

Mathematical Analysis and Modeling of Epidemics of Rubber Tree Root Diseases: Probability of Infection of an Individual Tree

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ABSTRACT. The spread of root diseases in rubber tree (*Hevea brasiliensis*) due to *Rigidoporus lignosus* and *Phellinus noxius* was investigated epidemiologically using data collected every 6 months during a 6-year survey in a plantation. The aim of the present study is to see what factors could predict whether a given tree would be infested at the following inspection. Using a qualitative regression method we expressed the probability of pathogenic attack on a tree in terms of three factors: the state of health of the surrounding trees, the method used to clear the forest prior to planting, and evolution with time. The effects of each factor were ranked, and the roles of the various classes of neighbors were established and quantified. Variability between successive inspections was small, and the method of forest clearing was important only while primary inocula in the soil were still infectious. The state of health of the immediate neighbors was most significant; more distant neighbors in the same row had some effect; interrow spread was extremely rare. This investigation dealt only with trees as individuals, and further study of the interrelationships of groups of trees is needed. FOR. SCI. 34(4):831-845.

ADDITIONAL KEY WORDS: *Hevea brasiliensis*, *Rigidoporus lignosus*, *Phellinus noxius*, pathogen spread, qualitative regression, infection probability, epidemiology.

IN THE IVORY COAST, root rot diseases due to the fungal pathogens *Rigidoporus lignosus* (Kl.) Imaz. and *Phellinus noxius* (Corner) G. H. Cunn cause serious problems in rubber tree (*Hevea brasiliensis*) industrial plantations. Unlike most pathogenic fungi in above-ground organs of plants, these root rot agents are spread, not by spores, but by mycelial filaments in the soil. *R. lignosus* and *P. noxius* are characterized respectively by rhizomorphs (fast-growing strands of mycelial filaments) and by a mycelial sleeve surrounding the infected roots. In the spread phase these mycelial formations run along the lateral and superficial tree roots, sometimes for several meters without penetration (for *R. lignosus*). The wood decays later when the hyphae reach the tree's taproot, usually quite deep in the soil. In spite of the various operations to prepare the ground before planting rubber trees, most of the centers of infection (consisting of infected stumps of forest trees) remain active and constitute the primary inoculum. Mycelial filaments develop from these stumps and spread through the soil establishing contacts with the roots of healthy rubber trees. Once infected and decayed, these

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trees in turn become a secondary inoculum allowing the disease centers to extend by successive infection of neighboring trees (Nandris et al., 1987).

Faced with this problem, the Office de la Recherche Scientifique et Technique Outre-mer (O.R.S.T.O.M.) Plant Pathological Laboratory in Abidjan has investigated various aspects of the biology of these pathogens and their interactions with rubber trees since 1965 (Boisson 1972, 1973, Geiger et al. 1976, 1985, Nandris et al 1983, Nandris 1985, Nicole et al. 1983, Nicole 1984). As part of these investigations, an epidemiological study was carried out to quantify the spread of the fungi and the mortality of trees affected by root diseases in a young rubber plantation established after forest felling (see details in Materials and Methods). This *in situ* study has produced extensive information on the incidence of the fungi, dynamics of the diseases, infection chain, and root rotting fungi pathogenicity (Nandris et al. 1987), which has led to the elaboration of a mathematical model of the epidemic of these root diseases. Up to the last 10 years, most of the modeling studies for quantifying the dynamic process of epidemics in plants have dealt with pathogenic fungi of above-ground organs, especially with foliar diseases (Zadoks and Schein 1979). By contrast, few investigations had attempted to model root diseases due to soil-borne pathogens in general and to root rot fungi in particular. With new approaches in soil-borne pathogens epidemiology in temperate countries (reviewed by Campbell 1986 and by Gilligan 1985) and particularly in forest pathology (Bloomberg 1983, Williams and Marsden 1982), these types of investigations are becoming more common.

The present study aims to analyze the development of rubber root diseases in a population of rubber trees in a rainy tropical environment and to model these root diseases to allow the prediction of the severity and incidence of pathogens from the very first years of cultivation, so that control methods can be adopted accordingly. In practice this investigation concentrates on describing and quantifying the two complementary phases of the infection chain:

1. mycelial spread from infected trees to neighboring healthy trees, and
2. infection of roots, wood tissues colonization, and death of the tree.

