (Lund, 1934; Quednau, 1957). The activity of the adults and fecundity also increase with temperature. The optimum is 28°C and 32°C for *T. cacaeciae* and *T. minutum*, respectively, but the grey race of the latter (probably *T. fasciatum*) develops more quickly than the yellow at high temperatures and more slowly at low (Flanders, 1931; Lund, 1934; Marchal, 1936; Peterson, 1930; Quednau, 1957). Consequently, seasonal and regional temperatures affect the potential of *Trichogramma*, particularly by way of the annual number of generations. This ranges from 2 for *T. cacaeciae* in Europe, to approaching 50 for *Trichogramma* spp. in the tropics (Brenière, 1963; Kuwana, 1930; Marchal, 1936; Peterson, 1930).

The darkening of the body of the adult is intensified at low rearing temperatures, and is characteristic of different species. The body colour of individuals reared at variable temperatures cannot be used as a diagnostic character (Flanders, 1931; Quednau, 1957). Quednau (1960) has established a colour spectrum based on the intensity of darkening when reared at temperatures of 15, 20, 25, 30 and 35°C.

Temperature affects the sex ratio through adverse effects on the vitality of the sperm. Schread and Garman (1933) noticed that an excess of males appeared in the progeny of *Trichogramma* adults kept for two weeks at 3–8°C.

Humidity

Adult *Trichogramma* are very susceptible to desiccation, and optimum humidity is between 80% and 100% r.h., varying slightly for different species (Lund, 1934). The immature stages are affected only to the extent that the hosts are, but host eggs laid on living leaves are unaffected by humidity provided the plant is transpiring normally (Peterson, 1930).

Light

Trichogramma adults show a well-marked positive phototaxis, and under natural conditions are found on the most exposed parts of a plant. Their activity increases with light intensity (Quednau, 1958), this reaction being important for host-finding. Under laboratory conditions, Costas (1951) noticed that parasitism was higher in light than shade, and attributed it to greater activity on the part of the adults rather than to better visibility. On the other hand, *T. evanescens* can distinguish the host and oviposit in complete darkness (Salt, 1937). Brenière (1965*b*) found that diffuse light caused a slight increase in oviposition. Quednau (1957) stated that light has no effect on rate of development, mortality or fecundity.

Behaviour — host-finding and oviposition

Host-finding is essentially a consequence of the exposed leaves of the cane plant being the point where adult *Trichogramma* tend to congregate and Pyralid borers prefer to oviposit. There is little or no attraction exerted over a distance by the host, the parasites being drawn to the host environment rather than to the host itself (Laing, 1938; Stein, 1961). Under natural conditions the chances of the host being found depend not only on the size of the *Trichogramma* population, but also on light and temperature which affect the general activity of the parasites.

Before drilling and oviposition take place the female determines the size of the host egg by drumming it with her antennae (Klomp and Teerink, 1962). The number of eggs per host egg increases with host size (Salt, 1934, 1937) being 1 in *Sitotroga cerealella* Ol., 2 in *Corcyra cephalonica*, 2–3 in *Diatraea saccharalis* (F.), 3–4 in *Chilo sacchariphagus* (Boj.) and 8–10 in *Papilio demodocus* Esp. (Brenière, 1965*b*; Metcalfe, 1959). These numbers are very variable, and under laboratory conditions superparasitism may occur (Brenière, 1965*b*; Lund, 1938). The parasite will oviposit or at least drill through the chorion regardless of the stage of development of the host egg (Brenière, 1965*b*; Clausen, 1940; Quednau 1960; Tothill *et al.*, 1930). Drilling, even without oviposition, inhibits embryonic development of the host (Martin, 1928).

Oviposition is hindered by a thick chorion (Salt, 1938). Tothill *et al.* (1930) found that the advantage lay with the larger species and races, for smaller ones were restricted to eggs with a thin chorion.

The female can distinguish parasitized eggs by the smell left by itself or other individuals (Salt, 1937) and oviposition in eggs already parasitized is avoided. Under the suboptimal conditions that sometimes arise in the laboratory this capacity is lost, particularly when there is an excess of *Trichogramma*. The result is superparasitism, too many eggs being laid in the same host, leading to competition among the developing larvae (Smith, 1916). In extreme cases development is not completed (Brenière, 1965*b*; Salt, 1936). Mild superparasitism

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leads to slower development, smaller adults with lower fecundity, and progressive degeneration of the breeding stock (Brenière, 1965*b*; Lund, 1938; Salt, 1936). Superparasitism might be expected under natural conditions, but has not been observed (Brenière, 1965*b*).

Adaptation

Trichogramma species and races have different host preferences, and specificity, although fairly loose under laboratory conditions, is undoubtedly stricter in nature. Each species or race may not only respond characteristically to the environment, but also become changed by the very conditions to which it is responding. Such adaptations are made possible by the short life cycle and the considerable genetic variability of the species. Mayer (1960) noticed that in dense populations new inheritable behaviour patterns emerged as ecological adaptations. This could explain the existence of several species or ecotypes within the same habitat. Stark (1944) found that *Trichogramma* reared at constant temperature and humidity congregated after liberation in zones where conditions resembled those of the laboratory. It is now accepted that *Trichogramma* reared at alternating high and low temperatures give better results in the field than those reared at constant temperature and humidity (Schepetilnikova, 1960; Stein and Franz, 1960). Similarly, Stein (1960) obtained better field results on *Carpocapsa pomonella* (L.) from a strain reared on *Galleria mellonella* (L.) at variable humidity and temperature, than from one reared on *Sitotroga cerealella* at 27°C and 80% r.h.

There is also adaptation to hosts. Brenière (1965*d*), experimenting with *T. fasciatum* and *T. australicum*, observed important differences in the ability to lay in eggs of *Chilo sacchariphagus*. *T. fasciatum* laid indiscriminately in the eggs of *C. sacchariphagus* or *Corcyra cephalonica* when it had been reared on the latter; conversely, *T. australicum*, which is a natural parasite of *C. sacchariphagus*, laid preferentially in the eggs of the species on which it had been reared. This adaptation, although it does not always occur (see Salt, 1935), could ultimately lead to the appearance during mass-rearing of strains entirely unable to lay in their original host. The nutritional qualities of the host through pre-imaginal conditioning produce a new inheritable adaptation in the adult (Flanders, 1935; Marchal, 1936; Mayer and Quednau, 1959; Telenga, 1956; Urquijo, 1946, 1951).

4. Significance of Egg Parasitism

Egg parasitism, as well as all other mortality and natality factors, is continually changing, so that its full significance is not immediately apparent. Isolated data on per cent parasitism, so frequently quoted in connection with *Trichogramma*, are of no value. Also, conclusions relating per cent parasitism and subsequent borer or egg populations, while ignoring other mortality and natality factors, are invalid. The importance of *Trichogramma* and other egg parasites may be interpreted only in relation to the host egg population per unit area (the absolute population). Egg destruction can be assessed, but to determine whether *Trichogramma* is a key factor in natural control would necessitate the intensive study of borer populations over several generations.

