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Spatial patterns of spear rot in oil palm plantations in Surinam

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As the aetiology of spear rot of oil palm is unknown, indirect methods were applied to study its putative infectiousness by analysing data from commercial oil palm plantations in Surinam. Geostatistics and gradient analysis were used to examine the spatial variation of spear rot disease in 13 blocks at two plantations. In two blocks, which had low spear rot incidence initially, the variogram indicated that affected trees were not spatially related, suggesting that infection came from various distant sources. Later, the semivariances in one of these two blocks and in seven others, calculated for successive dates, showed a linear increase with distance. The variograms for four blocks showed a nonlinear increase in variance. Over the years, the variograms suggested that the variation in spear rot was anisotropic, with more spatial dependence in a westerly direction. Classical analysis of disease gradients over time confirmed that there was a preferential direction of disease spread. The data are compatible with the following hypotheses: (1) spear rot is an infectious disease; (2) the causal agent of spear rot is vector-borne, the vector being displaceable by wind; and (3) spear rot appears in two distinct phases, phase 1 being characterized by few randomly scattered trees, phase 2 by focal spread of disease starting from such scattered trees. The trigger of the change from phase 1 to phase 2 remains unknown.

Keywords: disease gradient, disease pattern, *Elaeis guineensis*, fatal yellowing, geostatistics, spatio-temporal dynamics

Introduction

Spear rot of oil palm (*Elaeis guineensis*) is a fatal disease of unknown aetiology (Van de Lande, 1986). The disease was recognized at the Victoria oil palm plantation (Fig. 1a) in Surinam around 1976. At Phedra (Fig. 1b), a plantation 30 kilometres north of Victoria, the first tree affected by spear rot was noticed in 1981. Palms with spear rot exhibit chlorosis in the youngest leaves, with one or more spears rotting. The continuous breaking of spears and leaves results in gradual deterioration, and finally in the death of the tree. Previous research involving isolations and application of Koch's postulates to leaves, both *in vitro* and *in vivo*, did not indicate involvement of pathogenic fungi or bacteria (Van de Lande, 1984; 1991). Effective means of control of spear rot are not yet available (Van de Lande, 1990). In 1982 a dramatic change occurred in the spatial arrangement of diseased trees, from isolated affected trees to a pattern of focal development of spear rot.

The increase in the number of trees affected or killed by spear rot with time can be described by the logistic model (Van de Lande, 1993a). Temporal studies of the progress of the disease help to characterize its development and might lead to statements regarding future disease levels. When yield reduction is taken into consideration, the spatial pattern of affected plants is often neglected (Hughes, 1990). The reduction in the proportion of productive trees per unit area affects yield dramatically when diseased or removed trees are arranged in groups where interplant compensation for yield loss becomes impossible (Zadoks & Schein, 1979; Walker, 1987; Hughes, 1988; Hughes *et al.*, 1989).

Disease gradients can provide clues about the mode of spread of the disease. A preferential direction, such as along rows, could indicate mechanical transmission through harvesting implements. Alternatively, a directional distribution associated with the prevalent wind might suggest airborne dispersal. Geostatistics (Journel & Huijbregts, 1978) provides a solution to two of the problems encountered in the field: missing trees (gaps) and irregular shapes of blocks. Geostatistics enables the spatial dependence between specific observation points to be measured by the *semivariance*. The semivariance is

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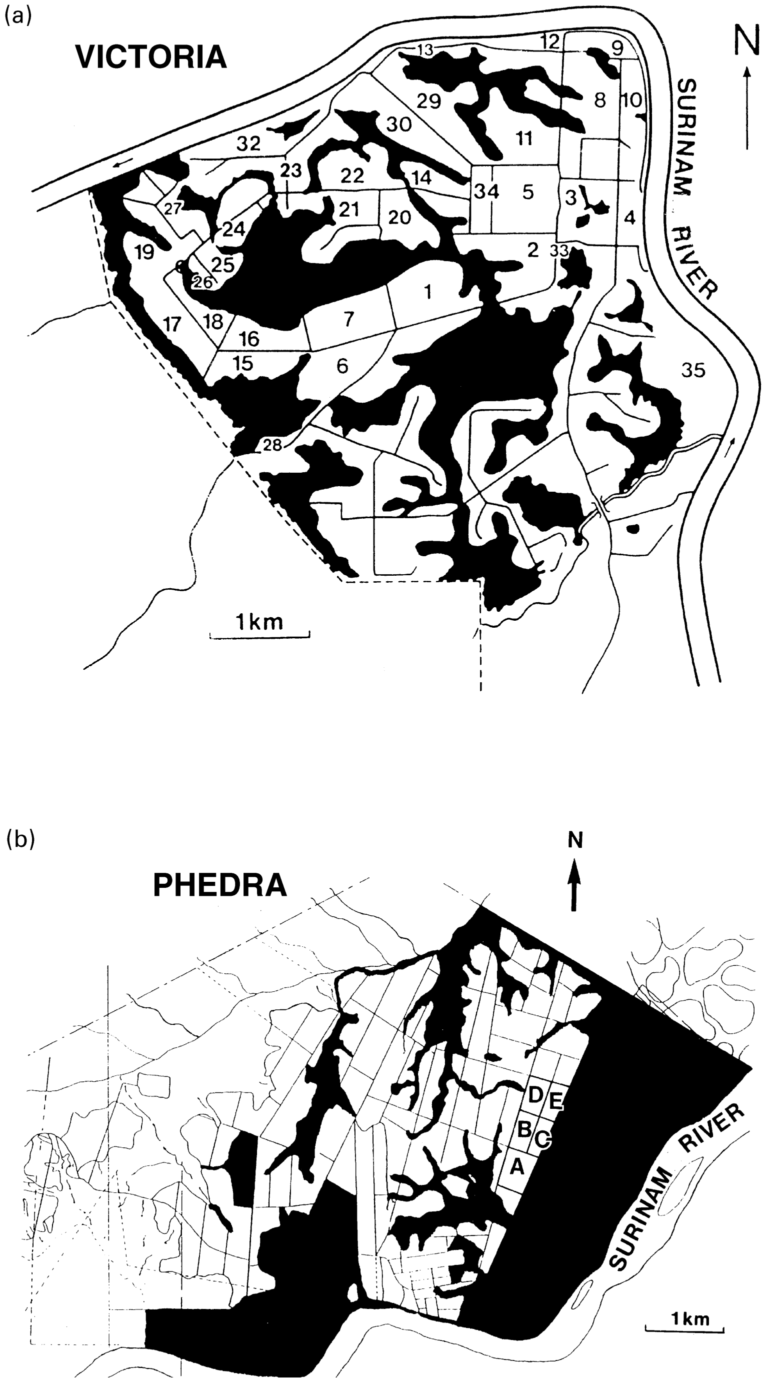

