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MODELING AUGMENTATIVE RELEASES OF *TRICHOGRAMMA PRETIOSUM*[1/]

J. L. Goodenough and J. A. Witz

Pest Control Equipment and Methods Research Unit
USDA, Agricultural Research Service, College Station, TX 77843

ABSTRACT

This paper summarizes several available models relating to the population dynamics of *Trichogramma pretiosum* Riley and lists assumptions, suggested model uses, and needs. All models included are lacking in one or more major elements: reproduction, development, parasitization rate, mortality, or movement.

We describe a model that has an improved component of temperature-based mortality during the first 4 h after augmentative release. Soil temperatures above 37°C, especially during the first h after release, are expected to dramatically reduce *Trichogramma* survival. The most serious limitations to modeling of *Trichogramma* are inadequate knowledge of movement and the inability to observe foraging behavior of individual *Trichogramma* in the field.

INTRODUCTION

Many available papers present theoretical aspects of modeling predator/parasite population dynamics, but relatively few deal explicitly with *Trichogramma*. Few if any include dynamic feedback of the impact of released parasites upon a predicted pest population. In this paper, we review several available models of *Trichogramma*, especially *T. pretiosum*, and present a model based on *T. pretiosum* population dynamics that is interactive with the dynamic *Heliothis* spp. model, MOTHZV, of Hartstack et al. (1976). This model has been adapted to COMPAQ-PLUS® PC (J. A. Witz, unpublished information). A selected list of available data for use in modeling *T. pretiosum* is presented in Table 1.

Early modeling of *Trichogramma* was done by Knipling and McGuire (1968). Using a theoretical appraisal of the limitations and potentialities of *Trichogramma*, they identified some principal factors governing the efficiency of *Trichogramma* and their effect on the relationship between parasite and host density. These factors included 1) parasite population density, searching behavior and efficiency; 2) host insect egg density, and 3) the area of host plant environment that must be searched by the parasites in finding host eggs.

Knipling and McGuire (1968) made a series of assumptions that, although validated only for sugarcane borer, *Diatraea saccharalis* (F.), they felt were biologically representative of such other economically important pests as the southwestern corn borer, *Zeadiatraea grandiosella* (Dyar); the corn earworm, CEW, *Heliothis zea* (Boddie); and the tobacco budworm, TBW, *H. virescens* (F.). They derived or assumed parameter estimates for the various efficiency factors that were identified. The population of adults from overwintered stages or migratory adults was assumed to be low: 74 individuals/ha (30/A). The host male:female ratio was assumed to be 1:1. Each female deposited 200

[1/] Hymenoptera: Trichogrammatidae

TABLE 1. Summary of Data Available for Modeling *Trichogramma pretiosum*.

Factor[a/]	Description	Reference
	Development	
AGM host	Mean no. days ca. 10 ± 0.5	Butler and Lopez 1980
	Mean no. days at 25°C = 10.4	Goodenough et al. 1983a
TBW host	Mean no. days at 25°C = 11.8	Goodenough et al. 1983a
T. ni host	Mean no. days ca. 9.2 ± 0.36	Butler and Lopez 1980
SWCB host	Mean no. days at 25°C = 9.8	Calvin et al. 1984
	Longevity	
AGM host	4.5 ± 0.47 days	Lewis et al. 1976
	4.0 days (50%)	Goodenough et al. 1983b
	Some decrease in longevity after stored for 4-10 days at 16.7°C	Stinner et al. 1974b
TBW host	4.3 days (50%)	Goodenough et al. 1983b
CEW host	10.6 to 12.2 days, increased by exposure to kairomones	Nordlund et al. 1976
SWCB host	1 day (35°C) to 2 days (20°C)	Calvin et al. 1984
High temperature mortality		
AGM host	Greatly reduced emergence when parasites held for 1 h at 37°C	Lopez and Morrison 1980
T. ni host	100% mortality - *T. minutum* in soil at >42°C for 3 h or less	Fye and Larsen 1969
Insecticidal mortality	75% killed 1.6 km downwind of methyl parathion ULV	Stinner et al. 1974a
	Increased by permethrin for 21 days, for only one day by endosulfan	Jacobs et al. 1984
	Reproduction efficiency	
AGM host	9.8 progeny/female	Stinner et al. 1974b
	8.6 to 11.2 progeny/female	Lewis et al. 1976
	8.3 eggs/female/24 h	Morrison et al. 1983
	154 emerged from 148 eggs at 25°C	Goodenough et al. 1983
TBW host	13.8 progeny/female	Stinner et al. 1974b
	66 emerged from 148 eggs at 25°C	Goodenough et al. 1983a
CEW host	2.5 adults/host egg	Oatman 1966
	Mean fecundity 8.64 to 11.16 progeny	Lewis et al. 1976
	Mean no. progeny increased by kairomones	Nordlund et al. 1976
SWCB host	10 to 16 ova/female depending on temperature	Calvin et al. 1984
Artificial Diet	8.9 eggs/female	Morrison et al. 1983
Insecticide	Diflubenzuron alone did not, but the addition of crop oil significantly reduced parasitism	House et al. 1980

TABLE 1. (continued)

	Inhibition in parasitism 70-100% by methomyl, permethrin and methyl parathion, 30% by chlordimeform	Bull and House 1983
% Females Produced	Sex ratio varied with parasite species and crowding	Kfir 1981
	1:1 to 1:5 M:F for 1 to 6 parasites/host egg	Calvin et al. 1984
	Movement of female *Trichogramma*	
Before parasitizing	Innate tendency to move	Lewis et al. 1976
Current knowledge	Literature review - physical and biotic factors	Keller et al.
Retention time	Increased by kairomone	Lewis et al. 1976
	Increased by prerelease exposure to host eggs	Gross et al. 1981
Wind	No effect detected	Schread 1932
	Downwind dispersion	Hendricks 1967
	Nonrandom movement, time-varying drift and diffusion rates	Allen and Gonzalez 1974
	Movement: substantial to at least 15 m the first day and some to 122 m within 2 days of release	Stinner et al. 1974a
	Upwind in apple trees	Yu et al. 1984
	Fitness or Quality	
Number/ha to parasitize 50% host eggs		
	Hypothesized = 12,400	Knipling and McGuire 1968
	Mass-reared 111,000	Hartstack et al. 1976
Field efficacy	Review of releases on several crops (49% to 85% parasitism) and for control of *Heliothis* spp. on cotton (24% to 81%).	Ridgway et al. 1981
Trichogramma parasitism rate	Peak at 2 days of age	Morrison (unpublished data used by Goodenough et al. 1983b)
Trichogramma host	Host spp. affected distance and rate of travel by parasites	Boldt 1974
Humidity	Distance traveled was less at 30% than 50%, 70% and 85% RH	Boldt 1974
Temperature	Affected distance traveled and time spent traveling	Boldt 1974
Search Area	Increased plant size reduces efficiency by factors of 1-6 during cotton and corn growing season	Knipling and McGuire 1968