Only the first part of this work is reported in the present article. Mathematical and statistical interpretations of epidemiological data collected in an industrial plantation allow the prediction of the infection of a given tree at time $t + 1$ from knowledge of the states of the adjacent trees at time t .

MATERIALS AND METHODS

PROCEDURE USED FOR THE EPIDEMIOLOGICAL INVESTIGATION

The methodology used for this study consisted in following the fate of a population of 7636 *Hevea* trees, 4 years old at the start of the investigation in 1977, arranged in 20 stands that were initially chosen considering the level of root rot infestation. The trees were planted the same year with a standard layout in contour lines (every 2 m in rows 8 m apart). The health of each tree in the experiment was monitored for 6 years, at six-month inspection rounds. The rounds of inspection were made each year in April and October, at the ends of the rainy and dry seasons, respectively. The root system of each tree was checked for infection by removing the soil around the collar and at the beginning of the lateral roots, then looking for the mycelial formations characteristic of the two pathogens. For each stand studied, the method of forest clearing, the position of the planting rows, and the locations of the rubber trees (healthy or diseased) and of missing trees in

each row, were marked on plans. At each inspection, newly infected trees and dates of detection were recorded: a tree infected by *P. Noxius* detected at survey j was noted N_j and the state infected by *R. Lignosus* detected at survey j was noted L_j .

PRINCIPLE OF ANALYSIS

Given the biology of these root pathogens, the study of the spread of the pathogens involves the use of a neighborhood model. In other words, the state of a tree at the time $t + 1$ of a given round of inspection will be considered in relation to the states of the adjacent trees in round t . In practice it is considered that a tree can be infected by mycelium spreading from its closest neighbors (secondary inoculum). Accordingly the study takes into account the ten closest neighbors of a given tree: the three trees on either side in the same row, and the two closest trees in each of the adjacent rows.

We have used the hypothesis that the phenomenon is spatially stationary. Within a treatment for cultivation, two central trees with neighbors in the same state are considered as two repetitions of the same phenomenon. So the probabilities of infection on the central tree at time $t + 1$ were estimated in each configuration from a knowledge of the state of health of the trees surrounding this individual at time t and from a knowledge of the treatment for cultivation. This calculation was based on statistical analysis of the data gathered by the epidemiological survey of the trees.

DATA ACQUISITION AND HANDLING

Data Encoding

A file was set up for each stand, containing the following variables:

- For each living tree at the start of the study: its coordinates on the map, its state of health, the nature of the pathogen (*R. lignosus* or *P. noxius*), and the date when it was detected (and the date when the tree died, if relevant).
- For each tree dead before the start of the study: its coordinates on the map. Note that we could not know *a posteriori*, in the field, the actual cause of death of a given tree (poor growth, damage due to animals, or pathogen attack).
- Whether each tree was in a manually or mechanically cleared site.

This information provided a virtual file containing the 7636 configurations adopted by the disease in the plantations. Individuals at the edge of a stand were removed from this file, and then 1200 independent (the independence is important for statistical reasons) configurations were selected according to the method suggested by Besag (1974), incorporating only "central" trees that were not neighbors. A central tree was chosen only if it was not a neighbor of another central tree, although central trees could share the same neighbors.

Probabilities of Tree Attack by Root Pathogen

A factorial analysis of correspondences (Lebart et al., 1984) was used first to establish the disease pattern of *R. Lignosus* on a stand (279 individual trees, a subset of the 1200 trees) at the second inspection. It was applied to the complete disjunctive table defined as follows. Each line (or individual) in the table refers to one tree. Each variable is a given state of a given neighbor (and equals 1 if the neighbor is in this state, 0 if not). There are 3 possible states (found infected by *R. Lignosus* at survey 0 (L0), found infected by *R. Lignosus* at survey 1 (L1), healthy) and 10 neighbors, so the complete disjunctive table has 30 variables. This analysis brings to the fore groups of

diseased trees corresponding to the *in situ* disease center opening in the forest. An individual is characterized by its position in relation to the neighboring center of infection. However, there is no very clear separation between the populations of diseased trees and the population of healthy trees.

Second, since factorial analysis revealed that deterministic prediction of infection was unreliable, we examined the probability of infection on a healthy tree as a function of its environment. The model proposed is a linear regression on conditional probabilities, which was studied in 1973 by Andrews and Messenger, developed particularly by Daudin (1978, 1979, 1980) and turned into a computer program (Meyniel 1983), which we used. Since this statistical method is the basis of our own work, we present it in some detail.

