FORUM

Timing of Control Based on the Stage Structure of Pest Populations: A Simulation Approach

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ABSTRACT Because susceptibility of pests to control agents varies among life stages, knowledge of the stage structure of a pest population is critical for implementation of control strategies. However, computer simulations based on traditional female age-specific life tables are inadequate in this respect. A computer simulation of population growth based on an age-stage, two-sex life table reveals the stage structure of a pest population at any time. Using this model, the most economical and efficient control strategies can be chosen and applied at the appropriate times.

KEY WORDS Insecta, life table, pest control timing, simulation

WITH PESTICIDES or their alternatives, proper timing is essential for an effective reduction of a pest population. Lack of proper timing in a pest management program can waste money, labor, and time; it can lead to failure of the control program and contamination of the environment. Proper timing in pest control should be based on the knowledge of population dynamics of pest species.

Different criteria have been proposed to time insecticide application. Among these criteria are plant stage, stage structure of pest population, accumulated degree-days, insect-days and pheromone trap data (Mueller & Stern 1974; Cooper et al. 1983; Hull & Starner 1983; Ruppel 1983, 1984; Gargiullo et al. 1984, 1985; Reissig et al. 1985; Stanley et al. 1987). More sophisticated models based on pest population ecology have also been reported and reviewed by Gutierrez et al. (1979), Rykiel et al. (1984), and Welch (1984). The importance of pest population ecology is discussed in these papers and textbooks of pest management (e.g., Metcalf & Luckmann 1982). Because pest susceptibility to control agents varies among life stages, knowledge of the stage structure of a pest population is critical to planning the most effective pesticide application schedule.

Traditional age-specific life tables (Lewis 1942; Leslie 1945, 1948; Birch 1948) offer little information in this respect. Furthermore, the traditional age-specific life table deals only with the female population and ignores variable developmental rates among individuals. In pest control programs, the consequences of ignoring variation in maturation rate may be serious (Plant & Wilson 1986). Incorporating both sexes and variable developmental rates among individuals, Chi & Liu (1985) reported the theory of an age-stage, two-sex life table. Because they give a complete age-stage description for each time period (Chi 1988), simulations based on an age-stage, two-sex life table offer a possible way to predict the most suitable time for pest control. In this paper, I describe a model for timing of pest control based on an age-stage, two-sex life table. Simulation examples are also given to illustrate the general features of pest management oriented to population stage and structure.

The Model: Timing

To take both sexes and variable developmental rates into account, raw data of development and fecundity for each individual are required. In this instance, data previously obtained and published (Chi 1988) for the potato tuberworm, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) are used for the model. To simplify the discussion and to focus on the effect of variable susceptibility and damaging capability among stages, I refer to the three preadult stages (egg, larva, and pupa) as A, B, and C, respectively. I assumed that individuals of stage B cause less damage than those of stage C, while individuals of stage A and adults cause no damage. Original data of the matrices of growth rate (*G*), developmental rate (*D*), and fecundity (*F*) are given in Chi's (1988) paper. Because fe-

Table 1. Assumed stage-specific weighting coefficients and mortalities used in simulations

Stage	Weighting coefficient	Control mortality		
		1st day	2nd day	3rd day
Stage A	0	0	0	0
Stage B	0.5	0.9	0.45	0.225
Stage C	1	0.8	0.4	0.2
Female	0	0.2	0.1	0.05
Male	0	0.2	0.1	0.05

