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Variation in virulence among Rigidoporus lignosus and Phellinus noxius isolates from West Africa[1]

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Abstract

Pathogenicity of isolates of the root rotting fungi *Rigidoporus lignosus* and *Phellinus noxius* was tested on rubber seedlings (*Hevea brasiliensis*) by artificial inoculation under controlled conditions. Variation in virulence within the isolates tested was demonstrated and discussed.

1 Introduction

In the zone of sub-equatorial dense forest, root rot fungi constitute one of the main disease problems affecting rubber plantations. Since the beginning of this century, several studies concerning the biology of the pathogens and the development of control methods have been performed in Southeast Asia (Fox 1977; Lim 1970; Peries et al. 1983; Peries and Irugalbandara 1973, *inter alia*). In West Africa, white and brown rots due to *Rigidoporus lignosus* (Kl.) Imaz. and *Phellinus noxius* (Corner) G. H. Cunn. respectively, have caused significant damages to rubber plantations established on cleared forest areas (Pichel 1956; Nandris et al. 1983 a) since the beginning of rubber culture in 1950. Extensive phytopathological researches have been undertaken on the pathogens, mainly in the Congo and the Ivory Coast. Various results concerning the biology, the ecology, and the epidemiology of these fungi have contributed to a better understanding of their pathogenesis and of the host-parasite interactions (Fassi 1964; Geiger et al. 1976; Martin and du Plessis 1969; Nandris 1985; Nicole et al. 1982; Pichel 1956).

However, attempts to extrapolate the methods recommended in Southeast Asia for controlling root diseases in West Africa have largely been unsuccessful. For that reason, other control measures are currently being developed in West Africa. They are based mainly on antifungal substances and on selecting resistant or tolerant rubber trees using natural inocula collected in various infested areas.

As no information on differences in pathogenicity between African isolates was available, three observations led us to investigate whether any variation in virulence exists: first, it could be presumed that the large spectrum of soil and climatic conditions under which these root pathogens have been observed and the wide host range recorded in West Africa, could be a source of variability; secondly, epidemiological surveys in Ivory Coast's rubber plantation have demonstrated differences in the course of infection among different foci of the same pathogen (Nandris et al., 1983 a); finally, evidence of variation in pathogenicity among different isolates of the root rot fungi *Armillaria mellea* (Vahl ex

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Fr.) Kummer (Guillaumin and Pierson 1978; Morrison 1982; Raabe 1967; Redfern 1975; Rishbeth 1982), *Heterobasidion annosum* (Fr.) Brefeld (Kuhlman 1970; Worrall et al. 1983) in temperate countries and *Rigidoporus lignosus* in Sri Lanka (Liyanage et al. 1977) has already been reported.

In the Ivory Coast, previous works have exemplified the effect of soil characteristics on the pathogenicity of *R. lignosus* (Nandris et al. 1981). These results have led to the development of a standardized system of rubber seedling inoculation that uses water saturation of the soil in the vegetation tubs to simulate a micro-aerophilic environment (Nandris et al. 1983b). Since 1981 this method has been used to investigate the existence of pathogenic variants of *R. lignosus* and *P. noxius*. The results of these tests are reported in this paper.

2 Materials and methods

2.1 Preparation of inoculum

The various isolates of *R. lignosus* and *P. noxius* originated from three countries of West Africa – Ivory Coast, Liberia, Cameroon (Table 1). Isolates were collected from roots of various trees encountered in primary forest, and from *Hevea brasiliensis* (rubber tree), *Tectona grandis* L. (teak) and *Cedrela odorata* L. (Cedro).

