



Coffee Leaf Rust

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To cite this article: F. J. Nutman & F. M. Roberts (1970) Coffee Leaf Rust, PANS Pest Articles & News Summaries, 16:4, 606-624, DOI: [10.1080/09670877009413428](https://doi.org/10.1080/09670877009413428)

To link to this article: <http://dx.doi.org/10.1080/09670877009413428>



Published online: 06 Jul 2009.



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F. J. NUTMAN and F. M. ROBERTS

Coffee Leaf Rust

Rosehill Cottage*
Bow, Crediton, N. Devon

Pathogen: *Hemileia vastatrix* Berk. & Br.
Uredinales.

Obligate parasite on the leaves of the genus *Coffea*. There are twenty-one physiologic forms.

Uredospores: Bright orange $25\text{-}35\mu \times 12\text{-}28\mu$, oval with one flattened side, surface highly sculptured: echinalate.

Teleutospores. Reported from India, Ceylon and South Africa.

Distribution: Tropical Africa, Asia, Indonesia, Oceania, South America.

Introduction

Coffee leaf rust was certainly the earliest of the major tropical plant diseases to be reported and studied. It has caused enormous financial losses since its occurrence was first reported in Ceylon in 1869, and it ultimately caused the abandonment of the coffee industry there. Since then all coffee-growing countries of Asia have suffered, and the disease has reached Fiji, Papua, the New Hebrides, and Samoa. In January 1970 the first report of its presence in South America was made, and large acreages in Brazil are affected (Wellman 1970).

Coffea arabica and *C. canephora* probably originated in East Africa (Wellman 1957) and this is also the most likely home of the pathogen. All commercially grown varieties are affected in East Africa and the disease has spread from there across central Africa to the West Coast and further south to Natal. It has also been reported from Madagascar and the islands of the Indian Ocean. All main coffee-growing regions of the world are now affected but within these a few areas, for example the Southern Highlands of Malawi (at least up to 1964) are free from the disease.

Symptoms

Hemileia vastatrix is an obligate parasite on the genus *Coffea* and no alternative hosts are known. Infection results in the formation of pale spots of up to 1.5 cm in diameter on the lower surfaces of the leaves, often with slight chlorosis of the upper side. Uredospores, abstricted from hyphae which protrude through the stomata, are produced on these spots, and eventually the surface becomes encrusted with spore-masses forming the characteristic bright orange pustule. In ageing pustules lighter coloured uredospores are produced at first centrally and later over the whole surface. These, the contents of which are almost colourless, are not viable (Nutman and Roberts, 1963), see Fig. 1, 2 and 3. The uredospores have rough and sculptured surfaces and adhere strongly together.

*Since this paper is of considerable topical interest reprints will be available from TPRH & IU, 56/62 Gray's Inn Road, London WC1X 8LU.

Fig. 1. Spray of coffee leaves showing young pustules and a few older ones. Occasional water-drops are to be seen on the under-surface of some leaves. This level of attack would be very severe economically.

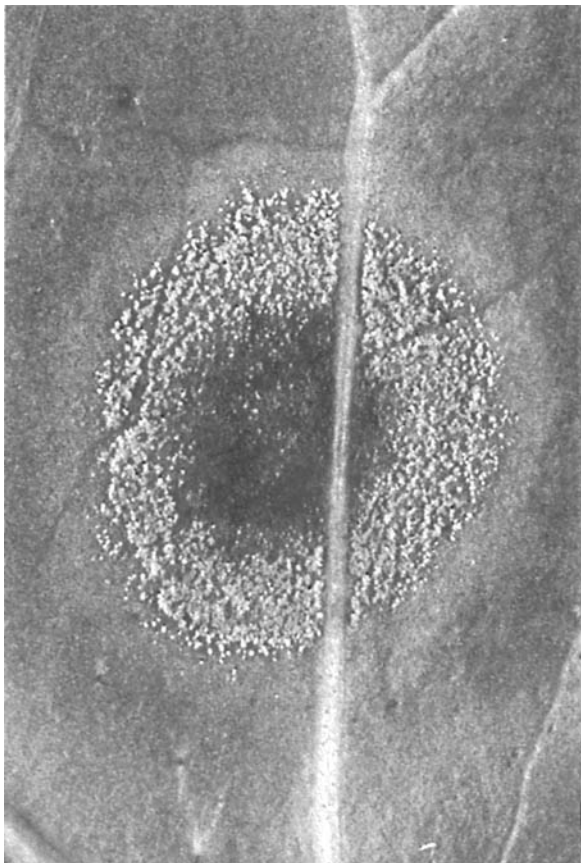


Fig. 2. Old pustule showing dark necrotic central portion bearing scanty light-coloured and non-viable uredospores. Surrounding this is a ring of orange-coloured masses of uredospores, surrounded by a faintly chlorotic halo.

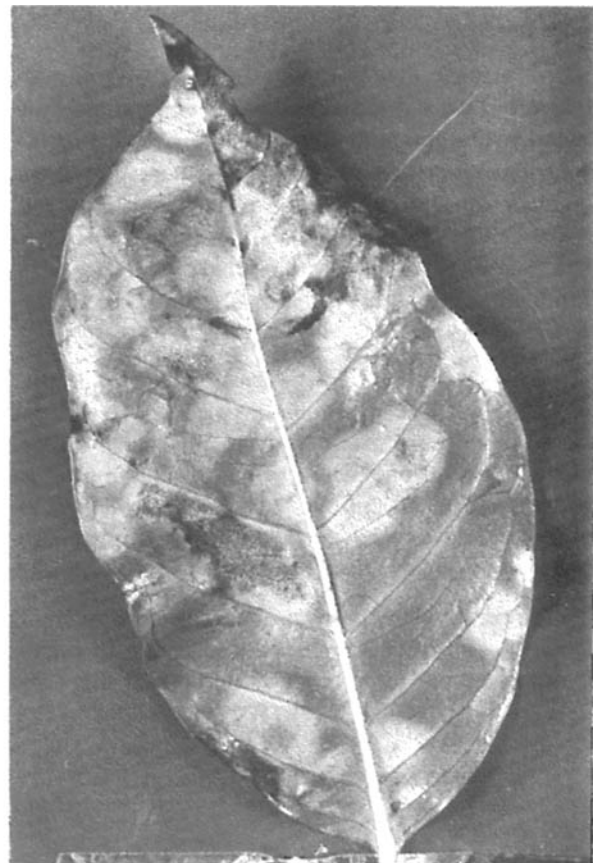


Fig. 3. Heavily attacked leaf, showing necrotic areas and coalescing pustules.

(Figs. 1, 2 and 3 — Shell copyright)

Marshall Ward (1881) reported the occurrence of teleutospores in Ceylon, while in India, Visveshwara and Tag Rag (1960) have observed them to develop in uredosori on *C. liberica*, *C. canephora*, and *C. arabica*. They were found to germinate *in situ*, and no reinfection of coffee leaves was obtained with the resulting basidiospores. Marshall Ward (1881, 1882), Pole Evans (1909), Gyde (1932) and Maine (1936) have all failed to infect coffee leaves with basidiospores. There is only one report of the occurrence of teleutospores in East Africa, and this was on dried herbarium material.

Sometimes the whole leaf becomes covered with pustules (Fig. 3), and over 700 have been counted on a single leaf. The presence of only 2 to 10 pustules on a leaf, however, represents an economically severe level of infestation. This is because even one pustule will cause premature abscission of the leaf, sometimes preceded by a general chlorosis. This abscission can readily be demonstrated by lightly tapping an infected leaf, when it is immediately detached from the branch. The ground under attacked trees soon becomes covered with a carpet of fallen leaves.

