Neth. J. Pl. Path. 97 (1991) 355-368

The spatial structure of spontaneous epidemics of different diseases in a groundnut plot

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Acepted 20 August 1991

Abstract

Spontaneous epidemics of rust, early leaf spot, late leaf spot, and *Rhizoctonia* blight simultaneously developed in a groundnut plot. Geostatistical techniques were used to describe and compare the spatial patterns of epidemics. *Rhizoctonia* blight exhibited a strong aggregative structure, contrasting with leaf spots and rust. The latter disease developed a general epidemic, in combination with local intensification. A strong negative interaction between rust and early leaf spot, and a close correspondence between rust intensification and *Rhizoctonia* blight development were indicated.

Additional keywords: semivariogram, correspondence analysis, disease intensification, disease extensification, *Cercosporidium personatum* (*Phaeoisariopsis personata*), *Cercospora arachidicola, Puccinia arachidis, Rhizoctonia solani.*

Introduction

The analysis of spatial characteristics of an epidemic can be undertaken along several directions, including doublet analysis (Van der Plank, 1946), analysis of runs (Madden et al., 1982), analysis of frequency distributions (Nicot et al., 1984), and analysis of quadrats (Shew et al., 1984; Schuh et al., 1986). These techniques were reviewed and compared by Nicot et al. (1984), and Campbell and Noe (1985).

This paper is a case-study on a single groundnut plot where four different disease epidemics developed. Its objective is to provide a pictorial description of the spatial patterns of these epidemics, and forward hypotheses on their possible interactions.

Material and methods

Plot

The plot under study was a 12 × 12 m square sown with an erect, short cycle, local groundnut cultivar. It was established at the ORSTOM Research Station, Adiopodoumé, Southern Ivory Coast. Sowing (March 3rd, 1988; $t = 0$) and replacements (shortly after emergence) were made in order to obtain a density of 6.25 plants/m^2, with equal distance between rows and plants in the row (0.4 m). Owing to the period of sowing (end of the dry season), overhead irrigation was applied weekly to the plot during the first 40 days after sowing. As usually practiced in farmers' fields, the plot was regularly hand-weeded. No pesticide was applied to the plot.

Sampling procedures

Four fungal diseases spontaneously developed in the plot, rust (*Puccinia arachidis* Speg.), *Rhizoctonia* blight (*Rhizoctonia solani* Kühn), late leaf spot (*Cercosporidium personatum* (Berk. & Curt.) Deighton), and early leaf spot (*Cercospora arachidicola* Hori).

Assessments of foliar diseases (rust and leaf spots) were made on one plant out of two in each row, the position of observed plants alternating in successive rows, totalling a population of 481 observed plants. Assessments were made at t = 30, 45, 60, 75, and 90. Severities were assessed on the fifth leaf (counted from top) of each main stem of each sampled plant using diagrammatic scales. The scale for rust included 7 classes (with centre of classes: 0, 1.2, 5.1, 13.7, 29.3, 58.6, and 86.6%; Savary, 1987a), and the scale for leaf spots 6 classes (with centre of classes: 0, 1, 5, 20, 50, and 84%; Blizoua-Bi, Lannou and Savary, unpublished). Only on the last assessment date (t = 90) were early leaf spot and late leaf spot assessed separately.

Incidence of *Rhizoctonia* blight was assessed at t = 80 and t = 90. Each plant of the plot was rated healthy (rb0) or diseased (rb1). The plants were further grouped into 225 adjacent quadrats of 4 individuals, each quadrat being represented by the frequence (0 to 4) of diseased plants. Intensities of the diseases (severities of individual plant for rust and leaf spots and *Rhizoctonia* blight frequency per quadrat) were recorded on maps of the plot.

Data analysis

Geostatistical methods. Each of the intensities of the four diseases at a given time was considered as a regionalized variable, $F(x_i)$, its value being assumed to depend on the position x of the considered sampling point i (Matheron, 1963). Assuming that the difference in F-value only depends on the distance h between two points, the semivariance G(h) is a measure of spatial variability (Lecoustre and de Reffye, 1986; Chellemi et al., 1988; Lecoustre et al., 1989). It can be calculated for a given distance as:

$$G(h) = [1/(2\,N_h)] * \{\Sigma\,[F(x_i + h) - F(x_i)]^2\}$$

where N_h is the number of pairs. In practice, the points considered were plants or quadrats, and a step of 0.8 m along and across rows was used. Results of calculations within a range of 6.8 m only are presented, in order to avoid edge effects. The mean of squares of deviates, G(h), can be plotted against h. The resulting semi-variogram can exhibit a variety of shapes (Lecoustre and de Reffye, 1986; Gascuel-Odoux, 1987; Chellemi et al., 1988), among which a horizontal line, which indicates a purely random pattern or a more or less regular increase of G(h) with h up to a threshold value of h, which indicates a maximum distance (range, Chellemi et al., 1988) beyond which there is no significant correlation between values of F. A 'nugget effect' is a sudden increase of G(h), representing a change in spatial pattern of F at a given scale, indicated by h. Such a discontinuity frequently occurs at the first step in h increase.