Many workers, including Barber (1936), Box (1932, 1951*b*) and Wolcott and Martorell (1943*b*), have noticed that the efficiency of *Trichogramma* as measured by per cent parasitism is related to the abundance of the host. Jaynes and Bynum (1941) found a direct linear relationship between the population of *Diatraea saccharalis* and per cent parasitism, with a correlation coefficient of 0.59. Correlation coefficients of 0.64 (subsequently corrected to 0.966, see p. 447) on *Chilo sacchariphagus* and 0.46 on *D. saccharalis* have been established by Brenière (1963) and Metcalfe and Van Whervin (1967), respectively. There is also some evidence for delayed density dependence and density independence (Metcalfe and Van Whervin, unpubl. data). The relative inefficiency of *Trichogramma* at low host densities is apparent. The inconsistencies among the correlations are probably due to different sampling techniques and sampling errors.

Competition between *Trichogramma* and other egg parasites and predators may be keen; nevertheless they all contribute to total egg mortality. The Scelionidae, especially *Telenomus alecto* (Crawford) in Barbados (Metcalfe and Van Whervin, 1967) and Argentina (Jaynes, 1932), and *T. beneficiens* in the Far East (Jepson, 1954), are important. *Trichogramma* is intrinsically superior to *Telenomus* in that it survives when multiparasitism occurs, and can kill and replace *Telenomus* up to the fourth day of its development (Jones, 1937; Metcalfe and Van Whervin, 1967). It is not known if this is important under field conditions. Predators (ants, mites, Blattids and Coccinellids) attack both parasitized and unparasitized eggs indiscriminately, and sometimes account for a large proportion of the eggs (Brenière, 1960; Metcalfe and Van Whervin, 1967; Wolcott and Martorell, 1943*b*; Tucker, 1933, 1935*b*).

The presence of other hosts for *Trichogramma* in or near cane fields has a direct bearing on the host-parasite balance. Myers (1935*a*) claimed that a significant wastage of *Trichogramma* would occur in their presence but, according to Tucker (1932), their availability in large tracts of cane is negligible. In the subtropical winter, alternative hosts guarantee the carry-over of *Trichogramma* when borer eggs are absent (Jaynes and Bynum, 1941; Anon., 1960).

During the early 1930's, the controversy as to the significance of egg parasitism when followed by a high early larval mortality hindered the settlement of the *Trichogramma* problem. Myers (1929, 1932*b*, 1935*a,b*) and Box (1932, 1933) maintained that early larval mortality was always over 90% and that it reduced the effect of egg parasitism by the same amount; thus the effective mortality achieved by 50% parasitism would be only 5%, and therefore of no significance. This is an obvious fallacy. Others (Hazelhoff, 1932; Pickles, 1936; Tucker, 1933) found that early larval mortality in fact varied within wide limits, and Tucker (1934*a,b*) and Pickles (1936), who followed Thompson's (1928) rational approach to the problem, showed that egg parasitism and early larval mortality were complementary. It is clear from hypothetical life-tables that changes in egg parasitism, particularly when it approaches 100%, could be an important factor in determining the size of borer populations.

5. The Host-Parasite Balance — Studies of Field Populations

Sampling methods

The basic requirement for population studies is a method of sampling to find the absolute borer egg population. This has not always been forthcoming. A method of estimating relative populations, popular in the U.S.A. and Puerto Rico, is the collection of eggs in a period measured in man-hours (Hinds and Osterberger, 1932*b*; Wolcott and Martorell, 1943*b*); various refinements have been introduced to avoid errors due to personnel differences (Burrell and McCormick, 1962; Wolcott and Martorell, 1943*b*). The main criticism is that height of cane and habit affect the area searched in a given time, so that data from one field at different stages of growth or from different fields may not be comparable. The absolute population can be estimated by collecting all eggs on selected stools or leaves (Box, 1932), but the time of oviposition and the fate of unhatched eggs remain a matter of conjecture. The best method is to sample from fixed plots, marking the eggs as they are laid and removing them when their eventual fate is known (Brenière, 1963; Gupta, 1951; Metcalfe, 1959; Simmonds, 1951; Tucker, 1933). By this means the number of eggs laid, the number that hatch and the extent of predation and parasitism, and the size of the *Trichogramma* population, may all be accurately determined. The only disadvantage is that, during periods of heavy oviposition, so much leaf tissue is picked off with the clusters that the suitability of the plant as an oviposition site may be temporarily affected.

Wolcott and Martorell (1943*b*) and Moutia (1943) estimated parasitism by counting the number of egg clusters attacked, but not all the eggs in a cluster suffer the same fate. Brenière (1963), working with very large samples, used a rapid visual scoring system for the level of parasitism in each cluster.

Dispersal of Trichogramma

The rate of colonization of fields of young cane from release points is determined by the dispersal of *Trichogramma*. Dispersal is largely passive, its direction and extent being influenced by wind.

Dispersal of *Trichogramma* in cane fields has not been studied in detail. Tucker (1951) relied on the wind for uniform distribution in Barbados, and Smyth (1939), although he did not give supporting data, stated that in Peru populations moved downwind from the release points at the rate of 1 mile/month, and that lateral and upwind movements were small or negligible. In Louisiana, experiments performed in April, when natural parasitism was nil, showed that *Trichogramma* moved downwind only 500 ft from the release points in three weeks (Hinds and Osterberger, 1932*a*). However, Jaynes and Bynum (1941), who placed test cards with *Sitotroga* eggs at known distances from the release points, found dispersal up to 75 ft in 24 hours, and 100 ft in 48 hours.

From parallel studies on *Heliothis* in corn, cotton and beans, Parsons and Ullyett (1936) concluded that dispersal of *Trichogramma* is rapid, extending from the centre to the outer part of 5-acre fields within 24 hours. The effect of wind was to form a cone of dispersal from the release point, modified by zones of concentration along field edges and sites of host abundance.

Fluctuations in the host-parasite balance

Fluctuations in the host-parasite balance result from many inter-related biotic, cultural and climatic factors. Climatic and cultural factors are dominant. During subtropical winters in Louisiana frosts kill the aerial portions of sugar cane, borer development stops, and the life cycle of *Trichogramma* is slow (Jaynes and Bynum, 1941). In the tropics, temperature stops neither cane growth nor borer development, but during the harvest period (determined primarily by climatic factors) cropping causes a drastic reduction of the borer population and changes the environment completely. Recolonization of fields by borers and borer parasites from older cane is facilitated by prolonged harvest periods. The effect of harvest is modified by the distribution and intensity of rainfall, which can act directly on both borer (Wolcott, 1915) and parasite populations, and indirectly through the growth of the cane.