TABLE 1. (continued)

	One searching unit = 2800 sq cm of leaf surface area	Need and Burbutis 1979
	Reduced parasitism on larger (62 cm) compared to smaller (33 cm) plants	Ables et al. 1980
	Increased release rate needed with increased leaf area	Kanour and Burbutis 1984
	Searching efficiency	
Naturally occurring Trichogramma		
% leaves discovered	Increase 40-100% with increasing host density	Morrison et al. 1980
% parasitism/ discovered leaf	Decrease 100-40% with increasing host density	Morrison et al. 1980
Cultured Trichogramma		
Location of eggs on corn and cotton	No preference corn vs cotton	Gonzalez et al. 1970; Orphanides and Gonzalez 1
	No preference upper or lower surface of leaves	Gonzalez et al. 1970; Orphanides and Gonzalez 1
	Eggs placed on leaves near top of plants preferred vs eggs placed on leaves near bottom	Gonzalez et al. 1970
	Latter especially for eggs placed on top of cotton leaves	Orphanides and Gonzalez 19
Release rate	47,000-960,000/ha resulted in 33-81% parasitism of *Heliothis* spp. eggs	Stinner et al. 1974a
% leaves discovered	Increase 40-100% with increasing host density	Morrison et al. 1980
% parasitism/ discovered leaf	Decrease 100-40% with increasing host density	Morrison et al. 1980
Time spent/egg	1st egg 7.22 min to 6th egg 2.66 min	Gross et al. 1981
Model of searching time allocation in host-containing patches	Total patch time only weakly correlated to host density; *T. pretiosum* tends to abandon patches quickly as the ratio of re-encounters to hosts attacked becomes large	Morrison and Lewis 1981

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a/ Hosts: AGM, angoumois grain moth, *Sitotroga cerealella* (Olivier); TBW, tobacco budworm; CEW, corn earworm; SWCB, southwestern corn borer; *T. ni*, cabbage looper, *Trichoplusia ni* (Hübner).

eggs/generation that were susceptible to parasitism. Any eggs produced in addition to the 200 were assumed destroyed by natural causes such as predation, etc. Four pest generations of 30 days from egg to egg/season were assumed and the population was assumed to be isolated from outside effects. The uncontrolled increase/generation was assumed to be 5-fold. Thus 74 adults produced 7400 first-generation eggs (37 females x 200 eggs) and 370 first-generation adults (74 adults x 5)/ha, etc. Finally, they assumed suppressive measures would be necessary during the second and third pest generations in order to adequately protect the crop.

The hypothetical Trichogramma population (Knipling and McGuire 1968) was assumed to have been created artificially by release of ca. 12,400 parasites/ha (5000/A). It was also assumed that each parasitized egg produced two parasites and that the life cycle of Trichogramma was 10 days. The parasite was assumed to find host eggs by randomly searching the plant surfaces where the host eggs occur (nonrandom distribution of host eggs). Further, they assumed that the 12,400 parasites (during their 10-day lifespan) could search for and parasitize 50% of the host eggs on 1 ha when the plant searching area was one unit. Timing of host crop-pest-parasite was assumed to be such that one unit of searching area was present during the first 10 days of the second host insect generation, which was assumed to coincide with the first parasite generation.

The model of Knipling and McGuire (1968) was developed using the above assumptions and parameter estimates to solve a differential equation for the time rate of change of an animal population. The model was used by Hartstack et al. (1976) to simulate parasite releases against simulated Heliothis populations on cotton. To generate relationships between parasite density, host density, and search area, the latter researchers used the convenient form:

$$P = 1 - e^{(-.693*n)/(N*SA)}, \qquad (1)$$

where P = probability of parasitism,
e = 2.7128 (natural logarithm base),
n = number of effective parasites/unit area,
N = number of parasites/unit area required for 50% parasitism at SA = 1, and
SA = search area; for cotton, 1 at first cotton flower bud (first square); for corn, 1 when corn plants are ca. 61 cm high: for both crops, SA increases 1 unit every 10 days for ca. 50 days).

This model (Fig. 1) predicts that, as the number of effective Trichogramma/ha (n) increases, the % parasitism (P) increases, but at a decreasing rate (negative exponential). The curves show that less efficient parasites result in lower probability of parasitism. The probability of parasitism also decreases with increasing search area. If search area is relatively high, or parasites are ineffective in searching, the predicted probability of parasitism will be low.

Ridgway et al. (1981) also used the model of Knipling and McGuire (1968) as adapted in the MOTHZV-2 Model (Hartstack et al. 1976) to develop decision-making indices based on numbers of naturally-occurring predators/ha and releases of Trichogramma to prevent economic loss on cotton due to Heliothis spp. Ridgway et al. (1981) predicted that, with Heliothis egg densities from ca. 62,000 to 250,000/ha (25,000 to 100,000/A) and 62,000 to 160,000 natural parasites/ha, no release of Trichogramma would be required to keep Heliothis below an economic threshold of ca. 6,200 large (4th to 6th stage) larvae/ha. With low numbers (0-25,000) of natural parasites, releases of ca. 86,000 to 350,000 Trichogramma/ha twice weekly were predicted to be needed. Ridgway et al. (1981) felt the predictions appeared reasonable, assuming that these levels of natural parasites exist, and that mass-reared parasites of quality assumed in the model (Table 1, N = 110,000/ha, from Hartstack et al. 1976), are available for augmentative release.

Economic Analysis. Liapis (1980) computed the changes in yield necessary for cost-effective use of Trichogramma to control Heliothis spp. on cotton. By assuming that other inputs of production are independent of the insect control strategy (the technique of partial budget analysis), he compared current control measures under light, standard, and heavy insect

