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The *Coffea arabica* Fungal Pathosystem in New Caledonia: Interactions at Two Different Spatial Scales

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With 5 figures

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Abstract

The simultaneous analysis of epidemiological and environmental variables could contribute to the determination of the main factors which govern the epidemic dynamics of diseases (i.e. rust, anthracnose and Cercospora leaf spot) in *Coffea arabica*. With this in mind, the condition of previously marked leaves in 29 plots, which were grouped in 11 different sites in New Caledonia, were surveyed monthly. In the same period, the environmental characteristics of the plots (soil type, climate, etc.) were determined.

Statistical analysis of these data revealed significant correlations between pathology and the environment, at the sites' level (analysis of the mean site values) as well as at the plots' level (analysis of the deviations with the mean site value). The site effects predominated: at those sites in which rust was the major disease, leaf and branch mortality were more pronounced than at sites in which anthracnose or Cercospora leaf spot predominated. Rust was generally associated with soil pH values that were favourable for coffee tree development, with poor soil structure and with large temperature ranges. Within a site, plot exposure to sun and wind could enhance anthracnose and Cercospora leaf spot.

Finally, in New Caledonia the three variables soil pH, soil structure and temperature range allow a simple and satisfactory estimation of the epidemiological risks in a given plot.

Zusammenfassung

Das *Coffea arabica*-pilzliche Pathosystem in Neu Kaledonien: Interaktionen zwischen zwei verschiedenen räumlichen Ebenen

Die Simultananalyse von epidemiologischen und Umweltvariablen könnte bei der Bestimmung der Hauptfaktoren, die für die epidemiologische Dynamik einer Krankheit (d.h. Rost, Anthraknose bzw. Cercospora-Blattfleckenkrankheit) des Kaffees (*Coffea arabica*) von Bedeutung sind, behilflich sein. Mit diesem Ziel wurde der Zustand von markierten Blättern in 29 Parzellen, die in 11 verschiedenen Standorten in Neu Kaledonien gruppiert waren, monatlich ermittelt. Zur gleichen Zeit wurden die Umweltcharakteristika der Parzellen (Bodentyp, Witterungsdaten, usw.) gesammelt.

Die statistische Analyse dieser Daten zeigte, daß es signifikante Zusammenhänge zwischen der Pathologie und der Umwelt gab, sowohl auf der Ebene des Standortes (die Analyse der Durchschnittswerte der Standorte) als auch auf der Ebene der Parzellen (die Analyse der Abweichungen mit dem Standortdurchschnittswert). Die Einflüsse des Standortes waren von größter Bedeutung: in Standorten, wo der Rost als Hauptkrankheit herrschte, war die Absterberate der Blätter und Zweige deutlich höher als in Standorten mit Anthraknose der Cercospora-Blattfleckenkrankheit als Hauptkrankheitserreger. Rost wurde am häufigsten bei Böden mit pH-Werten, die für die Entwicklung des Kaffeestrauches am günstigsten waren, beobachtet sowie bei armen Böden und mit großen Temperaturschwankungen. An einem Standort konnte das Vorkommen der Anthraknose und der Cercospora-Blattfleckenkrankheit durch die Sonneneinstrahlung und den Wind in einer Parzelle positiv beeinflußt werden. In Neu Kaledonien können die drei Variablen Boden-pH-Wert, Bodenstruktur und Temperaturbereich für eine einfache und zufriedenstellende Vorhersage des epidemiologischen Risikos einer bestimmten Parzelle herangezogen werden.

Résumé

L'objectif de ces recherches concerne l'analyse simultanée de paramètres épidémiologiques et environnementaux afin de déterminer les facteurs majeurs régissant la dynamique des maladies (rouille, anthracnose, cercosporiose) affectant le caféier arabica.

Un échantillon de 29 parcelles appartenant à 11 sites répartis sur le Territoire a été retenu, afin de réaliser mensuellement un suivi feuille à feuille de leurs signatures épidémiques. Parallèlement, des données environnementales (climat, sol, etc.) ont été enregistrées dans chaque site.

Les analyses statistiques de ces diverses catégories de données révèlent, à l'échelle des sites (analyse des valeurs moyennes) et des parcelles (analyse des écarts aux moyennes) une liaison significative entre pathologie et environnement. C'est à l'échelle des sites qu'apparaissent les principaux phénomènes: les sites les plus concernés par la rouille, la défoliation et la mortalité des rameaux s'opposent à ceux qui sont plus infestés par l'anthracnose et la cercosporiose. La rouille se développe essentiellement sur les sites où le pH favorise le développement du caféier, où la structure du sol est pauvre et où les écarts de températures sont importants. Au sein des parcelles constituant un site, l'exposition au soleil et au vent semble favoriser le développement de l'anthracnose et de la cercosporiose. Enfin, il s'avère que les données concernant le pH, la structure du sol et la température ambiante permettent, à elles seules et dans le contexte néo-calédonien, de prédire de manière satisfaisante le niveau de sévérité de la rouille et de l'anthracnose sur une parcelle donnée.

Introduction

Because of the world-wide economic importance of coffee and of the phytosanitary constraints affecting its cultivation, numer-

ous studies have examined the fungal pathology of coffee. These studies have varied widely in their focus: biology of pathogenic agents, epidemiology, genetics of parasitism, control methods, etc. The great majority of research on *Coffea arabica* has been devoted to coffee leaf rust, a disease caused by *Hemileia vastatrix* Berk. et Br., a particularly serious threat to coffee production in many countries (Shieber 1972; Eskes et al., 1991).

Numerous publications in coffee epidemiology have examined the effects of environmental conditions on the development of rust (Pedro, 1983; Oseguera, 1985), generally focussing on one particular parameter such as the altitude of plantations (Avelino et al., 1991), the intensity of incident light (Eskes, 1982), the period during which free water remains on the leaves (Nascimento and Tubelis, 1980), the range and extremes of temperature fluctuations across the crop cycle (Schrödter, 1965), the physiological state of the host plant (Eskes and Toma-Braghini, 1982), etc. On the whole, these studies, carried out in the laboratory and/or research stations, have sought to quantify epidemiological phenomena either in a global manner (Zheng Fuchong et al., 1991) or by analysing in turn, the different phases of the epidemic process i.e. germination, penetration, sporulation and dissemination (Nutman and Roberts, 1963). These studies have clearly improved our understanding of the development of rust epidemics in coffee-producing zones. Predictive models developed by several authors (Kushalappa et al., 1984; Becker-Raterink, 1985) on the basis of these findings, have attempted to integrate the principle parameters influencing rust development. Because such models tend to incorporate considerable complexity defining the successive stages of the epidemic process, their results may be difficult to transfer from the station to the natural environment.

