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SPACE–TIME STRUCTURES IN A WINTER RAPE PEST POPULATION, *PSYLLIODES CHRYSOCEPHALA* (COL., CHRYSOMELIDAE): METHODOLOGICAL PROPOSALS AND BIOLOGICAL INTERPRETATIONS

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SUMMARY

(1) Graphical representations, non-parametric tests, and correspondence analysis are used to describe spatial and temporal structure in a population of a winter rape pest (*Psylliodes chrysocephala* L.) on three scales: between-plants, within-plots, and between-plots.

(2) The between-plants variability was related to the egg-laying of females and to the attractiveness of plants for young larvae. A density-dependent regulation mechanism occurs at this scale, either by differential mortality, or by dispersal of larvae.

(3) The within-plot structures were analysed in terms of static spatial structures, of spatial and temporal interactions, and of variation during the life history of the pest.

(4) The between-plots variability is described, and a qualitative model of plot invasion explains the between-plots variation in infestation.

(5) Data are discussed from the point of view of methodology and population biology.

INTRODUCTION

In a recent book, Legay & Debouzie (1985) emphasize the role of structures in the definition of natural populations: spatial, temporal, genetic, kinship, and social structures are to be analysed to understand how populations are organized and how they function. In non-social insect populations, spatial and temporal structures are directly observable. For Taylor (1984), spatial distribution of insects results from 'the population expression of the individual behaviour', and therefore leads to characteristic parameters of populations.

Four main characteristics are necessary for a study of spatial and temporal structures in insect populations:

(i) The life history and general biology of the species must be well known. This is so for the system we have been studying since 1981: the cabbage stem flea beetle (*Psylliodes chrysocephala* L.) and its host plant, the winter rape (*Brassica napus* L.). This pest has been thoroughly studied by Bonnemaison & Jourdheuil (1954) in France, by Kaufmann (1941) and Buhl (1959) in Germany, by Alford & Gould (1975) and Alford (1979) in England, and by Ebbe-Nyman (1952) in Sweden.

(ii) Favourable experimental conditions are required to lessen the complexity of natural situations. The agrosystem offers such conditions for studying the spatial distribution of insect pests (see a review in Stinner *et al.* 1983).

(iii) As a first step, all the sites occupied by insects in the area of study must be controlled. This control may be ensured by spreading the sampling intensity over the sites; systematic sampling is particularly well adapted to this.

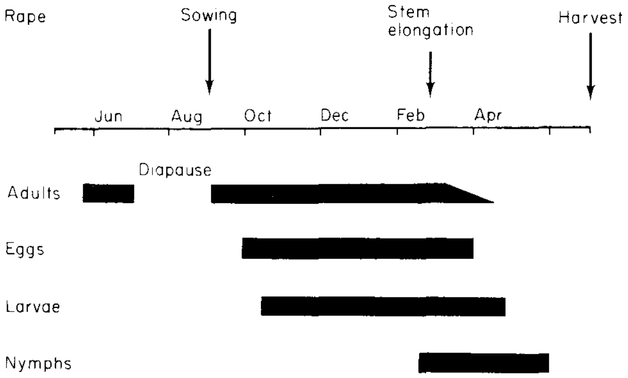

FIG. 1. Life history of *P. chrysocephala* and main stages of development of winter rape in St Thomas-En-Royans.

(iv) The whole life history of the insect must be sampled: data on the number and distribution of adults only are rarely sufficient for understanding and predicting the dynamics of an insect population.

Our objectives were to describe the various scales of heterogeneity in the distribution of *P. chrysocephala* in St Thomas-En-Royans, in relation to environmental or biological factors, and the consequences of these structures for the definition of a natural population of insects.

MATERIALS AND METHODS

Life history of insect

In the region of St Thomas-En-Royans, adults emerge from the soil in June (Fig. 1). After feeding on rape plants for about 2 weeks, they enter diapause. Activity resumes in early September, and is followed by a dispersal phase. Crop invasion takes place if young rape plants are present in the fields. Otherwise, insects disperse in temporary shelters, such as hedges or surrounding woods, and invasion of the rape crops is delayed until the appearance of the first plants. In St Thomas-En-Royans, winter rape is sown in the first half of September. Egg laying begins a few days after the invasion of crops (Fig. 1) and can extend until spring. Eggs are laid in batches, into the superficial layer of soil; larvae develop within rape stems. Three larval stages are defined and, at the end of their third instar, larvae drop into the soil, where they pupate.

The site of study

The site of St Thomas-En-Royans (Drôme, France) was chosen because it is favourable for isolated rape cultivation. The area is surrounded by hills, 100–1000 m high, creating a natural barrier to insect movements (Fig. 2). Field work to implement our sampling designs was carried out by the field laboratory of CETIOM (Interprofessional Technical Centre of Metropolitan Oilseed Crops). Contracts between farmers and CETIOM made control of cultivated areas and practices possible; no insecticide was applied during the study. Each year since 1981, rape cultivation was limited to *c.* 5 ha and the fields were within an area of 2 km^2.

