

## STUDIES ON THE BIOLOGY OF *PHYTOPHTHORA MEADII*\*

BY

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*The cardinal temperatures for growth of P. meadii McRae in vitro were 5, 28–30 and 36° C. The fungus remained viable for 96 hr at 36°. The optimum for the production of sporangia was 28°, and zoospores were liberated readily between 20 and 28°, the maximum zoospore liberation being recorded at temperatures about 2° below those at which the sporangia were produced. Sporangia took longer to germinate and lost viability as they aged, becoming completely non-viable after 16 days incubation at 28°. Zoospores came to rest within 1 hr at 28°, but remained motile for 9 hr at 15 to 20°.*

*Very few sporangia formed germ-tubes directly, and chlamydospores were produced rarely by this fungus; both occurred only above 30°.*

*Sporangia liberated zoospores only in the presence of free water and lost viability rapidly on exposure to lower humidities, being rendered completely inactive after 4 hr at 75% RH. Zoospores germinated poorly and produced little germ-tube growth on dry surfaces, even under highly humid conditions (approaching 100% RH).*

*The optimum pH for growth and sporulation of the fungus was 6.*

*Exposure to direct sunlight and UV radiation for 5–20 min completely inactivated both sporangia and zoospores.*

*Zoospores were produced only at low temperatures (<20°), and all attempts to germinate them failed.*

*The significance of the available data on the biology of the fungus in formulating a scheme for forecasting Phytophthora leaf disease epidemics on Hevea is discussed.*

Four diseases of *Hevea brasiliensis* Müll-Arg., named abnormal leaf-fall, bark rot, dieback of shoots and pod rot, all caused by *Phytophthora meadii*, have been known in Ceylon since 1905 (Petch, 1921). These diseases have been observed on *Hevea* in all parts of the world, but no detailed studies have been made on the biology of the causal fungus since McRae (1918). The present investigations were undertaken mainly to provide a basis for forecasting the incidence of *Phytophthora* leaf disease epidemics.

Tucker (1931), in his study of the taxonomy of *Phytophthora* de Bary, grouped ten of the species described earlier, including *P. meadii*, under *P. palmivora* (Butl.) Butl.; subsequently *P. meadii* was overlooked until Waterhouse (1963) confirmed that McRae's (1918) *P. meadii* is a distinct species. Waterhouse has since identified a number of *Phytophthora* cultures, isolated from different parts of the rubber tree in Ceylon, as *P. meadii*. McRae (1918) observed that *P. meadii* was homothallic, and this has been confirmed by Waterhouse (1963). Peries & Dantanarayana (1965) have recently shown that in addition to being homothallic, *P. meadii* is sexually compatible with the 'rubber' group isolates (Ashby, 1929) of *P. palmivora*.

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## MATERIALS AND METHODS

A culture of the fungus (No. 65 of the collection of the Rubber Research Institute, Ceylon) isolated from the endocarp of a rubber pod and identified by the Commonwealth Mycological Institute, England, as *P. meadii*, was used throughout these studies. The stock culture was maintained on Difco Lima bean agar (LBA) in the laboratory at room temperature ( $28^{\circ} \pm 2$ ), and subcultured once a year.

Bean, carrot, maize meal and oatmeal extract agar, LBA, potato dextrose, potato glucose and water agar were tested as culture media. The most satisfactory was LBA, prepared from the standard Difco medium and used at 2.3% in water and this was employed in all experiments, unless otherwise stated. All media, unless otherwise stated, were brought to pH 5.6 with 0.1N hydrochloric acid or potassium hydroxide, and solidified with 20 g/l of agar.

Glucose-asparagine (Lilly & Barnett, 1951) with 0.0005 g/l vitamin B<sub>1</sub> was used as the standard liquid medium for these studies.

Solid media were inoculated with a 4 mm disk from the growing edge of a 5-day old colony on water agar, and liquid media with 0.1 ml of a mycelial macerate of a 4-day old culture in glucose-asparagine medium.

The number of sporangia per unit area in 7-day old agar cultures was determined by pressing surface sections of known area of the test cultures under coverslips on glass slides, and counting the sporangia under the microscope using a squared eyepiece.

The rate of release of zoospores from sporangia was determined by placing small pieces of the sporulating culture in water, the fungus being killed and stained at different intervals by introducing a drop of lactophenol cotton blue into the water. The number of zoospores produced per sporangium was counted with the aid of a telecounter, while observing zoospore release under the microscope. Standard 5-day old cultures were used for all studies on sporangial germination, and the figures given are based on averages of five replicates, at least 500 sporangia per replicate being counted.

