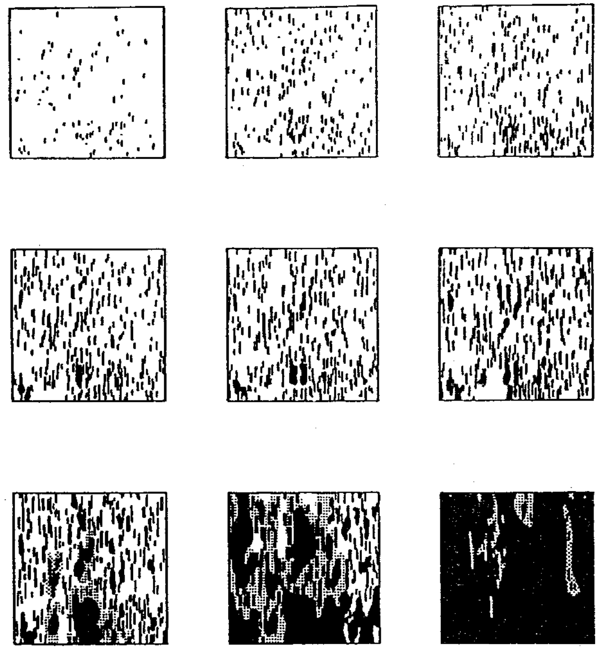
Epidemiology and Ecology of Black Sigatoka

(*Mycosphaerella fijiensis* Morelet) on Plantain and Banana (*Musa* spp.) in Costa Rica, Central America

by Friedhelm Gauhl



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Contents

1. INTRODUCTION

The causal organisms of the leaf spot diseases of the "Sigatoka-complex" (Lehmann-Danzinger 1988) to be found on banana and plantain are closely related to one another, and were at first classified as two species and a subspecies (Mulder and Stover 1976). Yellow Sigatoka (*Mycosphaerella musicola* Leach ex Mulder) was first investigated by Zimmermann (1902), who described the asexual *Cercospora* form. The disease was named after the first great epidemic 11 years later (1913) in the Sigatoka district on Viti-Levu Island (Fiji) (Meredith 1970). Leach (1946) described the sexual stage as *Mycosphaerella musicola*. The disease spread rapidly world-wide. In 1970, it was common on all continents - apart from Europe - in 75 countries (Stover 1962, Meredith 1970). Black Sigatoka (*Mycosphaerella fijiensis* Morelet) was discovered in 1963 as "black leaf streak" on Fiji, again in the Sigatoka district (Rhodes 1964). Leach (1964) described the morphology of the fungus and suggested the name *Mycosphaerella fijiensis*. The agent spread from southeast Asia and led to great losses in Zambia (Africa) in 1973 (Raemaekers 1975).

A decade after the discovery of *M. fijiensis*, an epidemic of a most virulent leaf spot disease on banana was observed in Honduras in 1972 (Stover and Dickson 1976). As this new agent seemed to show characteristics of both *M. musicola* and *M. fijiensis*, it was described as a new variety *M. fijiensis* Morelet var. *difformis* Mulder ex Stover (Mulder and Stover 1976). According to Pons (1987), however, *Mycosphaerella fijiensis* and *M. fijiensis* var. *difformis* are synonymous. In this document, therefore, the agent of black Sigatoka will be named *M. fijiensis*. The disease spread rapidly from Honduras into the neighboring countries (Stover 1980b). In 1979, the disease appeared in Costa Rica for the first time (Stover 1980b), and invaded the banana and plantain cultivation areas in the Atlantic lowlands (Araya 1982). In Central America black Sigatoka is the greatest threat to banana and plantain cultivation. In banana cultivation, the cost of disease control amounts to 27% of production costs (Stover 1986).

In contrast to yellow Sigatoka, black Sigatoka leads to great losses in plantain cultivation, too. In Costa Rica, plantain is mostly cultivated on small farms, where there is no chemical disease control. Thus, black Sigatoka has become a threat to the peasant farmers' existence. Stover (1983a) estimates that losses in plantain cultivation amount to 50-100%.

Plantain and banana belong to the cultivars of the genus *Musa* Section Eumusa. The plantain cultivar in Costa Rica named Curraré belongs to the Horn plantain type (Stover and Simmonds 1987). Following Swennen (1990), this cultivar is a False Horn plantain, because its inflorescence is incomplete at maturity with hands consisting of large fingers followed by few hermaphrodite flowers. The banana cultivar in Costa Rica belongs to the Giant Cavendish group in the Cavendish subgroup and is called Valery (Stover and Simmonds 1987).

Yellow and black Sigatoka may be controlled by the same methods (Stover 1971b). Since the first epidemic of *M. fijiensis* in 1972/73, experience has been gained with chemical control of black Sigatoka in Central and South America (Beugnon *et al.* 1982, De Leon E. 1980, Fulton 1980, Grove 1980, PANS 1977, Pasberg-Gauhl 1989, Stover 1977, 1979b, 1980a, 1980b, 1983a, Stover and Dickson 1987). The same applies to the Pacific Islands (Firman and Hoskin 1970, Long 1971, 1973, 1979), and Africa (Fouré 1983, 1985, 1988a, 1988b, Fouré and Grisoni 1984, Fouré and Mouliom Pefoura 1988, Frossard 1980).

A series of papers has been published on the morphology and biology of the black Sigatoka fungus (Firman 1972, Fouré 1982, Fouré *et al.* 1984, Laville 1983a, Meredith and Lawrence 1969, 1970, Meredith *et al.* 1973, Pons 1987, Stover 1976, 1978, 1980b, 1983b). However, there is still little knowledge about the behavior of *M. fijiensis* and about the relation between the fungus and climatic factors (Ganry 1986).

There are several investigations on yellow Sigatoka dealing with epidemiological aspects, the interrelations between disease and weather, and disease development forecast (Brun 1963, Bureau 1984, 1986, Bureau and Ganry 1987, Cronshaw 1982, Ganry 1986, Ganry and Laville

1983, Ganry and Meyer 1972a, 1972b, Stover 1964, 1965, 1968, 1970, 1971a and Stover and Dickson 1970). In contrast, as yet there have been only two investigations of forecast systems with regard to black Sigatoka until now (Chuang and Jeger 1987a, 1987b). More detailed epidemiological investigations on black Sigatoka have so far not been carried out.

The investigations presented here were carried out with a view to gaining basic knowledge on the epidemiology and ecology of black Sigatoka. For this purpose, disease development on plantain and banana and its relationship to weather factors were examined over a long period of time. The investigations were as comprehensive as possible. The simultaneity of weather and disease development was not the only factor to be examined. A more exact analysis of the relationship between the parameter groups was achieved by adjusting the weather data against the disease data.

As part of the investigation was carried out in commercial plantations where fungicides are used, the aim of the investigation was to gain knowledge especially on the influence of the fungicide on the reciprocal effects of climate and disease. The same methods were applied to both plantain and banana. This permits direct comparison of the results.

The main emphasis was placed on the plantain investigations, because as yet there exists hardly any information about black Sigatoka on plantain. The possibility of integrated control in the cultivation of plantain on small farms was taken into consideration. The maintenance of plantain plantations is important for the provision of food for consumption, because plantain is part of basic diets in Costa Rica.

Fieldwork was carried out from 1984 to 1986 at three sites (two fincas of the Asociación Bananera Nacional, ASBANA, near Waldeck and on a small peasant plantation in Estrada) in the Costa Rican Atlantic lowland.

This document is based on a PhD thesis at the University of Goettingen: "Investigations of the epidemiology and ecology of black Sigatoka disease (*Mycosphaerella fijiensis* Morelet) on plantain (*Musa* spp.) in Costa Rica" (Gauhl 1989) and an MSc thesis (Univ. Goettingen): "Investigations of disease development of black Sigatoka (*Mycosphaerella fijiensis* Morelet) on banana (*Musa* spp.) in Costa Rica" (Gauhl 1990a). These two investigations were edited and summarized for translation into English. Because of the great interest shown in Latin America in these investigations, the PhD thesis (Gauhl 1989) was translated into Spanish by the Unión de Países Exportadores de Banano (UPEB) in Panamá (Gauhl 1990b).

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Note

For the sake of clarity, the following distinctions are made in terminology: the terms 'banana' and 'plantain' (i.e., singular) refer to the crops. The terms 'bananas' and 'plantains' (i.e., plural) refer to the fruit of these crops (INIBAP 1989).

2. Study Area

Location, geomorphology and soils

Costa Rica lies on the Central American isthmus between Nicaragua in the north and Panama in the south, and occupies an area of 51,000 km² (8°-11°N, 82°30'-86°W). A central mountain range with altitudes up to 3820 m above sea level reaches from northwest to southeast separating the Pacific lowlands from the Atlantic lowlands (Fig. 1). These cover about 20% of the land.

The study area is located in the province of Limón, at the foot of the Cordillera. Three experimental areas were situated in Waldeck (Fig. 2) and one near the village Estrada (Fig. 3). Here, flat, slightly sloping and undulating lowland plains reach from the mountains in the south to the swamps in the north. The soils range from well to poorly drained alluviums (Nuhn 1978) which form a triangle between Limón in the southeast and Guápiles and Río Frío in the northwest.

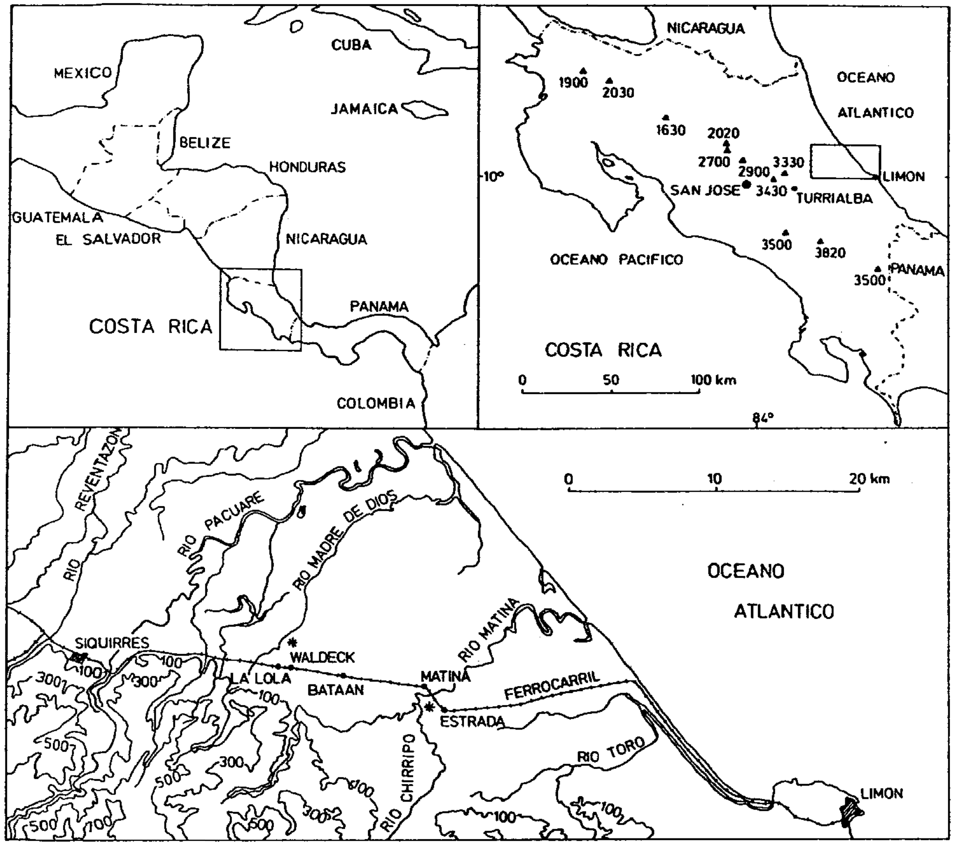


Fig. 1: Situation of experimental area (= experimental sites: Finca San Pablo north of, and Finca Semillero south of, Río Madre de Dios, Estrada, east of Río Chirripó)*

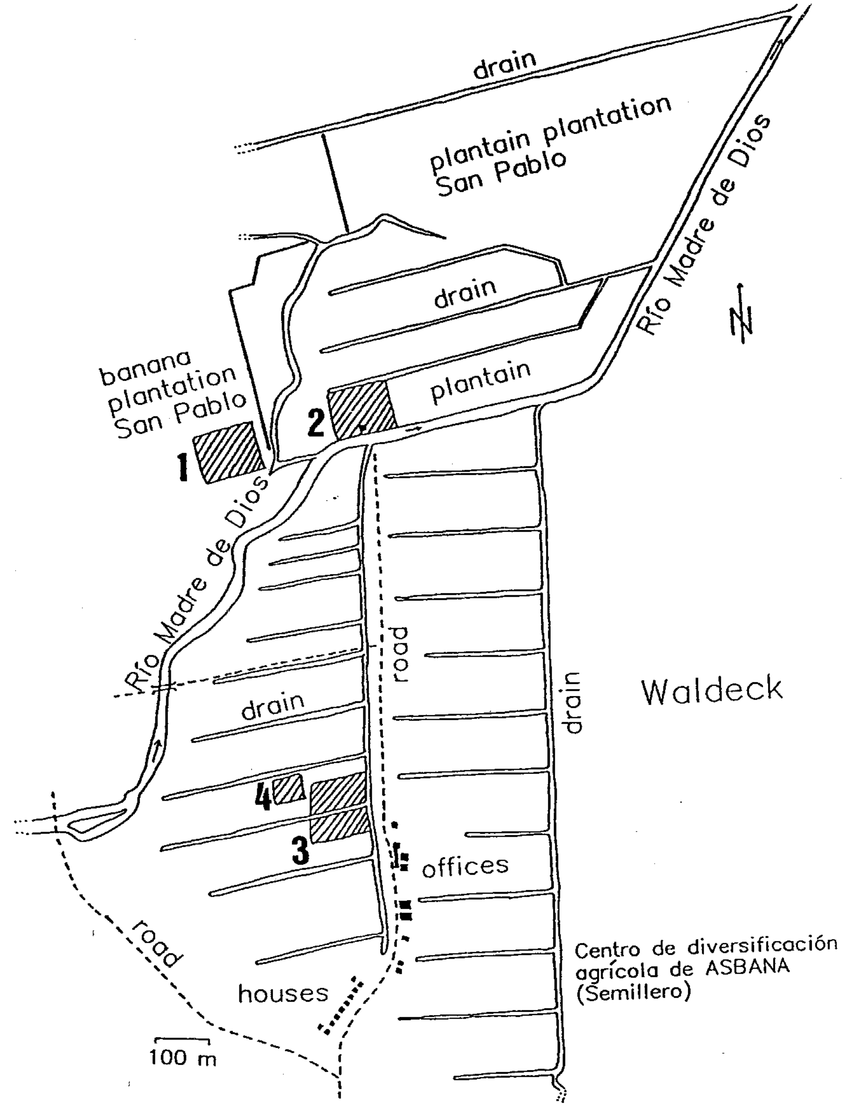


Fig. 2: Experimental site Waldeck

1: Experimental plot, San Pablo, banana;
2: Experimental plot, San Pablo, plantain;
3: Experimental plot, Semillero, plantain plantation with climate-measuring instruments and spore trap (north quarter with good drainage; south threequarters with impeded drainage);
4: Experimental plot, Semillero, banana

Banana cultivation is strictly limited to these soils (Hall 1984). Plantain cultivation in the form of monoculture is also concentrated here (Araya 1982). Further soils suitable for banana and plantain monoculture are to be found south of Limón near the Río Estrella and the Río Sixaola. Banana makes higher demands on the quality of the soil than plantain. The best soils, therefore, are used for the cultivation of banana. These plantations must be of at least 200 ha in size if they are to be economical. Plantain is often cultivated on less suitable soils and is only seldom exported. These plantations are scattered and much smaller: 84% of the plantations in the Atlantic lowlands are smaller than 10 ha. Often, plantain is not cultivated in monoculture but is planted together with cocoa (lowlands) and coffee (highlands).

The study area belongs to the thermic belt of the "tierra caliente". According to the classification often applied in Latin America in "life zones" by Holdridge (1967) and the map by Tosi (1969), the area belongs to the tropical moist forest with a transition to premontane wet forest.

Description of experimental sites

Experiments were carried out in two locations and in four different plantations. The plantations were differentiated according to the way they were managed and to their soils. The main experimental site was Waldeck (Veintiochomillas) with the two fincas: San Pablo and Semillero (Fig. 2); a further site was situated near the village Estrada (Fig. 3).

The San Pablo finca was a commercial banana plantation 214 ha in size, north of the Río Madre de Dios (Table 1). The banana plants were sprayed with a fungicide from an airplane about once every 10 days (Tables 3 and 5). The experimental site was on the east side of the finca (Fig. 2, No. 1), adjoining a plantain plantation of 35 ha. The experimental plantain site lay about 100 m east of the banana plot (Fig. 2, No. 2). The plantain was cultivated in exactly the same way as the banana (Table 2). However, the intervals between the spraying of fungicides against black Sigatoka disease were longer than those in the banana plantation (Tables 4 and 5). The loams of the experimental area were drained sufficiently by means of a normal network of drainage ditches. The groundwater table was between 1.5 and 2 m deep. The banana and plantain on the San Pablo finca were harvested weekly and exported directly to the USA.

South of the Río Madre de Dios lay the "Centro de Diversificación Agrícola de ASBANA, 28 Millas, Limón" (Fig. 2), locally just called "Semillero". On this finca, about 800 m south of the first two experimental sites, there was a small plantain plantation of about 1 ha (Fig. 2, No. 3). Here, climate-measuring instruments and a spore trap were installed. This plantation was solely for experimental use but was managed in the same way as the plantain plantation in San Pablo. However, no fungicides were applied here; dead leaves were left on the plants (Table 6).

This plantation was divided into two parts according to the physical properties of the soil. In the southern three-quarters of the area, plant growth was severely restricted. The upper layers of soil consisted of clayey loams with a gray-stained gleyish horizon about 15 cm thick with rust-colored mottles. This horizon was at a depth of 30-60 cm. Below this, there were sandy loams which did not impede drainage. Additional drainage ditches, with beds below the gleyish horizon, reduced the drainage problems but could not eliminate them. After heavy rainfall, the groundwater level was often only a few centimeters below the soil surface. However, not only too much, but also too little water caused problems on these soils. Drier periods without rainfall or with only low rainfall resulted in water deficiency , because the upper soil layers dried out. Plantain roots could hardly penetrate the gleyish layer, so that the plants were not able to utilize the water in the deeper layers. Both impeded drainage and drought resulted in slower plant growth. There were no drainage problems in the northern quarter of the plantation, as there was no layer impeding drainage. The soil consisted entirely of sandy loams, which, in the upper layers, were mixed with large amounts of organic material.

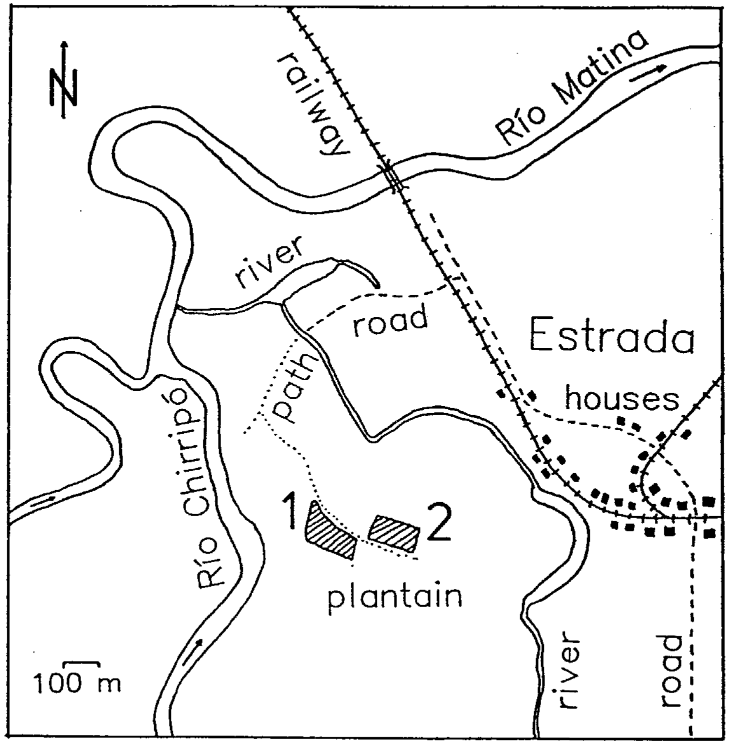


Fig. 3: Experimental site, Estrada
1: Experimental plot, Estrada, plantain
2: Plantain plantation for fungicide tests (Pasberg-Gauhl 1989)

On these well drained, sandy loams, on the northwest corner, a small banana plantation bordered directly onto this plantain plantation (Fig. 2, No. 4). The plantation consisted of only a dozen banana plants, which had been planted in May 1985 and were only for experimental use. Fertilization was in the form of 215 kg N, 25 kg P_2O_5, 190 kg K_2O and 13 kg Mg per hectare per annum. Weed control was about every 4 weeks, manually (machete) and chemically (herbicides) in rotation. This plantation was also not treated with fungicides.

The fourth plantation was located west of Estrada village on the alluvial soils of the Río Chirripó between the village and the river, in the midst of large plantain plantations (Fig. 3). It was situated about 10 km from Waldeck. The soils were sandy loams without drainage problems. Even after heavy rainfall, the groundwater table never rose higher than 1 m. The plantation belonged to the farmer Juan Dunn from Estrada, and it was cultivated in the traditional way, i.e. the farmer worked on it only now and again without using chemicals (Table 7). Fruit was harvested about once a fortnight. In contrast to the other two plantain plantations, the age of the fruit bunches was assessed by experience and the harvest sold to local traders.

Table 1: Site description and agricultural measures: Banana plantation at Waldeck, San Pablo.

Site: Waldeck, San Pablo, Atlantic lowlands, Costa Rica

Altitude: 25 m above sea level

Situation of plantation: north of Río Madre de Dios

Soil: clayey loam

Size of plantation: 212 ha

Size of experimental plot: 1 ha

Age of experimental plot: several years

Cultivar: Cavendish banana Valery, group AAA

Planting system: equilateral triangle; plant spacing 2.6 m

Population: 1720 plants ha^{-1}

Plantation structure: 3 generations per production unit

Management:

- Pruning of suckers (deshija): every 6 weeks
- Sanitation deleafing (deshoja): once a week
- Replanting: every 4 weeks (if necessary)
- Propping of fruit bunches (apuntalamiento): once a week
- Debudding and dehanding (desmane): once a week
- Marking of fruit bunches (cintaje): once a week
- Fertilization: 115 kg N, 55 kg K_2O, 45 kg Mg per hectare in August and September; 260 kg ha^{-1} Ca in April-June
- Sigatoka control: approx. every 10 days (cf. Tables 3 and 5)
- Nematode control: Nemacur 10G (Fenamifos) in June (38 g/plant) and in November (31 g/plant)
- Weed control: if necessary mechanical (machete) or chemical (herbicides); agent according to infestation (amount/15 L water): Dalapon (Dalapon) 180 - 230 g; Radex (Glyphosate) 50-75 mL Gramoxone (Paraquat) 45 mL; Diuron (Diuron) 70 g

Table 2: Site description and agricultural measures: plantain plantation at Waldeck, San Pablo.

Site: Waldeck, San Pablo, Atlantic lowlands, Costa Rica

Altitude: 25 m above sea level

Situation of plantation: north of Río Madre de Dios

Soil: clayey loam

Size of plantation: 35 ha

Size of experimental plot: 1 ha

Age of experimental plot: several years

Cultivar: False Horn plantain Curraré, group AAB

Planting system: equilateral triangle; plant spacing 2.6 m

Population: 1720 plants ha^{-1}

Plantation structure: 3 generations per production unit

Management:

- Pruning of suckers (deshija): every 6 weeks
- Sanitation deleafing (deshoja): once a week
- Replanting: every 4 weeks (if necessary)
- Propping of fruit bunches (apuntalamiento): once a week
- Debudding and dehanding (desmane): once a week
- Marking of fruit bunches (cintaje): once a week
- Fertilization: every 3-4 months (215 kg N, 25 kg P_2O_5, 190 kg K_2O, 13 kg Mg, 17 kg Ca per hectare per year (ha^{-1} a^{-1})
- Sigatoka control: approx. every 20 days (cf. Tables 4 and 5)
- Nematode control: once a year (June) with Nemacur 10G (Fenamifos) 40 g/plant
- Weed control: every 4 weeks; mechanical (machete) or chemical (herbicides) in rotation; agent according to infestation (amount/15 L water): Dalapon (Dalapon) 180-230 g; Radex (Glyphosate) 50-75 mL; Gramoxone (Paraquat) 45 mL; Diuron (Diuron) 70 g

Table 3: Applications of fungicide (35 per year) from the air (airplane) against black Sigatoka during the study period in the banana plantation at Waldeck, San Pablo.

Date	Spraying interval (days)	Fungicide mixtures*
03.01.1985	--	Dithane Flowable
11.01.1985	8	Dithane Flowable
19.01.1985	8	Cocktail Benlate
30.01.1985	11	Cocktail Calixin
15.02.1985	16	Cocktail Benlate
28.02.1985	13	Cocktail Calixin
08.03.1985	8	Cocktail Calixin
19.03.1985	11	Dithane Flowable
29.03.1985	10	Cocktail Calixin
10.04.1985	12	Cocktail Calixin
21.04.1985	11	Cocktail Benlate
30.04.1985	9	Cocktail Benlate
10.05.1985	10	Manzate 200 + Oil
21.05.1985	11	Cocktail Calixin
30.05.1985	10	Cocktail Benlate
11.06.1985	11	Cocktail Benlate
24.06.1985	13	Cocktail Calixin
03.07.1985	9	Cocktail Benlate
13.07.1985	10	Manzate 200 + Oil
23.07.1985	10	Cocktail Calixin
30.07.1985	7	Cocktail Benlate
10.08.1985	11	Cocktail Benlate
21.08.1985	11	Cocktail Calixin
02.09.1985	12	Cocktail Calixin
13.09.1985	13	Manzate 200 + Oil
21.09.1985	8	Cocktail Calixin
06.10.1985	15	Cocktail Calixin
18.10.1985	12	Cocktail Calixin
28.10.1985	10	Cocktail Benlate
08.11.1985	11	Cocktail Benlate
19.11.1985	11	Cocktail Calixin
29.11.1985	10	Manzate 200 + Oil
10.12.1985	11	Cocktail Calixin
19.12.1985	9	Cocktail Benlate
29.12.1985	10	Manzate 200 + Oil
07.01.1986	9	Cocktail Calixin
18.01.1986	11	Dithane Flowable
27.01.1986	9	Cocktail Benlate
08.02.1986	12	Cocktail Benlate

* cf. Table 5.

Table 4: Applications of fungicide (19 per year) from the air (airplane) against black Sigatoka during the study period in the plantain plantation at Waldeck, San Pablo.

Date	Spraying interval (days)	Fungicide mixtures*
07.09.1984	--	Dithane Flowable
29.09.1984	23	Cocktail Benlate
10.10.1984	12	Cocktail Calixin
30.10.1984	21	Cocktail Calixin
20.11.1984	22	Manzate 200 + Oil
15.12.1984	26	Manzate 200 + Oil
03.01.1985	20	Dithane Flowable
19.01.1985	16	Cocktail Benlate
15.02.1985	27	Cocktail Benlate
08.03.1985	20	Cocktail Calixin
29.03.1985	20	Cocktail Calixin
18.04.1985	20	Cocktail Benlate
10.05.1985	22	Cocktail Calixin
30.05.1985	20	Cocktail Benlate
22.06.1985	23	Manzate 200 + Oil
13.07.1985	18	Manzate 200 + Oil
31.07.1985	18	Cocktail Benlate
20.08.1985	20	Cocktail Benlate
12.09.1985	23	Manzate 200 + Oil
21.09.1985	9	Cocktail Calixin
08.10.1985	17	Cocktail Benlate
26.10.1985	18	Cocktail Benlate
19.11.1985	24	Cocktail Calixin
10.12.1985	21	Cocktail Calixin
28.12.1985	18	Manzate 200 + Oil
18.01.1986	21	Dithane Flowable
08.02.1986	21	Cocktail Calixin

* cf. Table 5.

Table 5: Composition of fungicide mixtures (filled up with water to 23 L total volume) for control of black Sigatoka in the plantain and banana plantation at Waldeck, San Pablo.

Fungicide mixture	Dosis applied ha^{-1}
Cocktail Benlate	0.28 kg Benlate (Benomyl) 1.25 kg Manzate 200 (Mancozeb) 50 mL Triton 5.0 L Oil
Cocktail Calixin	0.6 L Calixin (Tridemorph) 1.75 kg Manzate 200 (Mancozeb) 50 mL Triton 5.0 L Oil
Dithane Flowable	6.0 L Dithane F. (Mancozeb) 55 mL Triton
Manzate 200 + Oil	2.0 kg Manzate 200 (Mancozeb) 50 mL Triton 5.0 L Oil

Table 6: Site description and agricultural measures: plantain plantation at Waldeck, Semillero.

Site: Waldeck, Semillero, Atlantic lowlands, Costa Rica

Altitude: 25 m above sea level

Situation of plantation: south of Río Madre de Dios

Soil: clayey loam with impeded drainage

Size of plantation (experimental plot): 1.2 ha

Cultivar: False Horn plantain Curraré, group AAB

Planting date of experimental plot: July 1984

Planting system: equilateral triangle; plant spacing 2.6 m

Population: 1720 plants ha^{-1}

Plantation structure: 3 generations per production unit

Management:

Pruning of suckers (deshija): every 3 months

Sanitation deleafing (deshoja): every 3 months

Replanting: every 4 weeks (if necessary)

Propping of fruit bunches (apuntalamiento): once a week

Debudding and dehanding (desmane): once a week

Marking of fruit bunches (cintaje): once a week

Fertilization: 16.11.84, 10.01.85, 16.05.85, 14.06.85, 22.07.85, 20.11.85. (215 kg N, 25 kg P_2O_5, 190 kg K_2O, 13 kg Mg, 17 kg Ca ha^{-1} a^{-1})

Sigatoka control: none

Nematode control: April 1985 Nemacur 10G (Fenamifos) 40 g/plant

Weed control: every 4 weeks; mechanical (machete) or chemical (herbicides) in rotation; agent according to infestation (amount/15 L water): Dalapon (Dalapon) 180-230 g; Radex (Glyphosate) 50-75 mL; Gramoxone (Paraquat) 45 mL; Diuron (Diuron) 70 g

Table 7: Site description and agricultural measures: plantain plantation at Estrada.

Site: Estrada, Atlantic lowlands, Costa Rica

Altitude: 15 m above sea level

Situation of plantation: east of Río Madre de Dios

Soil: sandy loam

Size of plantation: 3 ha

Size of experimental plot: 1 ha

Cultivar: False Horn plantain Curraré, group AAB

Age of plantation (experimental plot): several years

Planting system: none; plant spacing 3-4 m

Population: approx. 1200 plants ha^{-1}

Plantation structure: 3 generations per production unit

Management:

Pruning of suckers (deshija): every 6 months

Sanitation deleafing (deshoja): every 6 months

Replanting: every 6 months

Propping of fruit bunches (apuntalamiento): none

Debudding and dehanding (desmane): none

Marking of fruit bunches (cintaje): none

Fertilization: none

Sigatoka control: none

Nematode control: none

Weed control: every 6 months; mechanical (machete)

3. MATERIAL AND METHODS

3.1 Meteorological Recordings

Temperature and relative humidity were recorded using mechanical hygro-thermographs with a measuring range (MR) of 0...100% relative humidity (rH) and 0...+60°C (Thies, 1.0620.00.016) and hygro-thermo-transmitters with electrical output (Thies, 1.1005.51.515; MR 10...100% rH, -20...+60°C). Radiation (Wm^{-2}) was recorded with electronic radiation transmitters acc. to Dirmhirn (Thies, 7.1415.00.000; MR 0...1300 Wm^{-2}), wind velocity and direction with a mechanical wind recorder acc. to Wolf (Thies, 4.3900.10; MR 0.5...60 m s^{-1}, 0...360°). Precipitation was measured using a precipitation recorder acc. to Hellman (Thies, 5.4011.00.00; 7 days). The duration of leaf wetness was determined by means of electromechanical leaf wetness recorders (Lufft, 8301). Minimum and maximum temperatures were measured with extreme thermometers (Thies, 2.0446.00.001 and 2.0445.00.002), evaporation with an evaporimeter acc. to Piché (blotting paper 3 cm; Thies, 6.1425.00.000). The output of the electronic transmitters was recorded with a six-color point recorder (Schenck, Vienna; STDB 63; 35 days), operating with a 12-V car battery. The meteorological instruments were partly mounted on an aluminum telescopic mast (Thies, 4.3181.00.000) with hangers (Thies, 4.3185.00.004) and could be reached via the platform (4.2 m high) of the spore trap. The upper hygro-thermo-transmitter was installed inside a weather and thermal radiation shield (Thies, 1.1025.51.000), the lower one was fixed on a wooden post under a louvered roof. The recording instruments were set up in weather huts with louvered walls.

In Waldeck, the instruments were installed inside the plantain stand so that those microclimatic factors influencing spore release and the development of the disease in a plantain stand could be determined as precisely as possible. Measurements were carried out below and above the foliage of the plantain. Wind velocity and direction, temperature, humidity, radiation and leaf wetness were measured above or at the height of the foliage. All measurements were also made below the foliage except those concerning the wind (Fig. 4). A precipitation recorder and a weather hut with evaporimeter, minimum and maximum thermometer as well as a further hygro-thermograph (for safety) were placed close by outside the plantation.

In Estrada, a considerably smaller recording station was installed for registering temperature, humidity, precipitation and leaf wetness only. The hygro-thermograph and the leaf wetness recorder stood in a weather hut (1.6 m high) about 10 m away from the plantation. The sensor of the leaf wetness recorder was mounted on a wooden post of the same height at a distance of 3 m from the weather hut, as the recordings made inside the plantation did not correspond well with the wetness of the leaves.

The hygro-thermographs and hygro-thermo-transmitters were calibrated weekly using an aspiration psychrometer acc. to Assmann (Thies, 1.0400.00.010, MR -10...+60°C). The wetness of the plantain leaves and the vertical markings of the leaf wetness recorder were checked several times with regard to their correspondence. Depending on the weather, deviations of ± 0.5 h were registered on the instrument fixed at the height of 4.2 m; deviations of up to several hours were observed on the lower instrument, especially on rainy days. The accuracy of readings was 1 h.

3.2 Plant growth

Between October 1984 and July 1985, 30 plantain plants with a height of 0.5-1.5 m were marked in Waldeck (Semillero) and Estrada. One could be certain that newly planted plantain of at least this size were established. Every week, the height of these plants (from the ground up to

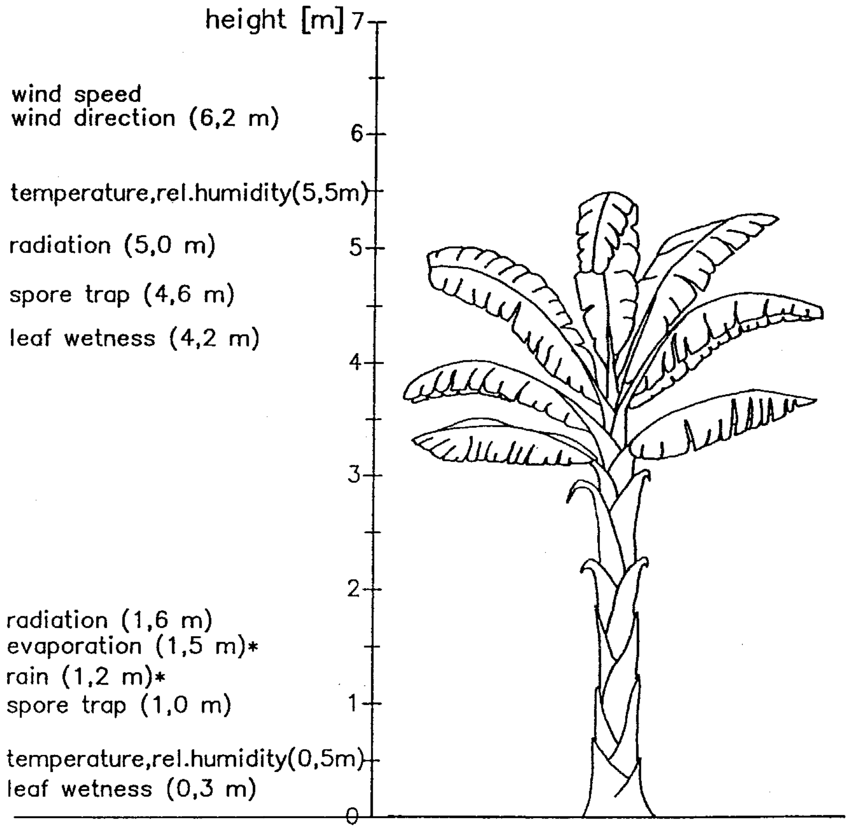


Fig. 4: Position of meteorological instruments and spore traps in a plantain plantation in relation to the height of the plants (measurements outside the plantation)*

the point where the leaf stalk of the second youngest leaf encloses that of the youngest one), and the girth of the pseudostem (at a height of 1 m above the ground), were measured. Once unfurled, each leaf was marked with a colored plastic label and given a number. From October 1984 to March 1986, the length and width of the blade were measured on a weekly basis. These plants stood on very different kinds of soil. Fifteen grew on soils with impeded drainage (Waldeck, Semillero, southern part; Fig. 2), and 15 on good soils without drainage problems (Estrada and Waldeck, Semillero, northern part; Fig. 2.). No differences in growth between the 10 plants in the northern part of Semillero and those in Estrada were observed. They were, therefore, grouped together for the interpretation. The 15 plants in the southern part of Semillero formed a second group. The sites were differentiated briefly according to their main characteristic as being "with impeded drainage" (Semillero) or "with good drainage" (Semillero and Estrada).

In September 1986, 23 leaves were marked on plantain plants of various ages. As soon as the leaves were completely unfurled, they were cut off and their outlines traced on brown paper. Until the results were analysed, the brown paper was stored under constant conditions. The leaves were then cut out and weighed. Using the weight (average value of n = 10) of a referential area of 100 cm², the leaf area was calculated. In order to established the factor for the determination of the leaf area by means of the measurements of the length and width of the blade, this area value was divided by the length and the width of the blade.

3.3 Development of symptoms and leaf area with symptoms

Marked leaves

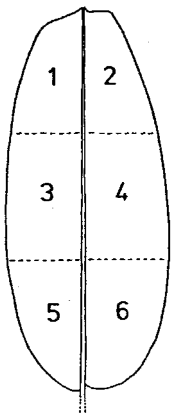


Fig. 5: Partitioning of plantain leaf in six sections for disease evaluation (Left side: odd numbers; right side: even numbers)

At weekly intervals, the grade of disease on the marked leaves (cf. Chap. 3.2) was observed in detail at a short distance. First, the diseased area of the whole leaf was given a value using Stover and Dickson's (1970) modified estimation scale (Table 8). Then the diseased area of each leaf section (Fig. 5) was evaluated separately, using the same scale. In addition, symptom of disease the most advanced was recorded both for the whole leaf and for each section by means of a numerical key (Table 9). These data were then used to calculate the following values for the leaves infected both before and after flowering:

- duration of incubation period;
- time of development of different symptoms of disease;
- development of leaf area with symptoms;
- life span of a leaf (unfurled until total [100%] necrosis);
- time until leaf hangs down.

The hanging leaves were left on the plants.

Development of symptoms (time of inoculation known)

In May 1986, during leaf emission, 25 plantain and three banana leaves were covered with transparent plastic bags (1.0 x 1.5 m) in order to prevent inoculation by spores. The blade of the youngest leaf was cut off so that the plastic bag could be placed over the petiole with the opening downwards on a bamboo tripod. The bag was then fixed so that it could not be blown away by the wind. As the following leaf first pushes up inside the petiole of the previous one, it thus grew into the plastic bag without having direct contact with the outside air. Leaf growth and the position of the plastic bag were checked and corrected daily, so that the new leaf did not become damaged. As soon as the leaf had unfurled, the bag was removed. Twelve of the plantain leaves were left in the bags for 4 weeks after unrolling, in order to investigate the manner of infection of older leaves.

Table 8: Disease grade and % leaf area with symptoms.

Grade A	Grade B	% leaf area with symptoms	
	0	0 %	without symptoms
0	1	<1 %	streaks and/or less than 10 spots
1	2	1 - 5 %	leaf area with symptoms
2	3	6 - 15 %	leaf area with symptoms
3	4	16 - 33 %	leaf area with symptoms
4	5	34 - 50 %	leaf area with symptoms
	6	51 -100 %	leaf area with symptoms

Grade A: (Stover and Dickson 1970)
Grade B: (Stover and Dickson 1970, modified)

Table 9: Symptoms of black Sigatoka.