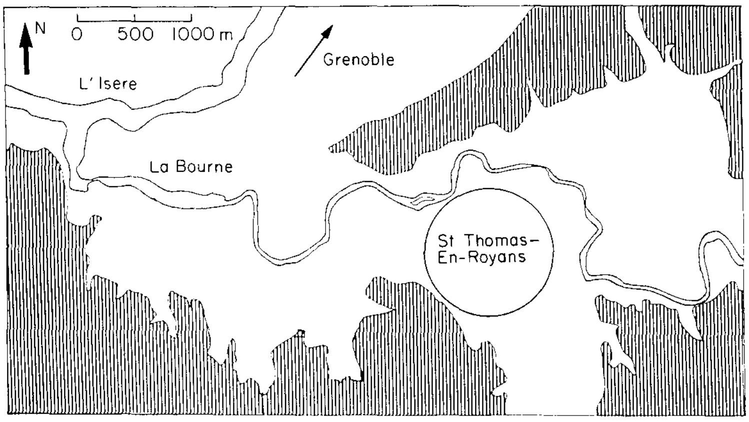

FIG. 2. General map of the region of St Thomas-En-Royans. Hatched areas correspond to an altitude >250 m.

Sampling methods

Each year, all winter rape plots were sampled according to a systematic design. A regular grid was defined within each plot; the nodes of this grid were 20 m apart, except for some plots in 1981–82, where the nodes were 10–40 m apart.

At each node of the grid, three sampling techniques were used, according to the insect development stage. A yellow water-trap (a plastic basin, 0·26 m in diameter, full of water and a few drops of detergent) was set into the ground. Adult insects that drowned in the traps were collected 1–3 times a week, from the invasion of the crops until the end of emergence of the new insect generation. A box was set up in the vicinity of each trap; two types of box were used in the first 2 years, a square one (1 m × 1m × 0·3 m) and a cylindrical one (diameter 0·5 m, 0·3 m high). In 1983–84, only the square type was used. Boxes had two functions. (i) To collect adults trapped underneath; the efficiency of this technique was tested by Ballanger (1979) who obtained good estimates of infestation during the invasion phase, in September and October. However, in winter, the efficiency decreased because of the decrease in insect activity, so boxes were used in early autumn and spring only. (ii) To collect young adults at emergence. Larvae were numbered by dissecting two adjacent plants at each sampling point. Plants were picked once a week or twice a month, from November to May; during this period, larvae of the three instars were present.

Table 1 summarizes information about the sampling devices for each plot from 1981 to 1984.

In the first days of September, adults were collected by sweep-net in all the bushes, hedges and coppices around, mainly near the rape fields of the previous year. Water-traps were placed in these fields. About forty traps were set up along two transects (three in 1982–83), one outside the area to provide information on its isolation, and the other within it, to check insect movements.

Data analysis methods

For the first 3 years, the data obtained represent *c.* 27 000 water-trap collections, 4800 box collections, and 12 000 plant dissections.

TABLE 1. Main characteristics of the sampling devices used for each plot from 1981 to 1984. Plots are numbered following a three digit code, the first two corresponding to the year of harvest. In 1981–82, the number of sampling points was divided by four during spring to reduce sampling intensity

1981–82

Plots	821	822	823	824	825	826	827
Area (ha)	1·65	0·84	0·25	0·69	0·63	0·78	0·72
Distance between grid nodes (m)	20	15	10	10	20	20	20
Number of sampling points	47	40	24	72	19	21	20

1982–83

Plots	831	832	833	834
Area (ha)	1·45	1·57	1·26	0·96
Number of sampling points	38	40	32	28

1983–84

Plots	841	842	843	844	845
Area (ha)	0·69	0·80	0·98	1·32	1·24
Number of sampling points	16	18	24	32	33

A computer database set up to store this information gave simple and quick access to any required subset of data and stored data on other winter rape pests, such as the stem weevil (*Ceuthorrhynchus napi* Gyll).

Three methods were used to analyse the data from each plot. Our objectives were to describe how the insects were distributed within each plot, so we used methods very different from those of Taylor (1984) or Iwao (1968). See Debouzie & Thioulouse (1986) for a discussion of these two approaches, and Bouxin & Gautier (1979), Bouxin (1983), and Bouxin & Le Boulengé (1983) for examples of applications of these methods to phytosociological problems. The between-plots and within-plot heterogeneity was studied by graphical mapping and by non-parametric statistics described by Chessel (1978, 1981) and Debouzie & Thioulouse (1986). Correspondence analysis (CA) was used for studying the temporal collections of grids. The main interest of the above mentioned non-parametric tests is that the spatial structure of data is used in the analysis, by the mean of the neighbouring relationships inside blocks. This is not true for the methods based on adjustments to theoretical distributions (i.e. Poisson, Negative Binomial, Log Normal, Neyman type A, etc.) or on indices derived from the variance-to-mean ratio; in both cases, the spatial location of measures is *not* used in the analysis.

