The use of a population model for the mass production of natural enemies of the cassava green mite

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Several Phytoseiid mite species from the Neotropics are being tested as control agents of the cassava green mite in Africa. Since large numbers of these predators are required for releases, an adequate mass rearing procedure must be developed. This is planned to be done by means of a population model, in order to adapt the production level to that of the prey food for which such a procedure was already empirically developed. While describing the mathematical framework of the model chosen here, the importance of considering certain factors such as variability in development within a cohort and a predator's searching capacity is stressed. According to given rearing conditions, the size and the age structure of the initial predator colonies are defined in order to reduce lab work. As the model provides a comprehensive data set regarding the growth pattern of such colonies, the food requirements of the predators in terms of prey can be scheduled in advance. As a result of this prey material can be used optimally.

INTRODUCTION

Classical biological control is the attempt to restore an ecological balance by introducing natural enemies that keep a pest in check in its native habitat (MEGEVAND *et al.*, 1987). Programmes using classical biological control usually require mass production of such natural control agents. Often this involves solving biological and technical problems in order to optimize the rearing procedures. In this context, demographic models appear to be a very useful tool to predict population increase of the control agents under laboratory conditions.

The International Institute of Tropical Agriculture (IITA) is currently testing several exotic predatory mite species of the family Phytoseiidae (Acari) for the control of the cassava green mite (CGM), *Mononychellus tanajoa* BONDAR in Africa (YANINEK & HERREN 1988). The area infested by this pest includes different ecological zones over an area larger than twice the size of western Europe. The magnitude of the problem requires massive numbers of predators for experimental releases in these areas.

Mass-rearing of the cosmopolitan two spotted mite (TSM), *Tetranychus urticae* KOCH is quite feasible, and it is a suitable alternative prey for most of these predators under laboratory conditions (FRIESE *et al.*, 1987). Currently, the daily production of 6 million eggs can be achieved (B. MEGEVAND, in prep.), and the problem is to develop a mass-rearing scheme to maximize phytoseiid production. The presesent work shows which parameters should be considered when developing such a scheme, and how the resulting production of predators can be adapted to the supply of prey using a population model.

Predicting the population increase

To predict population growth, the initial size and age structure of a given population must be specified. This is usually not a problem with insects a many species can be collected easily at particular stages in their life cycle, thus allowing to initiate cultures with cohorts. This does not hold for phytoseiid mites for which collecting individuals of the same age is difficult and time consuming. Thus, cultures of phytoseiids are best started with adult females picked randomly from an old colony that is going to be harvested. For technical reasons it has actually been necessary to maintain stock colonies for each species or strain separated from production cultures, undergoing more strict protection measures to prevent immigration of possible contaminants. Meanwhile, this pratice should not affect the fact that a sample of randomly selected females consists of same fractions of each age class related to adult female stage. Hence, age structure in such samples does not deviate much from stable age distribution, provided the sample size is large enough.

Existing demographic models pertaining to mass rearing assume stable age structure of populations (CAREY & KRAINACKER, 1988; CHI & GETZ, 1988), and identical developmental rates for all individuals of a cohort (CAREY & KRAINACKER, *l.c.*). Our model showed not be restricted by these assumptions. The so-called time distributed delay model (MANETSCH, 1976), which takes variability in developmental durations among individuals into account, is such a model. In other words, this model simulates a stochastic process. It differs from simple deterministic models in that individuals belonging to a cohort and moving from one developmental stage into another do not leave this stage and enter the next all at the same time, but dispersed in time according to a positively skewed frequency distribution. The latter is conveniently described by a probability density function of the Erlang family (MANETSCH, 1976). The density function is completely defined by two parameters: the mean transit time D of entities passing through a distributed delay process, i.e. the mean developmental duration of individuals of a given stage, and the parameter $k = D^2/s^2$, where s^2 is the estimated variance. Another reason to prefer this model is that it can be easily extended to include density dependent phenomena, relevant predator-prey interactions, effect of variable temperatures, and other factors found to be important, and which generally affectg age structure (see e.g. ZAHNER & BAUMGÄRTNER, 1988).