Table 1

Origins of the various isolates tested

	Isolate (No)	Country of origin	Host	Collection Date
Rigidoporus lignosus	1	Southeast Ivory Coast	*Hevea brasiliensis*	1978
	9	East Ivory Coast	Primary forest tree	1978
	13	West Ivory Coast	Primary forest tree	1978
	21	Southeast Liberia	*Hevea brasiliensis*	1979
	37	Southeast Ivory Coast	*Hevea brasiliensis*	1981
	38	Cameroon	*Hevea brasiliensis*	1981
	42	Southwest Ivory Coast	*Hevea brasiliensis*	1981
	52	East Ivory Coast	*Tectona grandis*	1981
Phellinus noxius	7	West Ivory Coast	Primary forest tree	1978
	45	East Ivory Coast	*Cedrela odorata*	1981
	31	Southwest Ivory Coast	*Hevea brasiliensis*	1980
	4	Southeast Ivory Coast	*Hevea brasiliensis*	1978
	35	East Ivory Coast	*Hevea brasiliensi*	1981
	39	Cameroon	*Hevea brasiliensis*	1981
	2	Southwest Ivory Coast	*Hevea brasiliensis*	1977
	32	Southwest Ivory Coast	*Cedrela odorata*	1980

Segments of rubber tree branches (8 cm long, 2 cm diam.) were sterilized in Roux flasks (1 l) with 0.5 l of water at 110°C for 1.5 h, and seeded with eight mycelial starter disks cut from malt-agar cultures of each fungus. Since the wood degrading abilities of these two fungi differ considerably, sticks seeded with *P. noxius* were incubated for five months at 28°C whereas those seeded with *R. lignosus* were incubated for eleven months at the same temperature, in order to obtain comparable inoculum potentials.

2.2 Method of inoculation

Young rubber trees (clone GT_1) growing under controlled greenhouse conditions were inoculated using a technique previously described (Nandris et al. 1983b). Plant growth tubs (1×1×1 m) were filled layer by layer with unsterilized forest soil, watered to satura-

tion. Soil moisture level was checked every two days using a neutron moisture gauge (Solo 20, Nardeux Usine ZI 37600, BP 109 LOCHES France). Each year, (in August) before beginning a new experiment the tubs were emptied, washed and re-filled with fresh forest soil collected from the same area.

Each tub contained 30 one-month-old rubber tree seedlings. Plants were inoculated by placing five infected sticks close to the tap root of each seedling at 20 cm depth. Any plant that died during the course of the experiment was uprooted and examined for disease quantification. To evaluate the early stages of infection, ten plants chosen at random were excavated and examined two months after inoculation. At the termination of the experiment – 5 months after inoculation – the surviving plants were removed from the soil and examined. Non-inoculated seedlings and seedlings inoculated with sterile sticks were used as controls.

2.3 Evaluation of pathogenicity

In order to quantify the rate of infection of each inoculated plant dead or living, several criteria were used: time between inoculation and plant death, presence of rhizomorphs on roots, length of stem and tap root, occurrence of reactional rhizogenesis i. e. neo-formation of lateral roots that replaced the original decayed tap root, colonization rate of root tissues.

A 0–9 scale was used for rating the severity of the attack of each plant (Table 2). The virulence of each isolate was determined by calculating the severity index (S.I.) as the mean of the severity scores of the seedlings recorded after either 2 or 5 months. Statistical treatment of the data was made using a multivariate (principal component) analysis.

The experiments with isolates of *R. lignosus* were repeated each year for 3 years, those with *P. noxius* for only two successive years.

Table 2

Scales used for rating the severity of attack

Rigidoporus lignosus	*Phellinus noxius*
0 no mycelium on roots	0 no mycelium on roots
1 non aggregate hyphae	1 mycelial crust withouth root penetration
2 rhizomorphs without root penetration	2 well-formed mycelial crust without root penetration
3 rhizomorphs and penetration	3 mycelial crust and penetration
4 rhizomorphs and localized necrosis	4 mycelial crust and localized necrosis
5 rhizomorphs and partial root decay < 20 %	5 mycelial crust and partial root decay < 20 %
6 rhizomorphs and 20 to 50 % root decay	6 mycelial crust and 20 to 50 % root decay
7 rhizomorphs and root decay > 50 %	7 mycelial crust and root decay > 50 %
8 foliar symptoms	8 foliar symptoms
9 plant death	9 plant death

