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Importance of different sources of inoculum and dispersal methods of conidia of *Colletotrichum musae*, the causal agent of banana anthracnose, for fruit contamination

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Different populations of *Colletotrichum* were characterized and quantified on floral parts of banana plants from flowering until harvest. Isolates of *Colletotrichum* found to be pathogenic and attributed to the species *C. musae* (77% of isolates) were differentiated from other species by abundant sporulation, a short mycelium, and rapid growth. *Colletotrichum musae* was isolated from floral parts mainly during the month following bunch emergence. The respective involvement of different sources of inoculum (leaves, bunch bracts, floral parts) in the levels of fruit contamination was evaluated. When the floral parts and bunch bracts were removed at flowering, the severity of anthracnose disease was considerably reduced. The severity of the disease is strongly correlated with cumulative rainfall during the first 35 days after bunch emergence, and was considerably reduced when rainwater runoff over the bunches was limited by placing plastic sleeves over them. The disease was not observed on banana fruit grown under shelters, protected from rain. The results obtained from this study show clearly that contamination of fruit by conidia takes place largely due to the trickling of rainfall over the floral parts, which are the main source of inoculum. The application of these results for integrated control is discussed.

Keywords: *Colletotrichum*, contamination, dispersal, epidemiology, inoculum sources, *Musa*

Introduction

The quality of bananas produced in the French West Indies is severely affected by skin defects due to brown rots caused by anthracnose disease during fruit ripening. *Colletotrichum musae*, the fungus responsible for this disease, can form lesions on fruits even without skin bruising, but produces larger lesions that appear more rapidly when fruit are damaged (Meredith, 1960). Fruit contamination occurs in the field when a conidium landing on a fruit germinates and forms a melanized appressorium that remains inactive until the fruit ripens (Muirhead & Deverall, 1981). A penetration hypha then develops, and the mycelium enters the skin and later the fruit pulp, forming brown lesions. In the case of banana anthracnose, the concept of contamination (Rappilly, 1991) applies better to the formation of dark appressoria. Indeed, the pathogen is then permanently installed on the host, although penetration has not occurred (de Lapeyre de Bellaire, 1999).

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This disease is, in practice, controlled by postharvest fungicide treatments (Frossard, 1969; Rippon, 1972; Shillingford, 1978; Slabaugh & Grove, 1982; de Lapeyre de Bellaire & Nolin, 1994). However, under conditions in Guadeloupe chemical control is now problematic, for three main reasons: (i) aerial fungicidal sprays to control Sigatoka disease have resulted in the appearance of strains of *C. musae* resistant to the active ingredients used for postharvest treatments (de Lapeyre de Bellaire & Dubois, 1997); (ii) the fungicidal treatments are not effective in all the production zones, apart from the appearance of resistant strains (Chillet et al., 1998); (iii) consumer demand is for a reduction in pesticide use, especially postharvest. Thus research programmes have been working on new control strategies that would rely on a better understanding of the epidemiological aspects of the disease.

Some work on the epidemiology of banana anthracnose has already been carried out (Agati, 1922; Simmonds & Mitchell, 1940; Meredith, 1962a; Shillingford, 1976), but the methodology used was often unsuitable for the study of a disease generally dispersed by rain.

All the fruit within a bunch are synchronous and close together, so they should be regarded as a uniform

epidemiological unit (de Lapeyre de Bellaire, 1999). In a previous study, populations of *Colletotrichum* spp. reaching a banana bunch were quantified in rainwater runoff (de Lapeyre de Bellaire & Mourichon, 1997). This showed that populations were of greatest importance within 6 weeks after the emergence of the inflorescence, and that the floral parts and main bract were the principal sites of production of the inoculum collected by spore trapping. Thus the hypothesis was proposed that conidial colonization of fruit within a bunch takes place mainly from 'auto-inoculum' produced on the floral parts and the main bract of this bunch. This auto-inoculum would be supplemented by 'allo-inoculum' coming from other banana plants or other organs of the same plant through splashing, insects or aerial dissemination of ascospores (de Lapeyre de Bellaire & Mourichon, 1997).

