A comparative study of yellow fever in Africa and South America

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In order to look for an ecoepidemiological model of sylvatic yellow fever (YF) transmission in South America, differences from and similarities to available African YF data are considered. Strains from both areas, representing various topotypes, are distinct serologically, genetically and biochemically. In Africa, all vector mosquitoes are *Aedes* species, some related to the forest cycle and others responsible for the transmission in dryer areas. In South America, and particularly in Brazil, the main vector is *Haemagogus janthinomys. Hg. albomaculatus* has been incriminated in human peridomestic transmission in Central Amazonia. In the two continents, monkeys are the only regular vertebrate hosts of YF but the indigenous neotropical monkeys, show higher mortality rates. The South American and African vectors are diurnal and crespuscular/nocturnal in habit, respectively. The urban vector (*Ae. aegypti*) has the same habits in both continents, but its competence in transmitting the virus is very variable, and no urban epidemic has been notified in South America since the 40s. A general ecoepidemiological model was elaborated to explain the maintenance and circulation of YF virus in West and Central Africa, which are related to the phytoclimatical regions. Because no such hypothesis has yet been presented in the case of YF in South America, we tested this with the available data from Brazil. All occurrences (of which 386 were lab-confirmed) were distributed in five phytogeographical zones: dense rain forest (189), open rain forest (30), savannah with gallery forest (147), ecotones (10) and decidual seasonal forest (7). For each of these zones mean intervals between years with occurrences of YF were estimated. They were all found to be lower than 3 years, and lower than 5 years when standard deviation was added. Despite the close values obtained for the means, the distribution of the years as a function of number of occurrences of YF showed two groups: *a*) gallery forest and dense forest and *b*) open forest and ecotones. However, more data are necessary to enable the study of such variations which are thought to be related to ecological differences in YF transmission.

Até o presente não foi elaborada nenhuma hipótese válida para explicar a manutenção e os vários modos de transmissão do vírus da febre amarela na América do Sul. Um primeiro passo na elaboração de tal hipótese é analisar os dados disponíveis à luz do esquema eco-epidemiológico estabelecido para FA na África, há muito mais tempo estudada. Embora as amostras sejam geneticamente distintas, as maiores diferenças entre FA nos dois continentes evidenciam-se nos aspectos ecológicos, e particularmente na natureza e comportamento dos vetores. Na África, esses são mosquitos do gênero **Aedes**, *com hábitos principalmente crepusculares ou noturnos, enquanto, nas Américas, os vetores pertencem aos gêneros* **Haemagogus** *e* **Sabethes**, *mosquitos diurnos. O vetor urbano da FA é o mesmo em ambos os continentes:* **Aedes aegypti**. *Os hospedeiros vertebrados são macacos em ambos os casos. Os dados disponíveis de casos humanos confirmados e outras evidências de circulação da FA no Brasil, no período de 1954 a 1991, foram agrupados segundo localização em cinco grandes zonas fitogeográficas. Para cada zona, foi avaliado o intervalo médio entre manifestações de FA. Os valores obtidos não ultrapassaram três anos, ou cinco, levando em conta os desvios padrões. A distribuição dos anos, em função do número de casos notificados, também sugere diferenças entre dois grupos: i) floresta tropical densa e florestas galerias, e ii) floresta tropical aberta e ecótonos. Somente estudos ecológicos mais detalhados permitirão estabelecer um esquema, com o objetivo de mapear corretamente as regiões de maior risco epidemiológico.*

The yellow fever (YF) virus was among the world's first isolated arboviruses (1), and at present it is among the most studied, either in the laboratory, or in nature.

A great number of strains were isolated during epidemics, interepidemic periods and during experimental studies. Epidemiological studies, related or not to the use of vaccine, have been done in almost all endemic areas. Reviews have been published (2), including the more recent developments on molecular biology (3). Thus, are there still new facts to be discovered about YF?!

Among the questions which have not received satisfactory answers are the following:

a) What are the eco-epidemiological factors which determine the transmission mode of YF?

b) What are the ecological factors which determine the geographical distribution of YF?

Because of the different answers obtained when dealing with New World or Old World ecoepidemiology of YF, the following review was written to emphasize the comparative aspects between the two main areas where YF is encountered: West and Central Africa and South America.