Figure 1 Location of blocks at the Victoria (a) and Phedra (b) plantations in Surinam. In black: forest, swamp area and gullies. Numbers indicate locations of blocks in north Victoria. Phedra blocks studied are indicated by capital letters (A = block 42A, B = block 46A, C = block 46B, D = block 46C and E = block 46D).

plotted against the distance separating observation points in the variogram function (Chellemi *et al.*, 1988; Lecoustre *et al.*, 1989; Stein *et al.*, 1994). A recent summary of geostatistics is found in Webster & Oliver (1990).

In this study, the spatial pattern of spear rot disease was examined over a period of up to four years, using geostatistics and gradient analysis (Zadoks & Schein, 1979) to gain insight into the behaviour of this disease of unknown aetiology.

Materials and methods

General setting

Two plantations in Surinam, Victoria and Phedra, were studied during a period of severe economic and political stress. The study focused on selected blocks within the plantations. A block or field is an agronomic and administrative unit within which all trees have the same genetic background and age. A block is bordered

Table 1 The geographic position of palm number one in the first row of the various blocks studied at Victoria and Phedra

Position[a]	Blocks
SW	3, 7, 46A, 46C
SE	5, 9, 16, 34
NE	6, 15
NW	42B, 46B, 46D

[a]Indicates starting point of harvest and pruning procedures.

by roads and surrounded by other blocks, or by primary or secondary forest. The size and form of the block were determined by the layout of the plantation and modified by the topography of the hilly and swampy terrain. Representative blocks were selected, of which the disease history was known over several years.

Sample locations

Spear rot data from blocks 3, 5, 6, 7, 9, 15, 16 and 34 of the Victoria plantation and from blocks 42B, 46A, 46B, 46C and 46D of the Phedra plantation were analysed. Most blocks in Victoria border primary or secondary forest, road or river verges, or swampy areas, on one or more sides (Fig. 1a). The blocks of interest at Phedra are in the east of the plantation (Fig. 1b). Three out of the five blocks border a strip of primary forest, over 1 kilometre wide, on their eastern side. The blocks studied at Victoria and Phedra differed in age and their year of planting varied from 1972 to 1981. Blocks varied in area from 10 to 45 hectares.

Planting material

The planting material in blocks 3, 5, 6, 7, 9, 15 and 16 was Deli-Dura, originating from crosses made in Surinam. The remaining blocks were planted with Harrison Crossfield material originating from Papua New Guinea. The palms were planted in a triangular design of either 9 × 9 (Victoria) or 8·5 × 8·5 m (Phedra). The rows were generally oriented perpendicular to the main road along the block side where the first palm in the first row was located. In blocks 3, 5, 9, 15, 16 and 34 the rows were oriented in a north–south direction (0°N), and in blocks 6 and 7 at about – 20°N. In the five Phedra blocks the rows were oriented at approximately – 70°N (Table 1).

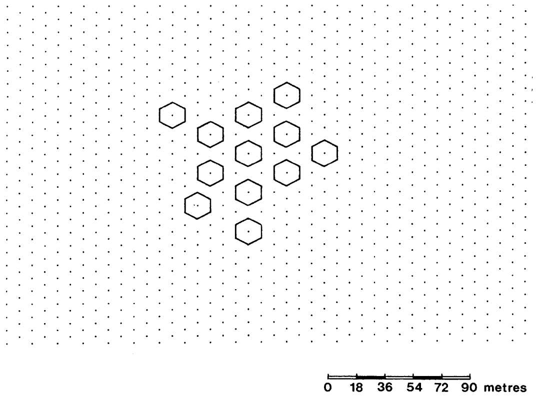

Figure 2 Grid of trees with hexagonal 'sample points' consisting of seven trees used in geostatistical studies at Victoria and Phedra, Surinam. Each point of the grid represents one palm tree. The distance between trees is 8·5 m (Phedra) or 9 m (Victoria).

Regular plantation operations

The symptoms of the disease are well documented (Van de Lande, 1986; Mariau *et al.*, 1992). Affected palms were detected and removed through phytosanitary rounds about once every two months. In general, harvesting and pruning were carried out every 2 weeks and 6 months, respectively, starting with the first palm in row number one and proceeding up and down along the consecutive rows. The direction in which the harvesters moved depended on their starting position (Table 1).

Sample units

Sample units comprised hexagons of six trees with one central tree. The seven trees per sample unit covered three rows (Fig. 2). Trees were scored as healthy (0) or diseased (1). Once a tree was designated diseased it remained thus, even when it had been cut down. Sample units were chosen on a regular grid, except when palms were lacking (gullies, unplanted area, palms missing for other reasons than spear rot). The sample units were spaced at 27 (Victoria) or 25·5 (Phedra) m distances, centre to centre, in a hexagonal pattern (Fig. 2). This separating distance enabled at least 75% of the trees per block to be included in the analyses.

Disease incidence per sample unit was defined as the proportion of diseased trees in the sample unit, running from 0 (all trees healthy) to 1 (all trees diseased). Disease incidence per block was defined as the proportion of diseased trees, relative to the total number of trees, summarized over all sample units of a block. Disease incidence could therefore vary from 0 to 1.

Sampling and the computation of the variograms

The variogram is a function of separating distance, h, the 'lag' between two sample units. In this study the smallest lag was the distance between rows of sample units (Fig. 2): 27 m for Victoria and 25·5 m for Phedra. To compute the omnidirectional variograms, the calculations were based on all pairs of points separated by $h \leq 0{\cdot}5$ times the length of the longest side of the area to be evaluated (Journel & Huijbregts, 1978; Spatanal program by A. Stein (1986) Wageningen Agricultural University, unpublished; Spatcor and Gamfit programs written by R. Rossi (1991), Washington State University, Pullman, unpublished).

