INSECT POPULATION SIMULATION

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ABSTRACT

Simulation of insect populations using systems dynamics methodology is discussed. The differences between the mathematical processes used to project long-term population regeneration and growth, and the processes used to project short-term within generation growth and development are presented. Both involve projection of a population level at a future time based on present population numbers. A framework is described for using systems dynamics methodology and the GASP IV simulation language to simulate the growth and development of the population of an insect having complete metamorphosis, i.e. staged development. Progression from stage to stage within the life cycle is either related to chronological or to physiological time depending on whether the nutrients for growth are contained within the insect at the beginning of the developmental stage or whether feeding occurs. Progression and mortality are continuous functions of heat energy accumulation in the environment and both are related to physiological age. Both progression and mortality are attenuated by environmental factors such as air temperature, air moisture content, air movement, and rain. An example simulation of a Hessian fly population is presented.

INTRODUCTION

The techniques used in analyzing dynamic systems were initially applied to insect population simulation and insect pest management in the early 1960's. The first reference found was Watt in 1961. (37) Research and development expanded rapidly during the 1970's. Presently, much progress is being made to change the "arts" that have developed into a "science" that can be validly used to supply information to people managing agro-ecosystems.

"Pest management may be (ideally) defined as the reduction of pest problems by actions selected after the life systems of the pests are understood and the ecologic as well as economic consequences of these actions have been predicted, as accurately as possible, to be in the best interest of mankind." (30)

Many authors have discussed the advantages of using the systems approach in agro-ecosystem and insect pest management. A few are: Arnold and de Wit (1); Berryman and Pienaar (4); Caswell, et al. (6); Coulman et al. (7); Loewer (20); Peart and Barrett (25,26); Ruesink (31); and Stark (33). Others are listed by Ruesink in a biologically oriented review that covers literature up to mid-1975. (31) Articles strictly related to engineering, systems science, and simulation are not necessarily included. Ruesink lists a number of examples of insect models which are usually simulations. Our bibliography does not repeat nor completely update the listing.

The life cycle of insects involves all the changes in form and habits from the beginning of life until death. This cycle is phased according to the type of metamorphosis. The two major types of metamorphosis are the gradual exopterygotous process exemplified by grasshoppers and dragonflies in which the young are nymphs which resemble adults, and the complete endopterygotous process exemplified by bees and butterflies in which there is a staged developmental sequence of egg, larva, pupa, and adult.

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Simulation is a logical tool for use in describing and projecting insect population growth and development. Both types of life cycles may be simulated to detail within generation development, or to show the generation to generation population progression in general. Either way, the whole procedure becomes a single or multiple server queing problem with associated bookkeeping. In this article, we will present an overview of insect population simulation starting with a brief discussion of mathematical modeling as used in classical population dynamics, followed by a discussion of insect population simulation in general. To conclude, an example GASP IV simulation of a Hessian fly population will be presented.

PHILOSOPHIES

Classically, ecologists have described animal population in terms of regeneration cycles, density dependence and independence, nutrient availability, behavioral characteristics, intra- and inter-specific competition, environment, and a host of other factors. Mathematical relationships have been developed that may, or may not, be biologically sound. A few references are: Crowe and Crowe (9), MacArthur and Connell (22), Pielou (28), Slobodkin (32) and Watt (37).

Ecologically, over long periods of time involving many generations, steady states will be disrupted only by evolutionary changes. Original interest was in modeling long-term patterns to define these evolutionary population changes.

Two frequently used expressions for the growth and regulation of populations are the exponential (E) and the logistic (S) growth curves. E is self-explanatory, while S is a sigmoidal relationship. The shapes of E and S are shown in Figure 1 (S=S1 or S2). Both relate number of individuals (N) to time (t), and both have N expressed as functions of birth, immigration, death, and emigration. Conceptually, the logistic curve projects N first with density limited due to small numbers, then with rapid expansion during a period of adequate numbers and food. This is followed with a leveling off over a period when the environmentally related carrying capacity is reached, and finally N decreases as resources become limiting. The decreasing section is not in Figure 1.