Kriging (Matheron, 1963; Lecoustre and de Reffye, 1986) is a technique for estimating F on all x positions, on the basis of the observation data and the correlation structure between sample points at different distances, as characterized by the semivariance function $G(h)$. It produces an unbiased estimate of F in any x position on the basis of $G(h)$. The estimate is given by:

$$F(x) = \Sigma L_j F(x_j),$$

where L_j is the weighting coefficient corresponding to the sampling points j. The number j of sample points needed, and the corresponding weights L_j are calculated using the shape of the semi-variogram in order to minimize the expected variance of $F(x)$, and have: $\Sigma L_j = 1$.

For the purpose of this case-study, attention was focused on the shape of, and on comparisons between semi-variograms pertaining to each date or particular disease. Kriging was primarily used as a mapping technique, i.e. to draw contour plots, rather than an estimation procedure.

Correspondence analyses. Correspondence analysis (Benzécri, 1973) is a multivariate method for graphically presenting the essential information contained in complex contingency tables. The technique was first developed and described by Benzécri (1973). An introduction is given by de Lagarde (1983). An English reference is Greenacer (1984). First the contingency table is built. We used the observation data on rust and on early and late leaf spot of day 90. Three tables were built:
- rust severity (7 classes as defined before and denoted as r0 – r6) × early leaf spot severity (a0 – a5): [r × a],
- rust severity × late leaf spot severity (p0 – p5): [r × p], and
- early leaf spot severity × late leaf spot severity: [a × p].

Next the multivariate calculations implied in correspondence analysis are performed (Benzécri, 1973; de Lagarde, 1983). This analysis results in axes along which the data points (entries of the contingency table) are grouped. The interpretation of these axes is complex as they involve all classes considered in the contingency table. The correspondence between different classified objects is indicated by the closeness of data points in the figure. As we are dealing with successive severity levels, closeness is indicated by the closeness of trajectories of data points. Parallel move along two paths indicates correspondence, whereas orthogonality indicates independence (Lebart and Fénelon, 1975; de Lagarde, 1983; Savary, 1987a, 1987b). As there were only two possible classes for *Rhizoctonia* blight, this disease was not considered for correspondence analysis. Chi-square tests were made to test for independence of *Rhizoctonia* blight with rust, early leaf spot, and late leaf spot.

Results

Initial disease intensities

On the first assessment ($t = 30$) the plot had the expected total number of plants, 961, and the canopy was uniform. Out of the 481 assessed plants, 8 (1.7%) had rust lesions, vs. 57 (11.9%) with leaf spots. The patterns of these first spontaneous infections are shown in Figure 1 (Fig. 1A, R30 and Fig. 1B, S30). The corresponding semivariograms (Fig. 2A, R30 and Fig. 2B, S30) are flat with high $G(h)$ values at low h values and indicate a random pattern.