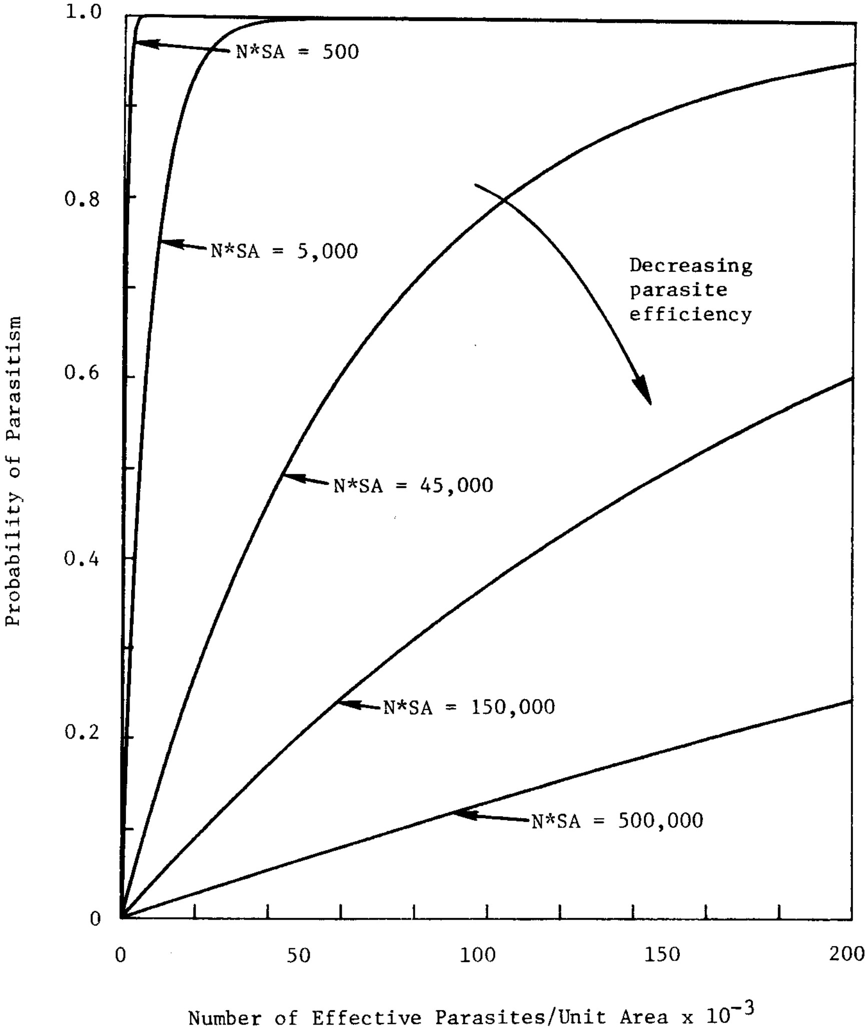

FIG. 1. Egg parasitism curves generated by the model of Knipling and McGuire (1968) (See equation (1) in text.).

pressure with simulated applications of *Trichogramma*, *Bacillus thuringiensis* (*B.t.*, a bacterial pathogen), and *Trichogramma* plus *B.t.* Under the assumptions made, break-even yields using only *Trichogramma* to maintain the same net returns as would have been expected with conventional controls ranged from a 56.04 kg/ha (50 lb/A) yield loss to a 4.48 kg/ha (4 lb/A) yield increase. The range in break-even yield was caused by the ranges in price and application rates of *Trichogramma* that he used.

Three major limitations in existing data were cited by Liapis (1980) as assumptions he was required to make. The expected cotton yields in relation to the use of *Trichogramma* or *B.t.* were lacking. Also lacking was information relating the yield obtained with the integrated pest management strategies and the level of other inputs of production. Further, knowledge of the behavior of field-produced *Trichogramma* compared to that of mass-released is important. Lastly, only direct private production costs of the biological controls could be compared, because quantitative data on the possible long-term social costs of using the techniques were not available. Because of the assumptions required, Liapis (1980) concluded that the analysis could not be utilized for control recommendations. However, he concluded that, on the basis of private costs only, either *Trichogramma* or *B.t.* alone appeared a viable economic alternative to conventional practice.

Additional benefits possible when using *Trichogramma* (Liapis 1980) are savings due to conserving natural enemies of *Heliothis*, and the possibility of *Trichogramma* reproduction in the field during the season. He estimated the cost of this control scenario by assuming a variable use rate.

Simulations with Dynamic Pest Population Models. Goodenough et al. (1983c) simulated the application of *Trichogramma* against *Heliothis* on cotton using the population dynamics model of Hartstack et al. (1976). Assuming there was no *Trichogramma* mortality from pesticide drift, Goodenough et al. (1983c) determined that the greatest potential for savings of direct cost was through early-season application when pest numbers were low. They simulated effects of pesticides on natural enemies and *Trichogramma* that were released by reducing the simulated natural enemy population by $1/n^2$, where n was the number of insecticide applications in a 14-day period. Their simulations did not include a dynamic feedback component to allow for *Trichogramma* reproduction in the field. Their control/no control criteria for *Heliothis* were determined by the numbers of control applications required to maintain the predicted yield within 90% of the expected yield.

In an attempt to simulate the population dynamics of *T. pretiosum* in the field, Goodenough et al. (1983b) developed a model incorporating *T. pretiosum* development, natural mortality, and fecundity. The model calculated the number of effective female *T. pretiosum* (based on physiological age) available to parasitize a host egg population after an initial augmentative release. The model was interfaced with the modified MOTHZV model (Hartstack 1982) and effectively modeled dramatic increases in parasitism.

Goodenough et al. (1983b) admit to inadequate validation of their model, but suggested ". . . present predictions indicate that even with continuous populations of host eggs, *Trichogramma* are unlikely to build, or even sustain their numbers sufficiently to control *Heliothis* spp. without continued release of parasites."

Trichogramma Movement. None of the models discussed above includes a simulation of the conditions under which *Trichogramma* may move from a field; such movement could be a factor contributing to low parasitization rates. Movement of *Trichogramma* is very complex (Keller et al., this monograph). Data are available on effects of temperature and humidity (Boldt 1974), mass-rearing host (Boldt 1974), kairomones (Lewis et al. 1976), wind (Schread 1932; Hendricks 1967; Allen and Gonzalez 1974; Stinner et al. 1974a; and Yu et al. 1984), and parasitization history of female (Lewis et al. 1976).

Hendricks (1967) found that *T. semifumatum* Perkins dispersed downwind in a cornfield. Stinner et al. (1974a) reported movement of released *T. pretiosum* up to 122 m within 2 days of release in cotton. Allen and Gonzalez (1974) found non-random movement of *T. pretiosum* attacking cabbage looper host eggs placed 20/cotton plant at 20 equidistant host stations located in a cross pattern centered on and extending up to 19 m from the release point. In one test they concluded that 15% background parasitization had resulted from a large-scale release experiment conducted 200 m away. Gross et al. (1975) and Lewis et al. (1976) reported that *T. pretiosum* has an innate response upon release to disperse before settling into a searching-type behavioral pattern. In point releases of *T. minutum* Riley, Yu et al. (1984) found eggs of the codling moth, *Cydia pomonella* L., more heavily parasitized in apple trees downwind of the release point than in trees upwind. However, the directional dispersal within a tree was random. Results with *T. pretiosum* within a caged tree agreed with those using *T. minutum* in noncaged trees. Other authors report no measureable effects due to wind. Schread (1932) found no directional effects due to wind on *T. minutum* dispersion in a peach orchard.

Keller and Lewis (this monograph) found movement an unlikely cause of low field parasitization rates with T. pretiosum released into cotton. Keller et al. (this monograph) present an in-depth review of literature describing physical and biotic factors affecting Trichogramma movement and foraging behavior; factors cited include temperature, humidity, dew, rain, light, wind, size of host, and Trichogramma age and genotype.