PRESENTATION OF QUALITATIVE REGRESSION

Let Y be the dependent qualitative variable, and J its number of possible states. Let (X_1, X_2, \dots, X_p) be the p independent qualitative variables, and I_k the number of possible states for X_k . Expressing Y as a function of (X_1, \dots, X_p) consists in determining the probability of Y for a known set of (X_1, X_2, \dots, X_p) . Set

$$P_{i,j,\dots,n}^q = P(Y = q | X_1 = i, X_2 = j, \dots, X_p = n)$$

the probability that

$$Y = q \text{ if } X_1 = i, X_2 = j, \dots, X_p = n$$

We can break down this probability into an additive model analogous to that of analysis of variance:

$$P_{i,j,\dots,n}^q = \mu^q + a_i^q + b_j^q + \dots + e_n^q + (ab)_{ij}^q + \dots$$

(Note that an additive model assumes independence among the effect of the dependent variables, but the variables can be correlated).

The parameters can be interpreted:

- μ^q is the mean of the q th state of Y .
- a_i^q is the contribution of the i th state of variable X_1 to the q th state of Y , and similarly b_j^q is the contribution of the j th state of variable X_2 . These are called "principal effects."
- $(ab)_{ij}^q$ is the contribution of the combination of the i th state of X_1 and the j th state of X_2 . This is called the "interaction term of order 2."

It is shown that the parameter estimators, calculated by the method of unweighted least squares, are consistent and asymptotically normal (Daudin 1978). The normality assumption can then be used to obtain a test of null hypothesis about the parameters. The statistical test is calculated as the difference between the sums of the squares in the complete model (comparison model) and in the model from which the parameters to be tested have been removed. This statistic tends asymptotically to a chi-square distribution, with its number of degrees of freedom (df) equal to the differences in df for each model.

A bootstrap method (Efron 1982, Freedman and Peters 1984), was used to calculate standard deviations of the estimates. Twenty bootstrap samples were selected and had 6 hours on a DPS6 computer.

DISEASED TREES AT THE BEGINNING OF THE INVESTIGATION

At the beginning of the investigation certain trees were found to be missing or dead from undetermined causes (bad growth of seedlings, animal damage on young plants, root rot diseases on young trees). We looked to see whether a healthy tree was at greater risk if it was near a dead one before the investigation.

The dependent variable Y is the state of health of the central tree at $t = 0$. Three states are possible: healthy, found infected by *P. noxius* at initial survey, found infected by *R. lignosus* at initial survey (L_0). It must be noted that simultaneous infections of the same tree by these two pathogens are very scarce. In this case, only the "first installed" fungus could be considered parasitic and responsible for wood decay; the second was generally only saprophytic.

The 11 independent variables considered are the states of the 10 neighboring trees [3 Neighbors Above (NA1, NA2, NA3), 3 Neighbors Below (NB1, NB2, NB3), 2 Neighbors Left (NL1, NL2), 2 Neighbors Right (NR1, NR2)] and the method of deforestation. Each neighbor has two possible states: dead before the experiment, or alive. The method of clearing has two possible states: manual, or mechanical with tree pusher.

The proposed model, fitted to the 1200 configurations selected, includes principal effects and all the interactions of order 2. It is written thus:

Set

$$P^j_{i_1, i_2, \dots, i_{10}, i_{11}}$$

the probability that $Y = j$ if the states of its neighbors and method of clearing are known.

$$P\{Y = j | NA1 = i_1, NA2 = i_2, NA3 = i_3, NB1 = i_4, NB2 = i_5, NB3 = i_6, \\ NL1 = i_7, NL2 = i_8, NR1 = i_9, NR2 = i_{10}, \text{method of clearing} \\ = i_{11}\}$$

$$P^j_{i_1, i_2, \dots, i_{10}, i_{11}} = \mu^j + a^j_{i_1} + b^j_{i_2} + c^j_{i_3} + d^j_{i_4} + e^j_{i_5} + f^j_{i_6} \\ + g^j_{i_7} + h^j_{i_8} + k^j_{i_9} + l^j_{i_{10}} + p^j_{i_{11}} \\ + (ab)_{i_1 i_2}^j + (ac)_{i_1 i_3}^j + \dots$$

On the basis of this model, the influence of neighbors and method of clearing was tested and the effects evaluated.