The E, S, and other curves have been described mathematically. The integrals of these mathematical functions are rates that have been used to project future from existing population levels. This procedure has been used to describe population dynamics over intervals of time involving generation to generation movement, or to define dynamics over a few generations.

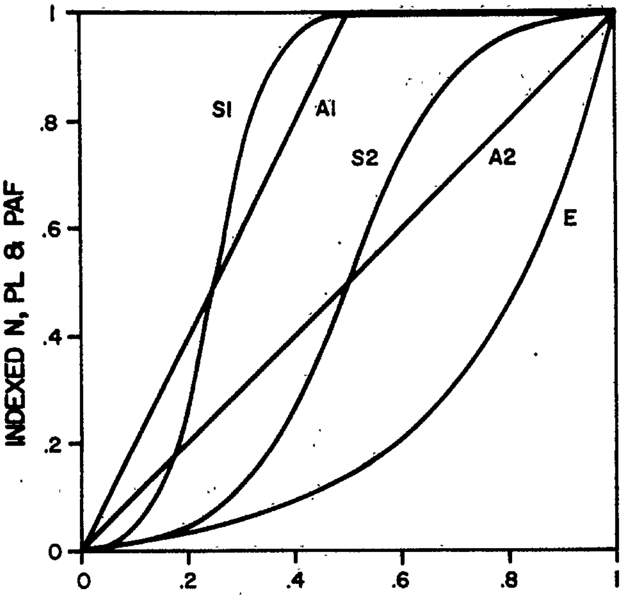

FIGURE I.

Now, more applied eco-scientists are interested in managing insect populations. (8,17,20) In contrast to the mathematical modeling of long-term population-dynamics, interest is primarily in using systems dynamics procedures to simulate and project insect populations over short intervals, either of the order of ten times the length of one generation, or more usually, of the growth and development pattern within one generation. Thus evolves what some call "Fortran ecology".

GENERAL INSECT SIMULATION METHODS

Scientists simulating insect populations have come to use a somewhat uniform set of methods and concepts in their procedures. These will be discussed next.

TIME FRAMES

Basic to understanding insect population simulation is recognition of the various time frames used. The differential expression, dN/dt, the incremental change, $\Delta N/\Delta t$, and the net change over a time period, all are used in essentially the same way. For dN/dt, the instant in time may be part of a day, a whole day, or some longer period up to the length of a regeneration cycle, or even several years. For $\Delta N/\Delta t$, the interval of Δt is the same as the "point" dt approaches. Likewise, net change may be defined to occur over any interval.

RATIOS, PROBABILITIES AND RATES

Conceptually, ratios, probabilities, and rates are used almost interchangeably to define the proportion, pro-rated number, percentage, or number per time interval, that a present level changes due to addition of new numbers, movement of numbers to other age or stage groupings, or movement out of a level caused by death. Good examples are Jones et al. (18) for probabilities, and Loewer et al. (21) for rates.

There may be concern over equating rates, probabilities, and ratios. This should disappear if you think in terms of a Markovian chain where the discrete stochastic process for each random variable depends upon the previous situation and affects only the subsequent situation. (27) Ratios are used to express the proportion of N that moves, and rates do essentially the same thing. Accurate prediction of levels has been and continues to be difficult. Other than the usual sources of experimental errors, are errors that are frequently caused by letting the matrix of probabilities, the sum of ratios, or the summed rates, exceed a unit factor. This results in the total number theoretically possible being exceeded.

POPULATION LEVELS (N)

Population level accounting is accomplished either on a numbers basis, or on a proportional or percentage basis where numbers are related to groupings. Groupings may be by stages, by time periods, or by totals of stages at a point in time.

CHANGES IN POPULATION LEVELS (Δ N)

The level at the present time (TNOW) is calculated by adding net changes to the past level. Thus, for each component of net change related to movement in, mortality, and progression out, this equation is used and the results summed:

$$\Delta N = A * PF * PL$$

"A" pro-rates the effect of discrete attenuation factors such as wind, rain, extreme temperatures, insecticide application and other management practices. A=a1*a2*a3...an, and is ≤ 1.0. Each attenuation factor is independent of the others. Therefore, as in probability theory, the a's can be multiplied.