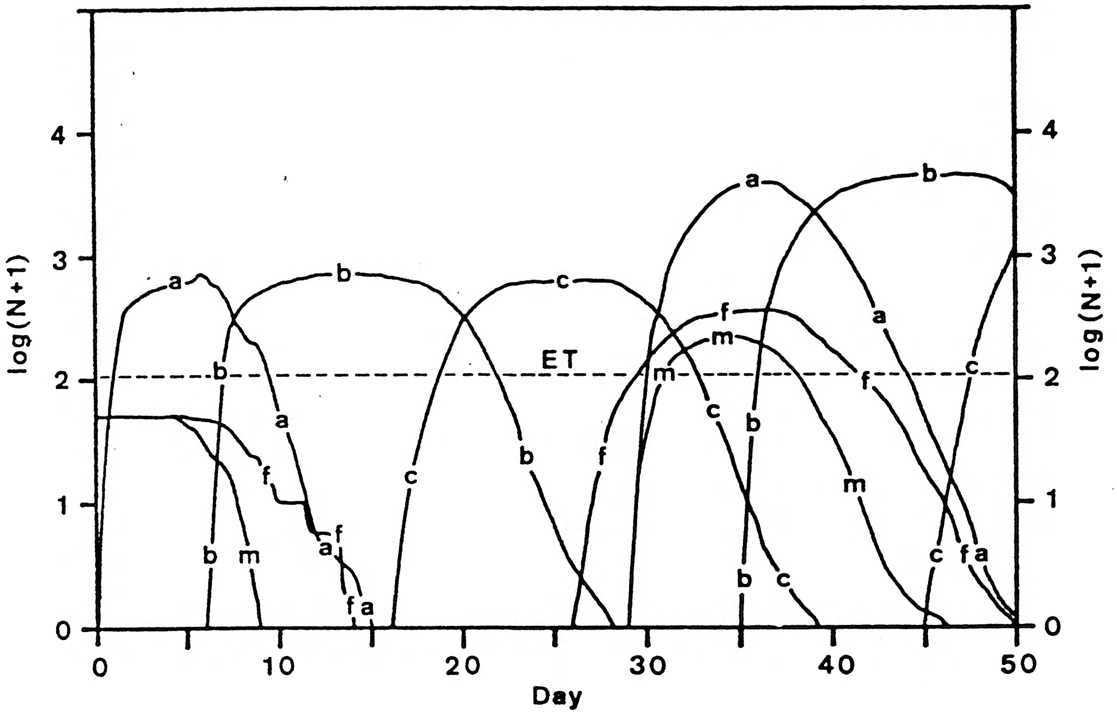

Fig. 1. Simulation of the population growth under unlimited conditions. Curves denoted by a, b, c, f, and m represent stages A, B, C, female, and male, respectively. ET is the economic threshold.

cundity and survival rate of potato tuberworm under laboratory conditions are very high, use of these data results in a very fast growth. To simplify the explanation, one tenth of original age-stage specific fecundity was used in all simulations. Besides life table data, the following additional data are required:

a. Time-specific economic threshold.
At equivalent densities, pests may cause more damage when infestations occur during susceptible stages of host plant (Johnston & Bishop 1987, Dripps & Smilowitz 1989). This phenomenon and many others should be considered in developing an IPM model (Onstad 1987). Here, the time-specific economic threshold in this model is described by the following equation:

$$Y(t) = a + b \cdot t + c \cdot t^2$$

where $Y(t)$ is the economic threshold at time t; a, b, and c are regression coefficients. Because my objective in this paper is to time pest control based on stage structure of pest population, I assigned the economic threshold for the entire simulation period as 100 equivalents of stage C (i.e., $a = 100$, $c = 0$, and $b = 0$).

b. Stage-specific weighting coefficients.
Because I assumed that individuals of stage A and adults are non-destructive, the correspondent weighting coefficients are 0. Weighting coefficients 0.5 and 1 are assigned to stage B and C, respectively (Table 1).

c. Stage-specific mortality.
Because the susceptibility of pest to control agents varies among stages, I assigned different mortalities to each stage (Table 1). I assumed an arbitrary 3-d period of residual mortality, with mortalities decreasing each day to half of that of the previous day.

Table 2. Number of treatments, cumulative stage-days and weighted stage-days of each simulation result

Simulation condition	No. treatments	Cumulative stage-days	Cumulative weighted stage-days
Unlimited (Fig. 1)	0	67,866	38,428
Calendar-based control without residue effect (Fig. 2)	4	5,295	2,817
Calendar-based control with residue effect (Fig. 3)	4	2,867	1,475
Control based on ET and stage size, without residue effect (Fig. 4)	6	2,595	1,666
Control based on ET and stage size, with residue effect (Fig. 5)	3	2,173	1,299
Control based on ET and weighted stage size, without residue effect (Fig. 6)	3	4,108	2,435
Control based on ET and weighted stage size, with residue effect (Fig. 7)	2	3,632	1,942

