Trans. Brit. mycol. Soc. **45** (3), 289–300 (1962).

SEASONAL PERIODICITY OF COFFEE LEAF RUST AND FACTORS AFFECTING THE SEVERITY OF OUTBREAKS IN KENYA COLONY

By K. R. BOCK*

Coffee Berry Disease Research Unit, Department of Agriculture, Kenya

(With 6 Text-figures)

The seasonal periodicity of *Hemileia vastatrix* Berk. & Br. in Kenya Colony differs markedly in districts east and west of the Rift Valley, this being attributable to the respective rainfall and climatic conditions of the two areas. The outbreaks in the east districts correspond to the monsoon rain pattern of two wet seasons; two disease peaks are always discernible, but their relationship to one another is often greatly affected by out-of-season rains. West of the Rift, the one extended epiphytotic is a result of the more or less continuous rainy season.

For any given disease cycle, three clearly defined phases are recognizable. There is also an inverse relationship between altitude and the severity of outbreaks.

Where temperature is not limiting, the course and severity of seasonal outbreaks are determined by the interaction of three factors, any one of which may be limiting. These are: (1) distribution and intensity of rainfall, (2) degree of leafiness of the tree, (3) amount of residual inoculum present at the end of the dry season.

The only study previously made of the seasonal periodicity of coffee leaf rust in Kenya was by Rayner (1956), but only for one district and not in any detail. Mayne (1930, 1932, 1939) investigated seasonal periodicity in Mysore. This paper reports field studies supplementary or additional to those of Mayne and of Rayner, with particular reference to recent observations on the dispersal of uredospores of *H. vastatrix* by rain splash rather than by dry air currents (Nutman, Roberts & Bock, 1960; Bock, 1962).

MEASUREMENT OF INFECTION

Observations were made on unsprayed plots of an extensive series of fungicidal timing and control experiments: guard trees surrounding blocks and experimental areas were also used. As the course of the disease differs east and west of the Rift Valley, these experiments were sited over a wide range of climatic zones and altitudes. Data were obtained from standard 20-tree plots, recordings being made weekly for periods of 12–30 months. One hundred leaves were collected at random from each plot, an average of five from each tree, and the numbers of individual rust spots counted on each leaf. These were taken from the lower half of the tree, where maximum infection usually occurs, since the inclusion of leaves from the upper parts of the tree in the sample greatly increases error. Table 1 illustrates the consistency of the results which may be obtained when sampling is from the

* Colonial Research Service.

Vol. 45, Part 2 was issued 25 June 1962

lower branches, compared with those from the upper. The differences in the amount of disease in the lower, middle and upper regions of the tree are a reflexion of the manner of uredospore dispersal. With air dispersal, the numbers of uredospores deposited on the leaves at the three levels would tend to be uniform. With water dispersal, however, spread from initial foci is mainly lateral and downwards, with limited distribution upwards by splash.

Table 1. *Leaf rust infection at different heights above ground*

Sample number	Mean no. rust spots/leaf for 100-leaf samples		
	1·5 m.	2·0 m.	2·5 m.
1	4·1	1·7	0·4
2	3·8	2·7	0·8
3	3·9	1·6	0·2
4	4·3	3·1	0·5
Mean	4·0	2·3	0·5

EPIPHYTOLOGICAL DATA

There are three clearly defined seasonal phases in the disease cycle. The first, which occurs towards the end of the dry season, may be described as a 'trough', with incidence constant at a low, or relatively low, level. During this, unless out-of-season showers of sufficient intensity occur, no fresh