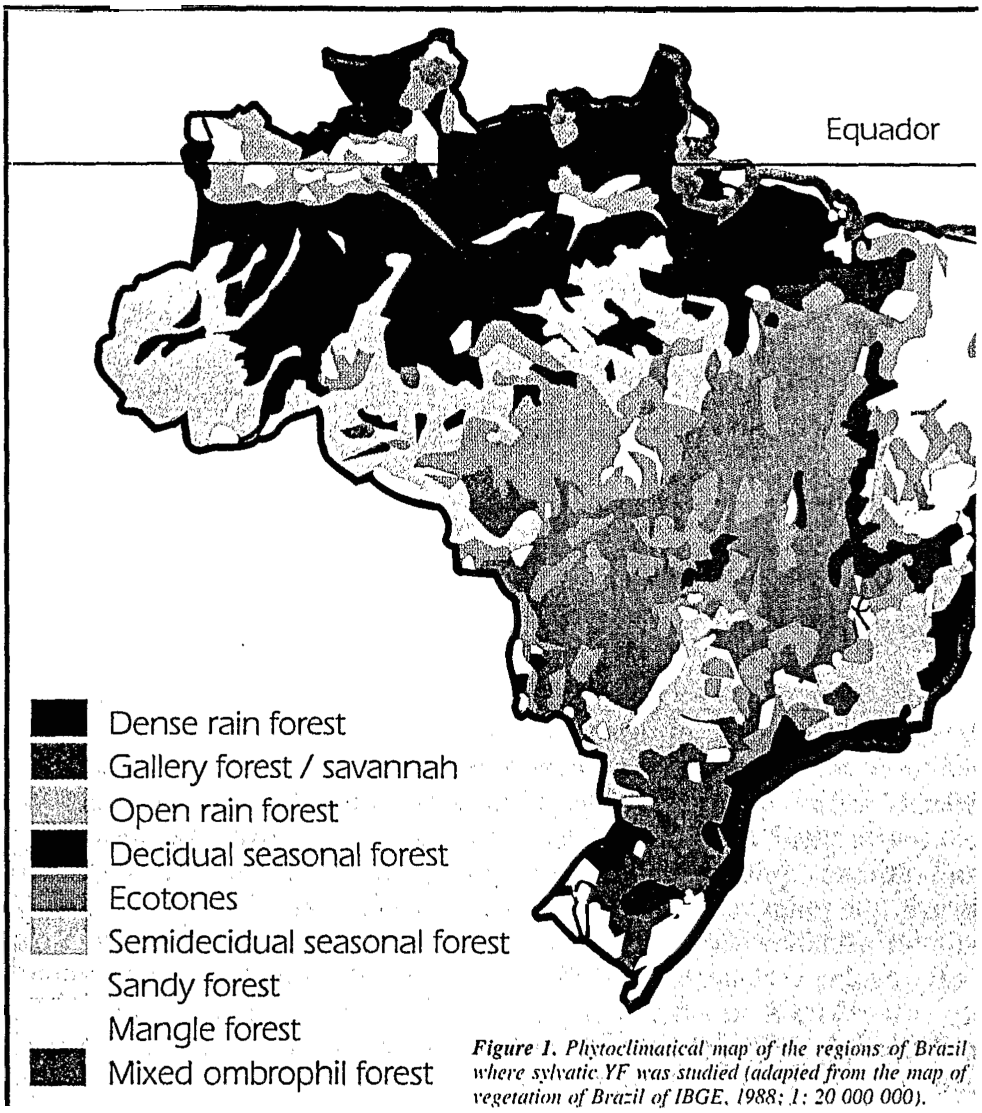

Figure 1. Phytoclimatical map of the regions of Brazil where sylvatic YF was studied (adapted from the map of vegetation of Brazil of IBGE, 1988; 1: 20 000 000).

Elements of comparison

Many similarities and differences may be noted in relation to the strains, hosts, sylvatic and urban cycles, and ecoepidemiological models.

The strains of YF virus

Many authors have contributed to the knowledge of the nucleotide base sequences of RNA and proteins of the virus (4-11).

Distinctive topotypes have been characterized by oligonucleotide fingerprinting for strains isolated in distinct regions and/or periods in both continents (8,12,13).

The South American strains were also distinctive from the African ones when their proteins were submitted to immunochemical analysis (8,12).

The vertebrate hosts

Man — In the Americas as in Africa, man is an accidental host of the sylvatic YF virus. He becomes infected sporadically when he enters the endemic zone.

When favorable ecoepidemiological conditions are met, i.e. high densities of the urban vector *Ae. aegypti* and low rate of serological protection of the people, epidemics can occur. The sick man is the carrier of the virus from the sylvatic environment to the city. In Africa, the "intermediate" vector *Ae. furcifer* also plays the role of carrier of the virus into towns (8,14). In Brazil, the mosquito *Ha. albomaculatus* has been suspected to play the same role in rural peridomestic environment (15,16).

No histopathological or clinical differences have been noted between YF cases of Africa and South America (17, 18).

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Table 1 — YF isolations, and human cases diagnosed by histopathology or seroconversion in Brazil, 1954 - June, 1992; notifications of cases already reported in the literature are referenced; an * means that the diagnosis was confirmed by another method (isolation of virus or serology); "s", "h", and "c" are isolations from a sentinel monkey, histological diagnosis, and seroconversion in monkey, respectively.