The objectives in most population studies have been to follow trends in populations and parasitism over a period of time, relating them so far as possible to major changes in climatic and cultural conditions. Wherever the role of *Trichogramma* in the natural control of borers has been critically discussed, there have been pleas for more detailed fundamental data (Box, 1933; Jepson, 1954; Myers, 1932*a,b*). These have been produced on an adequate scale in a few regions; elsewhere observations have been casual, showing only the state of the host-parasite balance at a particular time.

North America — The size of the first generation of *Diatraea saccharalis* in Louisiana depends on the number of diapausing larvae that survive the winter (Hinds and Osterberger, 1936; Charpentier, Mathes *et al.*, 1967); egg parasitism is generally very low and erratic, appreciable levels being found only in early maize crops. In the four subsequent generations, oviposition (expressed simply as no. of egg-masses/man-hour) and parasitism both increase, the latter up to 80% or 95%, although in some years it may be much lower. The first and second borer generations are distinct, so that little direct carry-over of *Trichogramma* from one to the next is possible (Burrell and McCormick, 1962; Dugas, 1939; Hinds and Spencer, 1928*b*, 1929; Hinds *et al.*, 1933*a*; Jaynes and Bynum, 1941). No estimate of the absolute *Trichogramma* population has been made. Dugas (1939) demonstrated a trend of increasing parasitism between 1928 and 1938 but, in view of the unreliability of figures for per cent parasitism before the fourth generation (Jaynes and Bynum, 1941), the validity of his conclusions is in some doubt. The course of events is similar for *D. saccharalis* and *Trichogramma* in Florida (Wilson, 1941), although parasitism is generally lower than in Louisiana (Charpentier, Gifford *et al.*, 1967), and for *D. grandiosella* Dyar and *Trichogramma* on maize in southwestern U.S.A. (Davis *et al.*, 1933).

Central and South America — The sparse data available indicate widely fluctuating parasitism. In Mexico, where the climate and borer species differ from one sugar cane area to another (Van Zwaluwenburg, 1951), Box (1951*a*) did not find any *Trichogramma* in March, while Flanders (1930*a*) recorded 7.1% and 30.3% parasitism in August for two species of *Diatraea*. Similarly, comparison of the data of Cleare (1928) and Bates (1954) in Guyana indicates a wide range in parasitism, the former quoting 40% average with a maximum of 75%, the latter 3.5% to 11.6% in March and April. According to Smyth (1939), parasitism in uncolonized fields in Peru increased from 8% to 78% during the period November-May, and declined between May and October. For some unknown reason he did not include data from the so-called autocolonized fields where parasitism was naturally high. Box (1951*b*) estimated the natural *Trichogramma* population at 1½ million/acre (time unit unspecified), and confirmed the wide variation in parasitism between fields. In Argentina, Jaynes (1932) found parasitism very variable between fields and years, and lower in young than mature cane.

Caribbean area — There is little detailed information available from the Greater Antilles, where *Diatraea saccharalis* is the main species of borer. Plank (1932) stated *Trichogramma* to be active throughout the year in Cuba, and Gowdey (1925, 1926) tentatively ascribed low borer damage in Jamaica to high egg parasitism. Wolcott and Martorell (1943*b*), in a five-year study in Puerto Rico, sampled only from young cane and therefore did not obtain the population trends within fields. Unfortunately, most of their data were summarized in graphs with no numerical scales for population or parasitism. Oviposition (expressed as no. of egg masses/man-hour) was very erratic except in the northwest, where it was seasonal with a prolonged flat peak in the summer. Parasitism tended to be lower in winter, particularly on the south coast, but there was considerable variation between fields. It was generally higher in ratoon (32% to 68%) than in plant cane (18% to 37%), but this was confounded with season. Their conclusion that *Trichogramma* was responsible for the fluctuations of borer populations in the northwest was not justified by the data presented.

The most detailed work on natural populations of *Trichogramma* comes from the Lesser Antilles where *D. saccharalis* is the dominant borer. Box (1932) in Antigua demonstrated the rapid increase in parasitism in large host populations, and estimated that in some fields the parasite population rose to 2½ million/acre (over a period of 2–3 months) or 245,000/acre/week. In Trinidad, Simmonds (1951) recorded in one heavily infested field in August 500,000 borer eggs/acre/week and over 95% parasitism, from which it can be calculated that the *Trichogramma* population was approximately 1¼ million/acre/week. The records from Barbados are conflicting. Maxwell-Lefroy (1900) stated that parasitism rose during the early part of the year to 75% in April and May. Tucker (1933, 1934*a*, *b*, 1935*b*) working on a very limited number of fields, found that in 1933 parasitism was very low to the end of April and had a maximum of 66.5% in October; even lower parasitism in 1934 was attributed to the dry weather. Borer oviposition had two peaks, March-June and September-October, respectively. Maximum oviposition was 27,605 and 42,359 eggs/acre/month in 1933 and 1934, respectively; the maximum *Trichogramma* population was 7,465/acre/month. Metcalfe and Van Whervin (1967) kept records from between 18 and 28 fields over a three-year period and concluded that Tucker's narrowly based data were not applicable to the whole island. They confirmed the existence of two oviposition peaks, the first, the result of immigration of moths from older fields, reached a maximum (average of all fields) of 136,000/acre/month. Egg mortality due to *Telenomus alecto* as well as *Trichogramma* and predators was always high in spite of periodic dry weather, and from February onwards was rarely much below 70%; as a result the parasite population paralleled the egg population, reaching a maximum (average of all fields) of 146,000/acre/month.

India — Data on the status of *Trichogramma* in India are for the most part incidental to experiments with liberations. In Bengal, parasitism of *Chilo tumidicostalis* (Hmps.) was 69% in September but only 30% in October (Gupta and Avasthy, 1960). In Uttar Pradesh, Gupta (1951), in a four-year study of *Chilo infuscatellus* Sn. and *Emmalocera depressella* Swinh., found peak oviposition in May (15,706 eggs/acre/week). Before the monsoon, when the temperature was 43°C and relative humidity 10%, parasitism was very low, but with the onset of more favourable conditions it rose as high as 100%, despite lower host populations. In the south *Trichogramma* could be found wherever infestations of *C. infuscatellus* were heavy, but it was never able to control them (Kunhi Khannan, 1931).

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Ramachandra Iyer *et al.* (1951), whose data cover eight successive years, found peak borer oviposition in May and June, this being presumably a response to the prevalence of young cane at that time. Parasitism is very variable. Subramaniam (1937) recorded 2% in July-September and 15% in October-December; Ramachandra Iyer *et al.* (1951) found that in April prior to liberations parasitism ranged from 4.4% to 41.0%, and for the following three months from nil to 26.8% in uncolonized areas.