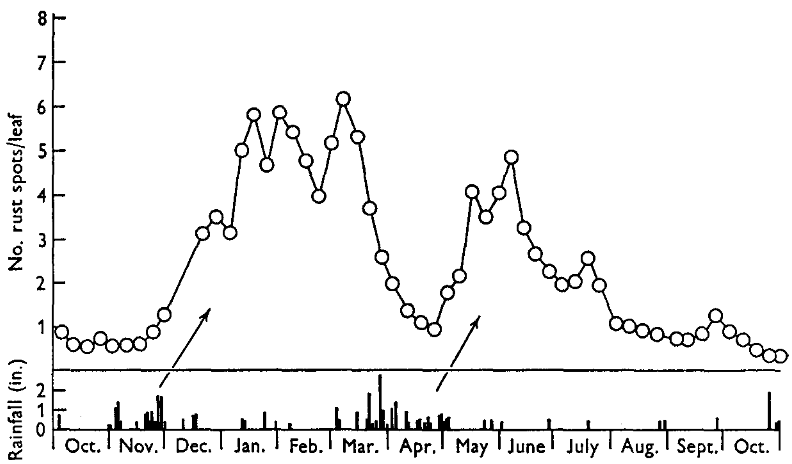

Fig. 1. Seasonal periodicity of leaf rust in districts east of the Rift Valley.

infection takes place. The second phase, which is one of marked fungal activity, commences after the onset of the rains. The rust pustules remaining on the tree are the reservoirs of infection, and spores from these are dispersed by rain to adjacent leaves, causing disease to increase to a maximum. This maximum or 'peak' period may or may not last long; its duration is dependent on further periods of rain and inoculum dispersal, interacting with leaf-fall. The third phase is one of a rapid and often spectacular decline, brought about by natural leaf-fall, accelerated by the premature shedding of infected leaves. Although further infection may appear at this time, this tends to be masked by leaf-fall. This phase is usually of short duration.

Figs. 1 and 2 illustrate this sequence of events for districts east and west of the Rift Valley respectively. It can be seen that the curves are closely related to the rainfall patterns of the two districts. Thus, where there are two periods of monsoon rains, separated by dry seasons, there is always a tendency for two distinct disease peaks. These are nearly always discernible, although they may be modified in seasons of atypical rainfall; they may

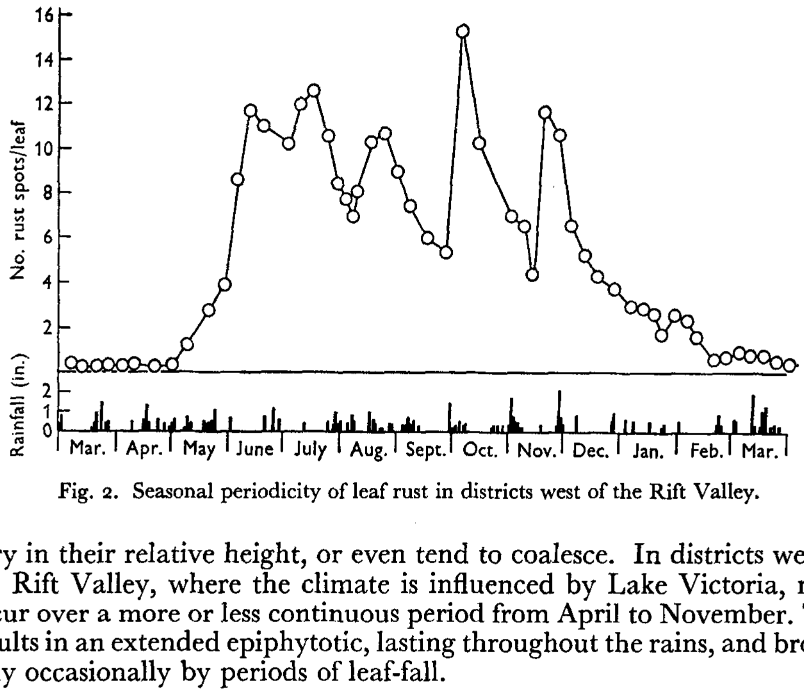

Fig. 2. Seasonal periodicity of leaf rust in districts west of the Rift Valley.

vary in their relative height, or even tend to coalesce. In districts west of the Rift Valley, where the climate is influenced by Lake Victoria, rains occur over a more or less continuous period from April to November. This results in an extended epiphytotic, lasting throughout the rains, and broken only occasionally by periods of leaf-fall.