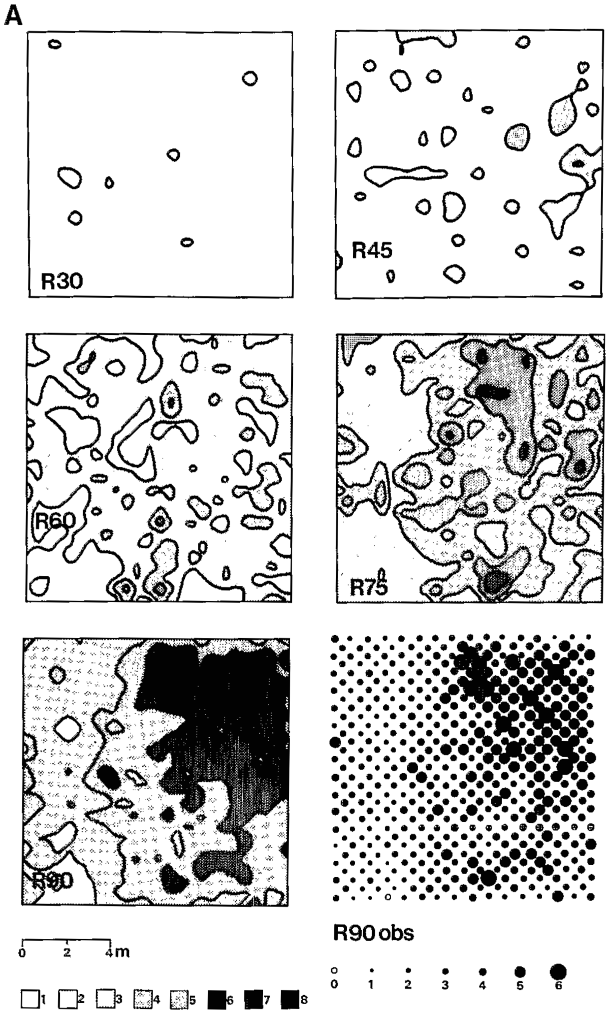


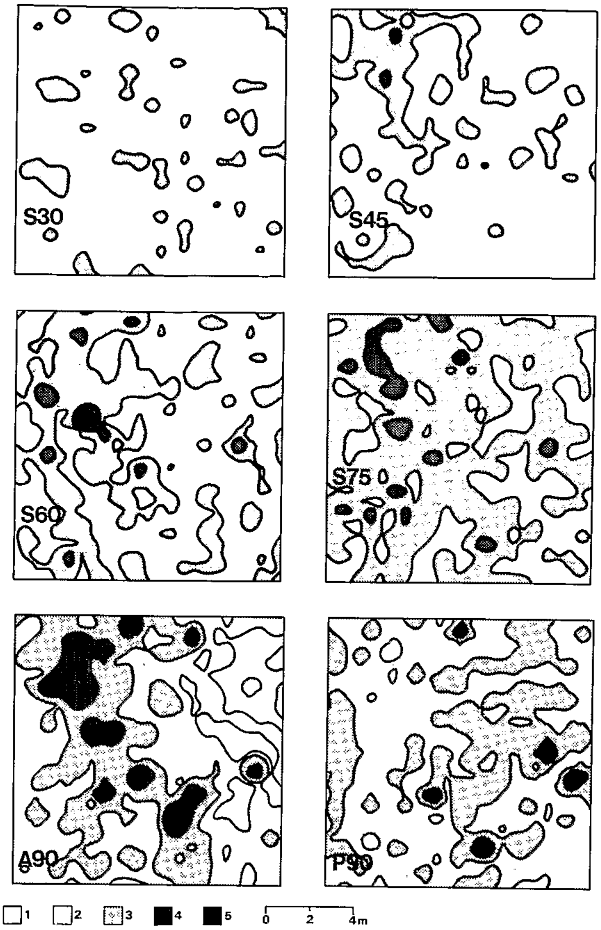
Fig. 1. Maps for rust, late leaf spot, early leaf spot and *Rhizoctonia* blight intensities in one groundnut plot.

Fig. 1A. Rust severity. Maps are derived from observation of 481 plants. Entries (R30, R45, R60, R75, R90) indicate the assessment date, in days after sowing. The northern direction corresponds to the top of the maps. Isopaths and severities between isopaths (1 to 8) are indicated: 1: 0-0.5%; 2: 0.5-2.5%; 3: 2.5-7%; 4: 7-20%; 5: 20-45%; 6: 45-60%; 7: 60-90%; 8: 90-100%.

Two maps for $t = 90$ are given, from automatic mapping (R90, left) and actual observations (R90 obs, right). For R90 obs, rust severity classes (0 to 6, see text) are indicated by dots of increasing size.

Fig. 1B. Severities of leaf spots. Maps are derived from observation of 481 plants. Cumulative severities are given from day 30 (S30) to day 75 (S75) after sowing. Early leaf spot (A90) and late leaf spot (P90) are mapped for day 90. Isopaths and severities between isopaths (1 to 5) are indicated: 1: 0-0.4%; 2: 0.4-2.0%; 3: 2.0-6.0%; 4: 6.0-15%; 5: 15-100%.