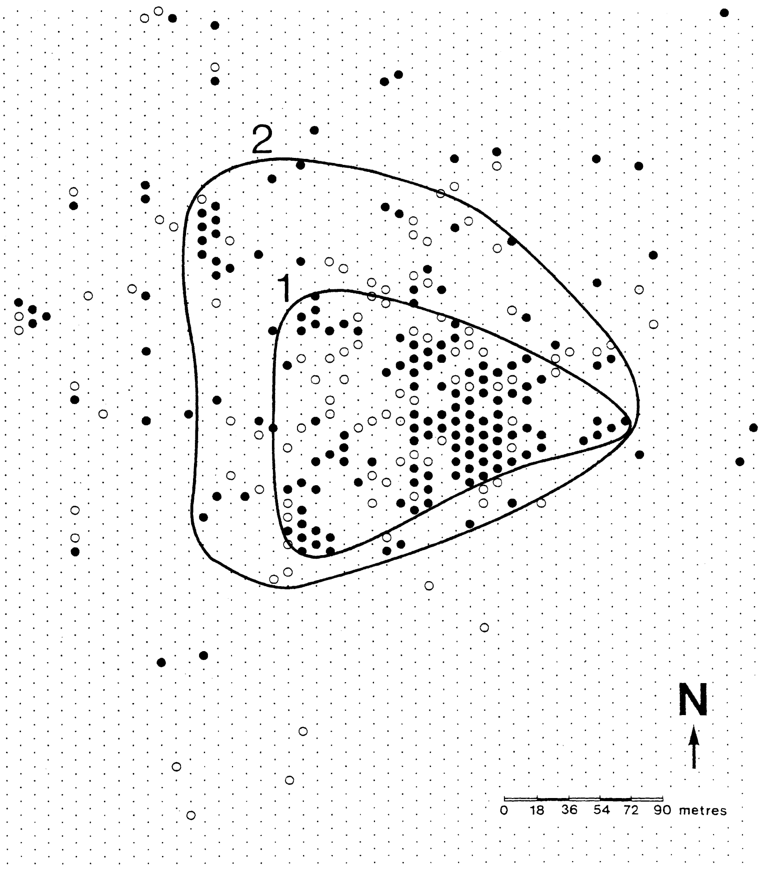

Figure 3 Spear rot of oil palm in Victoria, Surinam. Grid points represent individual trees (9 m apart). Pattern (areas 1 and 2) of diseased trees in the central part of block 6 West in (●) January 1986 and (○) January 1987.

An interesting feature of several blocks (3, 5, 6, 7 and 9) was the occurrence of clusters of diseased trees, indicating foci (Zadoks & van den Bosch, 1994). For validation, the remaining areas of blocks 6 and 7, with scattered diseased palms, were evaluated separately. To compare variograms from successive years, data from December of each year were used if available, otherwise (blocks 6 and 15) data from a date nearest to December. The results of geostatistical analyses are affected by the size, shape, orientation, scale and spatial arrangement of samples (Schotzko & O'Keefe, 1989). Therefore the same sampling lay-out was adhered to throughout this study (Fig. 2). Preliminary tests helped to determine a suitable size for sample units.

Variogram analysis

The semivariance, $\gamma(h)$, is estimated by calculating the mean of the squared differences between values of pairs of samples for a given lag distance (h) (Journel & Huijbregts, 1978).

$$\gamma(h) = \Sigma(\mathrm{F}x_{i+h} - \mathrm{F}x_i)^2 / 2\mathrm{N_h} \qquad (1)$$

where:

x_i = the position of a sample unit,
x_{i+h} = the position of another sample unit at distance h from x_i,
$\mathrm{F}x$ = the disease incidence measured at location x,
$\mathrm{N_h}$ = the number of sample pairs for distance h.

To obtain a reliable estimate of the semivariance, the number of sample pairs for each distance was at least 100. The variogram describes the relation between semivariance, $\gamma(h)$, and distance, h. Three types of variogram were fitted, following Matheron (1963):

1 No correlation between sample points, the variogram is flat (pure nugget effect).
2 The semivariance increases linearly with distance and remains unbounded.
3 The spherical model shows a maximum semivariance at some distance, called the range of spatial dependence.

Regression of semivariance on distance was calculated by means of regression analysis (Gamfit program by Rossi, 1991, Washington State University, Pullman, unpublished).

Directional effects

Compass direction was expressed in degrees (0–360) relative to the North (0°N). Disease gradients were analyzed in several directions, comparing two methods. Firstly, to detect anisotropy, variograms were calculated in a selected direction, usually that of the rows, and one perpendicular to it. The direction with the longest range (spherical model) or the most gentle slope (linear model)

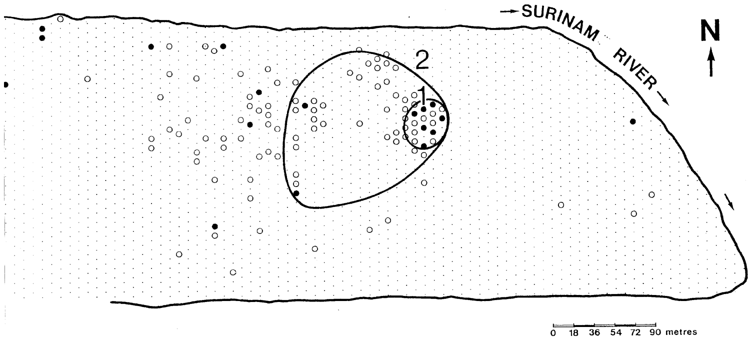

Figure 4 Spear rot of oil palm in Victoria, Surinam. Grid points (9 m apart) represent individual trees. Pattern (areas 1 and 2) of diseased trees in block 9 in (●) December 1985 and (○) December 1987.

is called the 'preferential direction'. Secondly, gradient analysis (Zadoks & Schein, 1979) was based on plots of disease intensity (here disease incidence) against distance from a putative source (here a clump of trees diseased at an early date). Plots were made on double log scales (Gregory, 1968) at different dates. However, the first diseased tree or the putative source of infection could not always be identified with certainty because of the time intervals between phytosanitary rounds. Disease gradients with early affected trees as sources were determined in various directions, for selected blocks with distinct and early clusters of trees, known to have been diseased at an early date.