		Number and origin of strains					
			Man				
Year	*Place/State*	*isol.*	*histop.*	*serol.*	*Monkey*	*Mosquitoes*	*References*
1954	Oriboca (PA)	10					(43,44)
1955	Oriboca (PA)	1			2s	4	(43,44)
1955	Apeú (PA)	11		2c		2	(43,44)
1955	Lazarópolis do Prata (PA)					1	(43)
1955	Utinga, Belém (PA)					7	(43)
1955	Ananindeua (PA)					1	(43)
1956	Acara (PA)		1				
1956	Porto Velho (RO)		1				
1957	Acara (PA)		1				
1957	Campo Grande (MS)		4				
1957	Coxim (MS)		1				
1957	Jataí (GO)		1				
1957	Manaus (AM)		1				
1957	Mineiros (GO)		1				
1957	Rosário Oeste (MT)		1				
1958	Anápolis (GO)		1				
1958	Aquidauana (MS)		1				
1958	Campo Grande (MS)		3				
1958	Coromandel (MG)		1				
1958	Goiânia (GO)		5				
1958	Ipameri (GO)		5				
1958	Ipora (GO)		2				
1958	Paracatu (MG)		2				
1958	Pires do Rio (GO)		1				
1958	Prata (MG)		1				
1958	Rio Verde (GO)		2				
1958	Uberlândia (MG)		1				
1959	Anápolis (GO)		1				
1959	Corinto (MG)		1				
1959	Cristalina (GO)		1				
1959	Patos de Minas (MG)		1				
1960	Belém-Brasília km 94 (PA)				1s		
1960	Marabá (PA)		1				
1961	Boa Vista (RR)		1				
1961	Lábrea (AM)		1				
1962	Belém-Brasília km 87 and km 94				2		
1962	São Paulo de Olivença (AM)		1				
1964	Barra de Bugres (MT)		1				
1964	Boa Vista (RR)		1				
1964	Campo Grande (MS)		6				
1964	Cuiabá (MT)		2				
1964	Mineiros (GO)		2				
1964	Utinga (PA)				1s		(45)
1965	Anápolis (GO)		1				
1965	Aquidauana (MS)		1				
1965	Bela Vista (MS)		1				
1965	Boa Vista (RR)		1				
1965	Campina Verde (MG)		1				
1965	Campo Grande (MS)		3				
1965	Ceres (GO)		1				
1965	Ituiutaba (MG)		2				
1965	Porto Nacional (TO)		1				
1965	Uberaba (MG)		1				
1965	Veríssimo (MG)		1				
1966	Anchieta (SC)		1				
1966	Barcelos (AM)		1				(46)
1966	Cascavel (PR)		3				
1966	Chapecó (SC)		1				
1966	Guaraniaçu (PR)		1				
1966	Iraí (RS)		2				
1966	Maravilha (SC)		1				
1966	Medianeira (PR)		1				
1966	Mondaí (SC)		2				
1966	Palma Sola (SC)		2				
1966	Passo Fundo (RS)		1				
1966	Piratuba (SC)		1				

(to be continued)

Sylvatic vertebrates — In both continents all monkey species are susceptible to YF virus. However, there are differences in lethality. In South America, only *Cebus* species (Cebidae) show low mortality rates. Other monkeys, like *Alouatta, Ateles* or the Callitrichidae are frequently encountered infected or immune but show higher mortality rates (19).

African monkeys do not show high lethality to YF infection (20).

Occasional and experimental hosts — A great number of vertebrate species were experimentally viremic or occasionally found infected in nature. More notable are marsupials (*Didelphis* sp. and *Caluromys* sp.) and rodents in South America (19), and the lemurs "Galagos" and "Potos" (20) and even bats in Africa (21).

The actual role of marsupials in the maintenance cycle of YF in South America is not known. In Africa, the nonsimian hosts are not considered to be important.

The arthropod hosts

Confirmed sylvatic hosts — In the New World the confirmed sylvatic vectors are *Haemagogus* species (*Hg. janthinomys, Hg. spegazzinii, Hg. albomaculatus* and *Hg. leucocelaenus* in Brazil), and *Sabethes chloropterus* (16,22).

In Africa the vectors are: *Ae. africanus* in forest areas; *Ae. simpsoni* only in East Africa at the ecotone between forest and cultivated areas (*Ae. lilii*, present in West Africa, is not anthropophilous: 23); *Ae. luteocephalus* and the *Ae. furcifer-taylori* complex in tropical and sub-tropical savannahs (24).

