EPIDEMIOLOGY OF FOOT ROT DISEASE OF BLACK PEPPER (*PIPER NIGRUM* L.) IN INDIA

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Foot rot (quick wilt) disease of black pepper (*Piper nigrum* L.) caused by *Phytophthora capsici* (*P. palmivora'* MF_4) is one of the major constraints in the production of black pepper in India. Although the fungus *Phytophthora* was isolated from black pepper as early as 1929 (Venkata Rao, 1929) in India, *Phytophthora* as the causal organism of black pepper wilt was reported only in 1966 (Samraj and Jose, 1966). Since then, it has been reviewed by Nambiar and Sarma (1977) and Sarma and Nambiar (1982). The epidemiological studies carried out so far in India have been reviewed in the present paper.

SYMPTOMATOLOGY

All parts of black pepper vine are susceptible to *P. capsici* as in the case of potatoes to *P. infestans*. Because of this, *Phytophthora* infection attains very severe proportion in black pepper and poses practical problems in disease management. According to Schwinn (1983) the infections caused by *Phytophthora* belong to three categories namely, (1) Infections on aerial parts like leaves and fruits, (2) Infections on shoot, crown and roots which are locally systemic, and (3) Infections on crown and roots.

Phytophthora infections in black pepper can be broadly classified into three categories namely, (1) Aerial infection, (2) Collar infection, and (3) Root infection.

AERIAL INFECTION

This includes (1) Stolon (or) runner shoot infection, (2) Leaf infection, (3) Spike infection and (4) Stem infection.

Stolon/runner shoot infection

The stolons arise from the base of the vine before the onset of south-west monsoon period, after receiving pre-monsoon showers in April-May. These runner shoots trail on the ground and produce roots at each node. Farmers in India, generally use these as planting material to raise rooted cuttings. These branches being very tender and succulent and also in direct contact with the soil, contract the infection first. Small dark brown lesions appear on the tender leaves and the succulent stem (Fig. 1). The rotten succulent runner shoots and leaves produce (Fig. 2) abundant sporulation. The sporulating tissues are responsible for the secondary spread of the pathogen (Ramachandran et al., 1988).

Leaf infection

Tender leaves to begin with and the older leaves later get infected. One to many dark brown lesions, which later turns to black, develop on the lamina at the tip or in the middle of the lamina, which has a characteristic fast advancing fimbriate margin (Holliday and Mowat, 1963). If unfavourable weather prevails, there may be concentric zonations (Nambiar and Sarma,

Fig. 1. Runner shoot (stolon) infection

1977). The infected leaves are shed prematurely before the entire lamina is covered by the spots. Severely affected vine shows defoliation and occasionally appear bare (Fig. 3).

Spike infection

When the foliar infection is severe, spikes also are infected. Black lesions develop either at the distal end (Holliday and Mowat, 1963) or on any part of the spike, including the tip, middle or the stalk ends. Tender berries are also infected. Infected spikes are shed by abscission.

Stem infection

When the foliar and spike infections are severe, infection occurs as dark brown lesions on the lateral branches and the leaves. The stem

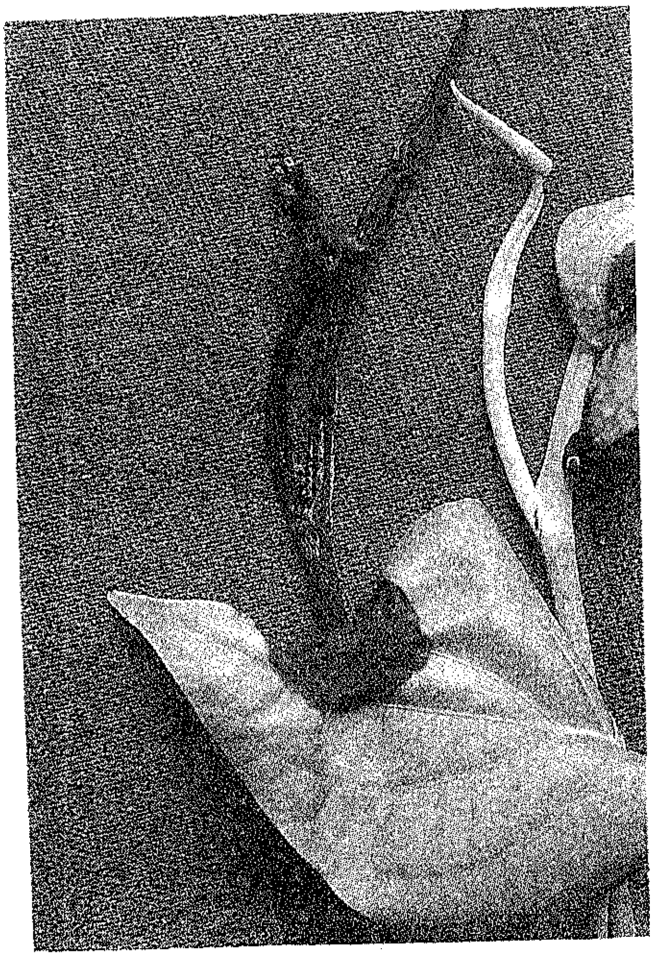

Fig. 2. Sporulating infected shoots

and leaves beyond the point of infection wilt and are shed. The tender berries in the spikes borne on such infected branches become shrivelled and the spikes are shed.

Succession of symptoms of aerial infection

The first visible symptoms of *Phytophthora* infection in black pepper occur on the runner shoots that emerge at the base of the vines soon after pre-monsoon showers. As the monsoon progresses soil moisture builds up and intermittant showers ensuring free water would make the conditions ideal for infection. Since soil with infected plant debris is the primary source of inoculum, the tender roots may also contract infection during the same period or even slightly earlier. The runner shoot infection is seen 2 to 3 weeks after the onset of monsoon. Since the mature dark brown lesions on

Fig. 3. Defoliated vine due to foliar infection

these succulent runner shoots and their tender foliage sporulate profusely, with the progress of monsoon in June-July period, the foliar infections gradually spread vertically over the entire height of vines in a stepwise manner, the rate of spread depending on the continuity of the monsoon. The tender leaves and spikes that are produced during this period help in faster spread of the infection. However, the maximum foliar infection is confined to the period starting from third week of June to second week of August (Figs. 4, 5, 6).