ATTACKS BETWEEN INSPECTIONS I_0 AND I_1

This period had to be studied separately, both because the epidemic was still in its explosive phase and because a year elapsed between these two inspections (instead of 6 months as for all the others). The dependent variable Y is the state of health of the tree at inspection 1. The three possible states are: healthy, N_1 (found infected by *P. Noxius* at survey 1), and L_1 (found infected by *L. lignosus* at survey 1). In theory the possible causative factors are the same as those considered in the previous section. However, in order to reduce the number of parameters, some factors were grouped, losing little information because of the symmetry of the configuration considered. So five factors were taken into consideration:

(i) The "neighborhood of rank 1" factor involves the two closest neighbors within the same row. This factor has five possible combinations:

- the two trees are healthy (at $t = 0$)
- one healthy tree and the other dead before survey
- one healthy tree and the other L_0 found infected by *L. lignosus* at survey 0 (L_0)
- one healthy tree and the other N_0 found infected by *P. noxius* at survey 0 (N_0)
- two diseased trees.

(ii, iii) The "neighborhood of rank 2" is the medial pair and "neighborhood of rank 3" is the distal pair; these factors group together with the same possible combinations as before.

(iv) The "lateral environment" factor groups the four nearest neighbors to the sides. It has six possible combinations:

- four healthy trees
- three healthy trees and the other in the state L_0
- three healthy trees and the other in the state N_0
- two healthy trees and the two other trees L_0
- two healthy trees and the two other trees N_0
- other configurations (two healthy trees, one L_0 , and one N_0 , for example)

A certain number of configurations placed in this last combination were difficult to analyze. In practice this is of little importance, since these configurations are rare.

(v) The clearing factor has two possible combinations: mechanical and manual.

The model includes the principal effects and the interactions of order 2 and of order 3 with the first factor. It is fitted to 1200 configurations as previously.

ATTACKS NOTED AT INSPECTION I_4 TO I_9

Our aim was to rank the causative factors, then to study changes with time (during three further semestrial inspections at most) of a diseased tree's effect on the probability that the adjacent tree would be attacked. We have thus applied for each round of inspection the same type of model as that presented in the previous section. The dependent variable is the state of the tree at the next inspection, denoted $t + 1$. It has three possible states: healthy, infected by *P. noxius* (N), infected by *R. lignosus* (L). Five possible causative factors were taken into account:

(i, ii, iii) Rank-1, rank-2, rank-3 neighborhood: ten possible combinations:

- two healthy trees
- one healthy tree and one diseased L at t
- one healthy tree and one diseased L at $t - 1$
- one healthy tree and one diseased L at $t - 2$
- one healthy tree and one diseased L at $t - 3$ or before $t - 3$
- one healthy tree and one diseased N at t
- one healthy tree and one diseased N at $t - 1$
- one healthy tree and one diseased N at $t - 2$
- one healthy tree and one diseased N at $t - 3$ or before $t - 3$
- no healthy tree

According to the time interval ($t - 3$) needed in the past, we have begun at I_4 .

(iv) Lateral environment: eight possible combinations:

- four healthy trees
- one or two diseased trees L at t and other trees are healthy
- one or two diseased trees L at $(t - 1)$ and other trees are healthy
- one or two diseased trees L at $(t - 2)$ and other trees are healthy
- one or two diseased trees N at t and other trees are healthy
- one or two diseased trees N at $(t - 1)$ and other trees are healthy
- one or two diseased trees N at $(t - 2)$ and other trees are healthy
- other configurations (more than two attacks)

(v) Forest clearing factor:

The model, fitted to 1200 configurations selected, includes the principal effects of the five factors and all the interactions of order 2.

RESULTS AND DISCUSSION

ATTACKS RECORDED AT THE BEGINNING OF THE INVESTIGATION (I_0)

Calculating the chi-square value (see previous section) showed that the effect of the missing or dead neighbors was not significant (for the principal effects, chi-square = 31 with $(3 - 1) \times (2 - 1) \times 10 = 20$ df, and chi square value = 37.5 at 1%). Thus we can suppose that at this age the state of a central tree was independent of the state of these neighbors. In biological terms, this may mean either that the majority of trees that died before the investigation did so from a cause independent of the presence of the parasite, or that the residual inoculum was no longer effective in the spread of the disease. They could thus be treated like "healthy trees."