B



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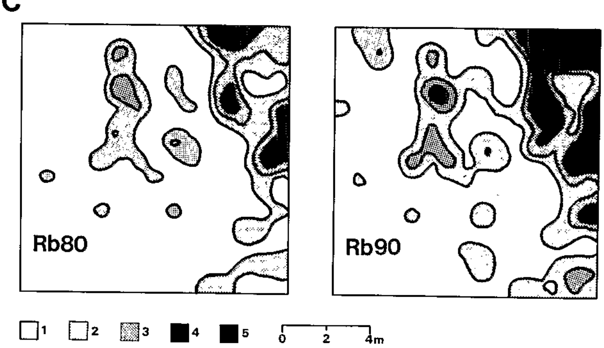


Fig. 1C. Intensity of *Rhizoctonia* blight. Maps are derived from automatic mapping on a sample of 225 quadrats of four individual plants 80 days (Rb80) and 90 days (Rb90) after sowing. Intensity is expressed as frequency of infected plants per quadrats. Isopaths and intensities between isopaths are indicated: 1: no infected plant; 2: one; 3: two; 4: three; 5: four plants infected per quadrat.

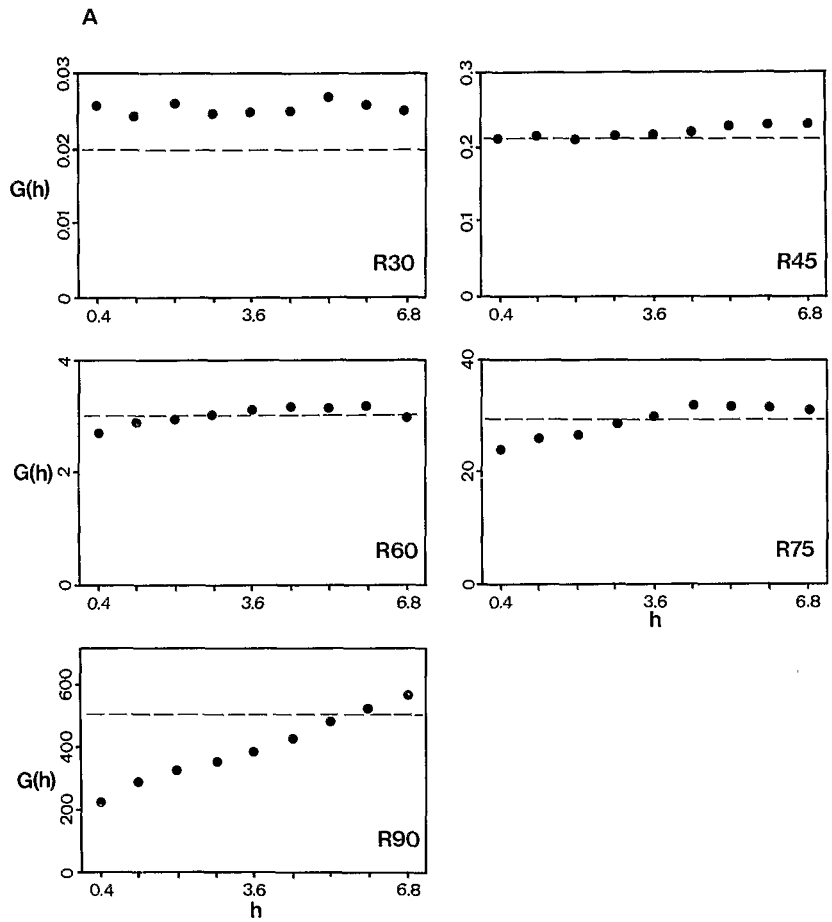
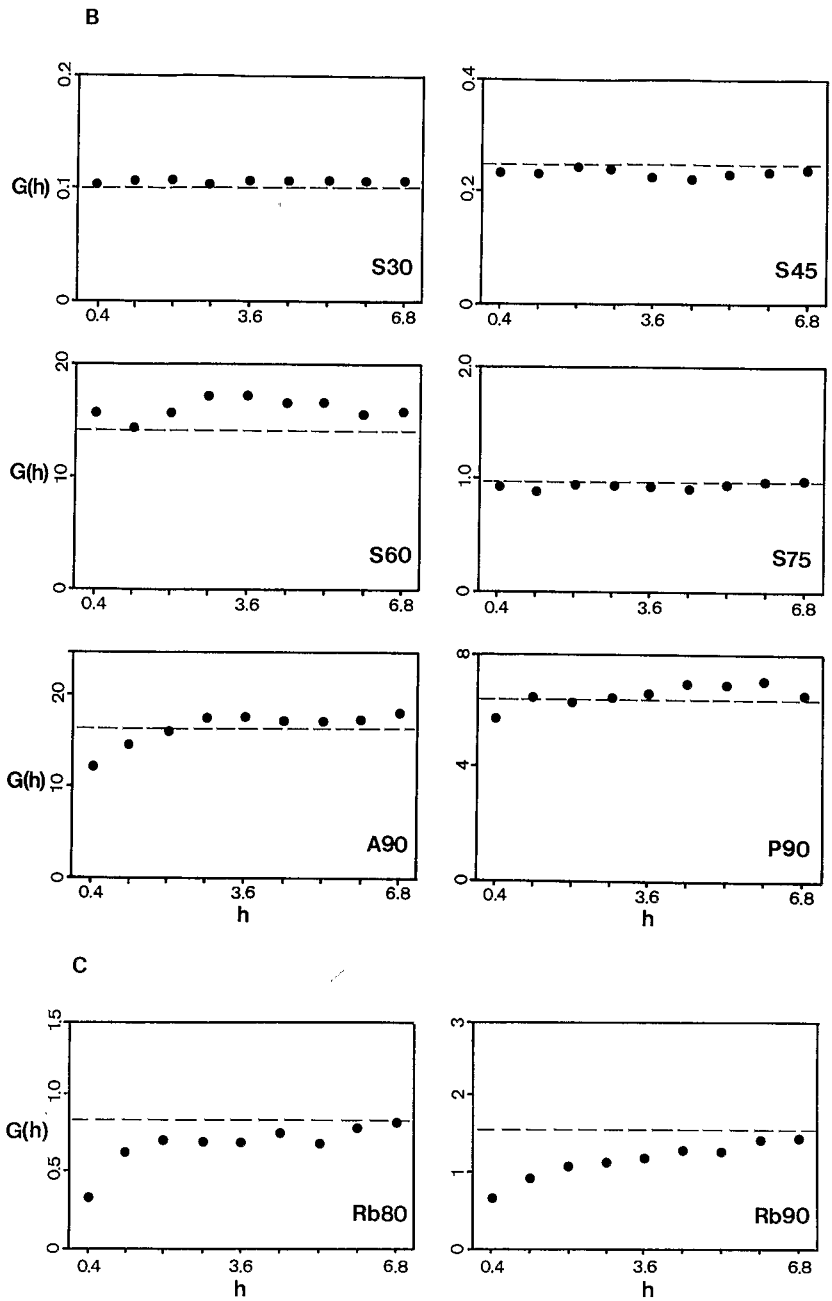