EFFECT OF ALTITUDE ON THE DISEASE

The effect of altitude on the seasonal outbreaks of disease was mentioned in the first report on coffee leaf rust in Kenya Colony by Dowson (1921), who observed that the severity of attack decreased with increase in altitude. The altitudes at which the present experiments were sited are given below, with the numbers of trials laid down in each, and with comments on the average disease incidence. The limits of these ranges do not correspond exactly to differences in disease incidence, but they represent convenient divisions into broad zones, which may themselves show considerable local climatic variation with topography (Table 2).

Figs. 3 and 4 illustrate the effect of altitude on disease incidence in districts east and west of the Rift Valley, respectively. The rainfall patterns for these curves are similar to those in Figs. 1 and 2. The relationship between altitude and disease is immediately apparent. The difference in the severity of infection displayed by the 5000–5500 ft. curve and the 5600–5800 ft. curve, respectively, is of interest in that the mean difference in altitude is only 400 ft., and the amount of rainfall for the two ranges—39·50 and 42·37 in.—is not dissimilar. Nutman & Roberts (1960) have

Table 2

Altitude range (ft.)	No. trials	Mean rainfall (in.)	Disease incidence
Districts east of the Rift Valley			
5000–5500	5	39·50	Generally severe
5600–5800	10	42·37	Often severe
6000–6200 (1)	1	48·66	Rarely severe
6000–6200 (2)	1	32·69	Never severe: local and rare occurrence only
Districts west of the Rift Valley			
5000–5500	3	47·77	Heavy and consistent disease
5800–6000	7	57·88	Often locally severe; occasionally very severe

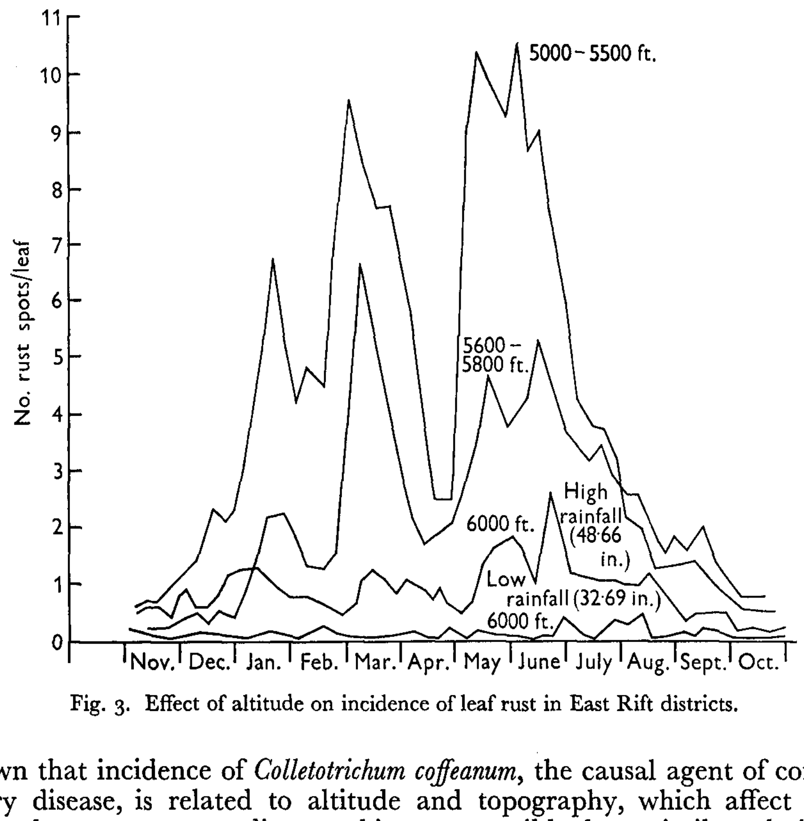

Fig. 3. Effect of altitude on incidence of leaf rust in East Rift districts.