Coffee trees demand a high carbohydrate supply for the successful maturation of the crop, which utilises not only the current production, but which draws heavily on reserves. For this reason the defoliation caused by the disease can have serious consequences. Towards harvest, even in the absence of disease, considerable strain on the tree is often evident and this is accentuated in trees which are partially defoliated by rust attack. The demands of the crop can exhaust starch reserves in the roots, and this results in the dying-back of the small woody rootlets which carry the actual absorbing roots. These are regenerated slowly, if at all (Nutman, 1934). Consequently the tree is left with a reduced absorbing system and it may be some years before full vigour is recovered. If, however, defoliation is repeated in a second year the accumulated strain may result in the death of the tree through its effect on the root system. Thus, although rust is not in itself a killing disease, it can become so after repeated attacks.

Spore dispersal

It was assumed until very recently, presumably by analogy with the cereal rusts, that uredospores of *H. vastatrix* were dispersed by air. For example, Rayner (1960) commenting on how rust moved from Africa to Ceylon wrote 'it would seem highly probable that it was blown there by the South-west monsoon from the horn of Africa.' He also surmised that the comparatively recent spread of leaf-rust in West Africa, with the inevitable build-up of inoculum there, presented a threat to the coffee-growing regions of the New World (at that time still unaffected) as uredospores might be carried there from Africa by the north-east trade winds. As long ago as 1918, however, Butler suggested that the pathogen might be carried on planting material, and considered that its introduction into Asia was probably the result of the movement of planting material from island to island across the Indian Ocean.

Later, workers in East Africa demonstrated that the uredospores are dispersed over very short distances by water, and not over very long distances by air (Nutman, Roberts and Bock, 1960). This, combined with strict quarantine measures, seems the most probable explanation of the long freedom of the New World from the disease. There is one record of an introduction of infected plant material into Puerto Rico in 1907, but this was fortunately intercepted. It is possible that the recent outbreaks in Brazil may have resulted from a similar but undetected introduction, although it is not impossible, with the increased speed and volume of air travel, for viable spores to be carried on the persons of visitors from countries in which the disease is endemic.

Since, as will appear later, a knowledge of the periods when spore-dispersal occurs is fundamental for successful control of leaf-rust, it is desirable to examine in some detail the evidence that dispersal is mainly by water and not by air. The main lines of this evidence are as follows:

Spore trapping

The highly efficient spore traps designed by Harrington, Gill and Warr (1959), were operated at different levels (1, 2, and 3m) among infected trees. Very few uredospores were trapped, and these were almost invariably at the lowest level, below the infected leaves which were the source of the spores. Thus, in 21 consecutive hours of trapping, Bock (1962a) recorded a total of only 34 uredospores (including one cluster of 22) trapped 1m above

the ground: at 2m, 12 were trapped: and at 3m, above the tops of the trees, one only and this was colourless and non-viable. Further, when trees are mechanically disturbed, and uredospores are shaken off the leaves into the air, these are trapped at the lowest of the three levels. Table 1 illustrates the results of trapping during a period when mechanical disturbance of the trees by harvesting operations took place at a known hour.

TABLE 1. EFFECT OF MECHANICAL DISTURBANCE ON THE
NUMBER OF UREDOSPORES IN THE AIR AT 1, 2, AND 3 M
ABOVE GROUND LEVEL
(After Bock, 1962a)

Time	Spore-trap height			Maximum recorded wind speed at 3 m (mph)
	1 m	2 m	3 m	
8.00- 9.00	1:5:1	0	0	3.5
9.00-10.00	7:1	1	0	4.5
10.00-11.00	0	0	0	3.8
11.00-12.00*	6:1:1:2:1: 1:5:1:2:5: 59:56:1:3: 5:1:10:2: 1:11:1:1:3: 2:2:12:1:1: 1:1:1:2:1:	0	0	4.9
12.00-13.00	1:4:4	0	0	4.1
13.00-14.00	0	0	0	3.0
14.00-15.00	0	0	0	2.7
15.00-16.00	0	0	0	1.8

*Period during which mechanical disturbance occurred.

Spore deposition on leaf surfaces in the field

Leaves selected for sampling were swabbed in the field with wet cotton wool to remove any uredospores present on them. After different intervals of time, and after days with and without rain, 1 cm² patches on these leaves were coated with a celloidin preparation. The films were then stripped off and examined microscopically for the presence of spores. The results are shown in Table 2 while Fig. 4 illustrates the clearly linear relation between the intensity of rainfall and the number of spores deposited.

TABLE 2. MOVEMENT OF SPORES ON DAYS WITH AND
WITHOUT RAIN
(After Bock, 1962a)

	Total days	Area cm ²	Spores	Mean no spores/cm ²
Days with rain*	14.	500	3600	7.2
Days without rain	50	1900	170	0.09

*The figures for all days with rain, varying from a trace to 2.25 in., are averaged. If the figures are limited to days with rain in excess of 0.3 in., the resultant mean number of spores/cm² is 37.9.

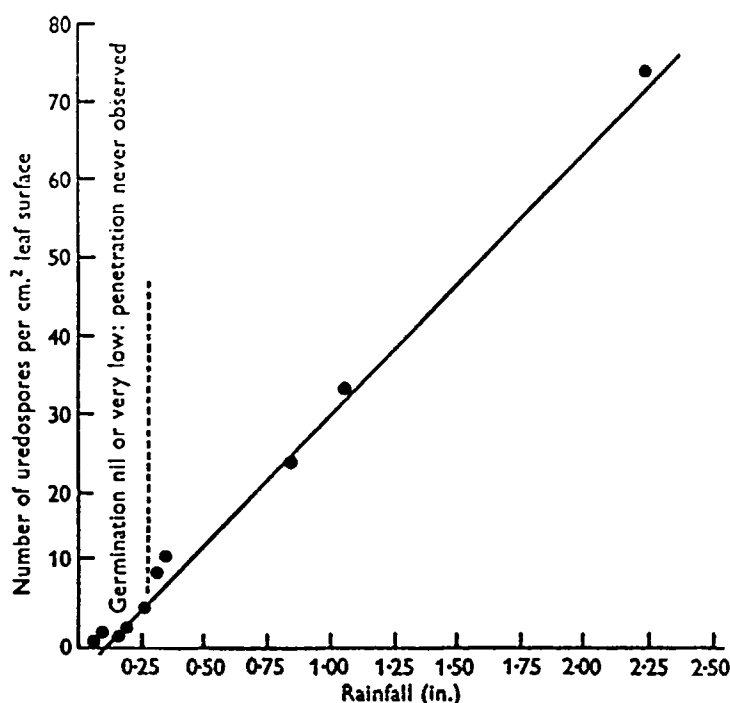


Fig. 4. Relation between intensity of individual showers and spore movement on healthy leaves.
Reprinted from Bock (1962a) *Trans. Br. mycol. Soc.*, 45(1): 68.

What happens to uredospores following rainfall can be seen by selecting leaves in the field which are bearing young pustules, swabbing the lamina around them, and, after showers, coating the entire under-surface of the leaf with celloidin. The film is subsequently stripped for microscopic examination, and the position of the uredospores in it can be mapped. Fig. 5 shows that the deposition of uredospores after rain is from the pustules on the same leaf, and that their distribution follows clearly a pattern of water-trickle: there is no suggestion of the random and uniform scatter which would be expected were the spores deposited by air. This figure also illustrates the position of spores following heavy rain: a fall of over an inch (2.5 cm) has not, as might have been expected, washed the spores away but it has effected maximum dispersal. This is because, as will appear later, only a very small fraction of the raindrops reach the undersides of the leaves where the pustules occur.