COLLAR (FOOT) INFECTION

The name quick wilt is derived from the symptoms of collar rot. Foliar yellowing, sudden wilting of the vine with flaccidity of leaves leading to various degrees of defoliation and breaking off of the branches at nodal regions are some of the characteristic symptoms. Collar infection occurs in various ways. (1) Infection of the main stem at or just below the soil level; (2) Infection through roots and (3) Infection on branch of underground stem, (4) Infection through runner shoots.

Infection of the main stem (Foot or collar) at or just below the soil

This occurs during the south-west monsoon season (June-September). The visible symptoms are wilting of leaves followed by defoliation, spike shedding and breaking off of the lateral branches at nodes. If the infected collar portion is exposed by scraping the outer layers of the bark, a clear demarcation of the advancing dark lesion in the cortical yellowish healthy tissue would be discernible. The root system below the collar and the stem above appears normal (Fig. 7). Some times wilting and shedding of the leaves are seen without any foliar yellowing symptoms of the leaves. The complete death of the vine results within 20–30 days (Anonymous, 1979). The occurrence of this sort of wilting is sudden and hence the local terminology as 'quick wilt' for this disease.

Infection through root system

The symptom expression in this case is gradual. The infection spreads from the root system to the underground stem before it spreads to the collar (Fig. 8). The earliest symptoms are yellowing of the leaves, followed by defoliation. Before the infections girdles collar,

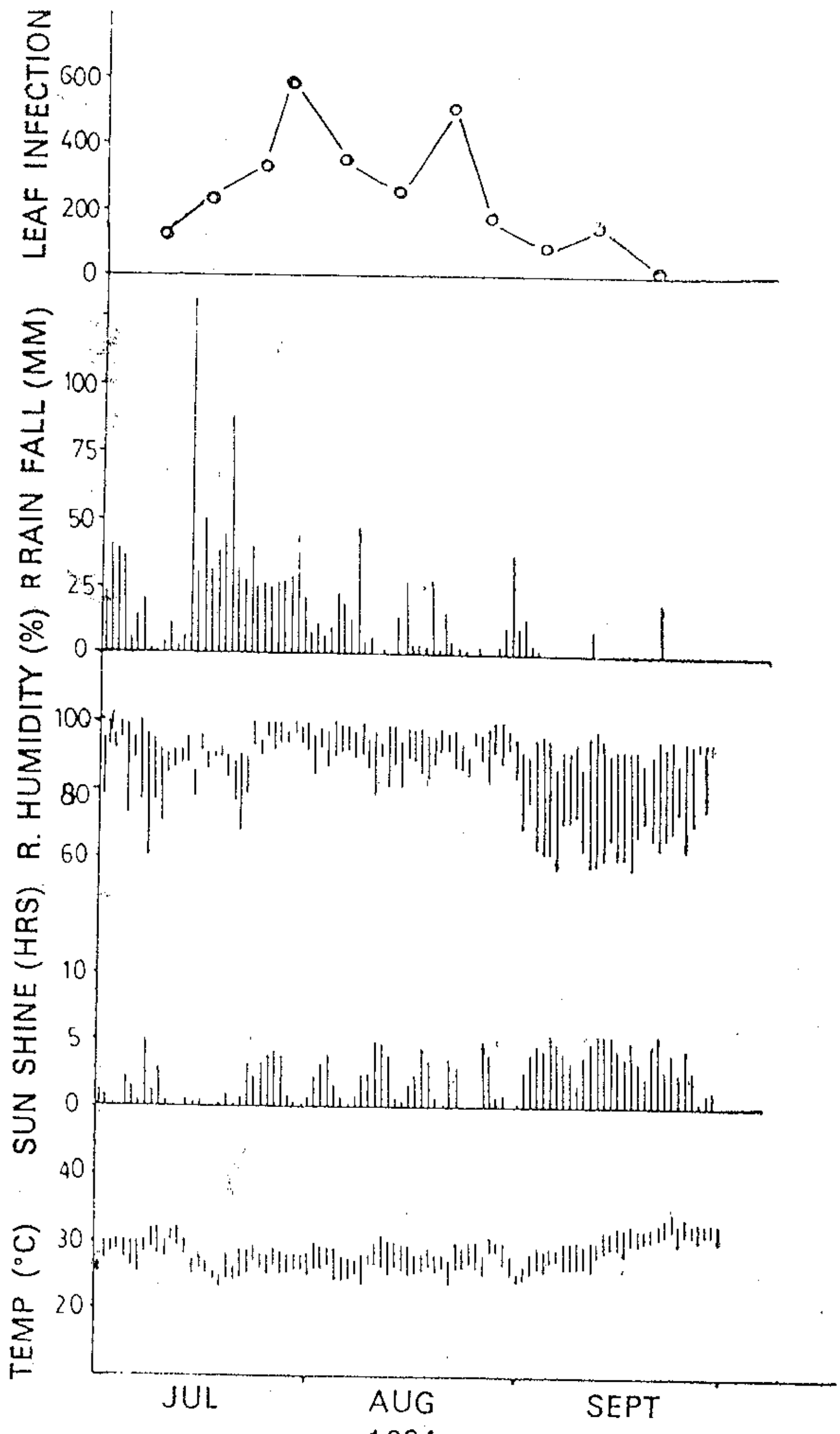

Fig. 4. Meteorological factors (vertical lines representing daily total of rainfall and sunshine and minimum and maximum of temperature and relative humidity) and *Phytophthora* leaf infection in black pepper during 1984