Meteorological data

Information on wind directions was obtained from the Meteorological Service in Paramaribo, Surinam. Data came from the Zanderij Airport, at about 30 and 60 kilometres from Phedra and Victoria respectively. Wind direction was measured at 1·5 m above soil level. The wind pattern in Surinam, dominated by the north-east trade winds, is fairly consistent over the indicated distances.

Topographical information

The topography of the plantations was obtained from the Central Institute for Aerial Mapping in Paramaribo. Contour lines on the maps represent an increase of 5 m in altitude. Generally, altitude increased from the block side bordering a swamp or marshy forest towards its centre. Blocks bordering the river generally had lower altitudes than blocks in the middle of the plantation.

Statistical analysis

Models were fitted iteratively to the experimental variograms using Gamfit (written by R. Rossi, 1991, Washington State University, Pullman; unpublished). The model was selected according to the largest coefficient of determination (R^2), and this was evaluated further with the *F*-test ($P < 0{\cdot}05$; Harnett, 1982). A *t*-test was used to test whether slopes ($P < 0{\cdot}05$) and y-intercepts in linear variograms and gradients differed significantly from zero ($P < 0{\cdot}05$), disregarding the objection that data points should be independent.

Results

Location and size of focal centres

The locations of early clusters of diseased trees, here called foci, varied between blocks. At an early stage of infection some blocks in Victoria and Phedra had a few scattered trees affected, sometimes only in one part of a block. Early foci appeared predominantly at a border near to other infested blocks (5, 34, 46A and 46C), or close to a forest or swamp (3, 7, 16, 42B, 46B and 46D), but seldom in the middle of a block (6 and 9, Figs 3 and

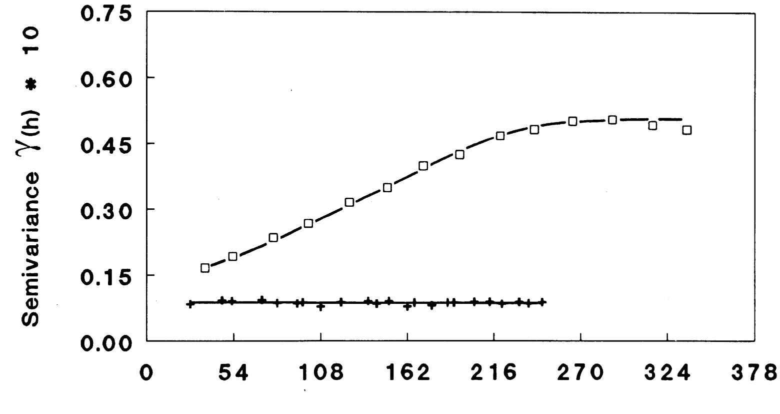

Figure 5 Omnidirectional semivariograms of spear rot distribution in the (+) Eastern (random) and (□) Western (focal) part of block 6 in 1987.

Table 2 Spear rot of oil palm in Surinam. Geostatistical analysis of blocks in the plantations Victoria and Phedra. The linear model, ($G(h) = C + b*h$, was fitted to the variograms of spear rot incidence

Block	Year[a]	Direction[b]	C	*b*	R^2	Incidence[c]
Victoria						
3	1983	omni	0·0117*	0·000024*	0·74*	0·061
		45	–	–	0·01	0·061
		135	0·0079	0·000072*	0·83*	0·061
	1984	omni	0·0148*	0·000141*	0·94*	0·127
	1986	omni	0·0216*	0·000480*	0·99*	0·415
		45	0·0295*	0·000253*	0·84*	0·415
		135	0·0216*	0·000484*	0·99*	0·415
5	1983	omni	–	–	0·15	0·021
	1986	omni	0·0267	0·000175*	0·97*	0·326
		45	0·0263	0·000260*	0·95*	0·326
		135	0·0354	0·000050*	0·65*	0·326
6	1987E	omni	–	–	0·12	0·151
7	1982E	omni	–	–	0·00	0·002
	1982W	omni	0·0022*	0·000004*	0·94*	0·018
	1986E	omni	–	–	0·02	0·047
	1986W	25	–	–	0·16	0·152
		115	0·0133*	0·000303*	0·98*	0·152
9	1985E	omni	–	–	0·02	0·007
	1986E	omni	–	–	0·03	0·007
15	1986	omni	0·0025*	0·000002*	0·68*	0·016
	1986	omni	0·0037*	0·000004*	0·60*	0·020
	1987	omni	0·0071	0·000004*	0·59*	0·036
		0	0·0052*	0·000023*	0·85*	0·036
		90	–	–	0·06	0·036
16	1984	0	–	–	0·49	0·009
		45	0·0012*	0·000001*	0·58*	0·009
		135	0·0012*	0·000008	0·59*	0·009
34	1986	45	0·0180*	0·000076*	0·83*	0·155
		135	–	–	0·62	0·155
Phedra						
42B	1990	omni	0·0040*	0·000278*	0·97*	0·758
		0	0·0520*	0·000201*	0·95*	0·758
		90	0·0066*	0·000413*	0·95*	0·758
46A	1990	omni	0·0189*	0·000024*	0·54*	0·118
		0	0·0146*	0·000094*	0·98*	0·118
		90	0·0151*	0·000045*	0·86*	0·118
46B	1990	omni	–	–	0·23	0·190
46C	1990	omni	–	–	0·13	0·081
46D	1985	omni	0·0037*	0·000024*	0·90*	0·022
	1988	omni	0·0105*	0·000030*	0·99*	0·109
		0	0·0063*	0·000050*	0·99*	0·109
		90	0·0205*	0·000057*	0·88*	0·109

[a] E = east, W = west.

[b] Direction in degrees relative to compass North, clockwise.

[c] Mean incidence of block.

*Value significant at $P \leq 0·05$.

4). Only in block 15 were trees with spear rot scattered over the entire area.

Variogram analysis

Pure nugget model

The variograms of blocks 5 (1983, Table 2), 6 East (1987, Fig. 5) and 7 East (Tables 2 and 3) were pure nuggets, i.e. no relation existed between semivariance and separating distance. Semivariance values in block 7 West were about 10 times larger than in 7 East, as were disease incidences per block.