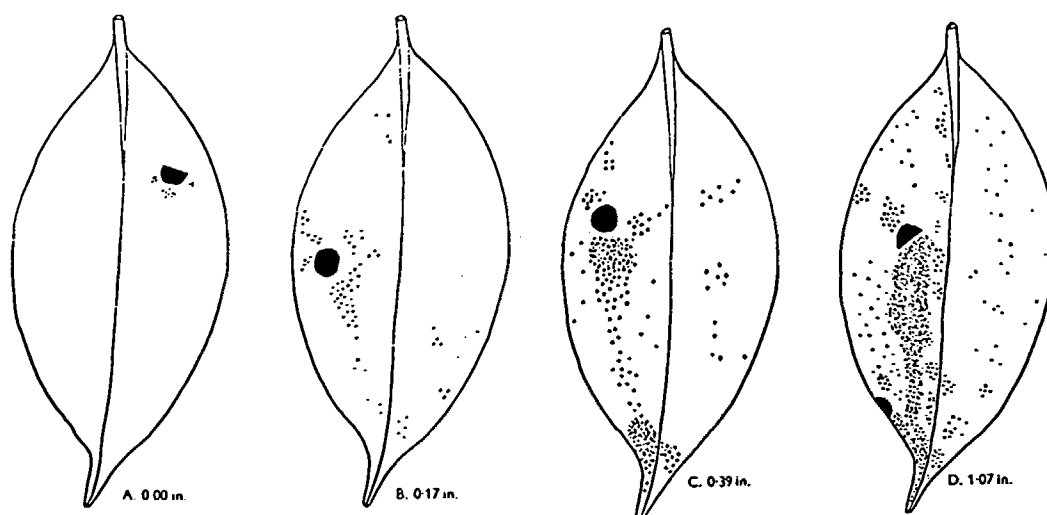


Fig. 5. Distribution of spores after rainfall of different intensities.
Reprinted from Bock (1962a) *Trans. Br. mycol. Soc.*, 45: 70

Relation of secondary to primary pustules

Under Kenya conditions secondary pustules appear on leaves about three weeks after a heavy shower and their distribution is significant. Fig. 6 illustrates this, with each dot representing one very small secondary pustule. It can be seen that these bear a very definite relationship to the primary lesion, from which they are obviously derived. The pattern of their development too is consistent in every particular with water-carriage of inoculum: this is particularly clear in C, where the water which carried the uredospores was channelled by the raised mid-rib of the leaf.

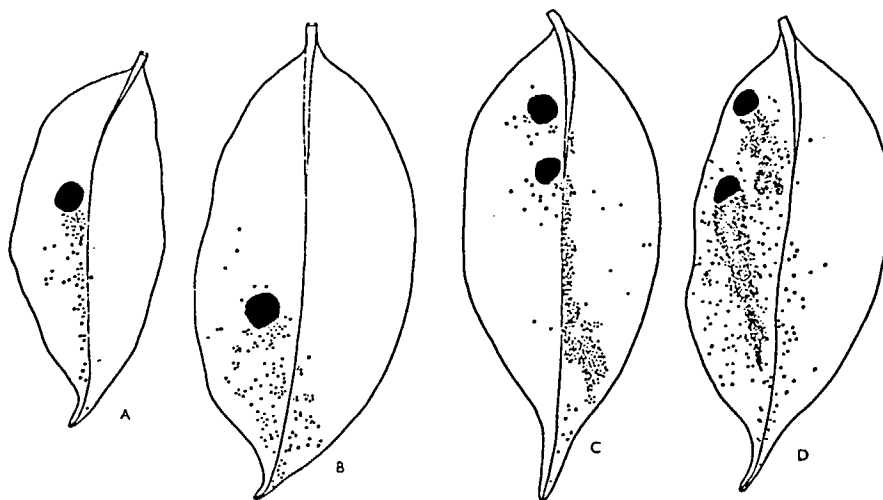


Fig. 6. Development of secondary rust spots on selected leaves from the field, 5 weeks after 1.07 in. rain.
Reprinted from Bock (1962a) *Trans. Br. mycol. Soc.*, 45: 71.

Photographic recording

What actually happens when rain is falling can be recorded by high-speed flash photography. When a drop strikes the surface of a leaf it fragments, and is dispersed in all directions. Some of these minute droplets, which can be projected by the impact some inches in a vertical direction, are intercepted by the lower surfaces of neighbouring leaves and, after a shower of about 0.3 in. (7.5 mm) these become wetted sufficiently for larger droplets to form, and for some run-off to begin. Plate 1 shows some water-droplets on the lower surfaces of the leaves. When a sporangium pustule is present on the leaf the water collects many uredospores: some of these are deposited on the same leaf and form secondary pustules, as is shown in Fig. 6: the remainder are carried to the tip, from which they stream off and are again dispersed by rebound from the upper surfaces of other leaves, to build up effective concentrations elsewhere (Nutman and Roberts, 1963).

Experiments with air currents

When wheat leaves infected with *Puccinia graminis* were exposed in the laboratory to air currents of only one mile per hour the uredospores were blown away. Pustules of *H. vastatrix*, on the other hand, remained unaffected even when subjected to air currents of up to 12 miles per hour (19 kph) (Nutman, Roberts and Bock, 1960). Such currents were sufficient to cause some movement in groups of uredospores on the surface of the pustule, but photographs taken before and after exposure showed that these groups did not become detached from the spor mass, (Fig. 7). In contrast with the minor role played by air currents, however, small water droplets, deposited delicately on the surface of a pustule, immediately released the spores from their mutual adhesion and they floated individually to the surface of the droplet.

Air currents of gradually increasing velocities up to 12.5 mph (20 kph) were directed against cut coffee branches with rusted leaves in the laboratory. Spore traps operating in the lee of these branches showed that spores were not blown free until, at the maximum velocity, the leaves began to flutter and vibrate. Under this violent motion spores did become detached, not as individuals, but as large groups, which were jerked into the air and collected, as groups, on the spore traps. Studies of the rate of fall of such groups of uredospores in still air,

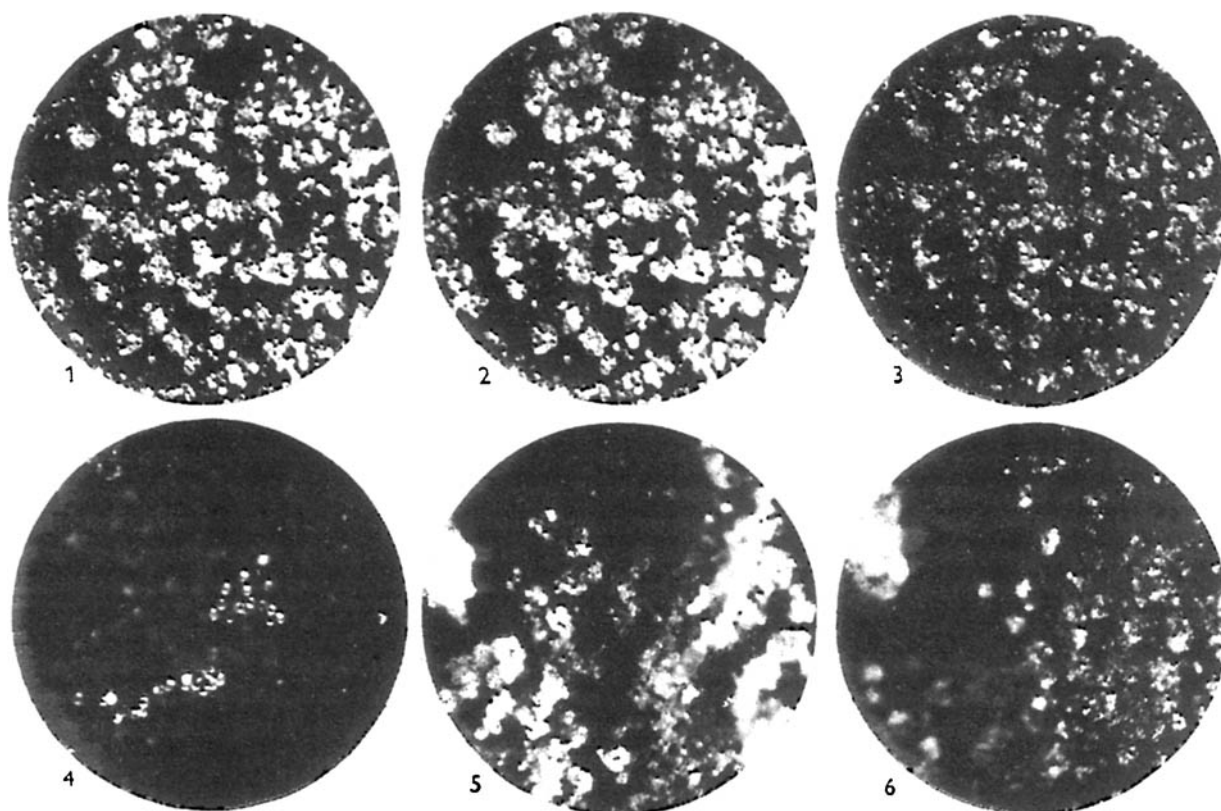


Fig. 7.

