TWO NEW METHODS FOR THE STUDY OF INSECT POPULATION ECOLOGY

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Hsin Chi and Hsi Liu (1985) Two New Methods for the Study of Insect Population Ecology. *Bull. Inst. Zool., Academia Sinica* 24(2): 225-240. Based on the stage-frequency distribution, a multiple column matrix was used to express the age-stage-structure of animal populations with metamorphosis. Using this new method, the growth process of insect and mite populations (both female and male were included) can be studied with proper stage grouping. Algorithms of population growth and the calculation of intrinsic rate of increase and stable age-stage-distribution were described in detail.

For the simulation work of field population ecology, a multidimensional matrix was used to display the spatial distribution of host plants and the age-stage-structure of pest population. Computer programs were designed to simulate the growth and dispersion of field population at the same time. These methods made a way to approach to the agroecosystem simulation.

In the last forty years, since the matrix was used in the study of population growth (Lewis 1942, Leslie 1945, 1948), the age structure of a population was given in a single column matrix (column vector), and only the female population was considered. This method has been used in many works (Pennycuick *et al*.1968, Longstaff 1977, Chi 1981, Carey1982). In using the single column matrix, one had to always handle all the individuals in one age group as if they were in the same developmental stage. However, the significant stage overlapping phenomenon has been frequently observed in the study of life cycles for animal populations with different developmental stages, such as in many insect and mite species. As a matter of fact, this overlapping phenomenon occurs in both discrete models and continuous models, using either calendar time or physiological time. This fact limits the use of Lewis-Leslie matrix in insect and mite population ecology, and points out that the stage-grouping by cutting the life span into stages (e.g. Carey 1982) without considering the overlapping phenomenon must be used carefully. Some authors had developed analytical methods for stage grouping (Lefkovitch 1965, Manly 1974, Van Straalen 1982), however, this overlapping phenomenon had not been included. From the biological viewpoint, the stage overlapping is resulted from the differences in developmental rates of individuals reproduced at the same day. Based on this biological fact, we developed a new method using multiple column matrix to express the age-stage-structure of population. In this method, both male and female can be included. The details about this new method

are discussed in this paper.

The another problem in population ecology is that the growth and dispersion of population had been almost always separately studied. This can be seen in many simulation models, where only the relative density (insect/plant) had been used to represent the population. They gave the false impression that the individuals were uniformly distributed in space and the spatial distribution had no relation to population growth. Many authors had tried to study the growth of population with respect to distribution or used computer mapping to show the spatial distribution (Ashley1976, Fulton and Haynes 1975, Haynes and Tummala 1978, Wellington *et al.* 1975, Taylor and Taylor 1977). Among them, Taylor and Taylor (1977) gave a spatial concept for population and treated the anatomy of a real population as being in three dimensions, latitude×longitude through time. This concept is helpful in understanding the real population. For the study on this problem, we used a multidimensional matrix to express the spatial distribution and the age-stage-structure of population, and tried to simulate the growth and dispersion of population at the same time. The basic concept of this method is also discussed in this paper.

THE MULTIPLE COLUMN MATRIX MODEL

(1) The age-stage-structure matrix

The basic idea of the multiple column matrix model is displayed in Fig. 1. In this method, the population structure is given in matrix N with k rows and m columns-k is the number of age groups, m is the number of stages. In explanation of this new method an assumed matrix N with ten rows and five columns is used. Each column of matrix N represents one stage, e.g. egg, larva, pupa, female and male. Then, n_{ij} gives the number of individuals in age i and stage j. After one age interval, individuals in age i and stage j may grow to age $i+1$ but still be in the same
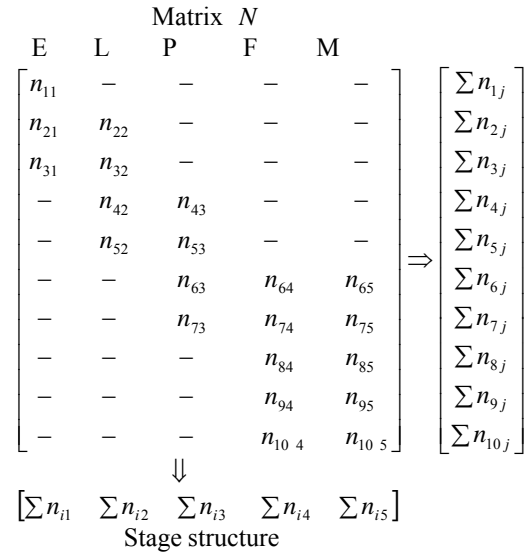

Fig. 1. The age-stage-structure matrix (N) of a population. Elements out of the range of stage distribution are denoted by "—". (E-egg stage, L-larval stage, P-pupal stage, F-female, M-male).

stage j, or develop to stage $j+1$ and then be in age $i+1$. The last two columns, female and male, are both developed from the last preimaginal stage-the pupa. A dash "—" is used where an element is nonexistent (out of the range of stage distribution), this also make the stage distribution more clear. All such elements will be set to zero in the calculation of the following sections.

(2) Age-stage-specific growth rate, developmental rate and fecundity

In The Lewis-Leslie matrix only age-specific survival rates and fecundity will be considered. In the present paper, we take the stage differentiation into consideration. Therefore, there are three factors which relate to all individuals, namely: age-stage-specific growth rate, developmental rate and fecundity. In order to make this method more comprehensible and to facilitate computer programming, we set these three factors into three matrices of the same dimension (Fig. 2).
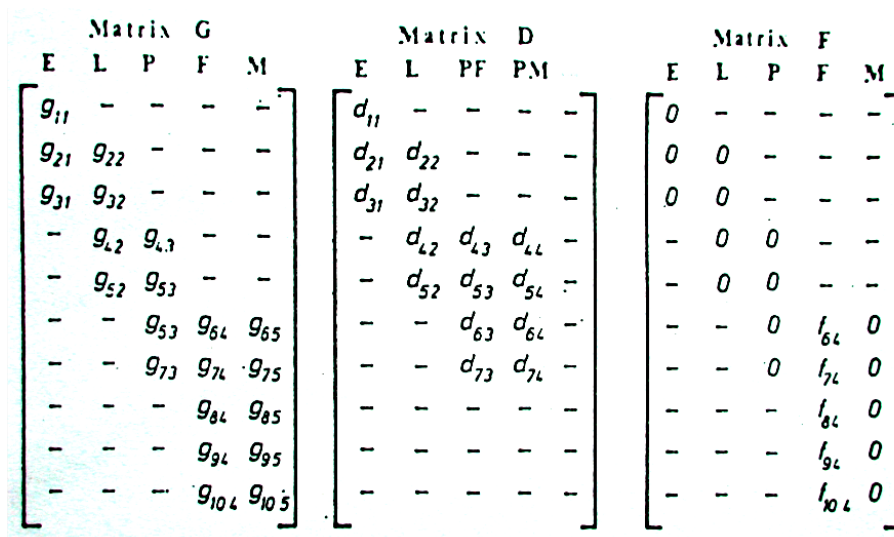
Matrix G