EXPERIMENTAL

A review of available literature indicated there is a definite need for a model that will be useful in determining the factors which limit field effectiveness of mass-reared Trichogramma. We present a candidate model (TGRAMMA) that includes extensive subroutines of temperature-related development and mortality. Functions incorporating searching behavior and movement are inadequate, although improved data are becoming available (Table 1).

Population Dynamics. Models for IPM decision-making should account for sufficient biological detail of pest insect responses to changing crop phenology/physiology (Barfield and Slansky 1981). These responses are: development, consumption, reproduction, mortality, and/or movement. These as categories of insect performance and their interactions are depicted in Fig. 2. We describe the theoretical dynamics of a Trichogramma population in the schematic shown in Fig. 3. The indigenous Trichogramma population may be increased through augmentation with laboratory-reared insects, immigration, or parasitization and reproduction within either target host or alternative host eggs. The Trichogramma population may be decreased through natural mortality, induced mortality (such as pesticides), movement from the crop and predation of host eggs (both parasitized and unparasitized).

TGRAMMA: Model Overview. To predict actual Trichogramma population dynamics, a model would require dynamic simulation of host egg density, Trichogramma emergence, and survival. The MOTHZV model (Hartstack et al. 1976, as modified by Hartstack 1982) is used to provide predictions of daily pest egg numbers and development. Numbers and quality of released Trichogramma (along with data on physiological age, % emergence and % of population as females), are used with the host egg data by the dynamic Trichogramma model, TGRAMMA, to predict the % of host eggs parasitized each day. Eggs not parasitized continue to develop and hatch into larvae. Both parasitized and nonparasitized eggs are available for predation. Parasites develop within parasitized eggs and emerging progeny (less estimates of mortality and movement) are added to naturally occurring Trichogramma; the total can parasitize additional new host eggs. Mortality is assessed according to physiological age, high soil or air temperature and insecticide application.

TGRAMMA: Developmental Routines. Developmental models for T. pretiosum reared on TBW or on the angoumois grain moth, AGM, Sitotroga cerealella (Olivier) were presented by Goodenough et al. (1983a). Poikilotherm (method of Sharpe and DeMichele 1977) and degree-day (DD) methods were compared. Goodenough et al. (1983) determined that emergence predictions using both models were sufficiently accurate when compared to observed values under field temperature regimes. However, predictions of the DD model were significantly different from observed values at constant temperatures of 15°C and 20°C for both hosts. Because the poikilotherm method was more accurate at low temperatures, we chose it for calculating development in TGRAMMA under mass-rearing regimes using cold programming (Stinner et al. 1974a). Because of the relative simplicity of the DD model, we used it in calculating development of Trichogramma under field temperature regimes.

Trichogramma pretiosum development is significantly faster (ca. 1 day) in TBW as compared to AGM host eggs (Goodenough et al. 1983a). Thus, we used separate developmental coefficients for mass-reared and field-reared Trichogramma. The percentages of T. pretiosum ready for emergence at the time

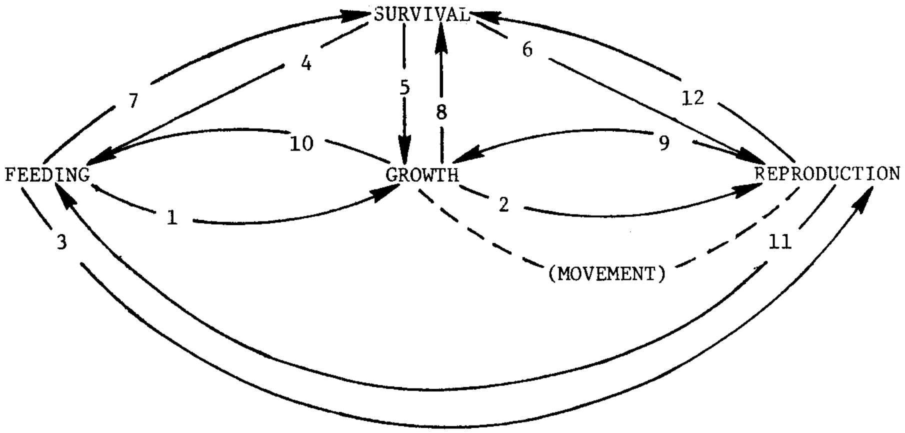

FIG. 2. Categories of insect performance and their interactions. From Barfield and Slansky 1981. (Used by permission.)

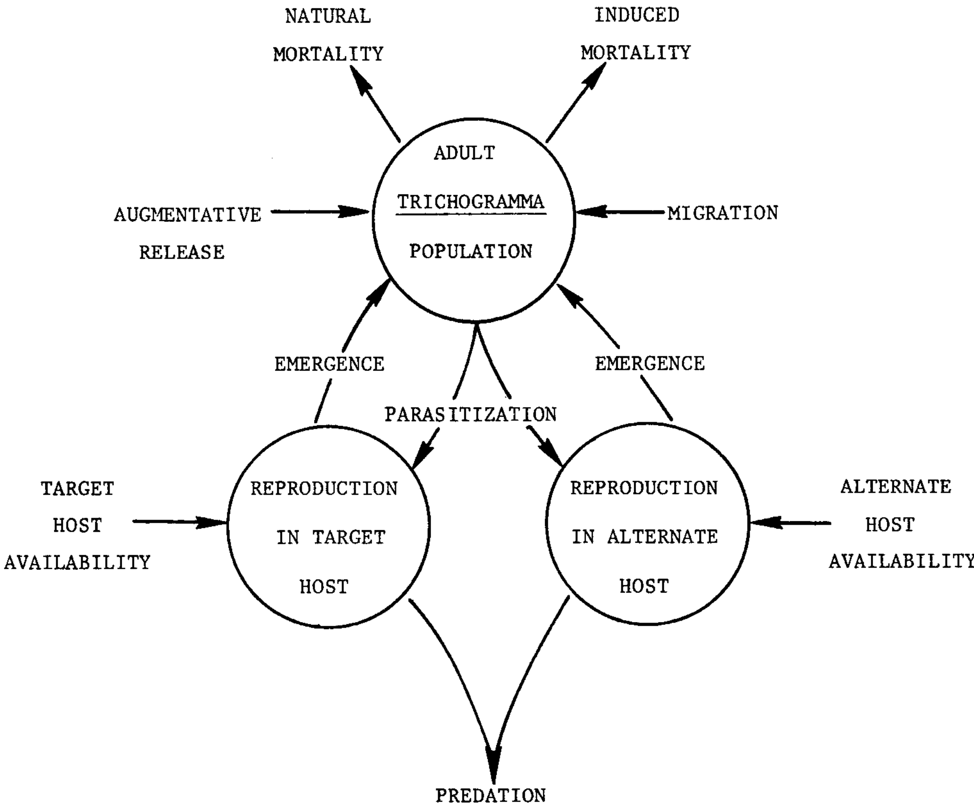

FIG. 3. Schematic description of a dynamic population of *Trichogramma*.

of augmentative release predicted by TGRAMMA are compared to observed values (R. K. Morrison, unpublished data) in Table 2. The calculations of fractional emergence were done as reported by Goodenough et al. (1983a), using a revised rearing temperature regime (R. K. Morrison, unpublished data).