1. Portion of pustule of *H. vastatrix* x 425.
2. The same after 20 min exposure to a wind of 6 mph, the last 10 min being with added vibration at a frequency of 400/min x 425.
3. The same, after two successive exposure to winds of 9 and 12 mph, the last half of each 20 min exposure being with added vibration x 425.
4. Surface of water-drop at edge of pustule showing floating spores x 500.
5. Portion of pustule showing surface incrustation of detached spores x 425.
6. The same, after a droplet of water has been applied and removed. The surface incrustation of mature spores has been removed, the small clusters of immature spores thus becoming visible. (The object at the left is the shank of a pin used as a marker) x 425.

Reprinted from Nutman, Roberts and Bock (1960) *Trans. Br. mycol. Soc.*, 43: facing p. 514.

however, showed that these are unlikely to be carried any appreciable distance by air currents of the maximum velocities normally experienced in plantations of coffee in Kenya (Nutman, Roberts and Bock, 1960). Kirkpatrick (1935) carried out a study of the wind velocities in such plantations and showed that the values used in this work were rare even on the edge rows, while inside the lines of trees air movement is still further reduced.

Long-range dispersal of H. vastatrix.

Dispersal of the uredospores of leaf rust by water-splash is, of course, extremely short-range and raises the problem not only of the world distribution of the disease, but also of the means of spread within countries where it has been introduced. When a new plantation is established in a region where rust is endemic it almost invariably remains apparently free from disease for some years. Rust eventually appears, however, and in the absence of any possibility of its having been carried in by water-splash, other explanations for its origin must be considered.

1. *Infected seedlings.* In Kenya new plantations are usually established with plants raised in nurseries, and these are subjected to a fair amount of handling by workers. Pustules of rust have been found by the writers on these young plants which are usually about 18 months old at the time of transplantation to the field. Small foci of infection such as these can remain inconspicuous for some years: when the trees come into bearing, however, the infections become obvious giving the impression that the disease has 'suddenly appeared'. Another aspect of this means of spread is that there is much more movement of planting material both between countries and within a country than is usually realised. Before legislation was introduced to prevent this, new plantations in Kenya were often established with seedlings grown

some hundreds of miles away — in some instances where coffee berry disease was endemic. An example from another crop is that clove seedlings were brought to Mauritius from Ceram on the other side of the Indian Ocean.

2. *Aberrant weather conditions.* Although winds in the coffee-growing districts of East Africa are rarely, if ever, strong enough to act as carriers of uredospores, yet small and very violent local whirlwinds occasionally occur. These can be seen to carry leaves and small branches to considerable heights, and transport of infected material could be effected in this manner.
3. *Transport by insects.* Uredospores can also be carried by insects. In East Africa, Crowe (1963) has shown that rust pustules are frequently inhabited by the larvae of two species of Cecidomyid midges (*Lestodiplosis* sp. and *Mycodiplosis* sp.) which burrow into them and feed on the uredospores. These larvae are parasitised by two species of wasps, *Leptasis kivuensis* and *Synopeas* sp. When searching in the rust pustules for larvae the wasps become heavily coated with uredospores which are carried off on the insect when it flies away. Crowe has also shown that these wasps can carry spore loads large enough to start a lesion and, because they are small, averaging only 1 mm long, they could be carried long distances by light air currents. Fifty-seven were caught 30 m away from the nearest coffee trees during two days of trapping and, of these, 26 were carrying spore loads. The wasps are extremely common, as populations of more than 20,000/ac have been recorded. In spite of this, however, it seems unlikely that uredospores transported in this way could give rise to more than an occasional infection at a distance.

In India the larvae and adults of two species of thrips, *Euphyothrips subramanni* and *Scirtothrips* sp. have been observed to feed on pustules, and to become covered with uredospores (Ananth and Chokanna, 1961). In East Africa *Taeniothrips xantherocerus* behaves similarly, and could, in the districts where it is common, also act as a carrier of spores. (Crowe *in lith.*)

The process of infection

Workers with *Hemileia* both in Asia and Africa have made use of discs cut from leaves and maintained in moist chambers for studying germination and infection. These discs, if cut with a very sharp cork-borer, can remain fresh for many weeks and their use enables adequate randomising of leaf material to be carried out. Infection is through the stomata, and as these are confined to the lower surfaces of the leaves the uredospores must germinate there. The one or more branched germ tubes which develop from each uredospore wander over the leaf surface and approximately 25% of them form appressoria over stomata. From the appressoria infection hyphae develop, which penetrate the stomatal opening and give rise to a branching mycelium in the tissues. Very rarely direct entry of a germ tube through a stoma without the formation of an appressorium has been observed.

For invasion to be successful it is necessary in general for a number of uredospores to germinate close to one another. This is in contrast to the cereal rusts, where one uredospore can usually give rise to a pustule. Table 3 illustrates the results of inoculating leaf discs with droplets containing known numbers of uredospores, under conditions in which about 150 in each droplet gave 90% of successful infections. It can be seen that very few lesions were obtained with droplets containing less than 20 uredospores in each.

TABLE 3. EFFECT OF INOCULATION WITH KNOWN
NUMBERS OF UREDOSPORES
(After Nutman and Roberts, 1963)

Number of spores	Number of transfers	Number of lesions	Percentage infection
1	591	2	0.3
2	502	0	0.0
4-5	150	2	1.3
10-20	534	9	1.6
Total	1786	13	0.7 mean

The threshold period for infection, or the time during which viable uredospores must be exposed to suitable conditions of moisture and temperature before infection results, is shown in Fig. 8 for optimum temperatures. In this, and also from the data illustrated in Fig. 11, it appears that the minimum threshold is about 3½h, and that the rate of eventual lesion formation increases with time for at least 12h. It will be shown later that pre-exposure to cold conditions shortens this period.

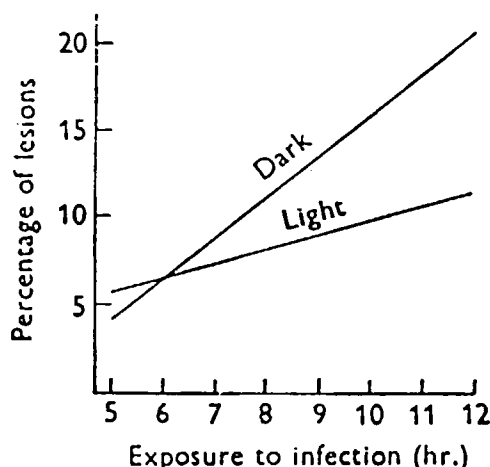


Fig. 8. Lesion production in relation to time of exposure to infective conditions in darkness and diffused light. Reprinted from Nutman and Roberts (1963) *Trans. Br. mycol. Soc.*, 46: 36.