shown that incidence of *Colletotrichum coffeanum*, the causal agent of coffee berry disease, is related to altitude and topography, which affect the diurnal temperature gradient, and it seems possible that a similar relationship may hold for *H. vastatrix*. The difference in degree of infection for the two 6000 ft. curves in the East Rift districts may, on the other hand, be attributable entirely to rainfall, as the difference is between 47·77 and 32·69 in. per annum. The severity of the disease in the higher altitudes in the West Rift calls for comment. The climate here differs markedly from that at similar altitudes east of the Rift. Temperatures are normally considerably higher, and the rainfall high (57·88 in.). Because of this, so far as disease incidence is concerned, these areas correspond more closely to the lower ranges east of the Rift Valley.

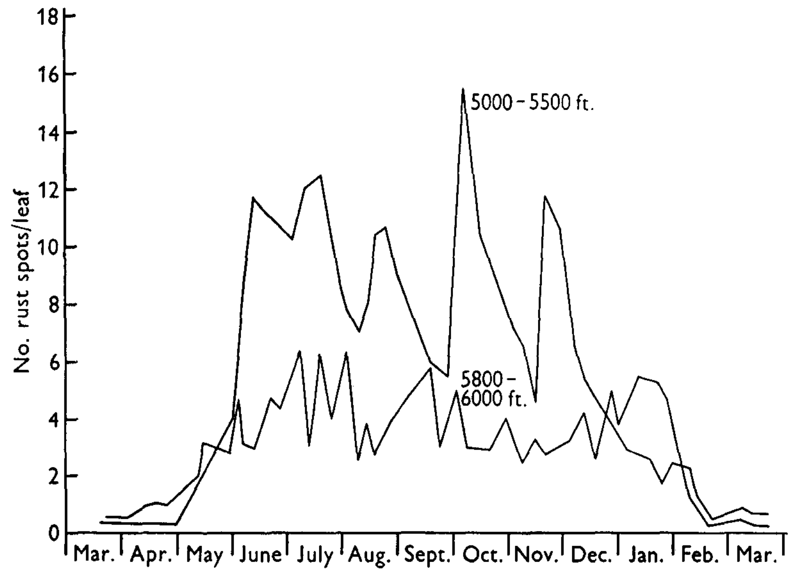

Fig. 4. Effect of altitude on incidence of leaf rust in West Rift districts.

FIELD INCUBATION PERIODS

Incubation periods in the field can be measured only approximately from epiphytological data. Often several dispersal periods (i.e. showers of a certain intensity) follow close upon each other, and the subsequent increase in disease is sometimes complicated by leaf-fall which may occur, for a limited period, at or near the peak. Thus, attempts to measure the period between effective dispersal and maximum development of rust may result in some inaccuracy. Nevertheless, remarkably uniform data have been obtained. The mean interval between rain and the first appearance of incipient leaf spots is 23 days, a figure which agrees very closely with average incubation periods obtained in the laboratory. In low-lying, warmer areas in West Rift districts the period averages 20 days, and may be as short as 18–19 days. These figures agree with those of Rayner (1956), who noted that incubation periods in Kenya were significantly longer than those recorded in India or Ceylon, where the average is 14 days; he also stated that incubation periods may vary from 4 to 7 weeks. The present investigations have shown that they rarely exceed 35 days and that even this period is exceptional and occurs only during the cool season in East

Rift areas: one cold-season record of 42 days has been obtained. Table 3 illustrates some field incubation periods measured from epiphytological data, averaged from four East Rift sites situated at 5600–5800 ft.

Table 3. *Incubation periods of* Hemileia vastatrix *in the field*

	Period from effective dispersal to incipient leaf-spot (days)	Period from effective dispersal to maximum rust-spot development (days)
January	23	28
February	23	29
March	23	31
April	23	27
May	21	28
June (cool)	26	33
July (cool)	24	36
August (cool)	27	40
September	22	29
October	23	29
November	21	28
December	22	27
Mean	23	30

FACTORS AFFECTING COURSE AND SEVERITY OF SEASONAL DISEASE CYCLES

For all conditions when temperature is not limiting, three interacting factors determine the course and severity of seasonal outbreaks of *H. vastatrix*. These are:

(1) Distribution and intensity of rainfall.