	E	L	P	F	M
	g_{11}	–	–	–	–
	g_{21}	g_{22}	–	–	–
	g_{31}	g_{32}	–	–	–
	–	g_{42}	g_{43}	–	–
	–	g_{52}	g_{53}	–	–
	–	–	g_{63}	g_{64}	g_{65}
	–	–	g_{73}	g_{74}	g_{75}
	–	–	–	g_{84}	g_{85}
	–	–	–	g_{94}	g_{95}
	–	–	–	g_{104}	g_{105}

Matrix D

	E	L	PF	PM	
	d_{11}	–	–	–	–
	d_{21}	d_{22}	–	–	–
	d_{31}	d_{32}	–	–	–
	–	d_{42}	d_{43}	d_{44}	–
	–	d_{52}	d_{53}	d_{54}	–
	–	–	d_{63}	d_{64}	–
	–	–	d_{73}	d_{74}	–
	–	–	–	–	–
	–	–	–	–	–
	–	–	–	–	–

Matrix F

	E	L	P	F	M
	0	–	–	–	–
	0	0	–	–	–
	0	0	–	–	–
	–	0	0	–	–
	–	0	0	–	–
	–	–	0	f_{64}	0
	–	–	0	f_{74}	0
	–	–	–	f_{84}	0
	–	–	–	f_{94}	0
	–	–	–	f_{104}	0

Fig. 2. The age-stage-specific growth rate matrix (**G**), developmental rate matrix (**D**) and fecundity matrix (F). In matrix G, g_{ij} is the probability that an individual from (i, j) will grow to ($i+1, j$) after one age interval. In matrix D, d_{ij} is the probability that an individual from (i, j) will develop to ($i+1, j+1$) after one age interval; in column PM, d_{ij} is the probability that an individual from ($i, j-1$) will develop to ($i+1, j+1$) (from pupa to male). In matrix F, f_{ij} is the number of offsprings that will be reproduced by every individual in age i and stage j.

In matrix **G**, the element g_{ij} (the age-stage-specific growth rate) is the probability that an individual in age i and stage j will grow to age $i+1$ but still be in stage j after one age interval. In matrix D, d_{ij} (the age-stage-specific developmental rate) is the probability that an individual in age i and stage j will develop to stage $j+1$ and be in age $i+1$ after one age interval. Because female and male will not develop to further stages, there are no d_{ij} for them. But the pupae can either develop into a female or male. We set the probability that a pupa will develop into a female in column **PF** and the probability for a male in column **PM**, thus the column $m-1$ (**PM**) contains the values for pupa to male, i. e. from $n_{i(m-2)}$ to $n_{(i+1)m}$ (Fig. 2). In matrix, F, f_{ij} (the age-stage-specific fecundity) are the number of offsprings that will be reproduced by every individual of n_{ij}. In general, only female have a $f_{ij} \geqq 0$, and the other f_{ij} have the value zero. All elements of these three matrices (**G**, **D** and **F**) can be obtained in the

basic life table study.

(3) Population growth

When the age-stage-structure of a population at time t is known, the age-stage-structure for time $t+1$ can be obtained through the combined operation of **G**, **D** and **F**:

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

The detail calculation procedures are:

$$n_{11(t+1)} = \sum_{i=1}^{k}\left(\sum_{j=1}^{m} n_{ijt}f_{ij}\right)$$

$$n_{ij(t+1)} = n_{(i-1)jt}\, g_{(i-1)j}$$
$$\text{for } j=1 \text{ and } i>1,$$

$$n_{ij(t+1)} = n_{(i-1)jt}\, g_{(i-1)j} + n_{(i-1)(j-1)t}\, d_{(i-1)(j-1)}$$
$$\text{for } 1<j<m,$$

$$n_{ij(t+1)} = n_{(i-1)jt}\, g_{(i-1)j} + n_{(i-1)(j-2)t}\, d_{(i-1)(j-1)}$$
$$\text{for } j=m \text{ (the male).}$$

We need only sum the elements in each row to get the age-structure, and sum the

elements in each column to get the stage-structure (Fig. 1). The total population size is given by $\sum\limits_{i=1}^{k}\left(\sum\limits_{j=1}^{m} n_{ij}\right)$.

With the total population size, the age-structure and stage-structure, it is easy to calculate the percent age distribution and percent stage distribution.

(4) Intrinsic rate of increase

The intrinsic rate of increase can be calculated indirectly with these **G**, **D** and **F** matrices. At first, the age-specific survival rate (l_x) and the age-specific fecundity (m_x) must be derived from matrices **G**, **D** and **F.** For this, the age-stage-specific survival rate (matrix **S**) must be obtained according to the following procedures:

let $s_{11} = 1$ then
$$s_{ij} = s_{(i-1)j}\, g_{(i-1)j}$$
$$\text{for } j=1 \text{ and } i>1,$$
$$s_{ij} = s_{(i-1)j}\, g_{(i-1)j} + s_{(i-1)(j-1)}\, d_{(i-1)(j-1)}$$
$$\text{for } 1<j<m,$$
$$s_{ij} = s_{(i-1)j}\, g_{(i-1)j} + s_{(i-1)(j-2)}\, d_{(i-1)(j-1)}$$
$$\text{for } j=m \text{ (the male).}$$

This s_{ij} gives the survivorship for the newborn individual to age i and stage j.

To obtain the age-specific survival rate (l_x), the sum of each row of matrix **S** is then calculated from

$$l_x = \sum_{j=1}^{m} s_{xj}.$$

The age-specific fecundity (m_x) can be calculated for each age group as follows:

$$m_x = (\sum_{j=1}^{m} s_{xj} f_{xj}) / \sum_{j=1}^{m} s_{xj}.$$

By using the well-known formula: $\sum e^{-rx} l_x m_x = 1$ (Lotka 1913), the intrinsic rate of increase (r) can be obtained, then the finite rate of increase (λ) and the mean length of a generation (T).

It is easy to verify that：

$$\sum_{x=1}^{k} e^{-rx} l_x m_x = \sum_{x=1}^{k} (e^{-rx} \sum_{j=1}^{m} f_{xj} s_{xj}) = 1.$$

Therefore, the intrinsic rate (r) can be also calculated directly from

$$\sum_{x=1}^{k}\left(e^{-rx} \sum_{j=1}^{m} s_{xj} f_{xj}\right) = 1$$

(5) Age-stage-specific mortality (Matrix Q) and the distribution of mortality (Matrix P)

The age-stage-specific mortality (q_{ij}) gives the probability that an individual in age i and stage j will die after one age interval; however, the distribution of mortality (p_{ij}) is the probability that a newborn individual will die in age i and stage j. According to the previous sections, an individual of age i and stage j may grow to age $i+1$ and still be in the same stage, or may develop to stage $j+1$ and then be in age $i+1$. The age-stage-specific mortality can be calculated as follows

$$q_{ij} = 1 - g_{ij} - d_{ij} \qquad \text{for } j<m-2,$$
$$q_{ij} = 1 - g_{ij} - d_{ij} - d_{i(j+1)} \qquad \text{for } j=m-2,$$
$$q_{ij} = 1 - g_{ij} \qquad \text{for } j>m-2,$$

The distribution of mortality over all ages and stages can be easily obtained by

$$p_{ij} = q_{ij}\, s_{ij}.$$

Furthermore, $\Sigma\, p_{i1}$, $\Sigma\, p_{i2}$, …, $\Sigma\, p_{im}$ give the probabilities that a newborn individual will die in stage 1, 2, …, respectively. These stage mortalities tell us the occurrence of mortality in each stage during the life history.