Samples of sporangia were simultaneously exposed to direct sunlight and to sunlight under glass, also to diffused sunlight inside the laboratory, and to ultraviolet (UV) light (10 cm below a Hanovia 'Detectolite', a low-pressure quartz mercury-vapour lamp). The effect of darkness on the fungus was assessed by wrapping the complete apparatus for the test in two thicknesses of black polythene.

The period of motility of zoospores was determined by periodical observations of a zoospore suspension in water. Zoospore germination on agar-coated glass slides was estimated *in situ* after staining with cotton blue, and on leaf surfaces by the Sellotape strip method described by Peries (1962).

All studies on sporangial germination and zoospore motility and germination were carried out using glass-distilled water.

## RESULTS

*Selection of growth medium*

The salient features of the growth of the fungus on the different media tested are summarized in Table 1. The colony grew best on oatmeal agar as was observed by McRae (1918), but sporulation was poor on this medium, which was also opaque and unsuitable for critical studies on the fungus. LBA is a clear medium on which *P. meadii* grew well and sporulated profusely; therefore, this medium was selected for all further studies on the fungus.

TABLE 1

DETAILS OF GROWTH OF *PHYTOPHTHORA MEADII* ON DIFFERENT MEDIA AT 28° C

	Agar media							
	Bean	Carrot	LBA	Maize meal	Oat meal	Potato dextrose	Potato glucose	Water agar
Diameter of colony (mm) after:								
(a) 2 days	30.75	26.75	26.75	32.25	34.25	24.00	28.00	23.00*
(b) 4 days	58.25	57.75	50.00	69.75	67.00	52.00	51.75	45.50*
(c) 6 days	78.00	78.75	64.50	90.75	93.25	74.25	68.50	62.25*
Aerial mycelium	+	—	—	+++	+++	—	+	—
Sporulation after 5 days incubation	+	+	+++	—	+	—	—	—
	* Mycelium very sparse.		+++	Profuse.	+	Sparse.	—	Nil.

*Effect of temperature on growth and reproduction*

*Growth of colony:* The optimum temperature for colony growth on solid media is 30° (Fig. 1). There was no growth at 5 and 36°. This agrees with Tucker's (1931) observations.

The fungal mat weights in Fig. 1 show that the cardinal temperatures for growth on liquid media differ very little from those on solid media, the optimum being 28°.

*Lethal temperature:* A number of Petri dish cultures were maintained at 36° and at intervals of 24 hr; five of them, selected at random, were transferred to the laboratory bench. This showed that though the fungus does not grow at 36°, it is not killed by short periods of exposure to this temperature, but will recommence growth if transferred to 28° within 96 hr. Longer exposures proved lethal.

*Production of sporangia:* Fig. 2 shows the time taken from the inoculation of media to the first appearance of sporangia at different temperatures. *P. meadii* produces sporangia in 48 hr under optimum conditions, 28—30°; this agrees with Gadd's (1924) observations for *P. faberi*, but is longer than the 24 hr recorded for *P. palmivora* by Waterhouse, (1930).

There was a close relationship between temperature and spore production (Fig. 3), the greatest numbers being produced at 28°. Few sporangia were produced above 30° and below 25°, showing that the ambient temperature has a more critical effect on reproduction than on growth (cf. Fig. 1).

*Germination of sporangia:* Sporangia can germinate directly by producing germ-tubes or indirectly by releasing zoospores. All further references to sporangial germination in this paper concern indirect germination, unless otherwise stated. Irrespective of the temperature at which they are produced, the optimum temperature for germination of sporangia lies between 20 and 28° (Table 2).

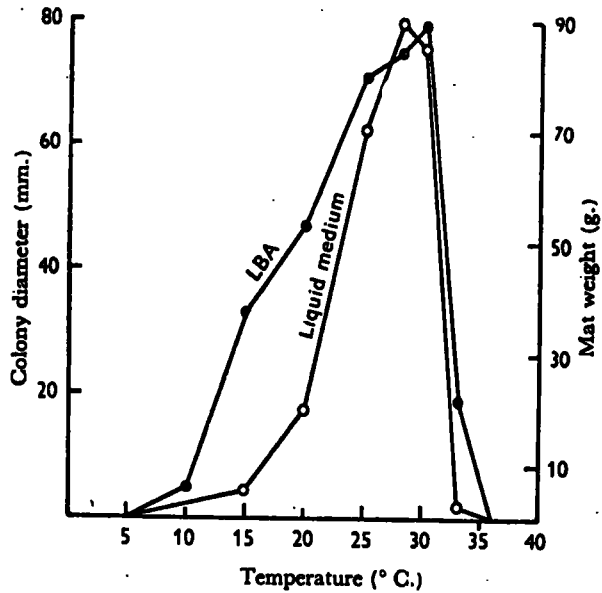


Fig. 1. Relationship between temperature and growth on solid and liquid media. Colony diameter (mm) on LBA and fungal mat weight on liquid medium (g.) 7 and 14 days, respectively, after inoculation.