Symptom score	Description of symptoms
0	without symptoms
1	speck
2	streak <5 mm long
3	streak 5 mm long
4	spot >2 mm wide
5	individual spots with a clear/dry center
6	several coalescent dry areas

For comparison, several leaves of both plantain and banana which had not been placed in bags were observed. Records were made of the leaf emergence, position in the sun, grade of shade and length and width of all leaves. The observations with respect to the development of symptoms were made every 3 days; as, due to the size of the leaf, the leaf-base was often no longer covered by the bag, the tip of the blade was examined.

As easy access to the leaves was necessary in order to observe and trace the symptoms (see below), plants of 1.5-2.0 m in height were chosen for this experiment. Therefore, the leaves were not always in full sunlight but in positions with different amounts of shade. The grade of shade was registered according to the following scheme: sunny (leaf not in the shade of other leaves), half-shade (leaf in the shade of other leaves at some time during the day) and shady (leaf also in the shade of neighboring plants and in the shade all day).

The symptoms were evaluated according to the following score: dots and light patches, specks (= streaks up to 1 mm in length), streaks up to 3 mm in length, brush streaks, spots and spots with a clear/dry center. The brush streak (Lehmann-Danzinger 1988) describes the transition from a streak to a spot. It consists of several very close streaks (almost a spot) with "ragged" ends in the direction of the leaf veins.

On four plantain leaves (three with bags, one without), and three banana leaves (two with bags, one without) squares measuring 5 x 5 cm² were marked using a pen (Rotring Isograph, 0.7 mm) with Indian ink (not damaging to the leaf tissue; Fig. 22). Within these squares, the symptoms which had developed were counted. In addition, always at the same time of day, the symptoms in four of the squares were traced to scale against the light, using a waterproof pen on a sheet of transparent plastic.

In order to determine the percentage of the diseased area, the traced squares were copied with Indian ink. These black and white patterns were evaluated quantitatively by means of an area meter (Area Meter, Delta-T Devices Ltd, Cambridge, England). However, the tissue which was yellow due to chlorosis was not taken into account.

Development of disease in four plantain and banana plantations

In the three plantain plantations — Semillero, San Pablo (Waldeck) and Estrada (February 1985 - February 1986) — and in the banana plantation San Pablo (May 1985 - February 1986), 10 plants each were evaluated weekly at the following stages:

- just before flowering;
- 6 weeks after flowering (approx. half-time until harvest);
- 11 weeks after flowering (1-2 weeks before harvest).

The leaves were evaluated from a distance of 2 m. The number of standing leaves, the youngest leaf with symptoms, and the stage of the disease on each leaf, were determined for every plant (Table 8). These data were then used to calculate leaf area, size of leaf area with symptoms and an index of the grade of disease (Lehmann-Danzinger 1988). The maximum average number of leaves occurring in the investigation period was inserted into the index per plant for each stage:

$$X = \frac{\sum_{n=1}^{L} LAWS_n \, (Z_{max} - L) \, LAWS_{max}}{Z_{max} \cdot LAWS_{max}}$$

Where:

$LAWS_n$ = leaf area with symptoms in % on nth leaf
$LAWS_{max}$ = maximum leaf area with symptoms in %
L = number of standing leaves
Z_{max} = maximum average leaf number

A choice of 10 plants was made, because each week about 15-20 plants of the same age were available on the experimental plots of approx. 1 ha. Therefore, even if some plants were lost, e.g. due to wind, at least 10 plants were left for evaluation. During the week in which the plants began to flower, they were marked with colored plastic tapes.

3.4 Spore trapping

Airborne spores were monitored with 7-day recording volumetric spore traps (Burkard Mfg. Co. Ltd, Rickmansworth, Hertfordshire, England). Neither ascospores nor conidiospores of *Mycosphaerella* spp. could be captured by means of slide traps. The use of water traps (glass bottle with funnel) was not possible due to the high precipitation (as much as 45 mm in 20 min) and because there were no facilities on the farm for reducing the water volume in order to obtain a concentration of spores countable under the microscope.

The volumetric spore traps were first set up in the San Pablo plantain plantation (Waldeck), where the plants were treated regularly with fungicides. Spore release was registered both in the upper part of the foliage and below it. The upper spore trap was mounted on a horizontal wooden platform on three legs at a height of 4.2 m, so that the trapping orifice of the trap was at a height of 4.65 m. The lower spore trap was placed on three posts in the ground in such a manner that the orifice was at a height of 1 m. From January 1985 onwards, only one spore trap (height of orifice 4.65 m) was used in the Semillero plantation (Waldeck).

Spores (asco- and conidiospores) were impacted onto Melinex tapes (Burkard Mfg. Co. Ltd) coated with a mixture of 20% paraffin (melting point 68-73°C) and 80% Vaseline in 5-10% toluene. The spore trap was operated at a flow rate of 9.5 L min^{-1}; this was checked several times a week with a volumetric flow meter. At the same time, the orifice was cleared of insects.

The tapes were cut into 48-mm lengths representing 24-h periods and mounted on glass microscope slides beneath 25 x 56 mm cover slides. The slides were kept in plastic boxes in the refrigerator at 4°C to prevent the germination of the spores or the growth of fungi or bacteria. The spores were counted directly in transmitted light using a 500-fold enlargement (Zeiss Universal microscope). This was done without staining, because, when Fuchsin red in lactophenole, Fastgreen or Aniline blue stains were used, it was more difficult to examine the spores. Tapes were examined at hourly intervals of deposition in 5-mm long traverses (corresponding to an area of 1.8 mm^2) perpendicular to the direction of movement. The results were used to calculate the hourly concentration of spores per cubic meter (m^{-3}) of air.

The efficiency of the spore trap varies with the wind velocity and the size of the particles. When the wind has a velocity of more than 3 m s^{-1}, objects of more than 10 µm can be withdrawn from the air taken in, with an efficiency of approx. 75% (Bartlett and Bainbridge 1978). The spore concentrations calculated are, therefore, always lower than the actual ones.

At first, three spore traps with 12-V motors (Maxon, Switzerland) were available. However, it was soon discovered that these motors were not suitable for use in the humid tropics and were burnt out after 25-50 days. It turned out to be extremely difficult to obtain new motors from Switzerland.

The potentiometers used for regulating the flow rate were a further problem. As the motors became worn out, they were found to be too weak and burnt out, too. There were no spare parts available in Costa Rica. However, a permanent substitute for the potentiometers was created using a simple heating coil for cookers (20 Ω, 900 W). This coil was connected to the circuit and the resistor regulating the suction capacity was tapped with a crocodile clip.

Failures of the spore traps were also caused by water entering the instrument during the heavy tropical rain, by the corrosion of ball bearings, by termites eating the wooden structures and by big black wasps which insisted on building their nests in the covers of the turbines and motors. In the end, due to the frequent failures, only one spore trap could be run in the field and the other two were used for spare parts.

From January 1985 onwards, motors run on the circuit (Burkard, 110 V - 50 Hz) were available, which caused no problems. There was then only one failure when a fieldworker cut the supply cable with his machete.

3.5 Production of ascospores by necrotic leaf tissue

From marked, hanging leaves showing symptoms of black Sigatoka, leaf samples with perithecia were repeatedly taken from the same plant at different times of the year. The samples were taken from the left or the right base of the blade. As it was known when the symptoms had developed, the age of the necrotic parts at the time of sampling could be determined. Thus, pieces of leaf with necrotic areas of different ages were available at the same time.

In March/April 1985, six leaves with necrotic areas aged 1 week were fixed to the ground with bamboo pegs. Three leaves lay with the lower side upward, the others the other way around. At intervals of 1-2 weeks, leaf samples with perithecia were taken. If possible, these samples were taken at noon on dry days and when the leaves were completely dry, and then stored in polyethylene bags.

The analysis in the laboratory took place 2-6 days later. From each sample, four pieces of leaf of 1 cm^2 with perithecia were cut out, and the ascospores collected according to the method described by Stover (1976). Deviating from this method, the samples were stored in dry conditions, then soaked in water for 5 min and, finally, left for 2 h over the agar so that the ascospores could be discharged. Two of the pieces of leaves were placed with the upper side facing the agar, two with the lower side.

Finally, under the microscope, ascospores were searched for on the surface of the agar using x 100 enlargement. In the sections with the largest amount of spores (eye measure), an optical field (0.1 mm^2) was counted out four times.

As this method cannot be standardized easily and contains subjective sources of errors (choice of pieces of leaf, eye measure for estimation of the amount of spores), the spore numbers were added and divided into classes.

3.6 Identification of pathogenic fungi

The fungi were determined according to morphological characteristics. Descriptions of pathogenic fungi on banana leaves have been published by, among others, DuPont (1982), Meredith and Lawrence (1969, 1970), Mulder and Stover (1976) and Stover (1963, 1969, 1972).

On plantain leaves, *Chloridium musae*, *Cladosporium musae*, *Cordana musae* and *Mycosphaerella fijiensis* were found. Apart from *M. fijiensis*, the other leaf diseases on plantain in the Costa Rican lowlands are of lesser importance.

The spores of the following banana leaf diseases were found on the spore trap tapes: *Cordana musae*, *Didymella* sp., *Leptosphaeria* sp., *Micronectriella* sp., *Mycosphaerella fijiensis*, *M. minima*, *M. musae* and *M. musicola*. The countings were, however, restricted to the spores of *Mycosphaerella fijiensis* and *M. musicola*. It is not possible to distinguish between the ascospores of these two species; therefore, one can only speak of the ascospore-type *M. fijiensis*/*M. musicola* (Meredith and Lawrence 1969). The conidiospores of both species, however, show distinct characteristics.

3.7 Data processing and statistical evaluation

All the data obtained were evaluated on the mainframe "Sperry 1100/80" of the Gesellschaft für wissenschaftliche Datenverarbeitung Goettingen (GWDG; Society for Scientific Data Processing Goettingen) using the program BMDP Statistical Software (Version: April 1985).

All data from the meteorological instruments were digitalized in hourly values and transferred to lists for punch cards. The spore values were recorded directly onto lists when counted. The disease evaluation, measurements of growth and size of the plants, as well as the harvest data, were recorded on these lists during fieldwork.

As, in the meantime, both card punchers and punched-card readers were out of use on the mainframe, the data had to be filed to an IBM-compatible personal computer (PC). Input, transformation, sorting and processing of the data were carried out using the author's own programs developed with the database system dBASE III (Ashton-Tate) supplied by the Institute for Plant Pathology at the University of Goettingen. The data were then read into the mainframe from the PC.

The data was processed by means of a one-factor variance analysis and significant differences checked with the Tukey Test. The correlations were examined with a two-sided F-test with respect to significance (Sachs 1978).

4. CLIMATE

The climate is a tropical perhumid rain forest climate with two rainfall maxima (July and December). Between these two maxima, there are two less rainy seasons in February/March ("verano") and September/October ("veranillo de San Juan"). Annual temperatures average about 25°C, annual precipitation is between 3500 mm and 4500 mm. The climate of the Atlantic lowland plain is very uniform (Fig. 6). About 3 km southwest of the experimental plots in Waldeck lies the experimental finca "La Lola" of CATIE (Centro Agronómico Tropical de Investigación y Enseñanza), where weather data have been recorded since 1949.

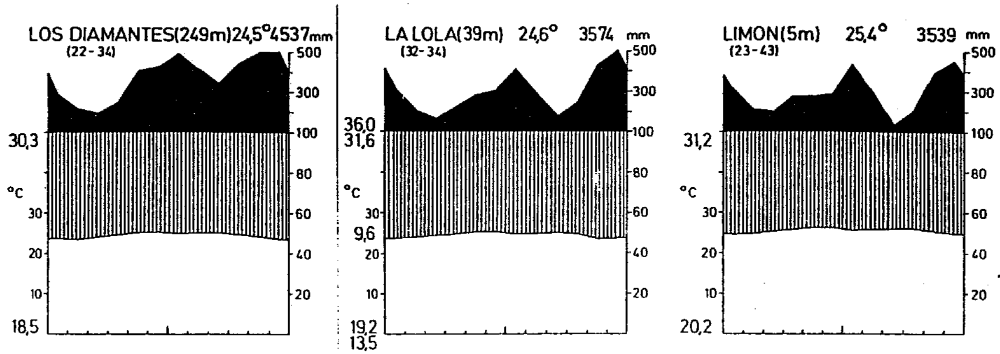


Fig. 6: Climatic diagrams of Los Diamantes (Guápiles), La Lola and Limón, Costa Rica. Data from CATIE (Centro Agronómico Tropical de Investigación y Enseñanza) and IMN (Instituto Meteorológico Nacional). (Standard diagram after Walter and Lieth 1960; left axis: temperature (°C), right axis: rainfall [mm], horizontal: months from January to December)

As can be seen from the climatogram of La Lola (Fig. 7) covering a period of 8 years, precipitation is much more variable than temperature. Although there are no relatively dry periods in the long-term mean values, in particular years dry periods can occur (e.g. March/April 1984, February 1986). For example, in March, when relatively little rain falls, precipitation fluctuates between 43.2 mm (1980) and 305.7 mm (1983), and that of the rainy month of November between 105.6 mm (1983) and 928.8 mm (1981).

As shown by the comparison of the weather at the two experimental sites in Waldeck and Estrada, there is no marked difference between the parameters that were measured (Figs. 8, 9, and 10); merely the frequency and the heaviness of the rainfall differed slightly, but the distribution pattern throughout the year was the same. In January, March, April/May, September/October 1985 and again in February 1986, there were periods lasting several weeks when only little rain fell. Between these drier periods, from the end of May to the beginning of September 1985 and from the end of October 1985 to January 1986, rainfall was very high (Figs. 8 A and 10 A). Evaporation showed three maxima, in January, March and April/May 1985, corresponding with the periods with little rainfall. The minimum was in the last two extremely rainy weeks of June (Fig. 8 B). The extreme temperatures also showed a marked annual periodicity, which was more noticeable in the case of the minimum temperatures. From January to April 1985 and from mid-November 1985 to February 1986, the minima were distinctly under 20°C; between those periods, the minimum temperatures rose to 23°C (Figs. 8 C and 10 C).

Naturally, the curves of the hours of rainfall per week showed the same periodicity as the precipitation curves. They were almost the same at both sites, too (Figs. 9 A and 10 B). The curves of the hours of leaf wetness were also related to rainfall and temperatures; however, an annual periodicity was not so marked here (Fig. 9 A and 10 B). The values of the leaf wetness recorder fixed at the height of 0.3 m deviated more strongly from the actual leaf wetness than those of the recorder fixed at the height of 4.2 m. Thus, the results regarding the leaf wetness obtained at the height of 0.3 m were of limited value for the statistical evaluation.

In Waldeck, the numbers of hours with temperatures <20°C and <23°C were calculated (Fig. 9 B), because laboratory experiments showed inhibited growth of *M. fijiensis* below these temperatures (Stover 1983b). Both these curves showed a marked annual periodicity with three maxima at the end of February, in July/August, and in December/January.

From May to July 1986, experiments concerning the development of symptoms of black Sigatoka disease were carried out. Rainfall was distributed evenly throughout this period, apart from two dry periods (Fig. 11). From 08.05.86 to 16.05.86, there were 9 days without any rain and from 30.05.86 to 03.06.86 another 5.

In 1985, in Waldeck, wind directions were investigated in more detail. During that year, in 45.9% of the cases the wind blew from east to northeast (Fig. 12). When one compares the frequency percentage of the wind directions in each month (Fig. 13), sea winds from east to northeast dominated in most months. Only during the months of August, October and November did the wind more often blow from west to northwest. Southwesterly winds coming from the direction of the mountains were very rare. Southeasterly winds were also relatively few.

From October 1984 to July 1986, the weather corresponded more or less to that of the long-term general climate (Figs. 6 and 7). Only in the case of the precipitation could a few deviations be observed. Thus, in comparison with other years, January 1985 was relatively dry with 89 mm rainfall and February 1986 with only 47 mm rainfall. In February 1986, however, most of the experiments had come to an end and the new ones did not begin until May 1986. Unusual events as regards the wind were two storms on 11.05.85 and 08.07.85, which devastated large areas with banana plantations and also caused some losses in the experimental plantations.

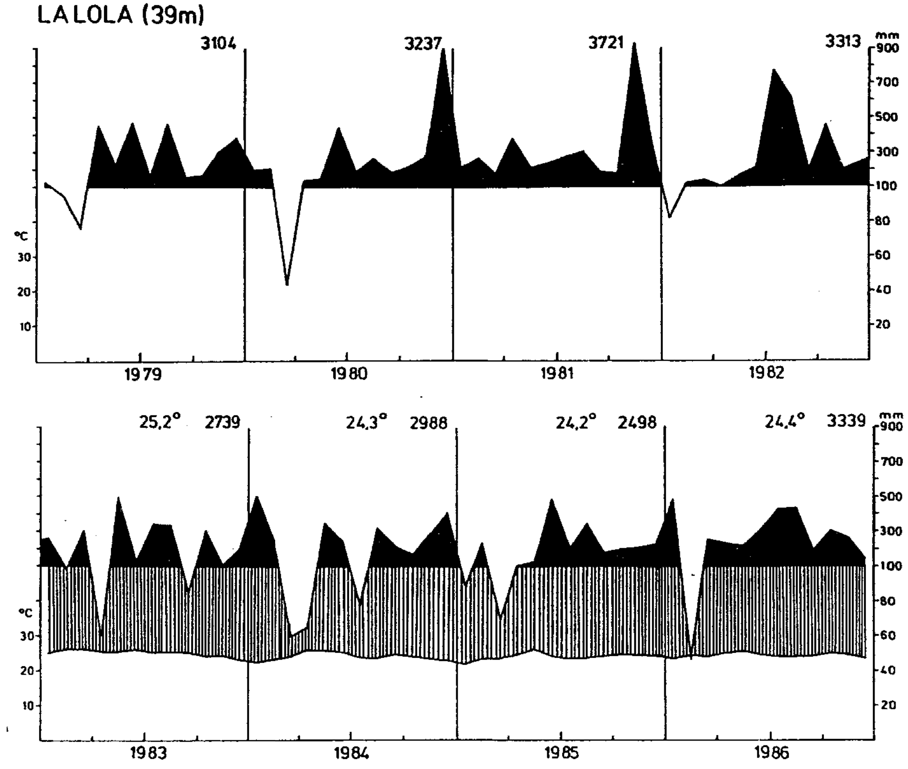


Fig. 7: Climatogram of La Lola over 8 years; from 1979 to 1982 no temperature data available. Data from CATIE (Centro Agronómico Tropical de Investigación y Enseñanza)

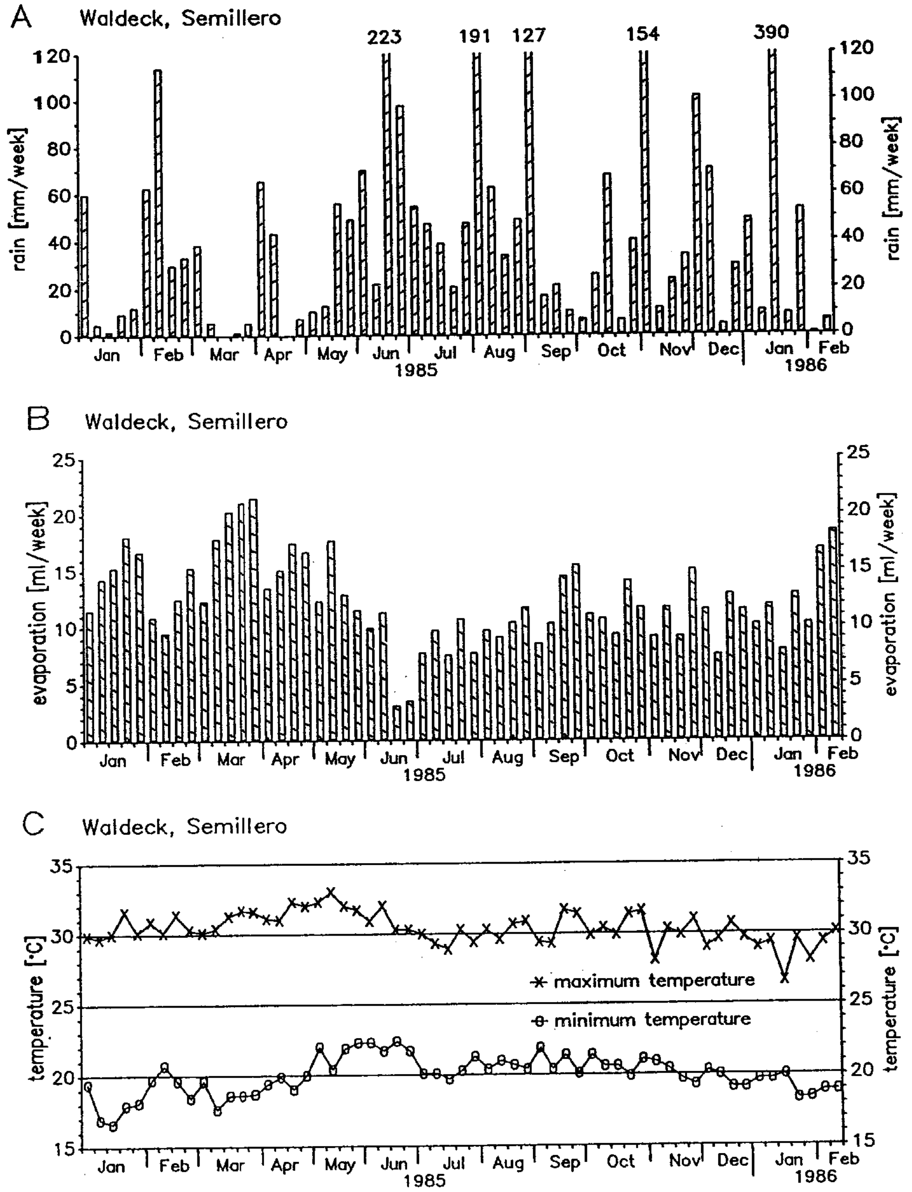


Fig. 8: Weekly totals of rainfall (A), evaporation (B) and weekly average of daily minimum and maximum temperatures (C) in Waldeck, Costa Rica.

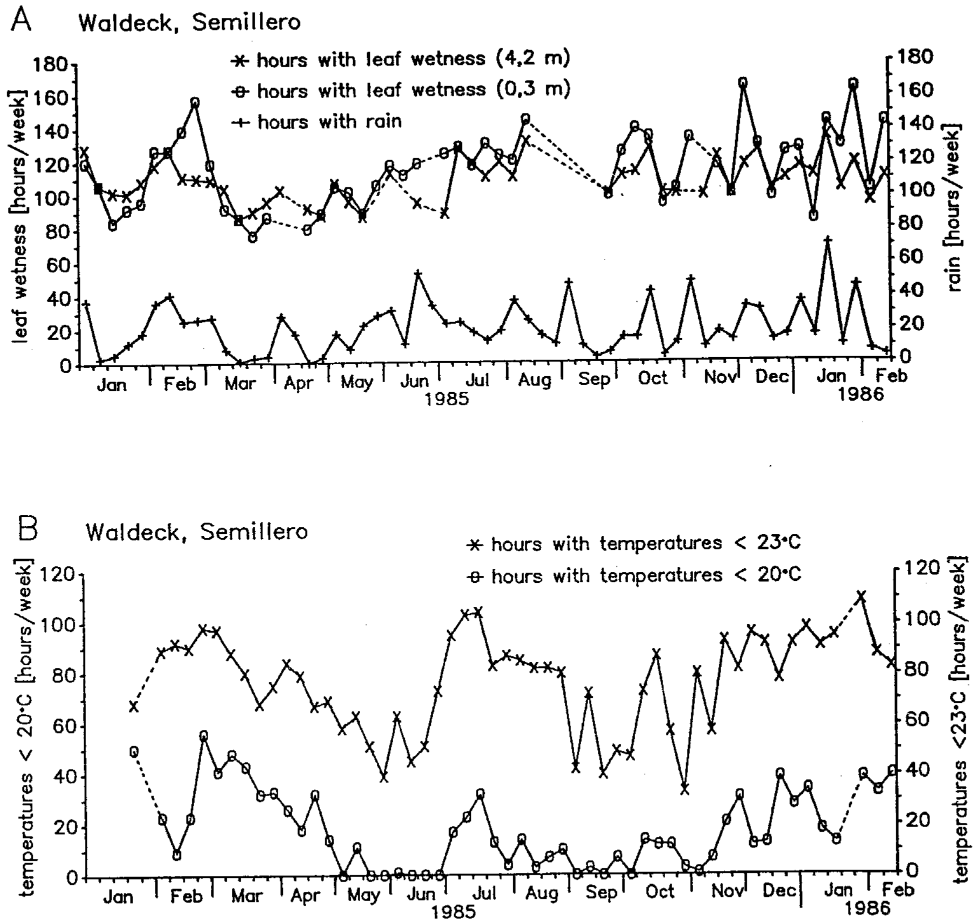


Fig. 9: Weekly hours with rain and leaf wetness (A) and hours with temperatures below 20°C and 23°C (B) in a False Horn plantain plantation in Waldeck, Costa Rica.

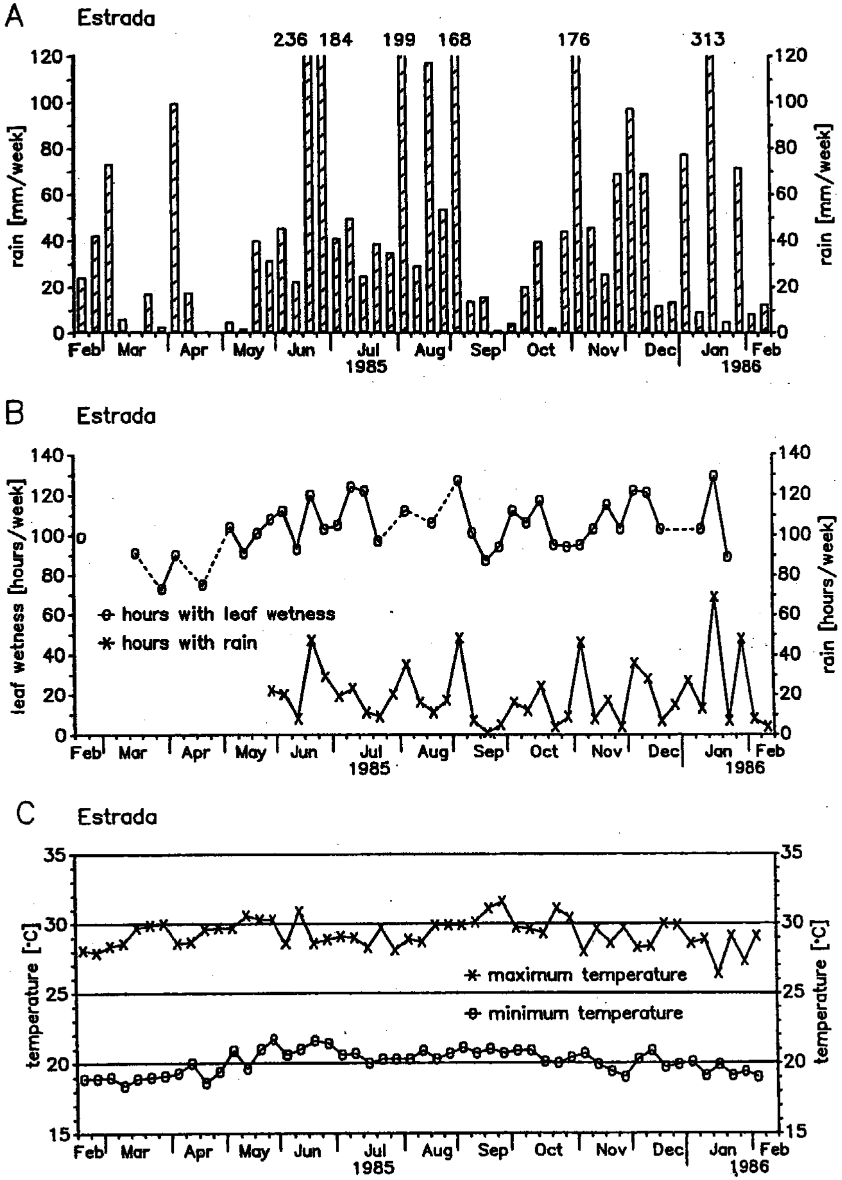


Fig. 10: Weekly totals of rainfall (A), hours with rain and leaf wetness (B) and weekly average of daily minimum and maximum temperatures (C) in Estrada, Costa Rica.

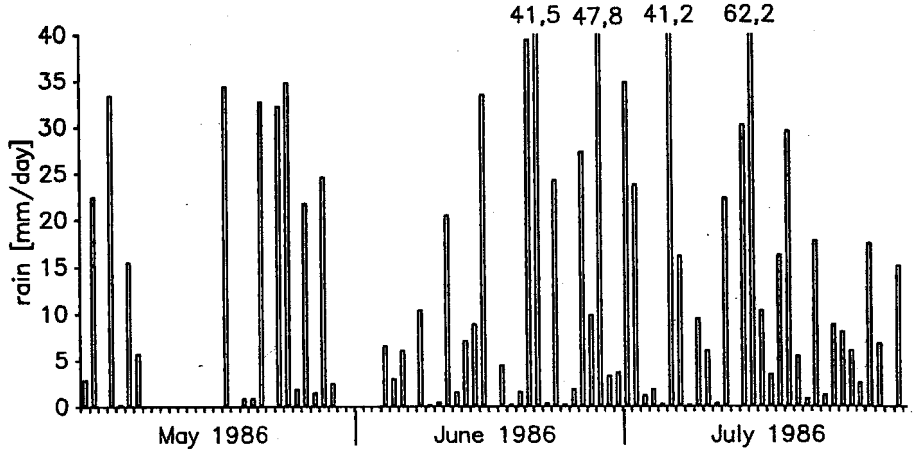


Fig. 11: Daily totals of rainfall from May to July 1986 in Waldeck, Costa Rica.

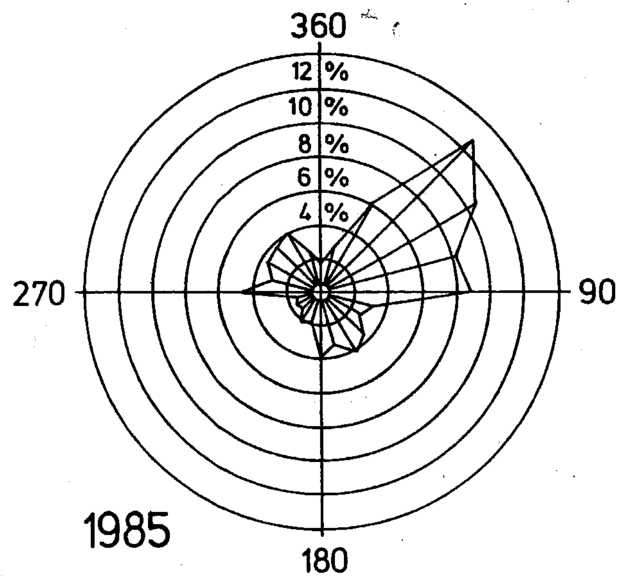


Fig. 12: Frequency of wind directions in Waldeck (Costa Rica) during 1985 at 7 m above ground in a False Horn plantain plantation; data from hourly values.

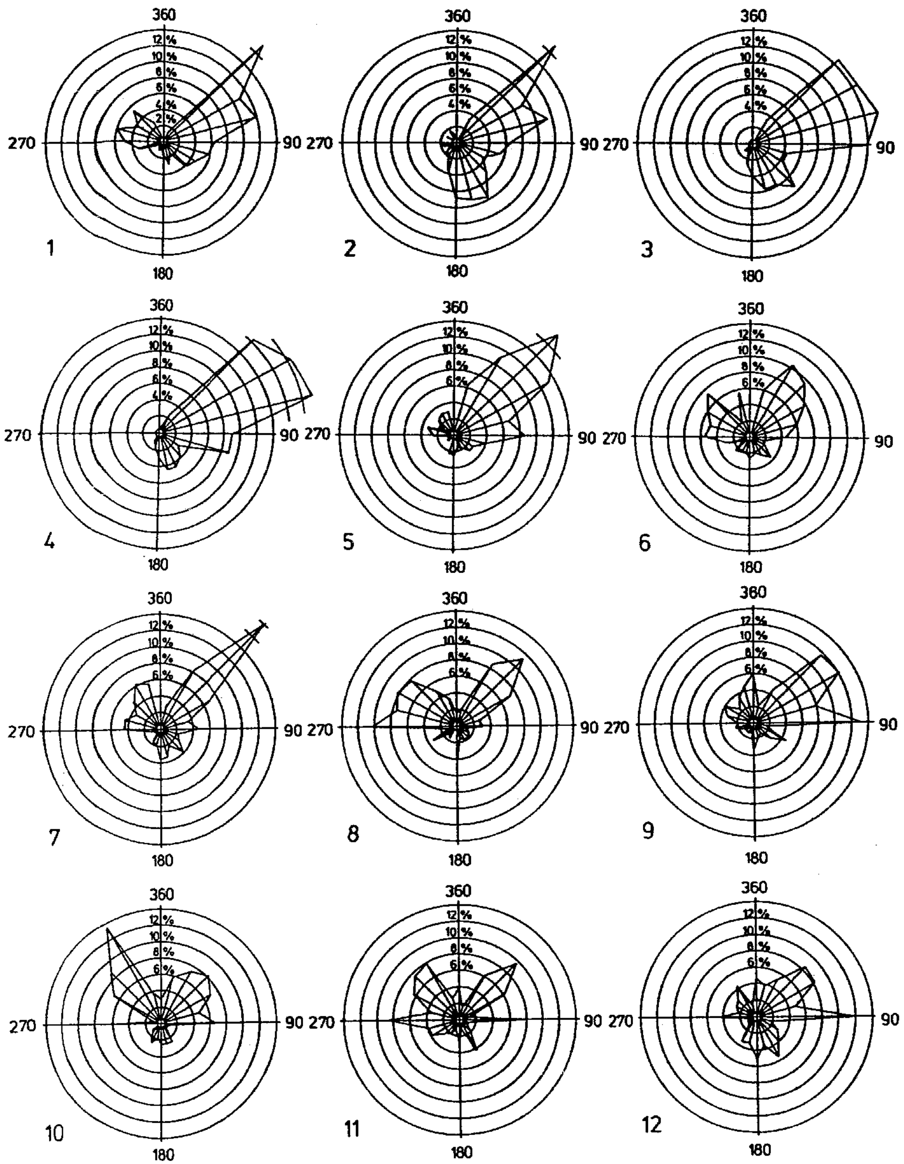


Fig. 13: Frequency of wind directions in Waldeck (Costa Rica) for the months January - December 1985 at 7 m above ground in a False Horn plantain plantation; data from hourly values.

5. STUDY OF PLANT GROWTH

On the soils with impeded drainage in Semillero and those with good drainage in the plantations Semillero and Estrada, plantain showed very different rates of growth. The growth of the pseudostem, the duration of leaf emergence as well as the size of the leaf differed significantly (Tables 10 and 11). In all cases, growth on the poorer soil with impeded drainage was greatly retarded. However, at both sites there was a highly significant correlation between the growth in height and the increase in girth of the pseudostem at a height of 1 m (Table 10).

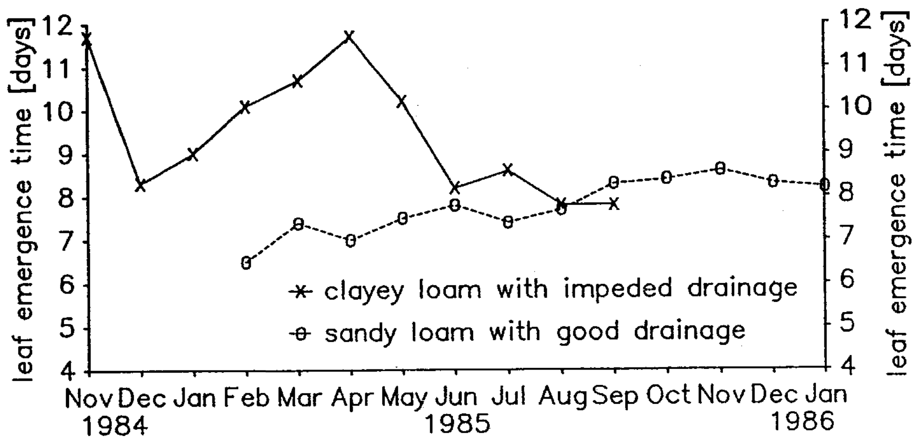


Fig. 14: Average time (days) of leaf emergence of False Horn plantain in stands on different soils (Semillero plantation with impeded drainage: n = 13 plants; Semillero and Estrada plantations with good drainage: n = 15 plants).

At the sites with good drainage, plant growth rate slowed down continuously until the final height was reached at flowering. With increasing plant age, the time of leaf emergence rose from 6.5 days to more than 8 days (Fig. 14). During this time, the additional growth in height of the pseudostem of more than 13 cm per week (13 cm w^{-1}) was about halved and the increment rate of the girth lessened from 1.9 to merely 0.3 cm w^{-1} (Fig. 15). The rate of growth was not influenced by the fertilizers; these were applied here at the same time as at the site with impeded drainage. Lassoudière (1977) also reports on a longer period of leaf emergence in the case of older plants of the banana cultivar Valery (Poyo). Stover (1979a) observed that, with increasing age, the cultivar Grande Naine showed a slower rate of growth in height.

At the site with impeded drainage, the time of leaf emergence fluctuated very strongly (Fig. 14), but, in contrast to the soils with good drainage, no dependency of growth on the age of the plants could be observed. Instead, growth fluctuated according to fertilization and climatic influences. During periods with high rainfall, impeded drainage retarded plant growth. On the other hand, dry periods led to water deficiency and, therefore, to slower plant growth, too. After fertilizers had been applied in November 1984, in the following month of December leaf emergence was in only 8.3 days instead of 11.7. During April and May when rainfall is low, time of emergence again slowed down to 11.7 days. After renewed applications of fertilizers in May, June and July and more regular rainfall leaf emergence was again only 8 days. The fertilizer also had a positive effect on the rate of growth in the height and the girth of the pseudostem (Fig. 15).

Table 10: Growth parameters of False Horn plantain from 60 cm height until flowering in stands on different soils (plantation at Semillero with impeded drainage: November 1984 - September 1985; plantations at Semillero and Estrada with good drainage: February 1985 - January 1986).

Measurements	Plantation with impeded drainage		Plantations with good drainage	
Growth in height (cm/week)	4.6*	(452)	8.7	(250)
Increase in girth (cm/week)	0.9*	(184)	1.3	(220)
Time of leaf emergence (days)	9.8*	(292)	7.6	(239)
Leaf area (m^2)	0.56*	(311)	1.24	(249)
Correlation height - girth (r)	0.9271***	(189)	0.9754***	(187)

* Differences between the stands significant at $P \leq 5\%$.
*** Significant with at $P \leq 0.1\%$.

Table 11: Growth parameters of False Horn plantain at flowering in stands on different soils (plantation at Semillero with impeded drainage: November 1984 - September 1985; plantations at Semillero and Estrada with good drainage: February 1985 - January 1986).

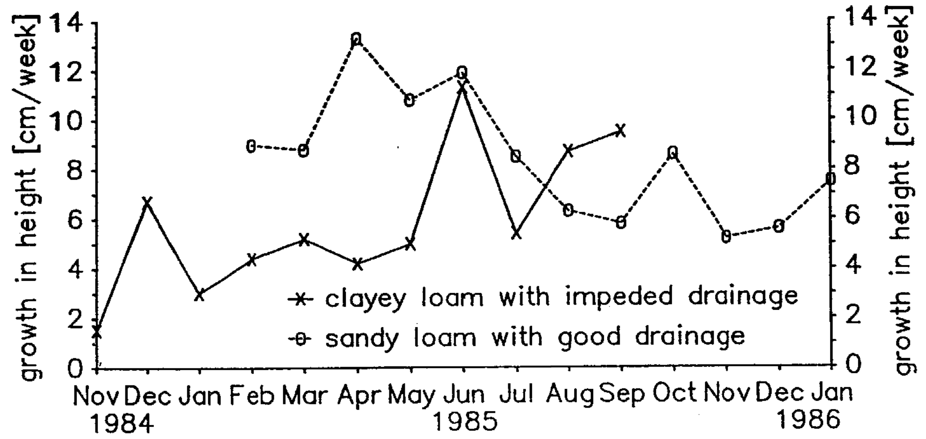
Measurements	Plantation with impeded drainage		Plantations with good drainage	
Height of pseudostem (cm)	244.0*	(10)	326.0	(15)
Girth of pseudostem (cm)	39.9*	(10)	53.8	(15)
Leaf length (cm)	144.2*	(64)	206.2	(128)
Leaf width (cm)	65.2*	(64)	81.1	(128)
Leaf area (m^2)	0.84*	(64)	1.51	(128)

* Differences between the stands significant with $p \leq 5\%$.