The distributed time delay is modeled by dividing a given developmental stage in k substages. Thus, the rates at which individuals move through the different substages can be described by the following set of differential equations:

$$\frac{dr_1(t)}{dt} = \frac{k}{D} [x(t) - r_1(t)]$$

$$\frac{dr_2(t)}{dt} = \frac{k}{D} [r_1(t) - r_2(t)]$$

$$\frac{dr_k(t)}{dt} = \frac{k}{D} [r_{k-1}(t) - y(t)]$$

with $x(t)$ being the input rate (i.e. the rate at which individuals enter a given stage), $y(t) = r_k(t)$ the output rate (or the rate at which individuals enter the next stage), and $r_1(t), r_2(t), \ldots, r_{k-1}(t)$ being the so-called «intermediate» rates of the delay process. The storage or the number of individuals in the ith substage at time t is:

$$Q_i(t) = \frac{D}{k} r_i(t)$$

MANETSCH & PARK (1974) wrote an algorithm in FORTRAN code (subroutine DELAY2) to generate time distributed delays according to the set of equations above. Our model uses the same algorithm, in which the time step $\Delta t = 1$ DD or day-degree (see below). Whereas the algorithm refers to a physicological time scale, the model, for more convenience, gives a daily output, i.e. related to calendar time. As n successive stages are defined ($n = 3$, i.e. egg, post-embryonic juvenile, and adult stages), D_j and k_j (with $j = 1, \ldots, 3$) designate the mean developmental duration (in DD above the developmental threshold; see below) and the number of substages for the jth stage respectively. Thus, the output rate of the first stage $y_1(t)$ represents the input rate of the second stage $x_2(t)$, and so on. The input of the first stage $x_1(t)$ is given by the number of offspring (total number of eggs laid) during the interval $[t - \Delta t, t]$, and the output of the last stage $y_n(t)$ denotes the number of individuals definitely leaving the process, i.e. those individuals which have reached the end of their life during the intervall $[t-\Delta t, t]$. Computation of offspring is based on m_x statistic (age x is defined in DD for each substage). The computer program written to calculate the population growth is initialized with the following data: 1) initial number of individuals for each stage and substage (substages are defined as age classes). 2) Mean developmental duration D and variance s^2 for each stage expressed in day-degrees, i.e. the cumulated number of degrees above threshold temperature for achievement of development (when temperature T is constant, conversion into days is given by: $D_j/(T-\vartheta_j)$, ϑ_j being the threshold temperature of stage j; when temperature fluctuates, development is achieved as soon as the sum of $[(T_{max}-T_{min})/2]-\vartheta_j$ over days reaches D, T_{max} and T_{min} being the daily maximum and minimum temperature respectively). 3) l_x and m_x statistics (note that for juvenile stages it may be sufficient to know the stage specific instead of the age specific survivorship) and the sex-ratio. 4) Daily temperature extrema (T_{max} and T_{min}) for computation of day-degrees.

Item 1) comes down to inscribe numbers of individuals into a matrix with respect to stage and substage; as mentioned above, the age structure of a sample consisting of randomly selected females is based on the stable age distribution (for details, see CAREY & KRAINACKER, 1988). For 2) and 3) data are found in ANONYMOUS (1987) and in BELLOTTI et al. (1987) for all species reared at IITA. Hence, the model can provide for any day data showing the expected population size and structure with respect to age and sex, so far under the assumption that food and space availability do not affect population increase.

Food requirements of predators

The amount of food with which we must provide a predator for optimal growth and reproduction is not simply the amount it is able to ingest, but it depends on the predator's searching capacity, on the size and the shape of the rearing setup or arena, and on the way food is distributed (spread or agreggated in

clumps). The actual amount of food needed can be extrapolated from a predator's functional response curve to prey density (HOLLING, 1959): the minimum prey food density allowing a predator to cover its demand is defined at the point where such a curve tends towards a plateau. The needed information could be extrapolated from BRAUN *et al.* (1987)'s data.

MODEL OUTPUT

The model was implemented to simulate population development of phytoseiids during a four week period at a constant temperature of 25 °C (all results reported below were generated for the phytoseiid mite *Neoseiulus idaeus* DENMARK & MUMA), which corresponds to a suitable rearing time considering the underlying lab work and the prevailing hygienic conditions during the last phase of culturing.

Preliminary simulations showed that, in order to prevent overcrowding and subsequent mutual interference (KUCHLEIN, 1966), cultures can be initiated with only 10 phytoseiid females. However, samples of females with sample size smaller than 10 individuals are likely to generate high variability in size of resulting populations at the end of the rearing cycle. Tab. 1 shows the pattern of growth of a population, starting with 10 females with standard age distribution (i.e. age

Table 1. Growth pattern of a colony of the phytoseiid mite *Neoseiulus idaeus*, with age structure (individuals/age class) and food requirements (µg of *Tetranychus urticae* eggs) at 25 °C.