Linear model

Linear models were fitted to 9 of the 13 blocks (Table 2). These blocks generally had a spear rot incidence greater than 0·01. Usually both intercept *C* and slope *b* differed significantly from zero at the $P < 0·05$ level. The linear

Table 3 Spear rot of oil palm at Victoria, Surinam. Average semivariance values of spear rot incidence in the Eastern and Western (focal) part of block 7 in the year 1982

	West		East	
h^a	G_h^b	N_h^c	G_h	N_h
36	0·0024	1782	0·00029	1810
53	0·0025	1148	0·00034	971
78	0·0024	3295	0·00031	3197
100	0·0027	2684	0·00031	2452
126	0·0028	4449	0·00030	4133
149	0·0029	3585	0·00029	3425
172	0·0029	4318	0·00031	4055
195	0·0029	4309	0·00029	4013
220	0·0031	5177	0·00029	4785
241	0·0031	3527	0·00030	3281
259	0·0033	2680	0·00033	2465

[a] h = average distance from source in m.

[b] G_h = value of the semivariance at distance h.

[c] N_h = number of sample pairs at distance h.

model, fitted to the data of blocks 5 (1983) and 7 East (1982), was not significant (Table 2). Incidence of spear rot in these two blocks was 0·02 and 0·002, respectively. The variogram values indicated a linear relationship in the data of block 7 West, and suggested early focal spread (disease incidence was 0·018). The linear model for the blocks 6 East (January 1987), 9 (1985 and 1986), 46B (1990) and 46C (1990) was nonsignificant (Table 2). In these four blocks no foci were seen.

The slope of the regression line increased with time in blocks 3, 7, 15 (January and September 1986) and 46D. In the directional variograms of block 3 (1986, Fig. 6) *b*(135°N) was significantly larger than *b*(45°N). In block 7 (1986) only *b*(115°N) was significant and in block 34 (1986) only *b*(45°N) was significant. In block 5 (1996, Fig. 7) *b* (135°N) exceeds *b* (45°N).

Spherical model

The spherical model could be fitted ($R^2 \geq 0{\cdot}79$) to the variograms (Table 4) for blocks 6 West (January 1987; Fig. 5) and 9 (1987 (Fig. 8) and 1988) at Victoria and block 46C (1990) at Phedra. The range increased over the years in blocks 6 (1986–87) and 9 (1985–87); see Figs 3 and 4.

Over the years 1986–87 (block 6) and 1987–88 (block 9) the sill increased with increasing incidence. The estimate of the slope of the regression line in the steep part of the variogram, tg α, increased over the years 1986–87 (block 6) and 1985–87 (block 9, Fig. 8). In block 9 (1987) the slope was least in direction 90°N, the direction of preference. Gradients within blocks had a directional preference between – 70°N and + 20°N at Phedra and between – 135° and 0°N at Victoria. In some cases, the direction of preference was more or less the same as the direction of rows (blocks 15, 16 at Victoria and 42B, 46A and 46D at Phedra), in other cases it was

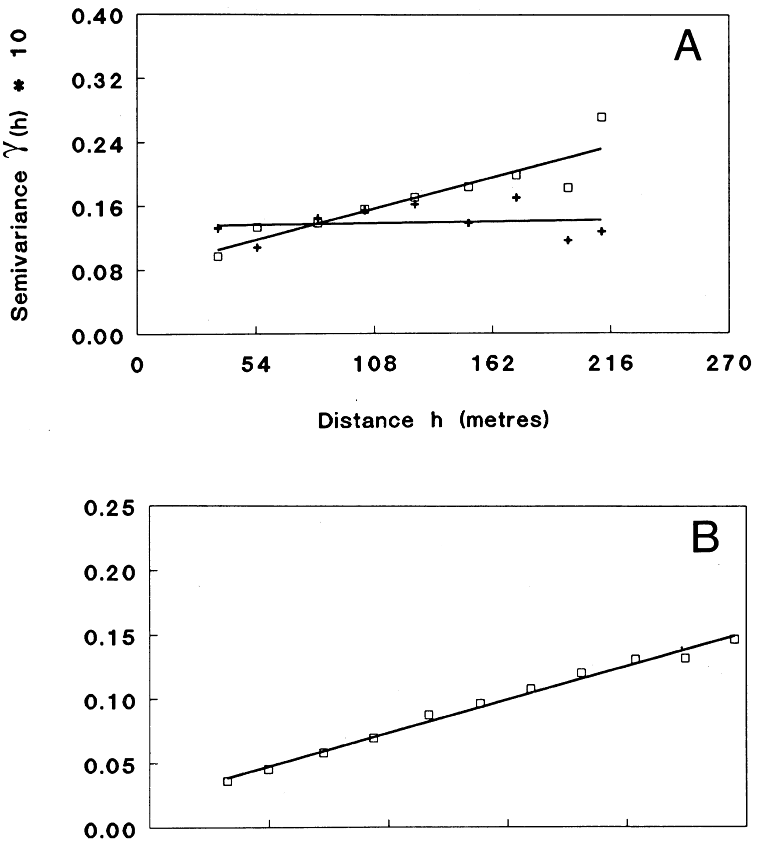

Figure 6 Variograms of spear rot distribution in block 3, in (a) 1983 at (+) 45°N and at (□) 135°N; and in (b) 1986, (□) omnidirectional.

Table 4 Spear rot of oil palm in Surinam. Geostatistical analysis of blocks in the plantations Victoria and Phedra. The spherical model was fitted to the variograms of selected blocks with spear rot incidence

Block	Year	Direction	C_0	C_1	Sill	Range	R^2	Incidence[a]	tg
Victoria									
6[b]	1986	omni	0·0072	0·0143	0·0215	225	0·98*	0·047	<0·0001
	1987	omni	0·0098	0·0596	0·0694	275	0·99*	0·151	0·0003
9	1986	omni	–	–	–	–	0·38	0·007	–
	1987	0	0·0009	0·0174	0·0183	94	0·99*	0·051	0·0003
		90	0·0085	0·0132	0·0217	250	0·87*	0·051	<0·0001
		omni	0·0051	0·0134	0·0185	116	0·94*	0·051	<0·0002
	1988	omni	0·0136	0·0728	0·0864	226	0·99*	0·231	0·0005
Phedra									
46B	1990	omni	–	–	–	–	0·52	0·190	–
46C	1990	omni	0·0044	0·0138	0·0183	51	0·79*	0·081	0·0004
		-70	–	–	–	–	0·52	0·081	–
		-160	–	–	–	–	0·14	0·081	–

[a] Mean incidence per block.