Lassoudière (1977) states that in Côte d'Ivoire, during the dry season on mineral soils (water deficiency), leaf emergence and growth in height of the banana cultivar Valery slowed down. On organic soils, he did not note any influence of drought on plant growth. Compared with the water budget, the temperature was of secondary importance. For Honduras, Stover (1979a) stated that low temperatures were responsible for a retarded growth in height and a prolonged leaf emergence in the case of the cultivar Grande Naine. The cooler months, however, were also the drier ones.

In order to determine the factor for the calculation of the leaf area, 23 leaves on plants between 1.6 m and 3.4 m tall were chosen. Both plants growing well in favorable sites and plants with retarded growth in unfavorable sites were taken into consideration. These leaves were between 81 cm and 259 cm long and between 42 cm and 83 cm wide. The factor for determining the leaf area by means of the length and width of the leaf was 0.898 ± 0.014, i.e. about 0.9. The values of both the small and the large leaves were scattered over the whole range of the factor and not concentrated at the upper or lower end. Thus, in contrast to the leaf area, the correction factor was not dependent on the age or the rate of growth of the plants.

A



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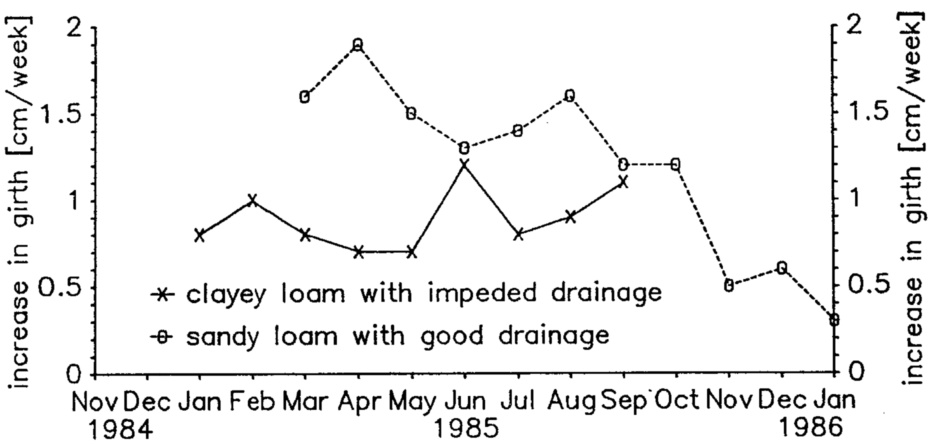


Fig. 15: Weekly growth of pseudostem of False Horn plantain in stands on different soils (Semillero plantation with impeded drainage: n = 13 plants; Semillero and Estrada plantations with good drainage: n = 15 plants).
A: Growth in height
B: Increase in girth at a height of 1 m

6. DEVELOPMENT OF BLACK SIGATOKA DISEASE ON PLANTAIN AND BANANA LEAVES

6.1 Time of development of symptoms and leaf area with symptoms on plantain dependent on season and weather

From October 1984 to March 1986, a total of 574 leaves were marked on 30 plantain plants. The development of symptoms and leaf area with symptoms were assessed for the whole leaf and then separately for each leaf section (Fig. 5), on a weekly basis. Data obtained during fieldwork had already indicated that the disease developed more rapidly before flowering than after. Therefore, the data gained "before flowering" and "after flowering" were presented separately (Table 12). Significant differences were observed with regard to the time of development of all symptoms and stages of leaf area with symptoms. Before flowering, the first symptoms, specks or streaks, developed about a week earlier than after flowering. Differences of even up to 3 weeks were observed in the case of 50% and 100% of the leaf area spotted.

Table 12: Time (days) required for appearance of symptoms and time to reach particular levels of leaf area with symptoms on False Horn plantain before and after flowering.

Symptoms / leaf area with symptoms	Before flowering (n)	(days)	After flowering (n)	(days)
First symptoms	(497)	23.3*	(65)	31.1
Specks	(182)	22.4*	(2)	32.0
Streaks	(436)	26.2*	(61)	31.9
Spots	(273)	34.1*	(60)	42.1
Spots with a dry center	(446)	42.3*	(103)	51.9
6-15% leaf area with symp.	(325)	50.2*	(95)	65.6
16-33% leaf area with symp.	(240)	56.0*	(83)	72.0
34-50% leaf area with symp.	(374)	64.2*	(122)	82.5
51-100% leaf area with symp.	(367)	66.0*	(117)	85.2
Leaf hanging	(356)	72.5*	(99)	93.2

* Difference before and after flowering significant at $P \leq 5\%$.

The following statements refer only to the leaves infected before flowering. The leaves infected after flowering were not taken into consideration because their number was considerably smaller. As plant growth varied noticeably on the different soils, the times of symptom development were also calculated separately for each soil.

The period up to the appearance of the various black Sigatoka symptoms in the different sections of the leaves is shown in Figs. 16-19. The corresponding values with the significant differences on four selected dates are presented in Tables 13-16. The graphs in Figs. 16-19 are so similar that they are discussed together.

All stages of the disease first appeared on the left half of the tip of the leaf (Sec. 1), and then, in most cases, on the right half (Sec. 2). Then, after a longer interval of time, the symptoms became visible on the middle Sections (3 and 4) and on the base of the leaf blade (Sec. 5 and 6). In all graphs, this order was not marked at the beginning of the curve; however, further on in the curve, it became obvious and, towards the end of the curve, the intervals were the longest. Moreover, these intervals increased according to each higher symptom stage. In the plantation with impeded drainage (Fig. 16 A-19 A), the intervals between the appearance of the symptoms in the first and the last section were as follows: first symptoms (specks and streaks) 3.2-6.8 days, streaks 2.0-8.0 days, spots 2.6-12.6 days, and spots with a dry center (necrosis) 3.0-12.4 days. In the plantations with good drainage (Fig. 16 B-19 B), the differences were greater. For the first symptoms, they were between 3.2-6.8 days, for streaks between 3.6-10.8 days, for spots between 0.0-17.4 days, and for spots with a dry center 1.1-30.0 days. These differences were significant (Tables 13-16).

The time of symptom development was longest in May and June, shortest in July and August and increased towards the end of the year. The differences between these maxima and minima also increased with each further symptom stage. In Section 1, the difference for the first symptoms was 10.0 days, for streaks 14.2 days, for spots 26.0 days, and for spots with a dry center 20.9 days. In Section 6, the corresponding values were 8.6, 12.1, 24.2 and 29.4 days.

Twice during the regular observation of the symptom development, an especially heavy infection of the leaves was noticed. In the plantations in Semillero (Waldeck) and Estrada, specks and streaks suddenly appeared at the beginning of May (04.05.85) in greater numbers than during the time before. The symptoms were spread out evenly and very densely over the whole blade. The lesions already became coalescent in the streak stage, and large areas of the leaf surface were evenly stained brown. The leaf tissue developed necrosis rapidly and the leaves died. This phenomenon was noted again on 22.06.85. These mass infections could be explained with the help of the spore trap data (cf. Chap. 7.1).

The period of time up to the appearance of different symptoms (first appearance independent of leaf section) is summarized in Fig. 20. Here, again, the time of symptom development and the increasing differences between minima and maxima of the higher symptom stages become clear. During the course of the year, in the plantations with impeded drainage, specks appeared on the unfurled leaves (Fig. 20 A) after 17.0-28.9 days (difference: 11.9), streaks after 20.0-34.6 (14.6) days, spots after 26.0-50.7 (24.7) days, and spots with a dry center after 33.7-55.7 (22.0) days. In the plantations with good drainage (Fig. 20 B), the corresponding values were 15.0-26.9 (11.9) days for specks, 18.7-30.1 (11.4) days for streaks, 24.6-43.6 (19.0) days for spots, and 33.9-49.3 (15.4) days for spots with a dry center. At both sites, the times of symptom development were longer during periods with low rainfall than during those with high. During the periods with low rainfall, development time for specks was about 11.9 days and for spots with a dry center about 15.4 days longer than during periods with higher rainfall. These fluctuations were more marked at the site with impeded drainage. In the months with higher rainfall, the times of symptom development were only 1 or 2 days longer on these soils than on the good soils; contrasting with this, in the months with lower rainfall symptom development was 12-25 days longer.

Firman (1972) estimated a latent period (period of time between inoculation and the first appearance of symptoms) of 25-35 days for *Musa* clones with the genome AAB on Fiji; Meredith and Lawrence (1970) also report 25-35 days for the Horn plantain on Hawaii. In Côte d'Ivoire, after the beginning of the dry season, the latent period increased greatly on numerous banana varieties (Fouré 1982, Fouré *et al.* 1984).

These results show that the leaves were infected throughout the whole year with slight time fluctuations. Within a week, first symptoms (latent period of specks or streaks) appeared in all six sections of the leaf. This applied to the whole study period. The later symptoms (spots and spots with a dry center) sometimes took twice as long to appear on the tip of the leaf during the drier periods than during the wetter ones. On the rest of the leaf blade, they appeared up to a month later than on the tip. With regard to each symptom stage, as the plants grew older the interval increased between the appearance of the symptoms on the tip of the leaf (Sections 1 and 2) and the rest of the leaf. As for the spot with a dry center, on the site with impeded drainage, just before flowering the interval was 12.4 days (September 1985) and 30.0 days (January 1986) on the sites with good drainage. These differences were observed in months with high rainfall when symptom development was not delayed. The reason for this is most likely age resistance of the plants. This assumption is supported by the calculations regarding the leaves which were infected after flowering. On these leaves, development times for symptoms and area affected were significantly longer than on leaves infected before flowering.

Table 13: Time after leaf emergence (days) until appearance of first symptoms of black Sigatoka on False Horn plantain leaves before flowering.

A: Plantation at Semillero with impeded drainage

Section	January 1985 (days)	(n)	May 1985 (days)	(n)	August 1985 (days)	(n)
1	21.2 A*	(52)	25.6 A	(21)	19.8 A	(5)
2	24.3 B	(51)	29.6 AB	(28)	21.3 A	(6)
3	22.2 A	(55)	29.0 AB	(21)	19.8 A	(6)
4	25.5 BC	(48)	31.8 B	(24)	24.5 A	(6)
5	22.5 A	(52)	29.5 AB	(20)	22.8 A	(6)
6	25.9 C	(49)	31.3 B	(23)	25.4 A	(5)

B: Plantations at Semillero and Estrada with good drainage

Section	May 1985 (days)	(n)	August 1985 (days)	(n)	December 1985 (days)	(n)
1	24.4 A*	(26)	18.4 A	(21)	24.6 A	(5)
2	28.7 BC	(30)	21.1 AB	(22)	25.4 A	(5)
3	26.2 AB	(24)	22.5 BC	(21)	30.6 A	(5)
4	29.6 C	(27)	24.9 CD	(20)	32.3 A	(4)
5	26.2 AB	(24)	24.5 CD	(23)	30.6 A	(5)
6	29.6 C	(27)	26.0 D	(21)	32.3 A	(4)

* Different letters indicate significant differences between sections at $P \leq 5\%$.

Table 14: Time after leaf emergence (days) until appearance of streaks of black Sigatoka on False Horn plantain leaves before flowering.

A: Plantation at Semillero with impeded drainage

Section	January 1985 (days)	(n)	May 1985 (days)	(n)	August 1985 (days)	(n)
1	23.9 A*	(50)	33.7 A	(29)	20.0 A	(2)
2	26.7 B	(46)	35.4 A	(29)	22.0 A	(4)
3	24.0 A	(50)	34.5 A	(27)	24.5 A	(4)
4	27.6 B	(45)	36.4 A	(27)	27.2 A	(5)
5	24.6 A	(49)	34.0 A	(26)	26.0 A	(4)
6	28.0 B	(46)	35.7 A	(26)	27.7 A	(6)

B: Plantations at Semillero and Estrada with good drainage

Section	May 1985 (days)	(n)	August 1985 (days)	(n)	December 1985 (days)	(n)
1	27.3 A*	(29)	18.7 A	(14)	24.6 A	(5)
2	32.9 BC	(38)	21.6 AB	(11)	25.0 AB	(4)
3	29.9 AB	(28)	23.3 B	(21)	32.4 BC	(7)
4	34.0 C	(34)	26.5 C	(22)	33.7 C	(6)
5	30.3 ABC	(27)	25.0 BC	(24)	34.7 C	(6)
6	34.2 C	(34)	26.7 C	(23)	34.7 C	(6)

* Different letters indicate significant differences between sections at $P \leq 5\%$.

Table 15: Time after leaf emergence (days) until appearance of spots of black Sigatoka on False Horn plantain leaves before flowering.

A: Plantation at Semillero with impeded drainage

Section	January 1985 (days)	(n)	May 1985 (days)	(n)	August 1985 (days)	(n)
1	33.4 A*	(18)	52.0 A	(19)	26.0 A	(6)
2	34.1 AB	(19)	52.6 A	(18)	28.0 AB	(6)
3	38.3 B	(48)	59.0 A	(21)	29.6 ABC	(5)
4	38.1 B	(44)	60.2 A	(20)	36.8 C	(6)
5	36.7 AB	(40)	58.2 A	(18)	34.7 BC	(7)
6	36.0 AB	(36)	59.1 A	(22)	37.8 C	(4)

B: Plantations at Semillero and Estrada with good drainage

Section	May 1985 (days)	(n)	August 1985 (days)	(n)	December 1985 (days)	(n)
1	44.1 A*	(19)	24.6 A	(23)	29.5 A	(4)
2	48.1 AB	(16)	25.2 A	(22)	27.7 A	(3)
3	48.8 AB	(26)	31.2 B	(19)	43.3 B	(4)
4	49.7 B	(26)	35.5 C	(14)	45.3 B	(4)
5	47.8 AB	(27)	34.3 BC	(16)	45.4 B	(5)
6	47.2 AB	(24)	35.6 C	(14)	46.8 B	(4)

* Different letters indicate significant differences between sections at $P \leq 5\%$.

Table 16: Time after leaf emergence (days) until appearance of spots with a dry center of black Sigatoka on False Horn plantain leaves before flowering.

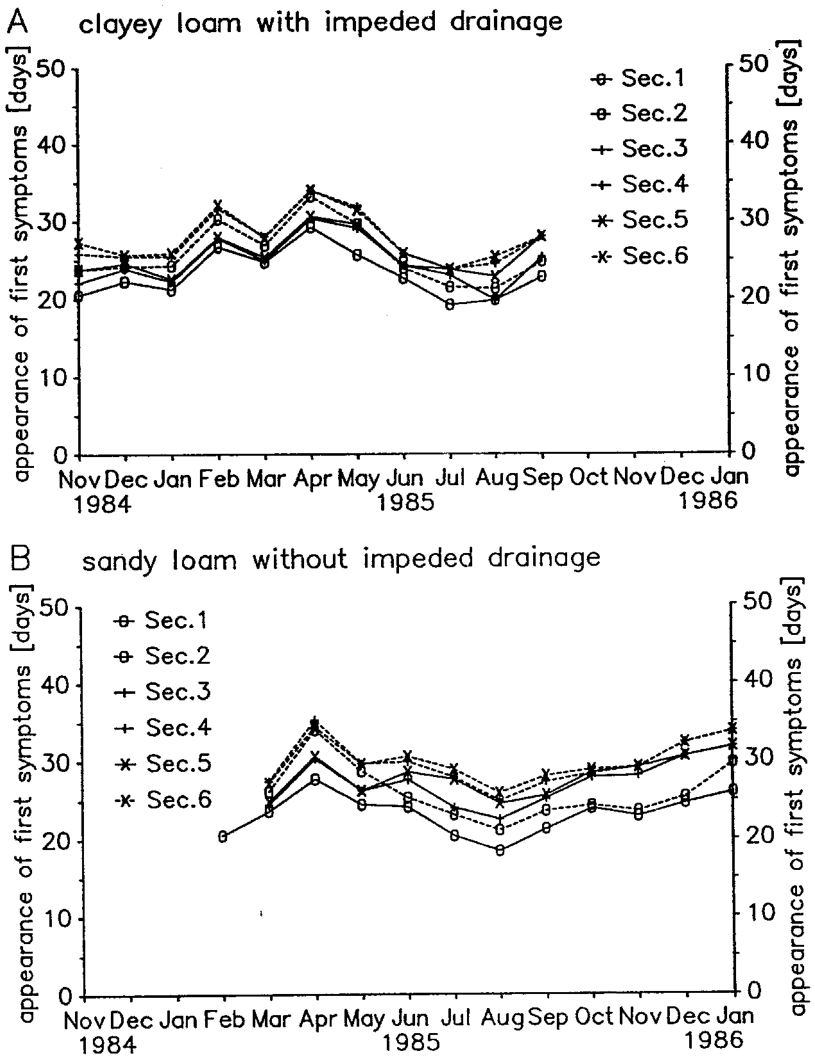
A: Plantation at Semillero with impeded drainage

Section	January 1985 (days)	(n)	May 1985 (days)	(n)	August 1985 (days)	(n)
1	38.5 A*	(58)	57.2 A	(11)	37.0 A	(5)
2	39.1 A	(54)	58.2 A	(12)	35.8 A	(4)
3	44.9 CD	(56)	69.9 A	(7)	45.6 AB	(5)
4	45.2 D	(57)	70.3 A	(6)	44.7 AB	(7)
5	42.2 BC	(58)	62.4 A	(5)	48.5 B	(4)
6	41.5 AB	(56)	67.8 A	(5)	45.4 AB	(5)

B: Plantations at Semillero and Estrada with good drainage

Section	May 1985 (days)	(n)	August 1985 (days)	(n)	December 1985 (days)	(n)
1	49.7 A*	(25)	31.8 A	(19)	40.7 A	(6)
2	51.7 AB	(27)	33.3 A	(17)	40.7 A	(6)
3	61.8 C	(13)	43.0 B	(12)	68.3 B	(9)
4	61.7 C	(19)	42.6 B	(9)	64.5 B	(11)
5	59.6 C	(17)	43.9 B	(8)	65.4 B	(7)
6	57.1 BC	(23)	44.7 B	(9)	69.5 B	(6)

* Different letters indicate significant differences between sections at $P \leq 5\%$.



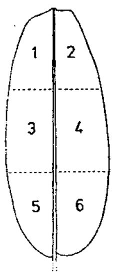
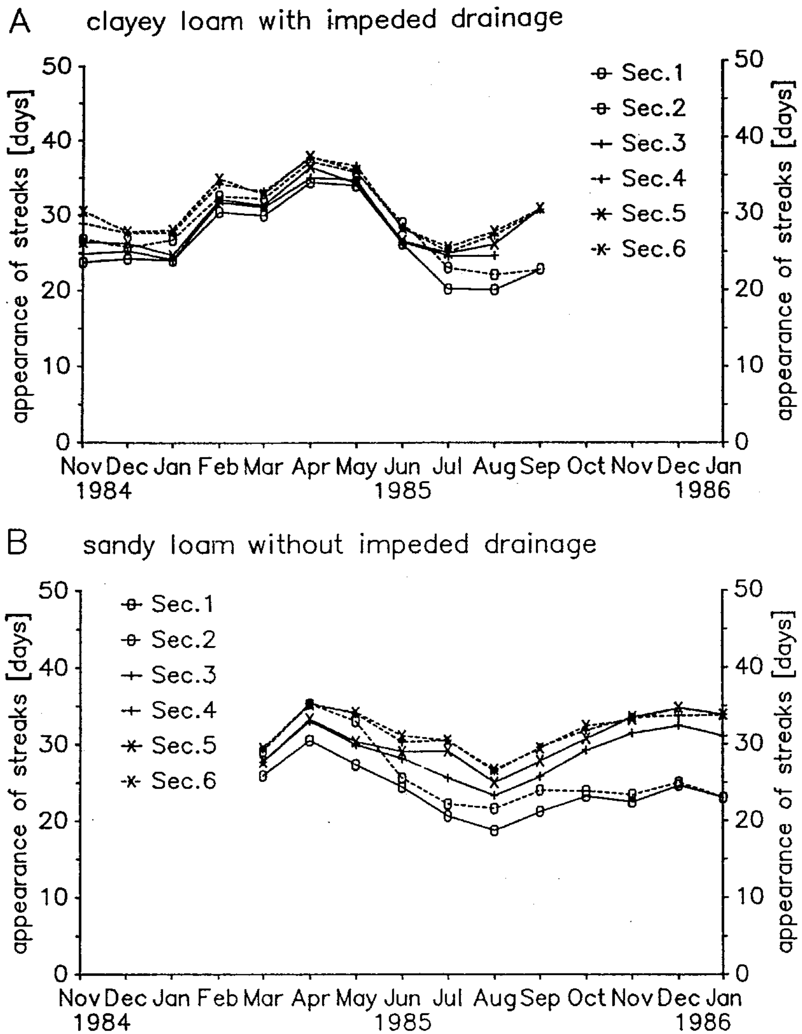


Fig. 16: Average time (days) after leaf emergence until appearance of first symptoms (speck, streak) on False Horn plantain leaves before flowering.
Statistical evaluation for selected months: cf. Table 13.
A: Plantation at Semillero with impeded drainage: n = 13 plants
B: Plantations at Semillero and Estrada with good drainage: n = 15 plants
Sec. = leaf sections



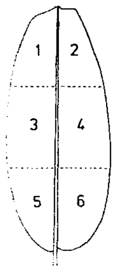
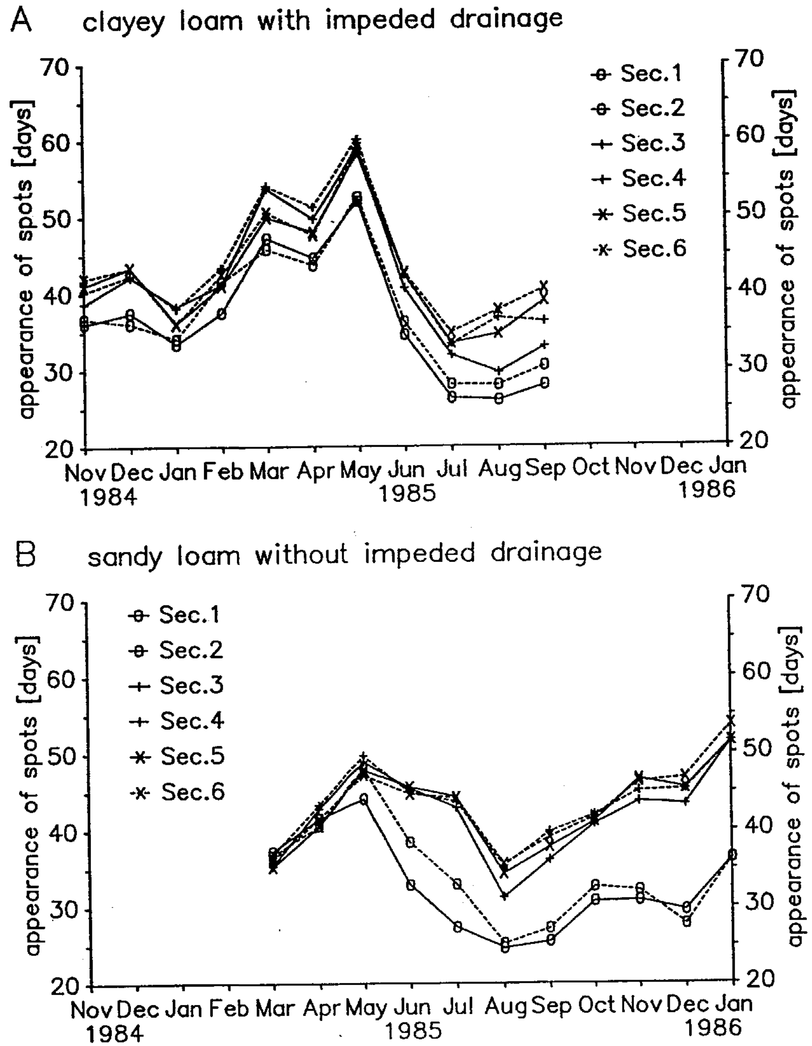


Fig. 17: Average time (days) after leaf emergence until appearance of streaks on False Horn plantain leaves before flowering. Statistical evaluation for selected months: cf. Table 14.
A: Plantation at Semillero with impeded drainage: n = 13 plants
B: Plantations at Semillero and Estrada with good drainage: n = 15 plants
Sec. = leaf sections



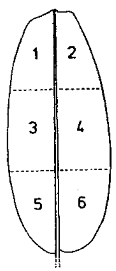
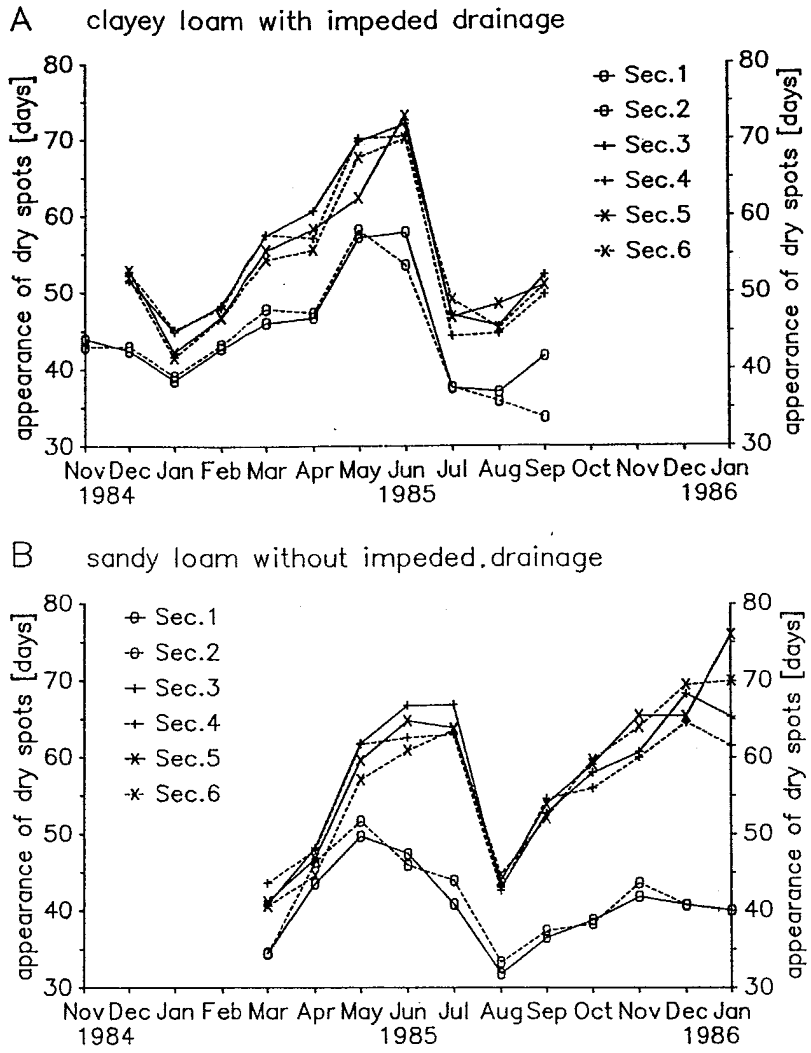


Fig. 18: Average time (days) after leaf emergence until appearance of spots on False Horn plantain leaves before flowering. Statistical evaluation for selected months: cf. Table 15.
A: Plantation at Semillero with impeded drainage: n = 13 plants
B: Plantations at Semillero and Estrada with good drainage: n = 15 plants
Sec. = leaf sections



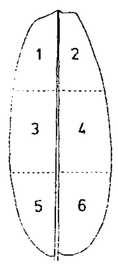


Fig. 19: Average time (days) after leaf emergence until appearance of spots with a dry center on False Horn plantain leaves before flowering.
Statistical evaluation for selected months: cf. Table 16.
A: Plantation at Semillero with impeded drainage: n = 13 plants
B: Plantations at Semillero and Estrada with good drainage: n = 15 plants
Sec. = leaf sections

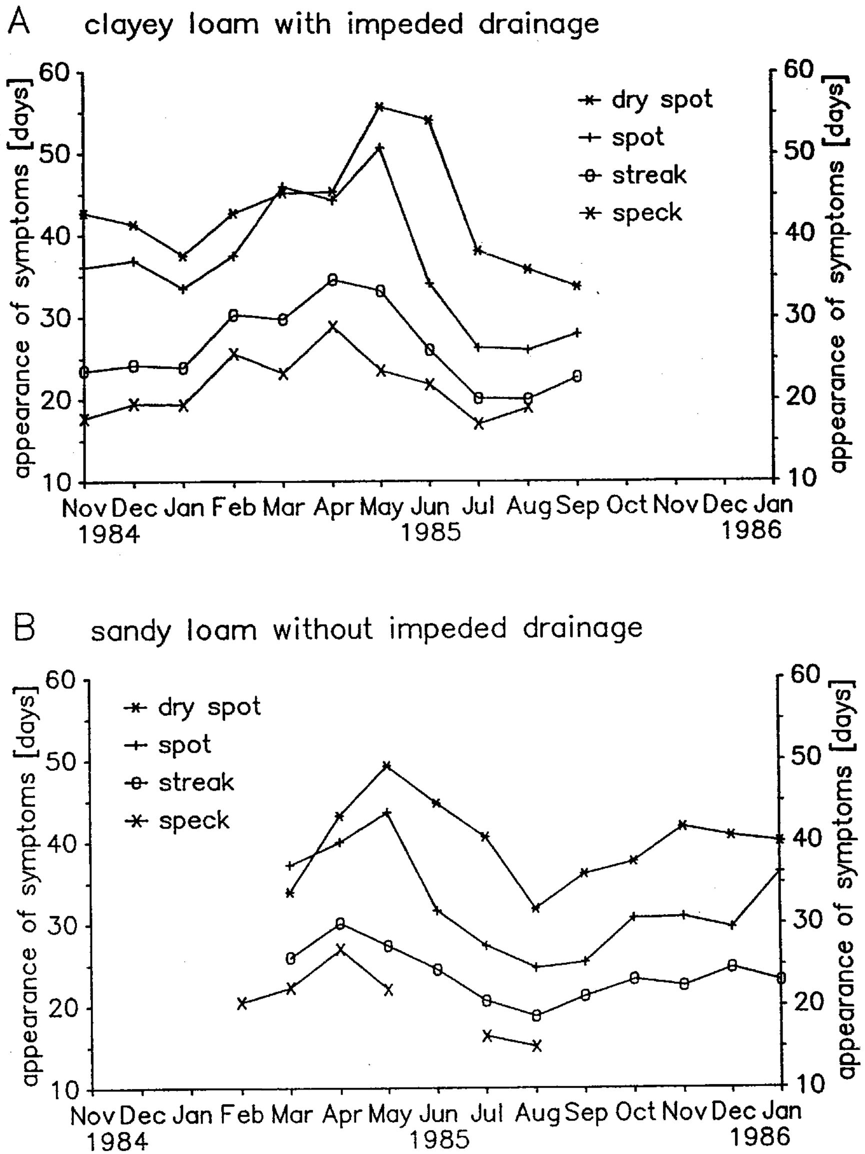


Fig. 20: Average time (days) after leaf emergence until appearance of different symptoms on False Horn plantain leaves before flowering.
A: Plantation at Semillero with impeded drainage: n = 13 plants
B: Plantations at Semillero and Estrada with good drainage: n = 15 plants

The first symptoms always appeared at the tip of the leaf, mostly on the left side, which unfurls first. The more rapid symptom development on the tip of the leaf was favored by the formation of the leaf tips: water was collected during the night in the canoe-shaped tip of the leaf, which mostly hung down. Thus, the tip remained wet after the rest of the leaf had dried. The symptoms appeared first here. The anatomy of the banana leaves also favors symptom development at the tip of the leaf. On the variety Gros Michel, Skutch (1927) found a larger number of stomata at the tip than at the base of the leaf blade. Furthermore, the leaf is thinner at the edges than near the midrib (Skutch 1927). Thus, the fungus can cause symptoms to appear more quickly in these areas.

The graphs depicting the number of days required until a certain area of the whole leaf became spotted are all similar (Fig. 21). In the plantations with impeded drainage (Fig. 21 A), the time until 6-15%, 16-33% and more than 50% of the leaf area became spotted was longest in May and June (64.6, 71.0 and 80.8 days), and shortest in July and August (36.9, 43.8 and 51.8 days). In the plantations without impeded drainage (Fig. 21 B), the corresponding values were 55.9, 61.5 and 68.4 days in May, 39.3, 43.2 and 52.0 days in August, and in December/January they increased again to 63.3, 71.0 and 77.7 days. The distance between the curves themselves remained relatively constant. The differences between minima and maxima of all curves ranged between 26.0 and 30.0 days.

When one examines the relationship between symptom development, leaf area with symptoms and weather (rainfall, hours of rainfall, temperature, evaporation, hours of leaf wetness), ascospore and conidiospore release by means of a correlation analysis, surprising results are obtained. At first, a statistical relationship between symptom development and rainfall seemed possible. However, no significant correlation could be demonstrated.

As regards the development time of all symptoms, calculations resulted in high, mostly significant, negative correlations with the hours of leaf wetness (Table 17). In the plantations with impeded drainage, there was a significant positive correlation between the maximum temperature with both symptom development and leaf area with symptoms. The relation between evaporation and the development of the first symptoms up to the spot stage was significantly positive. There was also a significant negative correlation regarding the connection between these symptoms and ascospore release.

No yield figures could be obtained from the marked plants. During two storms in May and June 1985, a large number of plants were blown down before the fruit had ripened. Fieldworkers harvested the bunches "by mistake" from several other plants.

6.2 Detailed investigation into symptom development of black Sigatoka on plantain and banana

From May to July 1986, symptom development was investigated on False Horn plantain (AAB) and banana (Valery; AAA) with inoculation time known. The experiments were carried out after the beginning of the rainy season, when the conditions for the development of the disease were favorable.

6.2.1 Symptom development on plantain

Investigation of leaves covered by plastic bags

On five plantain leaves, after the bags had been removed, all the symptoms appeared at the same time, with only slight differences (Table 18). Dots and light patches were visible after 21.3 days, specks after 23.4, streaks after 30.4, brush streaks (several brush-like streaks close together) after 34.6, spots after 36.6 and spots with a dry center after 42.8 days. These leaves were covered by the plastic bags until they were completely unfurled. Therefore, the whole leaf

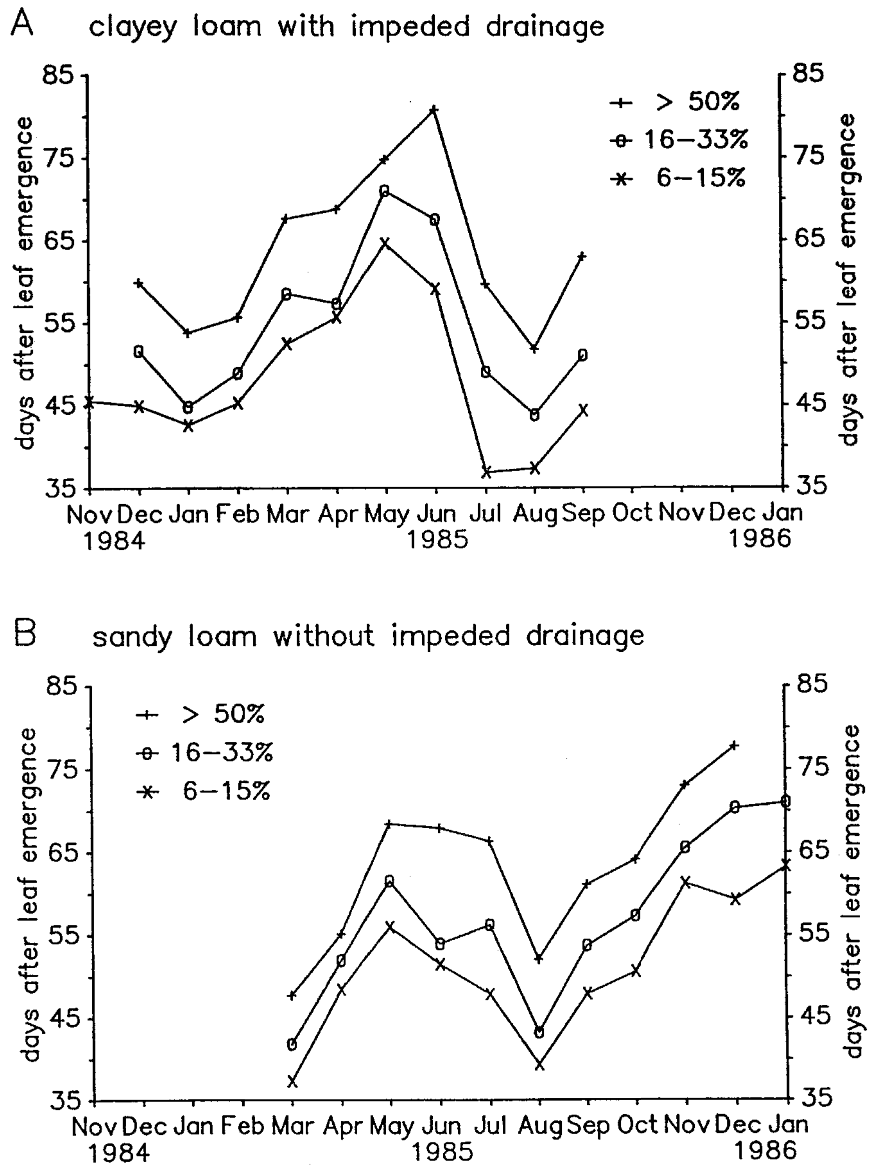


Fig. 21: Average time (days) after leaf emergence required to reach different stages of leaf area with symptoms on False Horn plantain leaves before flowering.
A: Plantation at Semillero with impeded drainage: n = 13 plants
B: Plantations at Semillero and Estrada with good drainage: n = 15 plants

Table 17: Correlations between time required for symptom development / leaf area with symptoms of black Sigatoka on False Horn plantain and hours of leaf wetness (in 4.2 m height), maximum temperatures, evaporation and ascospore release (monthly values) in plantations with impeded drainage (Semillero) and with good drainage (Semillero and Estrada).

		Correlations between time required for symptom development / leaf area with symptoms and							
Symptom / leaf area w. sym.	Plantations	Hours of leaf wetness (r)	(n)	Maximum temperature (r)	(n)	Evaporation (r)	(n)	Ascospore release (r)	(n)
First symptoms	Impeded drainage	-0.7552**	11	0.7152*	11	0.5726	9	-0.6168	9
	good drainage	-0.4594	12	0.1182	12	0.3629	12	-0.1916	12
Specks	Impeded drainage	-0.7935**	10	0.7503*	10	0.5026	8	-0.6697	8
	good drainage	---	--	---	--	---	--	---	--
Streaks	Impeded drainage	-0.8232**	11	0.7523**	11	0.6232	9	-0.7473*	9
	good drainage	-0.8663***	11	0.5882	11	0.6630*	11	-0.6282*	11
Spots	Impeded drainage	-0.6622*	11	0.5971	11	0.7127*	9	-0.7509*	9
	good drainage	-0.7794**	11	0.4962	11	0.6446*	11	-0.6406*	11
Dry spots	Impeded drainage	-0.5597	11	0.5655	11	0.0721	9	-0.6103	9
	good drainage	-0.5052	11	0.4147	11	0.0006	11	-0.3593	11
6-15% leaf area with symptoms	Impeded drainage	-0.6911*	11	0.7236*	11	0.3109	9	-0.5863	9
	good drainage	0.0833	11	-0.3093	11	-0.2818	11	0.2753	11
16-33% leaf area with symptoms	Impeded drainage	-0.4395	11	0.7679**	11	0.0960	9	-0.3993	9
	good drainage	0.2076	11	-0.3983	11	-0.2786	11	0.4305	11
34-50% leaf area with symptoms	Impeded drainage	-0.4009	11	0.7140*	11	-0.0206	9	-0.3231	9
	good drainage	-0.2434	11	0.5023	11	-0.0296	11	-0.1563	11

* Significant at $P \leq 5\%$. ** Significant at $P \leq 1\%$.*** Significant at $P \leq 0.1\%$.

Table 18: Time (dpi = days after inoculation) until first appearance of symptoms on five False Horn plantain leaves after natural inoculation with *Mycosphaerella fijiensis* (s = standard deviation). Until inoculation, leaves were covered by plastic bags.

Symptom development	Position of leaf in: full sunlight	full sunlight	full sunlight	full sunlight	half-shade	Average	
Inoculation	16.05.86	13.05.86	13.05.86	13.05.86	12.05.86	days	(s)
Dots and light patches	--(dpi)	--(dpi)	21(dpi)	21(dpi)	22(dpi)	21.3	(0.6)
Specks (streaks up to 1 mm)	21	21	23	24	28	23.4	(2.9)
Streaks up to 3 mm	25	31	32	32	32	30.4	(3.1)
Brush streaks	29	36	36	36	36	34.6	(3.1)
Spots	32	36	38	38	39	36.6	(2.8)
Spots with a dry center	39	45	42	42	46	42.8	(2.8)

blade was infected evenly, as could be seen by the distribution of the first symptoms. During further symptom development, there was a concentration of the symptoms at the edges of the leaves; they developed rather more quickly there. Four of these five leaves grew in full sunlight and one in the half-shade. There was no obvious difference as regards the symptom development in connection with different grades of shade.