"PF" is the maximum movement to next stage factor. It may be a ratio, probability, or rate. PF is ≤ 1.0 if pro-rated for staged development.

"PL" is the present level, either a number, or factor representing and relating numbers to unity, or 100%.

PHYSIOLOGICAL AND CHRONOLOGICAL TIME

Developmental rates are usually related to either the energy accumulation in the environment which is indexed to air temperature (T), or is directly related to T. Energy accumulation is indexed to growing conditions through heat units that are associated to physiological time. Heat units, sometimes called degree days, are usually defined as the average of maximum T (TMAX) and minimum temperature (TMIN) minus a base 10C (50F). This is limited by a T above which no development occurs and below which development continues at a minimum rate. The energy indexing system is used for feeding insect stages, while a direct age related chronological system is used for non-feeding stages. In either case the range of time is pro-rated to population age factors.

POPULATION AGE FACTORS (PAF or PF)

The distribution of ratios, probabilities, and rates over a life cycle, or a stage within a life cycle, can be accomplished by using relationships like those in Figure 1. PAF or PF is the mechanism that distributes the effect of the continuous relationship of the accumulation of energy in the environment to physiological age. They may span a particular part of the life cycle, a regeneration cycle, or several generation cycles. These progression and mortality relationships are difficult to define.

ATTENUATION FACTORS (A = a1 * a2...an)

Environmental conditions attenuate the maximum PAF's. These can be thought of as discrete attenuations caused by extremes in T, rain, wind, insecticide application, and other management decisions. These are independent of the continuous age-related factors.

DATA ACQUISITION

The choice of the location of the transducers used to acquire environmental data is a serious source of error in insect simulations. Usually, an important bridge must be made between the weather conditions recorded at standard meteorological observation sites and the micro-environmental conditions that exist where the insect population actually exists. An excellent explanation of micro-weather as a function of the properties of plants, pests, and soil has been written by Goudrian. (12) Monteith (24) discusses the principles of environmental physics in understandable language.

Banks of environmental data are hard to find and difficult to build. Historically, weather data were recorded to show climatic change or for air transportation use. Only recently have agricultural weather stations been maintained and these usually only record daily data. Generally, those developing an insect simulation must maintain a data acquisition system. (2)

Until recent years, biological data on insect populations was descriptive of point-in-time observations, or abnormal happenings. Very early and recent literature includes time related data. Generally, the researcher developing an insect simulation must acquire time oriented data on behavior and growth from field research. This is especially true for the processes of calibration and validation.

HESSIAN FLY SIMULATION (HFLYSIM)

Most insect simulations have been written in Fortran IV using no process oriented simulation language. (3,5,13,15,16,18,19, 34,35,36 and many others) In contrast, CSMP, SIMSCRIP, and other languages, have been sparsely used. The European corn borer simulation (SIMECOB) developed by Loewer, Huber, Barrett and Peart used Fortran IV and SPURT 70. (21) We chose to use GASP IV in HFLYSIM because it conviently allowed the inclusion of the generally accepted systems approach, because space and processor time were not critical, and because we wanted to develop a framework for insect population simulations that was easily understood, easily modified and adopted to other insect species, and that was for-the-most-part standardized. The standard GASP variables will not be herein defined. We assume the readers know the definitions or can find them in a description of the language. (29)

Some aspects of HFLYSIM can be part of any insect population simulation and some are uniquely insect dependent. The insect independent and dependent sections of the simulation will later be described by subroutines.