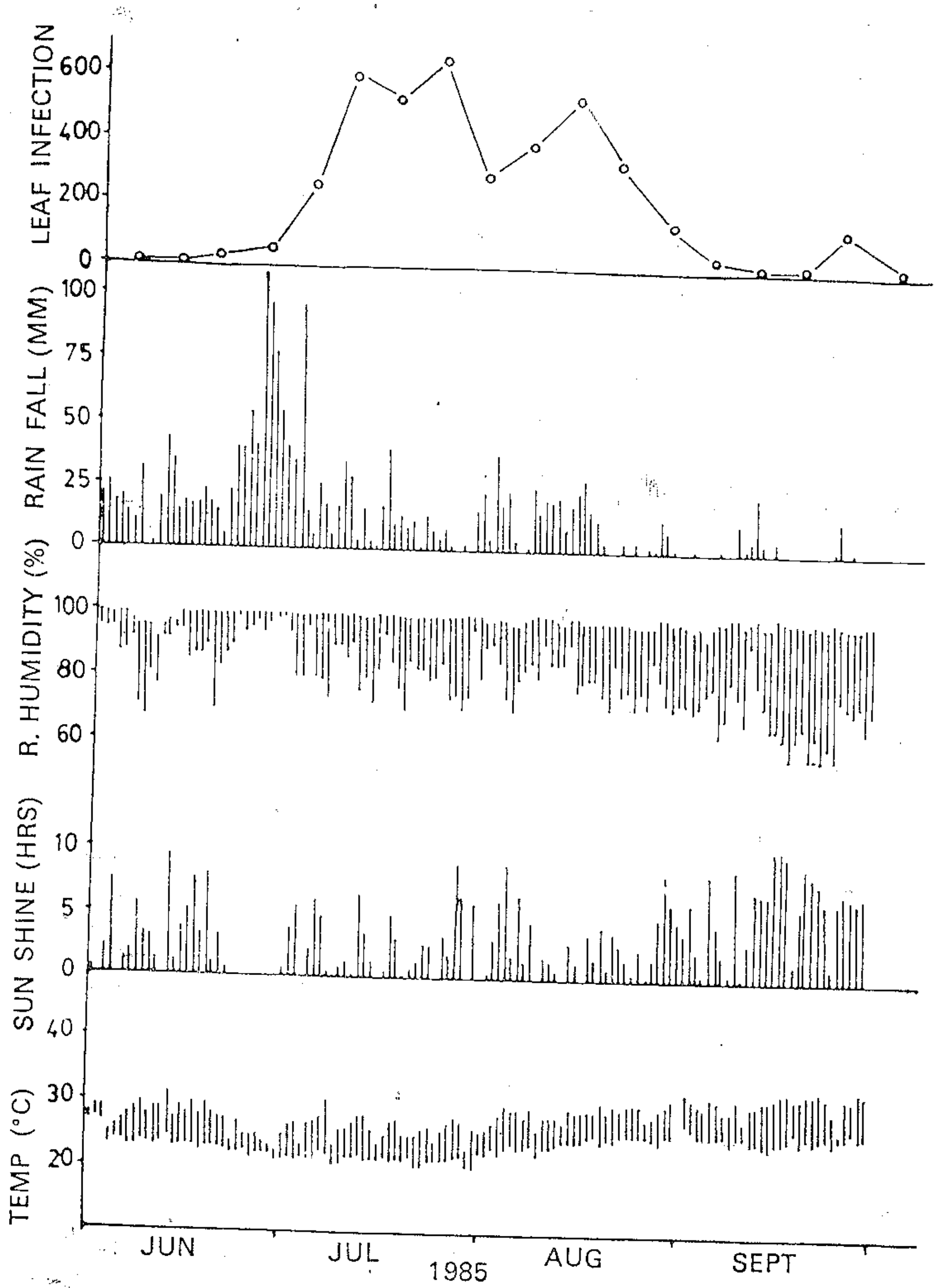

Fig. 5. Meteorological factors (vertical lines representing daily total of rainfall and sunshine and minimum and maximum of temperature and relative humidity) and *Phytophthora* leaf infection in black pepper during 1985