TABLE 2. Percentage of *Trichogramma* Ready to Emerge After Cold Programming at the Selected Temperature Regime.

After 8 days at 26.7°C, no. days at 16.7°C[a]	Predicted % for host: AGM	Predicted % for host: TBW	Actual % for AGM[b]
6 1/3	61.7	96.4	75.4
7 1/3	72.3	99.7	77.5
8 1/3	81.3	100	94.6
9 1/3	88.6	100	86.5

a/ The rearing regime needed to rear parasites for release at 8 a.m. after 14, 15, 16 or 17 days.

b/ Unpublished data of R. K. Morrison, presented at 1984 National Meeting, Entomol. Soc. Am., San Antonio, TX. 0-4 h emergence for *Trichogramma* held in continuous dark; does not include preemergence.

TGRAMMA: Simulation of Soil Temperature. Upon distribution by aircraft as described by Bouse et al. (1981), *Trichogramma*-infested eggs are scattered on the soil surface and the crop. The soil surface could be relatively smooth or rough and could be shaded by plants or mulch. Eggs might fall into cracks in the soil. Temperature of the soil surface depends on factors such as soil moisture, radiation, and soil type and slope. For the purpose of this paper, we estimated hourly soil-temperatures (ST) at 1 cm depth for typically clear days in 1984 for College Station, TX. We assumed moderately dry, bare soil. Soil temperatures were estimated by adding the differential between air temperature and soil temperature to air temperature for the respective hour. The soil temperature model of McCann (1985) was used to calculate the differential between air and soil temperature (Fig. 4). The cosine rule was used to calculate hourly air temperature from max/min air temperatures.

TGRAMMA: Emergence and Survival of Trichogramma After Augmentative Release. Lopez and Morrison (1980) reported dramatic reductions in emergence and survival of *T. pretiosum* from *S. cerealella* eggs that were held for as little as 1 h at high temperatures. They held eggs in vials in water baths at temperatures from 26.7 to 50°C. When parasitized *T. ni* eggs were covered with soil, Fye and McAda (1972) found even more drastic reductions in *Trichogramma* emergence.

To simulate increased mortality that would be expected if augmentative releases are made onto relatively hot soil, we calculated regressions (Table 3a) of % emergence and survival on temperature from adjusted data of Lopez and Morrison (1980). The equations are:

$$\mathrm{EMG} = \left|\begin{array}{ll} 52.04*(\mathrm{ST} - 16)/790 & \mathrm{ST} < 26 \\ (-5613 + 405.7*(\mathrm{ST}) - 6.516*(\mathrm{ST})^2)/790 & 26 \leq \mathrm{ST} \leq 40 \\ (169 - 6*(\mathrm{ST} - 40))/790 & \mathrm{ST} > 40 \end{array}\right. \qquad (2)$$

$$\mathrm{SURV} = \left|\begin{array}{ll} 10.97 & \mathrm{ST} < 26.7 \\ 1 - 0.7*e^{-.263(40.1 - \mathrm{ST})} & 26.7 \leq \mathrm{ST} < 40 \\ 0.3 - 0.03*(\mathrm{ST} - 40) & \mathrm{ST} \geq 40 \end{array}\right. \qquad (3)$$

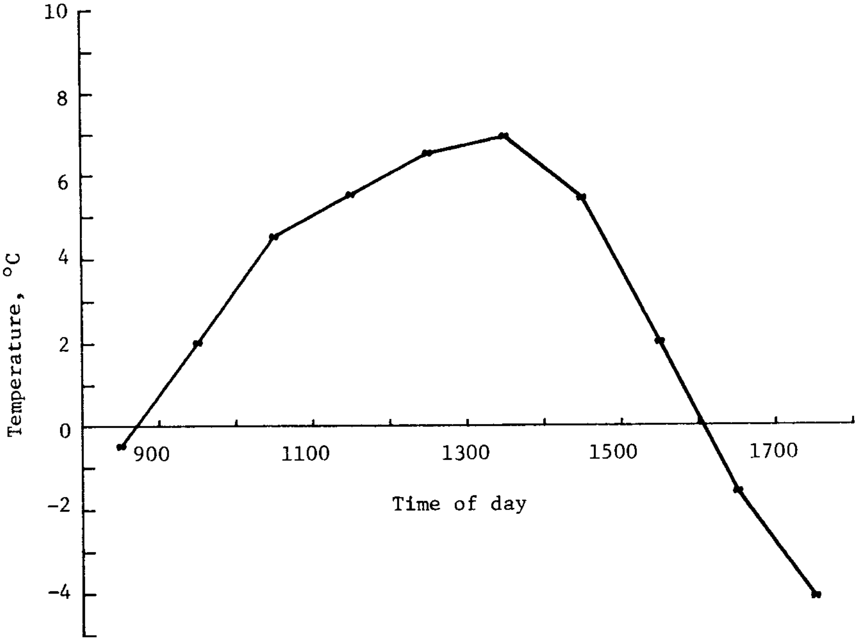

FIG. 4. Differential between air and soil temperature: moderately dry soil on a clear day - College Station, TX, March (from McCann 1985).

Simulated hourly values of emergence and survival are plotted in Fig. 5. The predicted values over time (Table 3b) agree very closely with observed data, Table 3a, with overall r^2 of 96.4. These equations are used with soil temperature (described above) to estimate Trichogramma emergence and mortality during the first 4 h after augmentative release.

TGRAMMA: Quality and Performance Factors. Trichogramma quality and field performance depend on many factors; some of these, which are referenced in Table 1, include laboratory host, temperature, field host species and density, plant size or search area, behavior-modifying chemicals, wind, and type, proximity and recency of insecticide use. Presently, the TGRAMMA model includes the factor of fecundity versus physiological age of Trichogramma (Goodenough et al. 1983b; from laboratory data of R. K. Morrison, personal communication). Reductions in numbers due to insecticide application are made in the MOTHZV model. The influence of increased search area is included as estimated by Knipling and McGuire (1976). Comparisons of other factors such as overall quality, % emergence, number of progeny/host, % females, and rearing host and strain of Trichogramma, may be input as decimal multiplicative constants (see Tables 4 and 5).