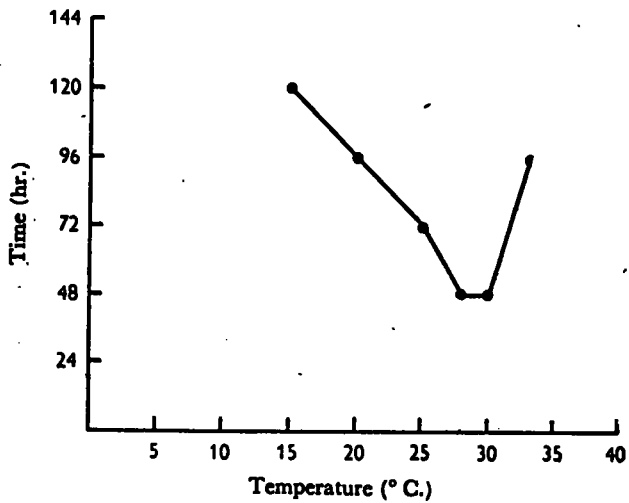


Fig. 2 Time taken for the production of sporangia at different temperatures

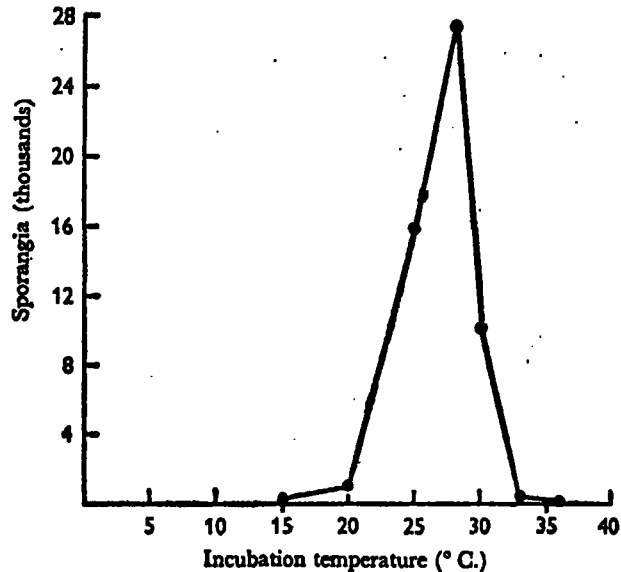


Fig. 3. Relationship between incubation temperature and number of sporangia (thousands) produced per cm<sup>2</sup> of agar surface on the 7th day of incubation.

TABLE 2

EFFECT OF TEMPERATURE ON MEAN PERCENTAGE GERMINATION, AFTER 45 MIN INCUBATION, OF SPORANGIA PRODUCED AT DIFFERENT TEMPERATURES

Temperature during sporangia production (°C)	Germination temperature (°C)						
	15	20	25	28	30	33	36
25	93	96	59	55	22	14	NG
28	75	95	96	58	3	Trace < 1	NG
30	78	91	96	95	47	7	NG

NG, No germination.

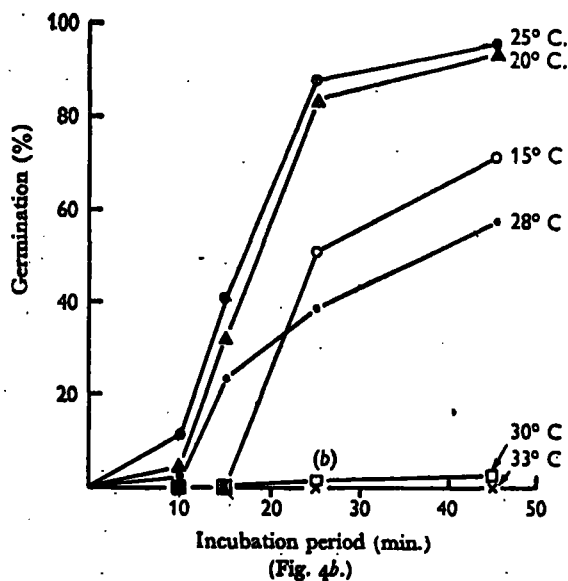
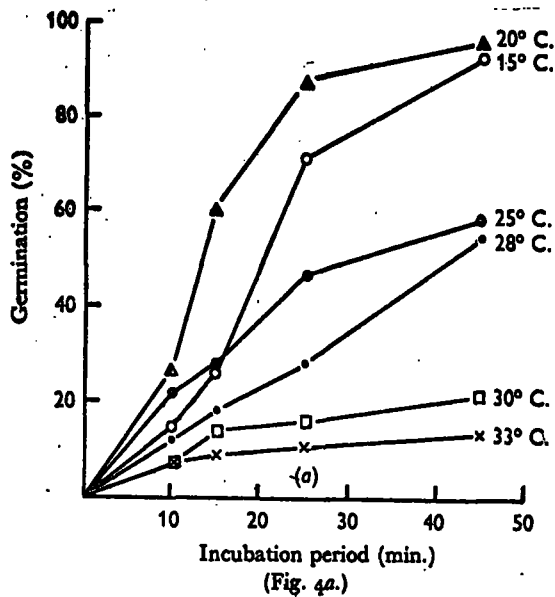
**Rate of germination of sporangia:** This was assessed for sporangia produced at different temperatures, and the results showed (Fig. 4) that there was a relationship between the temperatures of production and germination of sporangia. The optimum temperature for germination increased with that of production, sporangia always germinating most rapidly at a temperature slightly below that at which they were produced.