The objective of this work was to evaluate the role played by the floral parts as sites of inoculum production of the pathogenic species *C. musae*; to measure the relative involvement of auto-inoculum in the levels of fruit contamination; and to better understand the role of rainfall as a conidium dispersal factor and its effect on the levels of fruit contamination. Covering the bunches at flowering with a plastic sleeve, as currently practised by banana growers, was also tested for its effect on auto-inoculum production and subsequent levels of fruit contamination.

Materials and methods

Isolation and quantification of *C. musae* from floral parts

Experimental procedure

Two experiments were carried out on the same site in Guadeloupe, characterized by consistently high levels of anthracnose disease. All the banana plants belonged to the cultivar Grande Naine (a triploid cultivar of the species *Musa acuminata*, Cavendish group). For each experiment, 200 plants were selected on the same date, at the stage when the fruit were in a horizontal position (about 7 days after bunch emergence). The inflorescences on half of the plants were covered with a plastic sleeve (S = sleeved), whereas those of the other half were not (NS). The S and NS banana plants were arranged over the whole site in 10 plots of 10 plants per plot. The plots of the two treatments were arranged alternately. The two experiments were conducted over the course of two distinct seasons (March–June 1996, November 1996–March 1997) in order to obtain different rainfall regimes, at least during the first month after flowering.

Quantification by the suspension-dilution technique

Each week, from flowering until harvest (for 13 weeks), all the floral parts of one fruit from the same hand (hand no. 2) were sampled on each of 200 bunches. The floral parts of a given plot were mixed, placed in 100 mL sterile distilled water and shaken (180 oscillations min^{-1}) for 1 h. The suspension of conidia thus obtained was filtered through a 30 μm sieve and centrifuged at 4000 r.p.m. for 10 min. The pellet was then washed in 40 mL sterile distilled water, and the suspension of conidia diluted 10^2, 10^3 and 10^4 times. Ten platings were made, at the rate of 100 μL of each suspension, onto Mathur's medium enriched with antibiotics (2·5 g $MgSO_4 \cdot 7H_2O$, 2·7 g KH_2PO_4, 1 g peptone, 1 g yeast extract, 10 g saccharose, 15 g agar, 100 mg rifampicin, 0·8 mg ketoconazole, 1000 mL H_2O).

After 3 days' incubation the *Colletotrichum* colonies were identified, for one of the three dilutions, by morphology and microscopic examination of sporulation. One colony of *Colletotrichum* was then randomly chosen in each plate and transferred onto Mathur's medium without antibiotics to be characterized morphologically after 10 days' culture in darkness at 25°C. Hence at each isolation date, 100 cultures of *Colletotrichum* were analysed for each of the treatments S and NS. The pathogenic activity of these isolates was tested following inoculation of both wounded and unwounded green fruit with a suspension calibrated at 10^5 or 10^6 conidia mL^{-1}. Only pathogenic isolates were considered as belonging to the species *C. musae*. The total number of colonies belonging to the genus *Colletotrichum*, and the proportion of pathogenic isolates among these, provided an estimate of the number of conidia of *C. musae* for each sample taken from one plot.

The interpretation of the results is based on ANOVA of the cumulative number of conidia from flowering to harvest (mean of 10 samples), after logarithmic transformation using SAS software (SAS Institute Inc, 1996).

Effect of sleeving and elimination of auto-inoculum sources on levels of fruit contamination

This study was carried out on the same experimental site as before, which was divided into two equal parts. On one, all the floral parts were removed at flowering together with the bunch bract and the old, senescent leaves (treatment R = removed). On the other half, no such removal was done, except for the removal of leaves around the bunch (treatment NR). In each R and NR subplot some of the bunches were sleeved (S) and others not (NS). Sleeved and nonsleeved bunches were selected so as to distribute these two treatments as uniformly as possible over each of the R and NR areas, thus avoiding zone effects. The combined effect of these operations enabled the comparison of the four treatments NR/NS, NR/S, R/NS and R/S.