BACKGROUND ON THE HESSIAN FLY

The Hessian fly is a small Diptera, introduced into the US about 1776. It primarily attacks wheat. The larvae migrate to the base of the plant behind leaf sheaths during the critical spring and fall plant growth periods. This fly has discrete stages and generations. These are the egg; first, second, and third instar larva; flaxseed, or pre-pupa quiescent state; pupa; and adult stages. The fly overwinters, and passes the summer as a third instar larva. All larvae may, or may not, enter the flaxseed state sequencially. Background biological information was taken from experimental records and from the literature. (10,11,14,23) These data were sometimes incomplete for defining the effects of wind, of free moisture, and of the specific micro-climate on behavioral characteristics of the insect. Co-author Foster defined some missing relationships based on his observations and knowledge. A number of voids are presently being researched.

SOME MECHANICS

The conglomerate population, not individuals, is modeled. The total number of individuals in all stages at any point in time is considered to be 100% and the population levels of the different stages of the life cycle at each progressive day are expressed correspondingly as parts of unity, or 100%. Therefore, HFLYSIM does not keep track of distinct individuals, but rather interprets numbers as areas under curves expressed on a daily basis. Environmental effects were modeled from data about individual behavior and extrapolated to represent the whole population. The simulation is started with a fixed population size that is distributed across one or several stages. All changes are expressed relative to the original population.

The independent variables describing the environment were rain, wind, air temperature, and air moisture content. Data concerning these were taken from transducers located at standard weather station positions, not from locations in the microclimate where the insect exists. Our own data acquisition system was used to supply environmental data for calibration and validation. (2) Population growth and development data were recorded in nearby plots of wheat.

GENERAL USE OF GASP IV

The level of each stage is assigned a GASP SS(I) variable. Hence, interaction between stages is reflected in that the present level will affect movement to the next stage. The general DD, or net change equation is:

$$DD(I) = f(\Delta N\ \text{Into},\ \Delta N\ \text{Death},\ \Delta N\ \text{Out})$$

or

$$= f(\text{progress into stage},\ \text{mortality},\ \text{progress out.})$$

Each component of the total ΔN per day, or DD(I), is computed from:

$$\Delta N = (A * PAF * SS(I \text{ or } I-1))$$

ΔN's are summed and used as DD(I) in:

$$SS(I) = SSL(I) + DTNOW * DD(I)$$

The time unit is one chronological day. Therefore, all changes are implied rates per day. The maximum time step (DTMAX) is one hour, or 0.041666 days, and the minimum step (DTMIN) is 15 minutes.

INSECT-INDEPENDENT SUBROUTINES

Initial conditions (INTLC), thresholds (THRESH), events (EVNTS), STATE, WEATHER, and UPLOT are insect independent.

INTLC, user-written and called automatically by GASP at the start of a simulation, is used to load constants and variables detailing initial dates, times, levels and plotting arrays. The first day's environmental (weather) data is read, the next read-weather-data event is scheduled, and finally the first hourly auxilaries are computed.

THRESH, called only once from INTLC, computes stage durations and initializes duration within stages. The starting, ending, duration, and initial time accumulation within stages are recorded.

EVNTS, user-written, either calls daily the read-weather-data subroutine or calls the auxiliary subroutine hourly that keeps up with the time of day, indexes the weather data arrays, and determines certain attenuation factors.

STATE is called every time step and computes all stage levels.

WEATHER reads a day's environmental (weather) data and schedules the next call to itself. A value for the last hour of the previous day and 24-hourly values are recorded.

UPLOT is called from WEATHER and OTPUT to plot values of interest.

INSECT-SPECIFIC SUBROUTINES

Subroutines that are unique to the Hessian fly and that are species dependent are: Auxilary (AUXIL), hourly auxilary (HOURAUX), PAF, and RATE.

AUXIL processes some of the attenuation factors that are used in calculating the DD(I)'s. No calculations occur here because AUXIL is called every time step.

HOURAUX computes additional attenuation factors and is updated once each hour. It runs the time-of-day clock.

PAF computes the population, or physiological age factors. The relationship A, either A1 or A2, in Figure 1, was used to model the progression of the Hessian fly through its stages. PAF is used to calculate any age related progression or mortality factors that are used in calculating the DD(I)'s.