[b] Data refer to centre of block comprising the focus.

*Significant at $P \leq 0{\cdot}05$.

roughly perpendicular to the rows (blocks 6 and 9 at Victoria and 46B and 46C at Phedra).

In summary

Nine blocks had linear and four had spherical variograms. The slopes of the linear models, and the ranges and sills of the spherical models, increased significantly with time. With increasing ranges and sills, the slopes close to the origin in the spherical models decreased. The changes in spatial pattern of a few blocks at low disease incidence (e.g. 0·002), from a pure nugget variogram to a linear variogram, suggest that in these blocks the spatial independence at an early stage of disease development was replaced by a pattern. In most blocks, however, variogram analysis resulted in either a linear or a spherical relation even at low spear rot incidence (≥ 0·009). In eight blocks at Victoria and five blocks at Phedra a preferential direction could be determined, covering a range of directions from – 135° to + 20°N (average about – 57°N). This preferential direction was not related to the direction of tree rows or of harvest and maintenance procedures, but corresponded with the average direction of the prevailing trade winds.

Gradient analysis

Two blocks (7 West, 9) with clear focal development were selected to assess the disease spread in several directions and to find the dominant direction of spread. The slopes of the regression lines, *b*, were significant in all years and directions in both blocks ($P < 0{\cdot}05$). In block 7 the first affected tree occurred in the north-west corner. Here, long and shallow gradients were found in sectors of about 35°, spreading to the east-south-east (ESE) and south-south-east (SSE). In block 9, the approximate location of the first affected tree was in the centre of the eastern part. Apparently, the disease spread mainly towards the western part of the block, resulting in a V-shaped pattern of diseased trees (Fig. 4). The preferential direction was found by analysing gradients in directions SSW, W and NNW.

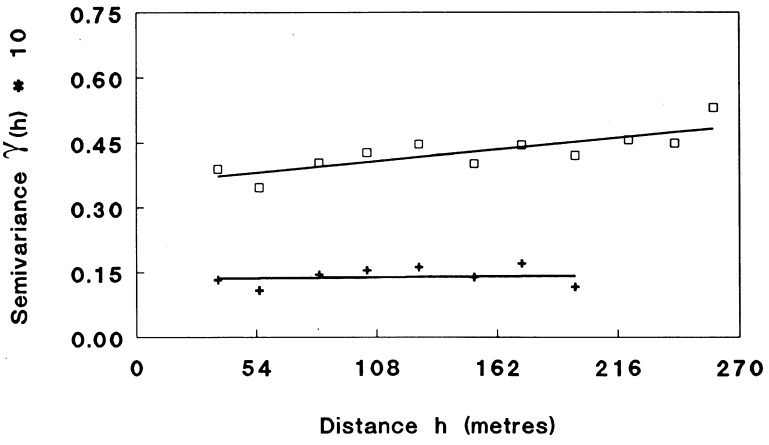

Figure 7 Unidirectional variograms of spear rot distribution in block 5 in December 1986, at (□)45°N and at (+) 135°N.

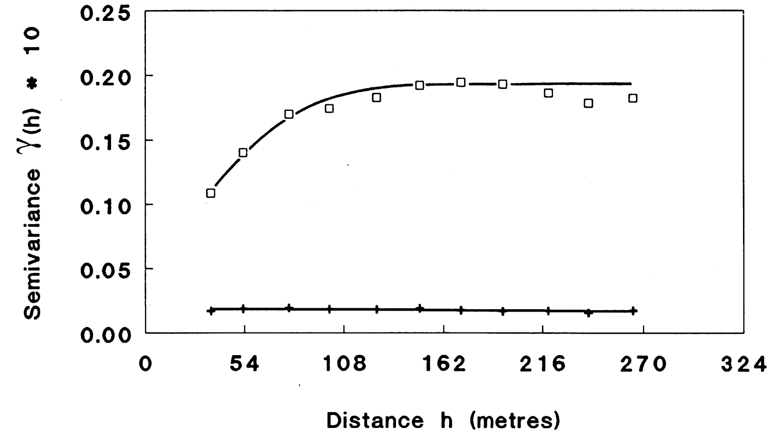

Figure 8 Omnidirectional variograms of spear rot distribution in block 9 in (+) 1985 and in (□) 1987.

Disease spread was very limited toward the east (Fig. 3).

Generally, the gradient of the linear models tended to decrease with time (Tables 5 and 6), and *b* was consistently smaller in the ESE sector than in the SSE sector of block 7, suggesting a preferential direction between − 90° and − 135°N. In block 9, the slope was flattest to the W or SSW (Table 6), suggesting a preferential spread at − 90° to − 157°N (Fig. 9). In block 9 the steep W and NNW gradients over the period 1985–87 flattened at a distance of about 95 m ($\log_{10}$ 95 = 1·96; Fig. 9a,b), and in the NNW direction 1987, at a distance of about 63 m ($\log_{10}$ 80 = 1·80; Fig. 9b).

Topography

Field observations in blocks 3, 7 and 9 indicated that the locations of the early foci corresponded with depressions in the field. Topographical maps were not detailed enough to show this.

Discussion

A methodological comment

According to medical history, at one time the infectious nature of cholera was suspected but its causal agent was unknown. Spatial analysis of a cholera epidemic in London led to an association of disease intensity with a water source (Snow, 1849; Shephard, 1995). This revolutionary insight was rejected at first (Gale, 1959). The cholera problem was solved by changing the water source. The causal organism of spear rot is still unknown but the disease is suspected to be infectious (Van de Lande, 1990). Spatial analysis may help to understand the nature of the disease (Cliff & Ord, 1981). Two complementary methods, variogram and gradient analysis, gave similar results. In epidemiology, statistical data for different points in time are used to make inferences as to the underlying processes of putative transmission, and ensuing spatio-temporal patterns, of disease.

The present study is largely an *ex post* analysis of an epidemic. It was performed under unusual circumstances, in plantations with hilly and marshy areas and irregular block shapes, where sanitation rounds were irregular because of economic problems and/or safety failures resulting from the political situation in the country. Data are typically ‘dirty’ field data, not ‘clean’ data from replicated experiments. Blocks that yielded interpretable data were selected, ignoring other blocks from which useful information could not be derived. Possible bias caused by selection is not considered to have seriously affected the conclusions, which did not contradict the early observations of the senior author, which triggered the present study.