(6) Stable age-stage-distribution

As $t \to \infty$, the age-stage-structure will settle down to a stable distribution and we have
$$N_{t+1} = \lambda N_t.$$
The stable age-stage-distribution can be obtained from the following equations：
for $j = 1$ (the first column)
$$\lambda n_{21} = g_{11} n_{11}$$
$$\lambda n_{31} = g_{21} n_{21}$$
$$\vdots$$
$$\lambda n_{k1} = g_{(k-1)1} n_{(k-1)1},$$
for $1<j<m$ [the second to $(m-1)$th column]
$$\lambda n_{ij} = d_{(i-1)(j-1)} n_{(i-1)(j-1)} + g_{(i-1)j} n_{(i-1)j}$$

for $j=m$ (the last column)

$$\lambda\, n_{ij} = d_{(i-1)(j-1)}\, n_{(i-1)(j-2)} + g_{(i-1)j}\, n_{(i-1)j}$$

To calculate the stable age-stage-distribution, we set $n_{11}=1$, and then derive the frequencies for all other ages and stages colum by column using the above equations. A computer program for this tedious calculation is inevitable. As the stable age-stage-distribution is obtained, the stable age distribution. and the stable stage distribution can be easily found by summation. For populations with stage differentiation, the stable stage distribution is obviously more interesting and meaningful than the stable age distribution.

AN EXAMPLE WITH DIAMONDBACK MOTH

(1) Material and Method

A laboratory population of diamondback moth, *Pultella xylostella* (L.), was used in this experiment. For the study on developmental time and survivorship of each preadult stages, 100 fresh leaves of *Brassica oleracea* L. var. *acephala* DC, each with one newly laid egg, were kept separately in petri dishes (9 cm dia.) until pupation. The fresh leaves were afforded every day and their stems were wrapped with wet cotton-wool to maintain the freshness of the leaves. The developmental and survival rate of eggs, four larval instars and pupae were recorded daily. When the pupae appeared, each pupa was removed into a finger tube (1cm dia., 4 cm height), then the developmental time and sex were recorded as the adults emerged.

The emerged adults were released by pairs into a plastic cylinder (15 cm dia., 20cm height) with a fresh leaf for egg laying. A small glass tube (1 cm dia., 1 cm height) with 30% honey solution was served as food for adults. All eggs laid in the previous day were counted and the number of surviving adults were recorded.

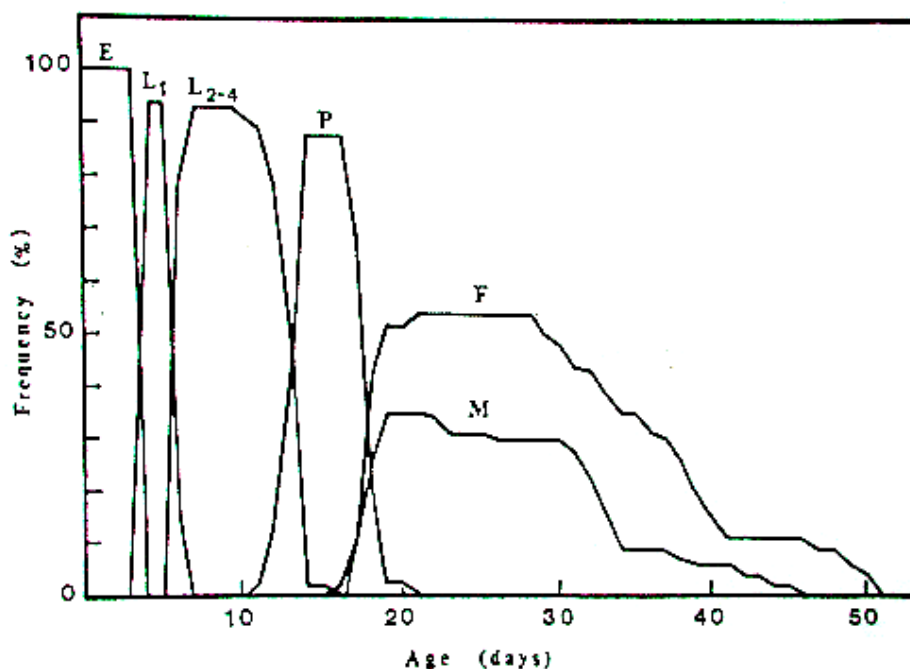The whole life table studies were conducted in the incubators (25℃, 60% RH).

Fig. 3. Stage-frequency distribution of *P. xylostella* at 25℃. (E-egg stage, L_1-first larval instar, L_{2-4}-second to fourth larval instars, P-pupal stage, F- female, M-male).

(2) The stage-frequency distribution

In order to compare the result with the glasshouse experiment, the data were grouped into 6 stages, namely: egg, L_1 (1st instar larva), L_{2-4} (2nd-4th instar larva), pupa, female and male. The stage frequency curve from birth to death presented a significant overlapping phenomenon (Fig. 3). This points to the fact that, when only the means are used to present the developmental times or a single curve (l_x) is plotted for the survivorship, many important features are neglected.

Matrix G

E	L_1	L_{2-4}	P	F	M
1.00	—	—	—	—	—
1.00	—	—	—	—	—
0	—	—	—	—	—
—	1.00	—	—	—	—
—	.16	—	—	—	—
—	0	1.00	—	—	—
—	—	1.00	—	—	—
—	—	1.00	—	—	—
—	—	.98	—	—	—
—	—	.98	—	—	—
—	—	.87	1.00	—	—
—	—	.62	1.00	—	—
—	—	.04	1.00	—	—
—	—	1.00	1.00	—	—
—	—	0	.98	—	—
—	—	—	.77	1.00	—
—	—	—	.30	1.00	1.00
—	—	—	.09	1.00	1.00
—	—	—	1.00	1.00	1.00
—	—	—	0	1.00	1.00
—	—	—	—	1.00	.95
—	—	—	—	1.00	.94
—	—	—	—	1.00	1.00
—	—	—	—	1.00	.94
—	—	—	—	1.00	1.00
—	—	—	—	1.00	1.00
—	—	—	—	1.00	1.00
—	—	—	—	.93	1.00
—	—	—	—	.96	.94
—	—	—	—	.92	.80
—	—	—	—	.96	.67
—	—	—	—	.91	.63
—	—	—	—	.90	1.00
—	—	—	—	1.00	1.00
—	—	—	—	.89	1.00
—	—	—	—	.94	.80
—	—	—	—	.88	.75
—	—	—	—	.71	1.00
—	—	—	—	.80	1.00
—	—	—	—	.75	.67
—	—	—	—	1.00	1.00
—	—	—	—	1.00	.50
—	—	—	—	1.00	1.00
—	—	—	—	1.00	0
—	—	—	—	1.00	—
—	—	—	—	.83	—
—	—	—	—	1.00	—
—	—	—	—	.60	—
—	—	—	—	.67	—
—	—	—	—	0	—

Fig. 4. The age-stage-specific growth rate (Matrix G) of *P. xylostella* at 25℃. (E-egg stage, L_1-first larval instar, L_{2-4}-second to fourth larval instars, P-pupal stage, F-female, M-male).