Epidemiological research on *C. arabica* presently being carried out in New Caledonia differs markedly in approach from the works cited above.

Our research objective is to analyse the overall functioning of a multiple pathosystem across various different sites, representative of the range of coffee growing conditions; in this case, the pathosystem associates the coffee, its principal pathogens *Hemileia vastatrix*, *Collectotrichum gloeosporioides* Penz., and *Cercospora coffeicola* Berk and Cooke and the environment. We note in this regard the striking scarcity of information available on the second and third pathogens listed (Hindorf, 1975; Tenckoff, 1982; Bailey and Jeger, 1992), a paradox unbalance given the importance of damage (attacks on branches, leaves, and/or berries) caused by these supposedly minor pathogens in certain ecological conditions. It is thus important to examine the role of these three pathogens throughout the entire cultural cycle in a systematic way. Thus, the chronology of appearance of each pathogen, the severity of their respective lesions, and the phenomena of competition or synergism on affected organs, are all three necessary elements for an integrated understanding of the infectious process.

Appropriate statistical methods have made it possible to expand significantly the range of environmental parameters examined, and to evaluate their effects on disease dynamics at each site. Thus, in addition to classic climatic descriptors, we have also gathered data on important characteristics of the soil (pH, structure, fertility, wilting point), and of the plot (topography, shade, planting density, ...).

Finally, the great ecological heterogeneity of New Caledonia has made it possible to maximize the diversity of environments examined, by choosing several plots from each of a large number of widely divergent sites. This study is marked in particular by the multi-local nature of our survey and the exclusive attention given to smallholders' shaded plots.

The objective of these investigations is to develop an epidemiological instrument enabling a better characterization of the disease risk. For varied practical problems, the optimal use of land converted to agriculture, the choice of rational control methods or the emergence of new diseases, the use of such a tool, applied to data describing a new context, should provide a rational contribution to decisions requiring predictions of the impact of diseases on a given crop.

This paper presents a first finding on the relationships between the environmental conditions and the global pathological and physiological status of coffee trees infected by fungal pathogens in New Caledonia. Particular attention is given to determination of (i) the spatial scale—between site differences vs. between plot (within site) differences—which best reflects the variability in susceptibility of trees in different plots; (ii) the environmental correlates of this variability at both scales; (iii) the evaluation of the accuracy of a decision tool based on these environmental observations in predicting the epidemiological risks for a given plot.

Materials and Methods

Data collection

In 1992, 11 sites (Fig. 1A) were chosen as a function both of geographic characteristics and of preliminary epidemiological data collected in 1991. The sites are located as follows: 2 lowland sites on the East side of the island at Yaté (YAT) and Canala (CAN); 2 elevated sites, one on the East slope of the central range, at Ema (EMA), the other on the West slope at Mou (MOU); 3 sites in isolated valleys of the central range, of which 2—Nérin (NER) and Kouaoua (KOU)—are on the East side, and one, Sarraméa (SAR), is on the West side; 2 lowland sites on the West Coast at Bangou (BAN) and Nessadiou (NES); 1 site on the hills of the West Coast at Moméa (MOM); and 1 site on the Isle of Pines (ILP). Within each site, 2–5 fields of arabica plants were chosen and monitored through the annual cycle. All of the 28 plots thus selected are traditional plantations of *C. arabica* var. Typica or Bourbon, grown under shade of varying density, and at least 20 years old. Field upkeep is in many cases limited to the harvest period, with little or no pruning or fertilization.

Pathological and physiological parameters

Within each field, 10 trees were sampled at regular intervals along a transect. Within each tree, 4 branches (chosen at 4 different heights from the bottom to the top) were marked. Epidemiological data was collected at approximately 5-week intervals using a 'leaf by leaf' observational methodology (Kushalappa, 1981; Avelino et al., 1991), in which the initial structure of each branch (position of leaves and presence of any pathogen) was recorded, and the history of each organ—leaf, branch and berry—was monitored throughout the cropping cycle. A foliar infection scale from 0 to 4 was developed thereby defining 5 levels of severity as a function of the number and the extent of lesions per leaf.

All these data were organised in a database (ORACLE), allowing the calculation, for each plot, of an annual pathological status (severity of infection of each pathogen, leaf fall, branch mortality etc.) and physiological status (leaf abundance, berries production, etc.). Definitions and values of the relevant variables are given in Table 1. The development, during the annual cycle, of the average severity of rust and anthracnosis on the different plots showed common dynamic patterns. In particular, attempts were made to define a date of occurrence and a propagation rate for the rust infections, but these only generated variables correlated with the maximum severity reached during the whole cycle ($r > 0.7$). Therefore, the maximum severity reached by the different pathogens during the cycle were the only parameters retained to describe the epidemic annual dynamics.

Table 1
This Pathology table contains for each plot: the maximum value reached during the annual cycle by the following parameters: the average number of living leaves per branch (NB. Leaves); the percentage of dead branches (Mortality); the average indices of severity of attack by rust (Rust), anthracnosis (Anthrac) and cercosporiosis (Cerco); the percentage of sampled branches bearing berries (Berries); the minimum value, during the annual cycle, attained by the average number of leaving leaves per leaving branch, divided by the maximum value attained by the same variable (Fall); the average life duration of the leaves (Leaves dur.) that appeared and fell during the annual cycle. The unit is the number of readings during the survey. The extreme values and the percentages of the within-site and between-site variances in the total variance, are displayed at the bottom of each column (see text for further details on data collection)