Graphical representations

Maps of each plot were drawn, using squares proportional to the number of insects captured for each sampling point. These maps are convenient for a qualitative analysis of the spatial distribution of insects within plots, but need to be complemented with statistical tests for the presence of spatial structures. Moreover, the temporal variations of spatial structures are difficult to assess by simply observing the chronological succession of maps. Multivariate analysis, and especially correspondence analysis, is well adapted to such designs.

Non-parametric tests

Several non-parametric tests were used; only three are presented here: the true aggregation index (TAI), the spatial autocorrelation matrix (SAM) and the trend test (TT).

The TAI (Chessel & De Belair 1973; Mead 1974, Debouzie *et al.* 1975; Chessel 1978) was used to check the presence of true aggregation (*sensu* Feller 1943): the difference in the numbers of insects captured in two adjacent points was compared with its expected value under a random distribution hypothesis:

$$\mathrm{TAI} = (1/\sqrt{n^*})\sum_{i=1}^{n^*}[D_i - E(D_i)]/\sqrt{\mathrm{Var}(D_i)},$$

n^*: number of pairs such that $L_i + R_i \geqslant 2$, $D_i = |L_i - R_i|$ L_i and R_i: number of insects in the left and right parts, respectively, of the ith pair.

$$E(D;\, 2) = 1,$$

$$\text{if } k \text{ even, } E(D;\, k) = E(D;\, k-1),$$
$$\text{if } k \text{ odd, } E(D;\, k) = E(D;\, k-1) + (k-1)!/\{2^{k-1}[(k-1)/2]!\}.$$
$$\mathrm{Var}(D;\, k) = k - [E(D;\, k)]^2.$$

If n^* is large and if the distribution of counts is random, the TAI follows a Gaussian law. Several scales of heterogeneity may be detected by grouping the sampling points into blocks of increasing size (see Mead 1974, or Ripley 1981 pp. 108–109 for a discussion of this technique, originally introduced by Greig-Smith 1952).

The SAM (Chessel 1981) is used to test the correlation between the values recorded at two adjacent points of a grid. It is derived from Geary's index (Geary 1954). The principle of the statistical test is to estimate the variability between two contiguous blocks as against the total variability of the grid.

The SAM has several useful characteristics: it applies to quantitative and qualitative data, to non-rectangular or incomplete grids, and allows several definitions for the contiguity relationship. By varying the size of the blocks, it is also possible to examine several scales of heterogeneity. If the grid is rectangular, the SAM is the non-parametric version of the analysis of variance of Greig-Smith (1952); for unequal blocks, it generalizes the statistical test of the number of pairs of Walter (1954) and, for binary data, it is equivalent to the non-parametric dispersion index of Chessel & Croze (1978).

Let V be the matrix of contiguity relationship of N points: $V_{ij} = 1$, if points (or blocks) P_i and P_j are neighbours, $V_{ij} = 0$ otherwise; x_i and x_j are the values measured at points (or inside blocks) P_i and P_j.

$$L_i = \sum_j V_{ij}$$
$$A(V) = \sum_i L_i = \sum_{i,j} V_{ij}$$
$$D(V) = \sum_i L_i(L_i - 1)$$

For each size of blocks, let $Z = H_v/H_T$, with:

$$H_T = [\sum_{i,j}(x_i - x_j)^2]/[N\,(N-1)] = 2\sum_i(x_i - \bar{x})^2/(N-1)$$

(total variability of measures),

$$H_v = [\sum_{i,j} V_{ij}(x_i - x_j)^2]/\sum_{i,j} V_{ij}$$

(variability of measures for two neighbouring points).

Then, the SAM is defined, for each size of blocks, by:

$$Z^* = [E(Z) - Z]/\sqrt{\mathrm{Var}(Z)}$$

$$E(Z) = 1$$
$$\mathrm{Var}(Z) = (X_1 + X_2 + X_3)/[A(V)^2 N(N-2)(N-3)]$$

with:

$$X_1 = [(N^2-3)-(N-1)^2 \mathrm{B}_2]A(V)$$
$$X_2 = 2\,A(V)\,(N-1)\,[N^2-3N+3]$$
$$X_3 = (N-1)\,[D(V)+A(V)]\,[(N^2-N+2)B_2-(N^2+3N-6)]$$

and:

$$B_2 = N\sum_i (x_i-\bar{x})^4/[\sum_i (x_i-\bar{x})^2]^2.$$

Cliff & Ord (1973) showed that Z^* approximately follows a Gaussian law, which allows one to test the significance of the observed values. If spatial autocorrelation exists, i.e. if the values measured at two adjacent points are more closely related than values measured at two points selected at random, then the observed value of Z decreases and Z^* becomes significantly positive.

The trend test (Chessel 1978) is used to test the presence of trends within data. If x_i is the ith value measured on a line of length N ($1 < i < N$), the statistic W:

$$W = \sum_{i=1}^{N} i x_i$$

is high if the high values of x_i are placed at the end of the line, and otherwise it is low.