Madagascar and Mauritius — In Madagascar, *Trichogramma australicum* is an important factor limiting the size of populations of *Chilo sacchariphagus* (Boj.). The long crop period (June to November) allows the migration of moths and parasites from old to young cane, and by November-December there are eggs in every field; parasitism is then very near zero. During the rainy season which follows, there is an increase in the egg population and a corresponding increase in parasitism; in 1960 the egg population (assessed from samples collected every 10–12 days) rose in a fortnight from 1.7 to 48.0 egg masses/acre and parasitism from 9% to 82%. In June, at the time of peak oviposition, there were 625 egg masses/acre and parasitism was about 90%, sometimes reaching 98% (Brenière, 1963, 1965*a*; Caresche and Brenière, 1962).

The contrast with the situation in Mauritius is striking. Parasitism was variable, being highest during the dry season (April to September) with a maximum of 55.1%; it varied also from year to year, being 1.8% and 10.3% in 1941 and 1942, respectively (Moutia, 1942, 1943; Moutia and Courtois, 1952).

Far East — The role of *Trichogramma* in Java is small compared with that of *Telenomus beneficiens*, perhaps because the eggs of the main borer, *Scirpophaga nivella* (F.), are covered with felted hairs, which *Trichogramma* may be unable to penetrate with its short ovipositor. Hazelhoff (1929) recorded that parasitism by *Telenomus* fell from 64.2% in the latter half of 1927 to 37.3% the following January, remaining at this level until August, when it reached 45%. Van der Goot and Van der Laan both expressed the view that the egg parasites did not exert economic control (Jepson, 1954).

In Taiwan, *Trichogramma australicum* is more important than *Telenomus beneficiens* on *Chilo venosatus* Wlk. It attained 58% parasitism in August, 74% in October, and then declined. In January and February no host eggs were available, but subsequently parasitism ranged between 7.6% and 65.4%. The annual mean was 63.8% (Takahashi, 1939).

Effects of field practice

Insecticides and weedicides

While there is no doubt that insecticides are deleterious to *Trichogramma*, the evidence regarding their effect under cane field conditions is contradictory. Parasitism is adversely affected by DDT, BHC, chlordane, toxaphene, parathion and sulphur, but not by ryania, cryolite or sodium fluosilicate (Dugas and Concienne, 1956; Hinds and Spencer, 1928*a*; Ingram *et al.*, 1951). On the other hand, Simmonds (1951) recorded that neither the level of parasitism nor *Diatraea* oviposition was affected by dusting with DDT. This differential response indicates that judicious selection of formulations and insecticides could avoid significant damage to *Trichogramma*. Granular formulations of endrin, gusathion and sevin control *Diatraea* but do not harm *Trichogramma* (Hensley *et al.*, 1961; Long *et al.*, 1961). Similarly, the bacterial insecticide, *Bacillus thuringiensis* Berliner, has possibilities (Long *et al.*, 1961).

Mathes *et al.* (1954) reported that *Trichogramma* parasitism was reduced by the esters of 2,4-D, but not by the amine or sodium salts. Further tests have confirmed that the amine has no adverse effects (Charpentier and Mathes, 1967).

Burning

The effect of burning on the host-parasite balance has always been a controversial issue and is now of immediate concern, for burning before harvest is being widely adopted to facilitate mechanical harvesting and loading.

In Louisiana the question was whether burning debris at the onset of winter had a greater overall effect on *Diatraea* than on *Trichogramma*. For many years conservation of trash was advocated (Holloway, 1933; Holloway *et al.*, 1928; Howard, 1921), but later it was demonstrated in exhaustive trials that burning reduces the overwintering population of borer larvae, and does not affect the level of parasitism the following season (Bynum *et al.*, 1939; Hinds *et al.*, 1934*b*).

In the tropics Cleare (1922) was in favour of burning on the grounds that it destroyed *Diatraea* larvae. It was widely opposed because of the inevitable loss of *Trichogramma* (Box, 1926; Quelch, 1914; Wolcott, 1915, 1933; Wolcott and Martorell, 1943*b*), and Wolcott (1933) considered that non-burning in Puerto Rico had brought considerable benefits. However, recolonization by both *Diatraea* and *Trichogramma* from adjoining fields is normally very rapid (Metcalfe and Van Whervin, 1967), and Box (1951*b*) remarked that this was true also in areas where burning was practised. In fact, burning seems to be of little significance (Brenière, 1965*a*; Myers, 1935*a*). Other agronomic factors such as block reaping and length of the crop period, which will affect the availability of borers and *Trichogramma* for recolonization, are far more important.

Possible integration of Trichogramma liberations

The relationship between *Trichogramma* and its host is very close, with parasite populations generally running parallel to host populations. The level of parasitism at any particular time is determined by the ability of *Trichogramma* to

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find and parasitize eggs; this in turn depends on the number of fecund *Trichogramma*, the number of hosts and the microclimate. The microclimate is limiting for relatively short periods, for instance during the spring in Louisiana, before the monsoon in North India, and possibly in very young cane during the crop season in Barbados. Normally, whenever there is an abundance of host eggs, a high level of parasitism is rapidly attained by virtue of the short life cycle and widespread occurrence of *Trichogramma*. Theoretically, mass-liberation of *Trichogramma* could be of benefit when the number released is a significant proportion of the total population, and particularly when parasitism is limited by the scarcity of *Trichogramma* or of host eggs, rather than by microclimate. In practice, such critical periods occur when the availability of host eggs is low. A prolonged critical period is found only in Louisiana where the egg population increases relatively slowly. In Puerto Rico, with its fluctuating populations, there is an ill-defined critical period during the winter. Where recolonization by *Trichogramma* is rapid, as in Madagascar and Barbados, the critical period is very brief or virtually non-existent. However, there is in all regions much variation in the egg population between fields; some fields suitable for liberations can be found, but they are of uncertain distribution and transient occurrence. The chances of integrating *Trichogramma* liberations into this dynamic equilibrium seem to be favourable only in continental subtropical regions.

6. Biological Control

History

In 1921 Cleare (1928) developed in Guyana a system of large scale liberation of *Trichogramma* and *Telenomus* from the old plantation means of borer control, namely collecting egg masses and deadhearts. This was the first practical step following Enock's (1895) proposals for '*Trichogramma* farming' and Harland's (1916) suggestion that *Trichogramma* could be increased in numbers in cane fields, either with liberations or by encouraging alternative hosts to windward. Production was limited at first by the supply of host eggs, but the discovery that *Sitotroga cerealella* was a satisfactory laboratory host for *Trichogramma* immediately made mass-production feasible (Flanders, 1927, 1928, 1930*c*). Preliminary trials for control of *Diatraea saccharalis* in Louisiana and Barbados by mass-liberation of *Trichogramma* (the '*Trichogramma* method') were apparently successful (Hinds and Osterberger, 1932*a,b*; Hinds and Spencer 1928*b*, 1929, 1930*a,b*; Tucker, 1930*a,b,c*, 1931*a,b*, 1932). However, these results and those on other crops were not universally accepted (Myers, 1929; Smith and Flanders, 1931), and the *Trichogramma* method became the centre of a violent controversy (e.g. Morrill, 1931). It was discussed at the 1932 Congress of the International Society of Sugar Cane Technologists which, influenced by Box's (1932) data on natural populations and early larval mortality, and Myers' arguments that early larval mortality reduced effective parasitism, concluded that it could not be recommended (Anon., 1932).