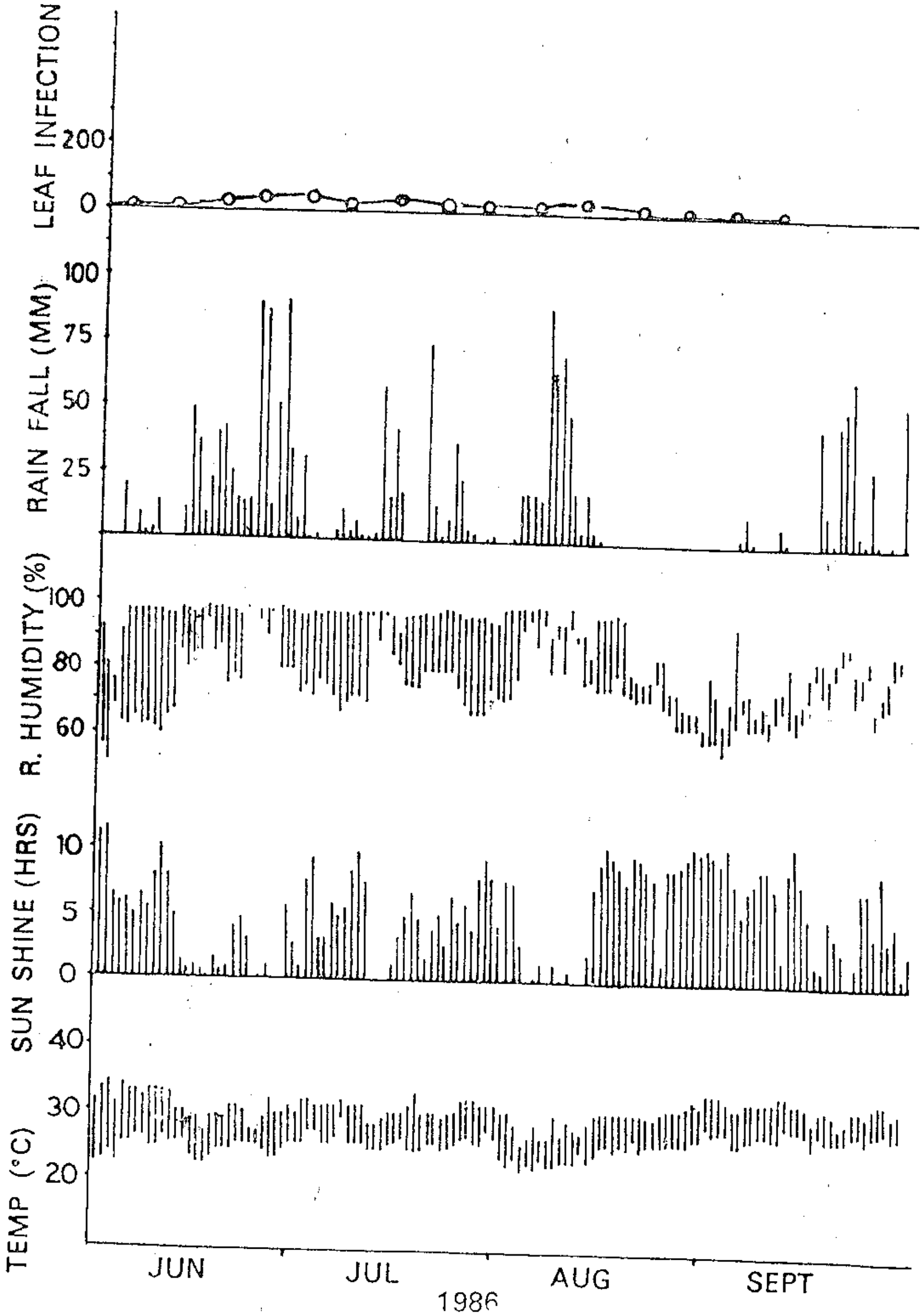

Fig. 6. Meteorological factors (vertical lines representing daily total of rainfall and sunshine and minimum and maximum of temperature and relative humidity) and *Phytophthora* leaf infection in black pepper during 1986

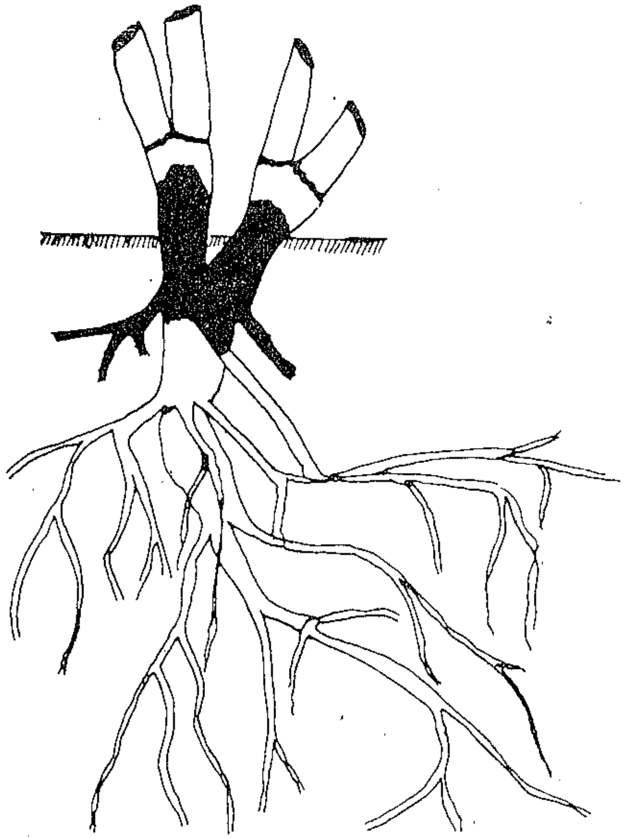

Fig. 7. Collar infection at or below soil level (diagrammatic)

one or two healthy roots at the collar region still sustain the vine for a prolonged period during the wet and monsoon period. When the root system is exposed at this stage of the infection, the spreading of the infection from the root system to the underground stem could be clearly seen.

Infection of a part of the vine

Black pepper vine produces several branches from the main stem, some of which arise from the main stem burried in the soil. If a single branch is infected either through root system (Fig. 9) or through direct infection, a part of the vine wilts showing all the symptoms of collar infection. In such cases the symptom expression may be delayed and expressed during dry periods. This type of infection results in partial death of a bush.

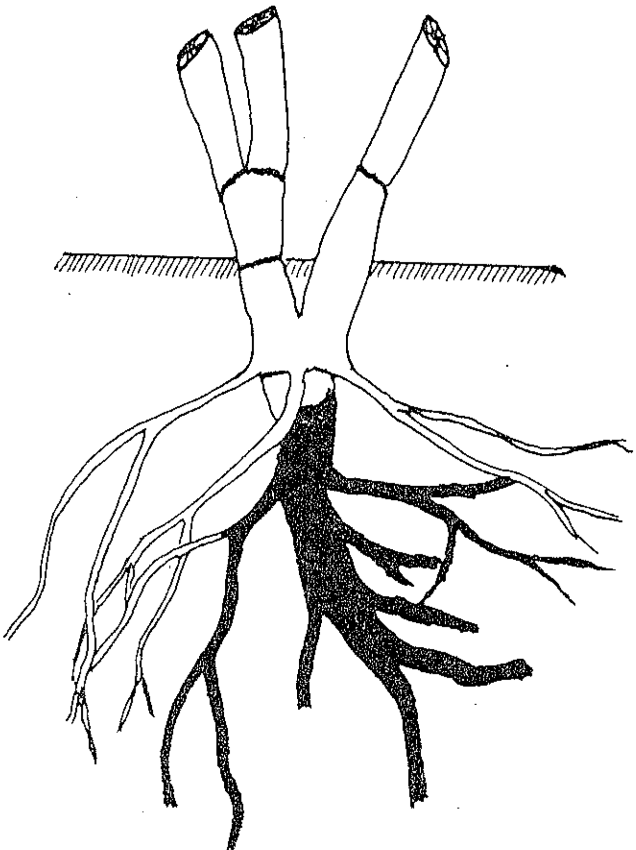

Fig. 8. Collar infection through roots and underground portion of the main stem (diagrammatic)