Plot	NB. Leaves	Fall (%)	Mortality (%)	Rust	Anthrac.	Cerco.	Berries (%)	Leaves Dur.
CAN1	6.6	44.2	25.0	2.16	0.20	0.00	27.5	3.86
CAN2	8.7	86.4	64.1	2.74	0.42	0.14	67.5	3.33
EMA1	9.4	69.9	25.0	2.68	0.16	0.00	82.5	4.43
EMA2	7.9	54.3	7.5	1.24	0.05	0.00	57.5	3.95
ILP4	8.4	68.6	50.0	0.01	1.53	0.60	55.0	2.95
ILP5	10.5	21.3	10.0	0.42	0.67	0.00	57.5	2.90
ILP6	8.9	40.9	18.4	0.14	1.13	0.01	40.0	3.41
MOM2	7.3	75.1	59.0	2.12	0.25	0.04	30.0	3.54
MOM3	7.7	87.0	51.3	2.88	0.47	0.02	12.5	4.88
MOM4	7.9	81.4	15.0	2.06	0.28	0.00	12.5	4.46
BAN1	7.3	39.8	12.5	1.15	0.11	0.36	52.5	4.89
BAN2	6.6	69.2	38.7	1.27	0.08	0.57	65.0	3.86
BAN3	9.1	47.2	27.5	1.34	0.08	0.20	72.5	4.79
KOU1	7.9	86.0	55.6	1.68	0.55	0.15	47.5	3.04
KOU2	8.1	71.6	65.8	2.06	0.37	0.08	15.4	3.11
KOU3	7.2	86.1	65.7	1.89	0.40	0.00	60.0	3.45
KOU4	6.3	71.5	72.5	1.82	0.30	0.00	47.5	2.67
KOU5	8.2	92.1	57.5	2.53	0.54	0.00	45.0	3.76
MOU1	8.5	62.6	10.3	1.75	0.46	0.00	85.0	4.46
MOU2	7.1	57.0	20.0	2.03	0.66	0.00	62.5	4.59
NER1	7.1	51.5	12.8	2.11	0.27	0.00	45.0	4.44
NER2	10.2	68.2	40.0	2.75	0.60	0.02	80.0	4.25
NES2	6.8	75.8	23.1	1.96	0.59	0.02	35.0	4.71
NES3	9.6	51.7	12.8	0.69	0.59	0.02	52.5	4.59
SAR4	6.1	74.8	70.0	3.19	0.19	0.00	15.0	4.43
SAR5	7.4	100.0	100.0	3.00	0.42	0.00	32.5	2.21
YAT1	6.2	50.7	5.1	1.00	1.61	0.00	15.0	3.47
YAT2	8.8	45.9	15.0	1.19	0.94	0.00	67.5	3.81
Min.	6.1	21.3	5.1	0.01	0.05	0	12.5	2.21
Max.	10.5	100	100	3.19	1.61	0.6	85	4.89
Within variance (%)	68	40	25	17	19	46	42	36
Between variance (%)	32	60	75	83	81	54	58	64

Environmental parameters

A number of descriptors were collected for each plot: local topography, daily rainfall and temperature maxima and minima, as measured either by the national weather service or by automated stations, soil quality, estimated from samples collected in the plots and analysed in the laboratory; planting density; canopy closure, estimated by scanning black and white photographs of the foliage; general condition of the crop; and exposure to dominant winds.

As previously, an 'Environment' table was produced from the annual estimates calculated from the environmental variables listed above. Definitions and values of the relevant variables are given in Table 2. Some of the environmental variables required preliminary processing. Variables estimated from soil samples were transformed into categories whose definitions were based on the current knowledge of coffee requirements (Coste, 1989). In addition, the extreme daily temperature logs included many missing values and therefore, as suggested by Graser (1990), required appropriate modelling. These logs were fit to sinusoidal curves with good agreements, using a multiple regression procedure. This model was used to estimate annual averages for minimum and maximum daily temperatures; the mean of these two values provided an estimate of the average annual temperature. Since this average annual temperature showed little variability among the different plots (from 21.6 to 23.2°C), it was not used in subsequent analyses. Instead, an annual temperature range was calculated as the difference between the highest value reached by the modelled daily maximum temperature, and the lowest value reached by the modelled daily minimum temperature. Finally, logs of daily total rainfall also included many missing values, but showed less characteristic patterns. Missing rain data at a given meteorological station were hence estimated by comparison with other periods or by using the rain data of the nearest available station. The average annual rainfall calculated in this way was highly correlated to the frequency of showering rains, and was therefore the only pluviometric variable considered.

Data analyses

Our analysis is based on the comparison of the two data sets which constitute the pathology and the environment tables. For each table, the rows correspond to different plots, and the columns are treated as quantitative variables though many of them are qualitative. In order to give the same weight to the different variables, both tables were normalized by column before any analysis.

As stated in the Introduction, the discrimination between the effects occurring between different sites and the differences observed within the plots of each site, is of primary interest. The environment and pathology tables were each decomposed into two tables: a 'between-site' table, whose 11 rows contain the site-averaged measurements and a 'within-site' table, whose 28 rows contain the deviations of the plot measurements from the averaged measurements for the relevant site. The comparison of the two between-site tables provides an analysis of the relationship between environmental and the pathological status at the scale of the site. The comparison of the two within-site tables reveals the relation at the scale of the plot. Such a decomposition is common

Table 2
This Environment table contains for each plot: the modelled annual temperature range (Temp. range); the annual average of daily rainfall (Av. rain); three descriptors of soil quality (adapted from Coste, 1989), namely: (a) pH scores: 1 for soils with unsuitable pH (<4.7 or >6.5); 2 for soils with suitable pH (>4.7 or <6.5); (b) structure (Soil struct.) scores: 1 indicates poor soil structure (organic matter content <3%); 2 indicates medium structure (3–4.5% O.M.), 3 indicates good structure (4.5–8% O.M.); (c) fertility (Fertility) scores: 1 indicates low soil fertility, 2 indicates to a medium fertility, 3 indicates good fertility. This classification was based on the degree of mineralisation of the soil samples and their contents in N, Ca, Mg, K and P2O5; coffee tree density (Density): 1 indicates low density (<4000 trees/ha); 2 indicates high density (>4000 trees/ha); relief (Relief): 1 indicates location in a plain; 2 indicates a mountainous loaction; plot shade (Shade): 1 refers to an unshaded plot; 2 refers to a shady plot; degree of plot clearing (State): 1 indicates poor ground clearing; 2 indicates good ground clearing; exposure to dominant winds (Wind): 1 refers to leeward plots, 2 refers to windward plots; the altitude (Alti.)