Matrix D

E	L_1	L_{2-4}	PF	PM	
0	—	—	—	—	—
0	—	—	—	—	—
.94	—	—	—	—	—
—	0	—	—	—	—
—	.82	—	—	—	—
—	1.00	0	—	—	—
—	—	0	—	—	—
—	—	0	—	—	—
—	—	0	—	—	—
—	—	.02	—	—	—
—	—	.12	0	0	—
—	—	.38	0	0	—
—	—	.96	0	0	—
—	—	0	0	0	—
—	—	1.00	.02	0	—
—	—	—	.10	.12	—
—	—	—	.46	.22	—
—	—	—	.45	.45	—
—	—	—	0	0	—
—	—	—	1.00	0	—

Fig. 5. The age-stage-specific developmental rate (Matrix D) of *P. xylostella* at 25℃. Column PF contains the developmental rates from pupal stage to female, column PM contains the rates from pupal stage to male.

(3) The matrices G, D, F, S and P

The age-stage-specific growth rate, developmental rate, and fecundity of *P. xylostella* are given in Fig. 4, Fig. 5 and Fig. 6, respectively. All of these three matrices have 50 rows and six columns. The matrix **S** (the age-stage-specific survival rate, Fig. 7) and the matrix **P** (the distribution of mortality, Fig. 8) are obtained according to the method of the previous sections. It is interesting to point out, that if the age-stage-specific survival rate is plotted against age, it gives exactly the same curve of stage frequency distribution (Fig. 3).

Matrix F

E	L_1	L_{2-4}	P	F	M
0	—	—	—	—	—
0	—	—	—	—	—
0	—	—	—	—	—
—	0	—	—	—	—
—	0	—	—	—	—
—	0	0	—	—	—
—	—	0	—	—	—
—	—	0	—	—	—
—	—	0	—	—	—
—	—	0	—	—	—
—	—	0	0	—	—
—	—	0	0	—	—
—	—	0	0	—	—
—	—	0	0	—	—
—	—	0	0	—	—
—	—	—	0	0	—
—	—	—	0	11.00	0
—	—	—	0	15.00	0
—	—	—	0	33.36	0
—	—	—	0	36.96	0
—	—	—	—	25.38	0
—	—	—	—	26.00	0
—	—	—	—	15.59	0
—	—	—	—	12.48	0
—	—	—	—	12.90	0
—	—	—	—	10.59	0
—	—	—	—	7.55	0
—	—	—	—	6.21	0
—	—	—	—	5.67	0
—	—	—	—	5.23	0
—	—	—	—	4.88	0
—	—	—	—	3.83	0
—	—	—	—	2.62	0
—	—	—	—	2.11	0
—	—	—	—	1.58	0
—	—	—	—	2.53	0
—	—	—	—	1.81	0
—	—	—	—	1.71	0
—	—	—	—	1.70	0
—	—	—	—	1.13	0
—	—	—	—	1.50	0
—	—	—	—	1.33	0
—	—	—	—	.67	0
—	—	—	—	.67	0
—	—	—	—	0	—
—	—	—	—	0	—
—	—	—	—	0	—
—	—	—	—	0	—
—	—	—	—	0	—
—	—	—	—	0	—

Fig. 6. The age-stage-specific fecundity (Matrix **F**) of *P. xylostella* at 25℃. (E-egg stage, L_1-first larval instar, L_{2-4}-second to fourth larval instars, P-pupal stage, F-female, M-male).

Matrix S

E	L_1	L_{2-4}	P	F	M
1.00	—	—	—	—	—
1.00	—	—	—	—	—
1.00	—	—	—	—	—
—	.94	—	—	—	—
—	.94	—	—	—	—
—	.15	.78	—	—	—
—	—	.93	—	—	—
—	—	.93	—	—	—
—	—	.93	—	—	—
—	—	.91	—	—	—
—	—	.89	.02	—	—
—	—	.78	.13	—	—
—	—	.48	.43	—	—
—	—	.02	.89	—	—
—	—	.02	.89	—	—
—	—	—	.89	.02	—
—	—	—	.69	.11	.11
—	—	—	.20	.43	.26
—	—	—	.02	.52	.35
—	—	—	.02	.52	.35
—	—	—	—	.54	.35
—	—	—	—	.54	.33
—	—	—	—	.54	.31
—	—	—	—	.54	.31
—	—	—	—	.54	.30
—	—	—	—	.54	.30
—	—	—	—	.54	.30
—	—	—	—	.54	.30
—	—	—	—	.50	.30
—	—	—	—	.48	.28
—	—	—	—	.44	.22
—	—	—	—	.43	.15
—	—	—	—	.39	.09
—	—	—	—	.35	.09
—	—	—	—	.35	.09
—	—	—	—	.31	.09
—	—	—	—	.30	.07
—	—	—	—	.26	.06
—	—	—	—	.19	.06
—	—	—	—	.15	.06
—	—	—	—	.11	.04
—	—	—	—	.11	.04
—	—	—	—	.11	.02
—	—	—	—	.11	.02
—	—	—	—	.11	—
—	—	—	—	.11	—
—	—	—	—	.09	—
—	—	—	—	.09	—
—	—	—	—	.06	—
—	—	—	—	.04	—