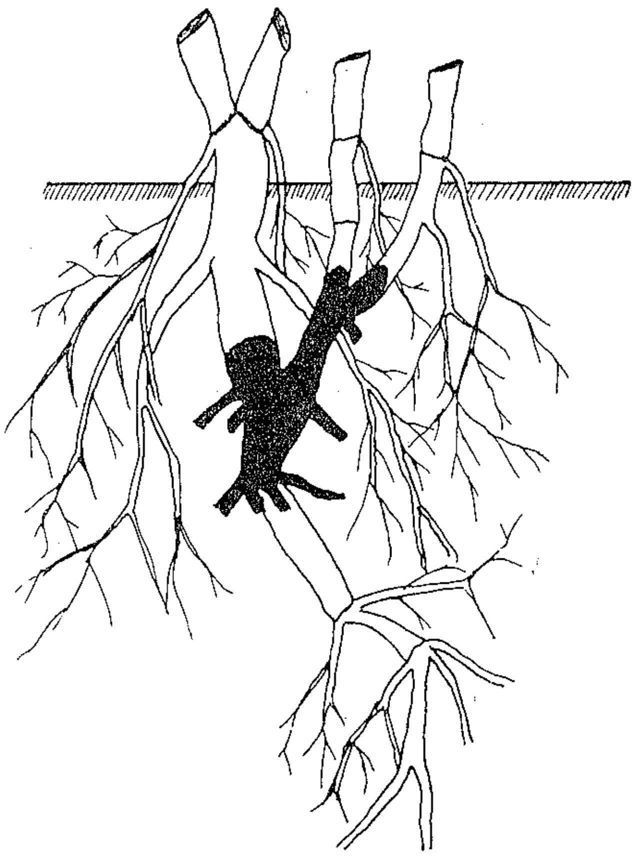

Fig. 9. Collar infection through roots of a single branch leading to partial death (diagrammatic)

Infection through runner shoots

Among the aerial parts of the vine tender leaves of the creeping stolons and the succulent stems are the first to take up infection. The infection spreads through the tender tissues of the runner shoots and enters the cortical tissue of the collar (Fig. 10). Once the infection encircles the collar, the entire vine wilts and defoliation occurs without yellowing.

ROOT INFECTION

Root infections which cause varying degrees of root rot go unnoticed without any visible aerial symptoms. To start with infection occurs on the fine feeder roots (Holliday and Mowat, 1963) and later spreads to the main roots and the collar. (Figs. 11 and 12). Visible symptoms are not expressed until large portions of the roots are damaged. With increased root rot, foliar yellowing, wilting of the vine and shedding of leaves, spikes and lateral branches

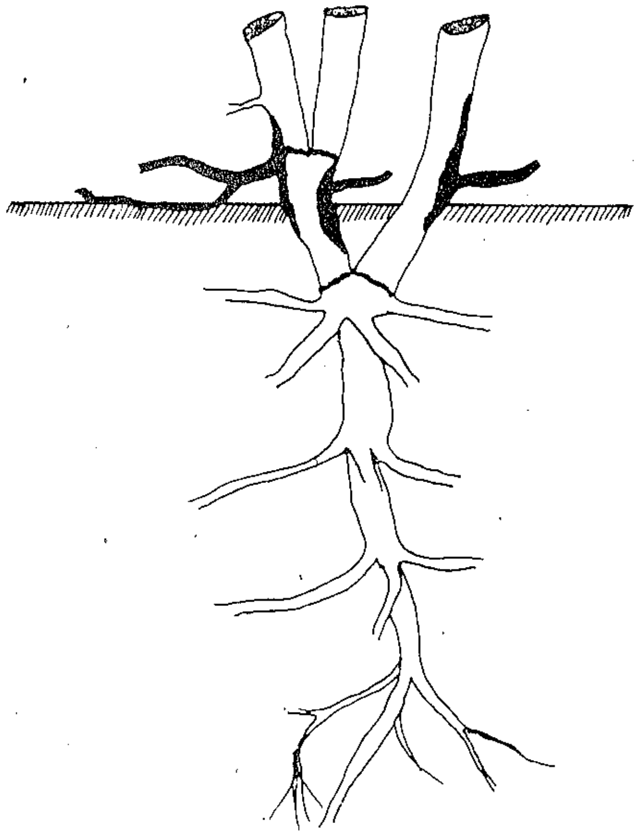

Fig. 10. Collar infection through runner shoots (diagrammatic)

are noticed. The amount of defoliation due to root infection is proportional to the root damage. Even if a portion of root system is healthy, the plant survives albeit with reduced canopy. The root loss to root regeneration determines the speed of the decline and death of the vine. After the cessation of rainy season with depletion of soil moisture if the remaining root system is unable to support the vine, the entire vine collapses with wilting and drying of leaves.

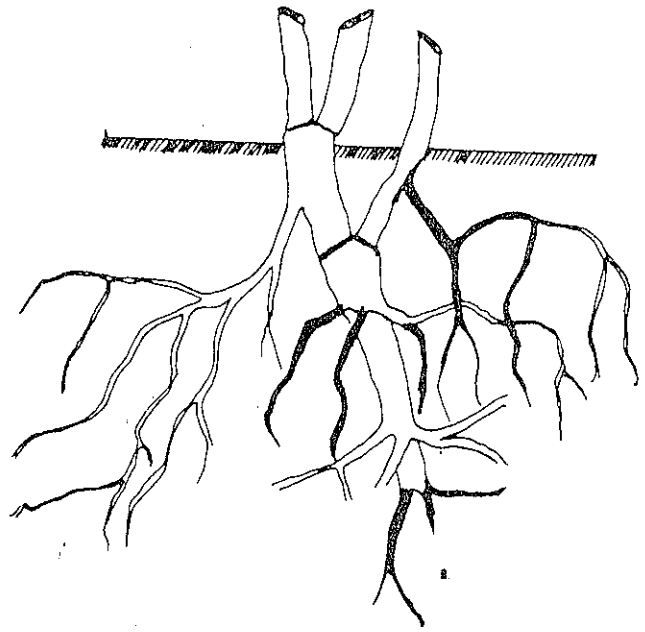

Fig. 12. Major root infection (diagrammatic)