Plot	Temp. range (cm)	Av. rain (mm)	pH	Soil struct.	Fertility	Density	Relief	Shade	State	Wind	Alti. (m)
CAN1	17.2	4.6	2	1	1	1	1	2	1	2	20
CAN2	17.2	4.6	2	1	2	2	1	2	1	2	10
EMA1	20.6	5.6	2	1	2	1	2	2	1	1	450
EMA2	20.6	5.6	2	1	2	1	2	2	1	1	420
ILP4	13.4	4.0	1	2	3	1	1	1	1	2	10
ILP5	13.4	4.0	1	2	3	1	1	2	1	1	10
ILP6	13.4	4.0	1	2	3	2	1	2	1	2	10
MOM2	16.1	3.9	2	1	2	1	2	2	2	2	160
MOM3	16.1	3.9	2	1	2	1	2	1	2	2	180
MOM4	16.1	3.9	2	1	2	2	2	2	1	2	160
BAN1	20.7	3.7	1	3	1	1	1	2	2	2	20
BAN2	20.7	3.7	1	3	1	1	1	1	2	2	20
BAN3	20.7	3.7	1	3	1	1	1	2	2	2	20
KOU1	14.6	5.5	1	1	1	1	1	1	1	2	10
KOU2	14.6	5.5	2	1	1	1	1	2	1	2	10
KOU3	20.1	5.6	2	1	1	2	2	1	1	1	40
KOU4	20.1	5.6	2	2	2	1	2	2	2	1	50
KOU5	20.1	5.6	2	1	1	1	2	2	2	1	40
MOU1	20.7	4.1	2	3	1	1	2	1	1	2	400
MOU2	20.7	4.1	2	3	1	2	2	2	1	2	400
NER1	18.7	4.6	2	1	1	1	2	2	2	1	100
NER2	18.7	4.6	2	1	1	1	2	2	1	1	100
NES2	15.0	2.8	1	1	2	2	1	2	2	2	10
NES3	15.0	2.8	1	3	3	2	1	2	2	2	10
SAR4	20.3	5.9	2	2	2	1	2	2	1	1	100
SAR5	20.3	5.9	2	2	2	1	2	1	1	1	80
YAT1	13.0	6.7	1	3	2	2	1	2	1	2	10
YAT2	13.0	6.7	2	3	1	2	1	2	1	2	10
Min.	13.0	2.8	1	1	1	1	1	1	1	1	10
Max.	20.7	6.7	2	3	3	2	2	2	2	2	450
Within variance (%)	15	0	20	14	16	51	17	80	37	29	0
Between variance (%)	85	100	80	86	84	49	83	20	63	71	100

The extreme values and the percentages of the within-site and between-site variances in the total variance, are displayed at the bottom of each column (see the text for further details on data collection).

in ecology, since it allows one to consider or to eliminate various scale effects (Doledec and Chessel, 1989).

The interactions between the two between-site tables as well as the interactions between the two within-site tables were analysed by a multivariate method. The method the most appropriate for our case was a connected analysis of the two tables, which aims to find successive couples of new environmental and pathological variables, being as covariant as possible. Such variables, called co-structure axes, reflect the relations between the main pathological phenomena and the main environmental differences among the sites or the plots. For an easier reading of this paper, the details about statistical procedures and graphical representations are given in the statistical appendix.

Results

The main pathology variables are represented in Figure 1. The different plots are principally infested by rust, which was found to be more wide-spread than anthracnosis and cercosporiosis. These last two diseases are observed mainly in a few plots in the South of New-Caledonia which have very little rust infestation. Surprisingly, rust attacks varied little in severity between the East and West Coasts, despite the systematically greater precipitation on the eastern side of the central mountain chain.

Tables 1 and 2 show how the variability of the different parameters depends on the spatial scale considered: between-site differences are the main effects in our data sets, accounting for 75% of the total variability of the environmental variables and 63% of the total variability of the pathology variables. These tables also show the contribution of each variable to the spatial decomposition of variability. Some variables typically vary at the scale of the site (rust, anthracnosis, mortality; soil and climate features, relief) and are therefore given prominence in the between-site analysis. Other variables typically vary at the scales of the plot (number of leaves, shade) and are therefore given prominence in the within-site analysis.

Connected between-site analysis

Figure 2 presents the connected analysis of the two between-site tables. The first co-structure axis is a rust-and-damage axis ('damage' refers to leaf fall and branch mortality), which opposes those sites more infected by rust and affected by leaves fall and branches mortality, to those sites more attacked by the other pathogens (Fig. 2B). This analysis thus confirms the opposition observed in Fig. 1 between *H. vastatrix* and the