The transition from descriptive statistics to narrative dynamics is a necessary methodological step, which is not unusual, and seems permissible when all experimental approaches fail. The existence of foci in ‘dirty’ oil palm plantations was obvious to the trained observer, not only in Surinam but also in other Latin American countries such as Brazil and Ecuador (personal observations by the junior author; Anonymous, 1992; Mariau *et al.*, 1992; Swinburne, 1993; Van de Lande, 1993b).

An epidemiological interpretation of patterns: from pattern to process

The spatial patterns represent instantaneous observations,

Table 5 Spear rot of oil palm in Victoria, Surinam. Statistical parameters of disease gradients in SSE and ESE directions in block 7 over 4 years

	SSE			ESE		
Year	R^2[a]	b[b]	SE[c]	R^2	b	SE
1983	0·88	− 0·45	0·04	0·78	− 0·35	0·05
1984	0·78	− 0·42	0·06	0·73	− 0·33	0·06
1985	0·65	− 0·25	0·05	0·75	− 0·24	0·04
1986	0·63	− 0·23	0·05	0·75	− 0·18	0·03

[a] R^2 = coefficient of determination of regression.
[b] b = slope of regression line, all b-values are significant at $P \leq 0{\cdot}05$.
[c] SE = standard error of b.

Table 6 Spear rot of oil palm in Victoria, Surinam. Regression parameters of disease gradients in SSW, W and NNW directions in block 9 over 4 years. All regression coefficients *b* were significant at $P<0{\cdot}05$

	SSW			W			NNW		
Year	R^{2a}	b^{b}	SE^{c}	R^2	b	SE	R^2	b	SE
1985	0·94	−1·22	0·13	0·95	−1·41	0·13	0·99	−1·81	0·02
1986	0·94	−1·21	0·13	0·97	−1·12	0·09	0·99	−1·69	0·08
1987	0·82	−0·87	0·17	0·87	−0·91	0·15	0·93	−0·83	0·13
1988	0·74	−0·38	0·09	0·88	−0·33	0·05	0·97	−0·49	0·05

[a] R^2 = coefficient of determination of regression.

[b] b = slope of regression line, all b-values are significant at $P \leq 0{\cdot}05$.

[c] SE = standard error of *b*.

whereas epidemiological interpretations look for processes linking successive patterns over time.

Absence of spatial relationships

A pure nugget variogram indicates spatial independence of the sample units, with no relationship between pairs of sample units at the smallest lag distance. The diseased palms are scattered at random over a block, as was the case in blocks 5, 6 East and 7 East, which had low disease incidences. The epidemiological implication of spatial independence is that, if the disease is infectious,

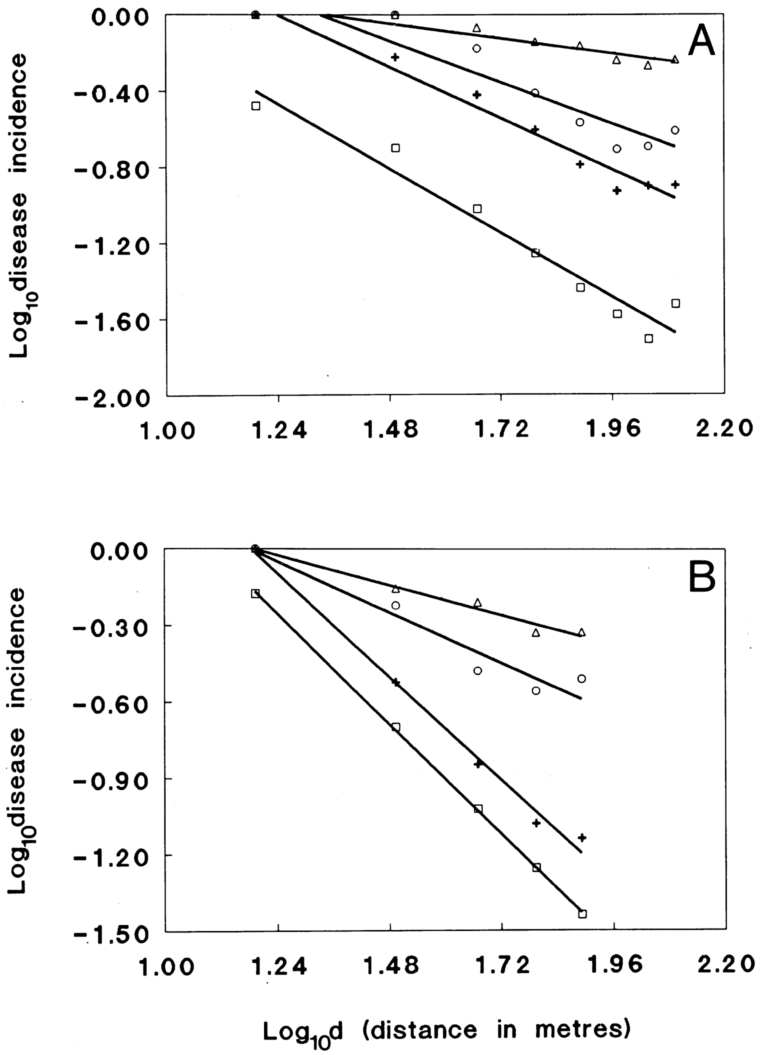

Figure 9 Spear rot of oil palm in the Victoria plantation, Surinam. Disease gradients of block 9 in (a) W and (b) NNW directions, on 4 separate dates, (□) 1985, (+) 1986, (○) 1987, and (△) 1988, calculated as regression lines of $\log_{10}$ incidence on $\log_{10}$ distance.

infection might come from distant sources, probably located outside the sampled area. Though the observations do not necessarily point to the infectiousness of spear rot disease, the hypothesis of inoculum sources far away from the diseased trees, in other parts of the plantation or outside, is compatible with the results.

Presence of spatial relationships

A linear variogram suggests a continuous relation between diseased trees, decreasing in degree with increased separating distance. Such a decrease of spatial interdependence of diseased trees is compatible with the epidemiological interpretation of a disease spreading from a source.