On the other hand, the effect of the method of clearing was significant (for the principal effects, chi-square = 24.2, with 2 df). The probability of attack was 2% higher in stands cleared manually (where there were more stumps) than in stands where mechanical clearing made it possible to uproot most of the stumps and woody debris in the forest. This is reflected in a disparity between the two types of stands, i.e. "delayed" spread in stands that were cleared mechanically.

ATTACKS BETWEEN FIRST (I_0) AND SECOND (I_1) INSPECTIONS

Incidence of the Various Factors

Table 1 presents the change of the sum of squares related to each factor studied. Two observations can be made:

1. Data revealed that principal effects are the most significant in this analysis.
 - Hierarchy of relationships: the state of a tree is related first to that of its closest neighbors on the line, then to the clearing method, and then to its other neighbors.
 - Relation among causative factors: Table 2 presents the sums of dependent squares for each factor taken alone. Each value is clearly greater than its corresponding value in the complete model (Table 1). The information provided by the factors of ranks 2 and 3 is already partially contained in the factor of the rank 1. Thus, in the absence of any other information, the state of the lateral neighbor gives information on the probability of attack; however, if the state of the neighbors in the same row is known, the information provided by the state of the neighbor on the lateral row is negligible.
2. Interactions of the order 3 are not significant, and interactions of the order 2 are significant, except those with the forest clearing. One explanation may be that spreading occurs in the same way whether the stands have been cleared manually or mechanically. The deforestation affects mainly the number of residual primary centers and contributes only additively to the probability of attack. For other interactions, a split of this chi-square table shows the terms that contribute most to the sum of the squares. However, they have large standard deviations, and we were thus unable to give a more refined analysis of these interactions.

Investigations on the Principal Effects

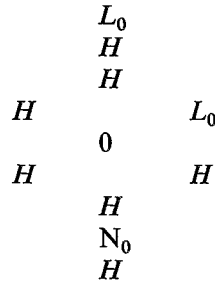
More detailed information on the principal effects are given in Table 3. The estimation of the parameters and their respective standard deviation have been calculated for each combination of the disease status in relation with the different configurations of the neighboring trees.

TABLE 1. Effects of the causative factors considered to evaluate the probability of infection of a rubber tree after the initial survey at inspection I₁.

	Model	Model number	Explicated squares	df	Comparison model	change	df	Chi square at 1%	Significant
	full model	1	946	424					
Factor removed									
Third-order interaction	with 1st rank	2	773	262	1	176	162	210	NS
All second-order interaction	with 1st rank	3	533	164	2	240	98	137	S
	with 2nd rank	4	536	162	2	237	100	139	S
	with 3rd rank	5	556	162	2	217	100	139	S
	with lateral lines	6	594	144	2	179	118	160	S
	with deforestation	7	722	228	2	51	34	56	NS
Principal effects									
	1st rank	8	428	156	3	105	8	20	S
	2nd rank	9	508	154	4	28	8	20	S
	3rd rank	10	533	154	5	23	8	20	S
	lateral lines	11	579	134	6	15	10	23	NS
	deforestation	12	702	226	7	20	2	9	S

The mean values of Y should be considered as the probabilities (expressed as a percent) of various states of the central tree at inspection 1 in the absence of any information concerning its environment. The effects of each possible causative factor were grouped within five subtables. Thus the first subtable includes the effect of the rank 1 neighbor tree. For example, if the rank 1 environment is characterized by one tree healthy and one tree dead before the experiment, the correction to be applied to the probability of being healthy (93.42) in inspection 1 is estimated at -1.12% , i.e., a probability of 92.30%.

So this table makes it possible to "reconstitute" the probability of infections in a certain configuration, even one that is not found in the field. For example, consider the following configuration after manual clearing with infected trees (two L_0 and one N_0) and seven healthy trees (H).



In this configuration, the probability of attack on the central tree (0) by *R. lignosus* will be:

mean attack	4.82%
principal effect of rank 1: two healthy trees	-1.29%
principal effect of rank 2: one infected tree (N_0)	-2.33%
principal effect of rank 3: one infected tree (L_0)	+1.89%
principal lateral effect: three healthy trees and one infected tree (L_0)	+1.37%
principal effect of clearing: manual	+2.00%
for a total probability of attack of	6.37%

This probability can be compared with the probability of attack in other configurations. If the lateral environment is represented only by healthy trees, the probability would be: $4.82 - 1.29 - 2.33 + 1.89 - 0.71 + 2 = 4.29\%$. And if the rank = 1 neighbors were one infected tree (L_0) and one healthy tree (H), the probability of attack would be: $4.82 + 12.57 - 2.33 + 1.89 + 1.37 + 2 = 17.65\%$.