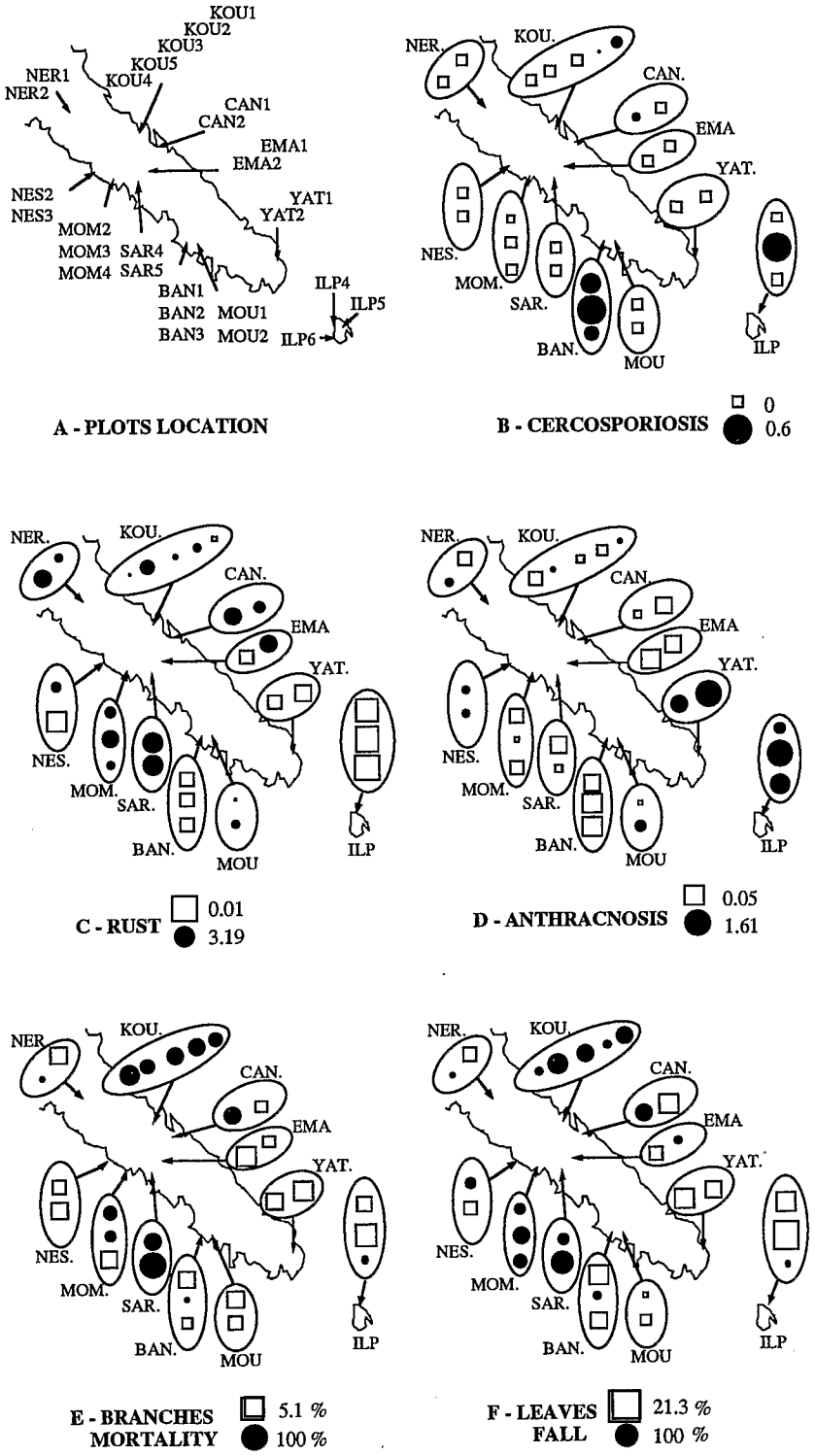
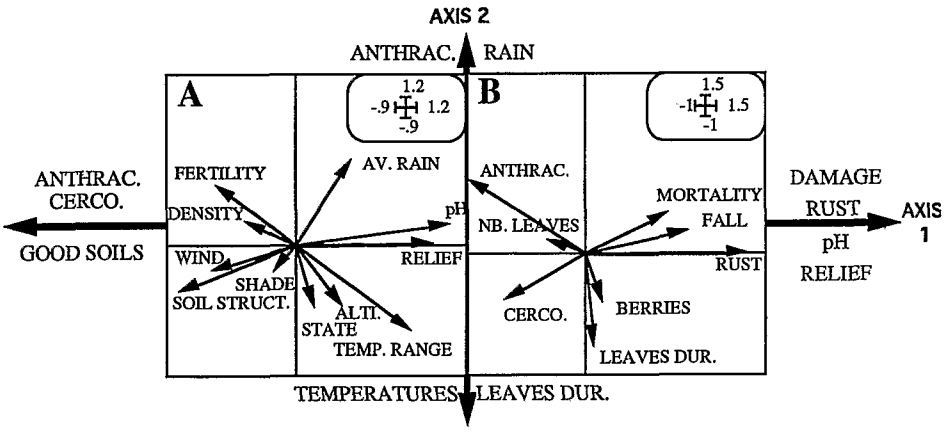
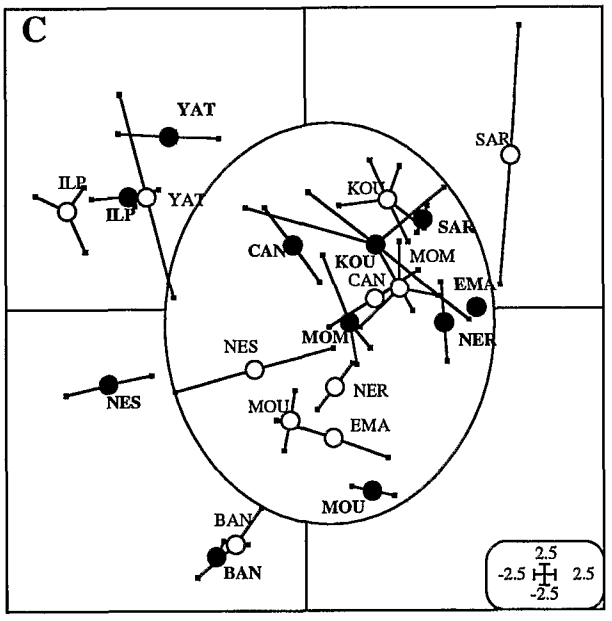


Fig. 1 Location of the plots and graphical representation of several pathological variables. Full circles represent positive differences from the mean value of each variable, whereas open squares represent negative differences from the mean value of each variable

other pathogens, and shows the association of damage with the rust. The grouping of sites by this classification is correlated with certain environmental variables. Thus rust and mortality are associated with some soil conditions (favourable pH, poor soil structure), higher altitude (RELIEF), and wide temperature ranges (Fig. 2A). We would emphasise that the physiological status (number of leaves, presence of berries) of affected sites is independent of the damage level (Fig. 2B). Figure 2D shows that the first co-structure axis reflects 44% of the variability of the Pathology table. Other investigations revealed that 49% of the variability of this table is reflected by the principal axis of a separate principal component analysis (PCA) of the between-site Pathology table, considered alone. This small loss of information on the pathology is more than compensated by the





D

	Environnement : variance explained	Pathological status : variance explained	Correlation
Co-structure axis 1	36 %	44 %	0.78
Co-structure axis 2	17 %	25 %	0.89