The levels of fruit contamination were estimated at harvest by the observation of an external fruit of hand no. 4 sampled from each bunch. The experiment lasted for 10 weeks of flowering and 10 subsequent weeks of harvesting.

Table 1 Percentage of pathogenic (731) and nonpathogenic isolates (259) of *Colletotrichum* obtained from floral parts of banana plants exhibiting different mycelial type, sporulation intensity and mycelial growth at 5 days

	Appearance of mycelium[a]			Sporulation intensity[b]				Growth at 5 days[c]	
Isolates	1	2	3	0	1	2	3	< 50 cm	> 50 cm
Pathogenic	81	17	2	0·1	0·7	10	89·2	10	90
Nonpathogenic	1	17	82	24	69	5	2	87	13

[a]1, short mycelium; 2, moderately fluffy mycelium; 3, very fluffy mycelium.
[b]0, no sporulation; 1, weak sporulation; 2, fairly active sporulation; 3, abundant sporulation.
[c]Incubated at 22°C without illumination.

Fruit contamination at harvest

The level of fruit contamination is represented by the quantity of dark appressoria formed on the surface of the fruit. This was estimated by the number of anthracnose lesions observed when fruit ripened. To ensure a good equivalence between the number of appressoria and the number of lesions, a technique perfected earlier was used that enables a maximum of quiescent infections to be detected (de Lapeyre de Bellaire *et al*., 2000). Fruit were stored for 5 days at 32°C and exposed continuously to 1000 μLL^{-1} ethylene during storage. The severity of the disease, corresponding to the level of fruit contamination, was measured by the number of anthracnose lesions per fruit (NLF), and the incidence of the disease by the percentage of necrotic fruit (PNF).

The weekly observations were treated as blocks. As the variances were not the same, the means of NLF were transformed to their square roots. The percentages of necrotic fruit were transformed to arcsin $[^2\sqrt{(PNF)}]$ before analysis. The different treatments were compared by ANOVA using SAS software (SAS Institute Inc, 1996) with the Newman–Keuls multiple comparison test.

Fruit contamination under shelters

The dispersion of conidia in the complete absence of rain was studied experimentally under shelter. For this purpose 10 banana plants were raised in a plastic tunnel. At the flowering stage, the floral parts of each fruit of five plants were inoculated by the deposit of one 25 μL droplet of a conidial suspension calibrated at 10^6 conidia mL^{-1}. The *C. musae* populations on the floral parts were assessed individually on each plant from flowering until harvest, using the methodology already described. At the same time the *C. musae* populations were also counted on eight plants in the open field. The levels of fruit contamination were estimated at harvest for each fruit of each bunch.

The data were interpreted using ANOVA of the cumulative number of conidia from flowering to harvest, and of the number of anthracnose lesions as described before, considering the means of eight banana plants in the open field, five plants under shelter whose floral parts were inoculated at flowering, and five plants under shelter whose floral parts were not inoculated.