(2) Amount of residual inoculum on the trees at the end of the trough phase immediately preceding the rains.

(3) Degree of leafiness of the tree at the onset and during the course of the rainy season.

Distribution and intensity of rainfall

This is the most important factor. The relation between rainfall intensity and uredospore dispersal is linear, and, under average conditions, only showers in excess of 0·3 in. will effectively disperse uredospores (Bock, 1962). Rainfall of 0·20–0·25 in. will disperse spores only when the inoculum level is high, that is, in excess of 2·0–2·5 actively sporing rust spots per leaf; this dispersal is virtually confined to the infected leaves, with adjacent ones only rarely becoming infected. Showers of less than 0·2 in. do not provide conditions suitable for germination and invasion by the fungus, even when temperature is not limiting.

Fig. 5 illustrates the effects of distribution and intensity of rain on the initiation and subsequent course of two outbreaks on different sites 5 miles apart, but within the same altitude range (5000–5500 ft.). Both sets of trees had about the same degree of foliation and, as can be seen in the figure, the residual inoculum in each was 0·25–0·5 rust-spots per leaf.

It is evident from the study of the two curves that the first increase occurred 21 days after the first group of showers. These were of similar intensities at both sites, the actual amounts being as follows:

Curve 1: 2·33, 0·86, 1·61, and 1·75 in.
Curve 2: 0·75, 2·5, 0·5, and 0·78 in.

The showers acted upon similar levels of residual inoculum, and, as expected, the maximum infection resulting from them was very similar, that is, 2·25–2·5 spots per leaf. At this point the course of the two outbreaks diverged. At Site 1, the last effective dispersal shower of the first group, common to both Sites 1 and 2, occurred on 19 November. At

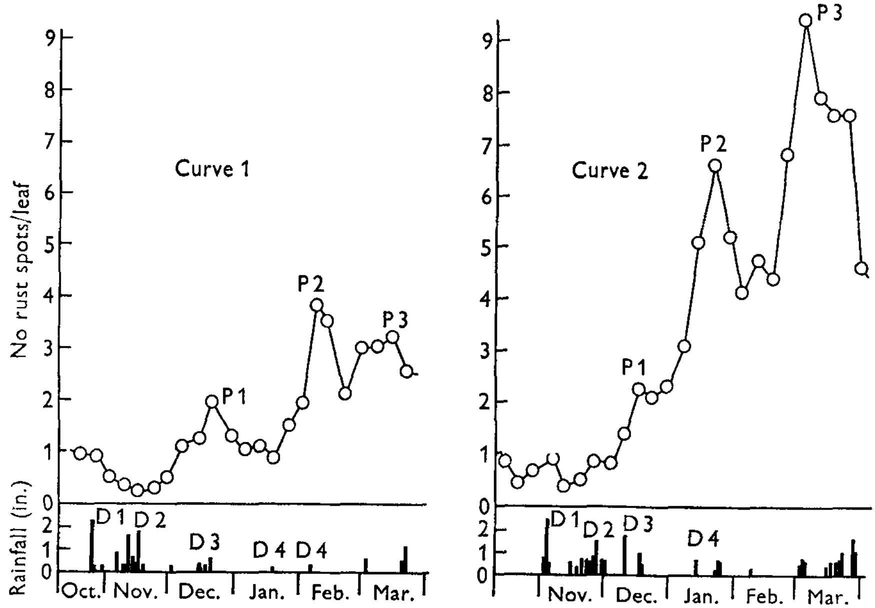

Fig. 5. Effects of distribution and intensity of rainfall on seasonal occurrence of leaf rust. For explanation, see text.