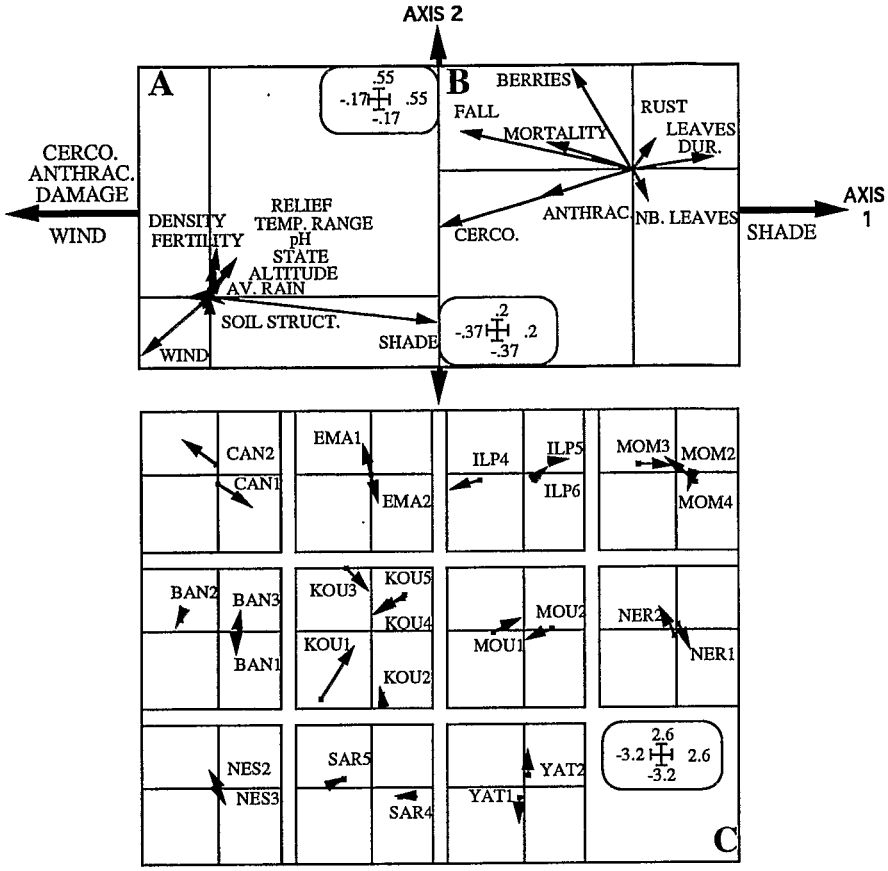
Fig. 2 Connected analysis of the two between-site tables, 'pathology' and 'environment'. A: Scores of the initial environmental variables on the two principal environmental axes. B: Scores of the initial pathological variables on the two principal pathological axes. C: Situation of the different sites for the environmental and pathological co-structure axes (full circles: normalized score of the sites on the environmental axes; open circles: normalized score of the sites on the pathological axes). The plots (small dots) are included though the analyses is based on the site-averaged measurements. D: Proportion of the variance of each initial data set taken into account by the co-structure axes. The correlation between the sites scores on the environmental and the pathological axes quantifies the reliability of the link between pathology and environment

high correlation (0.78) between the paired environment and pathology axes obtained using connected analysis (Figure 2D).

The second co-structure axis sheds light on differences between anthracnosis and cercosporiosis. Thus, anthracnosis, when contrasted to cercosporiosis, is more associated with a short leaf life duration, narrow temperature ranges and abundant rainfall (Fig. 2A, B).

The ordination of the sites along the pathological co-structure axes, and the ordination of the sites along the environmental co-structure axes are simultaneously represented in Fig. 2C. The observed structure is largely due to a small number of sites whose patterns are extreme: ILP, YAT, and to a lesser degree NES, are characterized by a low level of rust/damage and by infestation by anthracnosis/cercosporiosis. On the opposite side of the first axis, SAR shows high rust levels and heavy damage. Because BAN is less affected by anthracnosis and more affected by cercosporiosis than expected for a non-infected by rust site, is is opposed to ILP, YAT and SAR on the second axis.

Though the connected between-site analysis is based on the site-averaged variables of Tables 1 and 2, the positions of each plot are also given in Fig. 2C. A high degree of homogeneity of



D

	Environnement : variance explained	Pathological status : variance explained	Correlation
Co-structure axis 1	30 %	34 %	0.63
Co-structure axis 2	22 %	10 %	0.60

Fig. 3 Connected analysis of the two within-site tables, 'pathology' and 'environment'. A: Scores of the initial environment variables on the two principal environmental axes. B: Scores of the initial pathological variables on the two principal pathological axes. C: Situation of the different plots, grouped by site, for the environmental and the pathological co-structure axes (start of arrows: normalized scores on the environmental axes; end of arrows: normalized scores on the pathological axes). D: Proportion of the variance of each initial data set taken into account by the co-structure axes. The correlation between the plot scores on the environmental and the pathological axes quantifies the reliability of the link between pathology and environment

behaviour is observed between the different plots of a site for the effects revealed by the between-site analysis.

Connected within-site analysis

The connected analysis of the within-site tables is presented in Fig. 3. Within a site, damage generally increases with the severity of cercosporiosis and/or anthracnosis (Fig. 3B). This damage effect is essentially linked to the local exposure to light (SHADE) and to wind (WIND) (Fig. 3A). The importance given to light exposure in this analyses is largely due to the high within-site variability associated with the variable (Table 2). Nevertheless, the analysis reveals a high correlation (0.63) between the light exposure effect revealed along the environmental co-structure axis and the damage shown by the pathological co-structure axis (Fig. 3D).

Because of the low variability of the pathological table associated with the second co-structure axis (Fig. 3D), and because of the low between-sites variability in general, the effects revealed by this second axis are not considered significant.

The simultaneous representation of the scores of the plots associated with the pathological and the environmental axes (Fig. 3C) highlights the particular role played by plots within the ILP, SAR, BAN, CAN and KOU sites. The plots ILP4, BAN2 and to a lesser extent SAR5 match the co-structure described here since they experienced greater damage and were more exposed to light than the other plots of their sites. Thus, IPL4 was severely infested by *Cercospora*, whereas SAR5 was highly affected by damage, and BAN2 by both phenomena. In contrast, the particular positions of the plots of CAN and KOU do not match the common ordination, but are due, for CAN2, to high damage following a flood and for KOU, to the heterogenous environmental conditions of the plots, spaced along the valley of Kouaoua.

Predicting levels of rust and anthracnosis levels in new plots

To test the significance of the previously described relations between pathology and environment, the connected analysis was performed on 100 paired sets of tables obtained by random

Table 3
Probabilities associated with the hypothesis of non-influence of several environmental variables on the development of rust and the anthracnosis (Fisher's *F*-test on ANOVA). For this particular test, two groups only of similar size (n = 14) were considered for each pathogen

	Rust	Anthrac.
Temp. range	$9 \cdot 10^{-2}$	$9 \cdot 10^{-3}$
Soil struct.	$2 \cdot 10^{-2}$	$19 \cdot 10^{-2}$
pH	$< 10^{-5}$	$5 \cdot 10^{-2}$

permutation of the rows of our data sets. This test indicated that, under the null hypothesis of no common structure, the observed co-structure had a probability P = 0.01 for the within-site analysis and P = 0.18 for the between-site analysis. This latter elevated value was related to the high number of variables, in comparison with the low number of sites, which facilitates the random emergence of two highly covariant pathological and environmental axes.