3 Results

3.1 Virulence of Rigidoporus lignosus

Within two months, all isolates had developed rhizomorphs at the surface of tap roots of all plants inoculated (Table 3). Fungal penetration was observed in all plants except for a few inoculated with isolates 1 and 37. Differences in virulence are obvious considering the variation in root necrosis (8 to 70 %) and in mortality (0 to 50 %) inflicted by the various isolates. Weekly measurements of height of seedlings showed that, from two months on, inoculated plants were smaller than controls (Fig. 1). The differences become more accen-

Table 3

Incidence of isolates of Rigidoporus lignosus on rubber seedlings, 2 months after inoculation
(Plants showing foliar symptoms at the sampling date died in less than 2 weeks)

Isolate (No)	Severity index (a)	% of plants showing: (a)				Tap root necrosis ratio (%) (a)	Mortality rate (%) (a)
		Rhizomorphs on root system	Root penetration	Foliar symptoms	Reactional rhizogenesis		
42	7.7	100	100	20	10	70	30
13	7.7	100	100	0	0	75	50
52	7.5	100	100	20	10	72	20
38	7.4	100	100	0	10	70	40
21	6.2	100	100	10	10	33	10
1	6.0	100	90	0	0	40	20
9	5.7	100	100	10	10	31	10
37	3.3	100	70	0	20	8	0

(a) = mean of 10 plants
(b) = proportion between colonized tissues and total rap root length.

tuated towards the end of the experiment but, for some isolates, there was no relationship between virulence (as measured by the various criteria used in this study) and plant growth reduction.

Comparing the parameters recorded at 2 and 5 months, infection rate of all isolates increased with time although the differences in virulence between them remained clear (Table 4).

Secondary root formation was observed on few of the inoculated plants but no clear cut differences could be demonstrated between isolates with the exception of isolate 37 (60% of the number of plants examined). The order of virulence of the different isolates changed with time but strains 9 and 37 kept their rank as the least virulent ones. Six out of the eight isolates were extremely virulent as indicated by severity indexes of 8 or more and by a mortality rate of 70 to 95%.

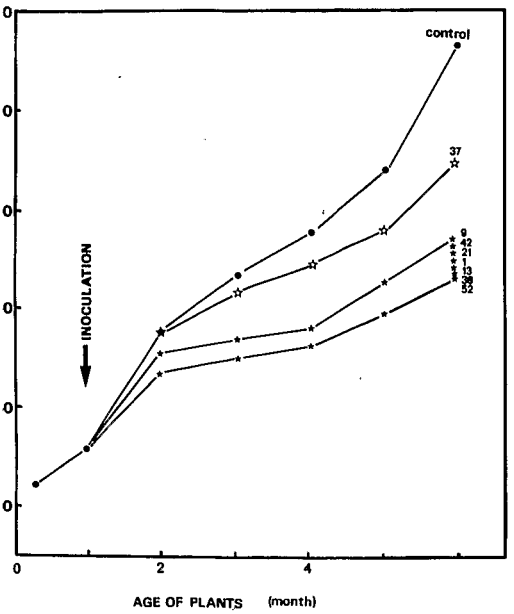
Plotting mortality against time (Fig. 2) indicated that during the first three months, a great proportion of plants died, the mortality decreases slightly towards the end of the experiment. Strains 52 and 42 are particularly aggressive killing 70% or more of the inoculated plants within the first three months. Statistical analysis (Fig. 3) confirmed the varia-

Table 4

Incidence and severity of isolates of Rigidoporus lignosus on rubber seedlings, 5 months after inoculation