Fig. 2. Semivariograms for rust, late leaf spot, early leaf spot and *Rhizoctonia* blight in one groundnut plot. Abscissa (h) is distance in m between two sampled plants. Ordinate is the (half) mean square of deviates (G(h), see text). Note that the units used for the ordinates differ from one graph to another. The variance of the sample (481 plants) is indicated by a dotted line. It provides a reference for comparison of amplitude of semivariances.

Fig. 2A. Semivariograms for rust severity. Entries (R30, R45, R60, R75, R90) indicate the assessment date, in days after sowing.

Fig. 2B. Semivariograms for severities of leaf spots. Entries indicate assessment dates. The data used are accumulated severities of early leaf spot and late leaf spot from day 30 (S30) to day 75 (S75). On day 90, severities of early (A90) and late (P90) leaf spot are analysed separately.

Fig. 2C. Semivariograms for intensity (disease frequency per quadrat) of *Rhizoctonia* blight. Semivariograms are derived from a sample of 225 quadrats of four individual plants 80 days (Rb80) and 90 days Rb90) after sowing.



Rust epidemic

The development of the rust epidemic in space can be followed in the maps of Figure 1A (R30 to R90). Automatic mapping by kriging provides appropriate representations of the actual field situations, as exemplified by the comparison of maps R90 and