The number of symptoms and the leaf area with symptoms were examined in detail on three leaves; only one leaf, however, is presented here as an example in Fig. 23 and Tables 19 and 20. First, at 20 days after inoculation (20 dpi), a large number of small, light dots appeared on the leaves, sometimes amounting to more than 200 in the 5 x 5 cm^2 squares (Table 19). From 23 dpi onwards, streaks were to be seen on the leaves; their number rose to 290.5 per 25 square centimeters (290.5 25 cm^{-2}) on 49 dpi. After that, the number of symptoms decreased rapidly, as the streaks merged into spots. From 42 dpi, spots were to be found on the leaves. Their number rose from 9.8 25 cm^{-2} to 44.2 25 cm^{-2} (59 dpi). After 56 dpi, spots with a dry center (necrosis) were observed which, however, often merged into larger, dry areas.

Using square No. 2 (Fig. 22 A) of the same leaf as an example (leaf inoculated on 13.05.86, Table 18, 2nd column), the development of the number of symptoms and the leaf area spotted is shown. During a period of almost 1 month (31-59 dpi), the square was traced every 3-4 days (Fig. 23). Table 20 contains the values for the symptoms and the leaf area with symptoms.

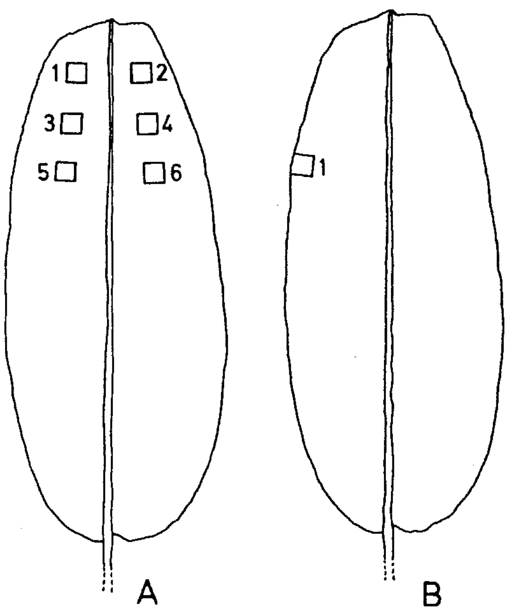


Fig. 22: Positions of 5 x 5 cm^2 squares marked on plantain and banana leaves.
A: cf. Figs. 23 and 25
B: cf. Figs. 24 and 26

After 31 dpi, there were 147 streaks in the square; these were up to 3 mm long and covered 4.4% of the leaf area. Five days later (36 dpi), the leaf area with symptoms had doubled (8.8%), and the streaks were so close together that they had the appearance of a wide, ragged brush

Table 19: Number of symptoms (average of 6 squares 5 x 5 cm^2; away from edge) at tip of False Horn plantain leaf in full sunlight on different dates after natural inoculation (dpi) with *Mycosphaerella fijiensis* at Waldeck (Semillero), Costa Rica (s = standard deviation).

Dates	dpi	Dots (number)	(s)	Streaks (number)	(s)	Spots (number)	(s)	Dry spots (number)	(s)
31.5.86	17	0	-	0	-	0	-	0	-
03.6.86	20	144.0	(34.9)	0	-	0	-	0	-
06.6.86	23	239.7	(71.4)	8.0	(3.4)	0	-	0	-
10.6.86	27	-	-	64.0	(23.9)	0	-	0	-
13.6.86	31	-	-	117.5	(34.0)	0	-	0	-
18.6.86	36	-	-	233.3	(50.5)	0	-	0	-
24.6.86	42	-	-	221.7	(12.8)	9.8	(3.7)	0	-
27.6.86	45	-	-	253.0	(32.1)	15.3	(5.4)	0	-
01.7.86	49	-	-	290.5	(85.0)	17.5	(6.5)	0	-
04.7.86	52	-	-	216.8	(23.6)	33.7	(14.1)	0	-
08.7.86	56	-	-	157.5	(21.8)	33.5	(9.0)	12.2	(3.3)
11.7.86	59	-	-	87.2	(24.3)	44.2	(15.9)	33.0	(8.7)
15.7.86	63	-	-	42.8	(18.5)	34.8	(13.5)	33.0	(20.3)

Position of squares on leaf: cf. Fig. 22 A.

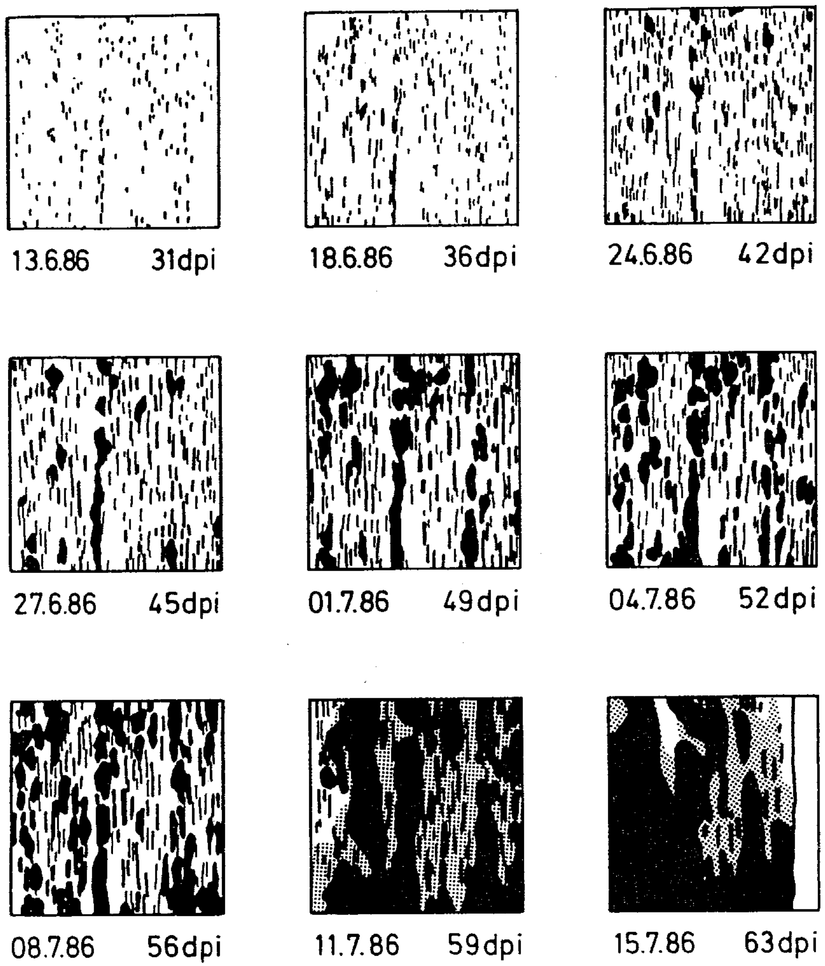


Fig. 23: Symptom development in a 5 x 5 cm² square at the tip (away from edge) of a False Horn plantain leaf after natural inoculation with Mycosphaerella fijiensis. *Until inoculation (13.05.86), leaf was covered by a plastic bag. On 15.07.86 area marked had shrunk to less than 5 cm in width.*
black: lesions
shaded: chlorosis
dpi: days after inoculation
(Position of square on leaf: cf. Fig. 22 A2; values for symptoms: cf. Table 20)

streak. After 42 dpi, 240 streaks and 11 spots were counted on the leaf, some of which came from the brush streak. The leaf area with symptoms was then 14.0%, again almost double the size. The number of spots rose to 18 and the area covered by spots increased. After 45 dpi, the number of streaks began to decrease (to 224). The disease now covered almost a fifth (19.6%) of the marked area. On 01.07.86 (49 dpi), the leaf area with symptoms had increased to 30.4%, the number of spots, however, remained the same; the number of streaks sank to 191. Three days later (52 dpi), the leaf area with symptoms had only slightly increased; the number of spots, however, had more than doubled, whereas the number of streaks decreased further. On 08.07.86 (56 dpi), the first spots with dry center were to be found. The number of streaks and spots decreased, the percentage of the marked leaf area with symptoms rose to 41.6%.

Another 3 days later (59 dpi), the lesions began to merge into large, dry areas with wide, yellow, chlorotic edges. The symptoms now covered 59.2% of the area (without the yellow tissue). At 63 dpi (15.07.86), the leaf tissue had already shrunk considerably and was, apart from small areas, completely covered by black Sigatoka. Individual stages of the symptoms could hardly be distinguished. As the leaves had shrunk, it was no use measuring the area with the video equipment.

Twelve plantain leaves were covered with bags for 4 weeks after they had unfurled, in order to investigate whether older leaves also became infected. As the evaluations were carried out only on a weekly basis, no exact details concerning the time of symptom development can be given. All leaves showed streak symptoms of black Sigatoka after 39.3 ± 6.8 days.

Investigation of leaves not covered by plastic bags

Parallel to the investigations of the leaves which had unfurled inside the bags, three additional leaves that had not emerged in plastic bags were observed (Table 21). These leaves were inoculated naturally when the heart leaf was still firmly rolled and a little more than half emerged. This could be concluded later from the development of the symptoms. On these leaves, the symptoms first appeared in the upper third of the left edge of the leaf.

This was the area of the leaf which was exposed to the air during the stage described above. In these areas, symptom development was more rapid than on the rest of the leaf. Here, the first symptom stage could not be registered. Streaks appeared after 31.0 days, brush streaks after 38.3, spots after 41.7 and spots with a dry center after 49.7 days. Symptoms developed more slowly on these leaves than on those in the bags. This was especially noticeable with regard to the higher symptom stages. Here, solar radiation could have played a part. Two of the three leaves grew in the half-shade. On these leaves, the development of the last symptom stage was distinctly longer (51 and 52 days compared with 46 days; Table 21).

Leaves that had been inoculated while unfurling were also examined in detail: here, too, at regular intervals, a 5 x 5 cm² square (edge of leaf) was traced exactly (Fig. 22 B1, Fig. 24, Table 22; leaf inoculated on 07.05.86, Table 21). This leaf belongs to the group of plants growing in the half-shade where symptoms developed somewhat more slowly. Inoculation took place here on 07.05.86: this was concluded from the formation of the symptoms. The stages traced (Fig. 24) can be well compared with those in Fig. 23. Except for slight differences, the area covered by the symptoms also corresponds (Tables 20 and 22). In contrast to this, the number of streaks in the square on the edge of the leaf was always higher (Fig. 24). There was also a marked concentration of streaks on the areas near the edge. Later, the first spots appeared here, too. On 04.07.86, however, an additional infection by *Cordana musae* took place, so that the areas between the edge of the leaf and the *Cordana* spots became quickly yellow and necrotized. For this reason, the number of spots and necrotic areas (spots with a dry center) remained smaller. Therefore, after 08.07.86 the percentage of leaf area with symptoms could not be determined either.

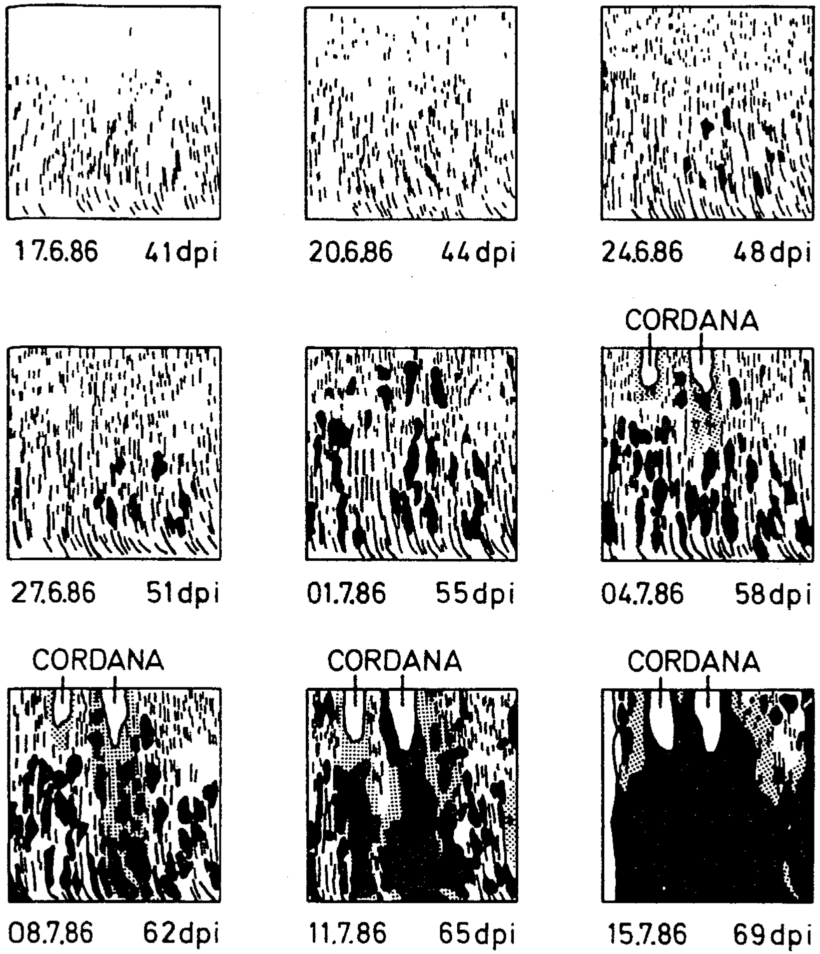


Fig. 24: Symptom development in a 5 x 5 cm² square on the left edge of a False Horn plantain leaf after natural inoculation (07.05.86) with Mycosphaerella fijiensis. *On 04.07.86, an infection with* Cordana musae *took place, which caused chlorosis. On 15.07.86, area marked had shrunk to less than 5 cm in width.*
black: lesions
shaded: chlorosis
dpi: days after inoculation
(Position of square on leaf: cf. Fig. 22 B1; values for symptoms: cf. Table 22)

Table 20: Number of symptoms and leaf area covered in the 5x5 cm² square in Fig. 23 (away from edge) of a False Horn plantain leaf on different dates after natural inoculation (dpi) with *Mycosphaerella fijiensis* at Waldeck (Semillero), Costa Rica.

Dates	dpi	Streaks (number)	Spots (number)	Dry spots (number)	Area (%)
13.6.86	31	147	0	0	4.4
18.6.86	36	231	0	0	8.8
24.6.86	42	240	11	0	14.0
27.6.86	45	224	18	0	19.6
01.7.86	49	191	18	0	30.4
04.7.86	52	160	41	0	32.8
08.7.86	56	143	34	13	41.6
11.7.86	59	5	17	48	59.2

Table 21: Time (dpi = days after inoculation) until first appearance of symptoms on three False Horn plantain leaves after natural inoculation with *Mycosphaerella fijiensis* (s = standard deviation).

Symptom development	Position of leaf in: full sunlight	half-shade	half-shade	Average days	(s)
Inoculation	10.05.86	06.05.86	07.05.86		
Dots and light patches	-- (dpi)	-- (dpi)	-- (dpi)	--	-
Specks (streaks up to 1 mm)	25	--	--	--	-
Streaks up to 3 mm	32	31	30	31.0	(1.0)
Brush streaks	39	35	41	38.3	(3.1)
Spots	42	39	44	41.7	(2.5)
Spots with a dry center	46	52	51	49.7	(3.2)

6.2.2 Symptom development on banana

Investigation of leaves covered by plastic bags

When the bags were removed from three banana leaves, the symptoms also appeared immediately with only slight differences (Table 23). These leaves all grew in the half-shade. Dots and light patches were visible after 17.0 days, specks after 28.0 days, streaks after 32.4 days, brush streaks after 36.0 days, spots after 39.3 and spots with a dry center after 41.3 days.

As in the case of the plantain, the first symptoms were also distributed evenly over the whole leaf. Later, the symptoms appeared more often on the edges of the leaves and also developed a little more quickly there.

The number of symptoms and their size were assessed exactly on two leaves, but here, too, only one leaf is given as an example (Fig. 25, Tables 24 and 25). At first (13 dpi), a large number of small, light dots appeared on the leaves, sometimes amounting to more than 200 in the 5 x 5 cm^2 squares (Table 24). On dull days, these dots were difficult to see and could not be counted (20 dpi; Table 24). From 24 dpi, streaks were visible on the leaves: their number rose to 281.7 25 cm^{-2} on 37 dpi. After that, the number of symptoms decreased rapidly, as the streaks merged into spots. After 37 dpi, spots were to be found on the leaves; their number increased from 0.7 25 cm^{-2} to 22.7 25 cm^{-2} (51 dpi). After 51 dpi, spots with a dry center (necrosis) were present; these merged into large areas.

Table 22: Number of symptoms and leaf area covered in the 5x5 cm^2 square in Fig. 24 on left edge of a False Horn plantain leaf on different dates after natural inoculation (dpi) with *Mycosphaerella fijiensis* in Waldeck (Semillero), Costa Rica.

Dates	dpi	Streaks (number)	Spots (number)	Dry spots (number)	Area (%)
17.6.86	41	188	0	0	8.0
20.6.86	44	228	0	0	10.4
24.6.86	48	357	5	0	13.6
27.6.86	51	290	8	0	18.8
01.7.86	55	286	16	0	28.0
04.7.86	58	221	30	1	30.8
08.7.86	62	177	30	5	--
11.7.86	65	155	25	17	--

Table 23: Time (dpi = days after inoculation) until first appearance of symptoms on three banana leaves (Valery) after natural inoculation with *Mycosphaerella fijiensis* (s = standard deviation). Until inoculation, leaves were covered by plastic bags.

Symptom development	Position of leaf in: half-shade	half-shade	half-shade	Average	
Inoculation	20.05.86	14.05.86	14.05.86	days	(s)
Dots and light patches	13 (dpi)	19 (dpi)	19 (dpi)	17.0	(3.5)
Specks (streaks up to 1 mm)	24	30	30	28.0	(3.5)
Streaks up to 3 mm	24	34	34	32.0	(3.5)
Brush streaks	34	37	37	36.0	(1.7)
Spots	37	40	41	39.3	(2.1)
Spots with a dry center	37	43	44	41.3	(3.8)

Table 24: Number of symptoms (average of 6 squares 5 x 5 cm^2; away from edge) at tip of banana leaf (Valery) in half-shade on different dates after natural inoculation (dpi) with *Mycosphaerella fijiensis* at Waldeck (Semillero), Costa Rica (s = standard deviation).

Dates	dpi	Dots (number)	(s)	Streaks (number)	(s)	Spots (number)	(s)	Dry spots (number)	(s)
31.5.86	10	0	--	0	--	0	--	0	--
03.6.86	13	8.3	(5.9)	0	--	0	--	0	--
w06.6.86	16	40.8	(24.9)	0	--	0	--	0	--
10.6.86	20	--	--	0	--	0	--	0	--
14.6.86	24	180.8	(26.7)	0.5	(1.2)	0	--	0	--
18.6.86	28	--	--	103.3	(26.8)	0	--	0	--
24.6.86	34	--	--	217.2	(30.9)	0	--	0	--
27.6.86	37	--	--	281.7	(46.5)	0.7	(1.6)	0	--
01.7.86	41	--	--	208.5	(15.3)	1.7	(2.3)	0	--
04.7.86	44	--	--	261.8	(52.3)	3.0	(2.8)	0	--
08.7.86	48	--	--	214.2	(19.9)	7.0	(3.5)	0	--
11.7.86	51	--	--	174.2	(20.0)	22.7	(5.0)	11.2	(12.9)
15.7.86	55	--	--	72.7	(62.6)	17.3	(12.9)	32.5	(33.7)

Position of squares on leaf: cf. Fig. 22 A.

As in the case of the plantain, the development of the number of symptoms and the area of the leaf they covered is also shown by the example of the square No. 2 (Fig. 22 A) of the same leaf (leaf inoculated on 20.05.86, Table 23). This square was traced at regular intervals from 29-59 dpi onwards (Fig. 25). In Table 25, the values for the number of symptoms and the area covered are given.

After 29 dpi, there were already 85 streaks in the square; these were up to 3 mm long and covered 2.4% of the area. Six days later (35 dpi), the number of streaks had doubled (195), and the area covered even trebled (7.6%). After 41 dpi, 222 streaks and 3 spots were counted, some of which were formed by merged streaks (brush streaks). The area had again almost doubled (12.4%). After the spots had increased to 11 and grown in size, the number of streaks sank to 218 after 48 dpi. The disease now already covered a fifth (20.4%) of the area. On 11.07.86 (51 dpi), the area covered had increased only to 23.6%; the number of spots, however, rose to 20 and that of the streaks sank to 188. Yellow, chlorotic edges formed around the larger spots. Four days later (55 dpi), the lesions began to merge over large areas. They now covered 49.2% of the area. Chlorosis also spread over large areas. On 59 dpi (19.07.86), the leaf tissue had shrunk considerably and, except for small areas, was completely covered by black Sigatoka. Individual symptom stages could hardly be discerned; the leaf area with symptoms amounted to 85.2%.

Investigation of leaves not covered by plastic bags

Parallel to the investigations of the leaves which had unfurled inside the bags, three banana leaves that had not emerged in plastic bags were also observed. On these leaves, too, symptoms first appeared in the upper third of the left edge of the leaf. Here, symptom development proceeded distinctly faster compared with the rest of the leaf.

The first two symptom stages could be determined only on two leaves, the others on all leaves (Table 26). Dots and light patches appeared after 23.5 days, specks after 31.0 days, streaks after 32.0 days, spots after 41.7 days and spots with a dry center after 49.7 days. No brush streaks were found here.

On these leaves, there were marked differences in symptom development: these are made clear by the large standard deviations (Table 26). This is most likely the result of the different exposure of the leaves to sunlight. One of the leaves was in a sunny position, the second in the half-shade and the third completely in the shade. Symptom development was shortest on the first leaf. On the leaf in the shade, the intervals between each individual symptom stage were much longer. On the leaf in the half-shade, development times for the different stages were exactly between those of the other two leaves (Table 26).

On the leaf growing in the half-shade (cf. Table 26), at regular intervals a 5 x 5 cm^2 square (edge of leaf) was traced exactly (Fig. 22 B1, Fig. 26, Table 27). Inoculation took place on 16.05.86; this could be concluded from the formation of the symptoms.

The stages traced (Fig. 26) showed that symptom development was noticeably quicker here in comparison with the leaves in the bags (Fig. 25). The square on 23 dpi (Fig. 26) corresponded to the square on 35 dpi in Fig. 25 as far as both the number of symptoms and the leaf area with symptoms were concerned. After that, symptoms developed considerably faster on the square on the edge of the leaf; the final stage was reached more than 10 days earlier (Fig. 26).

6.2.3 Comparison of symptom development on plantain and banana

The detailed studies of symptom development from May to July 1986 resulted in the following sequence of symptoms and their shortest development times. On plantain they were: dot 21 days, speck 24 days, streak 30 days, brush streak 35 days, spot 38 days, spot with a dry center 44 days. On banana: dot 13 days, speck 24 days, streak 27 days, spot 30 days, spot with a dry center 34 days. Brush streaks could only rarely be observed on banana leaves, as the transition period from streak to spot was very short.

Table 25: Number of symptoms and leaf area covered in the 5x5 cm^2 square in Fig. 25 (away from edge) of a banana leaf (Valery) on different dates after natural inoculation (dpi) with *Mycosphaerella fijiensis* in Waldeck (Semillero), Costa Rica.

Dates	dpi	Streaks (number)	Spots (number)	Dry spots (number)	Area (%)
19.6.86	29	85	0	0	2.4
25.6.86	35	195	0	0	7.6
28.6.86	38	221	0	0	10.8
01.7.86	41	222	3	0	12.4
04.7.86	44	239	5	0	16.0
08.7.86	48	218	11	0	20.4
11.7.86	51	188	20	15	23.6
15.7.86	55	84	8	8	49.2
19.7.86	59	--	--	--	85.2

Table 26: Time (dpi = days after inoculation) until first appearance of symptoms on three banana leaves (Valery) after natural inoculation with *Mycosphaerella fijiensis* (s = standard deviation).

Symptom development	Position of leaf in: full sunlight	half-shade	shade	Average	
Inoculation	07.05.86	16.05.86	08.05.86	days	(s)
Dots and light patches	-- (dpi)	21 (dpi)	26 (dpi)	23.5	(3.5)
Specks (streaks up to 1 mm)	--	25	37	31.0	(8.5)
Streaks up to 3 mm	27	29	40	32.0	(7.0)
Brush streaks	--	--	--	--	-
Spots	30	35	43	36.0	(6.6)
Spots with a dry center	34	39	47	40.0	(6.6)

Table 27: Number of symptoms and leaf area covered in the 5 x 5 cm^2 square in Fig. 26 on left edge of a banana leaf (Valery) on different dates after natural inoculation (dpi) with *Mycosphaerella fijiensis* at Waldeck (Semillero), Costa Rica.

Dates	dpi	Streaks (number)	Spots (number)	Dry spots (number)	Area (%)
18.6.86	33	202	0	0	8.4
24.6.86	39	265	13	0	15.2
27.6.86	42	238	21	0	21.6
01.7.86	46	77	21	0	56.0
04.7.86	49	--	--	-	100.0

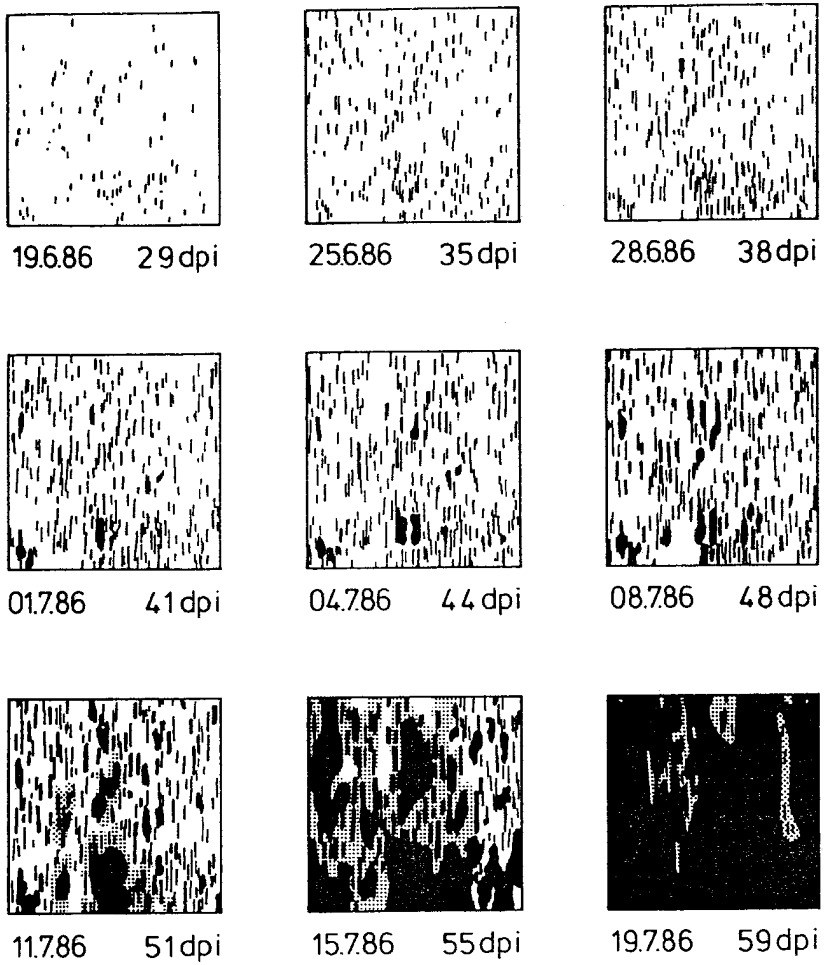


Fig. 25: Symptom development in a 5 x 5 cm² square at the tip (away from edge) of a banana leaf (Valery) after natural inoculation with Mycosphaerella fijiensis. *Until inoculation (20.05.86), leaf was covered by a plastic bag.*
black: lesions
shaded: chlorosis
dpi: days after inoculation
(Position of square on leaf: cf. Fig. 22 A2; values for symptoms: cf. Table 25)

The direct comparison between banana (Valery) and False Horn plantain, neither treated with fungicides, showed hardly any difference in the development time of early symptoms. On the banana, the more advanced symptoms from a spot onwards developed faster and spread more rapidly than on plantain; this led to the earlier death of the leaves. On a plantain leaf, the symptoms in a marked square (away from edge) covered 41.6% of the area after 56 dpi and 59.2% after 59 dpi (cf. Table 20 and Fig. 23). During the same time, in a marked square on a banana leaf, the symptoms already covered 49.2% of the area after 55 dpi and as much as 85.2% after 59 days (cf. Table 25 and Fig. 24) although, at the beginning, symptom density on the banana leaf was considerably lower (29 dpi, 85 streaks) than on the plantain leaf (31 dpi, 147 streaks). Symptom development was more rapid on the banana leaf although it was in a (half-shade) position which was more unfavorable to symptom development than that of the plantain leaf (full sunlight). Shade seems to slow down symptom development. Therefore, for both cultivars, the differences were even greater in the marked squares on the edges of the leaves, as both leaves were in the half-shade. On the banana leaf, 15.2% of the area was covered after 39 dpi and 100% only 10 days later (49 dpi; cf. Table 27 and Fig. 26). In contrast, on the plantain leaf 8.0% of the area was covered after 41 dpi and only 18.8% after 51 dpi (cf. Table 22 and Fig. 24).

As regards the sequence of black Sigatoka symptoms on banana, no generally valid statements can be made, as the formation of the symptoms depends both on the cultivar (Meredith and Lawrence 1969, 1970) and the density of the symptoms (Fouré 1982). The symptom stages described by Meredith and Lawrence (1969), Fouré (1982) and Lehmann-Danzinger (1986, 1988) only partly applied to black Sigatoka on False Horn plantain and banana (Valery) under the conditions of the Atlantic lowlands in Costa Rica. The dot corresponds to "stage 1" (small depigmentations on the underside of the leaf) specified by Fouré and the "initial speck" according to Meredith and Lawrence (1969). The speck, streak, and brush streak were according to the description given by Lehmann-Danzinger (1988). The spot corresponds largely to the uniform-colored spot 3.1 of Lehmann-Danzinger (1988). The spot with a dry center only rarely appeared as a single spot: the symptoms had mostly merged into larger patches at an early stage. In agreement with observations made by Fouré (1982), it was seen that, when the leaves are heavily diseased, the symptoms can already merge together from the speck stage onwards and cause large areas of the leaf to become necrotized. In these cases, therefore, symptom development progressed from a speck directly to larger necrotic patches without passing through the intermediate symptom stages.

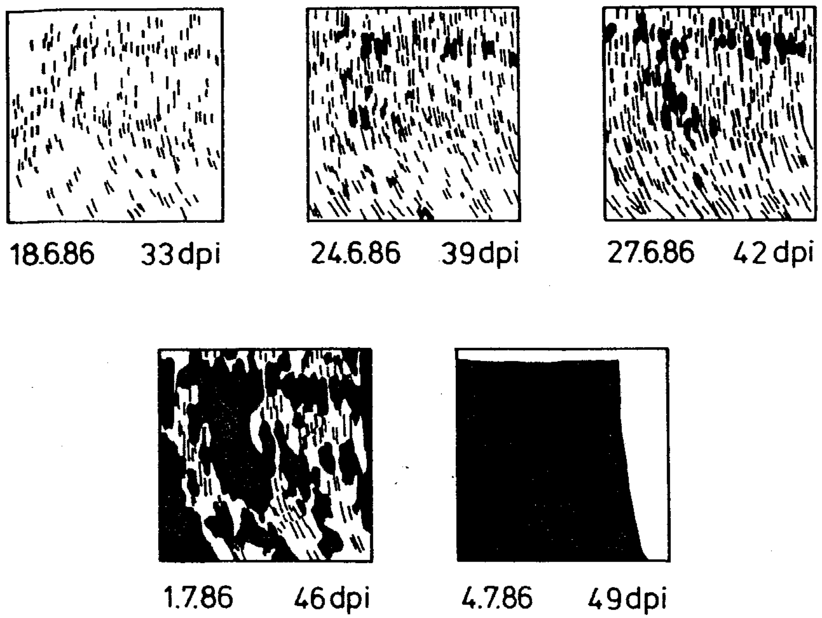


Fig. 26: Symptom development in a 5 x 5 cm² square on the left edge of a banana leaf (Valery) aft natural inoculation (16.05.86) with Mycosphaerella fijiensis. *On 04.07.86, marked area hı shrunk to 72% of its original size.*
black: lesions
dpi: days after inoculation
(Position of square on leaf: cf. Fig. 22 B1; values for symptoms: cf. Table 27)

7. STUDIES OF SPORE RELEASE AND PRODUCTION

7.1 Ascospore and conidiospore release

From July 1984 to February 1986, spore release was recorded in the San Pablo and Semillero plantain plantations, part of the time by means of several spore traps. Due to operating problems (cf. Chap. 3.4), the evaluation of the spores trapped during the first 6 months was limited.

A marked relation between rain and ascospore dispersal was already obvious without statistical evaluation (Fig. 27). An increased release of ascospores could be demonstrated during the hour when it actually rained or directly afterwards. Over the 48 hours before the 3 days depicted in Fig. 27, it had not rained. After such a long interval without rain, ascospores were also released just before 07:00 hours, without it having rained. This release was caused only by dew wetting the leaf surface. During the night of 12.01.86, very high ascospore concentrations were recorded immediately after the first rainfall of merely 1.6 mm. During the hours after rainfall, ascospore release decreased rapidly. Rainfall just before mid-day on 13.01.86 did not lead to such large amounts of ascospores being released again. This did not occur again until the heavy rainfall at 18:00 hours. During the following hours it rained continuously. Ascospore release sank to low values and, during the course of 14.01.86, it finally stopped. This pattern was typical and was observed repeatedly throughout the study period. The number of released ascospores diminished when it rained at short intervals. Apparently, the fungus required a period of about 24 h for new spores to mature. These results are consistent with the observations made by Meredith *et al.* (1973) in Hawaii. These also revealed an increase in the ascospore concentration shortly after rainfall, and only a few ascospores were found during longer periods with high rainfall.

The number of hours with a given amount of rainfall and a marked increase in the concentration of ascospores (more than 30 ascospores per cubic meter of air: >30 m^{-3}) was calculated, in order to determine the minimum amount of rainfall necessary to induce ascospore release. This occurred already with the smallest amount of rainfall (0.1 mm h^{-1}), as shown in Fig. 28. Rainfall can, therefore, always induce ascospore release if mature perithecia are present.

A complete annual cycle of the daily rainfall and ascospore release from one drier season to the next (January 1985 to February 1986) is depicted in Fig. 29. During the drier periods in January and March 1985, almost no ascospore release was recorded. The ascospores trapped at intervals of 6-13 days increased with a rising tendency (February, April and May 1985), only when rainfall was somewhat higher and more regular. This pattern was no longer observed after the two periods with higher rainfall in June. During the rainy period from the end of June to mid-January, ascospore concentrations were high. Almost every fall of rain led to a high ascospore release. The amount of released ascospores decreased again from mid-January onwards.

The highest ascospore concentration per cubic meter of air (6876 m^{-3}) per day was recorded on 26.12.85. The highest ascospore concentration per month (17 595 m^{-3}) was also recorded in December. Meredith *et al.* (1973) also found the highest daily ascospore concentrations during the rainy seasons in Hawaii and Fiji. They recorded the highest daily ascospore concentration (3597 m^{-3}) in Hawaii in December. They counted the highest monthly amount (33 461 m^{-3}) in November. In Fiji, comparable values were 3438 m^{-3} in March and 21 312 m^{-3} air in January.

Some interesting conclusions can be made, when the times of symptom development, ascospore release and two striking mass appearances of first symptoms (speck, streak) are considered. These mass infections were observed twice, on 04.05.85 and again on 22.06.85 (cf. Chap. 6.1).

The latent period of the first symptoms (speck, streak) in May was between 24 and 26 days. Therefore, the mass appearance of symptoms on 04.05.85 was probably caused by the high

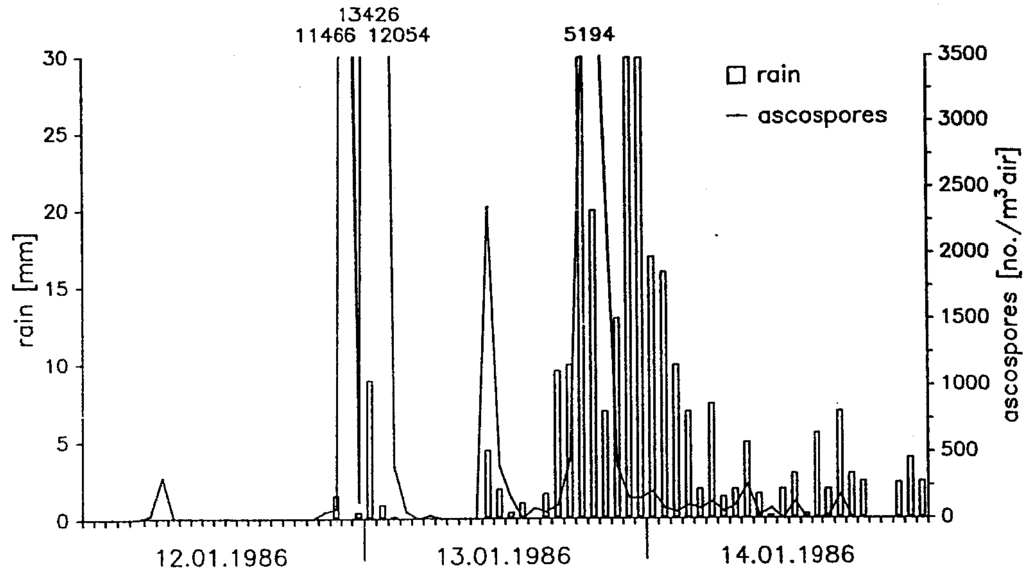


Fig. 27: Hourly release of ascospores of the Mycosphaerella fijiensis/M. musicola *type (height of spore trap 4.65 m) and rainfall in a False Horn plantain plantation on 3 days from 0 to 24 h respectively in January 1986 at Waldeck (Semillero), Costa Rica.*

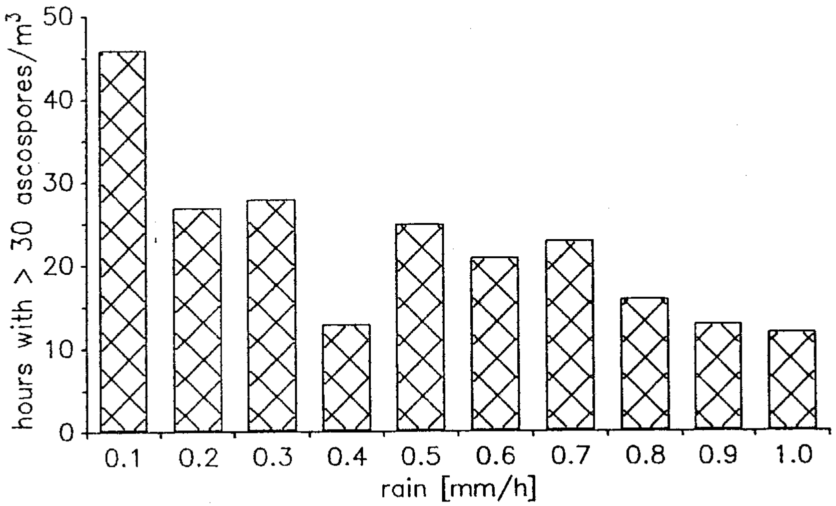


Fig. 28: Number of hours with more than 30 ascospores per cubic meter of air of the Mycosphaerella fijiensis/M. musicola *type and different amounts of rainfall per hour (January 85 - February 86).*

peak of ascospore release on 08.04.85 (25 days previously). This peak had the highest ascospore concentration after a longer period with low rainfall and almost no ascospore release (Fig. 29). In June, the latent period of the first symptoms was 23-24 days. There had been a high ascospore release 23 days before the mass appearance of the symptoms (22.06.85). This was probably responsible for the mass appearance of these symptoms.

The development period of spots with a dry center, i.e. the stage during which perithecia are formed, was between 49.3 and 55.7 days in May and between 44.7 and 54.1 days in June. It is, therefore, possible that the ascospores of 31.05.85 (Fig. 29) were released from spots with a dry center. These were the result of the ascospore maximum of 08.04.85 (53 days previously).