RATE is used to compute the final complete DD(I) variables. Equations that define the adult processes of mating, egg laying, and mortality of males and females, are solved here. Also, bookkeeping on hatching and initializing the first instar larvae levels is accomplished.

EXAMPLE OUTPUT

The outputs of simulations give information on insect presence and population abundance that is helpful when deciding if and when to apply control measures. These measures may be biological, as with predator releases; chemical, as with insecticide application; or physical, as with management practices other than insecticide application such as plowing, harvesting and delayed planting. Also, then simulation could serve to better time and synthesize release of Hessian fly in a genetic control program.

Figures 2 and 3 show the projected life cycles of the 1976 and 1977 spring generations of Hessian fly populations in wheat near Lafayette, IN. The dates validly reproduce field data within one to two days. The generations began on April 4 in 1976 and March 31 in 1977. Progression through the various stages was about as rapid as possible in 1977. In 1976, development was delayed due to the slowing effect of cold, adverse weather.

Eggs (E) are plotted only to show their presence. Their abundance was not included in the pro-rating procedure used to relate stages. The overwhelming effect of large numbers makes this necessary. The precise, abrupt ending of the adult and pupa stages is a result of plotting percentages.

IN CONCLUSION

We feel that simulation of insect populations has a prominent place in the management of food production. It will be used to relate measurable variables, such as those that describe environmental and existing population conditions, to potential reduced yields due to damage caused by future insect populations. Simulation will be used as a management tool both to time control measures and to estimate the likely results of these control measures.