Let m and s^2 be the observed mean and variance of the series; $E(W)$ and $\mathrm{Var}(W)$ are given by:

$$E(W) = [m\,N(N+1)]/2$$
$$\mathrm{Var}(W) = s^2 N\,(N+1)/12$$

Then the TT is defined by:

$$W^* = [W-E(W)]/\sqrt{\mathrm{Var}(W)}$$

and it is approximately Gaussian if $N \geqslant 20$.

Correspondence analysis

Correspondence analysis (CA) is a multivariate method used to analyse contingency tables; the table $T=[t_{ij}]$ has I rows and J columns ($I<J$), corresponding to the classes of two discrete variables. The value t_{ij} contained in the ith row and jth column represents the number of individuals belonging to class i of the first variable and class j of the second. Kendall & Stuart (1961), Benzecri (1973) and Hill (1973, 1974) have developed the mathematical theory of this analysis, and Nishisato (1980) gives a more recent synthesis of it, with a complete bibliography.

We used CA to interpret the results of sampling plans organized in space and time. Systematic sampling gives grid-organized data, which are often collected more than once, hence leading to three-dimensional data sets (i.e. time plus two dimensions in space) which cannot be analysed with classical statistical methods. Correspondence analysis can be performed on such data sets by reorganizing them into a two-dimensional table: the rows of this table correspond to the sampling dates, and each sampling point corresponds to a column, or inversely, since rows and columns are symmetrical for CA. The spatial structure of data (i.e. the location of measures) is thus not used as such in the analysis; but

TABLE 2. Values of the index of true aggregation for each plot and the three larval instars. The index is computed over all the pairs of plants picked at each sampling point. If the distribution of larvae within the plants of a pair is random, and if the number of pairs is large enough (which is always the case here), the distribution of the index is approximately normal

			1981–82				
Plots	821	822	823	824	825	826	827
First instar	4·3	5·6	2·3	6·2	4·4	3·9	5·7
Second instar	3·3	3·2	2·2	5·6	4·0	3·3	2·0
Third instar	3·7	7·5	1·3	6·1	2·9	5·6	5·6
			1982–83				
Plots	831	832	833	834			
First instar	8·9	8·6	8·8	10·2			
Second instar	5·1	6·4	8·1	6·4			
Third instar	3·9	3·8	2·6	3·8			
			1983–84				
Plots	841	842	843	844	845		
First instar	5·5	4·9	6·5	7·9	6·8		
Second instar	3·9	4·9	4·3	3·8	4·6		
Third instar	0·8	2·1	2·7	2·7	2·6		

we must point out that (i) it may be re-introduced when interpreting the results of the analysis (see next paragraphs); (ii) as remarked by Ripley (1981, p. 101), the theory of spatial processes may be extended to space–time processes (Bennett 1979), but 'these models are multivariate time series' and do not take into account the spatial nature of data.

Our objectives are: (i) to compare the curves of catches during the whole sampling period at each sampling point (i.e. to compare the distribution in each column of the table); (ii) to compare the maps of catches at each date (i.e. the distribution in each row).

This point of view is rather different from Hill's (1973) but the mathematical properties of CA are well adapted to these aims: (i) the scores of the sampling points maximize the between-dates variance (and minimize the within-dates variance); (ii) the scores of the sampling dates maximize the between-points variance (and minimize the within-points variance).

Correspondence analysis of spatio–temporal data sets (number of insects captured at point i and at time j) leads to canonical partitions of space (into homogeneous zones) and time (into homogeneous periods). The best way to represent these partitions is not the classical scatter diagram of the first two axes derived from commonly used multivariate methods. Instead, we suggest that the successive factors built by CA should be represented as functions of time or space. Homogeneous periods (i.e. periods during which spatial distribution of insects remains constant) appear by plotting the line-factor values (Y axis) against time (X axis). Homogeneous zones appear by plotting the column-factor values in space, for example by drawing squares proportional to the value of the score in each point of the grid. The sign of the factor value may be given by a symbol placed in the centre of each square (Auda 1983).

RESULTS

Spatio–temporal structures in the population of *P. chrysocephala* were observed in St Thomas-En-Royans on three scales:

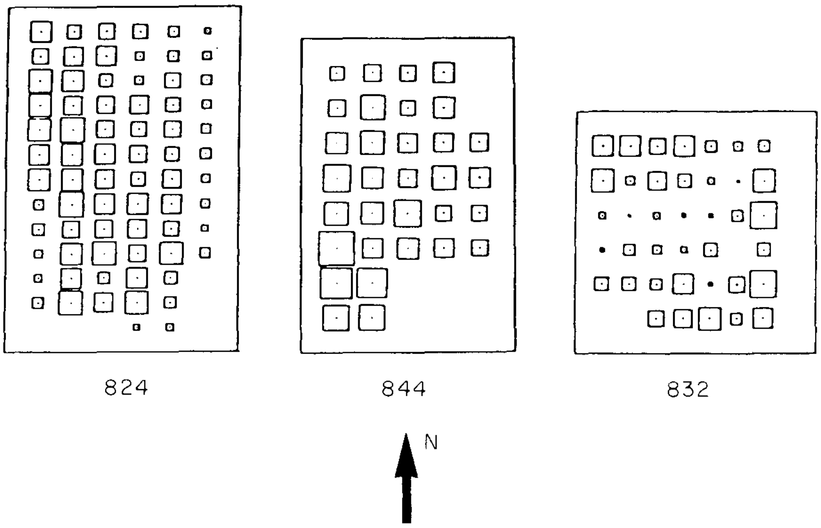

FIG. 3. Maps of plots 824 (1981–82), 832 (1982–83), and 844 (1983–84). Square sizes are proportional to the number of adults of *P. chrysocephala* captured at each sampling point in box traps.