Results

Morphology and population dynamics of *C. musae* on floral parts

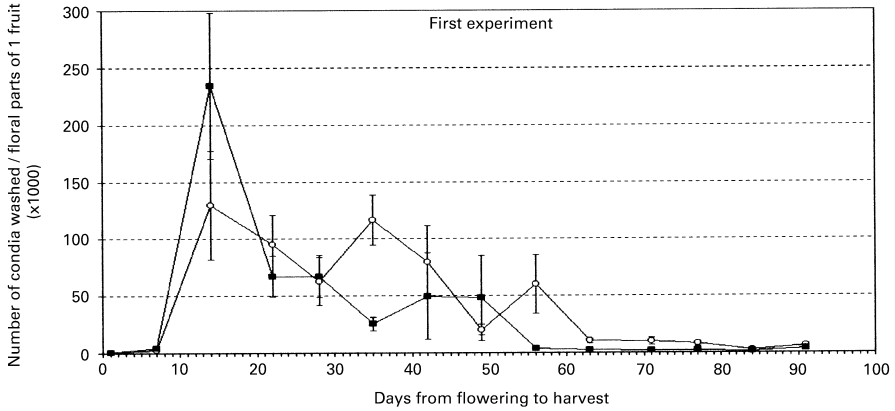
Two morphotypes characterize the 990 isolates of *Colletotrichum* obtained from floral parts (Table 1). The first morphotype, A, corresponds to isolates that sporulate abundantly or moderately in the dark, have a short, not very dense mycelium, and show rapid growth *in vitro* (more than 50 mm in 5 days). The second morphotype, B, is represented by isolates that sporulate very feebly or not at all in the dark, have a fluffy aerial mycelium, and slower growth (less than 50 mm in 5 days). The pathogenic isolates, 731 in number, were mostly of morphotype A, while the nonpathogenic isolates, numbering 259, were mostly of morphotype B (Table 1). Hence for all later observations the distinctive features of morphotype A were used to identify *C. musae*, and pathogenicity was no longer tested except for certain doubtful isolates.

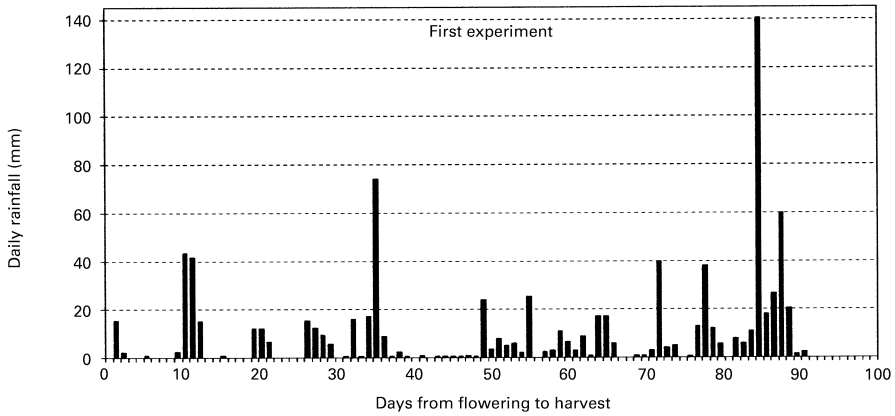
The majority of the isolates of *Colletotrichum* characterized morphologically during the 40 days after flowering (74 and 75% of the total number obtained from the first and second experiments, respectively) belonged to the species *C. musae*. Later the proportion was lower (54 and 56% for these two experiments). Finally, for the cumulative amounts of inoculum from flowering to harvest, calculated from isolations made on floral parts, *C. musae* appeared to predominate (74 and 82%, respectively, in the course of the two experiments).

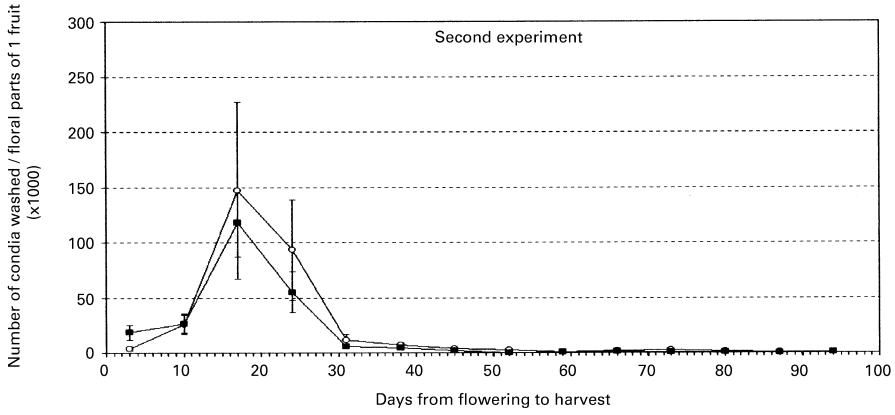
Figure 1 shows that most conidia of *C. musae* were produced within 40 days of flowering. In the course of the first experiment the population level was associated with an irregular rainfall distribution, in contrast to the second experiment, during which the expected production peak was observed, followed by a reduction probably caused by rapid washing away of *C. musae*.