The method was then re-investigated in a number of countries and, although some data in its favour were produced, it gradually fell into disrepute in the Americas. It was officially abandoned in Louisiana (Strong, 1936), but was practised by commercial pest control firms for many years (e.g. Dugas, 1958). In Barbados, Tucker, with the moral support of the Director of Agriculture (Miller, 1937) and the planting community, continued liberations on a commercial scale in the face of searing opposition (Myers, 1932*b*, 1935*b*, 1936) for over 25 years, and the decision to abandon the campaign was not taken until 1959 (Metcalfe, 1963). Similarly, after a varying length of time, disillusionment followed in Guyana (Cleare, 1934), Peru (Box, 1951*b*) (although here there has recently been renewed interest in the *Trichogramma* method (Risco, 1961, 1963, 1966 *in litt.*)), and Mexico (A. G. Gallardo, 1965 *in litt.*). In Puerto Rico, liberations, although recommended, were never made on a commercial scale (Wolcott, 1951).

The story has developed rather more slowly in the Old World. The method was given extensive trial in India (Gupta, 1951; Jepson, 1954; Ramachandra Iyer *et al.*, 1951; Rao *et al.*, 1956) and, although the results were for the most part inconclusive, it is still applied on a commercial scale in Mysore (V.P. Rao, 1965 *in litt.*). It was tried in Madagascar (Brenière, 1960, 1965*a*; Caresche and Brenière, 1962) and Mauritius (Moutia, 1942, 1943, 1944), with negative results. At the present time the only stronghold of the method is the Far East; liberations have been successful on a limited scale in China (Pu and Liu, 1962) and Taiwan (Chen, 1963), and are commercial practice in the Philippines (Porquez and Tabayoyong, 1959).

In many countries imported species or strains of *Trichogramma* have been liberated, sometimes simply because no rearing facilities were available locally (Llanos, 1940; Lobdell, 1933), or the indigenous species was difficult to rear on its factitious host (Tucker, 1954). The significance of the large genetic pool available in different biological species and geographical strains has long been appreciated (Evans, 1930; Harland and Atteck, 1933), and affords the most cogent reason for importation.

Mass rearing and liberation

The mass-production of *Trichogramma* has usually been based on the ready supply of a grain moth (e.g. *Sitotroga cerealella, Corcyra cephalonica*) as host (Brenière, 1965*c*; Flanders, 1930*c*; Kuwana, 1930; Porquez and Tabayoyong, 1959; Smyth, 1933; Spencer *et al.*, 1935; Takano, 1933; Tucker, 1931*b*, 1951), although phytophagous hosts - moth borer species (Cleare, 1928; Espino, 1955; Porquez and

Tabayoyong, 1959) and a Saturniid (Pu and Liu, 1962) - have also been used. The technique is essentially very simple. Grain moths from the rearing rooms (Figs. 3 and 4) are placed in small containers closed with wire mesh. Here oviposition occurs. The eggs, after being shaken through the mesh, freed from debris and glued to cards (Fig. 5) or some other convenient substrate, are exposed for 24 hours to newly emerged *Trichogramma* in well-lit containers of about 3/8 cu ft capacity (Fig. 6). The relative numbers of host and parasite are adjusted to avoid superparasitism. If the parasites are not required immediately, they may be stored under refrigerated conditions, provided development has reached the pupal stage. *T. australicum* may be kept for 15 days at 6°C (Brenière, 1965*c*; King, 1934; Schread and Garman, 1933), but many species may be stored indefinitely at a minimum of 1–2°C.

A number of difficulties may be encountered. High temperature and humidity allow the growth of mould on the host, and deter oviposition (Schepetilnikova, 1939). Larvae hatching from eggs that have escaped parasitism tend to be predacious, but exposure of the eggs to ultra violet light before parasitism kills the embryo without affecting the nutritive value (Brenière, 1965*b*, *c*). Mites are a nuisance (Meier, 1939) while *Tribolium* and parasites of the grain moths can reduce output considerably. Spotless sanitation, fumigation, effective screening, clean stock and the use of borax and sulphur are necessary to counter these factors (Tucker, 1951).

Trichogramma may be liberated as free adults or as parasitized eggs glued o cards. Egg cards are more convenient for large scale use, being placed either in

Fig. 3. Rearing room for *Sitotroga cerealella* Ol. in Barbados.

Fig. 4. Collecting adult *Sitotroga* in the rearing room. Note trays of wheat in which *Sitotroga* develops.

cane funnels throughout the fields (Kunhi Khannan, 1931; Tucker, 1931*b*) or in release boxes (Fig. 7) to windward (Brenière, 1965*a*; Cleare, 1928); the latter avoids the wastage due to rain, desiccation and predators. The use of adults (Jaynes and Bynum, 1941; Smyth, 1933) is limited, as temperature and humidity in the release jars have to be carefully controlled and liberations completed by the second day after hatching. Spraying the eggs on to the foliage (Schütte and Franz, 1961) has not been tried in sugar cane fields.

Two methods of liberation are recognized, accretitive and inundative (Flanders, 1930*b*). The accretitive method, which consists of a single critically timed liberation, was practised in Louisiana (Hinds *et al.*, 1933*a*) and Peru (Smyth 1939). Generally the use of *Trichogramma* tended to be inundative, a succession of liberations where parasites outnumber the hosts, the release period varying from a few weeks, as in Puerto Rico (Wolcott and Martorell, 1943*a*) and India (Gupta, 1951; Ramachandra Iyer *et al.*, 1951), to most of the year, as in Guyana (J. F. Bates, 1964 *in litt.*), Mauritius (Moutia, 1942, 1943) and China (Pu and Liu, 1962). Liberations ranged in size from a few hundred (Tucker, 1932) to 300,000 individuals/acre/month (J. F. Bates, 1964 *in litt.*).

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Fig. 5. Glueing *Sitotroga* eggs to cards for exposure to *Trichogramma*.

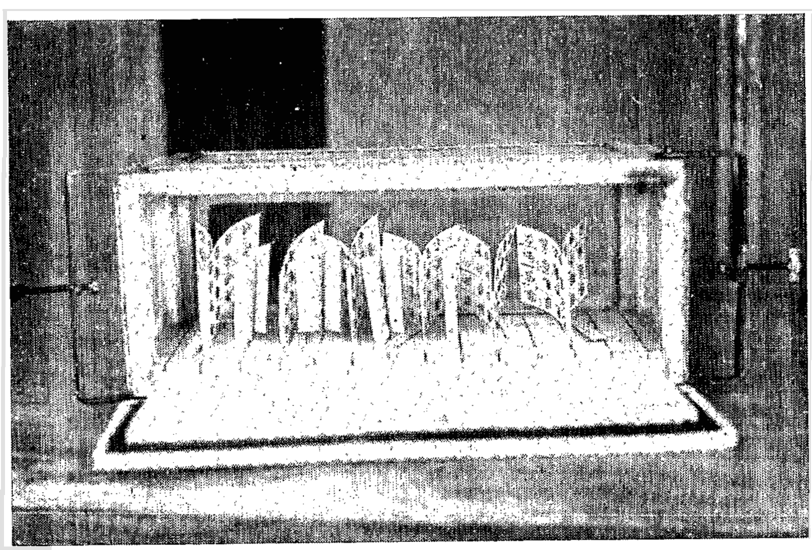

Fig. 6. Container in which *Sitotroga* eggs are exposed to *Trichogramma*.