Fig. 7. The age-stage-specific survival rate (Matrix **S**) of *P. xylostella* at 25℃. (E-egg stage, L_1-first larval instar, L_{2-4}-second to furth larval instars, P-pupal stage, F-female, M-male).
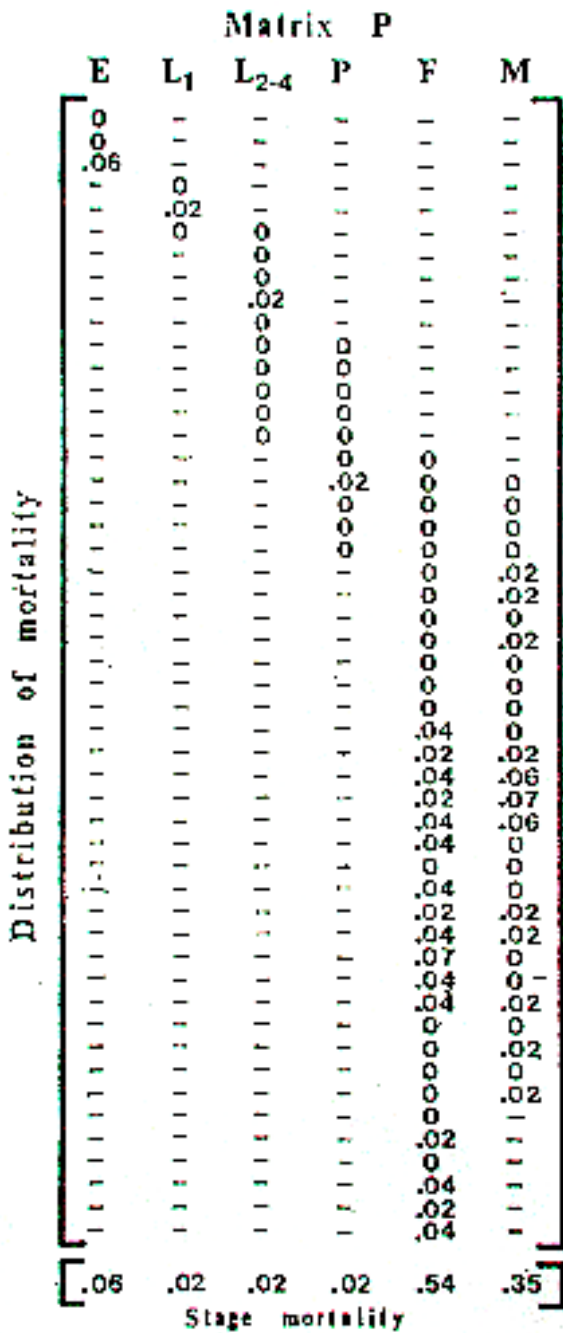
Matrix P

| E | L₁ | L₂₋₄ | P | F | M |

Fig. 8. The distribution of mortality (Matrix P) of *P. xylostella* at 25℃. (E-egg stage, L₁-first larval instar, L₂₋₄-second to fourth larval instars, P-pupal stage, F-female, M-male). (There are round-off errors).

(4) The intrinsic rate of increase and the stable age-stage-distribution of *P. xylostella* at 25℃.

With matrices F and S the intrinsic rate of increase are obtained by using formulae

The intrinsic rate of increase (r)	0.2229
The net reproductive rate (R_0)	120.93
The mean generation time (T)	21.51
The finite rate of increase (λ)	1.2497

$\sum e^{-rx} l_x m_x = 1$ and $\sum (e^{-rx} \sum s_{xj} f_{xj}) = 1$. The same results are obtained from both formulae. The detail data are given in Table 1.

The stable age-stage-distribution of *P. xylostella* is calculated according to the procedure of the previous section and is given in Fig. 9. In Fig. 9 the stable age distribution and stable stage distribution are also listed.

THE MULTIDIMENSIONAL MATRIX MODEL

(1) Basic concept

The basic concept of the spatial distribution of host plants and the age-structure of insects on them is displayed in Fig. 10. According to Fig. 10, if we use a three dimensional matrix N to represent this field population, then the element $n_{6,3,1}$ gives the number of individuals aged six and on the host plant (or in the habitat) located at third column and first row. For example, $n_{6,3,1}=5$ denotes that there are five individuals aged six on that host plant. Using this concept we can set the total field population into such a three dimensional matrix. Each hostplant has its own subpopulation and the spatial location is given by the subscripts.

However, for those animals with metamorphosis, such as insects and mites, the inadequacy of single column matrix for population structure has been discussed in previous sections. Combining this concept pf multidimensional matrix for spatial distribution and that of multiple column matrix for age-stage-structure, a four dimensional matrix is used to represent the age-stage-structure of insect population in field. Thus,
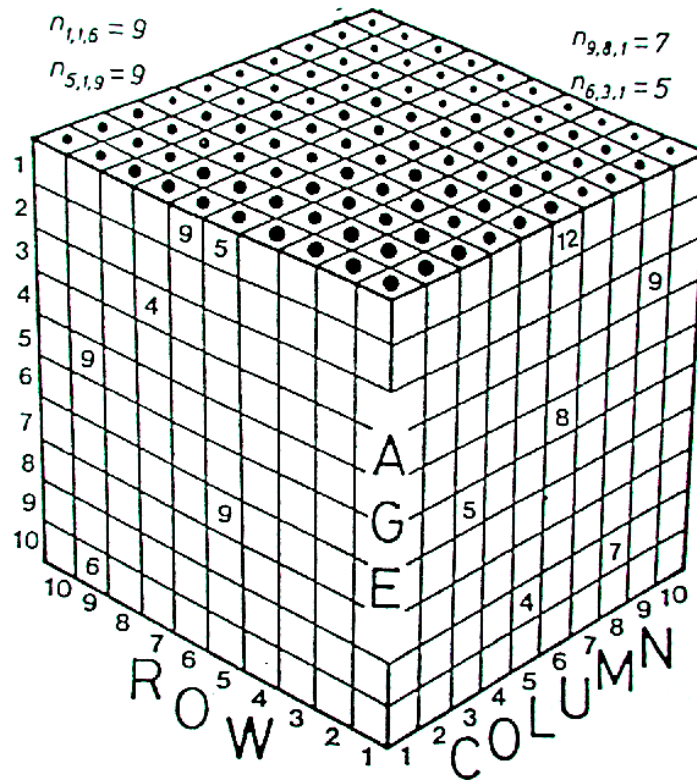
E	L_1	L_{2-4}	P	F	M		Stable age-distribution
20.78	—	—	—	—	—		20.78
16.63	—	—	—	—	—		16.63
13.30	—	—	—	—	—		13.30
—	10.05	—	—	—	—		10.05
—	8.05	—	—	—	—		8.05
—	1.01	5.30	—	—	—		6.31
—	—	5.05	—	—	—		5.05
—	—	4.04	—	—	—		4.04
—	—	3.23	—	—	—		3.23
—	—	2.54	—	—	—		2.54
—	—	1.99	.04	—	—		2.03
—	—	1.39	.23	—	—		1.62
—	—	.69	.61	—	—		1.30
—	—	.02	1.02	—	—		1.04
—	—	.02	.82	—	—		.83
—	—	—	.65	.01	—		.67
—	—	—	.40	.07	.07		.53
—	—	—	.10	.20	.12		.42
—	—	—	.01	.19	.13		.33
—	—	—	.01	.16	.11		.27
—	—	—	—	.13	.08		.21
—	—	—	—	.10	.06		.17
—	—	—	—	.08	.05		.13
—	—	—	—	.07	.04		.11
—	—	—	—	.05	.03		.08
—	—	—	—	.04	.02		.07
—	—	—	—	.03	.02		.05
—	—	—	—	.03	.01		.04
—	—	—	—	.02	.01		.03
—	—	—	—	.02	.01		.03
—	—	—	—	.01	.01		.02
—	—	—	—	.01	0		.01
—	—	—	—	.01	0		.01
—	—	—	—	0	0		.01
—	—	—	—	0	0		.01
—	—	—	—	0	0		0

Stable age-stage-distribution

| 50.71 | 19.11 | 24.27 | 3.88 | 1.25 | 0.78 |

Stable stage-distribution

Fig. 9. The stable age-stage-distribution, stable age-distribution and stable stage-distribution of *P. xylostella* at 25℃. (E-egg stage, L_1-first larval instar, L_{2-4}-second to fourth larval instars, P-pupal stage, F-female, M-male). (There are round-off errors).