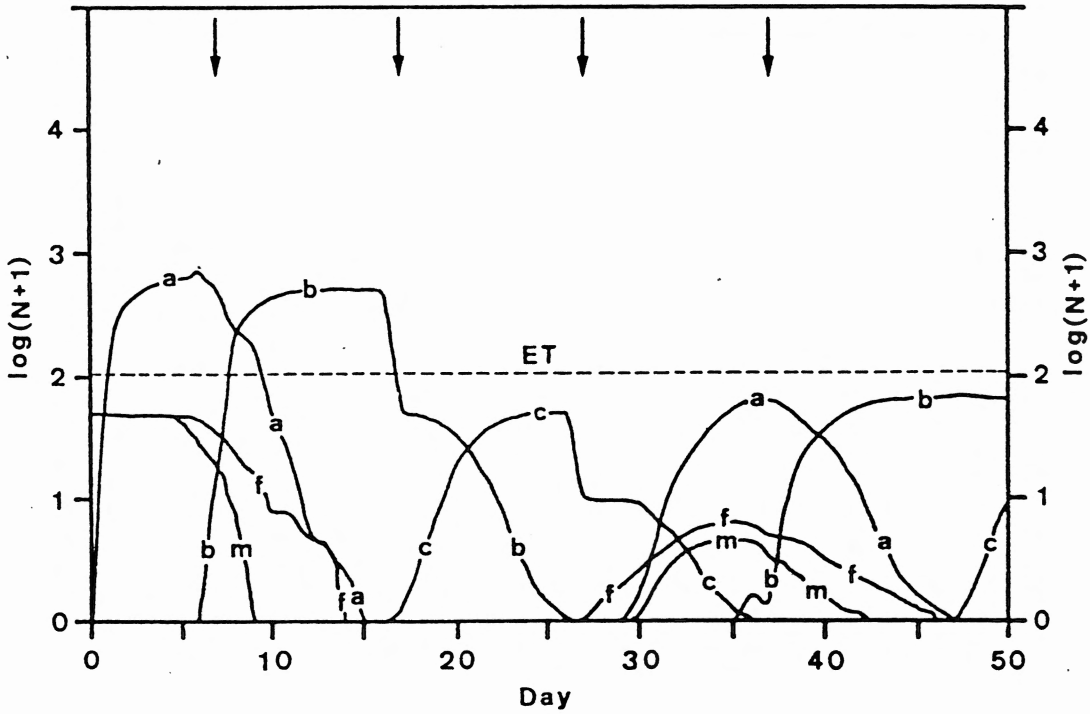

Fig. 2. Simulation of population growth under calendar-based control (without residue effect). Curves denoted by a, b, c, f, and m represent stages A, B, C, female, and male, respectively. Arrows represent application dates. ET is the economic threshold.

Detailed explanations and use of these data are given in the next sections. The model TIMING is described by using simulation examples as follows.

Unlimited Growth. In this section, the growth of a population without any restriction is simulated. The age-stage structure of pest population at time $t + 1$ can be obtained through the operation of matrices G, D, and F (Chi & Liu 1985):

$$N_t \xrightarrow{G,\,D,\,F} N_{t+1}$$

Starting with 100 adults, 30 d old (50 females and 50 males), the simulated result for 50 d is given in Fig. 1. This figure reveals the stage structure of the pest population at each time period. This can be considered as equivalent to a control treatment in pesticide experiments.

Calendar-Based Control without Residue Effect. To simulate calendar-based control, treatments were applied according to the schedule outlined in Table 2 regardless of the stage structure of the pest population. After each treatment, the surviving number in each age-stage class was calculated:

$$n'_{ij}(t) = n_{ij}(t) \cdot (1 - m_j)$$

where $n_{ij}(t)$ is the number of individuals in age i and stage j before treatment, m_j is the mortality to stage j, and $n'_{ij}(t)$ is the number that survived. Different values of m_j have been assigned to each stage to represent the variable susceptibilities among stages (Table 1). Fig. 2 illustrates the result of simulation in which the mortalities of the second and third days were ignored. The first treatment is on the 7th day, after that three successive treatments were applied at 10-d intervals. Because of the effects of control agents, the growth of the pest population differs from the untreated population (Fig. 1). According to the stage structure, the third treatment is applied when the target stage (B and C) is below the economic threshold; the fourth treatment is applied when the density of stage B and C are very low.