Site 2, however, there were several heavy showers between then and the point of maximum development. The result of these two different rainfall distribution patterns is reflected in the course of the outbreak after the first subpeak (indicated in the figures as P 1). At the first site, a heavy leaf-fall followed the subpeak; in Curve 2, on the other hand, it can be seen that while the beginning of leaf-fall is apparent, the rate of increase resulting from the showers after 19 November was far greater than the rate of decrease of disease effected by leaf-fall.

In the later phases of the outbreaks, the effect of intensity of rainfall is clearly apparent. Curve 1 shows that at the point of maximum disease incidence resulting from the first group of showers, two falls of 0·41 and 0·56 in. acted upon an average inoculum density of 2·23 spots per leaf to give rise to a second maximum (P 2) of 4 spots per leaf. On the other hand, two heavy showers of 1·65 in. and 1·03 in., acting on a similar inoculum density of 2·25 spots per leaf, resulted in a second subpeak (Curve 2) of 6·5 spots per leaf.

Finally (Curve 1), two light showers of 0·26 and 0·25 in. acted on an average of 2·5 spots per leaf; these succeeded only in maintaining the epiphytotic at an average level of 3 spots per leaf (P3); and (Curve 2) three showers of 0·55, 0·63 and 0·6 in. acted upon an average of 6·5 spots per leaf and gave rise to a final severe disease maximum (P3) of 9·5 spots per leaf.

The course of all the epiphytotics studied can be similarly traced and interpreted, and the two examples described above were selected from a total of twenty-seven similar sets of data from East and West Rift sites. It is thus the interaction of the intensity of rainfall with its distribution, operating on successively higher levels of inoculum, which determines the ultimate degree of severity of any given outbreak, and the rate of its development.

Residual inoculum

Table 4 presents data on the mean number of pustules per leaf in the trough periods at seven sites, and relates this residual inoculum to the degree of severity of the succeeding outbreaks.

Table 4. *Relationship between residual inoculum and ultimate degree of severity of outbreaks*

	Site no.	Level of infection in trough phase (no. pustules/leaf)	Maximum level of infection in ensuing outbreak (no. pustules/leaf)
5000–5500 ft.	1	0·50	7·00
	2	0·60	8·50
	3	2·60	15·10
5600–5800 ft.	4	0·20	1·60
	5	0·25	2·70
	6	0·90	5·50
	7	1·50	8·90

The level of infection present during the trough phase and immediately before the onset of the rains is influenced by leaf-fall and also, often to a greater extent, by out of season showers during the course of leaf-fall. When these occur, numbers of non-senescent leaves may become infected, and the trees thus carry a correspondingly higher amount of inoculum through into the rains. This often happens in certain districts east of the Rift where local showers are common in August and September. Mayne (1939) also mentioned this as one of the chief factors affecting the severity of outbreaks in India.

Foliage density

When uredospores are dispersed by rain-splash it seems likely that more will be retained in those trees bearing the denser foliage. Trees which have lost the majority of their leaves as a result of a heavy rust attack often remain relatively disease-free through several successive disease-cycles; it evidently takes a considerable time for an effective amount of inoculum to be built up again within such trees. Dowson (1921) observed this, and, in describing the spread of rust in the expanding coffee-producing areas of Kenya, stated that the first attack was usually severe, causing extensive defoliation, and this was followed by lighter attacks; he attributed this incorrectly, however, to an acquired resistance on the part of the host.

Table 5. *Mean numbers of uredospores/cm.²/leaf after 2·25 in. rain*

Each figure represents the mean of eight samples, each of 1 cm.²

Leaf sample number	On leaves from trees of low foliage density	On leaves from trees of high foliage density
I	0·22	83·00
II	0·00	169·00
III	1·00	54·75
IV	0·00	29·80
V	1·20	51·50
VI	0·00	64·50
VII	0·40	55·50
VIII	1·30	70·51
Mean	0·51	73·32