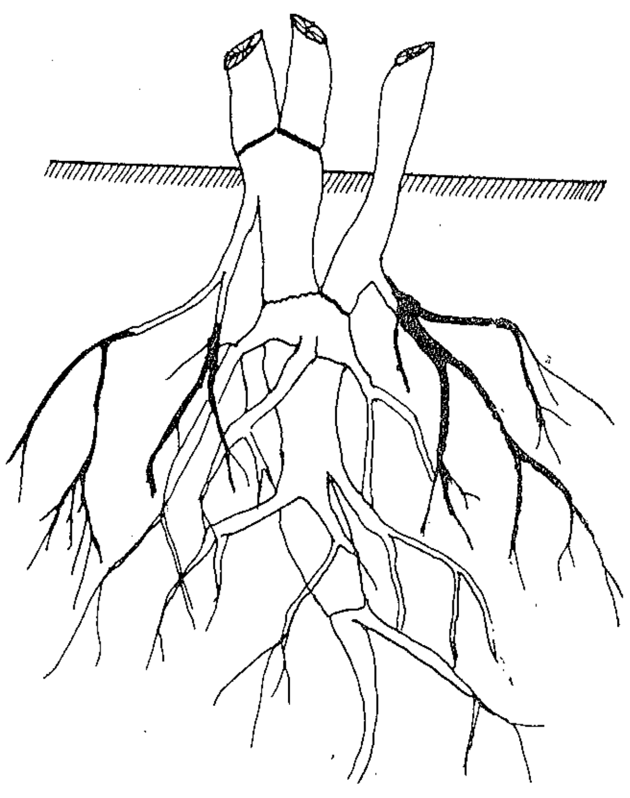

Fig. 11. Feeder root infection (diagrammatic)

EPIDEMIOLOGY

Although *Phytophthora* was isolated from the wilted black pepper vines as early as 1929 (Venkata Rao, 1929) the first authentic evidence of quick wilt of black pepper caused by *Phytophthora* (Muller, 1936) was reported in 1966 (Samraj and Jose, 1966). Based on the morphological studies, black pepper isolates of *Phytophthora* have been identified as *'Phytophthora palmivora'* MF_4 (Sarma, Ramachandran and Nambiar, 1982; Sastry and Hegde, 1987a).

Role of climatic factors in disease initiation

Phytophthora capsici (*'P. palmivora'* MF_4) being a wet weather pathogen is quite exacting in its requirements of physical environmental factors like temperature, moisture and relative humidity. In India the infections caused by this pathogen in black pepper is seasonal and is confined to the southwest monsoon period (June-September) as against Sarawak, where the infections are seen throughout the year, the maximum being in the wettest period of the year *i. e.*, October to March (Holliday and Mowat, 1963).

Disease initiation and the influence of pre-monsoon showers on the pathogen and the host

The first visible symptoms of the foliar infection occur on the runner shoots that emerge from the base of the vines, two or three weeks after the onset of the monsoon (Ramachandran et al., 1988). Since *Phytophthora* spp. survive in the soil saprophytically through survival structures like oospores and chlamydospores, high soil moisture is required to activate the fungus. This requirement is met by the pre-monsoon showers, which also trigger the flushing in black pepper vines. The flushing, thus initiated attains its peak either in the last week of June or in the first week of July providing highly susceptible host tissues for infection. Since soil is the primary source of inoculum, the runner shoots that are in contact with soil get infected first and promote profuse sporulation of the pathogen, providing the inoculum for further spread. This early phase of the disease is of utmost epidemiological importance and some of the climatic factors responsible for this are given in Table I.

A three year study conducted on the foliar infection in an areca-black pepper mixed cropping system in Kerala has shown that rainfall, number of rainy days and relative humidity had a positive correlation whereas temperature and sunshine hours had a negative correlation, (Figs. 4, 5, 6). The foliar infection increased when the daily rainfall of 15.8–23.0 mm, relative humidity 81–99%, temperature 22.7–29.6 °C and sunshine hours of 2.8 – 3.5/day (Table II) prevailed (Ramachandran et al., 1988). Unnikrishnan Nair et al., (1988) have reported that heavy rainfall, number of rainy days, relative humidity had positive correlation whereas, maximum temperature

Table I. *Rainfall and soil temperature preceding the initiation of runner shoot infection by* Phytophthora capsici *in black pepper*

Year	Date of onset of monsoon	Rainfall (mm)			Soil Temperature at 5 cm depth		Date of disease initiation
		Total until disease initiation	Average/day	Days with 10 mm and above	Min.	Max.	
1984	29 May	317.8	21.80	7	NR	NR	12 June
1985	23 May	259.5	17.30	13	24.27	27.50	6 June
1986	28 May	248.8	10.99	9	27.70	29.80	18 June

NR = Not recorded

(Ramachandran et al., 1988)

Table II. *Climatic factors (Means) during increasing and decreasing phases of* Phytophthora *leaf infection in black pepper*

	Year	No. of obser-vations	Temperature (°C)		Relative humidity (%)		Rainfall (mm)		Sunshine (h/day)
			min.	max.	min.	max.	per day	Days/week receiving 10 mm and above	
Increasing phase	1984	6	26.0	29.0	82.0	94.4	15.8	2.80	3.5
	1985	9	22.7	27.3	83.8	99.2	22.2	4.81	2.8
	1986	5	24.0	29.6	81.0	97.9	23.0	4.40	3.2
Decreasing phase	1984	5	26.3	28.6	82.4	95.6	8.4	1.80	4.8
	1985	8	23.6	28.7	76.4	97.9	8.4	2.20	3.5
	1986	10	24.7	30.8	70.9	88.9	10.0	1.80	6.8

(Ramachandran et al., 1988)

and sunshine hours had a negative correlation with foot rot incidence. Production of new leaves and spikes in black pepper starts in May-June and the peak flushing occurs during July. The occurrence of foliar infection is also maximum at this period coinciding with the peak monsoon season. Infection of underground parts of the vine must be taking place during this time.