A spherical variogram suggests a gradual decrease in dependence with increasing separating distance until the maximum, or sill, is reached. Beyond this distance sample points are no longer dependent. The epidemiological interpretation might be a focus of disease, spreading from a point source, surrounded by an area with randomly scattered diseased trees.

In the majority of blocks, where a linear or spherical model could be fitted to the incidence of spear rot, even at low disease levels, the pattern of diseased trees was structured. Linear relations extended over long distances within entire blocks.

Over the years, as disease incidences and sill variances increased, the ranges tended to enlarge independently of compass direction. Connecting successive gradients over time, the epidemiological interpretation of the observations suggests a process of focal spread of the disease.

Three hypotheses

The present work showed the following phenomena:

1 a structured pattern of diseased trees within the range at any point in time,

2 an increase of the range with time, and

3 beyond the range no structural pattern, suggesting random occurrence of diseased trees.

Similar phenomena are seen with focus development of infectious disease (Zadoks & Kampmeijer, 1977; Zawolek & Zadoks, 1989; Zawolek, 1993). Translating statistical evidence into epidemiological terms, hypothesis 1, 'spear rot is an infectious disease', is postulated, even though there is no clue about the nature of the infectious agent and its eventual vector(s).

The observations **1**, **2** and **3** (above) suggest the presence of two mechanisms of dispersal. One mechanism leads to diseased trees, scattered over larger distances and apparently spatially unrelated, indicating dispersal from various distant, and possibly outside, sources. The other mechanism works over short distances, causing a distinct focus around a tree infected by the first mechanism. The focus increases in intensity and enlarges in diameter (Lannou & Savary, 1991), indicating transmission between neighbouring trees (Lecoustre & de Reffye, 1986), typically within the block. Considering the relatively important downwind spread, hypothesis 2 is postulated, 'the causal agent of spear rot is vector-borne, the vector being displaceable by wind'.

The results are compatible with hypothesis 3, 'spear rot appears in two distinct phases'. Phase 1 has scattered diseased trees at very low incidence, supposedly after infection from inoculum sources beyond the borders of the investigated area. Phase 2 is characterised by the focal spread of disease starting from scattered trees infected in phase 1. Foci intensify and expand, either with or without clearly defined borders, as reflected by the spherical and the linear models of variograms, repectively.

Gradient analysis confirmed the existence of phase 2. Shallow disease gradients (Gregory, 1968; Zadoks & Kampmeijer, 1977) such as in blocks 7 and 9 indicate that diseased plants are scattered over a wide area. Vectors may be motile. In block 9 West (1986, 1987), flattening of gradients might be explained by background infection (Gregory, 1968). Steep gradients to the NNW indicate clumping of diseased plants near the initial focus (Van der Plank, 1963), and suggest vectors with low dispersability (Pedgley, 1982).

The three hypotheses seem plausible when other mechanisms that could explain the observed patterns can be excluded, such as topography, soils, farm operations, genetic background and plantation age.

Topography and soils

No indication was found that spear rot spread from high to low areas. Movement of inoculum, with or without vectors, through the soil by means of water is unlikely. Forest and swamp areas may have provided sources of infection (Mariau *et al.*, 1992), especially in phase 1, since the majority of blocks were bordering such areas. The disease occurred in fields with different soil types (Van de Lande, 1990), so that the effect of soil type on disease occurrence can be disregarded.

Plantation operations

Harvesting and pruning were carried out from the first row towards the last row of a block. If mechanical transmission had taken place, a disease gradient should have developed in the direction of movement. In 6 out of 13 blocks (5, 6, 9, 15, 16 and 34) the preferential direction of spread was westward, perpendicular to the direction of field operations. The hypothesis of disease spread by mechanical transmission through harvesting and pruning has no empirical support.

Genetic background and plantation age

As different blocks may have been planted to hybrids with genetically different backgrounds, topographic effects and genetic background could be confounded. The present study and other studies in Surinam quoted here gave no indication of a relation between disease spread and genetic background or tree age.

Wind effect

The mean wind direction in the interior of the country echoes that of the trade winds coming from the northeast. Considering the age of the palms (generally over 5 years) at the time of study, the canopy was closed and crown height of the trees was 2–5 m. Preferential direction of disease spread coincided more or less with the dominating winds. This result leads to the hypothesis that the causal agent of the disease or its eventual vector can be wind-borne, certainly in phase 2. The variation between blocks in the preferential direction in comparable years of observation may be the result of minor variations in wind direction (Pedgley, 1982), possibly combined with variation in the time of infection.

Infectious nature of spear rot

Disease spread in the direction of the prevailing winds was also observed in an oil palm plantation affected by amarelecimento fatal, a disease similar to spear rot, in Brazil (Van Slobbe, 1990b). In Ecuador, in plantations with *pudrición del cogollo*, a disease similar to spear rot, the association between affected trees and nearby forest was shown by variogram analysis (Anonymous, 1989).

Although the causal agent of spear rot is not yet known, the disease is generally believed to be infectious (Mariau *et al.*, 1992; Van Dijk & Van de Lande, 1990; Van de Lande, 1993a,b). This belief is corroborated by the present study. The trigger of the change from phase 1 to phase 2 remains unknown. The existence of two different vector populations seems plausible.

If spear rot is infectious, its control will be difficult, especially in phase 1. The lay-out of the plantation, with palm-free strips as a 'cordon sanitaire' (Thresh *et al.*, 1988) in blocks bordering forest or swamp areas, could be a temporary solution to keep infestation at a low level. Containment of the disease by eradication of disease foci should be performed as early as possible. Sanitation by frequent monitoring of disease and immediate felling of diseased trees, and possibly neighbouring trees too, is imperative.

Pattern analysis by geostatistics and gradient studies helped to define physical and biological mechanisms that underlie the evolution of spatial patterns. Such studies can be of importance for yield loss assessment, plantation management, and the selection of new planting locations. Pattern analysis may provide clues on the nature of other important fatal diseases of unknown aetiology in oil palm (Mariau *et al.*, 1992; Swinburne, 1993), 'amarelecimento fatal' in Brazil (Van de Lande, 1986; Celestino Filho & Lucchini, 1990; Martins e Silva & Das Chagas Oliveira Freire, 1990; Van Slobbe, 1990a,b) and *pudrición del cogollo* (Turner, 1981; Perthuis, 1990) in South and Central America.

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