The length of time between invasion and sporulation (the incubation period) is about 21 days on leaf discs (Nutman and Roberts, 1963). In the field it varies with the season (Bock, 1962b).

The above observations refer to conditions in Kenya. Here, in the cooler months of the year (June – August) the incubation period is appreciably prolonged. Rayner (1960) has reported periods of as long as five weeks. Marshall Ward (1882) found the incubation period in Ceylon to be 12-16 days and in Mysore, Mayne (1932) found it to be 15-16 days. These varying figures are probably a result of different temperatures, those quoted from Asia almost certainly reflecting results obtained in conditions warmer than are those normal in the high altitudes of the coffee-growing districts of Kenya.

TABLE 4. INCUBATION PERIODS OF
HEMILEIA VASTATRIX IN THE FIELD
(After Bock, 1962b)

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

Germination

Germination of uredospores is affected by the following factors:

Moisture

Water is essential, as no germination occurs even in a saturated atmosphere.

Temperature

The effect of this is complex. On potato dextrose agar the optimum is around 22°C, with 15° and 28°C as the limits. The curve relating temperature to germination is smooth and unimodal. On leaf surfaces, on the other hand, the curve is bi-modal, with one peak at about 21°C and another at just above 25°C separated by a marked depression of germination at between 23° and 24°C. The equation of this curve, illustrated in Fig. 9 and 10 is:

$$Y = -927.398 + 92.527x - 2.120x^2$$

where Y is the germination rate and x the temperature (Nutman and Roberts, 1963; Clarke, 1963).

No explanation has been advanced for this bi-modality. As it does occur *in vitro* even with spores drawn from the same populations as those used in the leaf tests, the cause would seem to lie in some effect of temperature in the region of 23°-24°C on the leaf, resulting in a depression of germination on its surface.

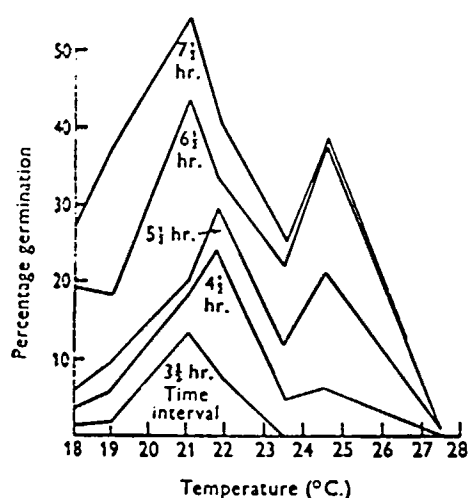


Fig. 9. Germination after different intervals of time on leaf discs as affected by temperature (2,000 spores per point: 70,000 spores). After Nutman and Roberts (1963) *Trans. Br. mycol. Soc.*, 46: 31.

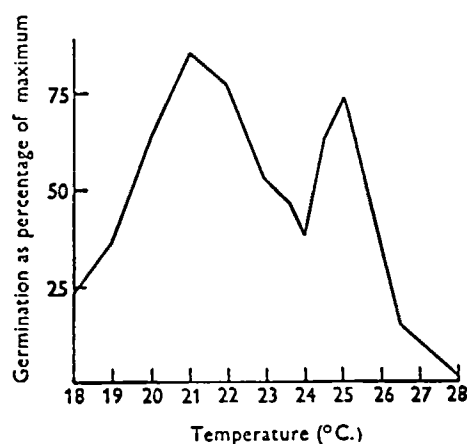


Fig. 10. Germination on leaf discs as affected by temperature. (5 experiments: 238,000 spore counts) Reprinted from Nutman and Roberts *Trans. Br. mycol. Soc.*, 46: 31.

Light

Direct bright light inhibits germinating completely, and because of this it was once thought that infection could take place only at night (Rayner, 1961). The light intensity at the under surfaces of leaves in the field, however, especially in dull weather or when these are shaded by others is low enough to permit germination, which can also take place in diffused light under laboratory conditions (Nutman and Roberts, 1963). Fig. 11 shows the strong interaction between light and temperature, and the regression curves of germination rate in darkness and diffused light are shown for three temperatures.

The ability of uredospores to germinate in diffused light has an important bearing on infection. Night-time temperatures in East Africa are almost invariably below 15°C for most of the time, and sometimes fall as low as 5°C. Similar conditions may well hold in other coffee-growing countries and, in these conditions, infection can usually occur only during daylight when temperatures in excess of the minimum are reached.

Pre-exposure to low temperatures

Exposure of wetted uredospores to sub-minimal temperatures for germination greatly stimulates the process when higher and more favourable temperatures occur. Nutman and Roberts (1963) found that the degree of stimulation increased with the length of the exposure to cool conditions, and was greatest at temperatures well below the minimum. Fig. 12 illustrates the stimulation after pre-exposure to a temperature of 15°C.

The importance of this cold-stimulation in relation to infection in the field is that uredospores, dispersed by rain during the night or the late afternoon, are subjected to temperatures which, in Kenya, can fall as low as 5°C (Woodhead, 1967). They will then germinate at an accelerated rate when the morning temperature rise takes place, and infection will occur more rapidly than would appear from the germination rate shown in Fig. 8

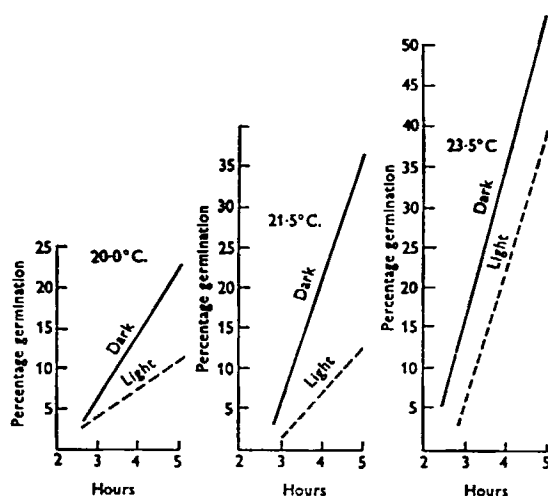


Fig. 11. Germination rates of uredospores in darkness and in light for 3 temperatures. After Nutman and Roberts (1963) *Trans. Br. mycol. Soc.*, 46: 34.

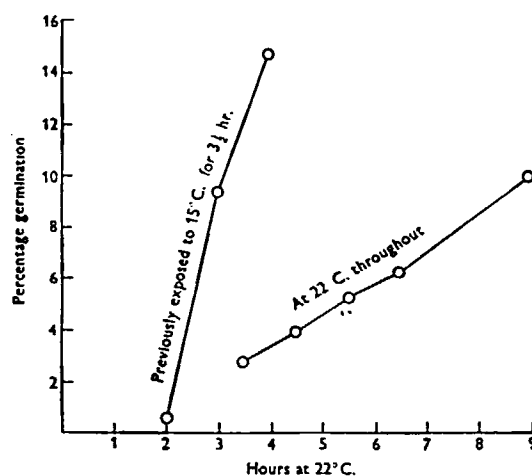


Fig. 12. Stimulation of germination by cold. Germination on leaf discs at the optimum temperature compared with that of spores previously subjected to cool conditions. Reprinted from Nutman and Roberts (1963) *Trans. Br. mycol. Soc.*, 46: 34.

Age of spores

Germination rate falls rapidly with increasing age of uredospores, following the equation

$$Y = 29.7 (x + 1) - 0.809$$

where Y is the germination rate and x is the age in days. The rate is halved in less than two days, and is negligible after fifteen (Nutman and Roberts, 1963). This loss of viability with age, however, is not sufficient to preclude the possibility of spores being carried from country to country by air transport, and for them to remain infective on arrival.

Age of leaf

Table 5 shows that there is more germination on young leaves than on older ones. There is also a difference in germination rate on different parts of the lamina, this being almost twice as great near the margin as it is near the mid-rib (Nutman and Roberts, 1963).