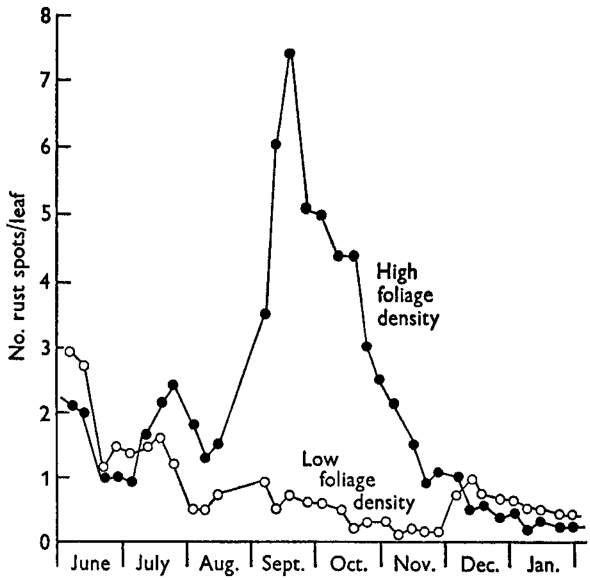

Fig. 6. Course of leaf rust development on trees of high and low foliage density, respectively.

A study of the numbers of uredospores actually dispersed to individual leaves of leafy and non-leafy trees by one heavy shower was made by a stripping technique (Bock, 1962). The level of inoculum in the two types of tree was similar, that is, 0·25–0·5 rust spots per leaf; the results (Table 5) show clearly that effective spore dispersal can take place only in fairly leafy trees. Thus, variations in foliar density at the time of dispersal will profoundly affect the severity of the ensuing outbreak. Different foliar densities may result from different causes, including cultural practices, e.g. from defoliation following attack by pests or diseases, or from prolongation of the period of leaf retention by fungicidal sprays (Rayner & Jones, 1948).

In certain field trials some of the treatments induced high foliage densities in some plots and in others low; there were twenty-seven such trials in all, and the development of outbreaks following spore dispersal in the leafy and non-leafy plots was recorded for each trial. The results from all were similar, a typical one being illustrated in Fig. 6; it is clear that disease incidence was higher where foliar density was high, though the actual number of leaves bearing pustules at the start of the outbreak was similar for all trees.

The implications of this are obvious; any cultural or spraying practices which increase the number of leaves on the tree at the time of spore dispersal must increase the severity of the resulting epiphytotic. This is of great practical importance, and the question is further discussed elsewhere (Bock, 1962).

DISCUSSION

The results presented here and in previous papers (Nutman, Roberts & Bock, 1960; Bock, 1962) do not support previous views on the mechanics of outbreaks of coffee leaf rust. It has been assumed that uredospores are dispersed by air currents as a more or less continuous process during dry weather, and over long distances (Rayner, 1956; Burdekin, 1960). This necessarily implies that an even distribution of spores over large areas is effected, and that, towards the end of the dry period, the leaves of trees in a plantation have already received inoculum; with the onset of suitable conditions, these spores were thought to germinate and infect the leaves. Rayner (1956) defined an 'infective period' as one in which the leaves remained wet after rain or heavy dew for a minimum period of 10 hr. during the night.

The present study has shown, on the other hand, that dispersal is not by air currents, but solely by rain-splash. Although Nutman *et al.* (1960) thought that a very limited amount of long-range dispersal might possibly be caused by air currents, this is now considered to be improbable. If single spores, or even small spore clusters, could thus be transported, infection is still unlikely to follow since Nutman & Roberts (private communication) have found that single spores are uninfective and that infection is rare even with clusters of as many as 20 spores.

The concept of long-range dispersal must now be replaced by one of extremely short-range dispersal. Actual assessments of distribution following showers (Bock, 1962) show that movement of spores from infected leaves even to adjacent ones on the same tree is not appreciable except during relatively heavy rain. Moreover, studies of the distribution of pustules on the leaf in the initial stages of an outbreak have shown that, when the original inoculum-density is low, the new pustules are normally confined to the same leaves, the total number of rust spots gradually increasing while the number of affected leaves remains more or less constant. This is obviously related to the small amount of inoculum to be dispersed.