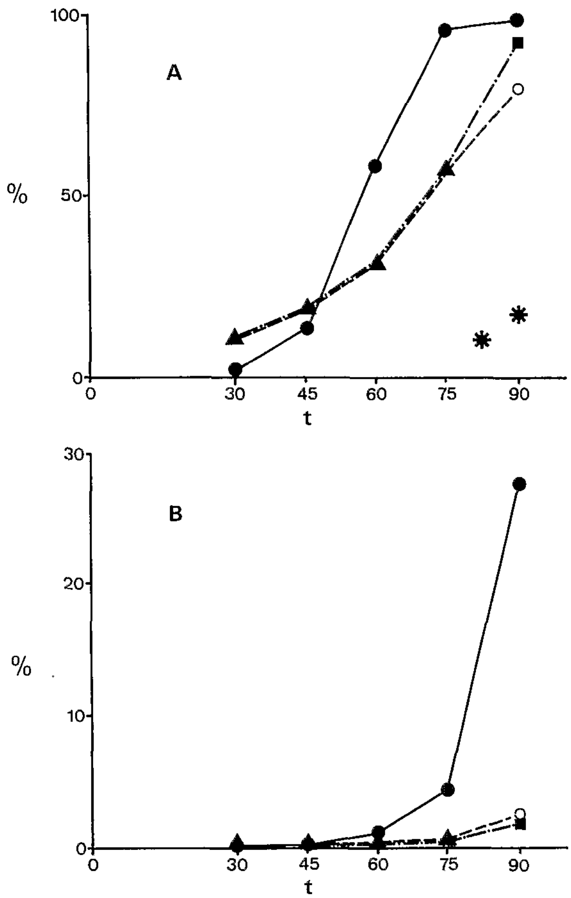


Fig. 3. Variation of incidences and severities of four groundnut diseases with time in one plot. Time (horizontal axis) is expressed in days after sowing. A) variation of disease incidences (%) with time (t); B) variation of disease severities (%) with time (t).

Each point represents observations made on 481 plants (rust and leaf spots) or 961 plants (*Rhizoctonia* blight). ● : rust; ▲: leaf spots (cumulative); ○ : early leaf spot; ■ : late leaf spot; *: *Rhizoctonia* blight.

R90-obs, where the pattern of the actual rust severity is shown. Figure 1A suggests the appearance of foci at t = 60, which further intensify and merge (t = 75) simultaneously with the increase in overall incidence and severity (Fig. 3A and 3B). At t = 90 (Fig. 1A, R90), an aggregative structure is indicated, with increasingly high rust severity in an east – north east direction. This description is consistent with the change in shape of the semivariograms, where a slight increase in mean square of deviates is apparent at t = 75 (Fig. 2A, R75), and further amplifies (Fig. 2A, R90).

Leaf spot epidemics

Early and late leaf spot progress in time is slower than that of rust (Fig. 3A and 3B). Maps for accumulated early and late leaf spot severities at t = 30 and 45 indicate a random pattern (Fig. 1B, S30 and S45), as do the corresponding semivariograms (Fig. 2B). Further spatial development (t = 60 and t = 75) suggests the appearance of an aggregated pattern, with foci appearing in several locations in the plot (Fig. 1B, S60 and S75). When the two diseases are considered separately (at t = 90, Fig. 1B, A90 and P90) a clear spatial pattern emerges: high early leaf spot severities are primarily concentrated in the western part of the plot, whereas late leaf spot is more randomly scattered over the area of study with, possibly, few small foci arising. The respective semivariograms are in agreement with this description, showing a regular increase in mean square of deviate with distance up to 4 m for early leaf spot (Fig. 2B, A90), and suggesting a slight increase for late leaf spot (Fig. 2B, P90).

Rhizoctonia blight epidemic

The *Rhizoctonia* blight epidemic develops at the end of the cropping season, with incidences of 10.2 and 17.4% at t = 80 and t = 90, respectively (Fig. 3A). The maps (Fig. 1C, Rb80 and Rb90) indicate an aggregated pattern, with conspicuous foci arising in the north-east part of the plot at t = 80. These foci quickly expand and merge (t = 90). This pattern is consistent with the shapes of semivariograms (Fig. 2C, Rb80 and Rb90), which show a clear increase in mean square of deviate with distance h.

Comparison of spatial patterns

Rust rapidly expands from a few, scattered infected plants to the whole plot, simultaneously with the appearance of areas with very high severities (Fig. 1). On the contrary, the development of leaf spots is initiated from numerous infections distributed all over the plot, and further expansion of the diseases is slower, with reduced local intensification. Comparison of maps is supported by comparison of incidence and severity progress curves (Fig. 3A and 3B). Fast increase in disease incidence corresponds to fast expansion in space, whereas fast increase in severity corresponds to rapid local intensification.

Comparison of maps at t = 90 shows that the area where rust intensifies most differs from the area where early leaf spot reaches noticeable severity; of the total number of plants observed, 7.7% only have simultaneous disease ratings equal or higher than 2 for early leaf spot and 4 for rust. Most of the area with high late leaf spot severity is superimposed on that of high rust severity. *Rhizoctonia* blight exclusively develops in areas of maximum rust severity. A chi-square test on the frequency distributions of low (r0 − r3) or high (r4 − r6) rust severity and absence (rb0) or presence (rb1) of *Rhizoctonia* blight indicates their non-independence (χ^2 = 17.6, P < 0.001).