Isolate (No)	Severity index (a)	% of plants showing: (a)				Tap root necrosis ratio (%) (a)	Mortality rate (%) (a)
		Rhizomorphs on root system	Root penetration	Foliar symptoms	Reactional rhizogenesis		
52	8.9	100	100	0	0	91	95
13	8.7	100	100	0	5	78	85
42	8.7	100	100	0	5	79	90
1	8.4	100	100	0	10	72	75
38	8.3	100	100	5	0	85	70
21	8.1	100	100	0	15	61	70
9	7.2	100	100	5	10	45	45
37	5.5	100	90	0	60	32	10

(a) = mean of 20 plants



1. Growth of rubber trees after inoculation with eight *doporus lignosus* strains. The stem length of each plant was measured each week

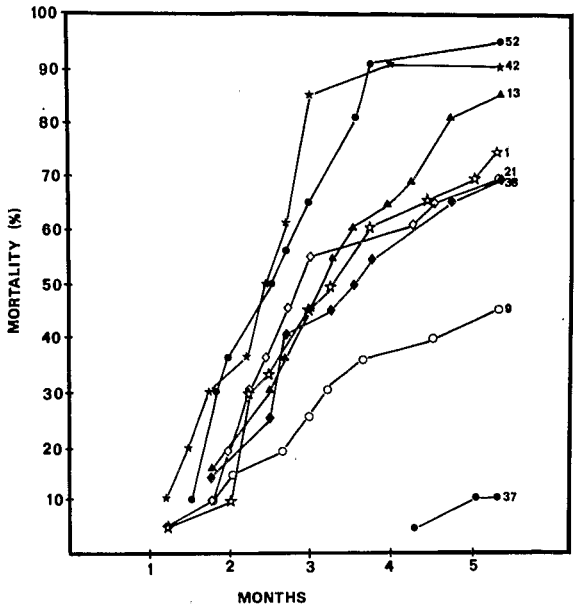


Fig. 2. Rates of mortality of rubber plants inoculated with isolates of *Rigidoporus lignosus* (mean of 20 plants)

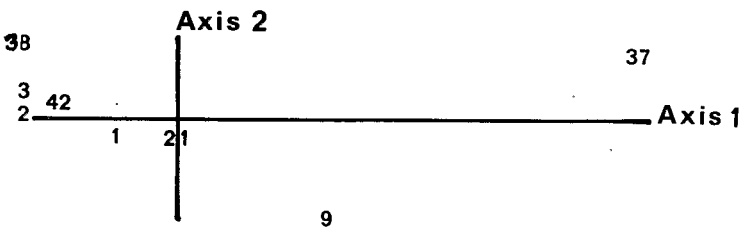


Fig. 3a. Position of each isolate on the plan 1–2 of the principal component analysis, five months after inoculation with *Rigidoporus lignosus* isolates. The most pathogenic strains lie on axis 1-negative

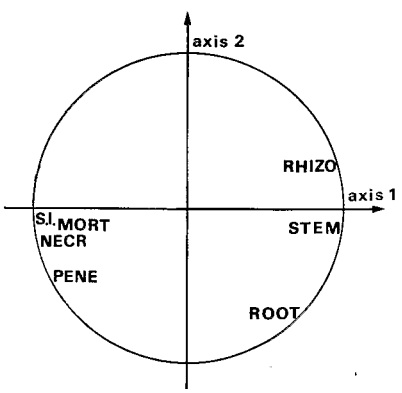


Fig. 3b. Position of the variables on the correlation circle. MORT = mortality; NECR = root necrosis; PENE = root penetration; RHIZO = reactional rhizogenesis; ROOT = length of root; S. I. = severity index; STEM = length of stem; variables MORT and S. I. have nearly the same coordinates

Table 5

Severity index of R. lignosus isolates tested on H. brasiliensis seedlings
(Results obtained after 5 months of inoculation in each of three years)

R. lignosus Isolate (No)	Severity Index[1]		
	1982	1983	1984
1	6.3	8.4	8.4
21	6.0	8.1	8.2
37	4.4	5.4	5.4
38	6.4	8.3	8.3
52	7.8	8.6	8.9
13	not tested	7.1	8.7

[1] mean of 20 plants

bility in pathogenicity described before. Thus, plan 1–2, which accounts for 85 and 12 % of the total variability, represents the structure of the population well, but it does not yield any new information with regard to the classification of isolates, beyond that obtained with the severity index.