The sequence of these events could thus be as follows: the ascospore peak on 08.04.85 led to a mass appearance of specks and streaks on 04.05.85. These symptoms developed into spots with a dry center which themselves again led to an ascospore maximum on 31.05.85. This second maximum again led to a mass appearance of symptoms on 22.06.85.

Further ascospore maxima were recorded during this period. A mass appearance of symptoms resulting from these maxima was not observed, or was perhaps just not noticed because it was not very visible. The height of the peaks increased continuously during this time. The development cycles of the fungus overlapped in time and had a promotive effect on one another during the transition period between the drier and the rainy season. This finally led to a constant release of large amounts of ascospores in July and the following months. From June onwards, these phenomena led to a steep increase in the area of the leaf infected by the disease, and a lower number (i.e. younger) of the youngest leaves with symptoms (cf. Chap. 8). The time which the fungus required to cover a given area of the leaf lessened considerably from May to July. This development was also favored by the time of symptom development, which decreased from May to August. In August, the development period for spots with a dry center was only 34 days.

The annual cycle becomes more marked, when the daily values of the ascospore release are summarized as weekly totals (Fig. 30). Only small amounts of ascospores were released in the period of lower rainfall from January to the end of May 1985. After a small peak at the end of May, a steep increase followed at the end of June. Ascospore release remained high with a few exceptions until the end of October. In the second half of October and in November, ascospore values sank with a minimum at the end of October/beginning of November. This was exactly 1 month after 2 very dry weeks (end of September/beginning of October). This period of 1 month corresponds approximately with the development time of spots with a dry center (34 days). The drought at the end of September, therefore, affected the ascospore production with a delay of 4 weeks. After that, ascospore numbers increased again considerably, and from mid-January there was again a marked decrease. The numbers of conidiospores registered were about 100 times lower than those of the ascospores. They were somewhat higher from May to November than during the other months. However, the amounts were not remarkable (Fig. 30). These low concentrations indicate that the conidiospores play only a secondary part in the spread of *M. fijiensis*.

Another factor that should be taken into consideration for ascospore production is the temperature. During the season of low ascospore production (January to June 1985, Fig. 29), the daily minimum temperatures were below 20°C (January to April 1985, cf. Figs. 8 and 10). Furthermore, the weekly totals of hours with temperatures below 20°C were high in the same period, i.e. there were many cool hours (cf. Fig. 9). These low temperatures coincide exactly with the hours of dew precipitation, which are required for spore germination.

Thus the low temperatures inhibited the spore germination and could have inhibited as well the fungus development inside the leaf. Stover (1983b) showed that temperatures below 20°C inhibited the germ tube growth of *M. fijiensis*.

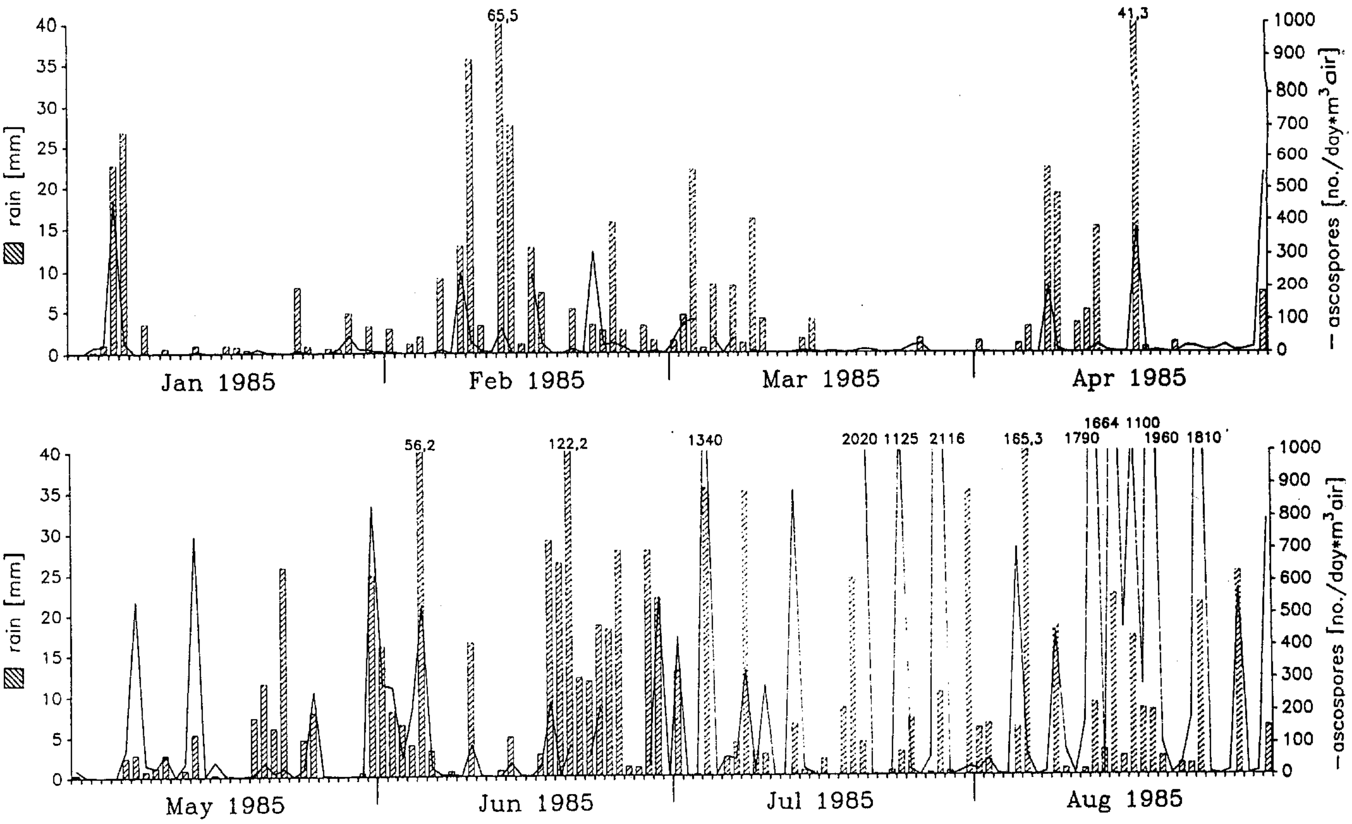


Fig. 29: Daily release of ascospores of the Mycosphaerella fijiensis/M. musicola *type (height of spore trap 4.65 m) and rainfall in a False Horn plantain plantation at Waldeck (Semillero), Costa Rica.*

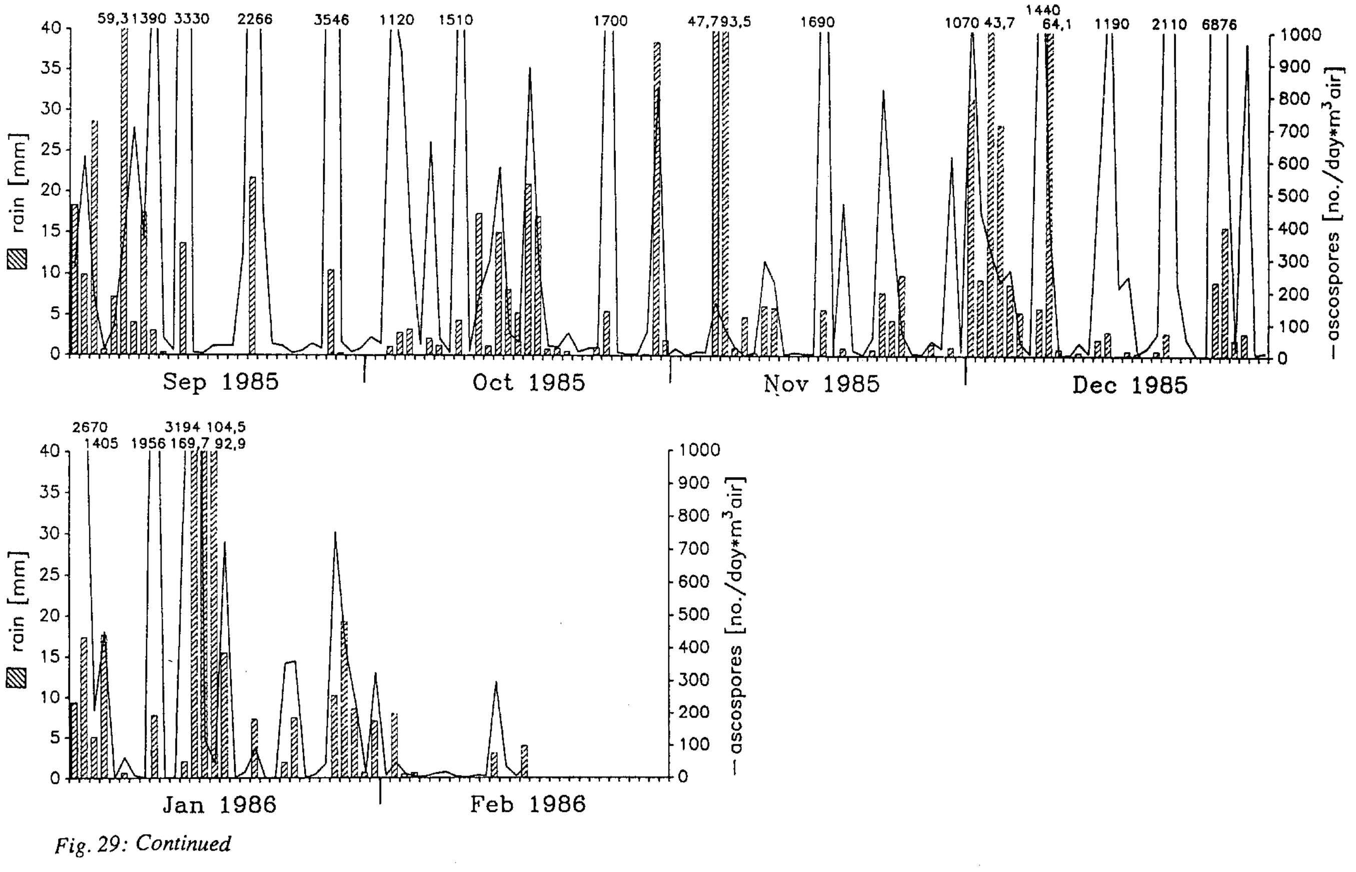


Fig. 29: Continued

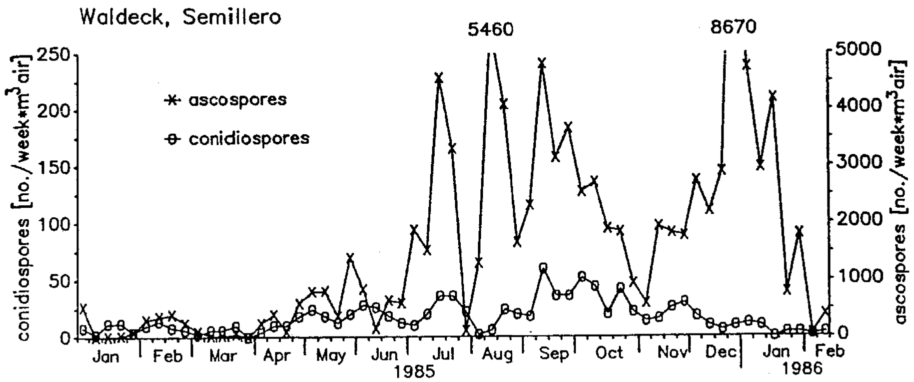


Fig. 30: Weekly release of ascospores of the Mycosphaerella fijiensis/M. musicola *type and conidiospores of* M. fijiensis *in a False Horn plantain plantation at Waldeck (Semillero), Costa Rica.*

At the end of June 1985 ascospores were released in large amounts, exactly 2 months after an increase of the temperatures. This period of 2 months corresponds with the development time of spots with a dry center (44.7 to 54.1 days in June). From November onwards, the temperatures decreased again and were unfavorable for the fungus. However, the highest ascospore concentrations were registered in December 1985. Possibly the effect of the lower temperatures did not influence ascospore production before January 1986.

Why was the number of conidiospores trapped so low? Was perhaps the reason the position (height 4.65 m) of the spore trap? In order to investigate whether the conidiospore concentration in the plantation was higher in the lower layers of air than in the foliage, part of the time two spore traps at a height of 1 m and 4.65 m were operated together. From these samples, only a period of barely a month could be evaluated (Fig. 31). As both these traps were installed in the San Pablo plantation, which was regularly treated with fungicides against black Sigatoka (Tables 4 and 5), the values obtained here cannot be directly compared with those already discussed.

As Fig. 31 A shows, ascospore concentrations in the air were the same at both heights. In contrast, on some days the number of conidiospores (Fig. 31 B) were noticeably higher at the height of 1 m than at 4.65 m. The maximum concentration of the conidiospores was, however, only about one-tenth of the highest ascospore concentration. These results, too, indicate that the conidiospores are only of secondary importance for the propagation and spread of *Mycosphaerella fijiensis.*

On days without rainfall, ascospore release (*M. fijiensis/M. musicola* type) and conidiospore release (*M. fijiensis*) showed a diurnal periodicity (Fig. 32). The clearly marked peak of ascospore release was recorded at 07:00 hours (Fig. 32 A), after the hours with the lowest temperatures and the highest dew, but before the wind had risen. Ascospore counting on 411 days showed that no ascospores could be observed in the morning if it had rained during the first half of the night of the day before. Meredith *et al.* (1973) are the only authors who have up to now published results of spore trapping of *M. fijiensis* on Hawaii. These authors also observed a diurnal periodicity. However, they had already recorded an increase in ascospore concentrations from 18:00 hours onwards after the beginning of dewfall, with a maximum at 06:00 hours.

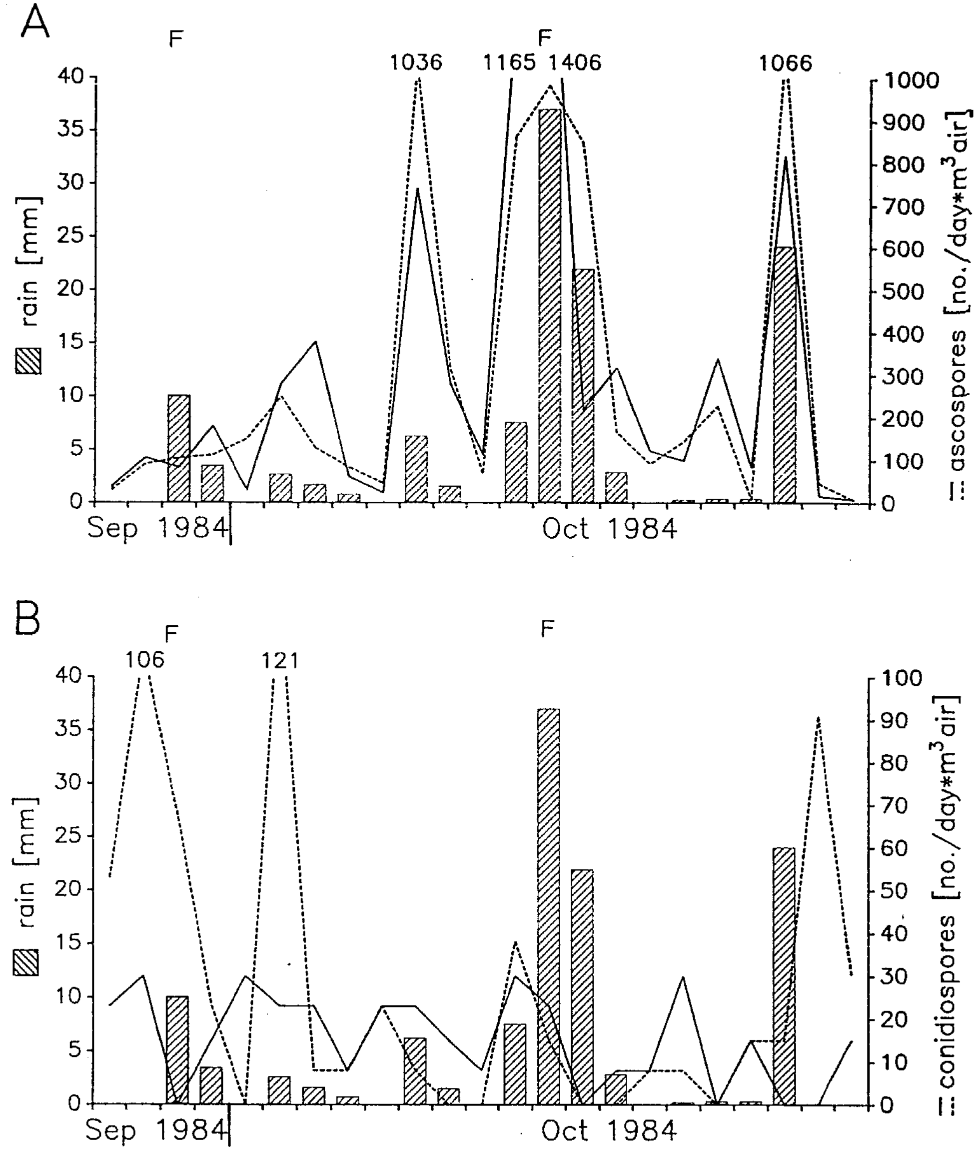


Fig. 31 Release of ascospores (A) of the Mycosphaerella fijiensis/M. musicola *type, conidiospores (B) of* M. fijiensis *at two heights and rainfall in a False Horn plantain plantation at Waldeck (San Pablo), Costa Rica.*
- - - - 1.0 m above ground
—— 4.65 m above ground
F = fungicide treatment (cf. Tables 4 and 5)

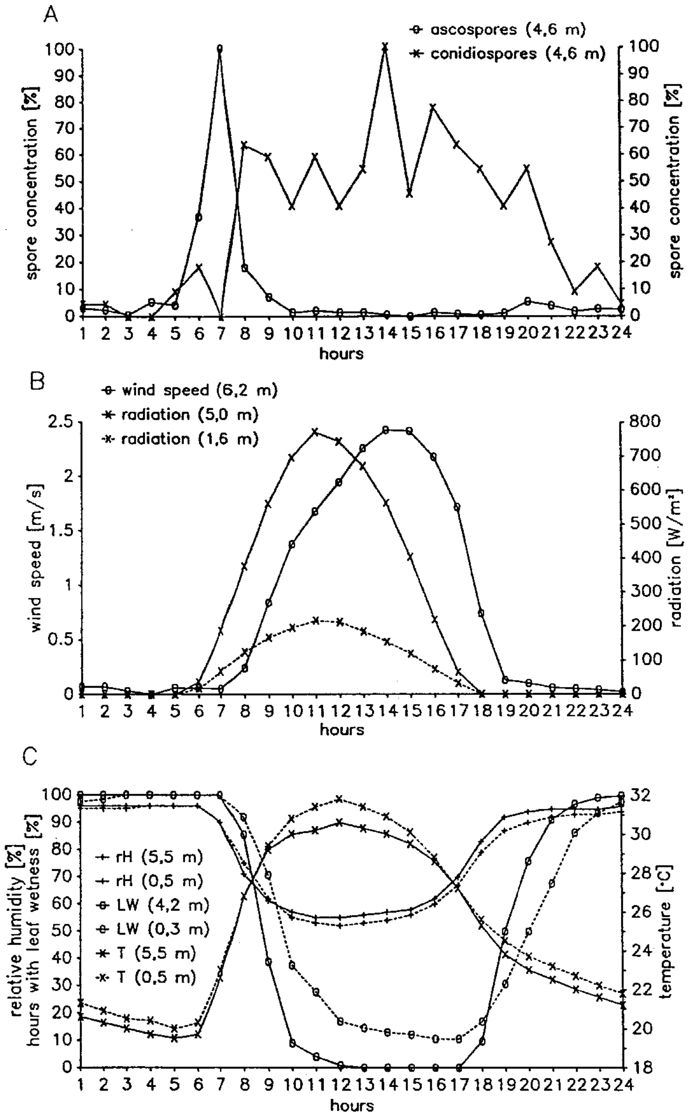


Fig. 32: Average values of spore concentration and weather on 141 rainless days in a False Horn plantain plantation at Waldeck (Semillero), Costa Rica.
A: Relative ascospore and conidiospore concentration; depicted as a percentage of the maximum of the average concentration values (ascospore = 64.2; conidiospore = 4.3)
B: Wind velocity and radiation above and below the foliage
C: Relative humidity (rH), number of hours with leaf wetness (LW) and temperature (T) above and below the foliage
----- above foliage
- - - below foliage

On days without rainfall, conidiospores, however, were recorded only after the wind had risen (Figs. 32 A, B). Then radiation, temperature, humidity and leaf wetness changed; these were also subject to a diurnal periodicity (Figs. 32 B, C). The conidiospore concentration was, however, about 15 times lower than that of the ascospore.

These relations between spore release and weather were also confirmed by statistical calculations. There was a highly significant correlation between ascospore release and rainfall, not only for the whole study period but also for each individual month (Table 28). For the whole period, significant correlations were also found with the temperature and humidity at different heights as well as with the leaf wetness at the height of 4.2 m. This relation becomes clear when one considers that, during rainfall, temperatures diminish and humidity increases. The upper leaf wetness sensor was wetted by the rain earlier than the one below, so that these values are also correlated. However, only the correlation with the rain can be termed a causal one. Ascospore and conidiospore release were completely independent of one another.

As regards conidiospore release, correlations were significant throughout the whole period with all meteorological parameters except rain (Table 29). These correlations could be determined for a large number of months. As conidiospore release changed according to the time of day, it correlated with all factors that are also subject to diurnal periodicity. The most important causal correlation was the one with the wind (significantly positive), but a cause for some of the other correlations cannot be excluded, either, e.g. for leaf wetness. There is a negative correlation between the number of hours of leaf wetness and conidiospore release. It is probable that a conidiospore is released more easily when the leaf has dried and there is no film of water on it any more. Generally, conidiospore release was significantly correlated with all weather factors subject to a diurnal periodicity. There were significant positive correlations with radiation and temperature and negative correlations with relative humidity and leaf wetness.

Banana farmers in the lowlands of Costa Rica have been concerned that inoculum was constantly carried by the wind from the highlands to the lowlands because, in the highlands, coffee and banana are cultivated together in large areas but are not treated with fungicides. However, the wind measurements in the lowlands proved exactly the contrary, because throughout the whole year the wind blows from the lowlands in the direction of the highlands. Furthermore, in Costa Rica black Sigatoka was found only up to 900 m above sea level, where it appeared together with yellow Sigatoka on the same leaf (Romero and Gauhl 1988). Higher up, even 6 years after black Sigatoka had appeared in Costa Rica, only yellow Sigatoka was found, whereas in the lowland areas this disease had been completely displaced by black Sigatoka.

7.2 Ascospore production by spots with a dry center

The age of the lesions on the marked leaves was known (cf. Chap 6.1). As the hanging leaves had not been removed from the plants, samples from leaves (and lesions) of different ages could be taken from one plant at the same time. Sampling took place twice in the drier season and once in the rainy season. The samples taken in March 1985 show ascospore production by lesions up to an age of 12 weeks (Table 30); due to the kind of experiment, there were no older leaves on the plants at this time. In contrast, in February/March 1986 the lesions were up to 20 weeks old. Ascospore amounts worth mentioning were, however, counted only up to the age of 12 weeks; after that only very small amounts were occasionally counted. The samples taken on 01.03.86 are an exception: on this day, it had rained heavily before sampling, all mature perithecia had emptied in the field and no more ascospores were to be found. In all other cases, it had not rained for at least 30 h before sampling. In August 1985, in the middle of the rainy season, an ascospore production by lesions was observed up to 21 weeks after the formation of the lesions. Ascospore production was mostly higher on the lower side of the leaf, but occasionally on the upper side. As the dead leaves are always left on the plants in typical plantations grown by peasant farmers, there is always a source of inoculum here, from which ascospores are released when dew forms and rain falls.

The experiment in March/April 1985 (Table 31), where the leaves were cut off and spread on the ground, was somewhat different. Here, samples of different ages were taken successively from the same leaves. Here, too, it had not rained for at least 30 h before sampling.

Large amounts of ascospores were found here only up to the 3rd week, and after that only small amounts. It was irrelevant whether the upper side of the leaf was upwards or downwards. The differences between the amounts of spores from the upper and lower side of the same leaf were also negligible. In the 10th week samples could no longer be taken, as the leaf tissue had already disintegrated (in the rainy season, decomposition of the leaves probably occurs even more rapidly).

As sampling was possible only a few times during the different seasons, no generally valid statements can be made about whether ascospore production takes place longer in the rainy than in the drier season. However, these experiments show quite clearly that, by regularly cutting off the old leaves which have died as a result of the disease, the inoculum can be greatly reduced in peasant farmers' plantations, too. Inoculum is also probably reduced by the only slight movement of air near the ground: the ascospores released from cut off leaves do not reach the leaves on the plants, especially if, in addition, the ground is covered by vegetation.

Table 28: Correlation coefficient (r) between ascospore release of the *Mycosphaerella fijiensis/M. musicola* type, meteorological factors at different heights above ground and conidiospore release of *M. fijiensis* (hourly values).

Month	No. (n)	Rain-fall	Wind speed	Radiation (1.6 m)	Radiation (5.0 m)	Temperature (0.5 m)	Temperature (5.5 m)	Rel.humidity (0.5 m)	Rel.humidity (5.5. m)	Leaf wetness (0.3 m)	Leaf wetness (4.2 m)	Conidio-spores
all	6014	0.1982***	0.0528*	-0.0364	-0.0412	-0.0482*	-0.0476*	0.0694**	0.0585**	0.0428	0.0577**	0.0034
Jan-85	119	0.4776***	-0.0388	-0.0249	-0.0619	-0.1009	-0.1065	0.1722	0.1340	0.1701	0.1366	-0.0056
Feb-85	508	0.1353***	0.0255	-0.0591	-0.0584	-0.0495	-0.0579	0.0754	0.0748	-0.0096	0.0676	0.0269
Mar-85	652	0.3810***	0.0459	-0.0023	-0.0432	-0.0879*	-0.0898*	0.1314**	0.1238**	0.1319***	0.1273**	0.1431***
Apr-85	400	0.4269***	0.0222	-0.0505	-0.0487	-0.0440	-0.0475	0.0719	0.0645	0.0568	0.0602	-0.0101
May-85	638	0.4966***	0.0408	-0.0436	-0.0456	-0.0442	-0.0348	0.0690	0.0697	-0.0298	0.0311	-0.0184
Jun-85	510	0.4522***	0.1178**	-0.0324	-0.0415	-0.0428	0.0001	0.0608	0.0645	0.0715	0.0939*	0.0066
Jul-85	630	0.3066***	0.1085*	-0.0651	-0.0665	-0.0807*	-0.0771	0.0933*	0.0796	0.0403	0.0561	0.0822*
Aug-85	528	0.1890***	0.0836	-0.0501	-0.0576	-0.0483	-0.0587	0.0748	0.0768	0.0739	0.0857*	-0.0215
Sep-85	713	0.1811***	---------	---------	---------	---------	---------	---------	---------	---------	---------	-0.0311
Oct-85	438	0.2703***	0.0775	0.0114	0.0055	-0.0030	-0.0070	0.0613	0.0701	0.0696	0.0841	-0.0394
Nov-85	407	0.2831***	0.0202	-0.0104	-0.0364	-0.0382	-0.0338	0.0790	0.0749	0.0912	0.0976	-0.0045
Dec-85	698	0.2145***	0.0811*	-0.0444	-0.0458	-0.0490	-0.0571	0.0709	0.0735	0.0360	0.0549	-0.0144
Jan-86	386	0.1487**	0.0439	-0.0797	-0.0678	-0.0581	-0.0588	0.0810	0.0960	0.0522	0.1117*	0.0552
Feb-86	333	0.7427***	---------	---------	---------	---------	---------	---------	---------	---------	---------	-0.0177

* Significant at $P \leq 5\%$. ** Significant at $P \leq 1\%$.*** Significant at $P \leq 0.1\%$.

Table 29: Correlation coefficient (r) between conidiospore release of *Mycosphaerella fijiensis* and meteorological factors at different heights above ground (hourly values).

Month	No. (n)	Rain-fall	Wind-speed	Radiation (1.6 m)	Radiation (5.0 m)	Temperature (0.5 m)	Temperature (5.5 m)	Rel.humidity (0.5 m)	Rel.humidity (5.5 m)	Leaf wetness (0.3 m)	Leaf wetness (4.2 m)
all	6014	0.0077	0.1029***	0.0999***	0.0919***	0.1283***	0.1267***	-0.1082***	-0.1083***	-0.0738***	-0.1089***
Jan-85	119	-0.0189	-0.0039	0.5869***	0.1215	0.0793	0.1096	-0.0501	-0.0883	0.0770	0.0618
Feb-85	508	0.1106*	0.1321**	0.1014*	0.1108**	0.1176**	0.1078*	-0.0939*	-0.0928*	-0.0437	-0.0599
Mar-85	652	0.1430***	0.0901*	0.0006	0.0065	0.0568	0.0459	-0.0481	-0.0227	-0.1054**	-0.1083**
Apr-85	400	-0.0292	0.0543	0.0929	0.1374**	0.1191*	0.1338**	-0.1312**	-0.1436**	-0.1231*	-0.1072*
May-85	638	0.0661	0.1597***	0.1469***	0.1632***	0.1803***	0.1765***	-0.1888***	-0.1800***	-0.1786***	-0.1998***
Jun-85	510	0.0114	0.1384**	0.1786***	0.1830***	0.1954***	0.1894***	-0.1760***	-0.1672***	-0.0926*	-0.1026*
Jul-85	630	0.0079	0.1930***	0.1796***	0.2103***	0.2195***	0.2215***	-0.2166***	-0.2175***	-0.0701	-0.1715***
Aug-85	528	-0.0123	0.1621***	0.0889*	0.1235**	0.1387**	0.1560***	-0.1560***	-0.1493***	-0.1582***	-0.0465
Sep-85	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------
Oct-85	438	0.0154	0.0751	0.1285**	0.0897	0.1616***	0.1716***	-0.1381**	-0.1261**	-0.1048*	-0.1846***
Nov-85	407	0.0491	0.0766	0.0057	-0.0128	0.0437	0.0418	-0.0251	-0.0150	-0.0557	-0.0810
Dec-85	698	-0.0251	0.0730	-0.0003	-0.0099	0.0609	0.0600	-0.0611	-0.0484	0.0213	-0.0702
Jan-86	386	-0.0347	0.0897	0.1290**	0.1244*	0.1176*	0.1184*	-0.1205*	-0.1012*	-0.1498**	-0.0931
Feb-86	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------	----------

* significantat $P \leq 5\%$. ** significant at $P \leq 1\%$. *** significant at $P \leq 0,1\%$.

Table 30: Ascospore production of *Mycosphaerella fijiensis* by spots with a dry center of different ages on hanging False Horn plantain leaves.

Sample date	Last rain before sampling date	Last rain before sampling amount (mm)	Side of leaf	Age of lesions in weeks 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
06.03.1985	05.03.1985	8.4	US*	0	-	-	-	++	++	++	++++	+	+	+++	+	-	-	-	-	-	-	-	-	-
			LS*	0	-	-	-	+++	++	+	+++	+	+	+++	+	-	-	-	-	-	-	-	-	-
13.03.1985	10.031985	4.2	US	-	+	-	-	++++	++++	++	-	++	+++	+	0	-	-	-	-	-	-	-	-	-
			LS	-	++	-	-	++++	++++	++	-	++++	+++	+	+	-	-	-	-	-	-	-	-	-
05.08.1985	02.08.1985	6.4	US	0	0	+++	++	++++	+	+++	+	-	-	0	+	0	+	+++	++	-	-	+	+++	+
			LS	++	++++	++++	++	++++	+++	++	0	-	-	+	+	++++	++++	+++	+	-	-	0	+++	+
21.02.1986	18.02.1986	1.5	US	-	-	-	-	+++	+++	++	+++	-	++++	++++	0	-	0	+	-	-	0	0	0	-
			LS	-	-	-	-	++++	++	++++	+++	-	++++	++++	++	-	0	0	-	-	0	+	0	-
01.03.1986	01.03.1986	22.5	US	-	0	0	0	-	-	0	0	-	0	0	0	0	0	0	-	-	0	0	0	-
			LS	-	0	0	0	-	-	0	0	-	0	0	0	0	0	0	-	-	0	0	0	-

Description of symbols:

-	no values available	
0	no spores	(0-5)
+	very few spores	(6-100)
++	few spores	(101-250)
+++	many spores	(251-500)
++++	very many spores	(more than 500).

* US = upper side; LS = lower side.

Table 31: Ascospore production of *Mycosphaerella fijiensis* by spots with a dry center of different ages from False Horn plantain leaves lying on the ground. First sample (age 1 week): 11.03.85; last sample (age 9 weeks): 30.04.85.

Position of leaf on the ground	Side of leaf	Age of lesions in weeks									
		1	2	3	4	5	6	7	8	9	10
Upper side upwards	US*	.	+++	+++	+	.	++	.	+	0	Leaf rotted
	LS*	.	++++	++++	+	.	+	.	++	+	Leaf rotted
Upper side downwards	US	.	++	+++	0	.	+	.	0	+	Leaf rotted
	LS	.	+++	++++	+	.	+	.	+	+	Leaf rotted

Description of symbols:

.	no values available	
0	no spores	(0-5)
+	very few spores	(6-100)
++	few spores	(101-250)
+++	many spores	(251-500)
++++	very many spores	(more than 500).

* US = upper side; LS = lower side.

8. COMPARATIVE STUDIES ON BLACK SIGATOKA INFECTION IN FOUR PLANTAIN AND BANANA PLANTATIONS

The most important differences between the three sites at Estrada, Semillero and San Pablo are briefly described here once more. The soil conditions at the three sites differed greatly (cf. Chap. 2). The plantain evaluated from the site at Semillero grew on soils with impeded drainage (cf. Fig. 2). The other sites had no such soil problems. Furthermore, the plantain and banana at San Pablo were both treated regularly with fungicides; the application intervals on the banana plantation were shorter (Tables 2 and 3). The different length of the curves in Figs. 33-48 is due to the different duration of the data-collection periods in the various plantations and age stages. The weather, however, was similar at all sites and only slight differences were recorded (cf. Chap.4).

8.1 Number of leaves and leaf area with symptoms per plant

Leaf numbers and leaf area per plant

Leaf numbers of the plantain showed an annual periodicity caused by the weather at all three sites and at all three age stages (before flowering (0 w); 6 weeks after flowering (6 w); 11 weeks after flowering (11 w); Figs. 33 and 34 A). Until June/July 1985, leaf numbers increased. The highest numbers were recorded in June, at the end of the warmer period when rainfall was lower. From August/September onwards, numbers decreased again. The plantain had the lowest leaf numbers during the rainy and cooler months of November and December. In San Pablo the leaf numbers of the plantain were always higher than in the two other sites. In Estrada, the values of the two advanced age stages (6 w, 11 w) were higher than those recorded in Semillero. The numbers during the stage before flowering were more or less the same in both plantations.

In San Pablo, during the stage before flowering, the highest leaf numbers of the plantain were 13.3 leaves/plant, 6 weeks after flowering they were 12.8, and 11 weeks after flowering 11.2. In Estrada, maximum values were 10.6 (0 w), 8.6 (6 w), and 6.4 (11 w), whereas in Semillero they amounted only to 9.7 (0 w), 7.4 (6 w), and 5.1 (11 w) leaves/plant. Minimum values were 9.1 (0 w), 7.6 (6 w), and 4.9 (11 w) in San Pablo, in Estrada 7.5 (0 w), 5.3 (6 w) and 1.7 (11 w), and in Semillero 7.7 (0 w), 4.7 (6 w), and 1.2 (11 w) leaves/plant. In San Pablo, before flowering, the banana had a maximum of 12.3 leaves/plant, 6 weeks after flowering 10.8, and 11 weeks after flowering 9.4. Minimum values were 10.2. (0 w), 8.9 (6 w), and 7.2 (11 w).

In contrast to the plantain, the curves for the banana were more uniform and without marked fluctuations (Fig. 34 B). There were no annual periodical fluctuations. Loss of leaves between flowering and harvest time was always about four, the same as in the case of the plantain undergoing fewer fungicide treatments. Why did the banana show no annual periodicity? Why were the leaf numbers independent of climatic influences?

This phenomenon is easily explained when one regards the management of the plots. The experimental plot was part of a commercial banana plantation and was managed in exactly the same way as the rest of the plantation. This meant that here, too, hanging leaves and leaves heavily infected with Sigatoka were cut off every week ("deshoja", sanitation deleafing). The workers had been told (and were repeatedly told during the study period) only to remove the hanging leaves from the plants in the experimental plot. Nevertheless, they were also often seen removing upright leaves which they felt were too heavily diseased. In addition, the leaves remaining on the plants were well protected against black Sigatoka by the frequent and regular fungicide treatments, so that there were hardly any leaf losses induced by the disease. Thus, leaf numbers remained almost constant and their curves were levelled. This also had an effect on the total leaf area, the diseased leaf area and the infection index.

In Costa Rica, at the end of October 1987 Lehmann-Danzinger (1988) observed plantain before flowering with 8.3-9.5 leaves/plant. At the end of October 1986, plants of the same age in Estrada and Semillero had 8.4 leaves/plant. In San Pablo, the number of leaves on plants before flowering and with fungicide treatment was 11.2. In Estrada, at the beginning of August 1986 shortly before flowering, Pasberg-Gauhl (1989) found False Horn plantain (Curraré) without fungicide treatment with 8.4 leaves/plant, and on plants with fungicide treatment 13.0-15.4 leaves/plant. At the Semillero site on soils with impeded drainage, for October 1986, she also noted 8.4 leaves/plant on those plantain plants not treated with fungicides and 9.2-11.7 leaves on the others. On untreated banana (Valery) she found 9.0 leaves/plant.

The shape of the curves for the total leaf area (Figs. 35 and 36) is similar to that of the leaf numbers (Figs 33 and 34), as the leaf area is calculated using the leaf number and the average leaf size (Table 11). Therefore, the previous discussion applies to the leaf area as well as to the leaf numbers. The leaf areas of the banana leaves were also calculated with the factor for the plantain leaves (0.9).

The plantain in San Pablo could develop a total leaf area of up to 20.0 m^2 (0 w). Six weeks after flowering, the plants still had a maximum of 18.9 m^2 (6 w), and shortly before harvest, a leaf area of 16.8 m^2 (11 w). The highest leaf area values in Estrada were 15.9 m^2 (0 w), 12.9 m^2 (6 w), and 9.6 m^2 (11 w), in Semillero 8.2 m^2 (0 w), 6.2 m^2 (6 w), and 4.3 m^2 (11 w) leaf area. The lowest leaf area values in San Pablo were 13.7 m^2 (0 w), 11.4 m^2 (6 w), and 7.3 m^2 (11 w), in Estrada 11.3 m^2 (0 w), 8.0 m^2 (6 w), and 2.9 m^2 (11 w), and in Semillero 6.5 m^2 (0 w), 4.0 m^2 (6 w), and 1.0 m^2 (11 w).

Leaf area values differed between the three plantain sites more markedly than the leaf number values. Just before flowering, the plants in San Pablo and Estrada had an average size of 1.51 m^2 and were double the size of those in Semillero, where they had an average area of 0.84 m^2 (cf. Table 11). This was undoubtedly due to the unfavorable soil conditions. Whereas, for example, in October 1986 leaf numbers in Estrada and Semillero were the same, there were great differences as regards the total leaf area: in Estrada it amounted to 12.7 m^2, and in Semillero 7.1 m^2. At that time, due to the fungicide treatment, the plants in San Pablo had a considerably larger total leaf area (16.9 m^2).

The banana in San Pablo (Fig. 36 B) had a maximum total leaf area of 18.5 m^2 (0 w), 6 weeks later still 16.2 m^2 (6 w), and shortly before harvest 14.1 m^2 (11 w). The lowest leaf area values for the banana in San Pablo were 15.3 m^2 (0 w), 13.4 m^2 (6 w), and 10.8 m^2 (11 w).

In Estrada, Pasberg-Gauhl (1989) recorded False Horn plantain of the first generation just before flowering with leaf areas of 12.7 m^2 on plants without fungicide treatment and up to 23.1 m^2 on those with. Lassoudière (1977) reports on the cultivar Valery in Côte d'Ivoire having a leaf area of 14.5-18.5 m^2 when flowering. In Honduras, Stover (1982) noted 23.5 m^2 also for Valery, and 16.9 m^2 for Grande Naine.

Leaf area with symptoms

The percentage of leaf area with symptoms for each plant was calculated by adding the maximum percentage of disease severity in the respective class and dividing this value by the number of standing leaves. The leaf area with symptoms in square meter was calculated from the total leaf area and the percentage of leaf area with symptoms. The curves for the leaf area with symptoms in Estrada and Semillero (Fig. 37) were quite different from those in San Pablo (Fig. 38). This was due to the fungicide applications in the plantations in San Pablo (Tables 3 and 4).