Correspondence analyses

The results of correspondence analyses performed on contingency tables (Table 1) from the last assessment date (t = 90) are given in Figure 4. As each analysis involved only two diseases at a time, all three analyses resulted in very large fractions of total variance accounted for by the first two axes. Figure 4A ([r × p]; 99.6% of total variance accounted for by axes) shows the paths for increasing rust and late leaf spot severities. These two paths essentially run parallel along axis 1. Figure 4A therefore indicates an overall correspondence between increasing rust and late leaf spot severities. Maximum late leaf spot (p3) and rust (r6) do not, however correspond; this contrast

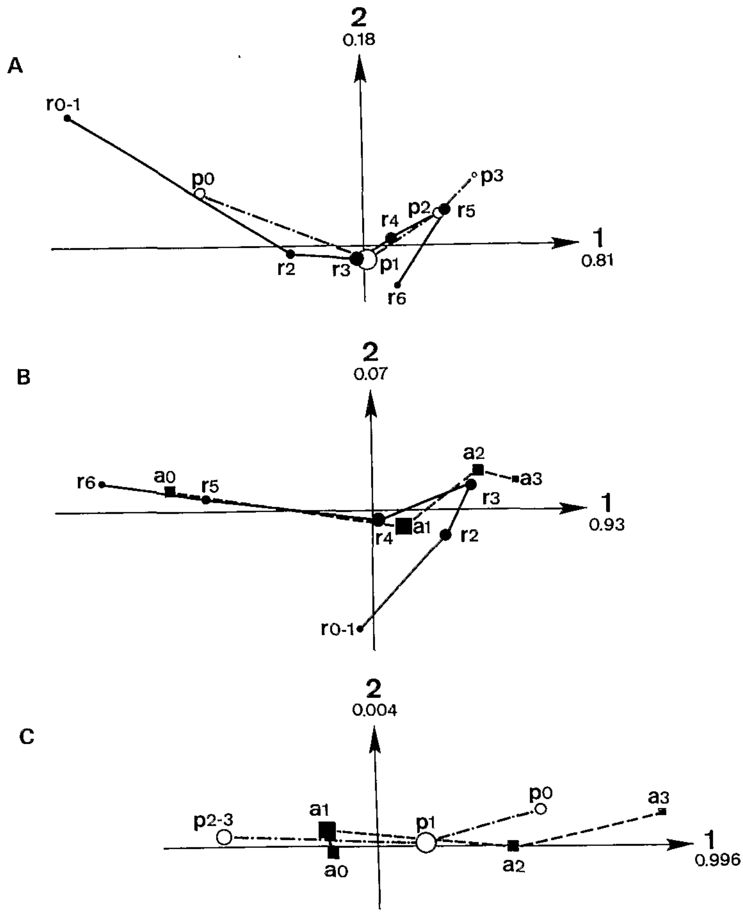


Fig. 4. Correspondence analyses among intensities of rust, early leaf spot, and late leaf spot in one groundnut plot, 90 days after sowing.

Classes for each disease are indicated by points and represent the centres of classes of diagrammatic scales (see text): rust: r0 to r6; early leaf spot: a0 to a3; late leaf spot: p0 to p6.

Size of dots is proportional to size (class filling, in number of individual plants) of classes. Classes with size smaller than 10 were grouped prior to analysis (e.g. r0-1). The paths representing increasing severity of each disease are drawn, and the proportion of variance accounted for by axes is indicated.

is accounted for by axis 2. Figures 4B and 4C ([r × a] and [a × p], respectively, almost 100% of total variance accounted for by axes in both cases) show that high early leaf spot severities are opposed to high rust (Fig. 4B) and high late leaf spot (Fig. 4C). Paths in Figure 4B however suggest that there is no opposition between initial increase in rust severity and variation of early leaf spot.

Table 1. Contingency tables built for the diseases severities observed at t = 90. Entries are plant numbers.

[r × p]		r0	r1	r2	r3	r4	r5	r6
	p0	1	3	10	13	6	1	0
	p1	0	3	46	135	81	52	12
	p2	0	0	5	35	32	38	3
	p3	0	0	0	1	2	2	0
[r × a]		r0	r1	r2	r3	r4	r5	r6
	a0	1	0	4	11	22	45	10
	a1	0	6	40	98	70	40	5
	a2	0	0	14	63	24	8	0
	a3	0	0	3	12	5	0	0
[a × p]		a0	a1	a2	a3			
	p0	5	15	11	3			
	p1	61	167	84	17			
	p2	25	75	13	0			
	p3	2	2	1	0			

Discussion

The analysis was conducted to pictorially document a case-study on a single, small groundnut plot, where four different epidemics simultaneously developed. Recent advances in the use of geostatistical methods in plant disease epidemiology mainly deal with soil-borne (Chellemi et al., 1988), or systemic vector-borne (Lecoustre and de Reffye, 1986, Lecoustre et al., 1989) diseases. Here, geostatistical techniques were applied to polycyclic foliar diseases.