The reliability of the main effect reflected by our data—the ordination of the plots from those affected by anthracnosis to those affected by rust, in connection with some environmental variables—had to be estimated in another way. In addition, the problem of quantifying the predictive power of the main environmental variables is of practical importance since rust and anthracnosis are definitely the main diseases observed in the sampled plots. Thus, we grouped the plots into 4 rust and 2 anthracnosis classes, according to severities reported in Table 2 and tried to discriminate these groups as a function of the main environmental variables (pH, soil structure, temperature range and relief). The relief parameter varies with the pH in all but four plots; this was therefore considered as redundant and therefore omitted.

The discriminating power of each of the three remaining environmental variables considered independently was tested (Table 3); rust severity levels are particularly related to pH, whereas anthracnosis severity levels are closely tied to a narrow temperature range. Then, a discriminant analysis of the plots grouped by rust and anthracnosis levels was performed as a function of the three variables together (the first axis of this analysis is the best combination of the three variables that discriminates the different groups). Figure 4 presents the observed probability distribution of the scores of the different groups on the first axis of the analysis. The discrimination of the different groups is particularly evident for the rust, for which classes 1 and 4 are strongly separated by the 3 environmental variables. The resultant model for the prediction of rust or anthracnosis level is detailed in the legend of Fig. 4.

The predictive power of this model was tested by exclusion of each site in turn from the discriminant analysis, and deduction of a new predictive model. This new model enabled predictions of the disease levels of the plots of the excluded site, as a function of the 3 environmental variables. The predicted and observed levels of disease severity are compared in Fig. 5. For rust, with 4 classes of infestation defined, 61% of the predictions were correct, while 32% fell in a neighbouring class. For anthracnosis, 2 groups were defined and 65% of the predictions were right. The probability of achieving at least this number of correct predictions by chance is $P < 10^{-6}$ for rust, and P = 0.06 for the anthracnosis.

Discussion

Our epidemiological monitoring of traditional plantations of *C. arabica* has revealed a great diversity in the spatial distribution of the diseases and in their severity; the comparison of the various epidemiological situations indicates that the bulk of variability is found at the between-site scale.

Rust, which is clearly the most widespread disease in New Caledonia, plays a preponderant role in the typology of sites. The most rust-infested sites proved to be those least affected by anthracnosis and cercosporiosis; these differences, evident in sites in close geographic proximity, generate a mosaic of epidemiological configurations and thus constitute an important step forward in our understanding of the function of the pathosystem.

H. vastatrix has also been shown to be the pathogen causing the greatest damage. First, certain heavily rust-infested plots were totally defoliated, even before the end of the crop cycle. The process by which infected leaves fall remains controversial; Kushalappa and Lagesse (1981) attribute this defoliation to the direct effect of the pathogen on infected organs, while Avelino et al. (1991) consider leaf fall to be a consequence of the reduced physiological status of plants heavily infested by rust.

Second, major withering of branches of severely defoliated plants was observed in these same plots. Cultures made from these dead or dying branches generally revealed the presence of *C. gloesporioides*, and an additional fungal flora which is probably secondary in nature (*Botryodiplodia*, *Fusarium*, *Phoma*, etc.). Given present knowledge on branch dieback (Hindorf, 1975), it remains difficult in New Caledonia to discriminate between an opportunistic infection by *C. gloeosporioides* and physiological withering following pathological defoliation.

The relationship between pathology and environment have been demonstrated to vary as a function of scale. The between-site analyses confirm the importance of temperature in the development of the diseases studied (Montoya and Chaves, 1974; Dodd et al., 1992). Thus, large temperature fluctuations are shown to be correlated with heavy rust infestations, while, conversely, anthracnosis is more likely to develop in sites with relatively constant temperatures.

In contrast, no effect was observed in the conditions of coffee growing in New Caledonia for a number of parameters found elsewhere to have an important role in the development of diseases, and of rust in particular. First, the heliophilic character of rust, established by Eskes and Toma-Braghini (1982), but contested by Machado and Matiello (1983), was not confirmed by our results; whereas shade is highly variable within sites, rust levels typically were most variable between sites. Second, contrasting with the results of Miguel et al. (1985), berry production is independent of rust level. Third, sites along the coast were significantly less infected by rust than were sites at higher elevations; these findings contrast with those of Brown et al. (1993) and Avelino et al. (1991). Fourth, several authors, including Pedro (1983), and Kushalappa and Eskes (1989), have reported that rainfall is important in the development of rust epidemics. However, under the conditions of this study, rainfall is in fact secondary to a variety of other edaphic, geographic, and climatic factors. We note though that *Cercospora* attacks tend to develop in sites with less rainfall. Finally, the demonstration of the role of a number of edaphic factors, namely soil pH, fertility, and soil structure, is apparently original to this study. Continuing analyses should determine more precisely the relationships linking them to the severity of coffee diseases.

Within given sites, shade and wind exposure are the principal variables observed which could increase the probability of occurrence and severity of cercosporiosis and/or anthacnosis.