**Germinability of sporangia:** Studies on the relationship between age of cultures and the rate of germination of sporangia produced by them (Fig. 5) showed that the germination rate was retarded as the period of incubation of cultures was increased, at all temperatures, the effect being more marked at high temperatures. This agrees with the observations of Blackwell & Waterhouse (1930) who recorded that young sporangia germinate more rapidly than the old, and concluded that the former had more readily available sources of energy.

**Viability of sporangia:** Culture plates were maintained at different temperatures and observed daily for the presence of empty sporangia. It was found (Table 3) that sporangia lost their contents and became non-viable more rapidly at high than at low temperatures.

**Number of zoospores per sporangium:** The figures in Table 4 are the average of five trials, at least twenty-five sporangia being sampled in each trial. There was no correlation between the temperature at which sporangia were produced and the average number of zoospores released by them.

**Motility of zoospores:** High virulence of certain strains of *P. parasitica* has been associated with long periods of motility of their zoospores (Dukes & Apple, 1962). The longer zoospores are motile, the greater their chance of reaching a suitable host; therefore the period of motility of zoospores under different conditions is of vital importance in the epidemiology of the disease.



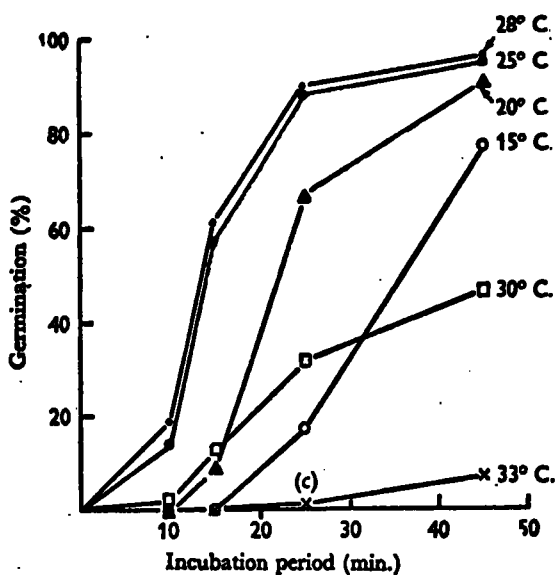


Fig. 4c

Figs. 4 a, 4 b and 4 c. Percentage germination of sporangia produced at (a) 25°, (b) 28° and (c) 30°C. after different periods of incubation at various temperatures.

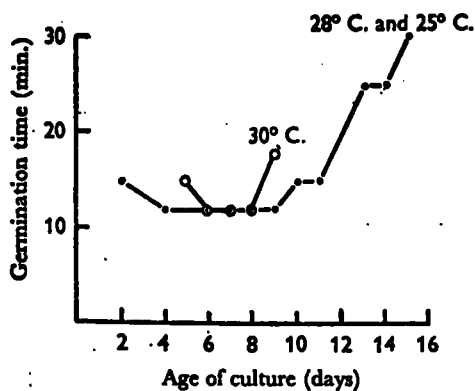


Fig. 5. Time taken for germination (at 20° C) of sporangia from cultures incubated at different temperatures for increasing periods of time.

TABLE 3

NUMBER OF DAYS AFTER THE PRODUCTION OF SPORANGIA FOR THE EARLIEST OCCURRENCE OF EMPTY SPORANGIA AND THEIR COMPLETE LOSS OF VIABILITY

Temperature (°C)	15	20	25	28	30	33
Empty sporangia first observed	12	12	11	10	9	6
Complete loss of viability	28	28	25	21	18	12

TABLE 4

NUMBER OF ZOOSPORES RELEASED FROM SPORANGIA PRODUCED AT DIFFERENT TEMPERATURES AND GERMINATED AT 28° C

Temperature at sporangia production (° C.)	No. of zoospores
25	42
28	38
30	39

It was found (Fig. 6) that zoospores of *P. meadii* remained motile for 9 hr at low temperatures (15-20°), but they ceased movement within 1 hr at temperatures above 25°. There were no clear differences between zoospores released from sporangia formed at different temperatures.