In the plantain plantations where no fungicides were applied, the leaf area with symptoms increased greatly from the end of June onwards. This date coincided with the beginning of the rainy season. The curves for the plantain in Estrada and Semillero showed peaks in July/August:

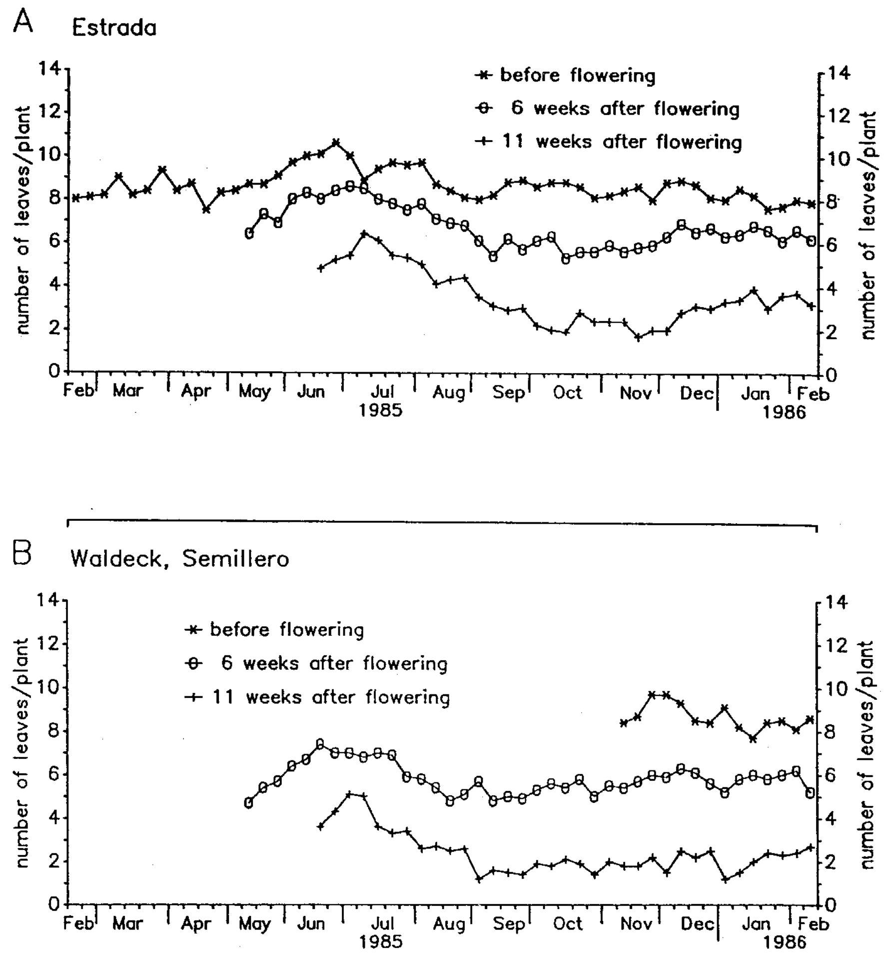


Fig. 33: Number of leaves on False Horn plantain of different ages (n = 10) at Estrada and Semillero, Atlantic lowlands, Costa Rica.

A: sandy loam; minimum management

B: clayey loam with impeded drainage; intensive management

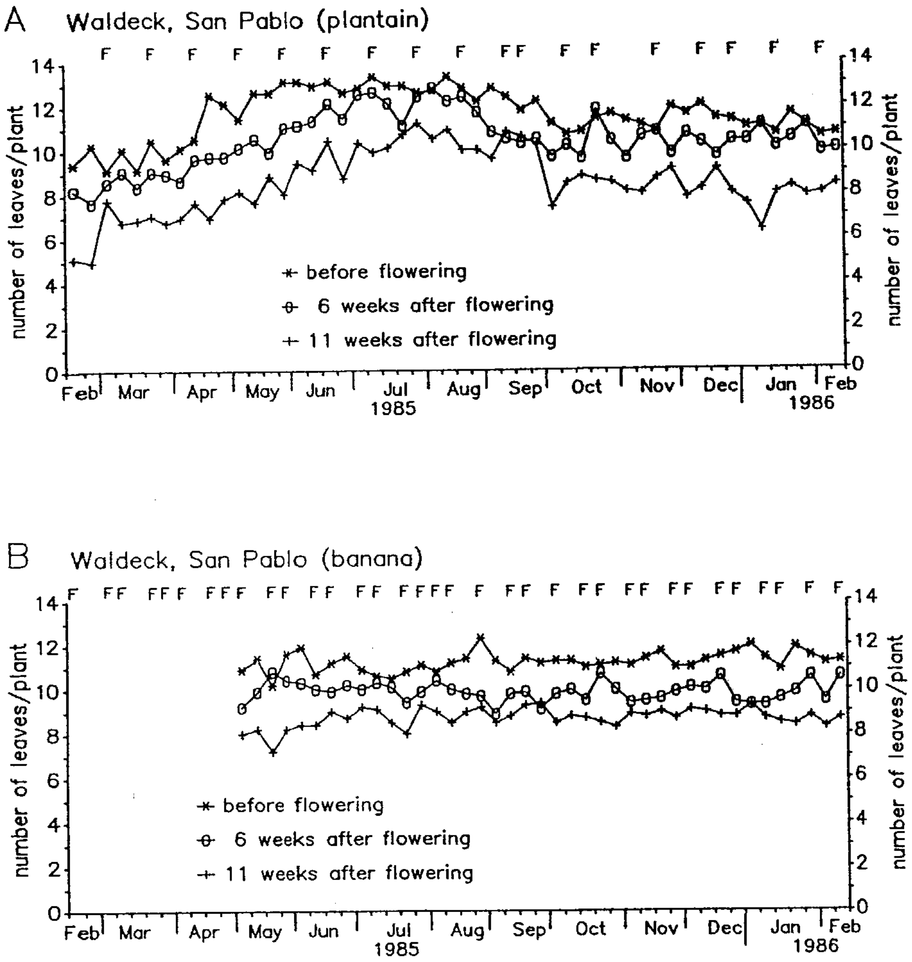


Fig. 34: Number of leaves on False Horn plantain and banana (Valery) of different ages (n = 10) at Waldeck, San Pablo, Atlantic lowlands, Costa Rica

A: Plantain; clayey loam; intensive management
B. Banana; clayey loam; intensive management
F: Fungicide treatment (cf. Tables 3, 4 and 5)

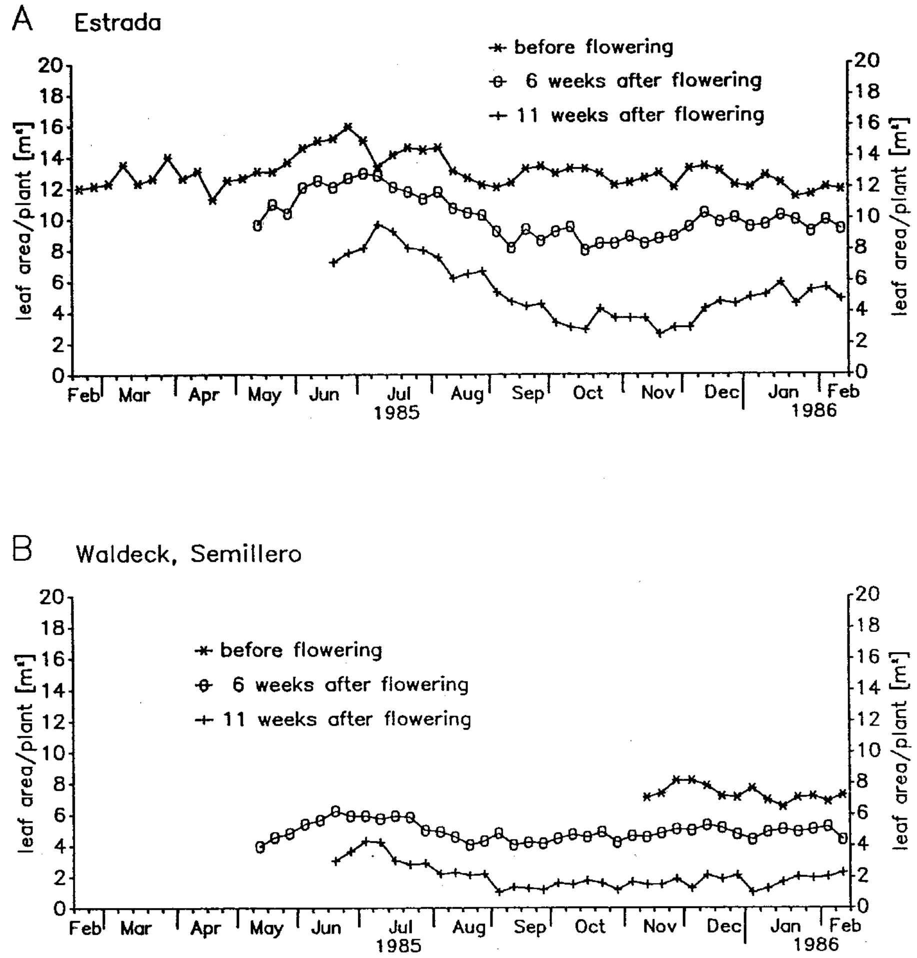


Fig. 35: Total leaf area (m^2) on False Horn plantain of different ages (n = 10) at Estrada and Semillero, Atlantic lowlands, Costa Rica.

A: sandy loam; minimum management
B: clayey loam with impeded drainage; intensive management

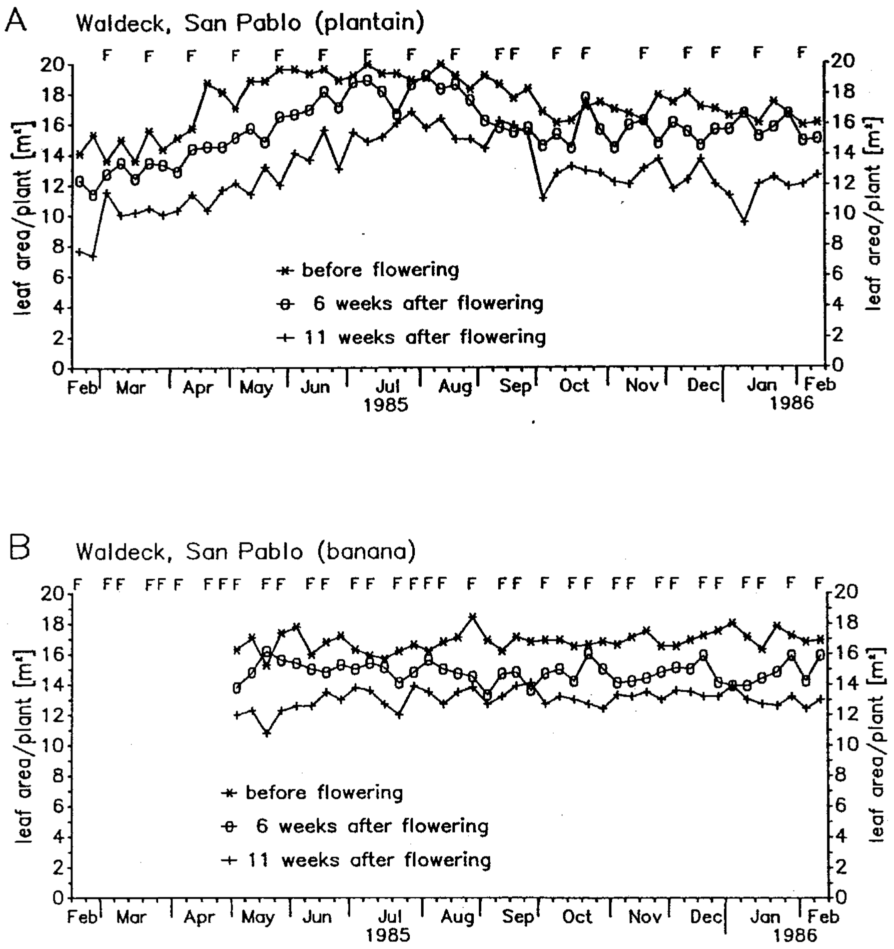


Fig. 36: Total leaf area (m²) on False Horn plantain and banana (Valery) of different ages (n = 10) at Waldeck, San Pablo, Atlantic lowlands, Costa Rica.

A: Plantain; clayey loam; intensive management
B. Banana; clayey loam; intensive management
F: Fungicide treatment (cf. Tables 3, 4 and 5)

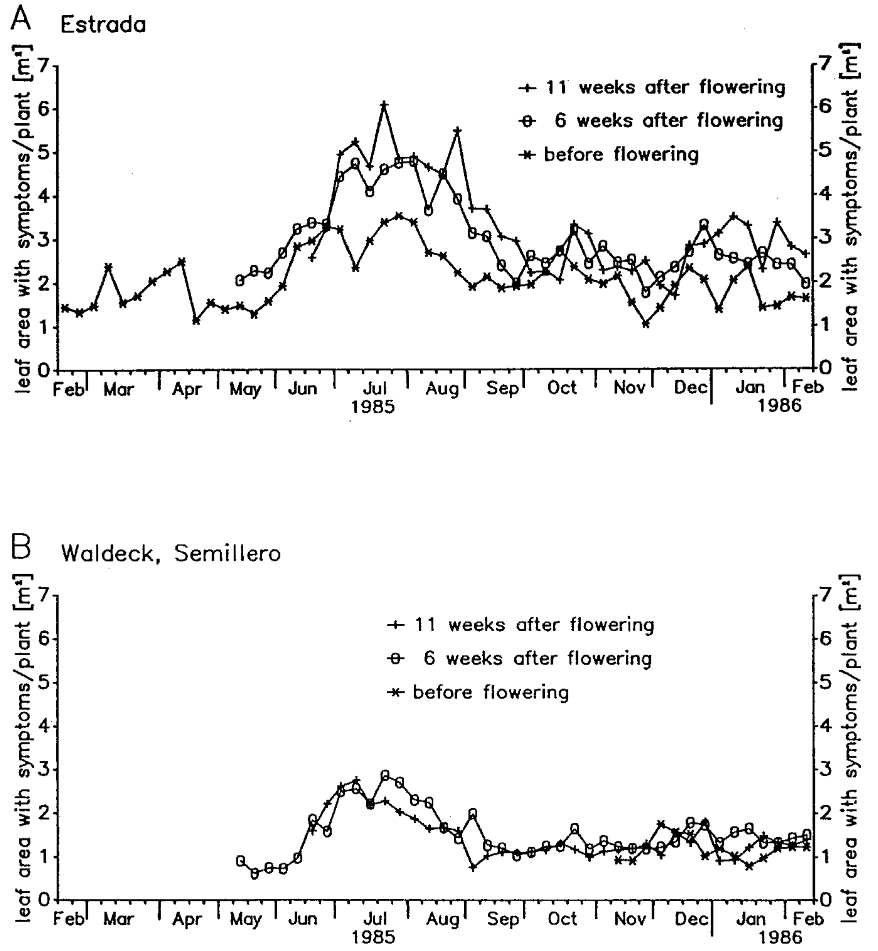
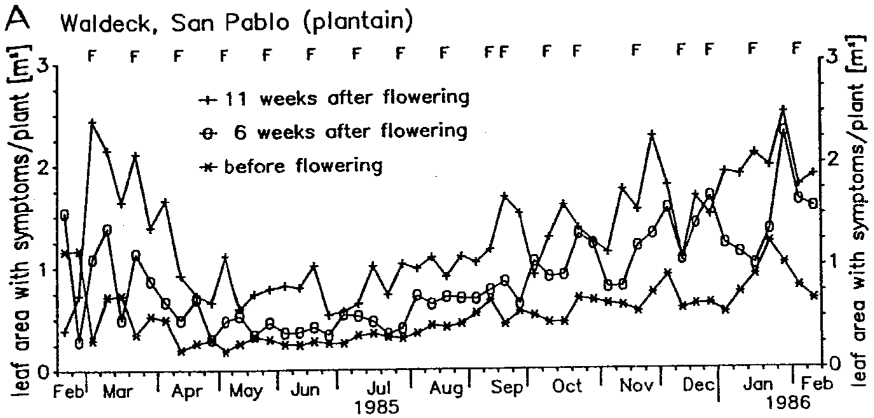


Fig. 37: Leaf area with symptoms (m²) of False Horn plantain of different ages (n = 10) at Estrada and Semillero, Atlantic lowlands, Costa Rica.

A: sandy loam; minimum management
B: clayey loam with impeded drainage; intensive management



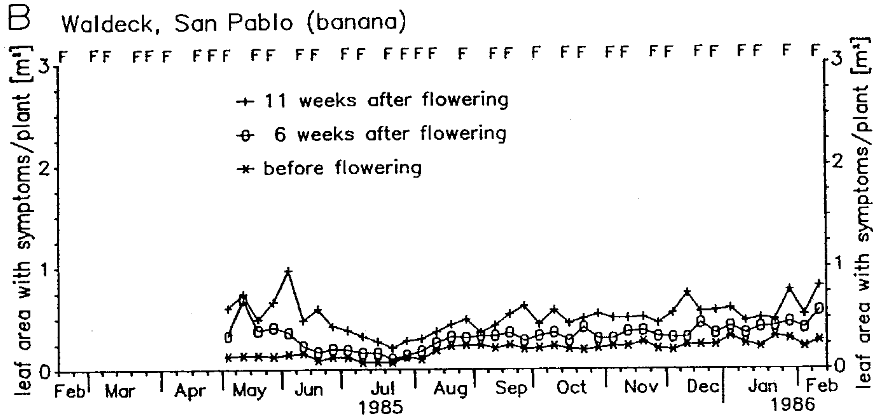


Fig. 38: Leaf area with symptoms (m^2) on False Horn plantain and banana (Valery) of different ages (n = 10) at Waldeck, San Pablo, Atlantic lowlands, Costa Rica.

A: Plantain; clayey loam; intensive management
B. Banana; clayey loam; intensive management
F: Fungicide treatment (cf. Tables 3, 4 and 5)

in Estrada 3.5 m^2 (0 w), 4.8 m^2 (6 w) and 6.1 m^2 (11 w) leaf area with symptoms, and in Semillero 1.7 m^2 (0 w), 2.9 m^2 (6 w), and 2.8 m^2 (11 w). The least values of the leaf area affected by the disease were 1.0 m^2 (0 w), 1.8 m^2 (6 w) and 1.7 m^2 (11 w) in Estrada, and 0.8 m^2 (0 w), 0.6 m^2 (6 w) and 0.8 m^2 (11 w) in Semillero.

In both plantations in San Pablo, the leaf area with symptoms was smaller than in Estrada and Semillero due to regular fungicide applications (Tables 3 and 4). Here the minima and maxima differed from those of the plantain not treated with fungicides. In the case of the plantain in San Pablo, the values 0.2 m^2 (0 w), 0.3 m^2 (6 w), and 0.5 m^2 (11 w) leaf area with symptoms were lowest in May/June. From August onwards the curves rose again slightly. Both at the beginning and the end of the study period, the leaf area with symptoms was larger, with values up to 1.2 m^2 (0 w), 2.3 m^2 (6 w), and 2.5 m^2 (11 w). In San Pablo, the values for the banana never exceeded 1 m^2. The curves showed a minimum in July with a leaf area with symptoms of 0.1 m^2 (0 w), 0.1 m^2 (6 w), and 0.2 m^2 (11 w). At the beginning and end of the study period the leaf area with symptoms was only slightly larger with values up to 0.3 m^2 (0 w), 0.7 m^2 (6 w), and 1.0 m^2 (11 w). Here, too, the deleafing may also have lowered the values, although the removal of the leaves had less effect here than on leaf numbers and total leaf area.

The curves for the leaf area with symptoms in the four plantations are all very close together and overlap more often than in the previous figures. As at all sites, the various age stages differed only very slightly. One can roughly say that the leaf area with symptoms at a given time of year, independent of the age of the plants, was about the same size. That means that the progressing infection of the younger leaves was in balance with the dying (or, in the case of the banana, cutting off) of the older leaves.

The curves of the percentage of leaf area with symptoms show the differences between the age stages more clearly than those of the absolute leaf area with symptoms (Fig. 39). This was due to the decrease in total leaf area with age, whereas the leaf area with symptoms remained on the same level. In Estrada and Semillero, therefore, the character of the curves changed. Clearly marked maxima and minima were no longer visible and the curves remained on more or less the same level for long periods. In both plantations in San Pablo, the older leaves were protected longer from the disease by the fungicide treatments, so that the percentage of infected leaves increased only slightly with increasing plant age and only a few leaves died (Fig. 40). As leaf numbers and total leaf area at the three age stages differed only to a slight degree, too, with increasing plant age the leaf area with symptoms as a percentage of the total leaf area changed only to a small degree. Thus, the curves for the leaf area with symptoms expressed in square meters were almost the same as those expressed in percentage, as the reference value for the latter changed only a little. The increase of the leaf area with symptoms (m^2 and %) was delayed for about 2 months until August, and after that was greatly reduced.

At the sites in Estrada and Semillero, at the end of June the leaf area with symptoms of those plants not treated with fungicides greatly increased at all age stages. This date coincided with the beginning of the rainy season. During this period, black Sigatoka took much less time to infect a given leaf area. As a result of the conditions which were apparently favorable to black Sigatoka from the end of June onwards, the disease developed more rapidly and was able to cover a larger area of the leaves. In Estrada, the increase of the leaf area with symptoms was not as marked during the stage before flowering (0 w) as it was when the plants were older. This was due to the fact that the plants in the 0 w stage had grown well (maximum leaf number in the 3rd week of June). During this period the plants had grown more quickly than black Sigatoka was able to infect the new leaves. In the stages 6 and 11 weeks after flowering (6 w and 11 w) there no longer was such a "lead", because after flowering no new leaves develop. For this reason, and because the leaves died as fast as new leaves were infected, in the 6 w and 11 w stages the leaf areas with symptoms were of the same size, i.e. the curves overlapped. From September

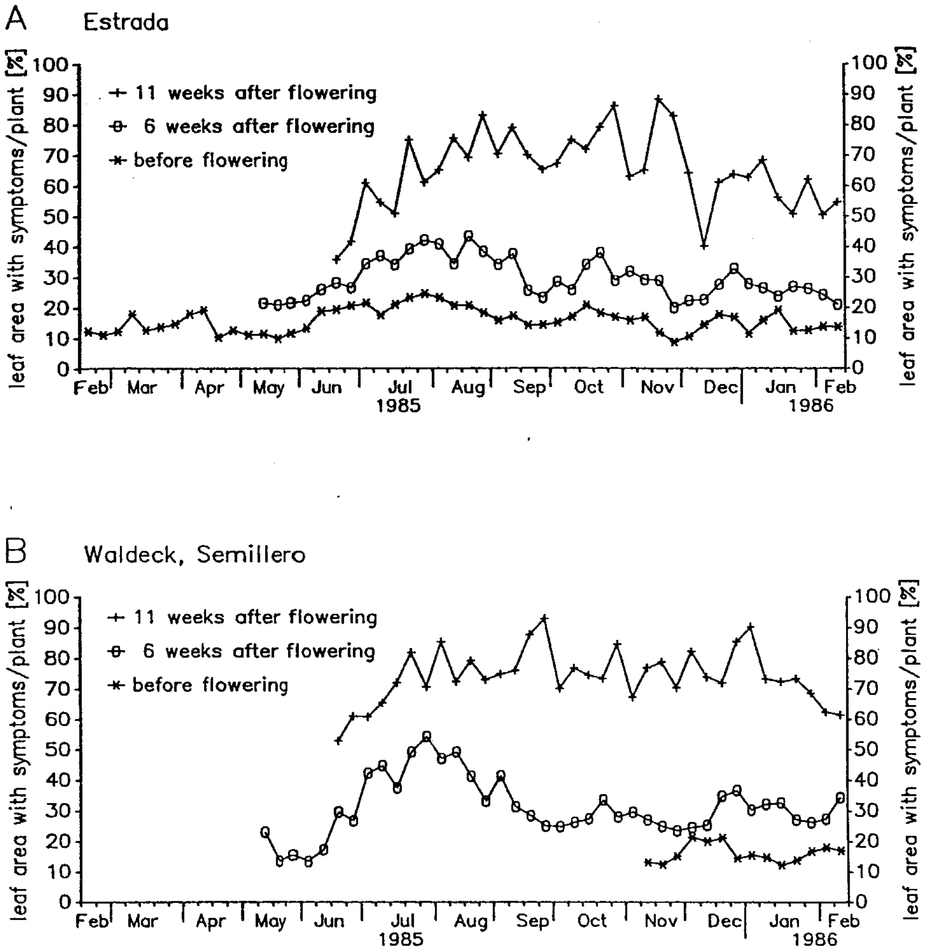


Fig. 39: Percentage of leaf area with symptoms (%) on False Horn plantain of different ages (n = 10) at Estrada and Semillero, Atlantic lowlands, Costa Rica.

A: sandy loam; minimum management

B: clayey loam with impeded drainage; intensive management

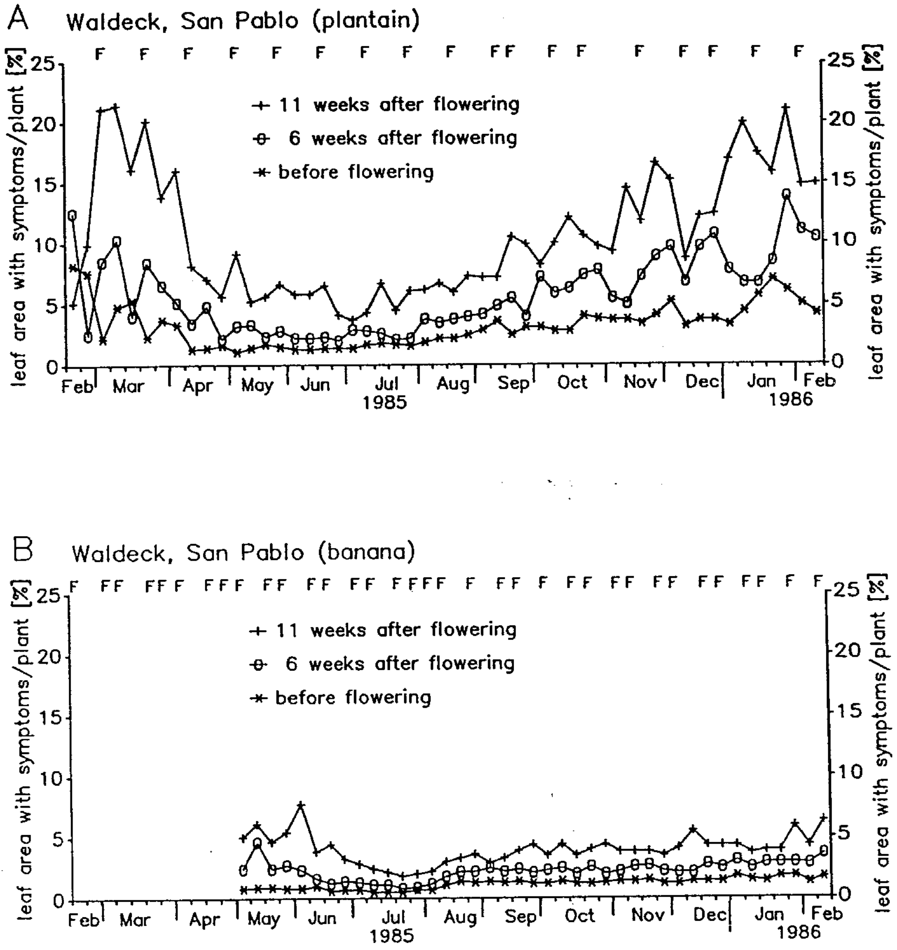


Fig. 40: Percentage of leaf area with symptoms (%) on False Horn plantain and banana (Valery) of different ages (n = 10) at Waldeck, San Pablo, Atlantic lowlands, Costa Rica.

A: Plantain; clayey loam; intensive management

B. Banana; clayey loam; intensive management

F: Fungicide treatment (cf Tables 3, 4 and 5) onwards, the leaf area with symptoms remained about the same at all stages. After 3 months, therefore, the "lead" of the 0 w stage was used up. These 3 months correspond almost exactly to the life-span of a leaf.

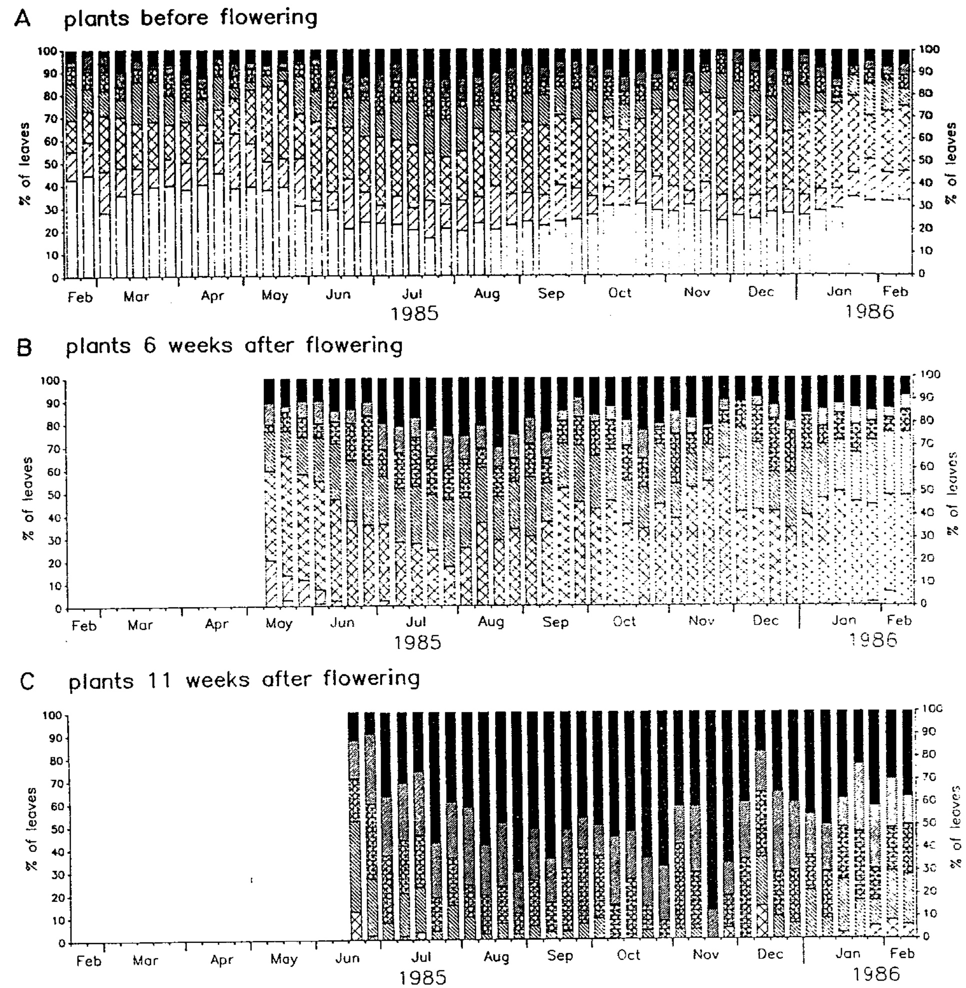
When the balance was reached at the end of September, the last leaves which had developed under the favorable conditions in June, therefore, had died. The same applies to Semillero. However, here the balance was already reached at the end of August, probably due to the poorer plant growth. No statements can be made as to the increase during the 0 w stage here, as no data are available for the period between May and September. In Estrada and Semillero, the leaf area with symptoms as a percentage of the total leaf area naturally increased in June, too. As, however, with increasing age leaves continually died, the leaf area with symptoms as a percentage of the total leaf area rose with increasing plant age. The distribution of the leaves within the disease grades in the different plantations is shown in Figs. 41-44. In Estrada (Fig. 41) the percentage of more heavily infected leaves was very high and showed a peak in July/August. At the highest age stages, however, this maximum was no longer visible as a clearly marked increase of infected leaves; here the heavy infection continued from July to December. The block diagrams representing Semillero (Fig. 42) resemble those of Estrada, as neither sites received fungicides treatment. The percentage of more heavily infected leaves in Semillero was, however, larger.

In San Pablo, the influence of the fungicide applications was very marked at all three age stages of both plantain (Fig. 43) and banana (Fig. 44): here, most of the block diagram referred to the disease grade 0-2. That means that the development of the spotted area was slowed down or even stopped by the fungicides. The percentage of more heavily infected leaves (increasingly darker hatching) was only somewhat higher at the beginning and end of the study period. In July, infection was the lowest at all age stages, and towards August/September infection increased. This increase in infection was especially noticeable at disease grade 2 (1-5%) and was greater during the stages after flowering (Figs. 43 B, C and 44 B, C). These changes occured almost exactly 1 month after the change of weather from drier to rainy in June, and were delayed by the use of fungicides.

When the intensive sanitation deleafing mentioned above is considered, the diagram illustrating the percentage of banana leaves in each disease grade is especially interesting (Fig. 44). Although there were fewer heavily infected leaves due to intensive deleafing, the percentage of leaves in the lower disease grades was not influenced by it.

The percentage of leaves without visible symptoms (disease grade 0%) was slightly higher from May to the end of July. Together with the percentage of leaves in the disease grade 1 (<1%) these differences were most prominent. From May to the end of July there were more healthy leaves, i.e. the conditions for Sigatoka were less favorable. These differences even increased in the higher age stages. In the group 11 weeks after flowering, the decrease in percentage of the only slightly infected leaves in fact shifted to almost the end of August. The leaves that had grown during more favorable periods were, therefore, effectively protected by the fungicides for up to 6-8 weeks. By depicting the values this way (Fig. 44), the annual periodicity, which was also observed in the case of the plantain, becomes visible for the first time in banana. In contrast to the plantain, though, this periodicity was visible only in the lowest grades of the evaluation scale (disease grades 0-2), due to the protective effect of the regular applications of fungicides. This means that, although the fungicides did not prevent infection, they greatly inhibited further development of the disease.

Leaf number and total leaf area increased during the drier season (March/April) until about mid-June. Afterwards, when the rainy season began, leaf numbers and total leaf area decreased once



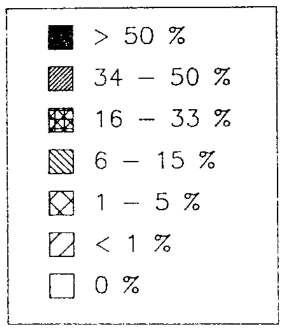
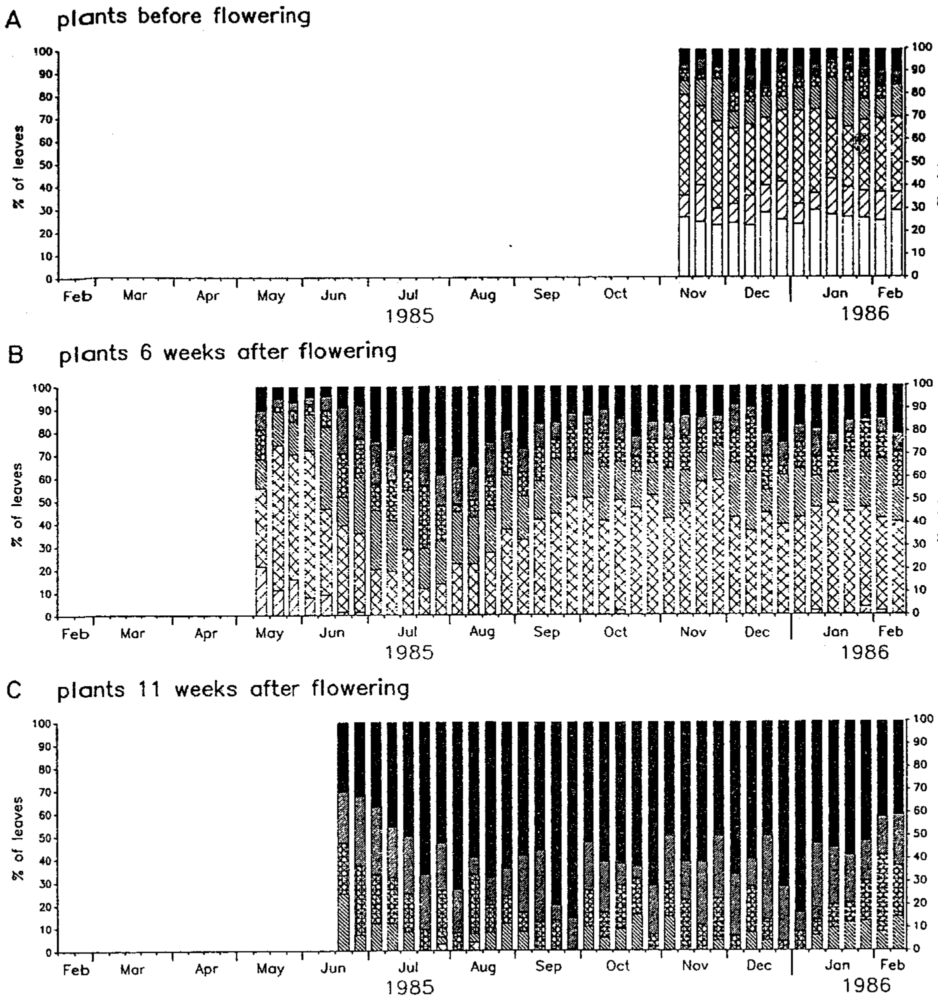


Fig. 41: Percentage of leaves (%) in each disease grade on False Horn plantain of different ages (n = 10) at Estrada, Costa Rica.
A: Plants before flowering
B: Plants 6 weeks after flowering
C: Plants 11 weeks after flowering



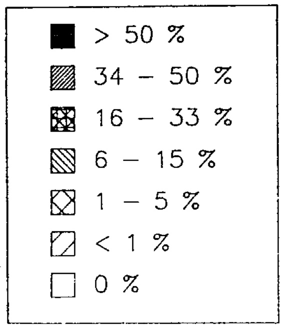
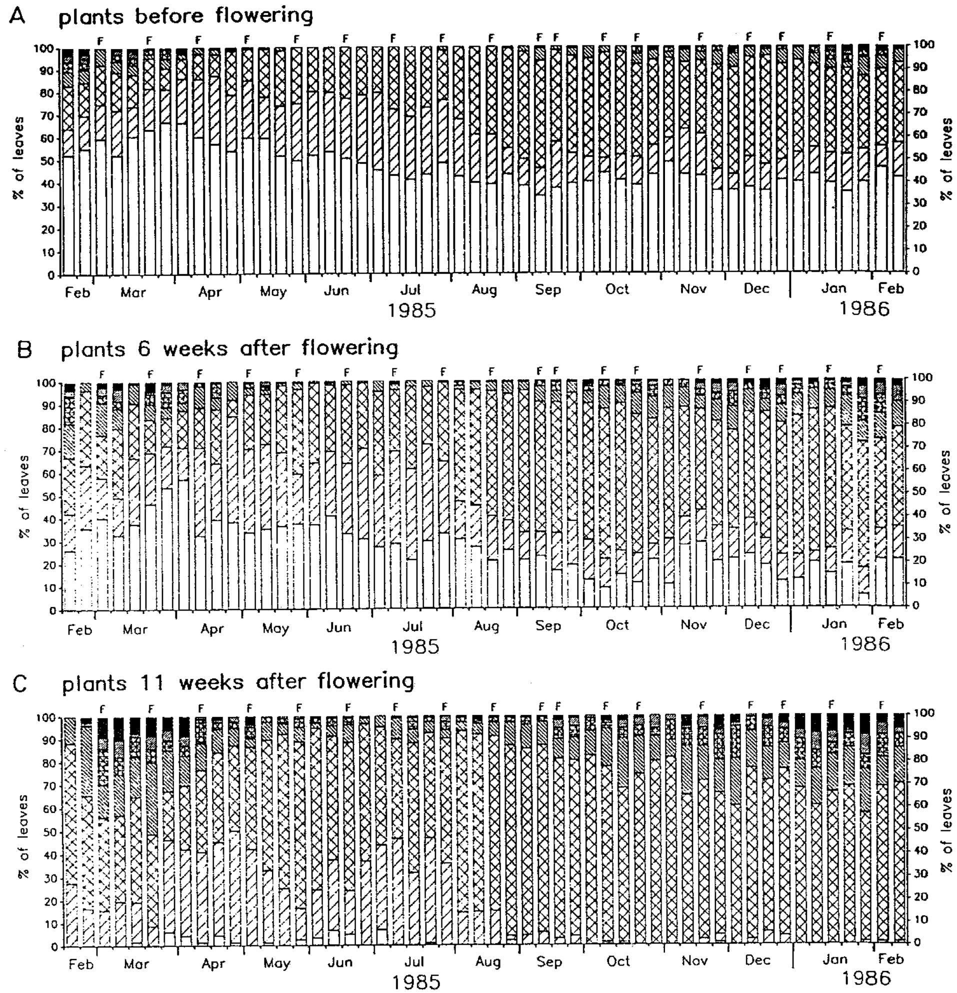


Fig. 42: Percentage of leaves (%) in each disease grade on False Horn plantain of different ages (n = 10); at Waldeck (Semillero), Costa Rica.