The effect of a diseased neighbor on the probability of attack on the central tree can thus be quantified in numerous configurations, and the essential role for pathogen spread of the closest neighbor in the same row is mathematically demonstrated. However, comparison of the probabilities of attack in various configurations requires the standard deviations of calculations of

TABLE 2. Effects of the factors considered alone to evaluate the probability of infection of a tree at inspection I_1 .

SOURCE	Explicated square	df	Chi square at 1%	S/NS
1st rank	150	8	20.1	S
2nd rank	87	8	20.1	S
3rd rank	39	8	20.1	S
Sideline	26	10	23.2	S
Deforestation	32	2	9.2	S

TABLE 3. Estimation of the probabilities (at inspection 1) to be healthy or infected for a tree in relation to its neighborhood configuration at initial survey I_0 (mean values of parameters and their standard deviations).

	Sanitary states			Standard deviation		
	Healthy tree	Infected tree by		Healthy	Infected by	
		Noxius	Lignosus		N	L
Mean value of Y	93.42	1.77	4.82	0.5	0.2	0.5
Causative Factors						
Rank 1						
both trees healthy	1.60	-0.40	-1.29	0.20	0.20	0.20
one dead before	-1.12	0.17	1.05	1.10	0.50	0.90
one diseased L_0	-11.72	-0.75	12.57	2.60	0.60	2.50
one diseased N_0	-23.68	23.72	-0.15	14.00	11.00	4.00
two diseased	-18.23	5.73	12.50	6.00	2.00	6.00
Rank 2						
both trees healthy	1.23	-0.05	-1.30	0.10	0.20	0.10
one dead before	-1.30	-1.17	2.35	0.90	0.30	1.00
one diseased L_0	-6.76	-0.31	7.00	3.00	0.60	3.00
one diseased N_0	-15.05	17.47	-2.33	7.00	7.00	3.00
two diseased	-8.29	-1.29	9.48	4.00	1.00	4.00
Rank 3						
both trees healthy	0.64	0.01	-0.65	0.40	0.10	0.40
one dead before	-1.90	-0.17	2.00	0.70	0.40	0.90
one diseased L_0	-1.44	-0.34	1.89	1.50	1.20	2.00
one diseased N_0	-14.33	5.47	9.00	6.70	2.00	6.00
two diseased	-4.24	2.80	2.36	3.00	0.20	3.00
Lateral Line						
all four trees healthy	0.74	-0.03	-0.71	0.30	0.20	0.30
one diseased L_0	0.29	-1.56	1.37	2.00	0.40	2.00
one diseased N_0	-6.76	3.34	3.32	4.00	4.00	4.00
two diseased L_0	-8.92	-0.38	9.15	3.00	2.00	3.00
two diseased N_0	-0.85	5.91	-5.05	7.00	7.00	1.00
other case	-34.51	7.94	26.67	15.00	7.00	16.00
Deforestation						
manual	-2.70	0.90	2.00	0.40	0.20	0.40
mechanical	3.60	-1.00	-2.70	0.60	0.20	0.60

effects to be taken into account. These standard deviations (Table 3) are generally relatively large: simple addition provides a very rough calculation of the standard deviation of the total probability. The probabilities of attack for the various configurations are thus difficult to compare, especially in the case of configurations that are rare in the plantation.

We can compare the effects of factors pairwise more confidently and can see that a few intuitive ideas are confirmed:

- Healthy configurations are associated with a low probability of attack $P = 4.82 - 1.29 - 1.30 - 0.65 - 0.71 = 0.87\%$. This may involve the risk of mycelial development from a residual woody inoculum under ground.
- Stands cleared manually are attacked more severely than stands cleared mechanically.
- An attack by *P. noxius* has a negative effect on attack by *R. lignosus*, and vice versa.
- The lateral environment has an effect only if it is made up of numerous diseased trees.

- The trees dead before the experiment are much "closer" to healthy trees than trees attacked in I_0 ; we reach the same conclusion as in the previous paragraph.
- The effect of a diseased adjacent tree seems greater when it involves *P. noxius* than when it involves *R. lignosus*. The trees colonized by *P. noxius* die more quickly, and this is difficult to explain since in the field this fungus spreads very slowly. Standard deviations for these values are relatively high, and this occurrence may be a random fluctuation.