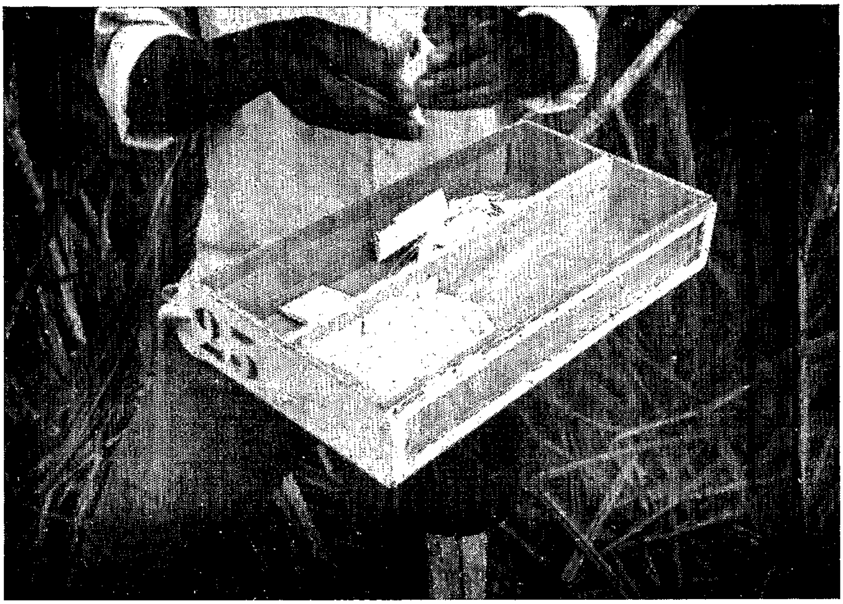

Fig. 7. Release point for *Trichogramma*. Egg cards are being placed in boxes from which the emerging *Trichogramma* can escape.

Effect of liberations

The natural dispersal of parasites, moths and first instar larvae has deterred many investigators from a statistical analysis of the effect of liberations, but accurate experiments should be possible, provided they are done on a sufficiently large scale. Trials have usually been conducted on plots of 3–10 acres (Gupta, 1951; Hinds *et al.*, 1933*a*; Jaynes and Bynum, 1941; Metcalfe and Van Whervin 1967), but no critical assessment of optimum plot size has been made. Brenière (1960) considered plots of 8–10 acres too small, and noticed a drop in parasitism due to *Trichogramma* dispersal even in a 25-acre plot. Only J. F. Bates' (1964 *in litt.*) trials (several blocks totalling between 200 and 300 acres in different years) have been beyond criticism.

A comparison of the numbers of liberated and naturally occurring parasites will show whether or not liberations could have any useful effect. Box (1932) and Myers (1932*b*) likened liberations to a drop in a bucket; conversely, J. F. Bates' (1964 *in litt.*) liberations of 300,000/acre/month must have outnumbered the natural population for most, if not all, of the time. The relationship is continually changing, and can be ascertained only by frequent sampling.

The most logical method of judging the effect of liberations is by weekly counts of the egg hatch per unit area. By this means the effects of host population, competition and density dependence are eliminated (Flanders, 1930*b*; Metcalfe

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and Van Whervin, 1967; Parsons and Ullyett, 1936). Most workers have relied largely on per cent parasitism (Brenière, 1965*a*; Gupta, 1951; Hinds *et al.*, 1933*a*; Smyth, 1939; Tucker, 1935*a*; Wolcott and Martorell, 1943*a*), but this is not necessarily valid. Counts of later stages of development such as borer larvae (Isaac, 1939) and pupae (as shown by pupal skins or exit holes) (Hinds *et al.*, 1933*a*; Jaynes and Bynum, 1941) have also been used, though other factors such as early larval mortality and larval parasitism may intervene. Trends in egg population (Tucker, 1933) may be affected by migration of moths and intervening mortality and natality factors. The amount of damage to the plant, which may be used as an index of the larval population or of loss in yield, has commonly been quoted (J. F. Bates, 1964 *in litt.*; Espino, 1955; Hinds *et al.*, 1933*a*; Jaynes and Bynum, 1941; Isaac, 1939; Moutia, 1943; Tucker, 1935*a*). Finally, the yield of sugar per acre (Jaynes and Bynum, 1941) affords a sound economic basis for assessing the problem.

Louisiana — Hinds and his colleagues experimented with liberations against *Diatraea saccharalis* for seven years, and claimed consistently beneficial results (Hinds and Osterberger, 1932*a, b*; Hinds *et al.*, 1933*a, b*, 1934*a, b*; Hinds and Spencer, 1928*b*, 1929, 1930*a,b*). Liberations against the first generation were suspended after two years as there was no carry-over to the second generation (Hinds and Spencer, 1929), and from then on were standardized at 5,000/acre against the second generation in June or 10,000/acre against the third or fourth in August. Parasitism was said to be raised by up to 50% by September, with a consequent reduction in borer damage and increase in yield. However, the relation of parasitism to host density was completely overlooked. Since the more heavily infested fields were, at least until 1932, selected for colonization (Hinds and Osterberger, 1932*b*) the effects of host density and liberations on the level of parasitism were confounded. Erratic parasitism in the first three generations due to the low host density meant that increases in parasitism before August were unreliable as an indication of borer control (Jaynes and Bynum, 1941). Jaynes and Bynum repeated Hinds' experiments over a three-year period with liberations at 10,000 to 45,000/acre in more than 50 sets of colonized and control plots separated by buffer areas. No increases in parasitism or yield were recorded. Recent experiments on a smaller scale have substantiated these findings (Burrell and McCormick, 1962).

Florida — Small-scale experimental liberations were conducted at various times between 1932 and 1941 (Ingram *et al.*, 1939; Lobdell, 1933, 1934, 1935; Wilson, 1941). Up to 11,000 *Trichogramma* / acre were liberated between April and August, but the results based on per cent joints bored and yield were inconclusive.

Mexico — Liberations led to increased parasitism in two species of *Diatraea* in August 1929 (Flanders, 1930*a*), and a certain degree of control has been claimed

(Aburto, 1942; Delgado de Garay, 1942). Flanders (1930*a*) regarded liberations impracticable commercially, as timing is very critical and the important borer species, *Acigona loftini* (Dyar), is rarely attacked.