The cumulative amount of inoculum on the floral parts was greater during the first experiment ($P < 0{\cdot}004$). For both experiments the cumulative amount of inoculum was greater on the floral parts of

Figure 1 Number of conidia of *C. musae* isolated from floral parts of banana plants each week from flowering until harvest, for 100 sleeved bunches (■) and 100 nonsleeved bunches (○). Bars represent the standard error of the mean calculated from 10 samples. Each sample consisted of the floral parts of 10 fruits. The daily rainfall is indicated below. Two experiments are shown.


First experiment
Number of condia washed / floral parts of 1 fruit (x1000)
Days from flowering to harvest


First experiment
Daily rainfall (mm)
Days from flowering to harvest


Second experiment
Number of condia washed / floral parts of 1 fruit (x1000)
Days from flowering to harvest

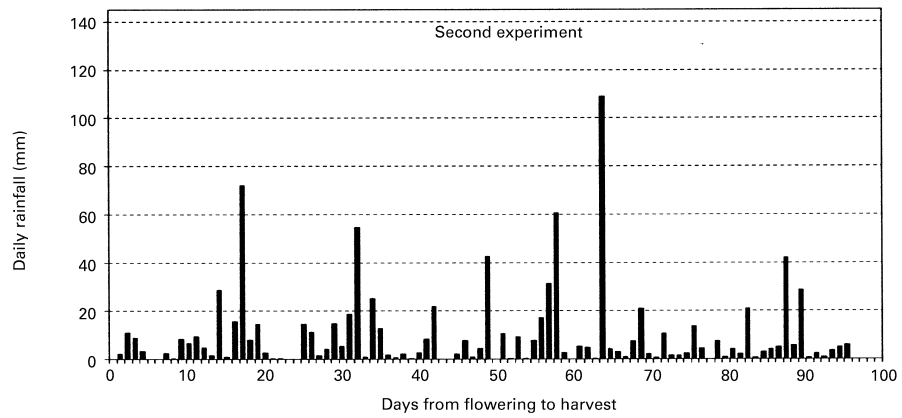

Second experiment
Daily rainfall (mm)
Days from flowering to harvest

Table 2 Comparison of cumulative number of conidia of *Colletotrichum musae* recovered from floral parts of banana plants, from flowering until harvest, for 100 sleeved and 100 nonsleeved bunches

	First experiment	Second experiment
Not sleeved	604·5[a]	302·7
Sleeved	511·6	235·3
F value[b]	< 1	< 1
P value[b]	NS	NS

[a]Mean of 10 samples, each consisting of the floral parts of 10 fruit.
[b]*F* and *P* values were determined by ANOVA of the sleeving effect after logarithmic transformation; NS, not significant; $P = 0{\cdot}05$.

the NS bunches than on those of S bunches, although the differences were not significant (Table 2).

Relative involvement of auto-inoculum in levels of fruit contamination

The severity and incidence of the disease measured on fruit from bunches that had received no treatment (NR/NS) were very high, and markedly greater than those of other treatments (Table 3). The degree of severity observed for this treatment makes it possible to quantify the level of fruit contamination in the presence of both allo- and auto-inoculum sources (total inoculum). The high values observed show that the conditions of this experiment were relatively favourable for disease development.

In the absence of sources of auto-inoculum (treatment R/NS), disease severity observed on fruit was no more than 28% of that measured in the presence of the total inoculum (Table 3). The auto-inoculum that develops on the floral parts and the main bunch bract thus contributes greatly to the level of fruit contamination. In the presence of a plastic sleeve, the relative contribution of this auto-inoculum is less, as shown by comparing the degrees of severity observed for the treatments NR/S and R/S (Table 3).