A: Plants before flowering
B: Plants 6 weeks after flowering
C: Plants 11 weeks after flowering



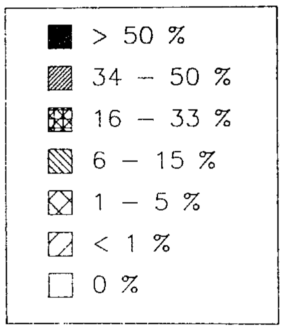
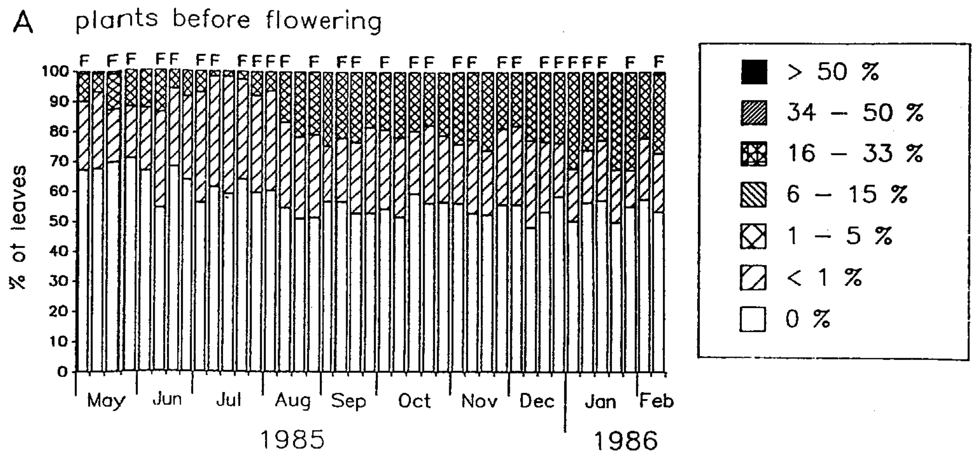
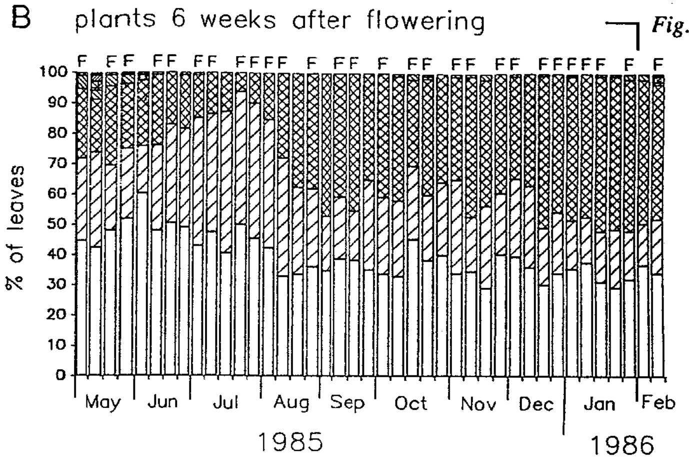


Fig. 43: Percentage of leaves (%) in each disease grade on False Horn plantain of different ages (n = 10) at Waldeck (San Pablo), Costa Rica.

A: Plants before flowering
B: Plants 6 weeks after flowering
C: Plants 11 weeks after flowering
F: Fungicide treatment (cf. Tables 4 and 5)





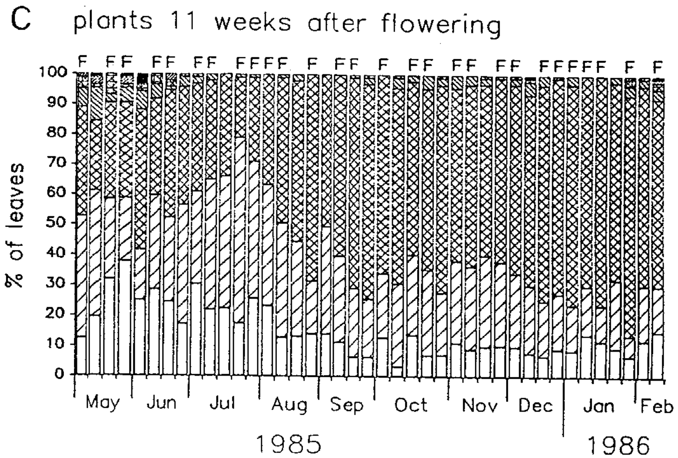


Fig. 44: Percentage of leaves (%) in each disease grade on banana (Valery) of different ages (n = 10) at Waldeck (San Pablo), Costa Rica.
A: Plants before flowering
B: Plants 6 weeks after flowering
C: Plants 11 weeks after flowering
F: Fungicide treatment (cf. Tables 3 and 5)

more. At the same time, the leaf area with symptoms and the percentage of leaf area with symptoms increase. In the case of the percentage of leaves per disease grade, the more heavily infected leaves increased from mid-June, too. These changes occurred in Semillero and Estrada at almost exactly the same time when the weather changed from drier to rainy. In contrast, in San Pablo these changes were delayed, weakened or even suppressed by the fungicides.

8.2 Disease severity index and youngest leaf with symptoms

Disease severity index

As the disease caused the leaves to die prematurely, evaluation always led to an underestimation of the severity of the disease, because the death of leaves was not recorded. In order to illustrate this "total disease severity", Lehmann-Danzinger (1988) suggested an index for the disease severity which would take the premature death of the leaves into account. For the calculation of the indices, the figure for the maximum number of leaves recorded in the study period (cf. Chap. 8.1) was inserted into the formula. These figures thus form the reference values of the best possible stage of development of the plants at each site.

In the case of the plantain, the curves for the severity indices (Figs. 45 and 46 A) closely resemble those of the percentage of the leaf area covered by the disease. They were merely somewhat stretched. The curves of the severity indices in Estrada and Semillero show minima in June and maxima in the more rainy period from September to December (Fig. 45). In Estrada, the minima severity indices were 0.21 (0 w), 0.28 (6 w), and 0.51 (11 w), and in Semillero 0.15 (0 w), 0.25 (6 w), and 0.61 (11 w). The maximum values were 0.38 (0 w), 0.61 (6 w), and 0.94 (11 w) in Estrada and 0.32 (0 w), 0.64 (6 w), and 0.98 (11) in Semillero.

In San Pablo, the lowest severity indices were recorded in the middle of the study period (July/August) and amounted the 0.02 (0 w), 0.04 (6 w), and 0.06 (11 w). Maxima were noted both at the beginning and end of the study period (Fig. 46 A). Here, the highest values were 0.35 (0 w), 0.44 (6 w), and 0.61 (11 w). The fungicide applications had a favorable effect on the "growing off" of the plants before infection during the period when rainfall was low (cf Chap 8.1). Thus, infection was heaviest at the beginning and end of the study period, and lightest in the middle. As in the case of the leaf area with symptoms, the increase in the disease severity index was delayed for about 2 months until the end of August. In comparison with the plantain not treated with fungicides, this increase was much smaller. Here, too, the more favorable growth conditions in the drier period before the end of June had an effect amounting almost to the life-duration of a leaf. The increase in the higher age stages was also small, because the fungicides limited the development of the disease to a leaf area of about 5% (disease grade 2).

As regards the banana, the curves of the severity indices (Fig. 46 B) show a pattern completely different from those discussed up to now. Whereas the curves of the plantain almost never overlap, the curves of the severity indices for the banana overlap completely, and do not show tendencies in any special direction or any differences between the age stages. Like the leaf numbers, the disease severity index was also affected most by the deleafing. Because the reference value — in this case the maximum number of leaves recorded during the study period — was already falsified by the deleafing, the calculation of the severity index offered no useful values. An interpretation of the curves was not possible here. Minimum indices are 0.02 (0 w), 0.04 (6 w), and 0.06 (11 w), maximum 0.35 (0 w), 0.44 (6 w), and 0.61 (11 w).

In the case of the banana in San Pablo, where there was no natural rhythm in the leaf numbers, the severity index no longer offers interpretable values whereas the curves for the proportion of leaf area with symptoms do.

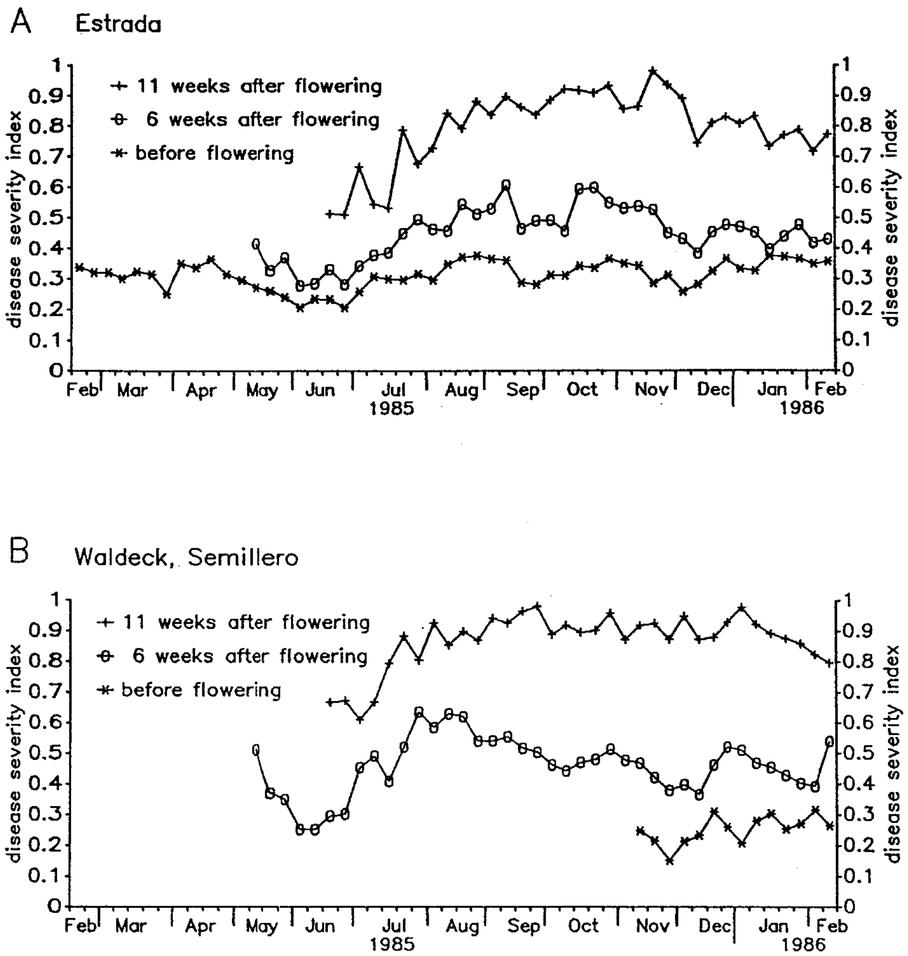


Fig. 45: Disease severity index on False Horn plantain of different ages (n = 10) at Estrada and Semillero, Atlantic lowlands, Costa Rica.

A: Sandy loam; minimum management
B: Clayey loam with impeded drainage; intensive management

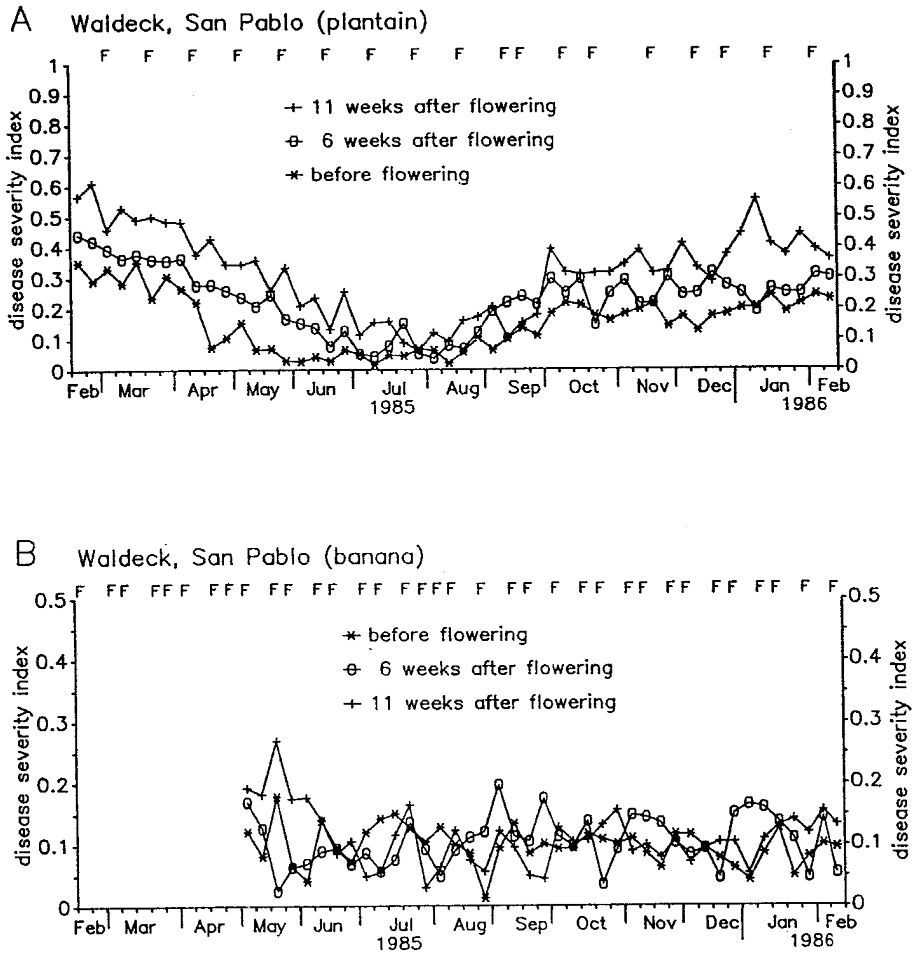


Fig. 46: Disease severity index on False Horn plantain and banana (Valery) of different ages (n = 10) at Waldeck, San Pablo, Atlantic lowlands, Costa Rica.

A: Plantain; clayey loam; intensive management
B: Banana; clayey loam; intensive management
F: Fungicide treatment (cf. Tables 3, 4 and 5)

Youngest leaf with symptoms (YLWS)

Another measure for the severity of the disease which is much easier to apply is the youngest leaf with symptoms (YLWS). This value, reduced by 1, corresponds to the number of healthy leaves. The YLWS is an indirect measure for the infection potential and latent period (Lehmann-Danzinger 1988). In all plantations, these curves show the same pattern (Figs. 47 and 48).

In the case of the plantain, the number of healthy leaves was highest in April/May and decreased again from June to about September/October 1985 (the position of the YLWS moved towards the top of the plant), as a result of the change of weather with more regular rainfall. From then onwards they remained on more or less the same level. However, in all three plantations the curves of the highest age stage (11 w) and the middle age stage (6 w) in Estrada and Semillero showed a more linear trend: apart from a few exceptions all leaves were always diseased here, because, after flowering, the plants develop no new leaves. The values decreased from San Pablo to Estrada to Semillero. In San Pablo, the highest values in the lowest age stage (0 w) were 8.5, in the others 5.9 (6 w), and 1.6 (11 w). In the group before flowering, the maximum in Estrada was 4.7 (0 w), and in Semillero 3.5 (0 w). In October/November (rainy period) the YLWS in Estrada was 3.5 (mean value), and in Semillero (with impeded drainage) 3.2. In October 1987, Lehmann-Danzinger (1988) observed similar differences in Costa Rica regarding Dwarf Horn plantain on soils without impeded drainage (YLWS 4.1) and with impeded drainage (YLWS 3.0). When treated with fungicides, in San Pablo the YLWS attained a value of 5.7.

Whereas the index of the disease severity for the banana did not allow any interpretation, the opposite was valid for the YLWS. This was the only evaluation measure determined in the field that was completely uninfluenced by the deleafing (Fig. 48 B). From the end of May onwards the position of the YLWS moved upwards (which corresponds to a higher infection pressure) as a result of the change of weather with more regular rainfall. From mid-August onwards the curves remained almost horizontal, and the mean YLWS-value before flowering was 7.0. Here, too, the annual periodicity correspond to that of the plantain.

In the case of the banana the number of healthy leaves was also highest in May/June and decreased again in July/August. From September 1985 onwards the number remained about the same. Due to the more intensive fungicide treatment, the curve of the highest age stage (11 w) also never sank to value 1 (= all leaves diseased). The highest values for the banana in the lowest age stage were 9.2 (0 w), in the others 7.2 (6 w), and 4.0 (11 w); the minima 6.4 (0 w); 3.8 (6 w), and 1.5 (11 w).

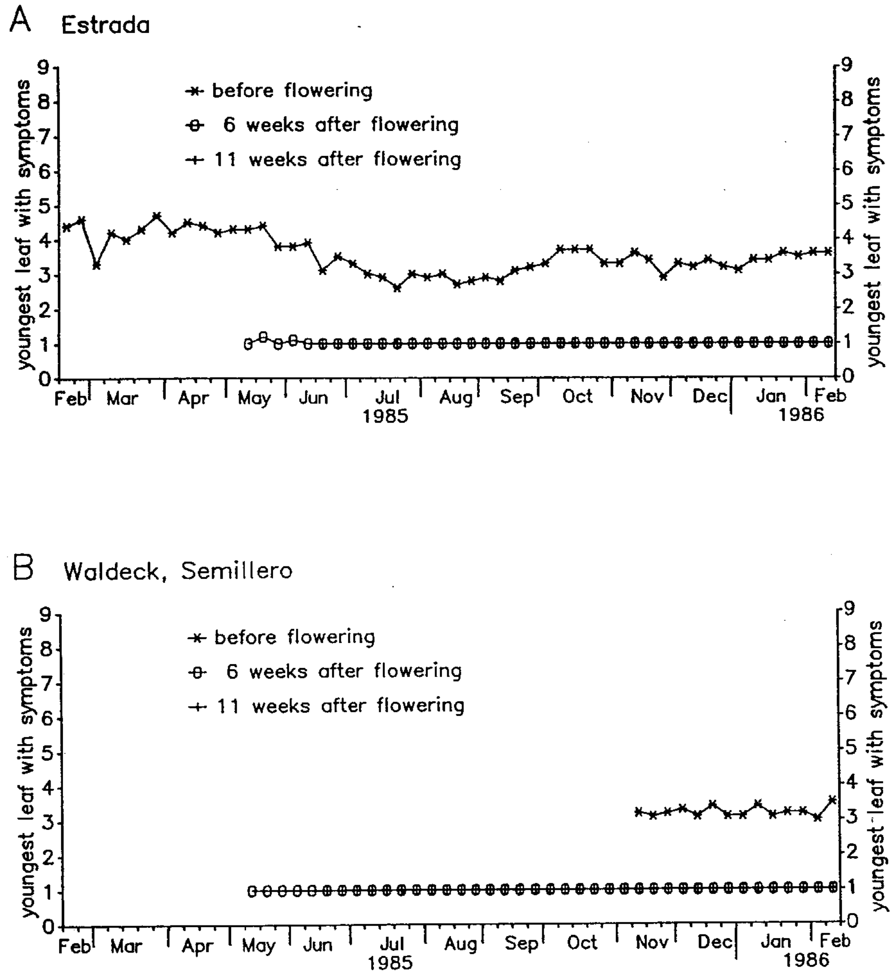
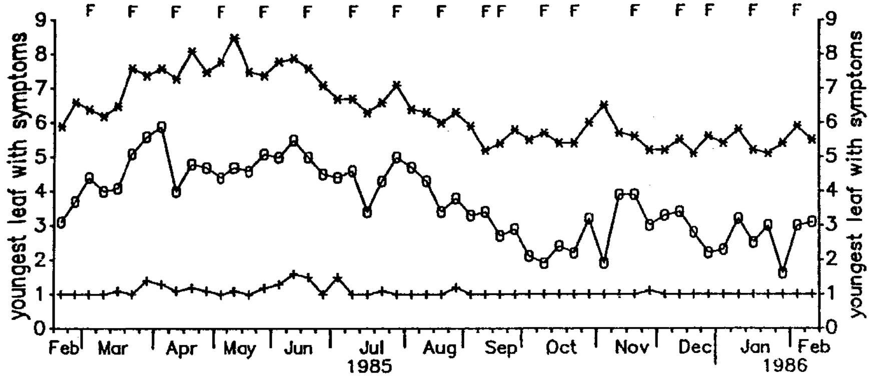


Fig. 47: Youngest leaf with symptoms (YLWS) per plant on False Horn plantain of different ages (n = 10) at Estrada and Semillero, Atlantic lowlands, Costa Rica.

A: Sandy loam; minimum management

B: Clayey loam with impeded drainage; intensive management

A Waldeck, San Pablo (plantain)



B Waldeck, San Pablo (banana)

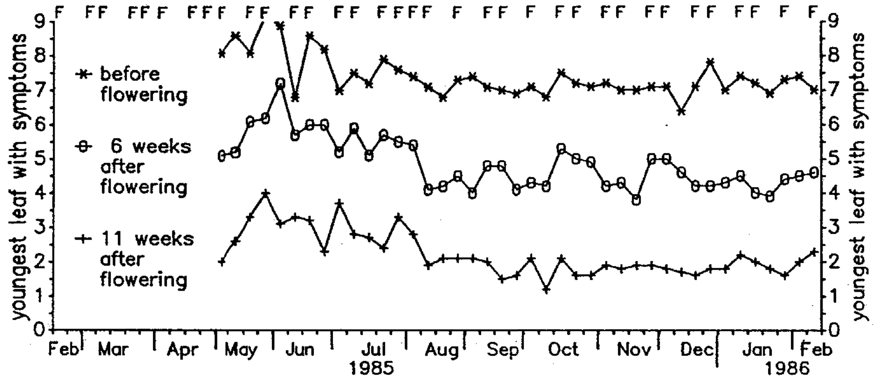


Fig. 48: Youngest leaf with symptoms (YLWS) per plant on False Horn plantain and banana (Valery) of different ages (n = 10) at Waldeck, San Pablo, Atlantic lowlands, Costa Rica.

A: Plantain; clayey loam; intensive management
B: Banana; clayey loam; intensive management
F: Fungicide treatment (cf. Tables 3, 4 and 5)

9. RELATIONS BETWEEN DISEASE DEVELOPMENT, SPORE RELEASE AND WEATHER

The relations between leaf numbers, leaf area with symptoms, youngest leaf with symptoms and spore release values on the one hand, and meteorological data on the other were investigated in correlation analyses. In order to work out more exactly the relation between disease development, spore release and weather, the spore release and disease data were adjusted weekly against the weather data (-1 to -8 weeks). New correlations were calculated for each stage of adjustment. By adjusting the data, the influence of certain weather parameters on the development of black Sigatoka became more obvious, and the relationship with the symptom development could be explained better. The calculations were carried out for the disease data on plantain and banana before flowering (youngest stage: 0 weeks) in Estrada and San Pablo. In Semillero there were too few data available at stage 0 w for such calculations. Naturally, the same correlations were obtained with respect to leaf area, percentage of leaf area with symptoms, or disease severity index calculated as with the above-mentioned original data. Therefore, only the correlations with the original data are noted here.

Regarding the ascospore release, there were significant correlations (Table 32) with rainfall (positive), evaporation (negative), hours with leaf wetness (positive), maximum temperature (negative), minimum temperature (positive) and hours with temperatures <20°C (negative) and <23°C (changing from positive to negative). All these values point to the same relation: a high ascospore release during periods with high rainfall and, therefore, low evaporation, higher minimum temperatures and thus fewer cool hours below 20°C and 23°C. The correlation coefficient of minimum temperatures (positive) on the one hand, and the hours with temperatures <20°C and <23°C (all negative) should always have reciprocal signs.

The relation is as follows: low minimum temperatures inhibit the disease agent, higher favor it (positive correlation). Lower minimum temperatures also mean more hours with cooler temperatures, which inhibit the fungus, too. Here, therefore, the relation is completely vice versa (negative correlation). With respect to the hours with temperatures <23°C, the sign in front of the correlation coefficient changes. At first the correlation coefficients are positive; only the last three (-6 to -8 weeks) have a negative sign as was to be expected: there were fewer ascospores during periods with lower temperatures and, therefore, more hours with cooler temperatures. When these results are regarded on their own, false conclusions can be made. The hours with temperatures <23°C proved to be not as exact with a lower correlation compared with the hours with temperatures <20°C. With the exception of hours with leaf wetness and maximum temperatures, the highest correlation coefficients were to be found with an adjustment of -7 to -8 weeks. The level of the correlation coefficient was at times distinctly higher at -5 to -8 weeks (= 35-56 days). These periods can be easily explained by the development times of spots with a dry center. This is the stage when perithecia are formed. Depending on site conditions, time of year and age of the plant, these development times fluctuated between 34-56 days in the case of the plantain (Chap. 6.1), and 34-51 days in the case of the banana. Pasberg-Gauhl (1989) noted a period of 5.7 ± 1.1 to 6.4 ± 1.0 weeks (= 39.9 ± 7.7 to 44.8 ± 7.0 days) for the development of spots with a dry center on young False Horn plantain (Curraré) and 5.3 ± 0.5 weeks (= 37.1 ± 3.5 days) on banana (Valery). Hours with leaf wetness showed direct influence on the ascospore values (0 week).

For conidiospore release, there were significant correlations (Table 32) only with rainfall (changing from negative to positive), minimum temperature (positive) and hours with temperatures <20°C and <23°C (each negative). As in the case of ascospore release, conidiospore release was reduced when temperatures were lower. The highest correlations here were found when the values were shifted -3 to -4 weeks (21-28 weeks). This is almost the same time the specks (15-29 days) and streaks (19-35 days) require to develop on plantain, depending on site conditions, season and age of the plants (Chap 6.1). On banana leaves, specks developed

Table 32: Correlation coefficients (r) between weather parameters and ascospore release of the *Mycosphaerella fijiensis/M. musicola*-type and conidiospore release of *Mycosphaerella fijiensis*, respectively, at Waldeck (Semillero), Costa Rica (weekly values). Spore release data were correlated with weather parameters, which each had been recorded 0-8 weeks earlier.

Correlated parameters		Number (n)	Weather parameters shifted by: 0 weeks	-1 weeks	-2 weeks	-3 weeks	-4 weeks	-5 weeks	-6 weeks	-7 weeks	-8 weeks
Ascospores	Rain (mm)	51-53	0.1004	0.0406	0.1570	0.0342	0.1360	0.2770*	0.0976	0.3656**	0.3252*
	Evaporation (mL)	51-53	-0.3289*	-0.2857*	-0.4025**	-0.3873**	-0.3807**	-0.4149**	-0.3550**	-0.4564***	-0.4624***
	h leaf wetness	40-42	0.4359**	0.2671	0.2551	0.1632	0.1806	0.3379*	0.1977	0.1376	0.0040
	Maximum temp.	51-53	-0.3999**	-0.2637	-0.2777*	-0.2349	-0.2203	-0.2491	-0.2482	-0.2984*	-0.1086
	Minimum temp.	51-53	0.0461	0.0847	0.1771	0.2646	0.2419	0.2674	0.3587**	0.4326**	0.5104***
	h with T <20°C	48-52	-0.1267	-0.0949	-0.2089	-0.3349*	-0.1889	-0.2297	-0.3184*	-0.3843**	-0.4016**
	h with T <23°C	48-52	0.1531	0.0402	0.1120	0.0381	0.0466	0.0717	-0.0060	-0.0518	-0.2865*
Conidiospores	Rain (mm)	51-53	-0.2289	-0.1027	-0.0597	-0.0157	0.0675	0.3296*	0.0519	0.0356	0.1384
	Evaporation (mL)	51-53	-0.1978	-0.1921	-0.1149	-0.2310	-0.2239	-0.1534	-0.1451	-0.1422	-0.1564
	h leaf wetness	40-42	0.0461	0.1060	-0.0883	-0.2149	-0.1486	-0.1046	0.0913	0.0945	0.0562
	Maximum temp.	51-53	0.1224	0.0605	0.1464	0.1032	0.1206	0.2114	0.0591	-0.0324	-0.0745
	Minimum temp.	51-53	0.4286**	0.4495***	0.3772**	0.5014***	0.4691***	0.4205**	0.3836**	0.3629**	0.2693
	h with T <20°C	48-52	-0.4810***	-0.4527***	-0.4326**	-0.5542***	-0.5807***	-0.4538***	-0.3530*	-0.2451	-0.1011
	h with T <23°C	48-52	-0.4036**	-0.4432***	-0.3803**	-0.4139**	-0.4682***	-0.3880**	-0.1400	-0.1013	0.0419

* Significant at $P \leq 5\%$. ** Significant at $P \leq 1\%$. *** Significant at $P \leq 0.1\%$.

in 24-37 days and streaks in 24-40 days. At this stage, conidiospores were seen under the microscope (Gauhl 1989). This adjustment thus corresponds exactly to the development time of the conidiospores. During the 5th week lower correlation coefficients were observed. This trend increased in the 6th week. When infection took place during hours with temperatures <20°C, fewer conidiospores developed 3-5 weeks later than when infection took place during hours with temperatures <23°C. Rainfall had a direct (0 week) negative influence on the number of conidiospores (they were probably washed out of the air). The significant positive value at -5 weeks is probably also related to the development of the symptoms.

In the plantain plantation in Estrada, the plantation with minimum care and without fungicide treatment, significant correlations (Table 33) were found between leaf number and evaporation (negative), hours with leaf wetness (negative), maximum temperature (positive), minimum temperature (positive), and hours with temperatures <20°C and <23°C (each negative).

Due to water stress, evaporation directly influenced plant growth (significant values only when values were shifted 0 to -1 week). On the other hand the relation "great leaf wetness - fewer leaves" seems at first to be contradictory. This can be explained by the interaction with the disease development: lesser leaf wetness had an inhibiting effect on black Sigatoka, but when the leaves were wetter the disease spread more easily. This led to the leaves dying more quickly and, thus, to a decrease in the number of leaves. Especially during the transition between the spot and the spot with a dry center, large leaf areas died due to the symptoms coalescing. The highest correlations were observed here at -5 to -8 weeks. This exactly corresponded to the transition period from spot to spot with a dry center (34-56 days). The maximum temperature had an effect on just this mechanism, too, but the other way round: when maximum temperatures were high, leaf numbers increased, because development of black Sigatoka was inhibited or leaf development increased. Correlations with minimum temperatures were mostly highly significant, i.e. the influence on plant growth was great (cold = fewer leaves). The values were especially high at the beginning (-1 week) due to direct inhibition of the rate of leaf emission and after -4 to -5 weeks. The latter values are most likely due to the fact that plant growth was not so greatly inhibited by the cold as by the spread of black Sigatoka. The same applies to the hours with temperatures <20°C and <23°C, although this was not quite so marked.

In Australia, Turner (1971) calculated significant increases in the production rate of Williams banana leaves when the mean monthly temperatures, wind velocity and relative humidity rose. With respect to the correlation coefficients, he did not state any limiting values as to their significance, but the relation between leaf production and wind, for example, was very weak.

In the plantain plantation in Estrada, significant correlations (Table 33) were found for the youngest leaf with symptoms with rainfall (negative), evaporation (positive), hours with leaf wetness (negative), maximum temperature (positive), minimum temperature (negative), and hours with temperatures <20°C (positive). These correlations were divided into two groups.

The first group was formed by the hours with leaf wetness and maximum temperatures. Many hours with leaf wetness and low maximum temperatures lead to the youngest leaf with symptoms "becoming younger". As the highest correlations were to be found when the values were not shifted (0 week) and significant correlations were observed up to -4 weeks, these weather parameters had a direct only effect on the infection itself and during a short time afterwards.

The second group was formed by rainfall, evaporation, minimum temperature and hours with temperatures <20°C. Heavy rainfall, resulting in low evaporation and higher minimum temperatures had a favorable effect on the disease and, thus, on the youngest leaf with symptoms. Even evaporation, whose influence was highly significant when values were shifted 0 to -8 weeks, increased markedly after -3 weeks. These 3 weeks corresponded to the

Table 33: Correlation coefficients (r) between weather parameters and leaf number, youngest leaf with symptoms and leaf area with symptoms (m^2), respectively, of False Horn plantain before flowering at Estrada, Costa Rica (weekly values). Leaf numbers and disease data, respectively, were correlated with weather parameters, which each had been recorded 0-8 weeks earlier.

Correlated parameters		Number (n)	Weather parameters shifted by: 0 weeks	-1 weeks	-2 weeks	-3 weeks	-4 weeks	-5 weeks	-6 weeks	-7 weeks	-8 weeks
Leaf number	Rain (mm)	51-53	0.1697	0.0506	-0.0435	-0.1003	0.0017	0.2232	0.1266	0.0576	-0.1489
	Evaporation (mL)	51-53	-0.4102**	-0.3388*	-0.1321	-0.1439	-0.2058	-0.1704	0.0171	0.1174	0.2063
	h leaf wetness	40-42	0.0511	-0.1385	-0.3535*	-0.2846*	-0.2342	-0.3239*	-0.4689**	-0.3600*	-0.3406*
	Maximum temp.	51-53	0.0987	0.1569	0.2594	0.3525**	0.3278*	0.3982**	0.5671***	0.6407***	0.5896***
	Minimum temp.	51-53	0.4610***	0.5493***	0.4714***	0.4665***	0.5529***	0.5296***	0.4580***	0.3605**	0.2106
	h with T <20°C	48-52	-0.3641**	-0.3460*	-0.2481	-0.2987*	-0.3853**	-0.4031**	-0.3553*	-0.2149	-0.1893
	h with T <23°C	48-52	-0.1460	-0.2796*	0.3415*	-0.3575*	-0.3007*	-0.3711**	-0.4211**	-0.4110**	-0.2892*
Youngest leaf with symptoms	Rain (mm)	51-53	-0.2492	-0.1224	-0.2060	-0.3164*	-0.2712*	-0.3593**	-0.2557	-0.2080	-0.2056
	Evaporation (mL)	51-53	0.5908***	0.5499***	0.6223***	0.7540***	0.7184***	0.6229***	0.5646***	0.5239***	0.4808***
	h leaf wetness	40-42	-0.5138***	-0.3764*	-0.3888*	-0.4059**	-0.2756*	-0.1908	-0.1935	0.0062	0.0952
	Maximum temp.	51-53	0.5203***	0.4348**	0.3903**	0.4285**	0.2800*	0.2287	0.0804	0.0876	0.0464
	Minimum temp.	51-53	-0.2536	-0.2103	-0.3274*	-0.5264***	-0.5857***	-0.5615***	-0.6572***	-0.5976***	-0.6102***
	h with T <20°C	48-52	0.2874*	0.2261	0.3598**	0.4972***	0.5966***	0.6003***	0.5020***	0.5325***	0.5060***
	h with T <23°C	48-52	0.1240	-0.0837	-0.0828	-0.0574	0.0973	0.1356	0.2301	0.2551	0.3584*
Leaf area with symptoms (m^2)	Rain (mm)	51-53	0.2859*	0.1422	0.0489	-0.0397	0.0523	0.3126*	0.3137*	0.1906	0.0818
	Evaporation (mL)	51-53	-0.5172***	-0.4975***	-0.2931*	-0.2748*	-0.3942**	-0.5014***	-0.3485*	-0.1994	-0.2196
	h leaf wetness	40-42	0.2133	0.1804	-0.0015	-0.0919	-0.0129	-0.0699	-0.2838	-0.3251*	*0.2067
	Maximum temp.	51-53	-0.2107	-0.1693	-0.0680	0.0616	0.0369	0.0214	0.1548	0.4381**	0.4382**
	Minimum temp.	51-53	0.2898*	0.3898**	0.3131*	0.3344*	0.4493***	0.5488***	0.6213***	0.5222***	0.5034***
	h with T <20°C	48-52	0.3093*	-0.2578	-0.1554	-0.1802	-0.2939*	-0.4298**	-0.4729***	-0.3139*	-0.4270**
	h with T <23°C	48-52	0.0642	-0.0003	-0.0685	-0.0953	-0.1007	-0.1940	-0.3408*	-0.3903**	-0.3377*

* Significant at $P \leq 5\%$. ** Significant at $P \leq 1\%$. *** Significant at $P \leq 0.1\%$.

development time of the first symptoms: specks (15-19 days) and streaks (19-35 days). These weather parameters apparently influenced the development of symptoms, i.e. the development of the fungi in the leaf.

In Estrada, with respect to the leaf area with symptoms, significant correlations were found with all investigated weather parameters (Table 33). However, the correlations between hours with leaf wetness and maximum temperature made no sense. If there had been some influence, it cannot be proved by this method. The other weather parameters showed increased or high correlations after -5 to -6 weeks. Here, too, high rainfall with the resulting low evaporation and higher minimum temperatures had a favorable effect on the leaf area with symptoms. The period of 5-6 weeks corresponds more or less to the transition of streak (19-35 days) to the larger spot (25-56 days) or spot with a dry center (34-56 days). Here, too, symptom development was influenced. At the time 0 week, rainfall and hours with temperatures <20°C showed significant correlation coefficients. Here an effect on the infection and the early stages of the disease is indicated, too.

The results of the investigations on the San Pablo plantations in Waldeck in some cases differ considerably from those of Estrada. This is due to the effect of the fungicide applications (cf. Tables 3, 4 and 5).

As regards the leaf number of plantain in San Pablo, the plantation with intensive care and fungicide treatment, significant correlations (Table 34) were found with the same weather parameters as in Estrada: with evaporation (negative), hours with leaf wetness (negative), maximum temperature (positive), minimum temperature (positive) and hours with temperatures <20°C and <23°C (each negative). In San Pablo, evaporation also had an immediate effect on plant growth as a result of water stress, but for a longer period than in Estrada (0 to -3 weeks). Hours with leaf wetness and maximum temperatures had the same effects on the leaf number as in Estrada. However, maximum correlations are found at -8 weeks, which is a difference of 2-3 weeks due to the fungicide treatment. The correlations with minimum temperatures were always very highly significant. The values were especially high at the beginning (0 to -3 weeks) due to a direct inhibition on the rate of leaf emission. In contrast to the values noted in Estrada, due to the effect of the fungicide the second maximum was after -4 to -5 weeks. The same applies to the hours with temperatures <20°C and <23°C, although this was not so marked.

With respect to the youngest leaf with symptoms on plantain in San Pablo, no significant correlations with rainfall were calculated (Table 34). Obviously, the influence of rainfall was neutralized by the effect of the fungicides. In the case of evaporation, the correlation coefficient of 0 week was not significant. Only after -4 to -8 weeks did the values become highly significant. Maxima were at -6 and -8 weeks. This was a shift in values of -3 weeks compared with Estrada. This shift is due to the effect of the fungicides, which intensified the inhibiting effect of water stress on black Sigatoka. In comparison with Estrada, the correlations with hours with leaf wetness and maximum temperatures were higher and highly significant from 0 to -8 weeks. The effects were intensified by the fungicides. The highest values were noted at -1 week, the difference of a week compared with Estrada. The correlation coefficients were higher than in Estrada: apparently the inhibiting effect of the fungicides was intensified here, too.

However, the picture was quite different in the case of minimum temperatures and the temperatures <20°C and <23°C. Here the logical relation (inhibition of black Sigatoka by low temperatures) seems to be cancelled by the fungicides. It seems as if black Sigatoka is inhibited by warmer minimum temperatures. However, this is not true, as black Sigatoka, too, can also develop more rapidly when temperatures are higher. But fungicides reduce the spread of black Sigatoka. In addition, the plants grow more quickly when temperatures are higher. As a result, black Sigatoka cannot spread over the new leaves so quickly. Due to this effect, when temperatures are higher, the youngest leaf with symptoms becomes older. Only after 7-8 weeks

Table 34: Correlation coefficients (r) between weather parameters and leaf number, youngest leaf with symptoms and leaf area with symptoms (m^2), respectively, of False Horn plantain before flowering at Waldeck (San Pablo), Costa Rica (weekly values; fungicide treatment: cf. Tables 4 and 5). Leaf numbers and disease data, respectively, were correlated with weather parameters, which each had been recorded 0-8 weeks earlier.