Puerto Rico — Much of the significance of the extensive experimental liberations against *Diatraea saccharalis* has been lost due to the unsatisfactory presentation of the results. Liberations, up to 1 million at each locality and including a xerophytic strain, were restricted to fields with many fresh eggs (> 5 egg masses/man-hour) and low parasitism (< 33%) (Wolcott and Martorell, 1943*a*). A net increase in parasitism (i.e. an increase in colonized fields and/or a decrease in control fields) occurred in 71% of the fields, but only 37% had been re-examined within two weeks of liberations. No comparative data on egg populations in colonized and control areas were given.

Barbados — Tucker (1929, 1930*b*, 1951) assumed at the outset of his campaign that, in the dry exposed conditions of young cane, *Trichogramma* was at a disadvantage compared with *Diatraea saccharalis*. At this critical stage, said to last from March to September, *Trichogramma* was liberated mainly in plant cane in numbers ranging from a few hundred to 5,000/acre/month (Tucker, 1931*a*, 1932, 1934*a*; Metcalfe and Van Whervin, 1967). The breeding stock was a mixture of races, and possibly species, originating from eight localities in North and Central America and in the Caribbean (Tucker, 1954). Claims for increased parasitism,

TABLE 2
THE EFFECT OF *TRICHOGRAMMA* LIBERATIONS ON PER CENT JOINTS BORED IN GUYANA
(J. F. Bates, 1964 in litt.)

Year	Crop	Per cent Joints Bored	
		Control	Colonized
1955	spring	6.7	6.4
	autumn	7.2	6.8
1956	spring	5.2	5.0
	autumn	8.1	6.7
1957	spring	6.6	7.8
	autumn	7.8	9.0
1958	spring	6.2	6.3
	autumn	6.0	5.2
1959	spring	7.5	6.8
	autumn	7.2	7.4
5-Year Mean	—	6.8	6.7

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smaller larval populations and reduced damage followed (Tucker, 1934*b*, 1935*a,b*, 1951). However, serious sampling errors in the assessment of per cent joints bored were revealed, and it was concluded that the annual records were of little value as a measure of the effect of liberations (Metcalfe, 1963; Myers, 1935*b*). Close scrutiny of Tucker's narrowly based field data convinced Metcalfe and Van Whervin that his claims were unjustified; furthermore, their liberations at 4,000 to 40,000/acre/month in 21 fields showed no consistent reduction in egg hatch or increase in parasitism (Metcalfe and Van Whervin, 1967). Although further experiments were desirable, these results, coupled with data on natural populations from Antigua (Box, 1932) and Trinidad (Simmonds, 1951), as well as from Barbados (Metcalfe and Van Whervin, 1967), were sufficient to condemn the method.

Guyana — The first liberations amounted to only 11 million on two estates over 18 months (Box, 1926). Although there was no evidence of successful control, the *Trichogramma* method was adopted on other estates and persisted with for many years on a small scale (Bates, 1954) despite Myers' (1932*b*) criticisms. Recently, J. F. Bates (1964 *in litt.*) conducted a series of experiments in which liberations of 300,000/acre/month were run over 200–300 acres for five consecutive years. The records of per cent joints bored, published here for the first time (Table 2), show no difference between colonized and control areas.

Colombia — 1 million *Trichogramma* imported from California were liberated in sugar cane. No assessment of the results was made (Llanos, 1940).

Peru — Smyth's (1939) claims of control of *D. saccharalis* in Peru with single liberations of 5,000/acre are not supported by many data. The validity of his comparisons of parasitism and borer damage in colonized and control areas is doubtful, for the autocolonized areas, where the *Trichogramma* population increased naturally, are ignored. The effect of liberations was said to extend up to 8 miles from the point of release but there were no data to distinguish such an effect from the natural recolonization from the stand-over cane that made up 25–35% of the total acreage. Box (1951*b*) was very critical. He found on occasion no parasitism where liberations had been made. Discussing the records of borer damage, he pointed out that the lack of differentiation between plants and ratoons might have confounded the effects of liberations, and that the damage even in colonized areas was severe. Commercial liberations at up to 87,000/acre/annum were resumed in 1961, since when borer damage has been at an unprecedented low level (Risco, 1963, 1966 *in litt.*). However, no experimental data are available.

India — Experimental liberations against *Chilo infuscatellus* and *C. indicus* (Kapur) were initiated in 1930 (Kunhi Khannan, 1931). According to Subramaniam

(1933, 1935, 1936, 1937, 1941) weekly liberations in one-acre plots for 2–3 months increased parasitism, from 2% to 50% and 10% to 92.4% being quoted in particular instances; smaller numbers of deadhearts and yield increases up to 8 tons cane/acre were also noted. These conclusions were based on very inadequate data, the release plots covering only 1, 2 and 12 acres in 1933, 1934 and 1935, respectively (Rao *et al.*, 1956). In 1933 only 14 egg masses were examined (Subramaniam, 1937). Increased yields between 1933 and 1938 attributed to liberations (Rao *et al.*, 1956) are inconclusive. Only three sets of data out of thirteen are based on an adequate number of control plots; in two, increases of 2.5 and 4.5 tons cane/acre, and in the third, a decrease of 3.95 tons cane/acre, were recorded.

These and similar results (Isaac, 1939) led to well-controlled experiments in eight states (Gupta, 1951). In Madras, Ramachandra Iyer *et al.* (1951) liberated up to 16,000 *Trichogramma*/acre/week for the 12 weeks following germination, over 7 years. Parasitism was erratic, but between 1946 and 1949 averaged 31.7% and 11.3% in colonized and control plots, respectively. Yield increases from 2.78 to 10.35 tons cane/acre were noted. There were no records of the egg populations or borer damage. In Uttar Pradesh, Gupta (1951), from 5 years' experiments, concluded that liberations were of no benefit due to unfavourable climatic conditions and low host density. In some years no parasitized eggs were found in the colonized plots, and the highest parasitism recorded was 7.4%. Reviewing the trials in other states, Gupta (1951), apparently unaware of the suggestive results in Madras, noted that only those in Bihar were considered successful.

Madagascar — Preliminary experimental liberations of *Trichogramma australicum* against *Chilo sacchariphagus* were inconclusive (Brenière, 1960). Accordingly, in 1960 liberations were made in a 25-acre block at the rate of 13,000/acre/week (Brenière, 1960, 1965*a*). The 9-week release period was timed to coincide with the rapid spring increase in the borer egg population. A noticeable, but temporary, increase in parasitism occurred, and shortly afterwards parasitism was equally high in colonized and control areas.

Trichogramma fasciatum was introduced (Brenière, 1965*d*), 7 million being liberated in a 12-acre field. In a short time it had almost entirely replaced *T. australicum*, but after two months the dilution of the stock, followed by the seasonal lack of *Chilo* eggs, led to its disappearance. Some individuals collected in the field possessed characters intermediate between the two species.