Comparing the results obtained for each of the three successive annual experiments (Table 5), it is important to notice that the S.I. of individual *R. lignosus* isolates was particularly stable over the last two years (except for isolate 13). Differences recorded in 1982 go back to perfection of the technique, but the ranking of isolates was similar.

3.2 Virulence of Phellinus noxius

In comparison to *R. lignosus*, isolates of *P. noxius* showed a much greater variability in virulence (Tables 6 and 7). This was particularly evident when mycelial development on roots and host-penetration were considered. Further more it was observed that attacks were definitely slower and less serious than those of *R. lignosus*; the mortality caused by the most aggressive isolate did not exceed 45 %, compared to a mortality of 75 % or more for 4 out of the 8 isolates of *R. lignosus*. Although mycelial development on roots for isolates 45, 32, 35 and 4 was comparable, mortality inflicted by these strains differed widely (10 to 45 %) indicating differences in pathogenicity. Infection of root systems by

Table 6

Incidence and severity of isolates Phellinus noxius on rubber seedlings, 2 months after inoculation

Isolate (No)	Severity index (a)	% of plants showing: (a)				Tap root necrosis ratio (%) (a)	Mortality rate (%) (a)
		Rhizomorphs on root system	Root penetration	Foliar symptoms	Reactional rhizogenesis		
45	6.3	100	100	10	0	40	40
32	3.6	80	60	0	0	21	20
2	3.4	50	50	0	0	28	20
4	3.0	70	70	0	0	0	0
35	1.2	30	0	0	0	0	0
7	0.8	30	10	0	0	3	0
39	0.3	10	10	0	0	0	0
31	0.2	20	0	0	0	0	0

(a) = mean of 10 plants

Table 7

Incidence and severity of isolates of Phellinus noxius on rubber seedlings, 5 months after inoculation

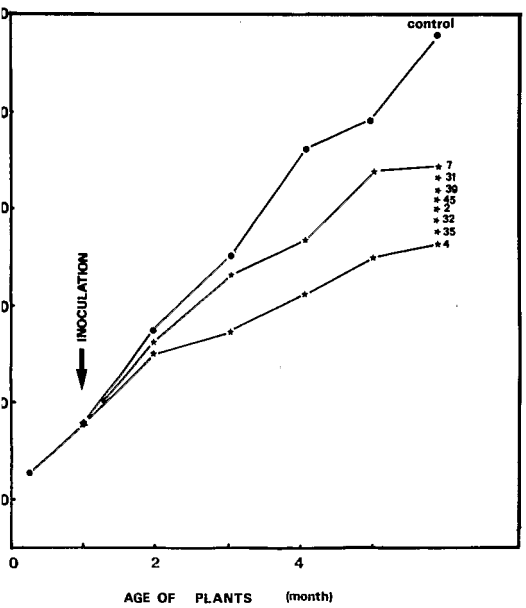
Isolate (No)	Severity index (a)	% of plants showing: (a)				Tap root necrosis ratio (%) (a)	Mortality rate (%) (a)
		Rhizomorphs on root system	Root penetration	Foliar symptoms	Reactional rhizogenesis		
45	6.5	90	80	20	5	53	45
32	6.2	95	95	5	25	24	35
35	5.1	85	80	15	30	30	15
4	4.8	85	80	5	5	22	10
2	4.5	65	65	5	25	16	20
7	2.6	60	60	5	5	7	0
39	1.5	35	30	0	10	5	5
31	0.4	10	10	0	0	0	0

(a) = mean of 20 plants

P. noxius reduced seedling growth for all isolates tested (Fig. 4); however, this reduction was not directly related to the virulence of individual isolates.