PATTERN OF SPREAD

Foliar infection

Though the pathogen is soil-borne, it also spreads aerially resulting in infections on foliage, spikes and stems. The foliar infection caused by *'P. palmivora'* MF_4, has been reported to spread from the lower portions of the vine to the upper portion and adjacent vines through rain splashes and wind-blown water droplets (Anonymous, 1986; Nambiar and Sarma, 1982; Ramachandran et al., 1988). The stolons/ runner shoots are the ones to be infected first and it spreads to the canopy in a ladder like hopping mechanism typical of splash dispersed pathogens. This is further evidenced by the splash dispersal studies. Splash traps installed at different heights in an areca-pepper mixed garden and water collected from the traps gave positive baiting with black pepper leaf discs (Table III) (Ramachandran, Sarma and Anandaraj, 1990).

Collar and root infection

The pattern of spread of foot rot in a garden is always from the infected vine. Soil, water, root contacts, movement of people and use of implements previously used in a diseased garden all contribute to the spread. The disease is reported to spread in a centrifugal pattern from the source of infection (Holliday and Mowat, 1963; Nambiar and Sarma, 1982). The pattern of spread and the rate at which the disease spreads has been studied over a period of five years in two locations and found that the disease tend to occur non-randomly in a garden and tend to cluster around the previously infected vine. As the pathogen propagules tend to aggregate around the infected vine (Ramachandran et al., 1986), the chances of the adjacent vine getting infected are more. Since, the inoculum from the previously infected vine contributes to the disease in the following season, the rate of spread of the epidemic follows a compound interest disease model.

Table III. *Percentage of bait infection in the rain splash water collected at three heights and three distances from the base of the vine*

Date	Rainfall (mm)	Percentage of bait infection					
		Distance (meters)			Height (meters)		
		1	2	3	0	0.5	1
17–7–1984	30.5[1]	10 (56)	30 (93)	0 (60)	10 (70)	*	*
19–7–1984	80.5[2]	100 (294)	0 (272)	0 (305)	100 (275)	60 (254)	0 (244)
21–7–1984	94.6[2]	100 (263)	0 (235)	*	100 (329)	0 (305)	40 (158)
24–7–1984	15.5[2]	90 (66)	20 (70)	20 (48)	40 (161)	30 (104)	20 (53)
30–7–1984	47.5[2]	50 (151)	10 (285)	0 (212)	50 (266)	10 (176)	30 (228)
1–8–1984	27.9[2]	0 (43)	20 (74)	60 (114)	50 (90)	10 (75)	0 (61)
4–8–1984	31.4[3]	0 (70)	0 (55)	0 (46)	20 (190)	0 (50)	0 (34)

*Samples not collected. (Ramachandran et al., 1990)
Figures in parenthesis are the amounts of water collected in splash traps in ml.
Figures superscripted with 1, 2 and 3 show the total rainfall during one, two and three days preceding the date of collection respectively.

Primary source of inoculum

It is well established that soil is the main source of inoculum (Anonymous, 1986; Nambiar and Sarma, 1982; Sastry and Hegde., 1988; Ramachandran et al., 1986). Soil containing infected plant debris or apparently healthy nursery stock with incipient root infection or runner shoots collected from infected gardens to raise rooted cuttings may also act as sources of inoculum.

Survival of the pathogen

The fungus has been found to survive in infected plant material. Infected plant material incorporated to soil yielded positive isolation of *Phytophthora* upto 19 months (Anonymous, 1986). The soil borne *Phytophthora* spp. are known to be weak saprophytes (Zentmyer, 1980; Gregory, 1983) and can survive in soil as chlamydospores and oospores. In black pepper the mode of survival of the pathogen is not studied. Though the fungus can produce chlamydospores and also oospores when paired with a compatible mating type *in vitro*, their presence in infected soil is yet to be established. Since, black pepper is grown as a mixed crop with arecanut, coconut, cocoa and cardamom, the possibility of natural hybridization among the different *Phytophthora* species infecting these crops has been studied (Anonymous, 1981; Santhakumari, 1987; Sastry and Hegde, 1987a). Black pepper isolates when paired with rubber and cocoa isolates have produced oospores (Sarma and Nambiar, 1982). Ten *Phytophthora* isolates from black pepper from Kerala and Karnataka studied have been found to be of A^1 mating type (Sarma, 1985). However, Sastry and Hegde (1987b) have reported the presence of A^1 and A^2 mating types in *P. palmivora* in the ratio of 6:4 and A^1 mating type in *P. meadii* infecting arecanut. Oospores were obtained by crossing *P. palmivora* A^2 x *P. meadii* A^1 suggesting the development of new strains by intra and interspecific hybridization. Studies on the distribution of *Phytophthora* propagules in black pepper plantations have shown that the density of the propagules decrease with increase in depth and distance from the infected vine (Table IV).

Methodology of quantification of inoculum

Isolation of the organism from the infected tissues and soils and its quantification is an essential pre-requisite from the epidemiological point of view. The methodology has been reviewed critically by Tsao (1983). In black pepper, isolation of the organism from the infected tissues of root and collar has been difficult compared to isolation from infected leaves (Sarma and Nambiar, 1982). However, leaching infected stems and roots in running water for 24 hours and plating the tissue on PVPH medium (Tsao and Guy, 1977) has increased the frequency of positive isolations (Unpublished). Several baits have been used for the isolation of pathogen from the soil. Apples (Holliday and Mowat, 1963; Nambiar and Sarma, 1982) castor (*Ricinis communis*) seeds (Narasimhan and Ramakrishnan, 1969; Nambiar and Sarma, 1982; Sastry and Hegde, 1988) and pepper leaf discs (Ramachandran et al., 1986) have been used. In all these cases, the infected baits were surface sterilised and

Table IV. *Percentage of infected baits in soil at different depths and distances from the base of the vines*

Distance from the base of the vine (cm)	Depth (cm)	Percentage of baits yielding *Phytophthora*	
		Diseased plants	Apparently healthy plants
90	0–10	21.5	9.0
	11–20	12.5	8.0
	21–30	6.5	1.0
60	0–10	27.5	11.0
	11–20	12.0	6.0
	21–30	4.0	12.0
30	0–10	43.0	6.0
	11–20	32.0	9.0
	21–30	18.0	11.0
0	0–10	45.0	15.0
	11–20	48.0	*
	21–30	38.0	*

*Samples not collected.