(i) the winter-rape plant,
(ii) the rape plot,
(iii) and the area of rape cultivation.

Between-plants variation in the number of larvae

Values of the index of true aggregation for each plot are shown in Table 2. For the seven plots of 1981–82, these values are almost always highly significant, hence denoting a high degree of true aggregation in the distribution of numbers of larvae within two neighbouring plants.

In 1981–82, no decrease in aggregation intensity was observed during larval development. This difference may be explained by less infestation in 1981–82: *c.* 1 first instar larva per plant (mean value for all plots), compared with >2 later.

Within-plots spatial and spatio–temporal variability of insect numbers

Three kinds of spatio–temporal structures were studied within plots:

(a) static spatial structures, obtained by summing the numbers of insects captured at each sampling point during crop invasion.

(b) spatio–temporal interactions, observed by comparing the successive systematic maps giving the number of captures from plot invasion until the emergence of the new generation of insects,

(c) variation of spatial structures during the life history of the insects.

Static spatial structures

Figure 3 shows the maps of three plots, one chosen in each year, where spatial structures can easily be seen. The presence of gradients, in plots 824 and 844, or of over-infested areas, in plot 832, can be explained by the proximity of sites from which insects

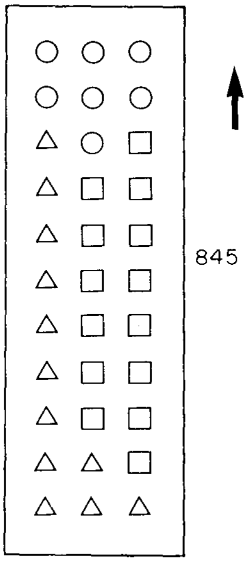

FIG. 4. Map of plot 845; the three zones detected by CA are represented by the following symbols: zone A (△), zone B (○), zone C (□).

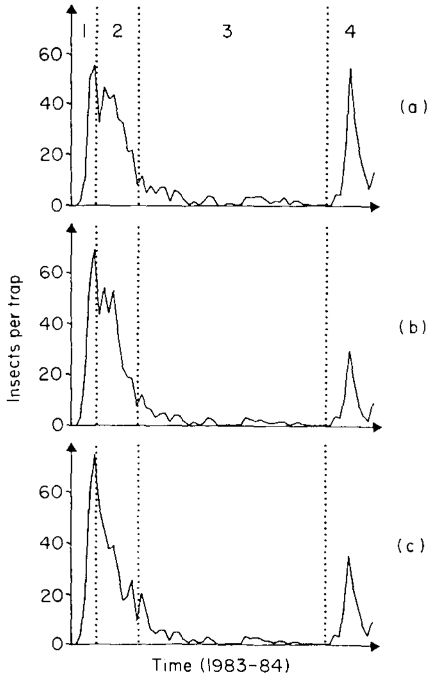

FIG. 5. Curves of mean numbers of adults of *P. chrysocephala* captured in plot 845. The three curves correspond to the three zones defined in Fig. 4. The four periods are delimited as follows: period 1, six dates from 12 September to 29 September 1983; period 2, eight dates from 30 September to 27 October 1983; period 3, forty-one dates from 28 October 1983 to 4 June 1984, period 4, nine dates from 5 June to 11 July 1984.

TABLE 3. Numbers of adults of *P. chrysocephala* captured in the water-traps of plot 845. Periods and areas are defined in the text and in Figs 4 and 5. The numbers correspond to the sum of captures for all the points within each area, during each period

	Areas		
Periods	A	B	C
1	152	218	265
2	249	232	194
3	101	67	97
4	167	61	112

originate (sprouts of last year, aestivation places, temporary shelters during dispersion). Gradients may also result from oriented invasion flights (W–E in plot 824 in 1981–82, Thioulouse, Debouzie & Ballanger 1984).

Spatio–temporal interactions

Among the sixteen plots studied since 1981, plot 845 was chosen to show how the evolution of the spatial distribution of insects can be described by correspondence analysis. Data are organized in a table: the columns represent the thirty-three sampling points and the lines correspond to the sixty-four dates of water-trap collections, from 12 September 1983 to 11 July 1984.

The first four factors of the CA defined three homogeneous zones (Fig. 4) and four periods (Fig. 5).

The first period (12–29 September 1983) corresponded to the arrival of insects in the crops. The number of catches per trap (26 September) was highest in zone C (ninety-three insects per trap) and lowest in zone A (fifty-five insects per trap), showing that insects did not invade the plot uniformly.