Fig. 10. The basic concept of multidimensional matrix model for field population. $n_{6,3,1}=5$ denotes that there are five individuals aged six on the host plant located at third column and first row. Each "•" denotes a host plant.

$n_{8,4,3,1}=5$ denotes that there are five individuals aged eight and in fourth stages on the plant located at third column and first row. This four dimensional matrix can not be displayed with a figure. Due to the complexity of data, computer is an inevitable tool in this work. Two large computer programs have been designed in FORTRAN V, one for three dimensional matrix model (program TDMSLBH) and the other for four dimensional matrix model (program FDMSLBH). In order to avoid the complicate subscripts of $n_{8,4,3,1}$, the expression of FORTRAN language can be used. For example, the general form of elements in population matrix is written as POPU (AGE,COLUMN,ROW) in TDMSLBH, or as POPU(AGE,STAGE COLUMN,ROW) in FDMSLBH. Thus, POPU (I, J, K, L)=5 denotes that there are five individuals in age I and stage J on the host-plant located at row L and column K. These expressions are more readable, but yet have not been generally used.

In accompany with matrix POPU, another matrix PLANT (or HABITAT) is used to express the existence of a hostplant or habitat. For example, PLANT (L, K)=0 denotes there is no plant located at row L and column K, PLANT (L, K)=1 denotes then the existence of a hostplant at row L and column K. Using matrix PLANT the configuration of field can be determined.

In the following sections only the general features of this new method will be discussed. For different insect species and hostplant other relevant factors can be inserted to make it more suitable for them.

(2) Population growth

If the field population structure at time t is known, then the population structure for time $t+1$ can be obtained through proper

calculations. When a single column matrix is used for the age structure of each sub-population (in program TDMSLBH), then the simple matrix multiplication can be followed in order to find the age structure of each subpopulation at time $t+1$. For this, a square matrix containing age-specific survival rate and fecundity is required (Lewis 1942). However, when there is significant stage overlapping phenomenon, e. g. in most insect and mite populations, the method of multiple column matrix should be followed (in program FDMSLBH). For this, the age-stage-specific growth rate, developmental rate and fecundity (matrices **G**, **D** and **F**) are required.

(3) The carrying capacity of host plant

The carrying capacity increases generally with the growth of host plant. Thus, it is necessary to know the carrying capacity (array name KVALUE(T) is used in computer program) of host plant for each time. These time-specific KVALUE(T) can be either direct input as real numbers or given with a function of time. Here, the unit of KVALUE must be properly selected. In our study, a fourth instar larva of the diamondback moth, *P. xylostella*, was used as a standard unit. A KVALUE(10)=20 means that the carrying capacity of host plant at $t=10$ is equivalent to twenty larvae of fourth instar. Although the carrying capacity may also depend on other factors, for the general introduction only the time-specific KVALUE is taken into account in this paper.

(4) Dispersion

The dispersion of an insect from a host plant to other may be density-dependent or density-independent and it may be variate from stage to stage; furthermore, the dispersal ability may be also different among stages. For example, the adults of flying insect may fly away from a host plant whatever the density is high or low. Whereas, a larva will crawl to next plant only when the density is high (in comparison with the time-specific KVALUE, and the other physical disturbances will not be considered). Here, the density is

not the sum of total population, a more convienient expression is the sum of the products of the number of individual in each stage multiplied by the respective stage-specific weighing coefficient (the array name KWEIGH is used in program). For practical use, we suggest that the stage-specific KWEIGH is to be experimentally determined and the difference among ages of the same stage can be neglected. For example, according to the leaf consumption of different larval instars, the stage-specific KWEIGH for the fourth larval instar is 1, for third is 0.6, for the second is 0.2 and for all other stages are 0. Then , the density of this pest on a host plant (the array name KDENSIT is use) can be calculated from :

$$KDENSIT = \Sigma (KWEIGH(J) \times STAGE(J)),$$

where STAGE(J) is the number of individuals in stage J on that host plant. The occurrence of density-dependent dispersion depends on the value of KDENSIT in comparison with KVALUE, the numerical relationship must be experimentally determined.

The dispersal distance depends on the behavior ability. For example, an adult of diamondback moth can fly to anywhere in a field, but a larva may only crawl to one of the surrounding plants. To each stage J a code can be assigned, this code is used to represent the stage-specific dispersal ability (the array name DISPAB(J) is used). The direction of dispersal will be determined by random number. If an individual fails to find a new host plant or the new plant has already a high KDENSIT, it will die. As a matter of fact, the spatial distribution of a population changes with time. In TDMSLBH and FDMSLBH, the means and variances will be calculated and the variance/mean ratios will be plotted against time. This gives a preliminary description of the dynamical change of distribution pattern. A mapping subroutine can be called at any time when a detail field distribution of pest population is needed, this

makes the change more comprehensible and is especially helpful in teaching entomology.

GLASSHOUSE RELEASE EXPERIMENT AND COMPUTER SIMULATION

(1) Material and method

Fifteen pairs of adults of diamondback moth, newly emerged from pupae, were released into the glasshouse. In the glasshouse, 100 pots of ca. 60 days-old *Brassica oleracea* L. var. *acephala* DC were arranged into three blocks, each with 33, 34 and 33 pots. The number of larvae (2nd-4th instars) and pupae were investigated every 3-5 days. The temperature and humidity were recorded every day. The results were compared with the simulation results by running program FDMSLBH. The released fifteen pairs of adults were assumed to be randomly distributed.

(2) Comparison between population growth in glasshouse and in computer simulation