Mauritius — 1½ million *Trichogramma evanescens*, imported originally from Ceylon, were liberated over 50 acres between January and July 1941 for control of *Chilo sacchariphagus*. Out of a sample of 35,120 eggs none was parasitized by *T. evanescens*, and the conclusion was that the species was not acclimatized to local conditions (Moutia, 1942).

During 1941–1942, 900,000 *Trichogramma australicum* were liberated at

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three localities covering 65 acres. The results were negative. The maximum parasitism recorded in a colonized field was 19.8%, less than that recorded in a control field (50%); parasitism was generally low, averaging 1.8% and 10.3% in 1941 and 1942, respectively. There was no consistent difference in borer damage in the three localities before and after liberations. No data on egg populations were given. The trials were abandoned in 1943 (Moutia, 1942, 1943, 1944).

Philippines — Three species, *Trichogramma minutum*, *T. japonicum* and *T. australicum* have been introduced into the Philippines, for, despite parasitism by the indigenous *T. nanum*, the borer *Argyroploce schistaceana* Sn. remains a major pest. The introduction of a small shipment of *T. minutum* in 1948 was followed by a three-year campaign with regular liberations over a 7-month period at the maximum rate of 50/acre/month. By the end of this period *T. minutum* was well established. However, the only data as to the effect of liberations were an increase in parasitism and a decrease in per cent deadhearts in the second and third years as compared with the first (Espino, 1955). About the same time, regular liberations of *T. australicum* and *T. japonicum* were started and 525 million were distributed over 31,000 acres in 1958 (Estioko, 1961; Porquez and Tabayoyong, 1959). There are no published data as to the efficacy of this programme.

Taiwan — Takano (1940) and Chen (1963) have reported good control of three borer species with liberations of *Trichogramma australicum*. Chen's trials cover eight years, and borer damage has been reduced by 80%. Owing to the language difficulty details are not available.

China — *Trichogramma evanescens* has been liberated on a large scale in three provinces, the recommended rate being 36,000–60,000 females/acre seven to nine times annually (Pu and Liu, 1962). Parasitism has been raised, being from 60.0% to 97.5% and 0% to 48.6% in colonized and control fields, respectively; damage has been reduced, per cent joints bored being 2.0–11.8 and 11.4–18.0 in colonized and control fields, respectively. Again, details are not available because of the language difficulty.

7. Conclusion

Much of the controversy surrounding *Trichogramma* in relation to sugar cane moth borers is the result of incomplete knowledge of their biology and ecology, and shortcomings in the technique used for their study in the field. Fundamental to all approaches to the subject is the taxonomy of the genus *Trichogramma*. Now that the principles of a biological classification are recognized, the determination and distribution of those species associated with sugar cane moth borers should be undertaken without delay. This will inevitably lead to treatment of the phenomenon of adaptation, and the concomitant problem of races and strains, subjects that have far-reaching significance in the practical aspects of the *Trichogramma* problem. In the field, methods of sampling absolute populations and studies of the dispersal of both host and parasite are essential to rationalize data on population changes and effects of liberations.

From the data that are available it is evident that a very close relationship exists between *Trichogramma* and its host, largely as a result of the short life cycle and rapid dispersal of the former. Critical periods where the equilibrium favours the host rather than *Trichogramma* are generally short, but their exact limits could be clarified by the field study of the survival of the host at varying host and parasite densities, a study that could be integrated with the effects of physical factors in relation to the microclimate. *Trichogramma* is undoubtedly an important limiting factor on the maximal size of borer populations, and for this reason any potentially harmful agronomic practice should be kept under surveillance.

Theoretical considerations suggest that liberations, when constituting a significant proportion of the total *Trichogramma* population, could contribute to the control of the sugar cane borers. Many claims of success have been made but, wherever re-examined from an ecological or experimental viewpoint, they have been shown to be unfounded, and there are still no data proving beyond all doubt the efficacy of the *Trichogramma* method. It is therefore highly desirable that critical studies be carried out in the remaining strongholds of the *Trichogramma* method, Peru, India and the Far East.

There remains one approach that has been comparatively neglected, and which offers perhaps the most hope for the future, the introduction and establishment of exotic species or strains of *Trichogramma*. Some preliminary success has been achieved in this direction. In addition, the vast genetic potential available suggests that strains of *Trichogramma* could be selected or even bred to suit particular environmental conditions.

8. Summary

The use of *Trichogramma* spp. in the biological control of sugar cane moth borers is reviewed in light of their biology and ecology. Five species are now associated with sugar cane moth borers, but a revision of the genus based on newly developed biological techniques may reveal many more. The life cycle of *Trichogramma* is very short (6–8 days at 28°–30°C); temperature, light and humidity have a critical influence on rate of development, host-finding and survival; the rapid adaptation to particular environments and hosts leads to the development of new strains or ecotypes, and is of particular significance to mass-rearing on factitious hosts.

Data on the absolute host egg population and parasitism give an accurate

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measure of egg destruction, but cannot explain population trends. Parasitism by *Trichogramma* tends to be density dependent; this, and destruction of eggs by predators and other parasites, make direct comparisons of per cent parasitism by *Trichogramma* misleading. The argument that early larval mortality reduces effective parasitism is unfounded; the two factors are complementary.

Methods of sampling the absolute host and parasite populations on sugar cane have been applied, but studies on dispersal of *Trichogramma* are still at a preliminary stage. Field data on host and parasite populations indicate their very close inter-relationship, with high parasitism generally being attained as soon as hosts are numerous. Harmful side effects of insecticides and weedicides on *Trichogramma* can be avoided by judicious selection of chemicals and formulations. Burning, before or after harvest, has no long-term deleterious effects on *Trichogramma* as recolonization from unburnt fields is rapid. Appraisal of the biology and ecology of *Trichogramma* suggests that the chances of usefully integrating liberations (the *Trichogramma* method) are limited to short critical periods in spring in continental subtropical regions.

After its initial application in Guyana in 1921 the *Trichogramma* method, despite considerable controversy, was widely adopted. It has now been largely discarded in the Americas, and at the present time is commercial practice only in Peru, India and the Far East. Mass-production is usually based on *Sitotroga*, but many variants of the original technique have been devised. Two methods of liberation are recognized, accretitive and inundative, the latter being most widely used. The evaluation of the effect of liberations is difficult, particularly as no data on optimum plot size are available. The most exact criteria are the numerical relationship between liberated and naturally occurring *Trichogramma* populations, and egg hatch per unit area; damage assessments and yield data are also useful. Critical examination of the data presented shows that many claims of success are not justified. Carefully controlled experiments, together with data on the natural host-parasite balance, have shown that liberations are of no value in the U.S.A., Barbados, Guyana, and Madagascar. It is concluded that the *Trichogramma* method should be re-examined in its remaining strongholds.

In view of their adaptability, the introduction and establishment of exotic species or selected strains of *Trichogramma* offers a possible new approach.

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