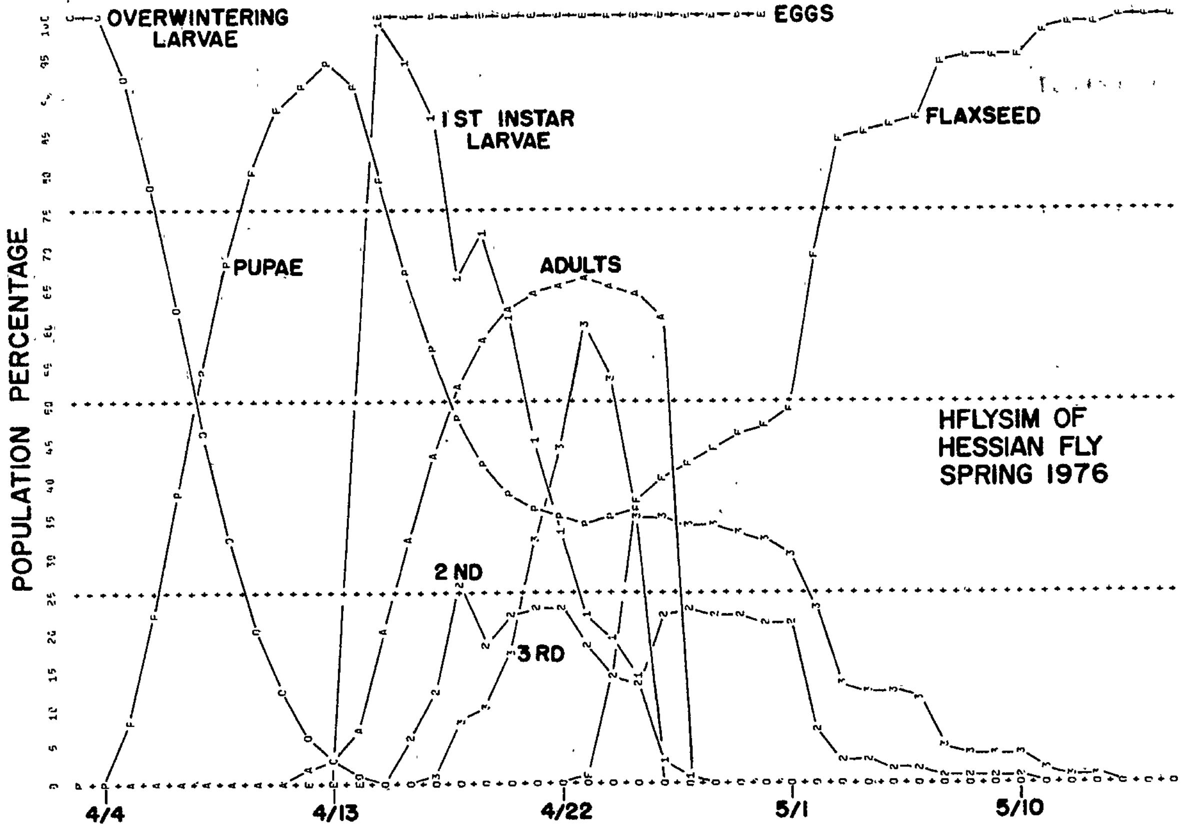

FIGURE 2.

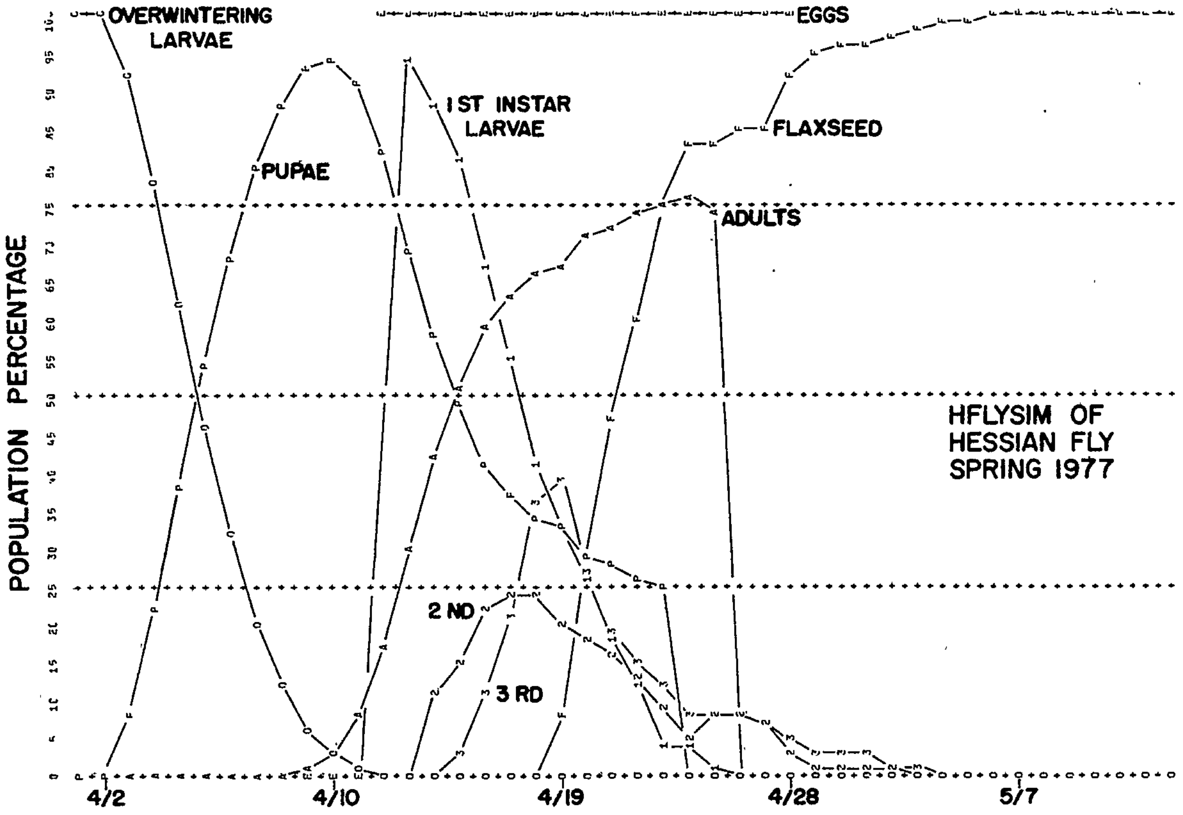

FIGURE 3.

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