The population growth curves obtained in the glasshouse release experiment are illustrated in Fig. 11 and Fig. 12. Due to the fact that the life table data were recorded under special laboratory conditions, it was reasonable to believe that there was a difference between the results of laboratory and of glasshouse conditions. Because the exact differences in growth rate, developmental rate and fecundity have not been experimentally studied, the half, the fifth, the tenth and the twentieth of the age-stage-specific fecundity were used in this preliminary simulation. The simulated growth curves are also plotted in Fig. 11 and Fig. 12. The curves of simulated and observed variance/mean ratios were plotted against time (Fig. 13). Due to the randomized random numbers were used in FDMSLBH, different results have been obtained from every simulations. (If the same result was obtained from every simulation, then the same sequence of random number had been used. This must be carefully avoided in programming). This can be used to simulate the variability in population growth and dispersion, which was as results of
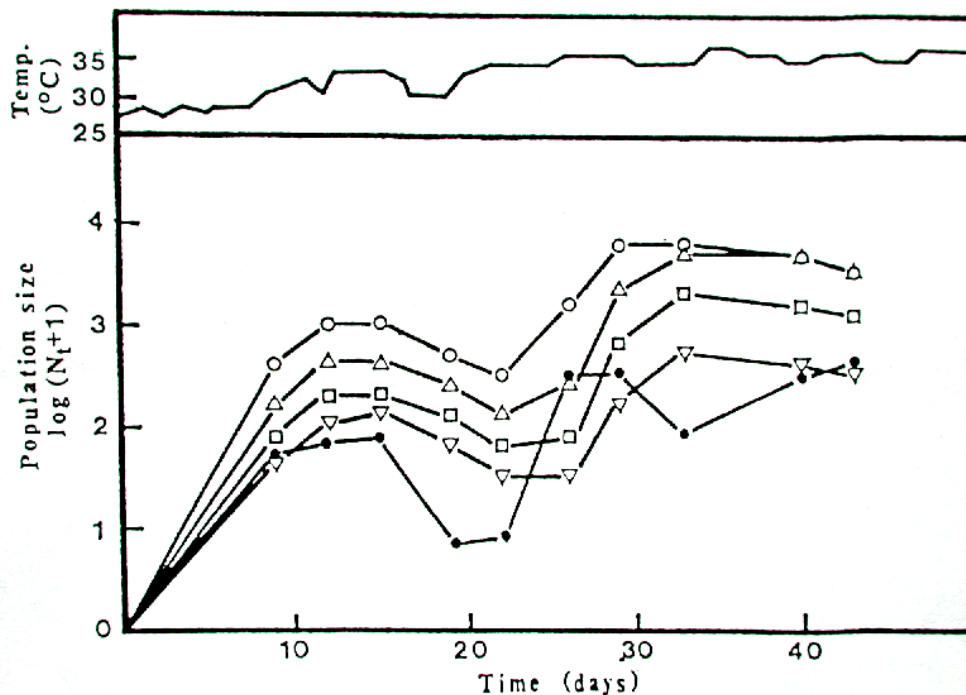
Fig. 11. The observed (●-●) and four simulated population growth curves for larvae (2nd-4th instars) of *P. xylostella*. The simulations were conducted by using $f_{ij}/2$ (○-○), $f_{ij}/5$ (△-△), $f_{ij}/10$ (□-□) and $f_{ij}/20$ (▽-▽), respectively.
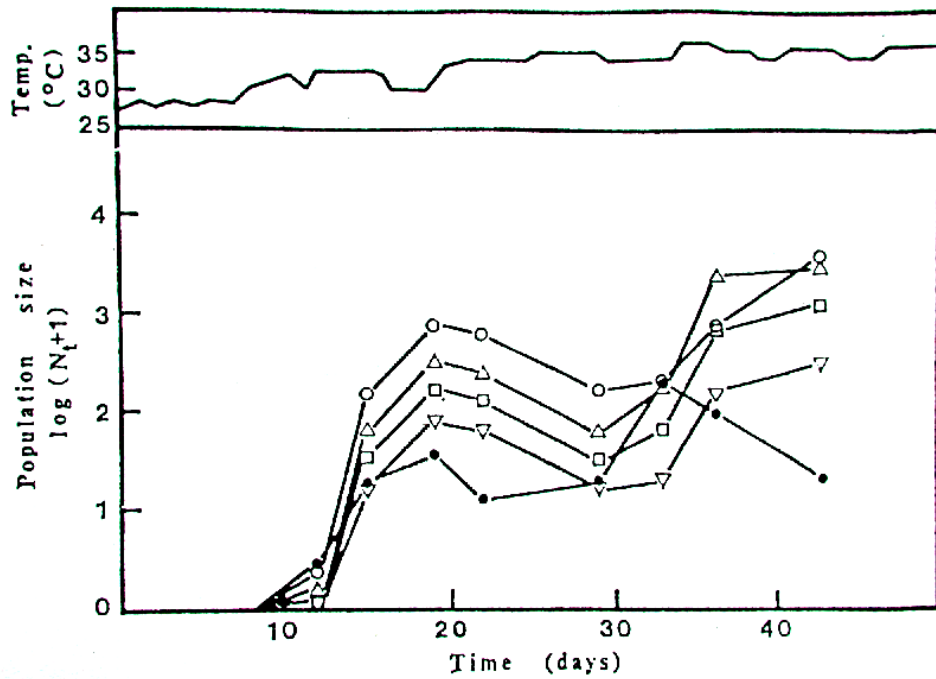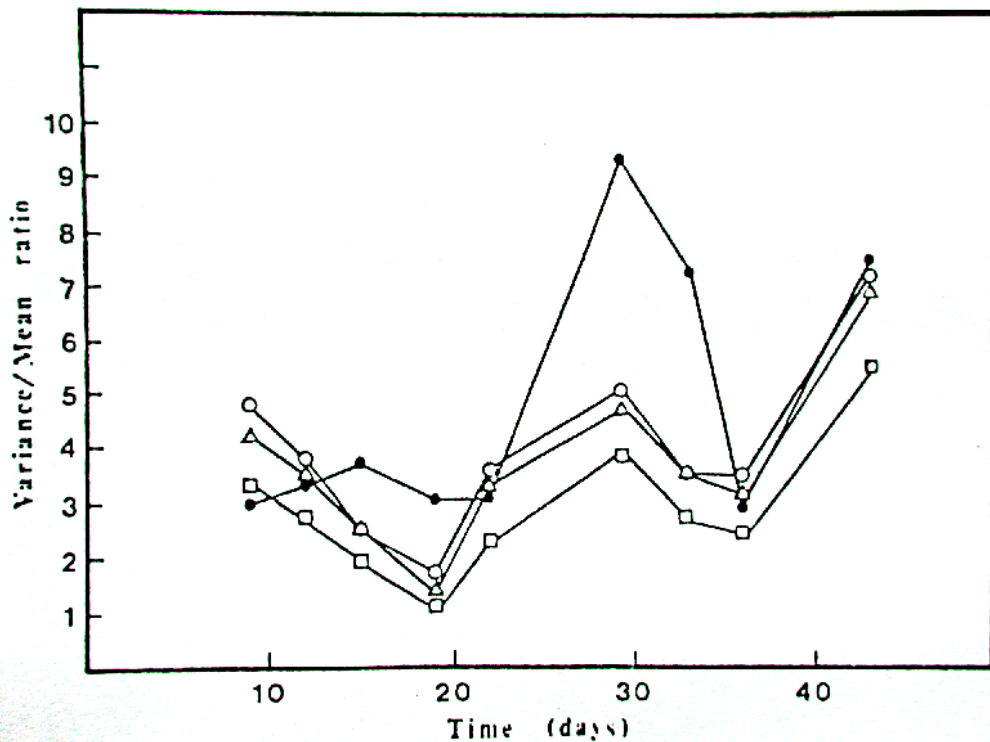
Fig. 12. The observed (●-●) and four simulated population growth curves for pupal stage of *P. xylostella*. The simulations were conducted by using $f_{ij}/2$ (○-○), $f_{ij}/5$ (△-△), $f_{ij}/10$ (□-□) and $f_{ij}/20$ (▽-▽), respectively.