Seedling mortality due to isolates 4, 7, 31 and 39 was low or zero during the first months and increased little with time. On the other hand, mortality of plants infected by isolates 2, 32 and 45 rose sharply during the first three months, and remained stable afterwards (Fig. 5).

The statistical analysis of these data separated isolates in a distinct order (Fig. 6). Isolates 45 and 32 were discriminated although they had nearly similar severity indexes. Iso-



4. Growth of rubber trees after inoculation with eight *linus noxius* strains. The stem length of each plant was measured each week

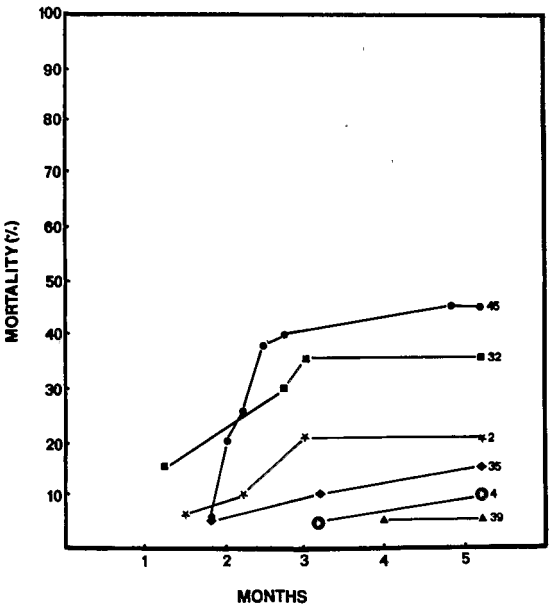


Fig. 5. Rates of mortality of rubber plants inoculated with *Phellinus noxius* strains (mean of 20 plants)

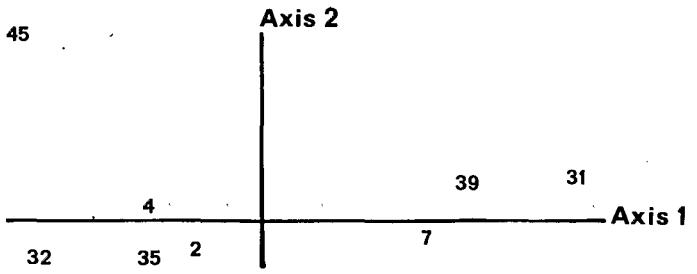


Fig. 6a. Position of each isolate on the plan 1–2 of the principal component analysis, five months after inoculation with *Phellinus noxius* isolates

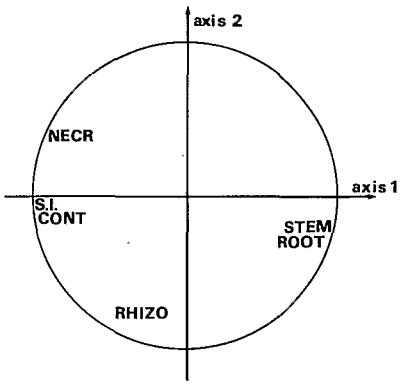


Fig. 6b. Position of the variables on the correlation circle. CONT = contamination; NECR = root necrosis; RHIZO = reactional rhizogenesis; ROOT = length of root; S.I. = severity index; STEM = length of stem

lates 4, 35 and 2 form one set distinct from isolates 7, 39 and 31. It is also interesting to note that strains 31 and 32, which differ greatly in pathogenicity, were nevertheless isolated from the same rubber plantation.