Occasional or experimental hosts — Some neotropical mosquito species of *Aedes, Tricho-*

Table 1 (continued)

Table 1 *(cont.)*

Year	Place/State	*Number and origin of strains* Man isol.	histop.	serol.	Monkey	Mosquitoes	References
1966	Quilombo (SC)		1				
1966	São Luis Gonzaga (RS)		3				
1966	Toledo (PR)		2				
1967	Boa Vista (RR)		1				
1967	Serra do Navio (AP)					1	
1967	Tomé Açu (PA)		1				
1968	Abaetetuba (PA)	1			3		
1968	Barcarena (PA)	1			1	1	
1969	Boa Vista (RR)		2				
1969	Itacoatiara (AM)		1				
1969	Itaituba (PA)	1	1*				
1970	Marabá (PA)		1				
1970	Portel (PA)		1				
1971	Boa Vista (RR)		4				
1971	Castanhal (PA)		1				
1971	Peixe Boi (PA)	1	1				
1971	Porto Velho (RO)		3				
1971	Salinópolis (PA)		1				
1972	Boa Vista (RR)		4				
1972	Carolina (MA)			>35			(47)
1972	Coari (AM)		1				
1972	Rio Branco (AC)		1				
1972	Silvania (GO)		3				
1973	Barra do Garças (MT)		1				
1973	Boa Vista (RR)		5				
1973	Cáceres (MT)		2				
1973	Carolina (MA)		1				
1973	Imperatriz (MA)		1				
1973	Jari (PA)		1				
1973	Paracatu (MG)		2				
1973	Rio Negro (MS)		1				
1973	Numerous localities in the southern half of Goiás State (see refs.)	1	44	14c,12	1	9	(48,49)
1974	Anastácio (MS)		1				
1974	Araguaína (TO)		1				
1974	Boa Vista (RR)		1				
1974	Cáceres (MT)		1				
1974	Coxim (MS)		1				
1974	Itupiranga (PA)		1				
1974	Rio Jaburú, Ilha Gurupá (PA)	1				1	
1974	Jaraguari (MS)		1				
1974	Jardim (MS)		1				
1974	Ladário (MS)		1				
1974	Marabá (PA)		1				
1974	Ponta Porã (MS)		1				
1974	Tomé Açu (PA)		1				
1975	Manacapuru (AM)		1				
1976	Alenquer (PA)		1			3	
1977	Altamira (PA)	1	1,1*				
1977	Araquatins (TO)		1				
1977	Itupiranga (PA)		1				
1977	Marabá (PA)		4				
1977	Miracema do Norte (TO)		2				
1977	Tocantinópolis (TO)		1				
1978	Altamira (PA)		1				
1978	Araguaína (TO)		1				
1978	Belterra (PA)	2	1*	1c*		2	(50)
1978	Boa Vista (RR)		2				
1978	Caracaraí (RR)		1				
1978	Tomé Açu (PA)	3	4,1*	3			(47)
1978	Conceição do Araguaia (PA)		2				
1978	Guaraí (TO)		1				
1978	Miracema do Norte (TO)		1				
1978	Santana do Araguaia (PA)		1				
1978	Santarém (PA)		1				
1978	Irituia (PA)		1				
1978	Rio Ouro, Vila Rondon (PA)		1				
1978	Tocantinópolis (TO)		1				

(to be continued)

prosopon, *Anopheles*, *Culex*, and *Amblyomma* ticks have been occasionally found naturally infected and/or experimentally susceptible to infection (25).

In Africa, many species of mosquitoes have been found occasionally infected but the more relevant fact is the isolation of YF virus from naturally infected ticks in Central Africa (23,26).

Despite the absence of YF in Malagasy, some lemurs have been found susceptible to the virus (27). Unfortunately, it is not known if the presence of West Nile virus, of the same serological group, may prevent YF from establishing itself in case of its accidental introduction.

The mosquito *Ae. albopictus*, recently introduced and established in Brazil (28), is a good candidate to be a rural or peridomestic vector of YF (29).

The sylvatic cycles (epienzootic)

In both continents, the cycles involve canopy-frequenting primatophilous mosquitoes, and monkeys. Furthermore, the mosquitoes lay drought-resistant eggs in tree holes.

In Africa, the vectors are principally crepuscular or nocturnal in habit, but in the New World, they are diurnal. However, in both cases they bite resting monkeys either at night or during the midday hours, respectively.

The epidemics

In both continents, the YF virus is introduced into *Ae. aegypti*-infested cities by the viremic man (30).

Various strains of *Ae. aegypti* have shown significant variations of vector competence but it has been demonstrated