TGRAMMA: Model Operation. The required responses for a sample model run are summarized in Table 4. After entering the days of run, daily max/min temperatures, and crop and pest data, the user can input Trichogramma-release data according to a desired regime, such as that suggested by a prior simulation, field experience, etc., or request the sampling option, which will stop the MOTHZV prediction on a specified day and then at specified intervals (e.g. at day 160 and every 3rd day thereafter). On successive sampling dates, the MOTHZV model prints estimates of Heliothis life stages and crop conditions. Based on the current insect and crop conditions, the user decides

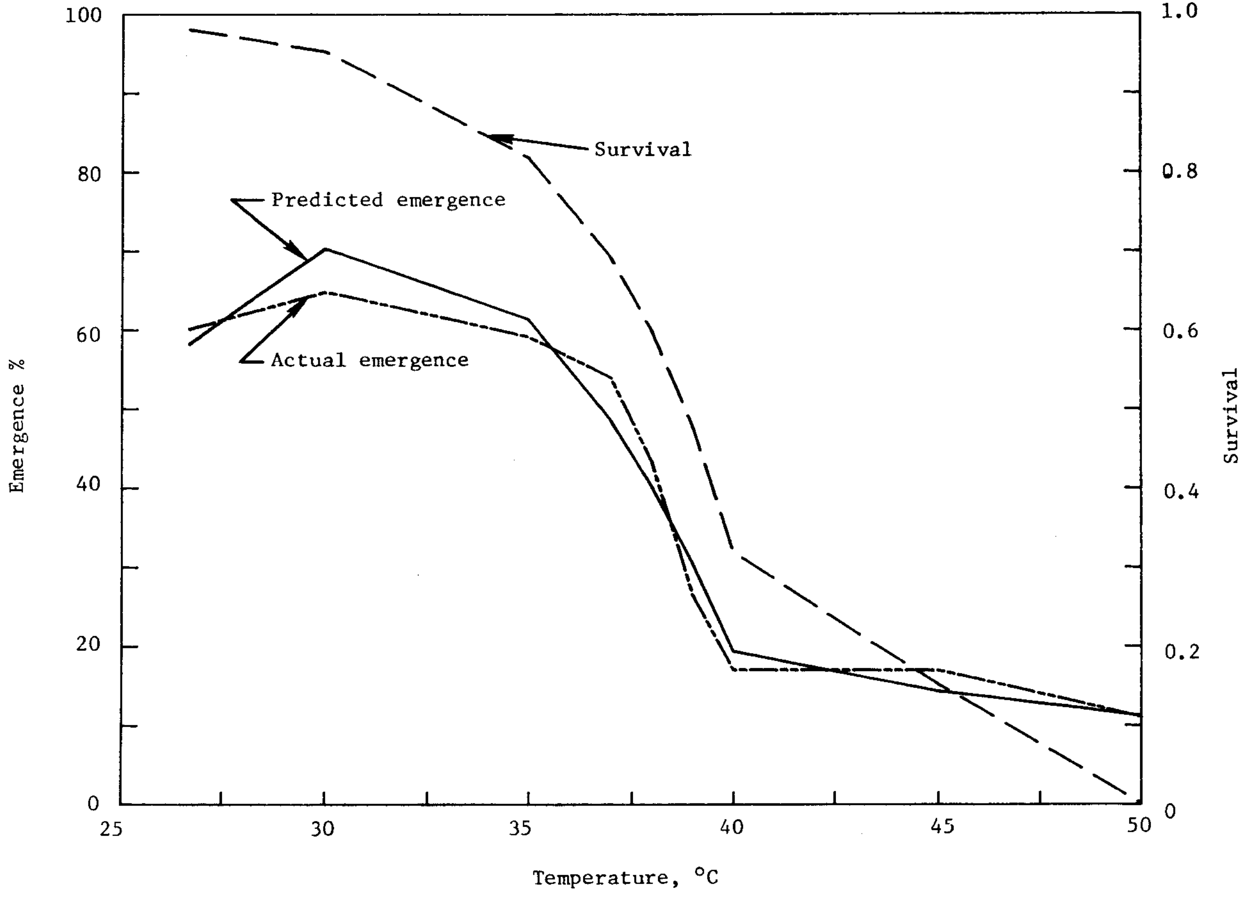

FIG. 5. Effect of soil temperature after release on hourly emergence and survival of _Trichogramma_.

TABLE 3. Effect of Soil Temperature After Augmentative Release on Emergence and Mortality of *Trichogramma pretiosum*.

A. Laboratory[a]

Temp °C	Time after release 1h	2h	3h	4h
26.7	600	682	740	790
30	647	690	646	723
35	590	638	664	693
37	538	611	651	679
38	431	480	536	500
39	263	436	368	360
40	169	160	156	174
45	168	99	157	69
50	109	146	103	102

B. Predicted values[b]

Soil Temp °C	Time after release 1h	2h	3h	4h
26.7	581	737	779	790
30	702	784	793	794
35	612	730	752	756
37	484	616	652	661
38	399	519	555	565
39	302	392	418	426
40	192	238	249	252
45	141	158	160	161
50	110	110	110	110

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a/Developed from data of Lopez and Morrison (1980). Emergence/1,000 eggs parasitized by *Trichogramma pretiosum* and programmed for field release. Values are after 1-4 h at the indicated temperatures.
b/Calculated as: 1st h, 1000 x 80% (assumed normal emergence) x %EMG(ST) x %SURV(ST) from equations 2 and 3; 2nd to 4th h: the number emerging each h is calculated from (number live not emerged) x %EMG(ST) X %SURV(ST) and added to number already emerged. During model operation, the % ready to emerge at each release (80% in this example) is calculated using the poikilotherm method and the rearing temperature regime.

whether *Heliothis* control is needed. He has the option of releasing *Trichogramma* or applying insecticide the following day. Whether or not the sampling option is chosen, the user is queried "Do you want to release *Trichogramma*?". If *Trichogramma* release(s) are specified, for each release the user enters data of mass-rearing host, day of release, h of release, number of *Trichogramma*/A (number/ha x 0.4047), mass-rearing temperature regime (choose 1 of 3, or construct from actual temperature) and any change in quality factors, for up to a total of 15 releases.

The MOTHZV model calculates pest and crop estimates for each day of the run. When the day of run is the same as a day of *Trichogramma* release, control is shifted back to TGRAMMA. Hourly predictions of development, mortality, etc. are used to calculate daily estimates of *Trichogramma* development, % emerged and adult numbers. This is done separately for

TABLE 4. Queries of a Sample Simulation of *Trichogramma* Release.