TABLE 5. % GERMINATION ON LEAVES IN DIFFERENT STAGES OF MATURITY AFTER 5 h
(After Nutman and Roberts 1963)

Tree No	State of maturity of leaf		
	Young	Intermediate	Old
1	41.5	29.5	20.3
2	22.5	10.3	8.5
3	26.4	11.2	5.8

Interruption of germination by drying

Once uredospores have been wetted (when presumably the initial processes of germination begin immediately) subsequent drying virtually inhibits further germination after the spores are again wetted. Table 6 shows this effect of interruption by drying, the total period of germination being 5 h in all cases. The duration of the first period of wetness, and also that of the period of dryness, appears to be immaterial.

TABLE 6. EFFECT OF INTERRUPTION OF GERMINATION BY DRYING
(After Nutman and Roberts 1963)

1st period of germination (min)	Period of dryness (min)	2nd period of germination		% germination
		h	min	
0	5	5	0	5.4
5	5	4	55	2.3
10	5	4	50	5.6
15	5	4	45	5.6
0	10	5	0	2.6
5	10	4	55	5.2
10	10	4	50	4.7
15	10	4	45	4.2
300 (5 h)	0	0	0	37.1

The disease in the field

Although Mayne (1930) and Rayner (1956) have both published accounts of the seasonal variation in disease level, the fullest and most recent account is that of Bock (1962b) who studied the disease in relation to rainfall patterns in Kenya. Disease level and rainfall in the main coffee growing districts are shown in Fig. 13, this together with Fig. 14 is based on weekly counts of the numbers of pustules on 150,000 leaves and consequently can be accepted as being highly accurate. The districts concerned have a monsoon climate with two distinct wet seasons. As a result there are two peaks in the annual rust cycle, the rise in disease level starting soon after the onset of each rainy season, with the maximum level extending into the following dry periods. During the latter the level of disease incidence falls, largely as a result of the rust-induced premature leaf fall, when most of the infected leaves absciss. West of the Rift Valley in Kenya (Fig. 14) the rainfall pattern is more uniform, as the climate is modified by the meteorological effect of Lake Victoria. Here, as a consequence, there is one extended peak to the annual outbreak, broken only by periods of heavy leaf fall.

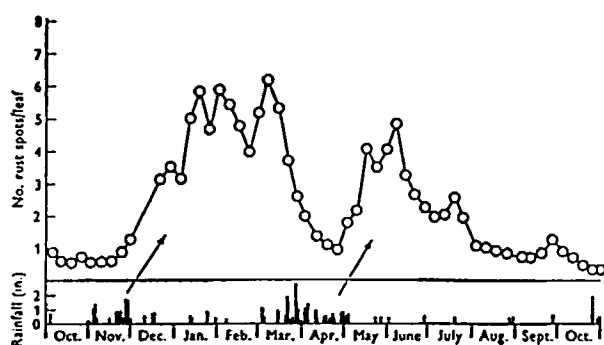


Fig. 13. Seasonal periodicity of leaf rust and daily rainfall in districts east of the Rift Valley in Kenya.
After Bock (1962b) *Trans. Br. mycol. Soc.*, 45: 290.

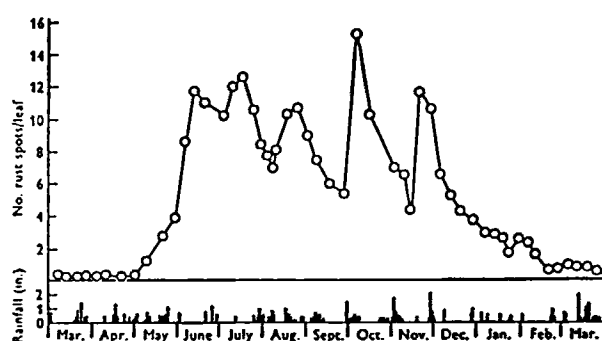


Fig. 14. Seasonal periodicity of rust and daily rainfall for districts west of the Rift Valley in Kenya
After Bock (1962b) *Trans. Br. mycol. Soc.*, 45: 291.

The effect of altitude on disease level is marked. In East Africa rust is much more severe in the lower and warmer districts than it is at over about 5,800 ft (1,902 m). Fig. 15 illustrates this for districts east of the Rift Valley. The figure also shows the two peaks which are much more defined at the lower altitudes.

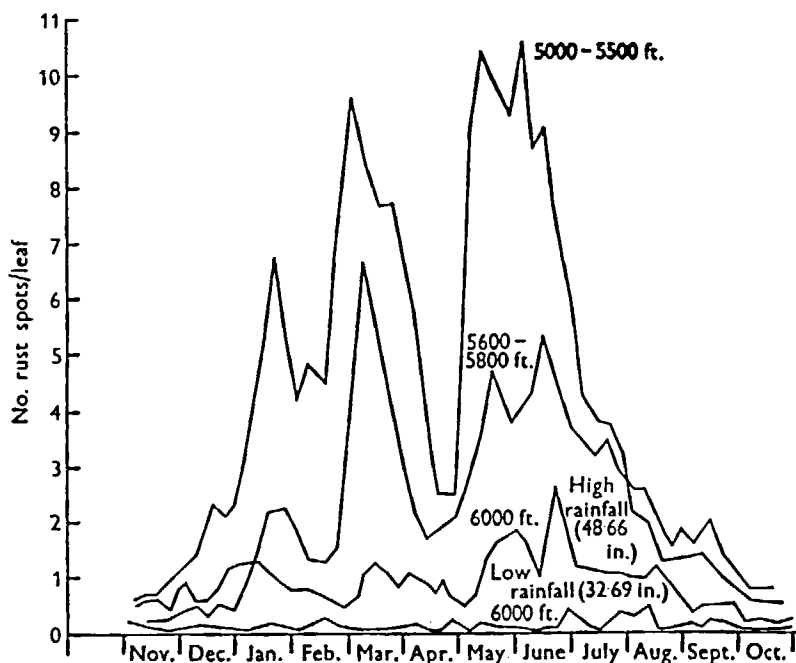


Fig. 15. Effect of altitude on incidence of leaf rust in East Rift districts.
Reprinted from Bock (1962b) *Trans. Br. mycol. Soc.*, 45: 292.

The intensity of the outbreak induced by each wet season depends mainly on three factors:

1. The amount of residual infection present at the time when the first shower of more than 0.3 in. (7.5 mm) falls. The higher the level of disease at this time, the more severe is the subsequent outbreak.
2. The density of the foliage: when there are few leaves on a tree much of the inoculum dispersed by rain falls to the ground because it is not intercepted by other leaves. On trees with dense foliage, however, there are many surfaces on which spores can be retained, and high concentrations of inoculum can be built up. Table 7 shows the differences in the amount of inoculum concentrations retained by the two different types of tree. The average is about 150 times greater on the densely foliated tree.

TABLE 7. MEAN NUMBER OF UREDOSPORES/cm²/LEAF AFTER 2.25 in. RAIN
(After Bock 1962b)
(Each figure represents the mean of eight samples, each of 1 cm²)

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. 16 illustrates the course of an epidemic on trees of high and low foliar densities respectively. Although both types had roughly the same level of disease in late June the more leafy ones reached a level of over 7 pustules per leaf which represents a severe attack compared with a consistently low pustule count on the thinly foliated trees.