Table 1 *(cont.)*

Year	Place/State	Number and origin of strains: Man isol.	Man histop.	Man serol.	Monkey	Mosquitoes	References
1979	Altamira (PA)	2					
1979	Araguaína (TO)		1				
1979	Barro Alto (GO)		1				
1979	Bujaru (PA)			1			
1979	Careiro (AM)			1			
1979	Goiânia (GO)		1				
1979	Ji-Paraná (RO)		1				
1979	Manaus (AM)			1			
1979	Oriximina (PA)			1			
1979	Porto Velho (RO)		1				
1979	Santa Maria (PA)		1				
1979	Santarém (PA)		1				
1980	Altamira (PA)	1	1				
1980	Ariquemes (RO)		1				
1980	Arraias (GO)		1				
1980	Barro Alto (GO)		1				
1980	Caldas Novas (GO)		1				
1980	Crixas (GO)		1				
1980	Formosa (GO)		2				
1980	Goiás Velho (GO)		1				
1980	Goiatuba (GO)		1				
1980	Iaciara (GO)		1				
1980	Imperatriz (MA)	1	1				
1980	Luziânia (GO)			1			
1980	Monte Altos (MA)	1	1	1			
1980	Uruaçu (GO)		1			3	(51)
1980	Niquelândia (GO)					1	(51)
1980	Novo Brasil (GO)		1				
1980	Ji-Paraná (RO)		1				
1980	Paraná (GO)		1				
1980	Pilar de Goiás (GO)		1				
1980	Porto Franco (MA)		1				
1980	Sanclerlândia (GO)		1				
1980	São João d'Aliança (GO)		2	1			
1980	Sta. Terezinha Goiás (GO)		2				
1981	Altamira (PA)		1				
1981	Ananás (GO)		1				
1981	Anastácio (MS)		2				
1981	Caracaraí (RR)		2				
1981	Conceição do Araguaia (PA)	3	1*				(47)
1981	Diamantino (MT)		1				
1981	Frieira (GO)		1				
1981	Igarapé Mirim (PA)		1				
1981	Jataí (GO)		1				
1981	Camapuã (MS)		1				
1981	Campo Grande (MS)		4				
1981	Nova Brasilândia (MT)		4				
1981	Garimpo do Mutum (RR)		1				
1981	Boa Vista (RR)		1				
1981	Macapá (AP)		1				
1981	Pedro Gomes (MS)		1				
1981	Tucuruí (PA)		1				
1981	Santarém (PA)		1				
1981	Vilhena (RO)		1				
1982	Lago da Pedra (MA)	3					
1982	Altamira (PA)	1	3	1*			
1982	Aquidauana (MS)			1			
1982	Cuiabá (MT)		2				
1982	Campo Grande (MS)		7				
1982	Antônio João (MS)		4				
1982	Caracol (MS)		4				
1982	Coxim (MS)		1*	1			
1982	Anastácio (MS)		2				
1982	Bela Vista (MS)		2				
1982	Boa Vista (RR)		2				
1982	Alto Alegre (RR)		1				
1982	Garimpo do Mutum (RR)		2				
1982	Grajaú (MA)		2				
1982	Jardim (MS)		2				

(to be continued)

that, under very high densities, a weak vector can sustain an epidemic (31).

Eco-epidemiological models

The Old World — The model which best fit the transmission of YF in West and Central Africa was elaborated by Cordellier (32,33), Germain et al (23,34) and Germain (35).

This model is characterized by two main areas, endemic and epidemic.

The southern part of the former is formed by dense equatorial rain forest. Sylvatic transmission is exclusively epienzootic and man-vector contacts are virtually inexistant. The northern part, made up of a mosaic of savannah and forest, with gallery forest, and drier savannahs in the North, is called the endemic emergence zone, where human sporadic cases (36) are common. Man-vector contacts are much more frequent and easy in this zone, due to the great development of clearings and ecotones. Local explosions of sporadic cases are named sylvatic epidemics. Natural transovarial transmission of YF virus has been shown in this same area (37).

The epidemic area is made up by: *i*) the northern dry or very dry savannahs where YF is known only as urban epidemics despite the presence of sylvatic vectors and primates, and *ii*) all cities located in the area where *Ae. aegypti* is present.

The New World — Until now, there has been no consensus theory about the maintenance and transmission of YF virus in the New World. Most authors think that the virus has to move about constantly in "epizootic waves", due to the relatively high mortality of the monkeys (18,38). Travassos da Rosa et al (16) have summarized the current data available on ecoepi-