Calendar-Based Control with Residue Effect. Most pesticides have residual toxicity. Although a major aim of integrated pest management is to decrease the total amounts of pesticide residues in the environment, short-term residual toxicity is still important for an effective control. The duration and toxicity of pesticide residues vary with chemical characteristics and environmental factors. Fig. 3 shows the simulated population growth under controls with 3 d of residual effects. The population size is significantly reduced from that in which the pesticide is without residual effect (Fig. 2), and the third and fourth treatments might be unnecessary.

Control Based on Stage Size and Economic Threshold. In the simulation based on the age-stage, two-sex life table, the curves for each stage can be obtained for each time period (Fig. 1–3).

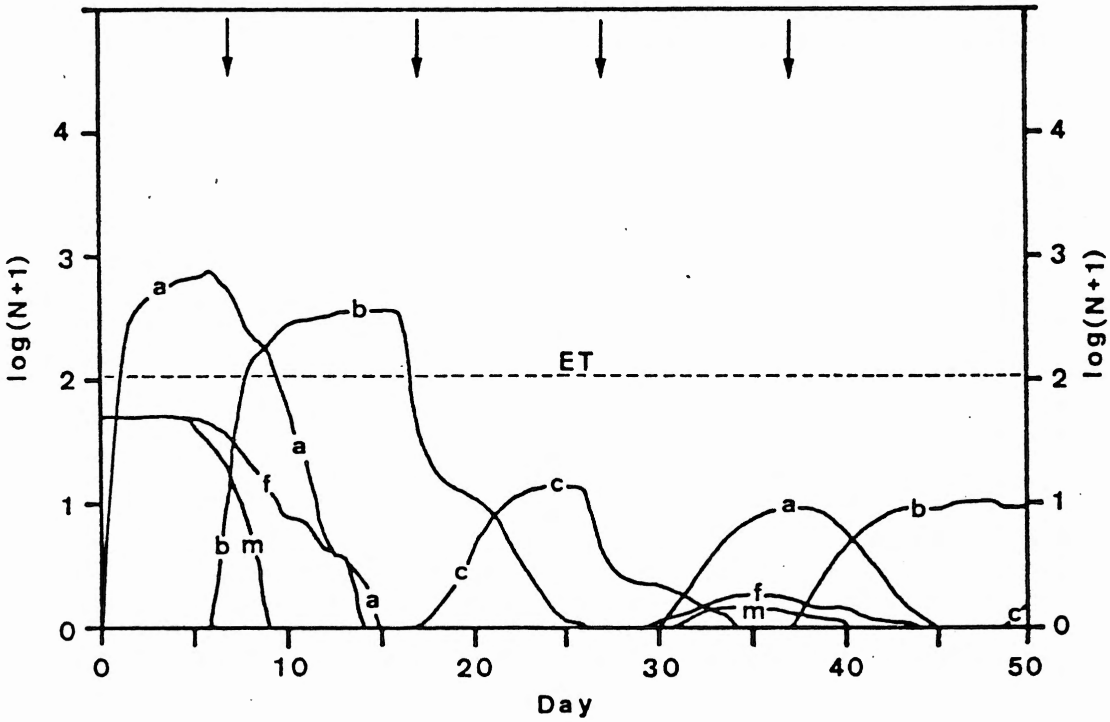

Fig. 3. Simulation of population growth under calendar-based control (with residue effect). Curves denoted by a, b, c, f, and m represent stages A, B, C, female, and male, respectively. Arrows represent application dates. ET is the economic threshold.