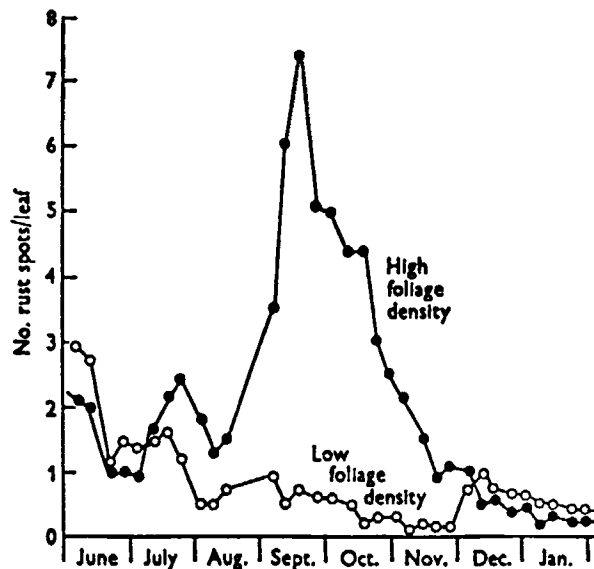


Fig. 16. Course of leaf rust development on trees. After Bock (1962b) *Trans. Br. mycol. Soc.*, 45: 297.

3. The distribution and intensity of rainfall during the build-up of an outbreak, is of fundamental importance. Fig. 13 shows the course of the disease on two plantation sites only 5 miles (8 km) distant from one another. At the start of the season the trees on each site had similar foliage densities and levels of residual inoculum. The early course of the outbreak was much the same on both, but in the early part of December the second site received a shower of almost 2 in. (50 mm); and subsequently also had heavier rainfall both in December and January. As a result the outbreak on this second site was almost twice as severe as that on the first.

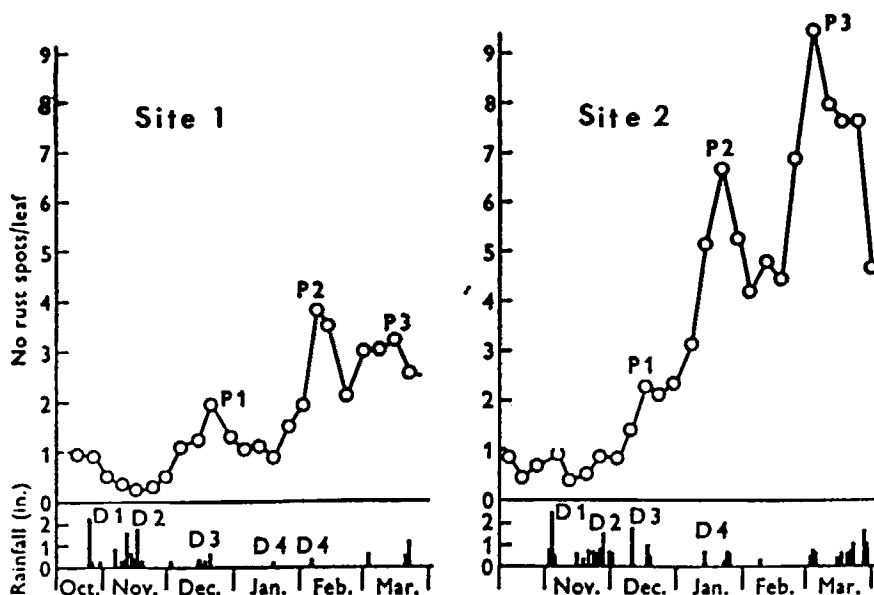


Fig. 17. Effects of distribution and intensity of rainfall on seasonal occurrence of leaf rust. After Bock (1962b) *Trans. Br. mycol. Soc.*, 45: 295

Control

All commercially grown varieties of *Coffea* are susceptible to leaf rust and it is certain that chemical control of the disease will be unavoidable for a long time.

Until very recently control was attempted on the assumption that air-borne inoculum, carried from a distance, was always present on the leaves and that nothing could be done about preventing its arrival. Efforts were directed, therefore, to maintaining a protective coating of copper fungicide during 'infective periods' (Rayner 1956). The recognition of the role of water in the dispersal of uredospores, however, has now made a different approach possible. The concept of a supposed long-range air dispersal has been replaced by the knowledge that dispersal by rain is extremely short-range and generally takes place mainly within an individual tree. It is further realised that movement of inoculum, and fresh infection, is virtually impossible until the first 'dispersal shower' of a rainy season. This shower is defined as being one of over 0.3in. (7.5mm) and, in general, the heavier it is the more effective is spore distribution. In regions such as East Africa it is usually possible to forecast its probable date with reasonable accuracy because of the comparative regularity in the onset of the rains. It will be shown later that there is a period of approximately 3 weeks before this dispersal shower during which sprays with a copper fungicide are effective.

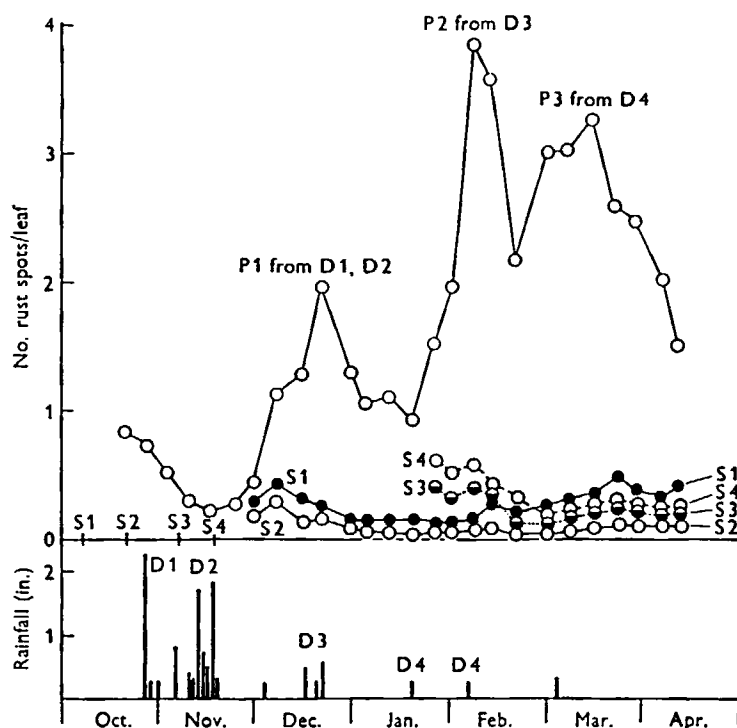


Fig. 18. Timing of sprays in relation to dispersal periods (D = dispersal period, S = spray application, P = disease peak).

After Bock (1962b) *Trans. Br. mycol. Soc.*, 45: 304.

That residual infection in Kenya is at a minimum before the start of the October rains is shown in Fig. 13 and 14. At this time most of the infected leaves have abscised, and as there has been no dispersal or re-infection for some time, any pustules remaining on the tree are fully formed with no new ones developing. New pustules appearing later therefore can only have been derived from these residual pustules which are the source of the fresh outbreak which follows the onset of the rains. Fig. 18 illustrates the separate effects of four copper sprays applied at various times around the critical period of the onset of rain. The actual sprays used were at the rate of 3lb/ac (2.67 kg/ha) of copper oxychloride. The figure also gives the time of each application, and the daily rainfall from October to April. The upper curve of Fig. 18 shows the disease level on unsprayed plots.

The first spray (S 1) went on about 3 weeks before the first heavy shower (dispersal period D 1), and the second (S 2) immediately before it. The third spray was between the first and second dispersal showers (D 1 and D 2) while the fourth went on immediately after D 2. As can be seen in Fig. 18 both the earlier sprays

controlled the disease for some months, although S 2, which was applied only a few days before the first dispersal shower, was more effective than S 1. This is because, even when copper residues are still visible on the leaves, the fungicidal effects of copper formulations are reduced after about 3 weeks (Bock, 1962c; Hislop, 1966). The second and third sprays had no reducing effect on the disease level which resulted from the first of the dispersal periods, since infection had already taken place before their application, but they did prevent subsequent infections, with their effect becoming apparent by mid-January; thereafter they kept the disease at a low level until the end of the cycle.