Table 1 *(cont.)*

Year Place/State	*Number and origin of strains* Man *isol.*	*histop.*	*serol.*	*Monkey*	*Mosquitoes*	*References*
1982 Sidrolândia (MS)		1				
1982 Terenos (MS)		1				
1983 Porto Velho (RO)	1					
1983 Ouro Preto (RO)		1				
1983 Presidente Figueiredo (AM)		1				
1983 Cacoal (RO)		2				
1983 Vila do Incra (RR)		1				
1983 Garimpo Serra Pelada (PA)		1				
1983 São João Araguaia (PA)		1				
1983 Xinguara (PA)		1				
1984 Faro (PA)	2	3	2c,10		1	
1984 Alenquer (PA)		1	6			
1984 Altamira (PA)		3				
1984 Bonfim (RR)		2				
1984 Santarém (PA)			5			
1984 Senador José Porfírio (PA)			4			
1984 Col. Ingles de Souza (PA)		1				
1984 Monte Alegre (PA)	3	1*,4	2c*,20		3	
1984 Tucuruí (PA)				1		
1984 São Domingos do Capim (PA)	1				3	
1984 Rio Curuatinga (PA)		1				
1984 Mariry, Oyampi (AP)	1					(47)
1984 Pedreire (RR)		1				
1984 Tefé (AM)		4				
1984 Parintins (AM)		1				
1984 Manaus-Itacoatiara km 42 (AM)	1					
1984 Monte Castelo (AM)		1				
1984 Nova Olinda Norte (AM)		1				
1984 Ilha do Cerubani (AM)		1				
1984 Porto Novo (AM)		1				
1984 Presidente Figueiredo (AM)		1				
1984 Macapé (AM)		1				
1984 Maraã (AM)		1				
1984 Rolim de Moura (RO)		1				
1984 Presidente Médici (RO)		1				
1984 Prainha (PA)		3				
1984 Urucura (AM)		1				
1985 Sinop (MT)	1	2,2*	3		1	
1985 Cacoal (RO)		1				
1985 Almeirim (PA)		1				
1986 Monte Dourado (PA)		1				
1986 Água Fria (RR)		1				
1986 Diamantino (MT)		1				
1986 Formosa (GO)		2				
1986 Mara Rosa (GO)		2				
1986 Nova Maringá (MT)		1	1			
1986 Nova Orixás (GO)		1				
1986 Jardim Oriente (GO)		1				
1987 Tucuruí (PA)		1*	1c,1			
1987 Alto Paraíso (GO)		1	1			
1987 Rio Laco, Sena Madureira (AC)		1				
1987 Goiânia (GO)			2			
1987 Goiás (GO)		1				
1987 Goiás Velho (GO)		1				
1987 Cristalina (GO)			1			
1987 São Luís de Montes Belos (GO)	1	1				
1987 Santana (GO)		1				
1987 Goiatuba (GO)		1				
1987 Fraternidade (GO)		1				
1987 Bela Vista (GO)		1				
1987 Formosa (GO)	1	1				
1987 Canutama (AM)		1				
1987 Carajás-Serra Norte (PA)				1h		
1987 Altamira (PA)			1			
1987 Ilha Japichaua, Breves (PA)			1		2	
1987 Palmeiras (GO)		1				
1987 Planaltina (GO)		1				
1987 Portel (PA)			1			
1987 Cametá (PA)			1			

(to be continued)

demiology of YF in Brazil. More precise data on the vector were obtained recently (39).

The "Old World model" tested by the New World data

Spatio-temporal distribution of YF

The periodicity of YF epidemics was first studied by Kumm (40). However he could not explain either the great variability of interepidemic periods, or the lack of concordance between epidemics in different South American countries. Furthermore, the relations between phytoclimatical zones and the ecology of YF was not considered. The present work will attempt to analyze the Brazilian data available from 1954 to June, 1992 (Table 1).

A first hypothesis which will be examined is that intervals between years with transmission evidence augment when the region is farther away from the endemic area.

Sampling and methods — It is obvious that, in such a large territory as Brazil — even if we consider only the Brazilian Amazonia — it is impossible to establish a nonbiased sample. The welfare centers are not sending us blood or viscera samples regularly. Furthermore, it was not possible to do surveys on each epidemic and/or each sporadic case. Thus, the present study will be valid only in the Brazilian context.

Eight phytoclimatical zones were chosen among those used in the map edited by the Brazilian Institute of Geography and Statistics (41) (Fig. 1). The localities with YF evidences were pooled according to their relevant phytoclimatic zones. Figure 2 shows the temporal distribution, as a percent of the total (386) YF transmission evi-

Table 1 *(cont.)*

		Number and origin of strains					
		Man					
Year	*Place/State*	*isol.*	*histop.*	*serol.*	*Monkey*	*Mosquitoes*	*References*
1987	Vieiras (GO)		1				
1987	Santa Cruz (GO)		1				
1987	Itaituba (PA)		1				
1988	São Félix do Xingu (PA)		1	1			
1988	Altamira (PA)			1			
1988	Abaetetuba (PA)			1			
1988	Manaquiri (AM)		1*	1			
1988	Camará (AM)			1c			
1988	Plácido de Castro (AC)		1				
1988	Santa Cruz (GO)		1				
1988	Caiapônia (GO)	1	1	1			
1988	Lavras (GO)			1			
1988	Jataí (GO)			1			
1988	Paracatu (MG)	1	2,3*	8			
1988	Unaí (MG)		1	1			
1988	Bonfinópolis (MG)		1				
1988	Doverlândia (GO)		1*	1			
1988	Novo Airão (AM)			1			
1988	Redenção (PA)		1				
1989	Cacoal (RO)		1				
1989	Francisco Dumont (MG)	1		5			
1989	Mineiros (GO)		1				
1989	Mirabela (MG)			1			
1990	Lajeado II (MA)		1				
1990	Tailândia (PA)			1			
1991	Locality ? (GO)				1		
1991	Catrimani, Yanomami (RR)	1	3,1*	4			
1991	Altamira-Itaituba km 30 (PA)			1			
1991	Campo Grande (MS)			1			
1991	Barcarena (PA)					1	
1991	Corguinho (MS)			1			
1991	Goiás (GO)				1		
1991	Jaraguari (MS)			3			
1991	São Gabriel do Oeste (MS)			1			
1991	Tucuruí (PA)			1			
1992	Camapuã (MS)			1			
1992	Campo Grande (MS)					1	
1992	Corguinho (MS)		1				
1992	Jaraguari (MS)					1	
1992	Paconé (MT)		1*	1			
1992	Pontes e Lacerda (MT)		1				
1992	Ribas do Rio Pardo (MS)		4				
1992	Sidrolândia (MS)		1*	1		4	
1992	Terenos (MS)		1				