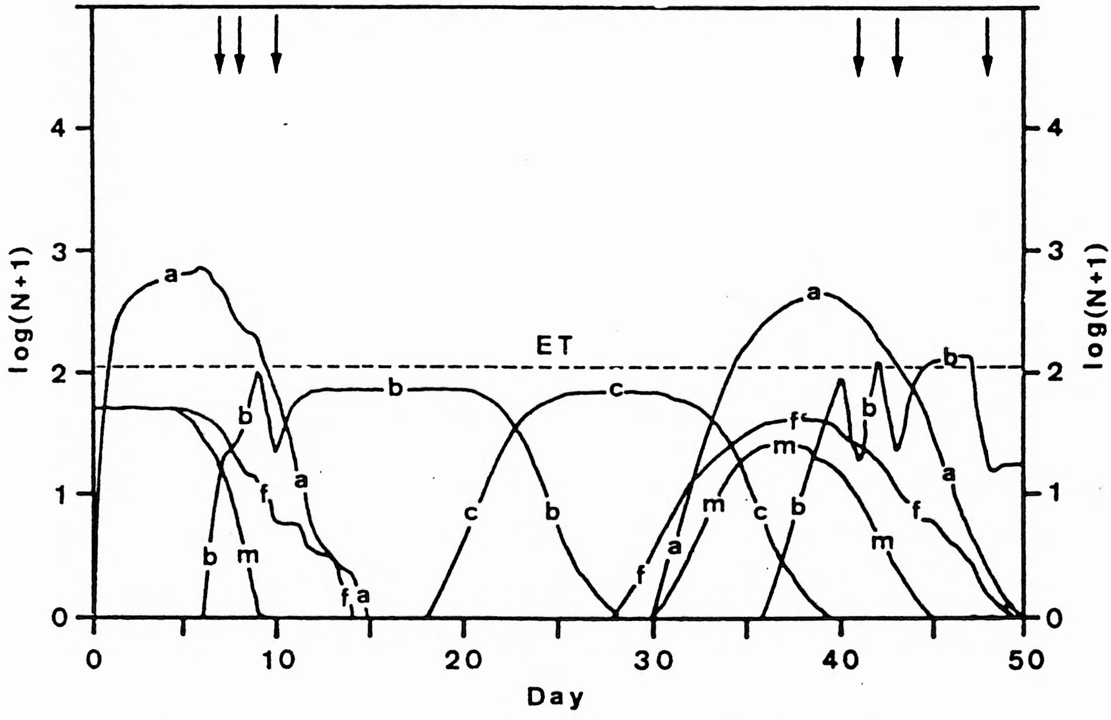

Fig. 4. Simulation of population growth. Treatments without residue effect are applied according to stage size. Arrows represent application dates. Curves denoted by a, b, c, f, and m represent stages A, B, C, female, and male, respectively. ET is the economic threshold.