During the second period (30 September to 27 October 1983), adults were still not dispersed uniformly, but fewer were caught in zone C (thirty-four adults per trap on 10 October) than in zone B (fifty adults per trap on 10 October). On average, the number of insects captured decreased during this period, because of a temperature decrease and natural mortality.

The third period corresponded to winter and spring (28 October 1983 to 7 June 1984); few adults were captured except in zone C on 2 and 7 November.

The fourth period was the emergence phase of the new generation (8 June to 11 July). More insects were caught in zone A (fifty-four insects per trap on 18 June) than in zones C (thirty-four inects per trap) and B (twenty-one insects per trap). The zone with the highest emergence (A) was that with the lowest invasion; no correlation between invasion and emergence rates was found for the other zones.

Table 3 summarizes the numbers of adult insects captured for each period and zone.

In other plots, similar results were found. For example, in plot 822, two areas of insect arrival during crop invasion were detected; one in the north of the plot, *c.* 300–500 m^2, the other in the south, *c.* 1000 m^2. In plot 834, variations in spatial structures were found between crop invasion (4 October 1982) and spring resumption of activity (11 April 1983). These variations were attributed either to differential survival rates within the plot, or to movements of adults. For now, it is impossible to distinguish between these two interpretations.

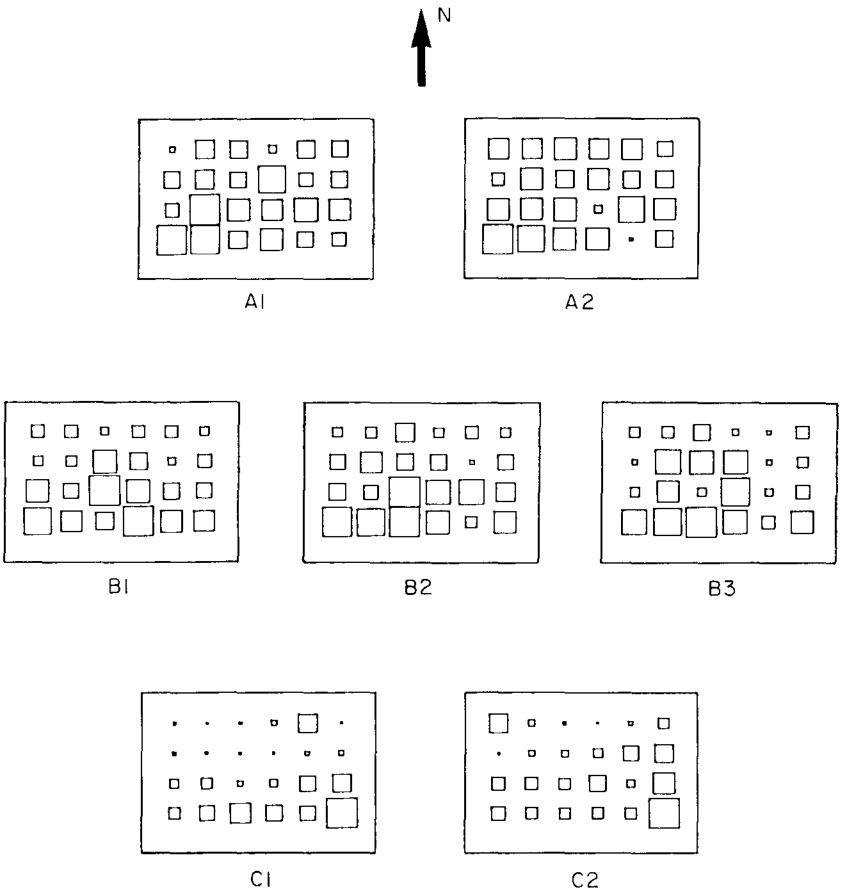

FIG. 6. Spatial structures in plot 843 (1983–84). Square sizes are proportional to: A1: number of adults of *P. chrysocephala* captured in boxes set out in autumn (27 September to 25 October 1983). A2: number of adults of *P. chrysocephala* captured in water-traps from 12 to 16 September 1983. B1-B2-B3: number of larvae of first, second and third instars per plant (sum from 17 October 1983 to 28 May 1984). C1: number of adults of the new generation captured in boxes during emergence (from 28 May to 11 July 1984). C2: number of adults of the new generation captured in water-traps during emergence (from 29 May to 11 July 1984).

Variation in spatial structures during the life history of the insect

Spatial structures detected for the various developmental stages of *P. chrysocephala* were compared.

In plot 843 (Fig. 6) a N–S gradient observed during invasion was still present for the three larval instars, and was also detected during emergence. But in plot 844, the gradient (Fig. 3) was not found again in larval infestation, or during emergence (Fig. 7).

If spatial structure set up during crop invasion are strongly marked, they can persist until emergence of the new generation. But spatial heterogeneity may be due to other factors, such as interactions between *P. chrysocephala* and rape, or variation in the surroundings of the plot, creating differences in the micro-environment.

