1. Introduction

In urban epidemics, transmission is solely inter-human and formerly the vector was considered to be always Aedes (Stegomyia) aegypti. This is probably true in towns, but is not always the case in rural areas.

For the last 30 years it has also been known that there are forest cycles of transmission in tropical Africa involving vertebrates and wild vectors and leading to the fortuitous infection of man. This type of cycle is of very great practical importance since it is in this way the virus can remain in circulation in the absence of epidemics, which it may initiate.

2. Cycles

The most thorough studies of yellow fever forest transmission cycles in Africa are those which have been made in Bwamba county, Uganda. They have revealed the vital part played by two vectors, Aedes (Stegomyia) africanus and Aedes (Stegomyia) simpsoni (Smithburn & Haddow, 1946; Haddow et al., 1948 & 1951; Mahaffy, 1949; Smithburn et al., 1949; Ross & Gillett, 1950; Haddow, 1965). Ae. africanus, which shows crepuscular activity in tree-tops and whose larvae live in tree-holes, transmits yellow fever from monkey to monkey when these take to the forest canopy to sleep. During the day the monkeys sometimes wander into plantations outside villages in search of food, and here they come into contact with Ae. simpsoni, whose larvae live in the axils of plants with sheath-like leaves (banana, taros, pineapple, Sanseveria, etc.). The adults of this species show diurnal activity. Ae. simpsoni bites both monkeys and man, thus causing sporadic cases of yellow fever in man. Ae. simpsoni may also at times penetrate into the forest and become infected after biting monkeys in the tree canopy (Haddow, 1950).

These transmission cycles, observed in a great rain-forest and in the villages nearby, call for a permanent population of non-immune monkeys and of Ae. africanus, and the presence at least from time to time of anthropophilic Ae. simpsoni. These conditions are only satisfied in limited areas of tropical Africa. Monkeys are frequently rare or little affected (Haddow, 1952; Lumsden et al., 1955 & 1956; Taylor, 1955). Ae. simpsoni is not always anthropophilic (Gillett, 1951 & 1955; Mattingly, 1952). Lastly, Ae. africanus is generally absent or rare outside densely wooded and humid areas. In addition, vectors seem to be absent for a large part of the year in all areas with a long dry season, which would apparently preclude maintenance of jungle yellow fever foci (Mattingly, in Mahaffy, 1949; Ross & Gillett, 1950), although the existence of such foci seems to have been proved serologically (Smithburn et al., 1949; Lumsden & Buxton, 1951; Haddow, 1952; Dick, 1953; Taylor, 1955).

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Analysis of some recent epidemics and cases of human infection in tropical Africa

3.1 Sudan

In 1940 a major urban yellow fever epidemic occurred in the Nuba mountains area. Aedes (Stegomyia) vittatus and Aedes (Diceromyia) of the taylori-furcifer group were considered mainly responsible for transmission with Ae. aegypti and Aedes (Stegomyia) metallicus (Kirk, 1941; Lewis, 1943; Lewis et al., 1942) also perhaps involved, to a minor extent.

In the 1959 epidemic in the Upper Nile and South Fung areas, the initial cases of human infection were put down to Aedes vittatus, with subsequent transmission from man to man through this mosquito or Ae. aegypti (Satti & Haseeb, 1966).

3.2 Ethiopia

In 1960-62 a major yellow fever epidemic was observed in Ethiopia. In forest galleries the epidemic was spread from monkey to monkey by Ae. africanus. In the Omo valley, monkeys from forest galleries infected Ae. simpsoni near villages and this mosquito was the sole vector responsible for an intensive inter-human transmission. In the Didesssa valley, where Ae. simpsoni is rare or absent, the majority of human cases were sporadic and transmitted directly from monkey to man through Ae. africanus in the forest or at the forest edge (Série et al., 1968 (a) and (b)). It is interesting to note that during this epidemic a yellow fever virus strain was isolated from a fruit bat of the genus Epomophorus (Série et al., 1968 (b)).

3.3 Kenya - Uganda

Surveys made in the Fortportal area in Kenya in 1953 and in Central Uganda in 1964, when scattered human cases occurred, showed that in this area Ae. africanus alone is responsible for transmission from monkey to monkey and from monkey to man (Haddow, 1953; Simpson et al., 1965).

3.4 Congo - Kinshasa

Apart from a few sporadic cases of jungle yellow fever, two minor epidemics were observed in 1958 in Eastern Province and in Equateur Province. In Eastern Province the transmission cycle was considered to be the same as that described for Bwamba county (Courtois et al., 1960). In the Equateur Province Ae. simpsoni and Ae. aegypti were regarded as responsible for inter-human transmission (Panthier et al., 1962; Lebrun, 1963).

3.5 Nigeria

Apart from sporadic cases, fairly large epidemics were recorded between 1946 and 1953 in the south-west and the east of the country but no detailed epidemiological study appears to have been published (MacNamara, 1954).