dences (strains isolated from human or sylvatic hosts, serological conversions or histopathological diagnostics) in each of the phytoclimatical zone. Thus, it was possible to study: *i*) qualitative aspects, such as the intervals between YF evidences, and *ii*) quantitative data, such as the distribution of years with variable levels of transmission.

Periodicity of YF transmission — For each phytoclimatical zone, we estimated the mean interval (and standard deviation) between years with YF transmission evidence (Fig. 3).

The first result is that in no single zone the mean interval exceeded five years. The means vary from 1.4 years for open rain forest to 2.7 years for the decidual forest and are therefore always lower than 7-10 years, usually cited in the literature (18). The decidual seasonal forests which lay at the division between the Amazonian belt and the East and Northeast regions of Brazil, represent probably the eastern limit of sylvatic YF. The zone, classified as an ecotone between the rain forests in the north and the southern mosaic of savannahs and gallery forest, is characterized by the relatively high value of 2.5 years.

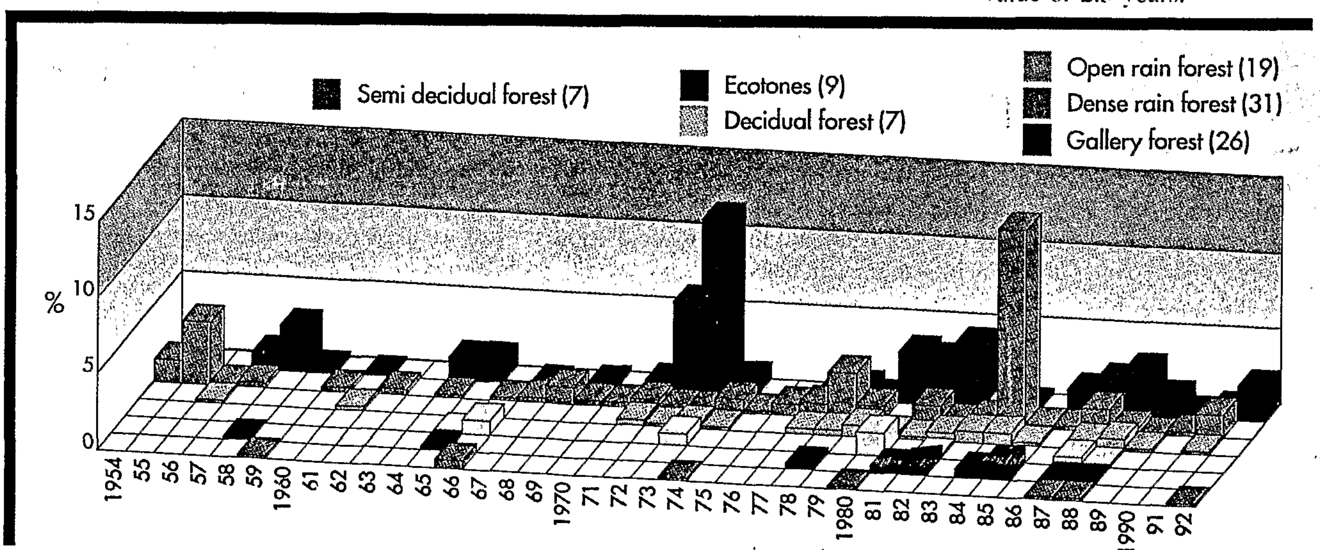

Figure 2. Annual positive strains (%) for YF virus, for each phytogeographical zone in Brazil, 1954 - June, 1992

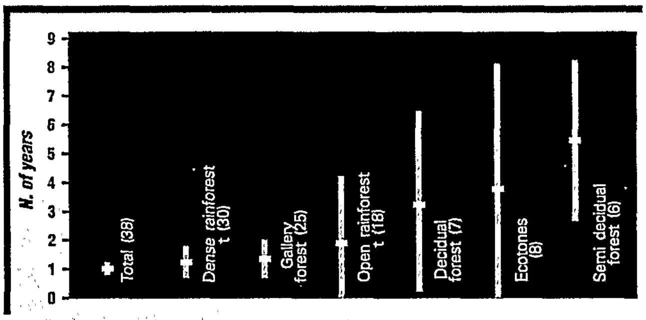

Figure 3. Mean interval, with standard deviation, between successive years of YF virus transmission, for each phytogeographical zone in Brazil (sample size), 1954 - June, 1992.