Between-plots variability

Several parameters of the cabbage stem flea beetle dynamics varied greatly from one

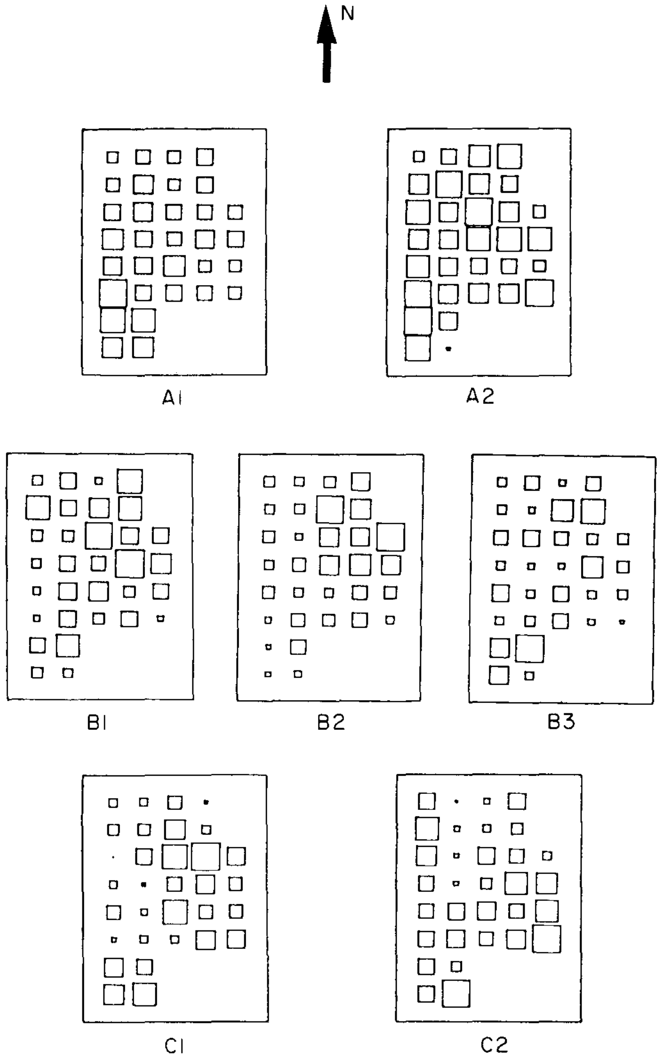

FIG. 7. Spatial structures in plot 844 (1983–84). See legend of Fig. 6.

plot to another for each year. For example, in 1983–84 (Table 4), infestation varied from 8 to 18 insects per m^2; winter survival of adults, calculated from October 1983 to April 1984, varied from 12 to 27%; 10–50% of the third instar larvae survived to the adult stage; emergence varied from 33 to 131 insects per m^2, and the multiplication ratio, calculated between two successive generations, from 4 to 12.

A qualitative model describing the invasion of the rape plots is proposed. It is based on the date of appearance of the first stems of rape in the plots, and on the position of plots within the area of rape cultivation.

The date of appearance of stems interacts with the date of dispersal of insects: the earliest plots will be more infested, even if differences are only 1–2 days. For example, in 1981–82, a delay of 2 days in rape shoot emergence corresponded to a decrease in infestation of 50% (Thioulouse, Debouzie & Ballanger 1984).

TABLE 4. Between-plot variation of several parameters of the population dynamics of *P. chrysocephala* in 1983–84. Infestation and emergence are calculated from box results in September (infestation) and June (emergence)

Plots	841	842	843	844	845
Infestation (adults m^{-2})	9	8	15	11	18
Winter survival of adults (%)	16	27	18	18	12
Larval/adult survival (%)	10	30	20	50	30
Emergence (adults m^{-2})	33	62	102	131	72
Multiplication ratio	4	8	7	12	4

The position of the plot, in relation to the position of plots of the previous year, of aestivation places, or of temporary shelters during dispersal, was also important in the determination of infestation. For example, in 1983–84, the most infested plots were plots 843 and 845: fifteen and eighteen insects per m^2, respectively. They were near former rape plots of 1982–83, and rape growth was early: 1–2 days before other plots. Early growth was also observed in plot 841, but remoteness of this plot in the west of the area resulted in much less infestation (nine insects per m^2). Plots 842 and 844 were in the centre of the site, near former plots 832 and 833, but rape was 1 or 2 days late in these fields; hence they were only moderately infested (eight and eleven insects per m^2, respectively).

In spite of its simplicity, this model allows us to explain the main between-plots variation in infestation in the autumn.

DISCUSSION

Knowledge of spatio–temporal heterogeneity among natural populations of insects is of interest at two levels: (a) in population biology, because it makes it easier to understand how populations are organized and regulated; (b) from a methodological point of view, it offers possibilities for reliable sampling designs, giving accurate estimates of the population parameters.