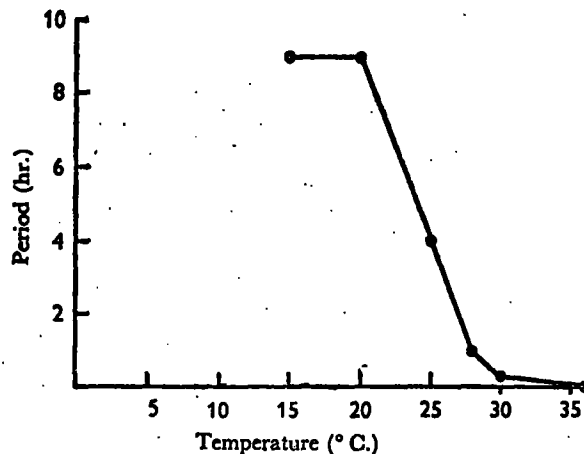
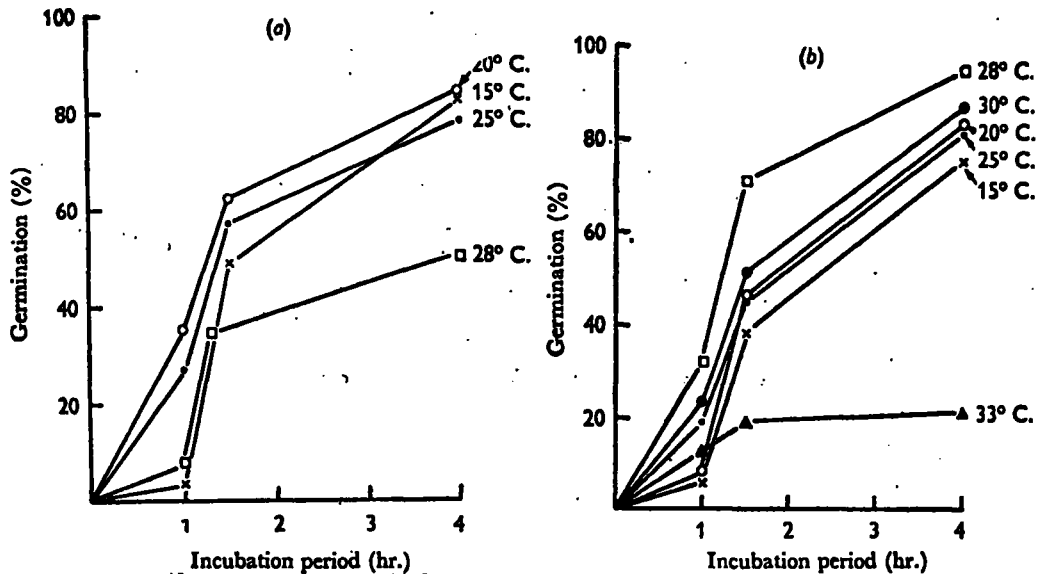


Fig. 6. Effect of incubation temperature on period of motility of zoospores released at 25, 28 and 30° C. Period for which zoospores remain motile at different temperatures.

**Direct germination of sporangia:** Crosier (1934) found that the maximum temperature for indirect germination of sporangia was the optimum temperature for direct germination in *P. infestans*. Very few sporangia (<5%) of *P. meadii* germinated directly, and these only at temperatures above 30°, the maximum numbers being recorded at 33°. Therefore, the general pattern of direct germination here is similar to that observed by Crosier in *P. infestans*.

**Chlamyospore production:** Observations, over a period of 8 weeks, on cultures incubated at different temperatures showed that very few chlamyospores were produced, and these only at temperatures above 30° after long periods of incubation (> 18 days). This is characteristic of *P. meadii* (Waterhouse, 1963).

**Rate of germination of zoospores at different temperatures:** Zoospores germinating in water, on agar-coated slides, were killed at various intervals with lactophenol cotton blue and the percentage germination estimated. The results (Fig. 7a) show that, when maintained at the temperature at which they are released, low temperatures are conducive to zoospore germination, the optimum being 20°. However, when zoospores released at low temperature (20°) are maintained at different temperatures, they germinate best at 28° (Fig. 7b); this may be related to the fact that zoospores come to rest rapidly (Fig. 6) at 28°, enabling them to germinate earlier.



Figs. 7a and 7b. Effect of temperature at which zoospores are released and subsequently incubated on their germination. (a) Percentage germination of zoospores incubated at the temperature at which they were released. (N.B. Insufficient zoospores were released at 30° and 33° C (cf. Table 2) for assessment). (b) Zoospores released at 20° C and germinated at different temperatures.