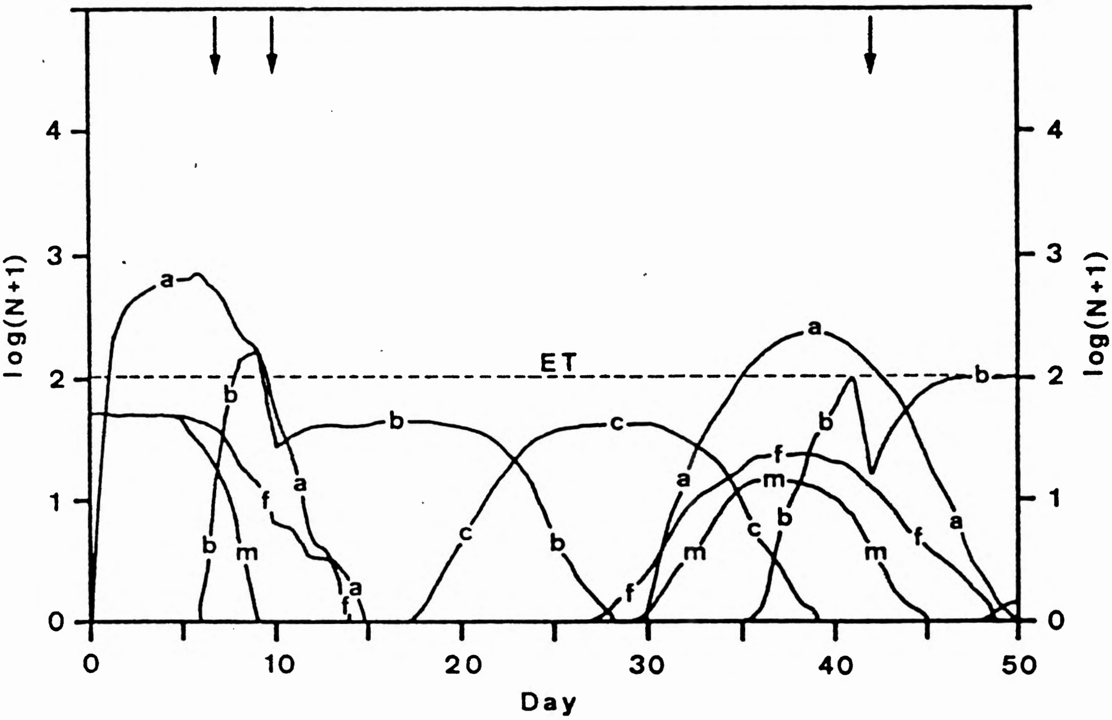

Fig. 5. Simulation of population growth. Treatments with residue effect are applied according to stage size. Arrows represent application dates. Curves denoted by a, b, c, f, and m represent stages A, B, C, female, and male, respectively. ET is the economic threshold.

If the economic threshold is defined as the number of individuals of a specific stage or the sum of individuals of several stages, application of pesticide can be justified by numbers of target stages over that threshold. Fig. 4 is the result of simulation without residual effect. No treatment is scheduled on any calendar day, but control is applied as soon as the size of target stage (B and C) exceeds the economic threshold. The interval between two successive controls depends on the surviving population and its growth rate. Therefore, if one treatment is more effective in decreasing the pest population to a lower level, the next application may be delayed. Alternatively, if the population grows rapidly, a second treatment may be required very soon. For a pesticide without residual effectiveness, six treatments are required to keep the pest population size under the economic threshold. However, when residual mortality does occur, only three applications are needed (Fig. 5).

Control Based on Weighted Stage Size. Rate of food consumption generally increases with the growth of pest. For most lepidopterous pests, younger instars consume less host plant material than do older instars. Therefore, younger instars usually cause less damage than do older instars. An economic threshold that does not consider this variation must be used with care. For practical purposes, the weighting coefficient for each stage can be calculated based on the consumption rate. The weighted stage size of pest population on day t can be calculated as follows:

$$n_w(t) = \Sigma\, \Sigma n_{ij}(t) \cdot w_j$$

where w_j is the weighting coefficient of stage j. The weighted stage size $n_w(t)$ is a more convenient value than the stage size to reflect the damaging potential of the pest population. Fig. 6 shows the simulation of control based on weighted stage size. Because food consumption rates among stages vary significantly in various pest species, this procedure is applicable when detailed life table data about each instar and the respective consumption rates are available. Therefore, the variable consumption rates among stages deserve greater attention not only in physiological studies, but also in pest management programs.

Because the residual activity is also considered, a clear difference is observed in Fig. 7: Only two treatments are necessary to keep the weighted population size under the economic threshold.

Ruppel (1983, 1984) suggested cumulative insect-days as an index for crop protection. Because insect-days represent the number and duration of pests surviving and causing damage to a crop, cumulative insect-days can be used as an index of the overall effectiveness of pest control. Because only