Some situations have negative probabilities. However, the model used is linear, and if all interactions are not included, the adjusted probabilities can be outside the 0, 1 interval. (Here, we cannot add many more interactions: the number of data must be greater than the number of parameters). Other models, logistic models, for example, automatically would restrict $P(Y|X)$ to its correct range. However, we would lose simplicity and easy interpretation, and interactions would become difficult to test. On the other hand, negative values or values exceeding 1 permit one to detect situations that are estimated poorly (often because they occur rarely in the data), and it may be quite acceptable to take such probabilities equal to 0 or 1 respectively.

ATTACKS NOTED AT INSPECTIONS I_4 TO I_9

Hierarchy of the Factors

Table 4 presents the analysis of data collected during inspection 4, which is taken as representative. The contribution of each of the factors to the sum of squares of the model makes it possible to rank the effects of the causative factors in an attack.

- The rank 1 environment factor (closest neighbor within the same row) is the most strongly causally related. Next, though much less strong, are the effects of the rank 2 and interinspections variabilities.
- The method of clearing has little effect. This is easily explained: new attacks originate less and less in stumps of forest trees and more and more from inoculum from infected rubber trees.
- At this stage the lateral environment is not significant: this confirms the almost total lack of row-to-row spreading of the mycelium (Nandris 1984).
- Although they are significant, the interactions were not analyzed because, as in previous cases, the major terms in the sum of the squares have been calculated on a low number of cases.

Principal Effects

Table 5 shows the mean principal effects of the various factors. It can be read like Table 3, and it gives rise to the following observations.

Between two inspections, when all the neighbors are healthy and the deforestation was manual, the probability of being attacked was 0.4% ($100 - (98.4 + 0.8 + 0.2 + 0.2 - 0.04)$). This may be considered an estimate of the minimal risk of a tree's being attacked by fungus in 6 months. This risk is of the same order of magnitude as that during the period between inspections 0 and 1 in a stand cleared mechanically. This is quite understandable, since the primary inoculum buried in the soil has disaggregated with time, and it reveals that at this stage the disease is developing mainly by spread from tree to tree.

When the immediate (rank 1) neighbor has been attacked by *R. lignosus*, the risk of attack is greatest after 1 year (9.3%) then decreases quite rapidly (to 3.7% a year later). For *P. noxius* the maximum risk of attack was when the neighbors has been diseased for 2 years. It confirms that *P. Noxius* spreads along the roots much more slowly than *R. lignosus*.

TABLE 4. Incidence of the causative factors studied on the probability of attack of a rubber tree at inspection 4.

	Model	Model number	Explicated squares	df	Comparison model	change	df	Chi square at 1%	Significant
	all principal effects	1	440	70					
Factor added									
All second order interaction									
	with 1st rank	2	2063	520	1	1623	450	530	S
	with 2nd rank	3	1537	530	1	1097	460	540	S
	with 3rd rank	4	1399	524	1	959	454	534	S
	with lateral lines	5	191	456	1	751	386	460	S
	with deforestation	6	553	148	1	158	78	113	NS
Second order interaction									
	with 1st rank								
	rank 1 × rank 2	7	956	240	1	516	126	170	S
	rank 1 × rank 3	8	1063	230	1	563	118	160	S
Factor removed									
Principal effects									
	1st rank	9	153	52	1	287	18	34	S
	2nd rank	10	394	53	1	46	18	34	S
	3rd rank	11	435	52	1	15	18	34	NS
	lateral lines	12	430	56	1	10	14	29	NS
	Deforestation	13	438	68	1	2	2	9	NS

The rank 2 and rank 3 factors have distinctly smaller effects and greater standard deviations than those of rank 1. Their secondary role is thus more difficult to analyze.

CONCLUSIONS

The method of qualitative regression, applied to interpretation of epidemiological data collected during a 6-year survey in rubber tree plantations, allowed us to estimate the probability of attack on trees by two root pathogens in all possible configurations. However, for configurations that

TABLE 5. Estimation of infection probability of a tree according to its neighborhood (healthy or diseased trees) considered at time t and at times 1, 2, and 3 semes-tral before.