#### *Effect of humidity on sporangia and zoospores*

**Germination of sporangia:** No germination was recorded in sporangia scraped off 5-day old cultures incubated at 25°, placed on dry slides, and maintained at 15, 20, 25, 28, 30 and 33° inside sealed jars, where the RH was kept constant at 100, 96, 75, 50 and 0%, with saturated salt solutions (Peries, 1961). However, 85-95% germination was recorded in controls where the sporangia were placed in water. It was concluded that the sporangia of *P. meadii* will germinate only in the presence of free water, unlike those of *P. infestans* which have been found to germinate on dry surfaces, under conditions of high humidity (Glendenning, Macdonald & Grainger, 1963).

**Viability of sporangia:** Thin blocks of agar, removed with a 4 mm cork borer from 5-day old cultures of the fungus growing in specially prepared plates, each containing 5 ml of medium, were placed under different conditions of humidity at 28°. Samples were placed in distilled water at 1 hr intervals and the percentage germination of sporangia determined. The results (Fig. 8) show that sporangia lose viability rapidly when maintained at low humidities even at temperatures conducive to the growth of the fungus. Similar results have been recorded by Crosier (1934), Zan (1962) and Glendenning *et al.* (1963) for *P. infestans*.

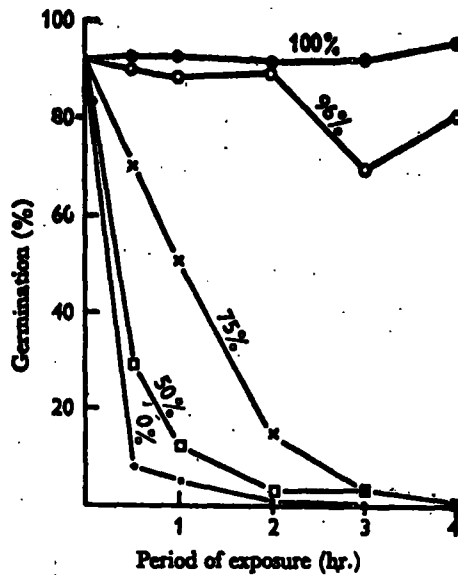
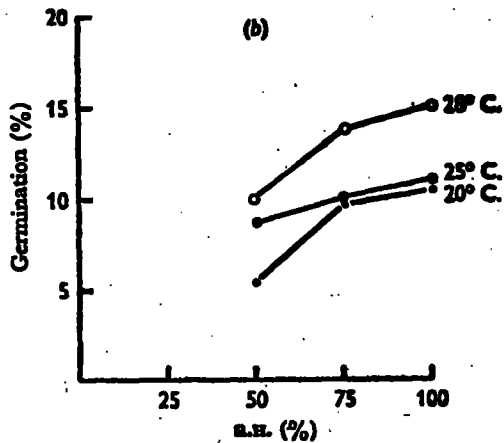
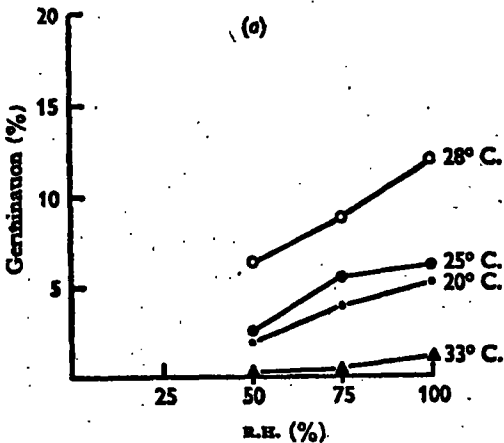


Fig. 8. Percentage germination of sporangia after exposure for various periods to different conditions of humidity.

**Zoospore germination:** Drops of a zoospore suspension in water were placed on agar-coated slides, and on rubber leaf surfaces, and the water dried off quickly under an electric fan. These preparations were then held under various combinations of temperature and humidity, and the percentage germination of zoospores determined at the end of 4 hr, the results being shown in Fig. 9a, b. Germination was poor under all conditions tested here, and little growth was made by the germ-tubes in the absence of free water, as shown below :

TABLE 5.  
LENGTH OF GERM-TUBES ( $\mu$ ) PRODUCED BY ZOOSPORES INCUBATED FOR 4 HR AT 28° C ON AGAR-COATED GLASS SLIDES OR LEAF SURFACES

	In free water	On dry surface	
Glass slides	120	6	} In saturated atmosphere
Leaf surfaces	160	6	



Figs. 6 a and 9 b. Percentage germination of zoospores on (a) dry agar-coated glass slides and (b) leaf surfaces at various temperatures under different conditions of humidity.