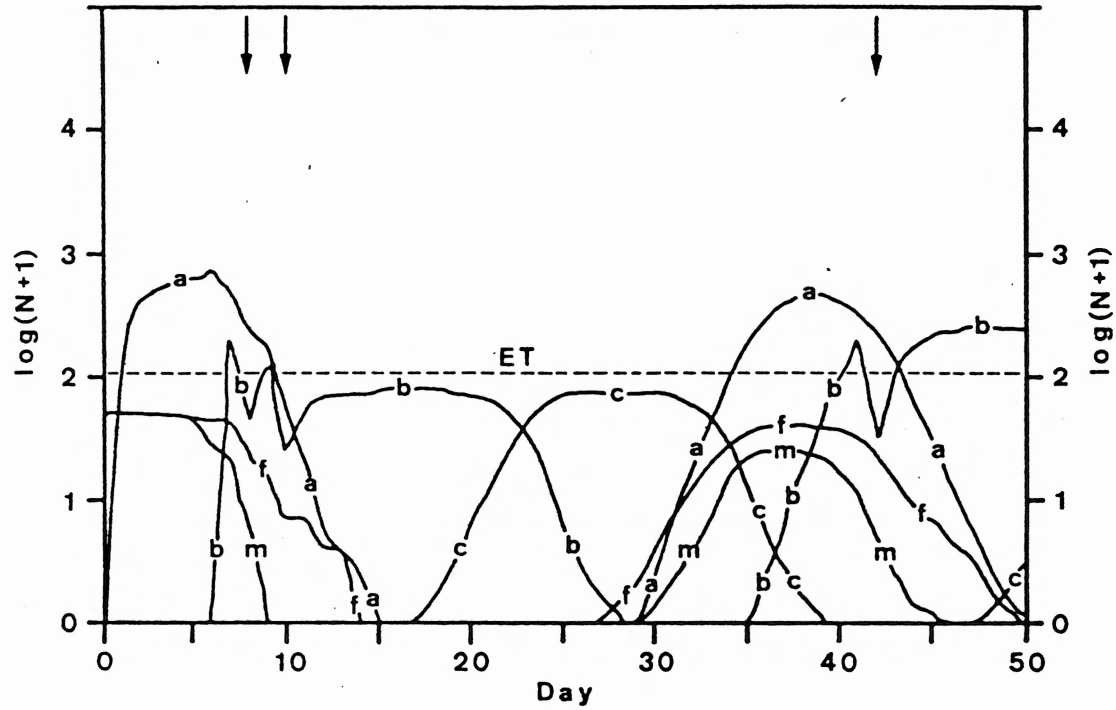

Fig. 6. Simulation of population growth. Treatments without residue effect are applied according to weighted stage size. Arrows represent application dates. Curves denoted by a, b, c, f, and m represent stages A, B, C, female, and male, respectively. ET is the economic threshold.

stages B and C cause damage, stage-days SD(t) of each calendar day t are calculated as follows:

$$SD(t) = \Sigma n_{i2}(t) + \Sigma n_{i3}(t)$$

where $\Sigma n_{i2}(t)$ and $\Sigma n_{i3}(t)$ are the respective sizes of stage B and C. The cumulative stage-days CumSD is then calculated as follows:

$$\text{CumSD} = \sum_{t=1}^{T} (\Sigma n_{i2}(t) + \Sigma n_{i3}(t))$$

where T is the length of growing season. The cumulative weighted stage-days CumWSD is obtained as follows:

$$\text{CumWSD} = \sum_{t=1}^{T} (\Sigma n_{i2}(t) \cdot w_2 + \Sigma n_{i3}(t) \cdot w_3)$$

where w_2 and w_3 is the weighting coefficient of stage B and C, respectively. Table 2 gives the values of cumulative stage-days and weighted stage-days corresponding to the population curves of previous sections. The stage-oriented control program (Fig. 5) gives the lowest cumulative stage-days (CumSD) and cumulative weighted stage-days (CumWSD), while the routine control without residue effect (Fig. 2) gives the highest. However, the weighted, stage-oriented control (Fig. 7) may be the most rational and economic one.

All these results were unforeseeable without the use of the age-stage, two-sex life table and computer simulation. Because no dynamic programming technique can be used in this biological system to find out the optimal control strategy, more efficient control can still possibly be obtained simply by applying the control earlier. Thus, stage-oriented pest control deserves greater attention in integrated pest management.

Discussion

Pesticides are the most widely used tool for pest control. While only a small portion of applied pesticide kills target pests, the rest becomes contaminant or pollutant. Unfortunately, pesticides will continue to be the major control method for the foreseeable future. Proper timing is one of the more helpful solutions in reducing the amount of pesticides, while simultaneously keeping the pest population under the economic threshold. Because simulations based on the age-stage, two-sex life table describe the stage structure of a pest population at each time period, they can be used to time pest control and to select the best control strategy according to the stage structure. Reports have shown that pesticide treatments applied at different times influence the control efficacy and number of treatments (Gednalske & Walgenbach 1984; Gargiullo et al. 1984, 1985; Reissig et al. 1985; Vittum 1985; Niemczyk 1987; Stanley et al. 1987). Among the many timing techniques, use of insect-day (Ruppel