	Sanitary states			Standard deviation		
	Healthy tree	Infected tree by		Healthy	Infected by	
		Noxious	Lignosus		N	L
Mean values of Y	98.4	0.5	1.1	0.15	0.05	0.12
Causative Factors						
Rank 1						
Healthy and Healthy	0.8	-0.2	-0.5	0.1	0.0	0.1
Healthy and $L(t)$	-1.2	-0.8	2.1	2.0	0.4	2.0
Healthy and $L(t - 1)$	-8.6	-0.7	9.3	1.0	0.2	1.0
Healthy and $L(t - 2)$	-3.7	-0.9	4.6	0.7	0.2	0.8
Healthy and $L(t - 3)$	-3.3	-0.4	3.7	1.2	0.3	1.1
Healthy and $N(t)$	-2.7	+3.0	-0.2	4.5	0.1	4.5
Healthy and $N(t - 1)$	-1.6	2.7	-1.0	2.6	2.0	0.3
Healthy and $N(t - 2)$	-2.5	1.6	0.9	3.5	2.0	2.8
Healthy and $N(t - 3)$	-5.5	5.5	-0.4	1.6	1.4	0.3
Other case	-9.8	5.5	4.2	4.3	2.9	2.1
Rank 2						
Healthy and healthy	0.2	-0.05	-0.1	0.1	0.0	0.1
Healthy and $L(t)$	-2.0	0.07	1.9	0.6	0.4	0.5
Healthy and $L(t - 1)$	-1.6	0.6	1.0	0.7	0.4	0.3
Healthy and $L(t - 2)$	-1.8	1.1	1.3	3.0	0.7	2.6
Healthy and $L(t - 3)$	-1.0	0.4	0.3	0.6	0.5	0.6
Healthy and $N(t)$	-2.0	3.1	-1.1	3.0	4.0	0.6
Healthy and $N(t - 1)$	-0.2	1.1	-1.0	1.1	1.3	0.2
Healthy and $N(t - 2)$	1.8	-1.0	-0.9	0.9	0.5	0.4
Healthy and $N(t - 3)$	1.8	-0.6	-1.2	0.7	0.3	0.4
Other case	-2.2	0.03	2.1	2.0	0.8	1.6
Rank 3						
Healthy and healthy	0.2	-0.02	-0.2	0.2	0.1	0.0
Healthy and $L(t)$	-2.0	0.9	1.9	1.4	1.1	2.3
Healthy and $L(t - 1)$	-1.5	0.8	0.7	1.8	0.6	1.3
Healthy and $L(t - 2)$	-3.0	1.0	2.2	1.2	0.7	1.4
Healthy and $L(t - 3)$	-0.1	0.0	0.2	0.6	0.4	0.2
Healthy and $N(t)$	0.9	1.0	-1.9	2.5	0.2	2.5
Healthy and $N(t - 1)$	-0.5	2.2	-1.7	1.3	1.7	0.5
Healthy and $N(t - 2)$	-0.6	0.0	0.7	2.4	0.1	2.4
Healthy and $N(t - 3)$	0.6	-0.4	-0.2	0.6	0.3	0.4
Other case	-1.1	-0.6	1.7	1.9	0.5	1.7
Deforestation						
Manual	-0.04	0.04	-0.05	0.1	0.1	0.0
Mechanical	0.05	-0.1	0.05	0.1	0.1	0.0

were seldom found in the plantation, the standard deviations are too large for suitable analysis.

Various factors were taken into account to explain these probabilities. It was thus possible to establish and rank their influence on the fate of a given tree as a function of a given configuration. In this respect the following results should be kept in mind:

1. The "roles" of the various neighbors were established, and although the rank 2 and rank 3 neighbors were an important influence, the rank 1 neighbor appears essential to account for the fate of the tree.
2. Mathematical analysis confirms that mycelium spreads from the infected tree in both directions within the same row, with spread between rows being extremely rare. This result confirmed that disease centers of rubber root rot develop not radially but rather along the planting line.
3. The method of forest felling before planting has a significant effect on the infectious process but exclusively at the beginning of the root epidemics during the first five years of cultivation.
4. A study of the evolution of the various probabilities of attack reveals that the time factor has a minimal influence. This may seem surprising at first, given the tree's increasing capacity for resistance with age (Nicole et al. 1983). In fact, in this specific case of mycelial contact with the roots of *Hevea*, there is reason to think that at this stage the tree still remains relatively "passive" towards the pathogen.

In conclusion, this study has made it possible to define a methodology allowing prediction of infection on a tree by a root pathogen according to its neighborhood, and then, to put forward hypotheses to explain the biological phenomena occurring during fungal spread and infection of roots.

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