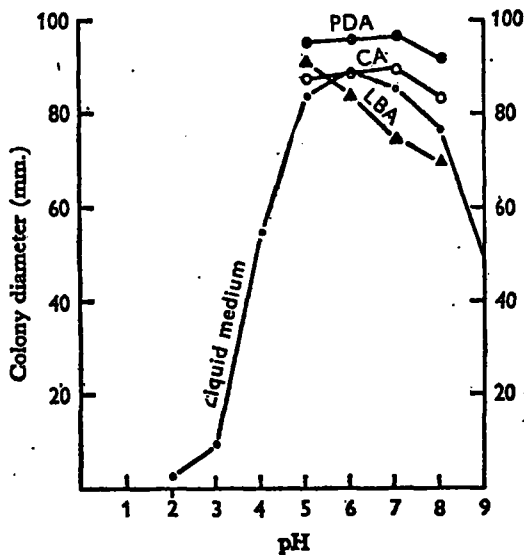


Fig. 10

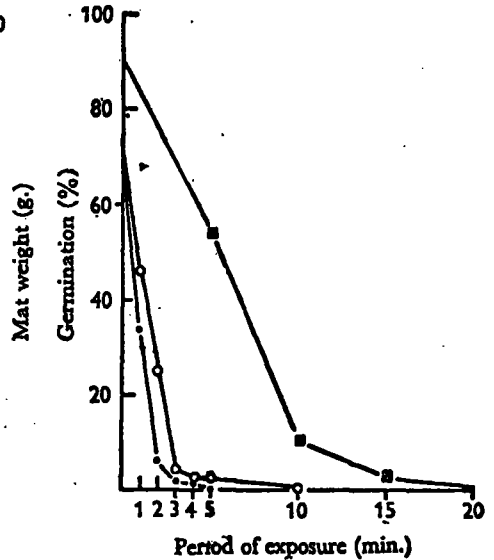


Fig. 11

Fig. 10. Effect of pH on growth of *Phytophthora meadii* on soil and liquid media. Colony diameter (mm) and mat wt (g), 7 and 14 days respectively after inoculation.

Fig. 11. Percentage germination of zoospores and sporangia exposed to UV radiation and sunlight for different periods of time. ■—■, Zoospore germination on exposure to UV radiation; O—O, Sporangial germination on exposure to UV radiation; ●—●, to direct sunlight.

#### *Effect of pH on growth and sporulation*

**Growth and sporulation:** The maximum growth on all media was recorded between pH 5 and 7 (Fig. 10). Agar media did not set below pH 5; therefore the optimum pH for growth on them cannot be clearly defined. On liquid media, however, the fungus grew best at pH 6. This agrees with the figure recorded by Stoughton-Harris (1926) for *P. palmivora* isolated from *Hevea*.

In further studies it was found that the curve for the relationship between sporulation and pH was very similar to that between growth and pH (Fig. 10); therefore the former is not illustrated in this paper.

#### *Effect of light and UV radiation on sporangia and zoospores*

**Production of sporangia:** Light can have a variable effect on the production of sporangia in different species of *Phytophthora*: Waterhouse (1930), Wills (1954) and Gooding & Lucas (1959) reported that it had no effect on certain species; Gadd (1924), Aragaki & Hine (1963) and Harnish (1965) observed that it stimulated spore production in others, and Zentmeyer & Marshall (1959) and Harnish (1965) found that it inhibited sporulation in some species.

There was no significant difference between the number of sporangia produced by *P. meadii* in complete darkness, in alternate light and darkness under natural laboratory conditions, and under continuous artificial light. Therefore, all the studies on the production of sporangia reported here were carried out in closed incubators and refrigerators.

*Inhibition of sporangial germination:* *Phytophthora* diseases of *Hevea* are most prevalent during the South-West monsoon season each year in Ceylon and South India (Peries, 1956; Ramakrishnan, 1961), and it is important to know what effects sunny periods occurring during this season have on the development of epidemics.

The sporulating fungus on thin agar blocks was exposed to direct sunlight, sunlight under glass and UV radiation, and sporangial germination in sample blocks assessed after every minute of exposure. It was found (Fig. 11) that sporangia were completely inactivated by exposure for 5 and 10 min to bright sunlight and UV radiation, respectively. The sporangial contents shrivel and disintegrate rapidly on exposure to direct sunlight or sunlight under glass, but UV radiation did not produce this effect.

*Effect of irradiation on zoospore germination:* Zoospores too are rapidly inactivated by exposure to sunlight and UV radiation. Motility and germination are completely suppressed and the zoospores disintegrate after 5 min exposure to sunlight. UV radiation was not as potent as sunlight and complete inactivation occurred only after 20 min exposure to it (Fig. 11).