With or without the plastic sleeve (S or NS), considering the individual data for 10 weeks of harvest, a good correlation occurred ($r = 0{\cdot}83$ and 0·97, respectively) between the severity measured on fruit for which the sources of auto-inoculum were eliminated at an early stage (R) and fruit for which they were not (NR).

Importance of rainfall as a conidium dispersal factor and its effect on levels of fruit contamination

Sleeving, which restricts the flow of rainwater and conidial transport from the source of auto-inoculum towards the surface of the fruit, caused a considerable reduction in the levels of contamination (Table 3). This sleeving effect was greater than that of removing the floral parts and the bract (Table 3). Sleeving interacts significantly with the elimination of sources of auto-inoculum, the latter having a more marked effect when the bunches are not sleeved.

Table 3 Effect of sleeving and of removal of sources of auto-inoculum of *Colletotrichum musae* on severity and incidence of anthracnose at harvest

Source	Severity[a]	Incidence[b]	Number of fruit
Removal of floral parts			
Not removed	47·2	95·8	967
Removed	16·2	86·0	980
F value	287	27·7	
P value	<0·001	<0·001	
Sleeving			
Not sleeved	55·1	97·4	847
Sleeved	12·0	82·7	1100
F value	554	64·2	
P value	<0·001	<0·001	
Sleeving × removal[c]			
NR/NS	94·1 a	99·7 a	396
R/NS	26·5 b	92·9 b	451
NR/S	16·4 c	87·5 c	571
R/S	8·4 d	77·3 d	529
F value	315	31	
P value	<0·001	<0·001	

[a]Mean of numbers of lesions per fruit (NLF) in the observed sample. Data were transformed to square roots for ANOVA.
[b]Mean of percentage of necrotic fruit (PNF). Data were transformed to arcsin (PNF) for ANOVA.
[c]Values followed by the same letter do not differ according to the Newman–Keuls test at $P = 0{\cdot}05$.

In the absence of the plastic sleeve, the levels of fruit contamination are strongly correlated with cumulative rainfall in the first 35 days after flowering (Fig. 2). In the presence of all inoculum sources (NR/NS) and in the absence of sources of auto-inoculum (R/NS), the coefficients of the correlation with rainfall are 0·836 and 0·864, respectively.

The amount of inoculum recovered from inoculated floral parts under shelter was very large, and exceeded the levels found in field-grown plants (Fig. 3). However, very few lesions were observed on fruit under shelter, and even fewer on fruit whose floral parts were not inoculated, in comparison with fruit harvested from plants in the field (Fig. 3).

Discussion

The study of the dynamics of *C. musae* isolated from floral parts by using a suspension-dilution technique confirms results obtained previously using spore traps (de Lapeyre de Bellaire & Mourichon, 1997). Most of the inoculum is produced in the first 30–40 days following flowering; after this critical period production decreases rapidly. Spore infestation of fruit occurs essentially during this critical period, which is most important to consider when assessing the level of fruit contamination. The technique used here has the advantage of distinguishing *C. musae* from other