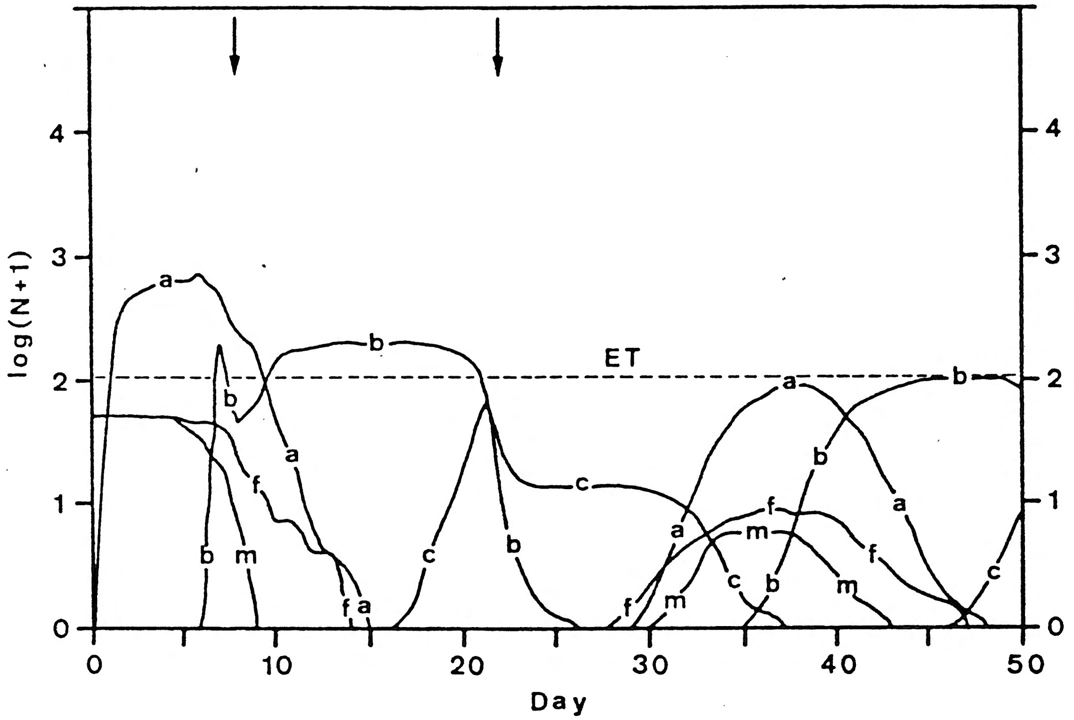

Fig. 7. Simulation of population growth. Treatments with residue effect are applied according to weighted stage size. Arrows represent application dates. Curves denoted by a, b, c, f, and m represent stages A, B, C, female, and male, respectively. ET is the economic threshold.

1984) and degree-day regression (Gargiullo et al. 1984, 1985) are worthwhile tools to be incorporated into an integrated pest management program. However, more research is needed in this area. The economics of pest control also play an important role in proper timing (Norgaard 1976). An economic threshold that is defined as the density of pest population alone may not produce the best treatment strategy (Mumford & Norton 1984). For a reasonable marginal analysis, more information must be collected. System analysis will continue to be the mainframe for pest management (Getz & Gutierrez 1982).

Ecologically sound pest management should be based on pest ecology. The two most important aspects in pest ecology are information in the life table and phenology. Life table includes the growth rate, developmental rate, and fecundity. These data are fundamental to simulation of population growth. On the other hand, phenology represents the influences of physical factors on the pest population. Because different life stages are variably susceptible to control agents, grouping by stage is important for use in a simulation model used in pest management. In this study, I have shown that an age-stage, two-sex life table is useful in this respect. For practical use in timing pest control, phenological data and economics of pest control should also be incorporated into the timing model. Because the variable susceptibilities among stages are also true for most biological control agents, the age-stage, two-sex life table can also be used in timing the application of those agents in pest management programs.

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