Initial discontinuities in semivariograms ('nugget effect') can be due to errors in observations, or the fact that clustering occurs at a scale smaller than the step size (Gascuel-Odoux, 1987). We believe that initial discontinuities primarily relate to the discontinuity in the observations, the distance step (0.8 m) representing the maximum size of a single plant. Initial discontinuities are stronger in late and early leaf spot than in rust (Fig. 2), suggesting that disease progress at plant scale is more intense in leaf spots than in rust. This interpretation agrees with the greater predominance of allo-infection over autoinfection (Robinson, 1976) in rust than in leaf spots (Fig. 3A and 3B). The shapes of semivariograms for *Rhizoctonia* blight indicate an initial discontinuity, which accounts in part for intensification at the plant and quadrat level. In other words, the magnitude of the initial discontinuity may be considered to represent partly disease intensification at a microscale.

Shapes of semivariograms at larger distances are representative of disease progress at a short mesoscale (Zadoks and Schein, 1979), i.e. disease extensification (Zadoks and Kampmeijer, 1977; Zawolek, 1989). The semivariograms for rust and leaf spots are initially flat, and progressively show an increase with increasing distance. This indicates a progressive change from a random to a more (rust) or less (late leaf spot) aggregated pattern over time. The semivariograms for *Rhizoctonia* blight are typical of a focal pattern (Lecoustre and de Reffye, 1986), with mean squares of deviates approaching a threshold value within 2 to 4 m. This range (Chellemi et al., 1988) approximately represents the size of *Rhizoctonia* blight foci according to field observations and maps.

At the end of the cropping season, the maps (Fig. 1) indicate that the areas where the diseases are established are not independent. Interpretation of maps is supported by correspondence analyses (Fig. 4) and chi-square tests. They suggest that heavy rust infection favours *Rhizoctonia* blight establishment. On the other hand the relative patterns of foliar disease corresponds to the conclusion drawn from a 3-year survey of over 300 farmers' fields in Ivory Coast (Savary, 1987b), which indicated that high late leaf spot and rust severity seldom coincide with high early leaf spot severity.

The pattern of the *Rhizoctonia* blight epidemic suggests that it was shaped by an uneven dispersion of inoculum and influenced by the rust epidemic. Epidemics of leaf spots were probably initiated by randomly distributed inoculum in the plot, or nearby infected groundnuts. Their further progress was to a large extent due to short distance dispersal mechanisms. The rust epidemic, being caused by an obligate parasite must have been initiated by external sources; this is accounted for by its initially random pattern. Its further development combined a general epidemic (Zadoks, 1961) with local intensification, leading to an increase in severity accross the plot.

The case-study involves pathogens well-documented in terms of dispersal and spread characteristics (Porter et al., 1984; Savary et al., 1988). Some typical features of the spatial structure of epidemics (focal and general epidemics, intensification and extensification of disease; Zadoks, 1961; Zadoks and Kempmeijer, 1977; Zadoks and Schein, 1979; Zawolek, 1989) are re-described, using geostatistical methods (Matheron, 1963) as adapted to epidemiology (Lecoustre and de Reffye, 1986). Some hypotheses can be forwarded on the relationships between diseases, and analogies between patterns pertaining to a single plot and those representing a population of farmer's fields are indicated. Multivariate structural analysis (co-kriging; Lecoustre and de Reffye, 1986) might also provide valuable information when several population characteristics are considered in the same area. In the present study, correspondence analysis was used to link the various disease variables. Although lacking any explanatory value, geostatistical techniques provide useful tools for future epidemiological investigations.

Acknowledgements

This research was supported in part by a fellowship provided to the second author by the International Agricultural Centre, Wageningen, the Netherlands, and by a joint research project between INERA (Burkina-Faso), ORSTOM, the Wageningen Agricultural University, and IRHO funded by the E.E.C. (grant No TS2 0102-M-CD).

We are grateful to Prof. J.C. Zadoks, Dr H.J. Schouten, and Ir A.M. van Veen, Department of Phytopathology, Wageningen Agricultural University, the Netherlands, for useful comments on the manuscript. We acknowledge gratefully A. Dezetter, Laboratoire d'Hydrologie, ORSTOM, Ivory Coast, for assistance in data analysis, and G. van Santen, B.S.H.R., United Kingdom, and P. Blizoua-Bi, M.R.S., Ivory Coast for assistance in field work.

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