day	eggs	active juveniles	adults	food required
0	-	-	10.000	-
1	18.426	0.000	9.950	248.75
2	31.531	5.441	9.924	302.51
3	34.083	20.296	9.896	450.35
4	33.677	36.550	10.825	636.12
5	32.089	48.024	17.298	912.69
6	33.155	48.901	31.349	1272.73
7	32.816	48.712	47.949	1685.83
8	35.039	48.675	64.766	2105.90
9	45.356	48.842	81.567	2527.60
10	67.825	51.333	97.943	2873.76
11	94.750	64.968	114.350	3302.59
12	123.610	94.880	130.341	3855.41
13	164.945	127.355	150.743	4499.45
14	199.254	173.376	182.259	5470.06
15	226.415	228.615	227.204	6739.36
16	270.234	273.624	282.741	8023.50
17	299.977	326.244	360.581	9680.78
18	324.412	382.335	457.046	11547.41
19	362.832	427.377	573.320	13962.90
20	452.087	457.076	705.848	16499.60
21	554.246	519.759	853.908	19628.63
22	670.527	646.826	1001.400	23391.90
23	872.261	769.446	1169.220	27454.30
24	1066.500	963.252	1385.254	33043.32
25	1263.040	1226.470	1653.761	40213.30
26	1593.402	1472.840	1959.763	47848.40
27	1885.792	1814.870	2374.443	58276.80
28	2176.964	2244.913	2891.180	71310.10

structure as in stable populations) after 28 days, and related food requirements in terms of TSM eggs (1 egg = ca. 1 μg). By means of simulations made for 30 different samples (consisting each of 10 randomly selected females in a colony whose adult population was made up of 200 females), variance in numbers of individuals (for each of the three developmental stages: egg, juvenile active, and adult) after 4 week population growth was estimated. The results in tab. 2 show that the coefficient of variation ($s/\bar{x}\cdot100\%$, $\bar{x}$ and s being respectively the mean number of individuals of a given stage and the standard deviation) is for all stages less than 10%.

Table 2. Variability in the production of the phytoseiid mite *Neoseiulus idaeus* after 28 rearing days at 25 °C for cultures started with 10 randomly selected adult remales, and confidence limits for the mean related to sets with varying numbers of cultures.

parameter	eggs	active juveniles	adults
population mean (n =30)	2144.6	2212.1	2847.9
standart deviation (n =30)	±200.8	±207.5	±266.3
coefficient of variation (%)	9.36	9.38	9.35
confidence limits (n =6; P >0.95)	±210.8	±217.8	±279.5
confidence limits (n =6; P >0.99)	±330.5	±341.6	±438.3
confidence limits (n =4; P >0.95)	±319.5	±330.1	±423.7
confidence limits (n =3; P >0.95)	±498.9	±515.3	±661.6
confidence limits (n =2; P >0.95)	±1804.1	±1864.3	±2392.6

The confidence limits reported in tab. 2 were calculated according to probabilistic statements and numbers of replicates denoted by P and n respectively, but using the variance estimated from 30 replicates. It can be seen that the confidence interval becomes large if one works with less than 4 rearing units, making the random selection of females in these cases unsuitable. But in these cases the amount of work involved is also so little that one should definitely operate with cohorts.

CONCLUSION

The population model presented here appears very suitable to predict the population growth of mass reared phytoseiid colonies. It shows for instance how it can be used to determine the adequate number of predators to start with to initiate cultures (given certain constraints and/or factors such as duration of cultures, temperature) after statistical considerations. The fact that the colony size can be predicted at any time also permits to foresee food requirements far in advance (provided the temperature is more or less predictable), hence, enabling rational use of prey food produced. Once the size of the initial predator colony is defined. It is then easy to determine the total number of rearing units necessary to use prey food optimally. The results shown here are not final, because from a biological point of view, there are missing inputs yet (e.g. effects of limited space as predator density becomes high, effects of small scale heterogeneity resulting from the accumulation of egg chorions, exuviae, carcasses, and the subsequent development of fungi). However, as already mentioned, the model may be easily

extended and include further details regarding the biology and the population dynamics.

RÉSUMÉ

Plusieurs espèces de phytoséiides d'origine néotropicale sont actuellement testées en vue de leur utilisation dans la lutte biologique contre l'acarien vert du manioc en Afrique. La nécessité de lâcher ces prédateurs en grands nombres rend impérative l'élaboration d'une procédure d'élevage de masses. Pour ce faire, il est prévu d'avoir recours à un modèle de population dans le but d'adapter la production des prédateurs à celle de leur proie, pour laquelle une telle procédure a déjà été développée de façon empirique. Outre les bases mathématiques auxquelles le modèle se réfère, on illustre le rôle de certains facteurs tels que la variabilité dans le taux de développement au sein d'une cohorte et la capacité de recherche d'un prédateur. Pour des conditions d'élevage données, la taille et la structure d'âge de la colonie initiale de prédateurs est définie, compte tenu du vœux d'économiser le travail de laboratoire. Comme le modèle génère des données complètes au plan démographique, les besoins alimentaires des prédateurs en termes de proies peuvent être planifiés à l'avance, permettant ainsi une utilisation optimale de ces dernières.

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