Outbreaks would thus be expected to be highly localized, and the correctness of this supposition is borne out by a weight of field evidence. For example, two adjacent trees, one with scanty and the other with dense foliage during the trough phase, will always exhibit very different levels of infection at the height of the disease cycle. In addition, effective fungicidal treatments give almost complete control which may persist for 6 months or longer, in spite of the fact that numerous showers have occurred during this period. Such trees carry a large and increasing number of leaves which have been produced after spraying, and which have thus never received any treatment; these trees are often immediately adjacent to others in untreated plots, where disease incidence may be as high as 20 spots per leaf. If wind dispersal were effective it would be expected that the trees in the treated plots would become infected from such neighbours, but this has never been observed to occur, and any hypothesis in favour of air movement of spores is untenable in the face of this fact. It is no exaggeration to say that each rust epiphytotic is an aggregate of separate outbreaks on individual trees, each one behaving to a considerable extent as an independent unit. Mayne (1930) came to the same conclusion, stating 'the incidence of the disease is regular, i.e. the number of pustules at a given date determines the number at a later one, indicating the absence of any considerable source of infection'.

The concept of the 'infective period' (Rayner, 1956), in which spores already distributed can germinate and infect when suitable conditions arise is replaced by that of a dispersal period, in which spores are distributed by rain, and germination and invasion follow immediately as a continuous process. Studies of dispersal and germination have indicated that the amount of rain necessary for this to occur is 0·3 in. or more, but epiphytological observations have shown that showers of 0·25 in. may be partially effective.

Uredospores of *H. vastatrix* do not germinate in strong sunlight, but germination followed by penetration does take place in light of low intensities, such as that reaching the lower side of a leaf during dull cloudy weather. Epiphytological studies confirm that appropriate amounts of rainfall result in a rise in disease incidence, whether this falls during the day or night.

Evidence on the processes of dispersal and infection presented herein not only explains the apparent inconsistencies in disease incidence so evident in the field, but also enables a rational approach to the control of the disease to be made.

REFERENCES

Bock, K. R. (1962). Dispersal of uredospores of *Hemileia vastatrix* under field conditions. *Trans. Brit. mycol. Soc.* **45**, 63–74.

Burdekin, D. A. (1960). Wind and water dispersal of coffee leaf rust in Tanganyika. *Kenya Coffee* (*Mon. Bull. Coffee Bd Kenya*), **25** (294), 212–213, 219.

Dowson, W. J. (1921). Some problems of economic botany in East Africa (Kenya Colony). *Ann. appl. Biol.* **8**, 83–100.

Mayne, W. W. (1930). Seasonal periodicity of coffee leaf disease (*Hemileia vastatrix* B. & Br.). *Bull. Mysore Coffee Exp. Sta.*, no. 4.

Mayne, W. W. (1932). Seasonal periodicity of coffee leaf disease (*Hemileia vastatrix*, B. & Br.). Second Report. *Bull. Mysore Coffee Exp. Sta.*, no. 6.

Mayne, W. W. (1939). A note on the origin of attacks of leaf disease (*Hemileia vastatrix*) in coffee estates. *Plant. Chron.* **34**, 14.

Nutman, F. J. & Roberts, F. M. (1960). Investigations on a disease of *Coffea arabica* caused by a form of *Colletotrichum coffeanum* Noack. II. Some factors affecting germination and infection, and their relation to disease distribution. *Trans. Brit. mycol. Soc.* **43**, 643–659.

Nutman, F. J., Roberts, F. M. & Bock, K. R. (1960). Method of uredospore dispersal of the coffee leaf-rust fungus, *Hemileia vastatrix*. *Trans. Brit. mycol. Soc.* **43**, 509–515.

Rayner, R. W. (1956). Leaf rust. *Mon. Bull. Coffee Bd Kenya*, **21** (243), 65–69, 75.

Rayner, R. W. & Jones, P. A. (1948). Tonic copper spraying. *Mon. Bull. Coffee Bd Kenya*, **16** (189), 212, 220.

(*Accepted for publication* 1 *June* 1961)