In 1969 an epidemic outbreak was reported in the Jos district. Adult males were infected to a much greater degree than women or children, seeming to indicate that transmission took place away from villages (Bres, 1970; Quenum, 1970). The epidemiological study, made somewhat belatedly, showed that Ae. africanus and Ae. luteocephalus were abundant and aggressive; Ae. simpsoni abundant and non-aggressive, while Ae. aegypti was rare. An earlier study in the same area had stressed the probable importance of Ae. vittatus and Ae. luteocephalus (Boorman, 1961). Transmission was thus apparently due mainly to forest vectors.
3.6 Upper Volta

A fairly large outbreak of yellow fever occurred in 1959 in the south-central part of the country in an area where An. aegypti was only moderately abundant in villages while An. luteocephalus, An. africanus and Aedes of the taylori-furculifer group were very abundant and aggressive in forest galleries. Human cases were scattered over an extensive area, while there appeared to be massive infection in monkeys. Transmission was probably ensured both by wild vectors and by An. aegypti (Pichon et al., 1969; Balay & Hamon, 1968; Gayral & Kambou, 1969; Compaore & Sentilhes, 1970; Cornet & Robin, 1970).

3.7 Ghana

Sporadic cases and minor epidemics were recorded at intervals in the south of the country. In the case of a small outbreak in the Ashanti region in 1957, transmission, which was of the forest type, was attributed to An. africanus, but An. luteocephalus was also present (Boorman & Porterfield, 1957).

A relatively large yellow fever epidemic occurred in the north of the country in 1969 and early 1970. Cases were scattered over an extensive area (Bres, 1970; Quenum, 1970). In the region affected An. aegypti was frequently very abundant in villages and could have been responsible for inter-human transmission (Mouchet, 1970).

3.8 Senegal

A serious yellow fever epidemic was observed in the west of the country in 1965. It was of the conventional type with transmission by An. aegypti and was limited to areas with a high density of this vector. This epidemic was halted both by insecticide treatment and by the fall in temperature in the winter (Wone et al., 1966; Bres et al., 1966 & 1967; Cornet et al., 1968). There was no local forest focus and the origin of the yellow fever virus could not be determined with any certainty since permanent foci seem to exist both in eastern Senegal and in Guinea - Bissau.

3.9 Other States

One case of human yellow fever was confirmed in 1970 in the Ayos district of Cameroon while positive serological tests were recorded in young non-vaccinated children in the south of the Central African Republic. In both these areas An. africanus and An. simpsoni are abundant and anthropophilic and monkeys are also present. The transmission cycle was perhaps the same as that described for Bwamba county (A. Rickenbach, F. X. Pajot & R. Cordellier, 1970).

Isolated cases and some grouped cases of yellow fever were confirmed in 1967 in Liberia, in 1969 in Mali and in 1969 and 1970 in Togo. They seem probably to have been of jungle origin (Robin & Pichon, 1968; Agbodjan, 1970; Scw, 1970; P. Pangalet, 1970, pers. comm.).

4. Discussion

A large proportion of yellow fever cases occurring in Africa are probably never diagnosed (Hamon & Bres, 1966), while most of the cases observed are not officially notified to WHO (Quenum, 1970). Under these conditions it is difficult to give an overall picture of the situation in tropical Africa.

An. aegypti is undeniably one of the major vectors in tropical Africa but it should be noted that it has played only a minor part, if any, in two of the major yellow fever epidemics of the last 30 years and that it has not always been the dominant component in lesser outbreaks, while all isolated cases appear to be jungle yellow fever.
Other potential vectors implicated in recent human cases all belong to the sub-genera Stegomyia and Diceromyia of the genus Aedes but it should not be forgotten that yellow fever virus has also been isolated from Aedes (Aedimorphus) dentatus (Serie et al., 1968 (a)) and from Phlebotomus (Smithburn et al., 1949) while it has been transmitted under laboratory conditions by Erethopodites group chrysogaster (Bauer, 1928), by Mansonia africana (Philip, 1930) by Culex thalassius (Kerr, 1932), and even by Culex pipiens fatigans (Davis, 1933). It should also be noted that the vector potentialities of many groups of African haematophagous arthropods have been studied only very superficially.

With a single exception, all African primates appear receptive to the yellow fever virus (Smithburn, 1949; Smithburn & Haddow, 1949). Only a few of the other African vertebrates studied circulate the virus, in particular one species of hedgehog, a genet (Dick, 1952), and bats belonging to the genera Eidolon, Epomophorus, Rousettus and Tadarida (Serie et al., 1968 (b); Simpson & O'Sullivan, 1968). Our knowledge of the real significance of the various species in the forest transmission cycle is far from satisfactory.

No study has yet been made to determine whether permanent natural yellow fever foci exist in Africa or whether the virus circulates in epizootic waves, as appears to be the case in Central America, or whether the two systems of maintaining and spreading the virus exist side by side. The two known transmission cycles may be no more than secondary cycles spreading from an unknown primary cycle involving none of the conventional vertebrates and vectors.

5. Conclusions

Yellow fever remains one of the major endemic diseases of tropical Africa, in both its epidemic and its jungle forms. Although Aedes aegypti may be responsible for transmission to man, the principal vectors in many areas are forest species of Aedes. Wild primates are frequently infected in endemic areas. The transmission cycles described for East Africa are probably valid for most forest areas in Central Africa, as far as Cameroon and the Central African Republic. Transmission cycles in forest areas in West Africa and in wooded areas and savannah with a long dry season have still to be determined. The mechanism whereby the virus persists during inter-epidemic periods is not known with any certainty.

7. References


Bres, P. et al. (1966) L'épidémie de fièvre jaune de 1965 au Sénégal, Méd. trop. (Marseille), 26, 21-38


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