In climates such as those of the East Rift districts of Kenya where there are two cycles of rust outbreaks in each year, each cycle required similar treatment. As would be expected successful control of the first of the seasonal outbreaks results in a low level of residual inoculum at the start of the second, and consequently in greater efficiency of control in the second outbreak.

Where there is an extended rainy season, however, such as in the districts west of the Rift Valley in Kenya, longer series of sprays are necessary. But, provided that the period when residual inoculum is at its lowest can be ascertained, and the first dispersal period predicted with reasonable accuracy, control of the disease can be effected.

In some circumstances chemical sprays applied for leaf rust control can have an unfortunate effect. It will be remembered that the presence of pustules of rust causes early abscission of infected leaves. Fungicidal sprays, including the copper formulations, tend to prevent abscission of both diseased and healthy leaves. In consequence the treated trees tend to be more leafy than untreated ones and, as has been shown earlier, these intercept more inoculum during dispersal periods. Thus they also tend to become more seriously attacked than the untreated and less densely foliated trees.

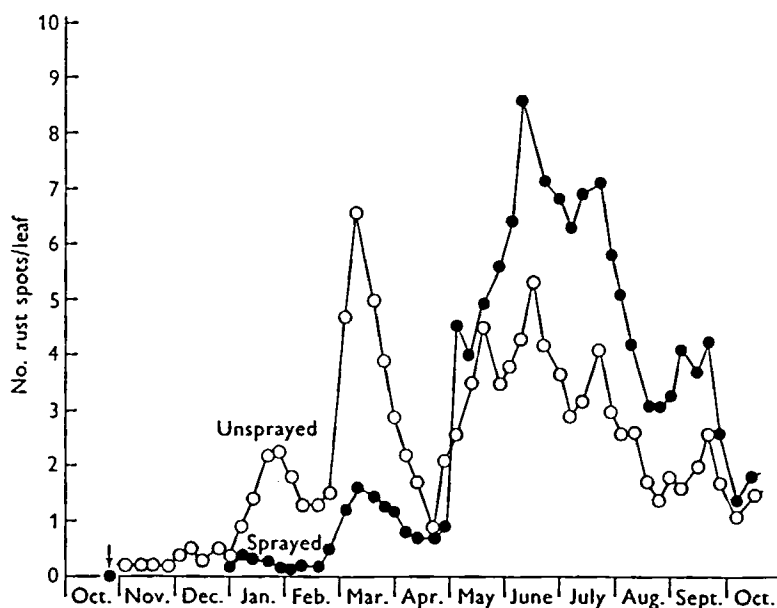


Fig. 19. Enhanced incidence of leaf-rust resulting from a single copper spray, applied 28 days before the rains, as indicated by arrow.

After Bock (1962b) *Trans. Br. mycol. Soc.*, 45: 310.

The result of badly-timed spray is shown in Fig. 19. In the instance shown the spray was applied in late October, 28 days before the first dispersal shower, by which time its effectiveness had been reduced by weathering. It did, however, control the January peak of the epidemic, and greatly reduced the March peak. The heavy fall on the unsprayed trees in early April (shown in the figure by the steep fall in the level of disease) resulted in both sprayed and unsprayed trees becoming similar in disease level at about an average of one pustule per leaf. The sprayed trees, however, being much more leafy, built up a higher disease level following dispersal by rain in April than did the unsprayed ones.

Basic principles of control

These can be summarised as follows:

1. The inoculum which gives rise to a rust outbreak is derived not from trees at a distance, but from pustules at very close range, usually within the same tree.
2. Inoculum is not spread during dry weather, but only by rainfall in excess of 0.3 in. (7.5 mm). This quantity is about the minimum required for run-off from the undersides of infected leaves.
3. There is a period, usually at the end of a dry season, when residual inoculum is at a minimum. It is at the end of this period, as precisely as possible before the onset of the first heavy rains of the season, that sprays have their maximum effect.
4. Of all the fungicides tested, copper formulations seemed to be the most effective (Bock, 1962c). These, however, lose much of their efficiency after a period of about 21 days. Many fungicides other than copper have also been found to give a measure of control.

Spraying schedules to be adopted in any country or region must, of course, be worked out empirically. The main object should be the prevention of infection arising from the first dispersal shower. This in itself normally results in successful control for a varying and often prolonged period. This spray should; however, be followed by others, applied at such times as to prevent disease level from rising to a point where rust-induced defoliation becomes serious. Once control sprays have been applied they must be continued as each rust cycle approaches, otherwise the 'induced' outbreaks such as are shown in Fig. 19 will occur.

Reference must also be made to another type of control carried out recently in Papua, where it seems that the disease may have been prevented from becoming established (Shaw, 1968). The method involved the elimination of all infected trees, and their possible contacts. This method is, of course, possible only when the pathogen has recently been introduced into a country hitherto free from the disease, where its presence has been detected before it has become widespread and where political conditions permit such an eradication campaign to be mounted.

Physiologic races

The greater part of the information given in this section is derived from the progress report for 1960-65 of the Oeiras Research Centre, (D'Oliveira, 1965) in Portugal. Cultivated species of *Coffea* which can become infected with *Hemileia vastatrix* include *Coffea arabica*, *C. abeokutae*, *C. canephora*, *C. eugenioides*, *C. dewevrei*, *C. kivuensis*, *C. liberica*, *C. racemosa*, *C. stenophylla*, and *C. salvatrix*. Wild species include *Coffea bengalensis*, *C. lebruniana*, *C. madurensis*, *C. mauritiana*, *C. wightiana*, and *C. travancorensis*.

Physiologic specialisation in coffee rust was first recognised by Mayne (1932) who differentiated three races in Southern India. The need for a comprehensive international survey of races in relation to geographic distribution and varietal susceptibility was met in 1955 by the establishment of the Coffee Rust Research Centre at Oeiras in Portugal.

By 1965, 23 races had been identified on the basis of their pathogenicity to a range of differential clones. They fall into two broad groups, one pathogenic to *C. arabica* and the other, smaller group pathogenic to other *Coffea* species; both groups infect *C. racemosa* and *C. bengalensis*. Both races I and II are geographically widespread. The distribution of the latter is probably correlated with the wide planting of the susceptible Bourbon-type coffee throughout many regions of the Old World. The other races are more or less confined to the areas of their particular host groups.

All the varieties cultivated in South America, including the most outstanding selections, are highly susceptible to both I and II, obviously the most widespread of all the races. It is this fact which emphasises the graveness of the threat to the industry in South America now that rust has become established there.

Coffee hybrids, cultivars and selections have been grouped on the basis of their reaction to physiologic races. These range from full resistance to all (Group A), to almost full susceptibility (Group B), with various intermediate types. A brief description of the more important groups will serve as an example.

Group A includes seedlings resistant to all known races of which the type is a clone derived from a 'Hybride de Timor' selection. One thousand seedlings of this have been tested and, while there is some segregation into susceptible types, 95% of them belong to Group A. This high degree of resistance which is transmissible, associated with tetraploidy, make these Timor hybrids valuable for breeding.

Group B includes the Bourbon-type coffees, and all cultivars and selections which are susceptible to all races with the exception of XIX and XX.

Group C is apparently entirely of Ethiopian and Sudanese origin and is characterised by susceptibility to races III, X, XII, XVI, XVII and XXIII. This group includes the important Geisha coffees which are well-known for resistance, vigour and yield.

Group D includes all selections susceptible to races, I, VIII, XII, XIV, XVI, XVII and XXIII, and many of the Kents selections fall into this group. These are of interest in that early in this century they displayed resistance to the local Southern Indian races and, accordingly, were introduced into other countries to be used for further selection and breeding.

This background knowledge makes it possible to synthesise new hybrids of known resistance to certain races. For example, crosses between Geisha (Group C) and Tanzania hybrid N. 66 (Group D) have resulted in selections of improved resistance.

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