However, the number of insects captured in one water-trap (or even in one box) cannot be representative of the number of insects in a plot, and this is also true for the number of larvae present in one plant. The spatial structures, either at the sampling point scale, or at the plot scale, require several sampling points to be spread out over the plot. The number of insects present on one plot cannot be representative of the number of insects present in a cultivated area: the infestation may vary from one to fivefold, depending on sowing date, or plot position and surroundings.

Systematic sampling within the plots, and survey of at least several plots is thus necessary to obtain good estimates of the real insect numbers. As far back as 1953, Cochran (1953) remarked that systematic sampling is both easier to set up in the field and more precise than simple random sampling, or even than stratified sampling in most cases. While, at that time, the analysis of data collected according to a systematic design lacked statistical analysis methods, now many well-adapted statistical tests are available (Chessel 1978, and for practical examples, Chessel *et al.* 1984, Chessel & Gautier 1984, Debouzie & Thioulouse 1986, Thioulouse 1985). Moreover, the theory of regionalized variables (Matheron 1965, 1970) allows one to calculate the accuracy of the estimates; two examples in the one-dimension case are given by Thioulouse, Mathy & Ploye (1985) in the field of stereology, and Thioulouse, Houllier & Onillon (1985) for insect counting (application to the sampling methodology of *Trialeurodes vaporariorum*). For plot 832, the accuracy of the estimation of the total number of insects obtained from box results is about 8% (coefficient of variation), but other experiments are needed to confirm this value and compare it with those obtained under other conditions.

The problem of reducing the sampling intensity must be approached according to the objectives of the study; to find spatial structures within a plot, i.e. to find invasion mechanisms (flight direction, sources of insects) or spatio–temporal interactions, a minimum of twenty sampling points per ha seems necessary. In order to calculate the total number of insects per plot (for a population dynamics study), the sampling intensity may vary greatly according to the desired accuracy of estimates. In our case, twenty-five points per ha gave sufficient accuracy.

Concerning the area of rape cultivation, one may ask to what extent the results obtained in St Thomas-En-Royans may be extrapolated to other situations. The geographical isolation of the site, though convenient for our objectives, hardly allows generalizations. However, in similar conditions, sampling techniques should take into account the spatial organization of plot infestation, by defining central and peripheral plots in the area. The date of appearance of young rape plants should also be considered, since we know that early plots will be invaded before the others. The survey then should give priority to plots with early rape, and to each kind of plot (central or peripheral).

The spatial and spatio–temporal structures found in the distribution of *P. chrysocephala* suggest that each of the three scales of heterogeneity has a biological meaning. The rape plant constitutes a significant unit for larval instars. Two facts may explain the high level of true aggregation observed between two adjacent plants: (i) the egg-laying behaviour of females: eggs are laid in batches (two to sixteen eggs per batch, Bonnemaison & Jourdheuil 1954); (ii) the attractiveness of rape plants for young larvae (Queinnec 1967).

Larvae from the same batch will make their way towards the nearest plant, and an adjacent plant may contain only a few larvae. Moreover, a density-dependent regulation appears at this level. The mechanism of this regulation may be either greater mortality of larvae in over-infested plants, or dispersal towards surrounding plants. The mortality seems to be important mainly during egg incubation, and remains low for larval instars. However, a quantitatively low mortality, but acting only on larvae present in over-infested plants, could be sufficient to explain the variation of true aggregation. The dispersal of larvae during host-plant senescence was observed by Bonnemaison & Jourdheuil (1954), and may take place even in healthy plants if the infestation is high. Xu (1985) showed that the decrease in aggregation during larval development of whiteflies (*Trialeurodes vaporariorum*) could result from mortality and dispersal, both being density-dependent.

The rape plot is also a meaningful unit, in that most of the life history of the insects occurs in the same plot, and that, after invasion, adults remain in the same plot. Nevertheless, the spatial structures in the within-plot distribution of insects show that this unit is not uniform in relation to insect behaviour or life conditions. These structures may be explained by several factors: (a) non-homogeneity of plot infestation during crop invasion, due to the proximity of shelters for insects, (b) interactions with rape quality or density of stems, (c) differential survival rates, or insect movements within the plots.

The area of rape cultivation in St Thomas-En-Royans represents the lowest organizational level where one population of *P. chrysocephala* may be defined. This level is also spatially and temporally structured, by the positions of plots and aestivation shelters within the area. The crop invasion model helps to explain the between-plots variation in infestation, and will be quantified and developed in the next year of study.

The study of spatial heterogeneity is a good way of assessing the nature of factors influencing the dynamics of populations on several scales. As pointed out by Hutchinson (1953) and recalled by Taylor (1984), this interpretation of spatial structures has to be based on experimental evidence, and not on theoretical arguments: the same factor may be of primary importance on one scale, and meaningless on another. For example, competition for food may be a limiting factor for larval development of *P. chrysocephala* at the scale of one plant, but certainly not at the plot scale. Addicott (1978) and Coulson (1979) gave other examples of variation of the factors to be taken into account according to the scale of study. Chessel *et al* (1984) showed that three scales of spatial heterogeneity in the distribution of the cockchafer larvae (*Melolontha melolontha* L.) could be explained by behavioural or environmental factors relating to each scale.

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