MOTHZV model:

Enter days of run, temperature files, crop data, and pest data into MOTHZV (e.g.: days 60-200; 1984 max/min temp. - College Station, TX; Corn with 50,000 plants/ha, and first silk on day 155; and *H. zea* pheromone trap catches on days 61-147.

```
DO YOU WANT TO RELEASE TRICHOGRAMMA?  ENTER <Y> OR <RETURN>.
? Y
```

Trichogramma submodel, TGRAMMA:

```
IT IS ASSUMED THAT THE HOST FOR MASS-REARED TRICHOGRAMMA IS
SITOTROGA CEREALELLA.  IF YOU WISH TO SIMULATE HELIOTHIS
VIRESCENS HOST ENTER <V>.  OTHERWISE PRESS <RETURN>.
? <RETURN>

ENTER DAY NO. OF RELEASE, IF NONE <RETURN>.
? 160

ENTER HOUR OF RELEASE OR <RETURN>.
EXAMPLE -- 8 a.m. IS 8   5 p.m. IS 17
IF YOU ENTER <RETURN> 8 a.m. WILL BE USED.
? <RETURN>

ENTER NUMBER TRICHOGRAMMA/A.
? 50,000

MODEL DEFAULT ASSUMES TRICHOGRAMMA HAVE BEEN MASS-REARED
ON A SCHEDULE APPROPRIATE FOR THIS RELEASE.

COLD PROGRAMMING: EMERGENCE NOT ALLOWED UNTIL TEMP. > 16.7°C.

ENTER ONE OF THE FOUR MASS-REARING TEMPERATURE REGIMES
FROM THE FOLLOWING LIST.
TYPE 1 - STANDARD, 8 DAYS AT 26.7°C THEN
         5 DAYS AT 16.7°C UNTIL RELEASE
     2 - 1° COOLER THAN STANDARD
     3 - 1° WARMER THAN STANDARD
     4 - YOU CONSTRUCT FROM ACTUAL/ASSUMED HOURLY TEMPS.
? 3

SUMMARY OF DATA FOR TRICHOGRAMMA RELEASE NO. 1
THE CUMULATIVE % READY TO EMERGE AT RELEASE: 72.3
THE DAY OF TRICHOGRAMMA RELEASE WAS 160
THE HOUR OF TRICHOGRAMMA RELEASE WAS 9
THE TRICHOGRAMMA REARING TEMPERATURE REGIME WAS 3

THE PRESENT QUALITY FACTORS ARE

SEARCHING                                      REARING
EFFICIENCY  % EMERGE  NO./HOST  % FEMALE    HOST     STRAIN
  0.80        0.85      1.50      0.60      0.60      1.00

DO YOU WANT TO CHANGE ANY QUALITY FACTOR?  ENTER <Y> OR <RETURN>.
? <RETURN>
```

TABLE 4. (continued)

```
ENTER DAY NO. OF RELEASE.  IF NONE <RETURN>.
? 165
```

etc. for each release - Here we simulated 4 releases:

```
SUMMARY OF TRICHOGRAMMA RELEASES:
 NUMBER OF RELEASES: 4
 THESE ARE THE DAYS TRICHOGRAMMA WERE RELEASED
  160 165 170 175 0 0 0 0 0 0 0 0 0 0 0
 THESE ARE THE HOURS TRICHOGRAMMA WERE RELEASED
  8 9 10 11 0 0 0 0 0 0 0 0 0 0 0 0
 THE NUMBER OF TRICHOGRAMMA RELEASED/A WERE
  50000 50000 50000 50000 0 0 0 0 0 0 0 0 0 0 0
 THE REARING TEMPERATURE REGIMES WERE
  3 3 3 3 0 0 0 0 0 0 0 0 0 0 0 0
 THE AIR TEMPERATURES AT RELEASE WERE
  26.6 27.2 29.4 32.1 0 0 0 0 0 0 0 0
 THE SOIL TEMPERATURES AT RELEASE WERE
  26.1 29.2 33.9 37.6 0 0 0 0 0 0 0 0
 THE CUMULATIVE % READY TO EMERGE AT RELEASE WERE
  .71862 .72329 .72792 .73251 0 0 0 0 0 0 0 0
 THE CUMULATIVE EMERGENCES 4 H AFTER RELEASE WERE
  35449.13 35802.26 34479.41 23527.39 0 0 0 0 0 0 0 0
```

(Model control now shifts back to MOTHZV model.)

```
INPUT DAY NO. OF INSECTICIDE APPLICATION -- IF NONE <RETURN>.
```

MOTHZV model calculates daily pest and crop estimates. Pest eggs parasitized by *Trichogramma* are removed from pest populations. *Trichogramma* emerging are added to the field population as "natural", Fig. 3.

The user may request a variety of printouts:

- *Heliothis* population - number of eggs, small larvae, large larvae, pupae, and adults/day.
- Insecticide effects on insects - % survival of egg, small larvae, large larvae, pupae, adults, beneficial insects, *Trichogramma*.
- Cotton population - number squares, small bolls, large bolls, open bolls.
- Damage to cotton - number of damaged squares, small bolls, large bolls, and % damaged squares, small bolls, large bolls.
- Temperature input data - mean daily temp., minimum temp., degree days/day and accumulated degree days for *Heliothis* and corn, adult activity of *Heliothis*, and moonlight activity of *Heliothis*.
- Crop and beneficial insect data - egglay probability (crop attractancy), probability of beneficial insect parasitism and predation (if model estimates are used), probability of egg and larvae predation (if numbers of common predators are known), plant search area estimate, probability of adult *Heliothis* migration from corn, and number of corn silks.

The user may request a variety of plots of the data available in printout form.

released and field-reared *Trichogramma*, so that effects of different environments, different hosts and quality factors may be assessed. Released, parasitized host eggs are assumed to be subjected to the temperature of the upper 2.54 cm of the soil profile (explained above). Quality of mass-reared *Trichogramma* is estimated as decimal equivalents of natural quality, considering natural as 1.0. Field offspring of mass-reared *Trichogramma* that develop in *Heliothis* eggs are added to "natural" numbers to calculate the total number of *Trichogramma* available to parasitize *Heliothis*. Numbers of parasitized *Heliothis* eggs are subtracted from those developing into larvae, but are left available to be reduced by predation and insecticidal mortality.

The four *Trichogramma* releases described in Table 4 were simulated using the TGRAMMA model with 1984 air temperature data of College Station, TX. Increasing soil temperature was predicted to decrease *Trichogramma* emergence and survival (Table 5). Release number two, at 9 a.m., resulted in slightly higher cumulative emergence (35,802) than the release at 8 a.m., because of the increased emergence during the first h after release. The adverse effect of higher air temperature at release was noticeable with the 10 a.m. release (Day of Year, DOY, 170), and was dramatic with the 11 a.m. release, which was also on a day of maximum temperature of 35.0°C.

TABLE 5. Demonstration of TGRAMMA Calculation for Emergence and Survival of Released *Trichogramma*[a].