Fig. 13. The observed (●-●) and three simulated (○-○, △-△, □-□) curves of variance / mean ratios for diamondback moth (*P. xylostella*)(2nd-4th instar larvae and pupae together). The three simulations were conducted by using the same $f_{ij}/10$.
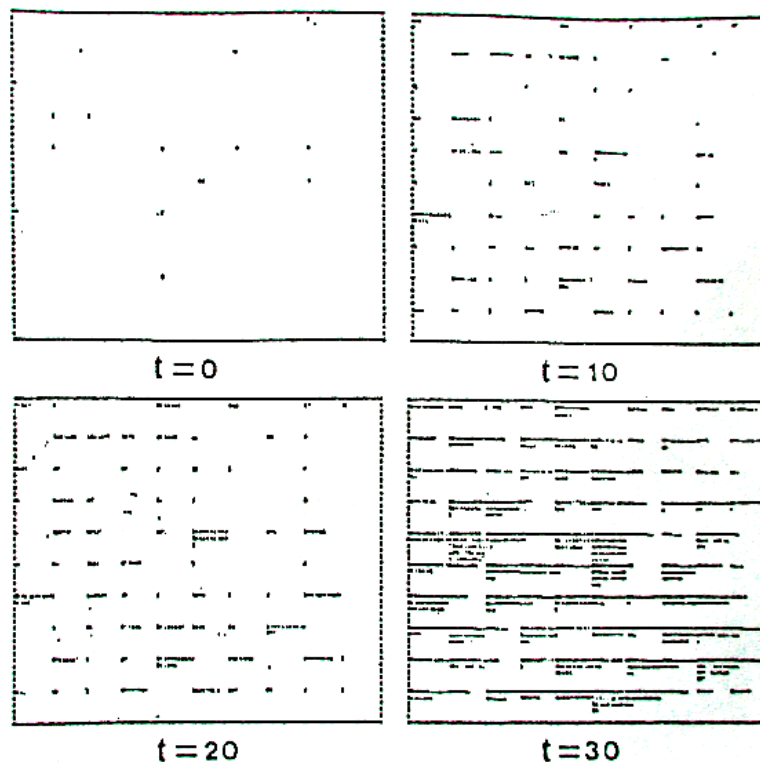
Fig. 14. Examples of computer mapping for the field distribution of *P. xylostella* at different time. The symbols are " • "-egg, "-"-larva, "*i*"-female and "/"-male. Overprinting allowed all stages to be printed in a single map. Due to reductions, the symbols cannot be distinguished.

dispersion in different directions or due to the occurrence of mortality, when movement ended in a hostile plant (i. e. already with a high pest density). This kind of variability has not been noted in other stochastic models, but it does play an important role in the true ecosystem (e. g. Jennings *et al.*, 1983). Although there were differences among simulated and observed curves, but the tendencies were alike. For this preliminary simulation, further explanations to these differences were not given.

Examples of computer mapping are displayed in Fig. 14. Different symbols were used to represent individuals of different stages and the overprinting allowed all stages to be printed in a single map. However, due to several reductions, the symbols cannot be distinguished. The mapping results of each simulation were also different from one another. This can be used to study the variability of field distribution.

DISCUSSION

In this paper, two new methods with respect to population growth of insects and mites have been introduced. The first method is concerned with stage overlapping. Here, the stage overlapping does not mean simply the occurrence of different stages in field at the same time. It means the overlapping of different stages during the development process of individuals reproduced at the same day. For a more precise and reasonable study of population growth, such stage overlapping phenomenon should never be neglected either in theoretical or applied ecology. In this paper, we have developed a straightforward and biologically realistic method, in which the survival rate is taken as a composition of growth rate and developmental rate and the age-stage-structure of population is given in a multiple column matrix. The detail algorithms for this new method have been described in respective sections.

However, the population growth is not merely an event of numerical change with time. As a matter of fact, individuals of population distributed themselves rather un-uniformly in fields (Taylor 1961). If we study the population growth without considering the spatial distribution, then we may lose ourselves in numbers and overlook some important features. On the other hand, if we study the spatial distribution but without considering the population growth, then we will lose the dynamic feature of spatial distribution. For the study of the growth of a "true" population, we have to set the population into a space and consider the changes in number and spatial distribution at the same time. Using a multidimensional matrix it is possible to do this work; the population is then taken as composition of subpopulations, each subpopulation lives on its host plant and has its own age structure (or age-stage-structure). Thus, we have the age structure and spatial distribution in one model. The basic concepts have been discussed in this paper. For practical application to specific pest and host plant, other relevant factors must be taken into account.

The multiple column matrix model is in principle developed for theoretical study on population growth with stage grouping. The multidimensional matrix model is then for the combined study of population growth and dispersion. If the predator or parasite is going to be included in this model, a five dimensional matrix is necessary. The matrix SYSTEM (SPECIES,AGE,STAGE,COLUMN,ROW) can be assigned for system simulation. Then, the experimental results such as Huffaker's report (1958) perhaps can be studied using this method. Furthermore, when using these concepts to study the intra-plant distribution on large host plant, such as trees, then another subscript HEIGHT must be used to construct the spatial structure ; for example, POPU(AGE,STAGE,COLUMN,ROW, HEIGHT) for the single species model or SYSTEM (SPECIES,AGE,STAGE,COLUMN,

ROW,HEIGHT) for system simulation. Of course, it needs large memory to store the matrix POPU and SYSTEM, and the simula-tion program can be run only on a large computer. However, it is not necessary to assign a large matrix for a field of hectares, but it must be large enough to reproduce the important features of a "real" population. If the simulation can give more precise infor-mation about field distribution, then it is possible to know how many host plants bear a pest number over the predefined economic injury level, and this will be better than to use a single value, the mean density. On the other hand, if the growth and dispersion of vector population can be precisely studied, then the research on epidemiology of plant disease transmitted by insect can be improved.

The combined study of the growth and dispersion is important not only for simu-lation works using calendar time, but also for those using physiological time. We are interested in incorporating these concepts in such simulation models. The main ongoing works in our laboratory are the further development of theories of population growth and their practical use in system simulation.

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研 究 昆 蟲 族 羣 生 態 的 兩 種 新 方 法

齊 心 劉 璽

依據齡期頻度分佈，本文利用一個多行矩陣表示具變態之動物族羣的年齡與齡期結構。用此新方法，可以研究昆蟲及蟎蜱族羣之增長過程（ 包含雌雄兩性 ），並適當的組合齡期。族群增長、內在增殖率以及穩定年齡與齡期分佈之計算，均詳述於文中。

為模擬田間族羣生態，本文利用一多維矩陣表示寄主植物之空間分佈及害蟲族羣之年齡與齡期結構，並設計電腦程式以同時模擬田間族羣之生長與分散。利用這兩種方法可以模擬農業生態系。