4 Discussion

To distinguish differences in virulence among fungal isolates we attempted to approach natural conditions. Therefore the inoculum was placed close to the tap root instead of inserting it, to avoid wounding the roots (KUHLMAN 1970; WORRALL et al. 1983). Indeed insertion of inoculum creates an artificial system and greatly enhances the infection (MERRILL and SHIGO 1979).

Generally, the virulence of root pathogens is estimated at the termination of the experiment which corresponds to the end of a sequence of wood decay events (MERRILL and SHIGO 1979). However, previous work had demonstrated that rhizomorphogenesis and initial penetration of *R. lignosus* occurred during the first two months (NICOLE et al. 1983). Therefore it was necessary to appraise the initial stages of pathogenesis. So, sampling during the course of the experiment and following the mortality rate of the inoculated plants, led us to a better description of the successive stages of infection for each isolate tested.

As all the plants were infected by all isolates of *R. lignosus* during the first weeks of the experiment, it appeared that no relation existed between pathogenicity and the capacity to produce rhizomorphs. This is in agreement with observations made by GUILLAUMIN and PIERSON (1978) on French isolates of *Armillaria mellea*, but contrasts with observations made on British isolates of *Armillaria* (MORRISON 1982). Secondly, as root penetration

generally occurred even with the least virulent strains (no. 31), it can be assumed that differences in pathogenicity would be revealed mainly during tap root colonization. On this point, the speed of development of root necrosis toward the collar seemed to play an important role in pathogenesis. Indeed, as established by GARRETT (1970) for the "ectotrophic infection habit", the more rapidly a parasite progresses into the tap root, the less time the plant has to react.

Comparing the ectotrophic development of *P. noxius* on plant roots (NANDRIS 1985), it appears that in these experiments, contact with the roots is asynchronous and accordingly the initial moment of infection will fluctuate. This may be the result of the biology of the fungus which does not possess a mycelial structure comparable to rhizomorphs of *R. lignosus*, but contacts the roots by means of a crusty mycelial sleeve which has a slower rate of development. This fact could explain the scattering of the results scored for each isolate of *P. noxius* at the termination of the experiment, and may involve an underestimation of the pathogenic potential of this fungus. Actually, failure to make contact with the host may be the weak point in the success of artificial inoculation with *P. noxius*.

With both pathogens, the mortality rate declined from the third month on, suggesting a reduction in fungal activity. This phenomenon has been described in previous works with rubber seedlings artificially infected by *R. lignosus* (NICOLE et al. 1983) and with *Eucalyptus* infected by *Armillaria* (LEACH 1937). To explain it, two hypotheses are proposed: a decrease of the fungal activity due to the exhaustion of trophic reserves in the woody sticks of the inoculum (GEIGER et al. 1986b), a delay of the colonization of the roots by the fungus induced by the development of host resistance that was demonstrated at molecular and morphological levels (GEIGER et al. 1986a; NICOLE et al. 1986) and confirmed by epidemiological observations in rubber plantation (NANDRIS 1985). The balance between mechanisms of fungal aggression and of plant reactions determines whether the host will survive.

In conclusion, our experimental system allowed us to describe differences in virulence among isolates, both of *R. lignosus* and of *P. noxius*. No relationship was detected between the virulence of the isolates and their geographic origin of the plant species from which the fungus was isolated. Similar results during successive years confirmed the stability of pathogenicity of the isolates which contrasts with the observations made by RISHBETH (1983), and demonstrate evidence of constitutive variations between them.

Finally, from a practical point of view, this heterogeneity in pathogenicity among isolates requires that many isolates should be tested when a control method is developed. This fact must be taken into account particularly in the case of resistance breeding. Investigations are currently in progress to evaluate the pathogenic variability among isolates collected on the same rubber estate. Furthermore the relationship between physiological characteristics of the fungi and their pathogenicity are to be studied in order to explain the origins of this variation.