DOY	Release	Time of day	Air temp	Soil temp	% Emergence	% Survival	Cumulative survival
160	1	0800	26.6	26.1	68.2	97.0	24,507
		0900	27.8	29.8	87.3	95.4	34,186
		1000	28.9	33.4	84.5	87.9	35,316
		1100	30.0	35.5	73.1	79.1	35,449
165	2	0900	27.2	29.2	85.8	96.0	31,047
		1000	28.5	33.0	85.9	89.1	35,268
		1100	29.7	35.2	75.0	80.6	35,730
		1200	30.8	37.3	57.9	66.8	35,802
170	3	1000	29.4	33.9	82.4	86.2	30,001
		1100	30.7	36.2	67.7	74.9	33,734
		1200	31.8	38.3	46.6	56.5	34,356
		1300	32.6	39.5	30.7	39.8	34,479
175	4	1100	32.1	37.6	54.5	63.9	19,965
		1200	33.3	39.8	27.0	35.5	22,838
		1300	34.2	41.1	20.5	26.6	23,404
		1400	34.8	40.2	21.2	29.4	23,527

[a] Simulated release of 50,000 *Trichogramma*/release: See Table 4 and text for conditions. Release made the first h shown each day. Temperatures were estimated via cosine rule from max/min air temperatures, College Station, TX, 1984: 32.2/23.3, 32.2/22.2, 33.3/22.8 and 35.0/23.3 for release 1, 2, 3, and 4, respectively.

Options allow a variety of rearing and field conditions to be simulated (Table 6). Host of mass-reared *Trichogramma* can be either AGM or TBW. Presently we have only data on TBW for field host. Special rearing temperature/release regimes can be used to simulate warm or cool mass-rearing

TABLE 6. Summary of Options in Using the Dynamic *Trichogramma* Model.

Released *Trichogramma* host = AGM/TBW (CEW data needed)	
Natural *Trichogramma* host = TBW (CEW data needed)	
Special rearing temperature regimes -	Warm/cool rearing temperatures
Timing, number of *Trichogramma* releases -	Frequency Number released Time of day: e.g., malfunction in distribution equipment, etc. causes delay in release
Quality factors[a] -	Rearing too hot or too cold affects performance Rearing host Strain of *Trichogramma* released
Searching efficiency -	More leaf surface as plant grows Effect of kairomone
Not yet included -	Non random movement after release Effect of wind Retention via kairomone

---

a/ Present input is via multiplicative constants.

conditions, malfunction in distribution cooling equipment, delays during release, etc. The timing and number of *Trichogramma* released can be adjusted as desired according to either actual or predicted pest numbers. Time of day parasites are released may affect the mortality of *Trichogramma*-parasitized host eggs exposed to hot soil, and is simulated by estimating soil temperature the first 4 h after an augmentative release of *Trichogramma* (for an example, see Table 7). Quality factors are needed that relate *Trichogramma* rearing conditions and strain to field performance. Estimates of these factors may be input as decimal reductions of the number of *Trichogramma* emerged. As described above, % emergence is calculated separately using the chosen rearing temperature regime (e.g., to simulate a reduction expected due to extended holding at cold temperatures).

TABLE 7. Effect of Time of Day on Emergence and Survival of Released *Trichogramma*[a].

Hour of release	Number of predicted adults 4 h after release with the indicated max/min temperature regime[b]:				
	32.2/23.3	35.0/23.3	35.0/26.7	39.8/26.7	40.6/26.7
8	35,449	35,544	35,525	35,299	34,862
9	35,782	35,435	34,725	32,546	28,579
10	35,105	32,058	28,796	20,365	11,295
11	32,509	23,527	19,482	9,605	8,415

---

a/Simulated release of 50,000 *Trichogramma* each release.

b/Each number is total predicted adults 4 h after a release simulated for that particular combination of hour of release and temperature regime. The first two temperature regimes are those of releases 1 and 4, Table 6.

A series of simulations were made to compare total predicted emergence at 4 h after Trichogramma release for releases made at 8, 9, 10, or 11 a.m. (Table 7). Slightly higher cumulative emergence was predicted for Trichogramma released at 9 a.m. with the first temperature regime. With the remaining temperature regimes, total emergence was lower for all releases made after 8 a.m. Emergence and survival were drastically reduced for late morning releases in max/min temperature regimes 39.8/26.7 and 40.6/26.7 - temperatures which commonly occur in Texas sometime during the cotton growing season. Predicted survival was reduced 67% and 76%, respectively, for simulated releases made at 10 and 11 a.m. compared to those made at 8 a.m. with the 40.6/26.7 max/min temperature regime. Corresponding soil temperature at release for this temperature regime was calculated as 31.3, 35.6, 39.9 and 42.6°C for releases made at 8, 9, 10 and 11 a.m., respectively.

CONCLUSION

A review of current models shows all lack one or more of the basic components; reproduction, development, field parasitization, mortality, or movement. The expanded temperature-dependent emergence and mortality function we developed and incorporated into a revised model, TGRAMMA, aids in understanding the importance of a timely augmentative release with respect to field soil temperature. Important aspects of Trichogramma efficiency and movement under field conditions are still needed. Conflicting reports, and lack of quantitative data on Trichogramma movement after release, hamper development of a subroutine to simulate the biological basis of movement as a possible cause of the rapid decline in Trichogramma field populations.

This revised model, TGRAMMA, coupled with the MOTHZV dynamic model of Heliothis allows simulation of various aspects of Trichogramma release, especially the time of application and impacts of insecticide application. The plots of Fig. 5 indicate that releases should be made when soil temperature is ca. 27 to 35°C. Thus, release on cloudy days, or holding Trichogramma until the next day should be considered if damaging soil temperatures are expected during the next few hours, and particularly during the first h after release.

Future Model Development. Routines should simulate effects of parasite quality or field performance because of their influence on numbers of parasites required to control the pest population. These routines should include quantitative data on movement, field search rate and handling times (time spent to parasitize host eggs as a function of parasitism history of both parasite and host). A movement component should be included in a dynamic Trichogramma model, but much research is needed before this aspect of Trichogramma behavior will be adequately understood (Keller et al., this monograph). Considerable data on efficiency-related factors (Table 1) will be incorporated into TGRAMMA as time permits. The effect of % discovery as presented by Need and Burbutis 1979, Morrison et al. 1980, and Kanour and Burbutis 1984, could be added. The reduction in parasite effectiveness due to insecticides should be estimated (House et al. 1980; Bull and House 1983). Data on host egg density (Ridgway et al. 1981), and handling time (Gross et al. 1981) are also available and important. Incorporation of these factors would be important steps toward predicting numbers of hosts parasitized, instead of simply % of the target population parasitized. It may be important to predict numbers of pest eggs parasitized because Trichogramma is not Heliothis-specific. Also needed in the model, are data on the field efficiency of various strains of Trichogramma on various hosts, as related to host density, plant phenology, presence of other natural enemies and other (nontarget) hosts. Costs of application should be included. Whether the assumption of equal yields under all pest control strategies (Liapis 1980) is valid will also be an important consideration if the model is to have reliability and credibility for use in pest management decision-making.

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