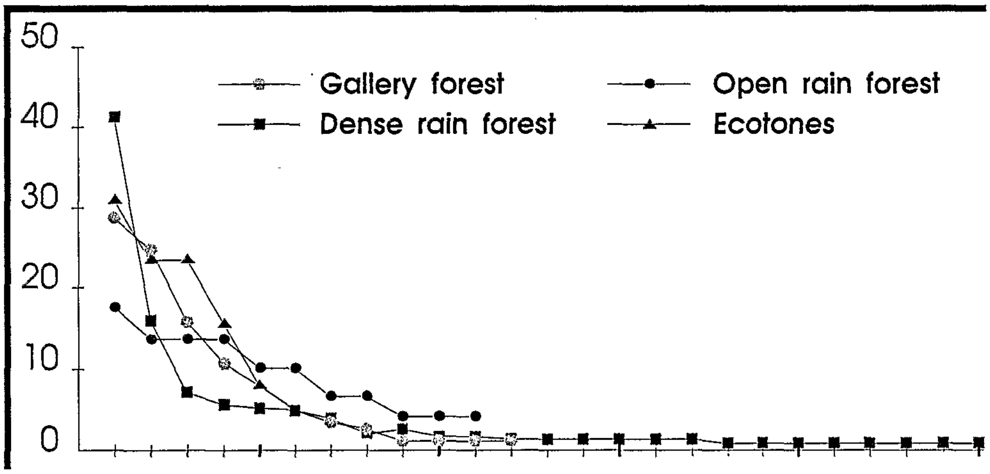

Figure 4. Distribution of years according to decreasing proportions of YF circulation evidences (% of cases), for each phytogeographical zone in Brazil (1954-1991).

Three phytoclimatic zones where the mean interval between epizootics is lower than two years may be good candidates for sheltering natural endemic focuses of YF: *i*) the dense Amazonian rain forest, *ii*) the open rain forest and *iii*) the gallery forests running through the arboreal savannahs in central and southwestern Brazil. The standard deviation increases from the open Amazonian rainforest to the dense rain forest and gallery forests.

Distribution of cases — YF was not transmitted by *Ae. aegypti* during our period of study (1954 to 1991). Thus, the frequency distribution of the years, according to the number of cases (or transmission evidences), would be characteristic of the transmission mode in each phytoclimatical zone (42). Figure 4 shows two types of distributions for the cases of YF: *i*) more or less linear ones in open rain forest and ecotones and *ii*) nonlinear ones in dense rain forest and gallery forest. Unfortunately, it is not known if these variations represent actual eco-epidemiological differences. It is as if the gallery forests were in continuity (and/or remains) of the dense Amazonian rain forest, and open rain forest and ecotones were more unstable (and heterogeneous) zones.

Due to the relative paucity of controlled data and the fact that human cases do not (at least quantitatively) represent the level of sylvatic circulation of YF virus, it remains difficult to evaluate the "Old World model" for explaining the YF epidemiology in Brazil. Nevertheless, three remarks are worthwhile here: *i*) in West and Central Africa, the level and seasonality of YF sylvatic transmissions are well correlated with the phytoclimatic zonation, justifying our present approach to the problem; *ii*) once the pooling of cases by zone is considered a valid method, the mean intervals between epienzootic manifestations do not exceed three years. Thus, inside the considered area, the YF virus may be thought of as always present and circulating. This area may be considered equivalent to the endemic area of Germain et al (24). The fluctuations of the transmission intensity would depend of the level of immunity of the human and simian populations; *iii*) the zones with higher ecological instability (naturally or man-modified biotopes), namely open rain forest, ecotones and decidual forest would correspond to an "emergent endemic area". A possible "epidemic area" would extend much southward.

Conclusions

This comparative ecoepidemiological analysis of YF shows the lack of data related to South America. However, an ecoclimatical approach must be projected for future studies. The most important aspects that are in need of detailed investigation are: *i*) the turnover of simian populations, *ii*) the macro and microclimatic parameters that determine the fluctuations of vector populations and *iii*) the relative importance of some ill-known vectors such as *Hg. albomaculatus.* ■

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52. *Acknowledgments:* We are deeply indebted to our colleagues Roger Cordellier, Max Germain and Michel Cornet from ORSTOM (Paris), whose discussions and advices were determinant for the elaboration of our present views about the natural history of YF virus. We sincerely thank the technical staff of the Evandro Chagas Institute that has always collected the material in the field and processed them in the laboratory with much competence and responsibility. The present work was performed under the joint auspices of the National Health Foundation (Ministry of Health, Brazil), CNPq and ORSTOM (France). Many data were collected in the Amazonia region during specific projects funded by these institutions and Eletronorte (Eletrobrás), SUDAM (Brazil).