(Ramachandran et al., 1986)

plated on PVPH medium (Nambiar and Sarma, 1982; Ramachandran et al., 1986) or on water agar (Sastry, 1982; Sastry and Hegde, 1988). The authors have successfully used *Albizzia falcatarea* leaflets as baits to isolate *Phytophthora capsici* from soil. The baits being smaller in size, large number of baits could be used in each container. Another advantage is that the fungus sporulates directly on the bait within 72 hr after placing the bait in the soil-water suspension. The confirmation of positive baiting is faster and easier (Anandaraj and Sarma, 1990). Soil dilution end point method (Tsao, 1960) has been adopted for quantification of inoculum in the soil. Studies carried out over a period of three years showed that the pathogen population in soil fluctuates during different periods of the year and in relation with moisture levels and soil temperatures.

Effect of age of the pepper vines on infection

Studies on the effect of age of the black pepper vines on infection was carried out on black pepper vines grown in microplots (1 m diam. cement tubs installed in the field). Plants of 5 age groups *viz.*, 5 year, 4 year, 3 year, 2 year and 1 year (20 each) were inoculated with *P. capsici* artificially showed that plants of all age groups are susceptible (Table V). As the development of disease is weather dependent, favourable period for the infection occurs only during monsoon period. Unless the infection occurs on the collar, the plant is not killed in that season. Generally, it is the root system which gets infected and the plant does not exhibit visible symptoms till considerable root damage has been caused (Figs. 11 and 12). In such cases of root infection, the yellowing, wilting and defoliation occurs even after the cessation of monsoon period. The correlation of such symptoms to the prevailing weather conditions (Unnikrishnan Nair et al., 1988) requires rethinking. Unless the collar is infected (through roots, stolon or direct infection) the entire vine is not killed. A portion of the vine may remain healthy and then it survives for several seasons. The survival or the death of the vine is the net result of rate at which the plant produces new roots and the rate at which the pathogen multiplies and colonises. If there is a break in the monsoon and the weather is unfavourable to the pathogen, the infection process is retarded; whereas the plant continues to grow since adequate soil moisture and good sunshine are available. Again at the start of monsoon the infection process is restarted. Once the south-west monsoon comes to an end in September, rainfall ceases and weather condition becomes unfavourable for the pathogen. Under irrigated conditions, especially in areca-black pepper mixed cropping system the favourable conditions are prolonged for longer duration and foot rot incidence is seen upto November. In cases of root infection, when the root system is damaged consider-

Table V. *Reaction of different age groups of pepper vines to artificial inoculation*

Age group	% of vine death	Collar infection	Root infection	Root + collar
5 year	50.0	25.0	—	25.0
4 year	83.0	8.3	16.6	58.3
3 year	50.0	—	16.6	33.3
2 year	—	—	—	—
1 year	41.6	25.0	8.3	8.3

Table VI. *Reaction of inoculated vines before and after monsoon*

Age group	Vines showing foliar yellowing and defoliation		No. of vines recovered (reduced canopy)	Subsequent vine death	
	Number of vines*	%		No.	%
5 year	4	33.3	3 (75)	1	25
4 year	11	91.6	8 (72)	1	9
3 year	10	83.3	10 (100)	1	10
2 year	4	33.3	4 (100)	—	—
1 year	3	25.0	2 (66)	—	—

* Out of 12 inoculated vines

Figures in parentheses are percentages of vines recovered

ably, after the monsoon period when the soil moisture depletes, the available root system is unable to cope up with the transpiration demands of the vine. Considerable defoliation occurs and a portion of the vine only survives till the next season. During the beginning of monsoon period sunlight and rainfall alternate, which facilitate the development of canopy. New roots and shoots are produced by the previous season's infected vine as well (Table VI). The survival of this depends upon the production of new roots and the colonization by the pathogen. In years where monsoon is prolonged and the favourable conditions prevail for a long time (Table VII) without break (1978, 1983, 1988) the incidence of foot rot also would be severe. The visual symptom express-

Table VII. *Weather data of National Research Centre for Spices, Experimental Farm, Peruvannamuzhi (Average for 4 years)*

Month	Rainfall (mm)	No. of rainy days	Relative humidity %		Temperature °C		Soil temperature °C at 15 cm depth
			Max.	Min.	Max.	Min.	
January	85.5	3	57.7	46.5	32.3	72.0	24.9
February	13.5	1	50.8	40.5	34.9	22.8	26.5
March	38.7	3	51.1	40.1	36.4	24.3	29.0
April	84.2	7	55.4	45.5	36.7	26.3	29.9
May	131.5	7	59.1	51.3	35.8	26.1	29.8
June	1178.9	25	83.2	75.9	28.5	23.7	26.9
July	785.5	25	84.3	79.5	27.8	23.4	26.2
August	609.2	22	84.2	78.7	26.9	21.8	26.5
September	305.5	14	75.5	68.0	29.5	22.2	26.1
October	482.5	15	71.6	64.3	31.1	24.0	34.2
November	220.2	8	65.6	56.5	30.9	22.7	25.6
December	83.7	3	59.1	50.3	30.7	22.1	24.5

ion is the result of the infection which occurred during favourable period.

The root exudates are known to influence root infection of *P. cinnamomi* in avocado (Zentmyer, 1961). In black pepper, soil population of '*P. palmivora*' is known to occur at higher concentration in the top 30 cm of the soil (Ramachandran et al., 1986). The rootlets are known to occur more in the top soil (Waard, 1969). To understand the exact nature of damage to the root system, detailed studies are warranted on root growth dynamics, root exudaates and other soil factors on the ecology of the pathogen and the infection process. These are necessary for a better understanding of the epidemiology of foot rot disease of black pepper.

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