Correlated parameters		Number (n)	Weather parameters shifted by: 0 weeks	-1 weeks	-2 weeks	-3 weeks	-4 weeks	-5 weeks	-6 weeks	-7 weeks	-8 weeks
Leaf number	Rain (mm)	51-53	0.1278	0.1969	0.1304	0.0819	0.0500	0.1236	0.0646	0.1255	0.0584
	Evaporation (mL)	51-53	-0.4714***	-0.4475***	-0.4117**	-0.3676**	-0.2101	-0.1428	-0.0957	-0.0854	0.0226
	h leaf wetness	40-42	0.0078	0.0002	-0.0427	-0.1323	-0.2306	-0.3121*	-0.3099*	-0.3802*	-0.3994*
	Maximum temp.	51-53	0.0470	0.0789	0.1131	0.1307	0.2172	0.3286*	0.2953*	0.3068*	0.3340*
	Minimum temp.	51-53	0.5819***	0.6422***	0.6077***	0.6157***	0.5401***	0.5263***	0.4788***	0.4505***	0.4059**
	h with T <20°C	48-52	-0.5792***	-0.5983***	-0.5551***	-0.5244***	-0.4503***	-0.3530*	-0.2639	-0.1014	-0.0202
	h with T <23°C	48-52	-0.3117*	-0.2714	-0.2280	-0.2382	-0.2929*	-0.2873*	-0.2546	-0.1848	-0.1740
Youngest leaf with symptoms	Rain (mm)	51-53	-0.0522	-0.1878	-0.1918	-0.1190	-0.2351	-0.1848	-0.2206	-0.2175	-0.1695
	Evaporation (mL)	51-53	0.1642	0.3214*	0.3959**	0.4179**	0.4620***	0.4535***	0.5465***	0.5181***	0.5060***
	h leaf wetness	40-42	-0.4936**	-0.5561***	-0.5493***	-0.4705**	-0.5485***	-0.5015***	-0.4965***	-0.4233**	-0.3229*
	Maximum temp.	51-53	0.5770***	0.6494***	0.5750***	0.5299***	0.5047***	0.4930***	0.5501***	0.4681***	0.3402*
	Minimum temp.	51-53	0.2951*	0.1877	0.0218	-0.0499	-0.1526	-0.1494	-0.2527	-0.2919*	-0.3473*
	h with T <20°C	48-52	-0.1565	-0.0324	0.0849	0.2347	0.2677	0.3156*	0.3803**	0.4252**	0.4487**
	h with T <23°C	48-52	-0.2845*	-0.2914*	-0.1916	-0.0866	-0.0237	0.0128	0.0139	0.0718	0.1278
Leaf area with symptoms (m^2)	Rain (mm)	51-53	0.0742	0.2361	0.1432	0.0114	0.0068	-0.0650	-0.0617	0.1125	0.1007
	Evaporation (mL)	51-53	0.1215	-0.0453	-0.1082	-0.0278	-0.0435	-0.0901	-0.1817	-0.2425	-0.2721
	h leaf wetness	40-42	0.2820	0.4071**	0.4652**	0.3068*	0.2941	0.2793	0.4238**	0.4820**	0.4156**
	Maximum temp.	51-53	-0.3947**	-0.3966**	-0.4591***	-0.3840**	-0.3935**	-0.3093*	-0.4557***	-0.4782***	-0.3923**
	Minimum temp.	51-53	-0.5052***	-0.3460*	-0.3105*	-0.3731**	-0.3856**	-0.3411*	-0.2916*	-0.1107	0.0206
	h with T <20°C	48-52	0.3825**	0.2000	0.1568	0.2690	0.1569	0.1401	-0.1734	-0.2086	-0.1916
	h with T <23°C	48-52	0.3622**	0.3338*	0.3800**	0.2476	0.1883	0.1070	0.1692	0.1360	-0.0651

* Significant at $P \leq 5\%$. ** Significant at $P \leq 1\%$. *** Significant at $P \leq 0.1\%$.

did the situation change. The fungicides lost their inhibiting effect, and the influence of temperatures on black Sigatoka predominated once more, so that the relations corresponded to the conditions to be expected.

The situation in the case of the leaf area with symptoms on plantain in San Pablo was again somewhat different. Here rainfall and evaporation had no evident effect on the leaf area with symptoms. In contrast to Estrada, hours with leaf wetness and maximum temperatures had a marked influence on the leaf area with symptoms. The correlation coefficients with the hours with leaf wetness of -1 to -3 weeks and -6 to -8 weeks were significant, and those of the maximum temperatures were, in fact, significant for the whole period (0 to 8 weeks). Values were especially high for -2 to -7 weeks. These maximum correlations agree with the development times of the first symptoms (specks 15-29 days, streaks 19-35 days) and the transition to a spot with a dry center (34-56 days). Especially during this last stage, coalescence of symptoms leads to large leaf areas being destroyed.

In the case of the minimum temperature and hours with temperatures <20°C and <23°C, the relations were similar to those of the youngest leaf with symptoms. In the case of the leaf area with symptoms, it seems that when temperatures are low the spread of black Sigatoka is no longer inhibited. Here, too, this effect was caused by stronger plant growth and simultaneous disease inhibition by fungicides. In the case of minimum temperatures up to -6 weeks, these effects were marked. For the hours with temperatures <20°C, these effects were marked only at 0 week, and for <23°C up to -3 weeks.

Leaf numbers in the banana plantation at San Pablo (intensive care with fungicide application and "deleafing") correlated significantly with hours with leaf wetness (positive), maximum temperature (negative), minimum temperature (negative), and hours with temperatures <20°C and <23°C (each positive). No significant correlations were proved with rainfall and evaporation (Table 35). The correlations would mean that there were more leaves when there were more hours with leaf wetness, lower minimum temperatures and many hours with temperatures <20°C and <23°C. These results are quite in contrast to those previously described in the case of plantain on nearby sites. As it cannot be assumed that plantain shows a fundamentally different kind of behavior from banana, the explanation can here, too, be found in the too-intensive "deleafing", which delinks the relation between leaf number and climatic conditions. Attention has already been drawn to this fact several times.

In the case of the youngest leaf with symptoms in the San Pablo banana plantation, significant correlations (Table 35) were observed with rainfall (negative), evaporation (positive), hours with leaf wetness (negative), maximum temperature (positive), minimum temperature (changing from positive to negative), and hours with temperatures <20°C and <23°C (each changing from negative to positive). These correlations were divided into three groups.

The first group was formed by rainfall and evaporation. With regard to rainfall, there was a significant value only at -8 weeks. In the case of evaporation, the correlation coefficients of 0 and -1 week were not significant, from -4 to -8 weeks onwards they were highly significant and maxima were observed at -7 to -8 weeks. The occurrence of significant values after -2 weeks is most probably connected with the development time of the first symptoms (specks and streaks). The fact that higher values did not occur before -4 and -5 weeks, and maximum temperatures not before -7 to -8 weeks, is due to the effect of the fungicides, which intensified the inhibiting effect of dryness on black Sigatoka.

The second group was formed by the hours with leaf wetness and maximum temperatures. A great number of hours with leaf wetness and lower maximum temperatures led to the youngest leaf with symptoms "becoming younger" (negative correlation), which meant a greater infection. Highest correlations were observed when values had not been shifted (0 week), i.e. these weather

Table 35: Correlation coefficients (r) between weather parameters and leaf number, youngest leaf with symptoms and leaf area with symptoms (m^2), respectively, of banana (Valery) before flowering at Waldeck (San Pablo), Costa Rica (weekly values; fungicide treatment: cf. Tables 3 and 5). Leaf numbers and disease data, respectively, were correlated with weather parameters, which each had been registered 0-8 weeks earlier.

Correlated parameters		Number (n)	Weather parameters shifted by:								
			0 weeks	-1 weeks	-2 weeks	-3 weeks	-4 weeks	-5 weeks	-6 weeks	-7 weeks	-8 weeks
Leaf number	Rain (mm)	41	0.1868	0.1101	0.0122	-0.0715	-0.2285	-0.1414	0.0352	0.1986	0.1162
	Evaporation (mL)	41	-0.0366	0.1724	0.1581	0.0061	0.1103	-0.0251	-0.2273	-0.1366	-0.1989
	h leaf wetness	30-32	0.1176	0.1226	0.3170	0.2551	0.0875	0.2661	0.4703**	-0.0278	0.1071
	Maximum temp.	41	-0.1437	-0.1443	-0.0197	-0.2207	-0.1369	-0.2254	-0.4477**	-0.2638	-0.1586
	Minimum temp.	41	-0.0413	-0.1521	-0.1657	-0.1001	-0.3902*	-0.3763*	-0.0826	-0.1136	-0.0662
	h with T <20°C	40-41	-0.0485	0.0449	0.1695	0.0296	0.3681*	0.3589*	-0.0587	0.0283	-0.0343
	h with T <23°C	40-41	-0.0835	0.0500	0.1199	0.2567	0.2734	0.3089*	0.2790	0.1600	-0.0223
Youngest leaf with symptoms	Rain (mm)	41	-0.1393	-0.1735	-0.0681	-0.1311	-0.1462	-0.1928	-0.0724	-0.2970	-0.3191*
	Evaporation (mL)	41	0.1144	0.2821	0.3483*	0.3090*	0.4363**	0.4751**	0.3863*	0.6248***	0.6482***
	h leaf wetness	30-32	-0.5533**	-0.3124	-0.2849	-0.4863**	-0.5530**	-0.4223*	-0.3306	-0.5455**	-0.4268*
	Maximum temp.	41	0.5356***	0.4452**	0.4195**	0.4588**	0.4947**	0.4406**	0.2547	0.4167**	0.2887
	Minimum temp.	41	0.3228*	0.1894	0.1182	0.0982	-0.2372	-0.2138	-0.1940	-0.4725**	-0.4875**
	h with T <20°C	40-41	-0.1257	-0.1365	0.0135	0.0205	0.2273	0.2499	0.2613	0.4955**	0.5176***
	h with T <23°C	40-41	-0.3238*	-0.1386	-0.1141	-0.1479	-0.0390	-0.1134	0.0415	-0.0317	0.0420
Leaf area with symptoms (m^2)	Rain (mm)	41	0.1244	0.1683	-0.0586	0.0527	-0.1371	-0.0419	-0.0253	0.2469	0.2799
	Evaporation (mL)	41	0.2193	0.1418	0.1346	0.0310	-0.0564	-0.1903	-0.2914	-0.3933*	-0.5022***
	h leaf wetness	30-32	0.3057	0.3457	0.4224*	0.5350**	0.5315**	0.5344**	0.5792***	0.4712**	0.4396*
	Maximum temp.	41	-0.3778*	-0.4014**	-0.3100*	-0.4866**	-0.5363***	-0.5568***	-0.6295***	-0.6696***	-0.5426***
	Minimum temp.	41	-0.4375**	-0.4009**	-0.4475**	-0.4697**	-0.4294**	-0.4172**	-0.2531	-0.0717	0.0339
	h with T <20°C	40-41	0.1893	0.2375	0.2469	0.3016	0.3407*	0.3316*	0.0581	-0.0486	-0.1471
	h with T <23°C	40-41	0.0938	0.1651	0.2436	0.3890*	0.3945*	0.4399**	0.3630*	0.3022	0.1301

* Significant at $P \leq 5\%$. ** Significant at $P \leq 1\%$. *** Significant at $P \leq 0.1\%$.

parameters had an especially strong direct effect on infection. The correlation with hours with leaf wetness and maximum temperature were, however, also significant at -4 and -7 weeks, and higher than the values in between. Here, too, the fungicide applications had an effect. The direct effect of hours with leaf wetness and maximum temperature on the youngest leaf with symptoms remained, but, due to the effect of the fungicides, it lasted longer. The infection on leaves protected by the fungicide became visible only later on.

In the case of the third group, minimum temperature and hours with temperatures <20°C and <23°C, the relations correspond exactly to those described for plantain in San Pablo.

With regard to the leaf area with symptoms on banana in San Pablo (Table 35), the "deleafing" effect must also be taken into consideration. This effect probably led to lower correlations, because hanging leaves as well as heavily infected leaves that were still upright were often removed. Significant correlations were noted with evaporation (negative), hours with leaf wetness (positive), maximum temperature (negative), minimum temperature (negative), and hours with temperatures <20°C and <23°C (each positive). Rainfall had no evident influence on the leaf area with symptoms.

As a result of the positive correlations at 0 to -3 weeks, the logical relation (inhibition of black Sigatoka by high evaporation) seems to be cancelled by the fungicides. It seems as if black Sigatoka were favored by high evaporation. However, this is not true, as black Sigatoka, too, can also develop more rapidly when evaporation is lower. This more rapid development and spread of the disease is, however, inhibited by the fungicides. As a result, black Sigatoka can spread over the leaf only slowly. Because of these effects, the leaf area with symptoms seems to increase when evaporation is higher. This effect is, in addition, favored by the fact that the plants also grow more quickly, because water stress is reduced and the new leaf areas are protected by the fungicides. The fungicides had no inhibiting effect only after 4 to 8 weeks, the influence of temperature on black Sigatoka predominated once more, and the relations corresponded once more to the conditions to be expected.

Hours with leaf wetness and maximum temperature had a marked influence on the leaf area with symptoms. Significant correlation coefficients were noted with hours with leaf wetness at -2 to -8 weeks, those with maximum temperatures were even noted during the whole period (0 to 8 weeks). Values were especially high at -6 and -7 weeks. These maximum correlations corresponded to the development times of the symptoms during the transition to spots with a dry center, where, due to coalescence, large areas of leaf were infected and caused to die.

With regard to minimum temperature and hours with temperatures <20°C and <23°C, the relations were similar to those of the plantain in San Pablo. The apparent cancellation of the inhibition of black Sigatoka by low temperatures was marked in the case of minimum temperature until -5 weeks, and hours with temperatures <20°C and <23°C especially at -4 to -5 weeks.

When the data of the youngest leaf with symptoms (YLWS) were compared with other disease data, significant negative correlations with the leaf area with symptoms and ascospore release were also proved (Table 36). This applied to both plantain and banana with and without fungicide treatment. Thus, the YLWS is also an indicator for disease severity. In the plantations without treatment, however, at the age stages of 6 and 11 weeks all leaves were always infected, i.e. the YLWS was always equal to 1. In Semillero, too few samples were available at the 0 w age stage to allow a statement to be made.

The results presented here represent only one of several approches to calculation and statistical analysis. The importance of individual climatic parameters and their combined effect on the development of the disease should be determined more exactly. On the basis of the data and

Table 36: Correlation coefficient (r) between youngest leaf with symptoms, ascospore release and leaf area with symptoms (m^2), respectively, at different age stages in the banana plantation at San Pablo and the plantain plantations at San Pablo, Estrada and Semillero (weekly values). (F): with fungicide treatment (cf. Tables 3, 4 and 5).

Plantation	Age stage	Numbers (n)	Youngest leaf with symptoms and: Ascospore release	Youngest leaf with symptoms and: Leaf area with symptoms
Waldeck, San Pablo, banana (F)	before flowering	41	-0.3416*	-0.5339***
	6 weeks after flowering	41	-0.3610*	-0.3265*
	11 weeks after flowering	41	-0.3656*	-0.1263
Waldeck, San Pablo, plantain (F)	before flowering	53	-0.5144***	-0.6129***
	6 weeks after flowering	53	-0.4656***	-0.5925***
	11 weeks after flowering	53	-0.2763*	-0.2730*
Estrada, plantain	before flowering	53	-0.5850***	-0.4098**
	6 weeks after flowering	40	------	------
	11 weeks after flowering	35	------	------
Waldeck, Semillero, plantain	before flowering	14	-0.2159	0.2723
	6 weeks after flowering	40	------	------
	11 weeks after flowering	35	------	------

* Significant at $P \leq 5\%$. ** Significant at $P \leq 1\%$. *** Significant at $P \leq 0.1\%$.

relations described in this document, a model could be developed which includes leaf wetness, evaporation, temperature, rainfall and the youngest leaf with symptoms. When such a model is developed, spore release can also be included, because that is important when one attempts to understand disease development. In practice, spore release will, however, be of no importance for the model, because the evaluation and calculation of spore release data causes far too much work and is too expensive.

In order to forecast disease development and the kind of fungicide applications necessary to control the disease, several forecast systems were developed for yellow Sigatoka (*M. musicola*). The French system (Ganry and Meyer 1972a, 1972b, Ganry and Laville 1983) is based on climatic data (evaporation and temperature) and the development of the disease (état d'évolution). In comparison, this system depends on complicated technical prerequisites, and evaluation places exacting demands on personnel. Ordinary technical personnel can certainly not apply it. Cronshaw's (1982) method is much simpler, as it requires no further prerequisites. It is based on the infection of the five youngest leaves of plants before flowering.

However, for two important reasons both methods cannot simply be transferred for use with black Sigatoka in Costa Rica:

1. They were developed for another, less virulent organism, which also reacts differently to climatic conditions.

2. They were developed in climates which show a marked dry period, simplifying control of the disease.

A forecast system for black Sigatoka in Taiwan was presented in 1987 by Chuang and Jeger (1987a, 1987b). This system is based on disease severity, total precipitation and days with $\geq 90\%$ relative humidity. But this climate has a dry period, too. Stover and Dickson's (1970) method of the youngest leaf with symptoms is applied to both yellow and black Sigatoka, in Costa Rica, also. This method, however, is not a forecast system, and permits the user only to react to conditions already existing. Such models as these can be checked with the data from the investigation described here, and, if necessary be adjusted and improved.

10. Insect and Nematode Infestation and Yield in the Three Plantain Plantations

When the three plantain sites are compared, infestation by pests and endoparasitic root nematodes also have to be taken into consideration as they, too, can greatly influence plant growth and yield.

Detailed surveys on this subject were not possible within the framework of the investigation presented here. However, in order to obtain an impression of the extent of the damage caused by the pests, sample investigations were carried out which, however, permit only general statements to be made.

The only *Musa* pest which caused greater damage to the plantain was the stem borer *Cosmopolites sordidus* Germ. (Coleoptera: Curculionidae). The larvae of this weevil bore tunnels into the rhizome and pseudostem, which can be up to 60 cm long with a diameter of 1.5 cm (Pans 1977). Infested plants show retarded development, are weaker and more susceptible to damage by wind.

Two methods were used to estimate infestation with *Cosmopolites sordidus*: traps were set up, and rhizomes were checked for damage. For the traps, the pseudostems of newly cut plantain were split lengthwise and the cut surface was placed downwards on the earth (Stover and Simmons 1987). During the night the weevils crept into the open tissue and were then collected in the morning. The rhizome investigations were carried out on plants blown over by the wind and on rhizomes which had been freshly cut for planting. In both cases, the numbers of tunnels and larvae were noted.

In San Pablo, 1-2 weevils were occasionally found in the traps, in Estrada 1-3, and in Semillero there were always several weevils (up to 8) in the traps. In San Pablo, the rhizomes investigated were sometimes infestation-free, in Estrada all rhizomes showed tunnels but only a few larvae could be found. In Semillero all rhizomes were damaged and sometimes several larvae were found. These results pointed to a relatively low infestation in San Pablo, a higher one in Estrada and a very high level of infestation in Semillero.

In order to determine nematode infestation, towards the end of the investigation period root samples were taken in all three plantations. With a special spade ("palín"), a hole 13 cm wide and 30 cm deep was dug directly at the foot of the plantain plant. All discernible roots were picked out of the excavated material and put into a plastic bag with part of the soil. The material originating from five different plants was mixed and the sample immediately sent to the Laboratorio de Nematología (ASBANA, San José) for examination. The roots were washed with water, sorted into living and dead, and weighed fresh. For the nematode analysis, the living roots were chopped up in a mixer. The nematodes were extracted by means of a fine sieve, and then determined under the microscope and counted (Figueroa 1985).

The results are shown in Table 37. The plants in San Pablo had the largest amount of roots. The plants in Estrada and Semillero had far fewer roots than those in San Pablo. The same applied to the amount of living roots, but the percentage of living roots was about the same in all plantations. In San Pablo, infestation by the especially harmful nematode genus *Radopholus* was very high. *Helicotylenchus* infestation was relatively low and *Pratylenchus* infestation moderate. In Estrada the values of the first two genera were low. However, those of the less harmful genus *Pratylenchus* were very high. In Semillero, the first sample was taken in January 1986. An extremely high level of *Radopholus* infestation and a high *Pratylenchus* infestation were observed. *Helicotylenchus* was missing here. The second sample was taken in May 1986, about 4 weeks after nematicides had been applied. The number of nematodes had been reduced to relatively low values. The nematode genera *Meioidogyne* and *Rotylenchus* could not be found in any of the three plantations.

From June until October 1985, in the three plantations at Estrada, Semillero and San Pablo, 10 of the marked fruit bunches (age 11 weeks) were measured every week after the harvest. For weighing, the rachis was cut off immediately above the first hand and directly below the last hand. On 2-week-old bunches in both plantations in Waldeck (Semillero and San Pablo), when all hands of the bunch had fully developed, the flower bud and the lowest, youngest hand with only a few fingers were broken off ("desmane", "debudding").

What was the effect of all these components (Sigatoka, pest and nematode infestation, soils and management) on the development of the fruit bunches?

The results of the measurements showed, apart from one exception, significant differences between the three sites in the case of all parameters (Tables 38 and 39). The number of hands and fingers per bunch (Table 38) was reduced ("debudding") in both plantations in Waldeck. Despite minimum care, the plantation in Estrada always (exception: number of hands) lay in between the two plantations in Waldeck. As was to be expected, the best results were obtained in San Pablo.

There is a great deal of literature on the per-hectare yields of banana, but not of plantain. Yield data over a longer period of time was available for two plantations. Close to the experimental plantation in Estrada there was another plantation 2.5 ha in size, which was managed in the same way. It was owned by a peasant (George Dunn) who had kept records of his yields for 2 years. In 1984, he harvested a total of 1394 bunches. That meant a yield of 557.6 bunches per hectare per year (ha^{-1} a^{-1}). In 1985, he harvested 1386 bunches, which was about the same yield: 554.4 bunches ha^{-1} a^{-1} (data from the records of George Dunn, Estrada). In the export-oriented ASBANA plantain plantation in Waldeck (San Pablo) in the "banana year" October 1984 to September 1985, 1424 bunches ha^{-1} a^{-1} were harvested, and during the same period of time (1985/1986) the yield was 955.4 bunches ha^{-1} a^{-1} (data from unpublished "informes anuales" by ASBANA).

Using these yield data and the average total weight per bunch (Table 38) the production in Estrada was calculated as being 4.8 t ha^{-1} a^{-1} and in San Pablo between 10.1 t ha^{-1} a^{-1} (1985/86) and 15.1 t ha^{-1} a^{-1} (1984/85).

Table 37: Nematode infestation of plantain roots (False Horn plantain) in three plantations in the Atlantic lowland of Costa Rica.

		Roots in 5 dm³ soil:			Nematodes 100 g⁻¹ living roots:		
Plantain plantation	Sample (date)	All roots (g)	Living roots (g)	(%)	Radopholus	Helicotylenchus	Pratylenchus
Waldeck, San Pablo	25.10.85	119	70	59	13500	5500	9500
	25.11.85	114	69	61	22670	7830	9670
Estrada	20.01.86	81	50	62	5500	4250	22750
Waldeck, Semillero	08.01.86	74	46	62	30500	0	12380
	06.05.86*	77	58	75	4750	0	2250

* Ca. 4 weeks after the application of 30 g Nemacur 10G (Fenamifos) per plant.

Table 38: Yield of False Horn plantain 11 weeks after flowering at three sites in the Atlantic lowland of Costa Rica (June to October 1985).

Plantation	No. of bunches	No. of hands/b.	No. of fingers/b.	No. of bunches	Total weight/ bunch (kg)	Weight of hands/b. (kg)
Waldeck. Semillero	197	4.8 A*	21.9 A	130	6.4 A	5.8 A
Estrada	189	7.1 C	24.4 B	127	8.6 B	7.8 B
Waldeck. San Pablo	180	5.3 B	27.6 C	130	10.6 C	9.6 C

* Numbers with different letters differ significantly at $P \leq 5\%$.

Table 39: Characteristic values for the fingers of the 2. and 4. hand of 11-week-old False Horn plantain bunches at three sites in the Atlantic lowland of Costa Rica (June to October 1985).

Plantation	No. of bunches	Central finger of 2. hand: girth (cm)	length (cm)	Central finger of 4. hand: girth (cm)	length (cm)
Waldeck. Semillero	197	14.6 A*	24.7 A	14.1 A	23.3 A
Estrada	189	14.8 A	26.3 B	14.7 B	24.8 B
Waldeck. San Pablo	180	15.2 B	27.0 C	15.4 C	25.7 C

* Numbers with different letters differ significantly at $P \leq 5\%$.

11. STUDIES OF THE SPECTRUM OF POTENTIAL HOST PLANTS OF BLACK SIGATOKA

It is known that many diseases have, apart from their specific host plants, secondary hosts on which they can survive and from which they can again infect the primary host. This has been observed in the case of Moko disease of banana caused by *Pseudomonas solanacearum* (Buddenhagen 1960, 1961). This bacterium was isolated from diseased Heliconias in, among other places, Costa Rica (Buddenhagen 1960).

In order to find out whether there are other host plants for *Mycosphaerella fijiensis* apart from the cultivated hybrids of the genus *Musa*, further Musaceae and species from other families of the Zingiberales order (Table 40) were examined with regard to natural infection with black Sigatoka.

The Heliconias were determined according to Daniels and Stiles (1979) and Kress (1984); other Zingiberales according to Gomez (1984). Small pieces of leaves with possible symptoms were lightened with Lactophenol (boiled for 5-10 min in Lactophenol: Stover 1964) and then examined under the microscope (Zeiss Standard) with a 312.5-500-fold enlargement. It was searched for the typical conidiophores of *Mycosphaerella fijiensis*. These investigations were carried out during the rainy months.

Table 40: System of the Zingiberales and the genus *Musa* (families according to Dahlgren and Clifford 1982, Takhtajan 1980, *Musa* according to Stover and Simmonds 1987).

Order	Families	Genera	Sections	Species
Zingiberales	Zingiberaceae	ca. 47	-	ca. 1300
	Costaceae	4	-	ca. 150
	Marantaceae	ca. 30	-	ca. 400
	Cannaceae	Canna	-	ca. 50
	Musaceae	Ensete	-	6
		Musa	Australimusa	5-6, e.g. *Musa textilis*
			Callimusa	5-6, e.g. *Musa coccinea*
			Eumusa	9-10, e.g. *Musa acuminata* *Musa balbisiana*
			Rodochlamys	5-6, e.g. *Musa ornata* *Musa velutina*
			Ingentimusa	*Musa ingens*
	Strelitziaceae	Strelitzia	-	4
		Ravenala	-	*R. madagascariensis*
		Phenacospermum	-	1
	Heliconiaceae	Heliconia	-	ca. 150
	Lowiaceae	Orchidantha	-	2

Black Sigatoka was identified only on the species *Musa acuminata* and *M. balbisiana* (*Musa* section Eumusa) (Table 41). In all the other cases findings were negative. Representatives of those genera where individual species could not be determined were not listed. From some of the genera *Costus*, *Renealmia* (Costaceae), *Maranta*, *Stromathe*, *Ischnosiphon*, and *Curcuma* (Marantaceae) several species were even found. In none of these cases was Sigatoka infection observed. Though ascospores of the *Mycosphaerella fijiensis/M. musicola* type occasionally germinated on the leaves, an infection was not recorded. This corresponds with Laville's observations (1983b).

Throughout the whole year, widely distributed common species such as *Musa textilis*, *Heliconia latispatha*, *H. mariae*, *H. wagneriana*, *Canna indica*, *Calathea insignis*, and *C. lutea* were repeatedly examined to see whether they were infected, so that the possibility could be excluded that the previous investigations had by chance been made during an infection-free period. In March 1985, the species *Musa ornata*, *M. velutina*, *Heliconia psittacorum*, *H.* 'Golden Torch', *Strelitzia reginae*, and *Alpinia purpurata* were planted in Waldeck immediately next to a heavily diseased plantain plantation. These plants were controlled regularly; however, until September 1986 black Sigatoka was not found on any of them. These findings were confirmed by microscopic investigations.

From spring 1986 onwards, a firm began the large-scale cultivation of *Heliconia* spp. as cut flowers for export. The farm was situated in the Atlantic lowlands near Guácimo in the vicinity of banana plantations and was visited repeatedly. In May and August 1986, none of the more than 80 *Heliconia* species and cultivars showed symptoms of black Sigatoka disease.

In all the studies it was repeatedly observed that, in the Costa Rican Atlantic lowlands, banana species and hybrids belonging to the Eumusa section were always infected by black Sigatoka, however isolated or scattered the plants were. Yet another observation indicated the ubiquitous presence of black Sigatoka spores: small, infection-free banana plants from shoot-tip culture in the Laboratorio de cultivo de tejidos, CATIE, were planted in plastic bags with earth and placed below the protruding gutter of the roof of our house in order to adapt them to the climatic conditions of the lowlands. The house was situated far away from any banana plant (600 m) on the southwest flank of a hill. In the north and east it was also surrounded by a pine forest with trees 15-20 m tall. Thus, it was completely protected against the main winds. The side of the house where the banana plants stood was facing the forest and the hill. Despite this protected and isolated position, after 3-8 weeks, according to susceptibility, the plants were infected by black Sigatoka.

Examination of Musaceae and the relations of the Zingiberales family such as Heliconiaceae showed only black Sigatoka infection of representatives of the genus *Musa* section Eumusa. In contrast to other banana diseases, e.g. Moko (Buddenhagen 1961, Berg 1971), *M. fijiensis* seems to be strictly limited to the genus *Musa* section Eumusa. The desultory spread of the disease also speaks in favor of such a host specificity (Stover 1980b). If *M. fijiensis* had a secondary host among such wild plants as *Heliconia latispatha*, which are spread over all tropical lowlands, the disease would have more likely spread continuously.

Table 41: Occurrence of black Sigatoka (*Mycosphaerella fijiensis*) in the Zingiberales order.

Species	Family	Locality	Altitude a.s.l. (m)	Occurrence	Sigatoka infestat.
Alpinia purpurata (Vieill.) K.Schum.	Zingiberaceae	Waldeck, garden	30	ornamental plant	no
Calathea insignis Peters	Marantaceae	coastal swamps	up to 150	wild	no
Calathea lutea (Aubl.) G.Mey	Marantaceae	coastal swamps	up to 150	wild	no
Canna indica L.	Cannaceae		up to 1300	introduced	no
Ensete spec.	Musaceae	highland,San José,garden	ca.1000	ornamental plant	no
Heliconia clinophila R.R.Smith	Heliconiaceae	Volcán Congo, wet rocks	ca.1000	wild	no
Heliconia imbricata (Kuntze) Baker	Heliconiaceae	lowlands, swamps	up to 100	wild	no
Heliconia irrasa					
ssp. irrasa R.R.Smith	Heliconiaceae	Cahuita, cocoa plantation	10	wild	no
ssp. undulata Daniels et Stiles	Heliconiaceae	Tortuguero, djungle	3	wild	no
Heliconia latispatha Bentham	Heliconiaceae	everywhere, road border	up to 1300	wild	no
Heliconia longa (Griggs) Winkler	Heliconiaceae	Río Chirripó, djungle	80	wild	no
Heliconia mariae J.D.Hooker	Heliconiaceae	lowlands, swamps	30	wild	no
Heliconia mariae x pogonantha	Heliconiaceae	Cahuita, swamps	10	wild	no
Heliconia mathiasii Daniels et Stiles	Heliconiaceae	Tortuguero, djungle	3	wild	no
Heliconia pogonantha					
var. holerythra Daniels et Stiles	Heliconiaceae	Río Chirripó, djungle	80	wild	no
var. pubescens Daniels et Stiles	Heliconiaceae	Linda Vista, road border	600	wild	no
Heliconia trichocarpa Daniels et Stiles	Heliconiaceae	Río Chirripó, djungle	80	wild	no
Heliconia wagneriana Petersen	Heliconiaceae	lowlands, moist sites	up to 100	wild	no
Heliconia psittacorum L.f.	Heliconiaceae	Waldeck, garden	30	ornamental plant	no
Heliconia 'Golden Torch'	Heliconiaceae	Waldeck, garden	30	ornamental plant	no
Hedychium coronarium Koenig in Retz	Zingiberaceae	everywhere, moist sites		introduced	no
Musa acuminata					
ssp. burmannica Simmonds	Musaceae	Guápiles, Turrialba	20, 640	CARIARI,CATIE*	yes
ssp. malaccensis (Ridley) Simmonds	Musaceae	Guápiles, Turrialba	20, 640	CARIARI,CATIE*	yes
ssp. microcarpa (Beccari) Simmonds	Musaceae	Guápiles, Turrialba	20, 640	CARIARI,CATIE*	yes
Musa balbisiana Colla	Musaceae	Guápiles, Turrialba	20, 640	CARIARI,CATIE*	yes
Musa coccinea Andrews	Musaceae	Guápiles, Turrialba	20, 640	CARIARI,CATIE*	no
Musa ornata Roxb.	Musaceae	Guápiles, Turrialba	20, 640	CARIARI,CATIE*	no
Musa textilis Née	Musaceae	lowlands, everywhere	up to 300	introduced	no
Musa velutina Wendl. et Drude	Musaceae	Guápiles, Turrialba	20, 640	CARIARI,CATIE*	no
Ravenala madagascariensis Sonn.	Strelitziaceae	Turrialba, CATIE	640	ornamental plant	no
Strelitzia reginae Ait.	Strelitziaceae	Waldeck, garden	30	ornamental plant	no

* *Musa* collections.

12. SUMMARY

From 1984 to 1986, the development of symptoms, leaf area with symptoms and spore release of black Sigatoka during the course of the year were investigated in the Atlantic lowland of Costa Rica. These investigations were carried out on False Horn plantain (Curraré, genome AAB) and banana (Valery, genome AAA) in four differently managed plantations with different soils: in Estrada and Semillero (Waldeck) plantain without fungicide applications, in San Pablo (Waldeck) plantain and banana with fungicide applications.

Microscopical investigations confirmed that the agent of black Sigatoka is *Mycosphaerella fijiensis* Morelet. Symptoms showing specific morphological structures of the black Sigatoka were found only on the two species *Musa acuminata* and *M. balbisiana* (Section Eumusa) and their hybrids. The disease was not observed on *Musa* species from other sections or representatives of five further families of the Zingiberales order.

Plantain growth was dependent on soil quality. On poor soils leaf emission was retarded, growth in height and thickness of the pseudostem and leaf size were reduced. Disease development is closely related to the growth of the host plant. The poorer this is, the greater is the disease's influence. In order to control black Sigatoka effectively, first of all the plants' growth conditions should be optimized.

In the case of plantain, an annual periodicity was observed with regard to leaf numbers. The highest leaf numbers were found in June, the end of the drier and warmer season. The lowest numbers were found in the rainy and cooler months of November and December. The number of leaves on the banana plants did not vary during the course of the year, because, due to the removal of hanging leaves as well as still upright but seriously diseased leaves ("deleafing"), they were delinked from climatic events.

Correlation calculations with an adjustment of 0 to -8 weeks against the leaf and disease data make obvious the relation between leaf number, youngest leaf with symptoms, leaf area with symptoms, weather and the effect of fungicides.

Even though evaporation has an influence on plant growth, it does not affect the development of symptoms, whereas humid periods accelerate black Sigatoka symptoms development. Hours of leaf wetness and the maximum temperature had an influence on the leaf number via the transition to the symptom stage spot with a dry center. The minimum temperature and hours with temperatures <20°C and <23°C had, on the one hand, an inhibiting effect on plant growth; on the other hand they also inhibited symptom development and, therefore, were favorable for the leaf numbers. On those plantain plants treated with fungicides, the same tendencies were to be observed, but correlations were lower. Due to "deleafing" in banana, there were no correlations calculated which made any sense.

Under favorable conditions, symptom development on plantain in the case of specks lasted 15 days, streaks 19 days, spots 25 days and spots with a dry center 34 days. During periods with low rainfall these development times could last as much as 15 days longer. Development time showed a significantly positive correlation with the number of hours with leaf wetness.

Detailed investigations of symptom development on plantain and banana showed hardly any difference in the development time of the symptoms. On banana, however, the more developed symptoms (spot and spot with a dry center) spread much more rapidly, leading to an earlier death of the leaf.

Disease development was also subject to an annual periodicity even under the seemingly constant climatic conditions of the humid tropics of Costa Rica. The development times of the fungi were longer in drier, cooler periods and shortened in the rainy, warmer ones. Especially

leaf wetness, evaporation and temperature showed a noticeable influence. The leaf area with symptoms and the youngest leaf with symptoms increased greatly after the beginning of the rainier period (end of June). At the same time, the fungus took less time to infect a certain area of the leaf. The youngest leaf with symptoms shows a significantly negative correlation with the leaf area with symptoms and spore release. In the course of the year, during the transition period from the drier to the rainier season, self-fortifying development cycles of the fungi were observed, rainfall being of special importance. This annual periodicity was observed on plantain both with and without fungicide applications as well as on banana with frequent fungicide applications. As a result of fungicides and intensive management ("deleafing"), the disease cycle was much less marked under commercial conditions. Chemical treatment prevented a marked fortifying of the fungi's development cycle during the transition period from the drier to the rainier season and delayed the increase in the leaf area with symptoms by 6 - 8 weeks.

When the weather parameters were shifted by 0 to -8 weeks against the disease data, the highest correlations of the youngest leaf with symptoms (YLWS) with leaf wetness and maximum temperatures were to be found at 0 to -2 weeks. Several hours of leaf wetness and lower maximum temperatures had an especially favorable direct effect on infection (lowering of the YLWS's age). All the other parameters had a marked effect on the development of the first symptoms (specks and streaks) after -2 to -4 weeks.

With regard to those plants treated with fungicides, higher correlations were found at -4 to -8 weeks, as infection of the leaves protected by fungicides was not marked until later on. Here, the growth rate was higher than that of the disease development. Fungicides delayed disease development by up to 5 weeks. During hours with low temperatures and those with temperatures <20°C and <23°C, the logical relation (inhibition of black Sigatoka by low temperatures) seemed to be offset by the fungicides. The fungicides inhibited the spread of the disease so that it could not cover new leaves so quickly. When temperatures were higher, the YLWS became older due to the concurrent more rapid plant growth. Only after 7-8 weeks did the fungicides lose their inhibiting effect, and the influence of temperatures on black Sigatoka predominated again, so that relations corresponded to those expected.

The influence of the weather on the leaf area with symptoms was largely connected with symptom development, particularly the transition from streak to spot symptoms. Especially during this stage, large areas of the leaf were caused to die as a result of coalescence of the symptoms (time adjustment of -5 to -6 weeks). Due to fungicide treatment, symptom development was inhibited and extensive infection delayed, i.e. it took longer. Thus, in the case of the plants treated with fungicides, growth rate of plants was higher than that of disease development. For minimum temperatures and hours with temperatures <20°C and <23°C, for example, the relations with the leaf area with symptoms on the plants treated with fungicides were similar to those of the youngest leaf with symptoms. The seeming neutralization of the inhibiting effect of low temperatures on black Sigatoka was especially marked at -4 to -5 weeks.

Conidiospore release showed a diurnal periodicity dependent on the weather. Significant correlations were determined for all weather parameters, which also show a diurnal periodicity. The most important causal correlation was the one with the wind. Conidiospore concentration inside the plantation was higher at 1 m above the ground than at the height of the foliage (4.65 m). In comparison with ascospore concentration, conidiospore concentration was, however, 10-100 times lower, so that conidiospores play only a minor part in spreading the disease.

On days without rain, ascospore release took place only in the morning (07:00 hours) after the hours with greatest dew. On days with rainfall, increased spore release was recorded at the time rain fell or during the hour following rainfall. Ascospore release was always induced by rain, even by 0.1 mm precipitation per hour. Ascospore concentration in the air decreased when rainfall lasted several hours. There was a significantly positive correlation between ascospore

release and rain. In the drier months from January to May, only small amounts of ascospores were recorded in comparison with the rainier season. The highest ascospore concentrations were registered in December: 6876 ascospores per cubic meter of air on 26.12.85 and a total of 17 595 m^{-3} per month.

The results of correlation calculations with a time adjustment of the weather parameters against spore release data of 0 to -8 weeks agreed with symptom development times. There were significant correlations between ascospore release and all weather parameters. High precipitation with low evaporation, higher minimum temperatures and, therefore, fewer cool hours under 20°C and 23°C led to high ascospore release. The highest correlations were recorded at a time adjustment of -7 to -8 weeks. This period of time could be explained by the development time of spots with a dry center, the symptom stage in which perithecia were formed. Among other things, therefore, low temperatures at the time of inoculation and infection respectively led to a lower ascospore release 7-8 weeks later. With regard to conidiospore release, significant correlations were determined only with rainfall, minimum temperature and the hours with temperatures <20°C and <23°C. Similar to ascospore release, conidiospore release was also lower when temperatures were low. The highest correlations were recorded at a time adjustment of -3 to -4 weeks, which corresponded exactly with the development time of specks and streaks, the symptom stages in which conidiospores were formed.

Spots with a dry center, which form the final stage of the symptom development of black Sigatoka, were able to produce ascospores on the leaves hanging down on the plants for up to 21 weeks. When the leaves were cut off and placed on the ground, as soon as 3 weeks later no ascospore production worth mentioning was recorded. By cutting off the dead leaves the inoculum in the plantation can be reduced considerably.

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