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Summary

Pathogenicity of isolates of *R. lignosus* and *P. noxius* collected from rubber and forest trees, was tested on young rubber plants (*Hevea brasiliensis*) using a technique of artificial inoculation under controlled conditions (e. g. soil moisture). After two months, almost all the plants inoculated with various isolates of *R. lignosus* were infected and differences in virulence were apparent. After five months, these differences were reflected in the mortality rates of the inoculated plants. For some isolates the attack begins early and abruptly, whereas for others, symptoms appear more gradually. With *P. noxius*, differences appear also very distinctly in the pathogenicity among the isolates during

the entire duration of the experiment. Principal-component analysis of the data recorded has demonstrated variations in pathogenicity among populations of *R. lignosus* and of *P. noxius*. This fact must be borne in mind when control methods of these diseases of rubber tree are developed.

Résumé

Variation pathogénique entre des isolats de Rigidoporus lignosus et Phellinus noxius d'Afrique occidentale

Le pouvoir pathogène d'isolats de *R. lignosus* et *P. noxius*, provenant de racines infectées d'*Hevea brasiliensis* et d'arbres de forêt, a été testé sur de jeunes plants d'hévéa. Les inoculations artificielles ont été réalisées, sous serre, en controllant strictement l'humidité de la terre des bacs. Deux mois après le début de l'expérimentation, la quasi-totalité des plantes inoculées avec les divers isolats de *R. lignosus* sont contaminées par les rhizomorphes et infectées au niveau du pivot. Cependant, des différences dans le pouvoir pathogène des souches infectantes sont déjà observables. Après cinq mois, ces différences sont confirmées et apparaissent en particulier au niveau des cinétiques de mortalité des plantes inoculées correspondant à chaque isolat. Ainsi pour certains, les attaques sont précoces et sévères alors que pour d'autres, les symptômes de l'infection apparaissent plus graduellement. En ce qui concerne *P. noxius*, des différences dans le pouvoir pathogène des isolats testés ont été également mises en évidence. Leur amplitude est cependant inférieure a celle observée pour *R. lignosus*, en raison de l'hétérogénéité liée à la contamination initiale des pivots d'hévéa par le manchon mycélien caractéristique de *P. noxius*. L'analyse en composantes principales (A. C. P.) des modalités des multiples variables utilisées pour quantifier le développement des infections dans le système racinaire des jeunes plants, confirme les variations de pouvoir pathogène au sein des populations parasitaires étudiées. Ce résultat doit être désormais pris en compte au moment de la conception puis de la réalisation des méthodes de lutte chimique et génétique contre ces maladies racinaires de l'hévéa.

Zusammenfassung

Schwankungsbreite in der Virulenz bei Isolaten von Rigidoporus lignosus und Phellinus noxius aus West-Afrika

Die Pathogenität von *R. lignosus*- und *P. noxius*-Isolaten aus Kautschuk und aus Waldbäumen wurde mittels künstlicher Inokulationen unter kontrollierten Bedingungen (insbesondere bei gleicher Bodenfeuchte) an jungen *Hevea brasiliensis*-Pflanzen ermittelt.

Nach 2 Monaten waren fast alle mit verschiedenen *R. lignosus*-Isolaten inokulierten Pflanzen befallen und Virulenzunterschiede wurden offenkundig. Nach 5 Monaten spiegelten sich diese Unterschiede in entsprechenden Mortalitätsraten der inokulierten Pflanzen wider. Bei einigen Isolaten setzte der Befall sehr früh und sehr plötzlich ein, bei anderen erschienen die Symptome nach und nach. Auch bei *P. noxius* waren Pathogenitätsunterschiede zwischen den Isolaten während der gesamten Versuchsdauer deutlich ausgeprägt. Die statistische Auswertung der Daten bestätigte die Existenz von Pathogenitätsunterschieden zwischen den getesteten Populationen von *R. lignosus* und *P. noxius*. Diese Gegebenheiten sollten bei der Entwicklung von Bekämpfungsmethoden beachtet werden.

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