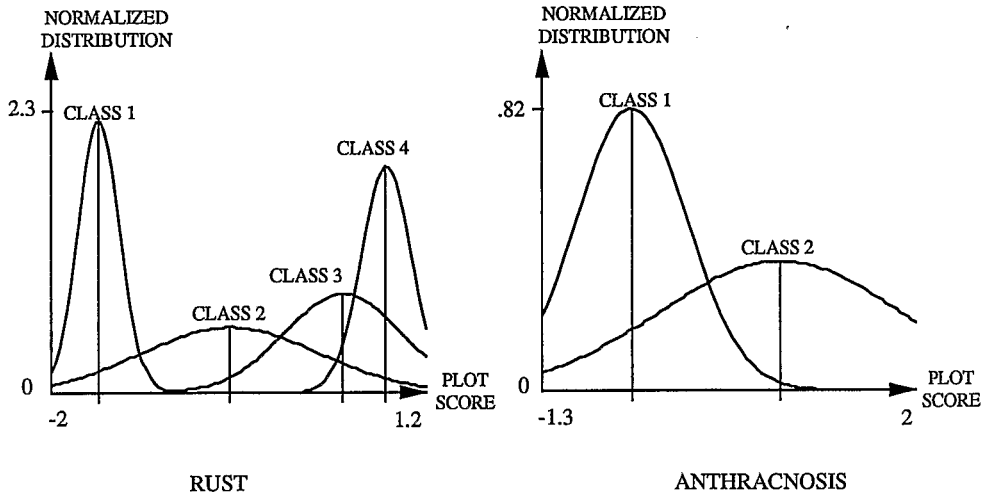


Fig. 4 Normalized distribution of the plots scores, grouped by rust or anthracnosis level, on the first axis of thre discriminant analysis based on pH, soil structure, and temperature range. The limits of the different groups are: rust (1 = [0,1]; 2 = [1,1.7]; 3 = [1.7,2.4]; 4 = [2.4,4]); anthracnosis (1 = [0,0.5]; 2 = [0.5,4]). The score x of a given plot is calculated as follows: Rust: $x = 1.44\ 10^{-2}$ (Temp. range) + 1.23 pH − 0.4 (Soil struct.) − 3.82. Anthrancosis: $x = 2.67\ 10^{-2}$ (Temp. range) − 0.69 pH + 0.24 (Soil struct.) + 5.39. The expected rust and anthracnosis levels in given environmental conditions can easily be read from this figure, by choosing the group whose probability density is maximal for the above scores (maximum likelihood method, Saporta, 1978)

Despite the limited number of sites included in the present study and the greater weight of a few of them in generating the variability observed, we have demonstrated the feasibility of developing decision instruments. Within the context of New Caledonia, three environmental variables—pH, soil structure, and temperature range—suffice to estimate in a simple and satisfactory manner the epidemiological risks in a given plot. The wide range of locations and parameters examined in this study compensate for the absence of precise measures carried out in the laboratory or research station on the detailed life cycle of the main fungal pathogens of *C. arabica* (Kushalappa and Carisse, 1990).

Nevertheless, actual growth processes are a function of a large number of interacting biological and environmental factors, some of which cannot be controlled and/or quantified. In order to minimize such sources of variability, certain parameters not considered in this study are now being characterized in greater detail. In particular, within the Typica and Bourbon strains, which constitute the majority of *C. arabica* planted in New Caledonia, there may exist significant varietal heterogeneity (Charmetant and Le Pierres, 1991). As a consequence, sampled trees were selected with regard to precise phenotype markers. The identification of genetically homogenous groups of individuals would make it possible to refine our analyses by reducing variability associated with the host, thus focusing only on that linked to the environment and with pathogens.

In this regard, one must also consider intraspecific variability of each of the three pathogens (Eskes, 1983; Boccas et al., 1985). Population studies are currently underway using zymograms and DNA probes in order to quantify precisely the role of each pathogen in the variations in epidemiological signatures registered within and between sites. A complementary component aims to test the pathogenicity of these fungal strains.

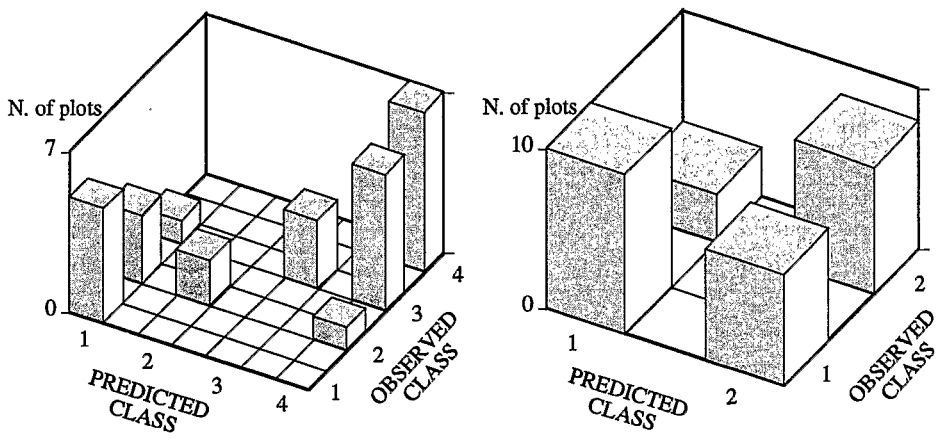


Fig. 5 Predictions of rust and anthracnosis levels in the different plots, using models based on data from which each site was deleted in turn: number of plots for a given predicted and observed class (see text for details on the procedure)

In pursuing these studies, attention will be given to temporal processes (dynamics of infection, climatic events triggering particular epidemiological phases, etc.) and spatial processes (study of phenomena at the scales of the plot, the tree and the branch). This approach, carried out in New Caledonia, will subsequently be validated in other ecological contexts within the Pacific.

Appendix: Connected analyses description

Various analytical tools are available to describe the common structure of two quantitative tables formed by two sets of variables measured on the same stands (Chessel and Mercier, 1993). These tools reflect several possible strategies. In our cases, the number of samples (11 for the between-site tables, 28 for the within-site tables) is of the same order of magnitude as the number of variables of each table. Therefore, any attempt to express one table as a function of the other, as in canonical correspondence analysis (Ter Braak, 1986), would be stymied by the presence of multicollinearity (Mercier et al., 1992). Canonical correlation analysis, in which correlations are maximized between two axes (linear combinations of the variables) computed from the two tables (Saporta, 1978), would face the same problem. Therefore, axes for each table were chosen so as to maximize their covariance. The result is a compromise between the main structure of the Pathology table (reflected by the variance of the plots scores on the pathology axis), the main structure of the Environment table (reflected by the variance of the plots scores on of the environment axis), and the common ordination of the different plots (reflected by the correlation of the scores of plots on the two axes). A mathematical description of such an approach, referred to as the 'symmetric connected analysis' of two data sets, is provided by Tucker (1958), by Mercier (1991) and in the review of Chessel and Mercier (1993).

Connected analysis computes the principal axes (linear combinations of the rows or columns) of the covariance table arising from two sets of variables. In our cases, these 'co-structure axes' can be expressed as linear combinations of the 11 environmental variables in an 11-dimensional space, or as linear combinations of the 8 pathological variables in an 8-dimensional space. Reciprocally, the initial variables can be expressed as linear combinations of the co-structure axes (Figs 2A, B, 3A, B). In both spaces defined by the two sets of variables, the points corresponding to the plots or sites can be projected onto the subspaces defined by successive co-structure axes. These projections make it possible to establish graphical representations of the two data sets (Figs 2C, 3C). In these figures, the spread of the projected points within each space reflect how the variance of each set is taken into account. The similarity of the normalized coordinates of the points in the two subspaces reflect the magnitude of correlation in the connected analysis.

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