The lethal action of sunlight to sporangia and zoospores cannot be ascribed entirely to the effect of UV radiation, as it was observed under glass too. Therefore, it appears that the longer light rays, especially the infra-red, and the drying action of sunlight are responsible for this effect. The temperature recorded in direct sunlight during the above trials was 42°, and later experiments, where sporangia exposed to a temperature of 42° disintegrated within 5 min, confirmed this conclusion. The observations made during these studies differ from those of Glendenning *et al.* (1963), who found that UV radiation had a more potent effect in inactivating sporangia than sunlight.

#### *Production and germination of oospores*

*Production:* Pure cultures of the selected isolate, and paired cultures of it with other isolates of the fungus from *Hevea*, were maintained at different temperatures and observed daily for oospore production. Oospores were produced only at low temperatures, 15-20°, as found by Turner (1961) and Satchuthanathavale (1963). The selected isolate produced oospores in 60 days in pure culture and in 5-7 days when paired with compatible strains of the fungus isolated from *Hevea*. This confirms the observation made by McRae (1918) and Peries & Dantanarayana (1965) that pure cultures of *P. meadii* characteristically produce oospores in vitro only after long periods of incubation.

*Germination:* Blackwell (1943) has given details on the method of germinating oospores of *P. cactorum*, but *Phytophthora* oospores have rarely been successfully germinated under laboratory conditions. All attempts to induce oospores to germinate during the present studies failed, but these organs may germinate in nature, and would then constitute the most important means by which variation of the fungus can occur, as suggested by Haasis & Nelson (1963).

#### DISCUSSION

*P. meadii* grows vigorously at normal temperatures recorded in the rubber-growing districts of Ceylon, but the optimum for the production of sporangia is 2-3° lower. Zoospores too remain motile for long periods at low temperature. Therefore a slight fall of the atmospheric temperature can be expected to stimulate the fungus, helping it to multiply rapidly and increasing its chances of dissemination

Free water is essential for the fungus, which hibernates in various parts of the rubber tree during dry weather periods (McRae, 1918; Peries, 1963; 1964) and recommences growth during rainy weather. Zoospore germination and germ-tube development are poor on dry surfaces, even under humidity conditions approaching saturation. It has been shown (Peries, 1964) that zoospores can cause infection of the plant only if the surface of the latter is kept wet for a period of at least 1 hr. Therefore a certain amount of rainfall, sufficient to wet the plant and maintain surface wetness, is essential for the spread of the disease. Intermittent rain accompanied by high humidity, which would help keep plant organs wet, would be ideally suited for rapid development of the disease.

The lethal effect of direct sunlight on field infections is likely to be limited; because all the plant organs, on which the fungus sporulates, are not likely to be exposed to the sun. However, in addition to its direct action, sunshine tends to increase the temperature and reduce atmospheric humidity, and both these effects are deleterious to the fungus. Therefore when a bright sunny day supervenes, after the disease has begun to spread, all sporangia produced prior to that day can be expected to dry out and lose viability, so that a new crop of sporangia would have to be produced, under suitable conditions, before the disease could spread farther (cf. Glendenning *et al.*, 1963).

Methods of forecasting *Phytophthora* late blight of potatoes have been known for a number of years in Europe and the U.K. All such methods are based on the occurrence of periods of weather during which certain specified conditions of temperature, humidity and rainfall prevail (Van Everdingen, 1926; Beaumont, 1947; Bourke, 1953; Smith, 1956). The present studies have shown that in addition to these factors, sunshine is likely to play an important role in governing the incidence of *Phytophthora* leaf disease of *Hevea*; a similar relationship has already been established in the case of blister blight (*Exobasidium vexans* Masee) of tea (*Camellia sinensis* L.) by Visser, Shanmuganathan & Sabanayagam (1961).

The data presented in this paper indicate that *Phytophthora* leaf disease of *Hevea* is likely to spread during the South-West monsoon season, in periods of dull, overcast, rainy weather. When there is little or no sunshine, the temperature falls below the normal for that time of the year, and the atmospheric humidity is consistently high, so that plant surfaces wetted by rain remain moist for long periods. From previous records of their incidence, Peries (1965) has recently elaborated the critical conditions of temperature, humidity, rainfall and sunshine on which epidemics of this disease may be forecast. It now remains to perfect the method on the basis of present knowledge on the biology of the causal fungus and further observations on the incidence of the disease.

These studies have indicated that control measures against the spread of *Phytophthora* leaf-fall in *Hevea* need be carried out only when certain weather conditions prevail, during the South-West monsoon season, and not throughout the duration of the latter, as suggested by Riegenbach (1957). It is clear that the control methods employed at present must be reassessed on the evidence presented here.

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