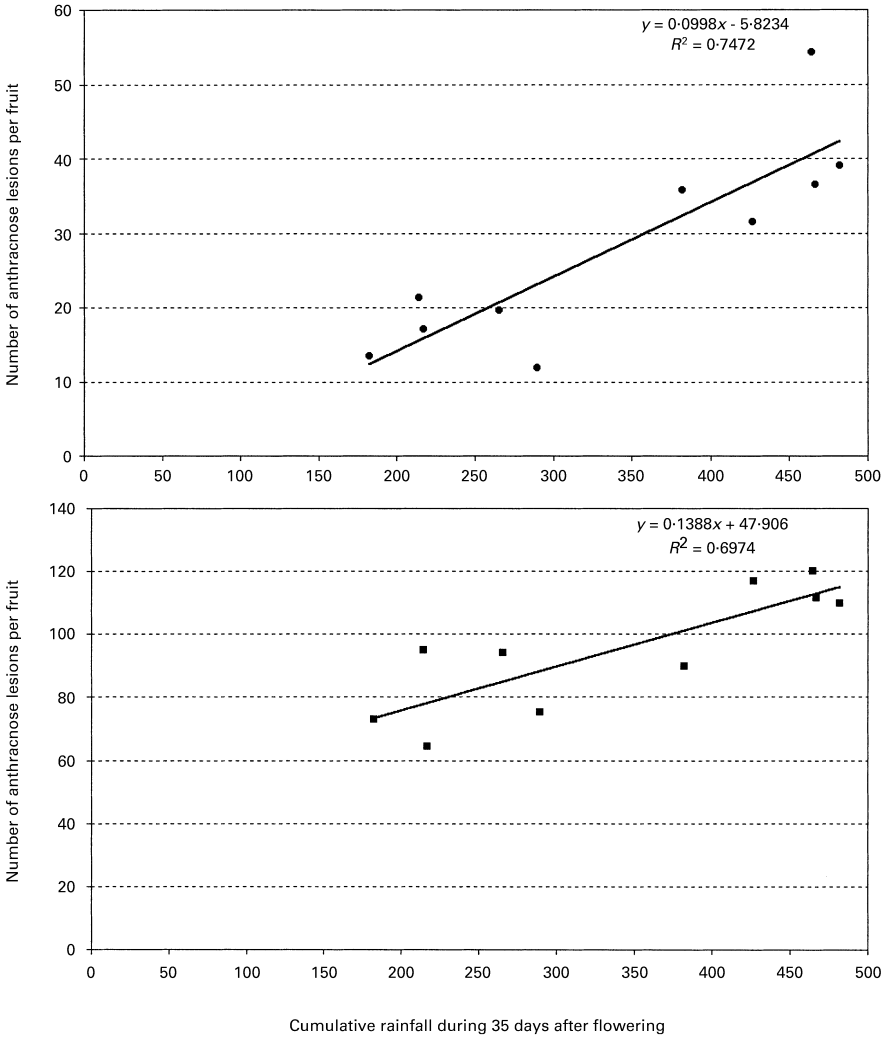


Figure 2 Relationship between allo-inoculum (●) or total inoculum (■) and cumulative rainfall in the first 35 days after flowering. Allo-inoculum was estimated by the severity of anthracnose measured on fruit for which the floral parts and the bunch bract were removed; total inoculum by the severity of anthracnose on fruit for which they were not removed. Each point corresponds to a different week of observation.

Colletotrichum species by the analysis of morphological and pathogenic characters. However, although the morphological characteristics of the pathogenic isolates attributed to *C. musae* appeared to be quite specific in the course of this study, there is no doubt that certain pathogenic isolates have characteristics that cause them to resemble nonpathogenic isolates. The different morphotypes described here have already been reported for *Colletotrichum* isolates from banana (Ashby, 1931; Simmonds & Mitchell, 1940; Kaiser & Lukezic, 1966), and have often been considered to belong to the same species, *C. musae*. Nevertheless, the morphological and pathological variations observed in the course of this study suggest the existence of a complex of species, as has been demonstrated for other models of anthracnose (Hindorf, 1970; Gunnell & Gubler, 1992; Bernstein *et al.*, 1995; Brown *et al.*, 1996).

The decrease in *C. musae* observed after the critical period may be likened to the observations of Meredith, (1962b), who showed that *C. musae* was a primary colonizer of leaves before disappearing progressively during their senescence. Thus it is likely that *C. musae* develops only on organs that are beginning to senesce. Such organs therefore constitute a support for inoculum that quickly runs out after a month. The inoculum present is then washed off by rainwater and the discharged acervuli no longer produce new conidia (Meredith, 1962b). If the rain is heavy, the acervuli quickly release the conidia, as shown by the rapid decrease in conidial numbers found on the floral parts during the second experiment. During the first experiment the inoculum was available over a longer period as it was less easily leached by the rain, which was irregular and interrupted by short dry spells of 4–8 days.

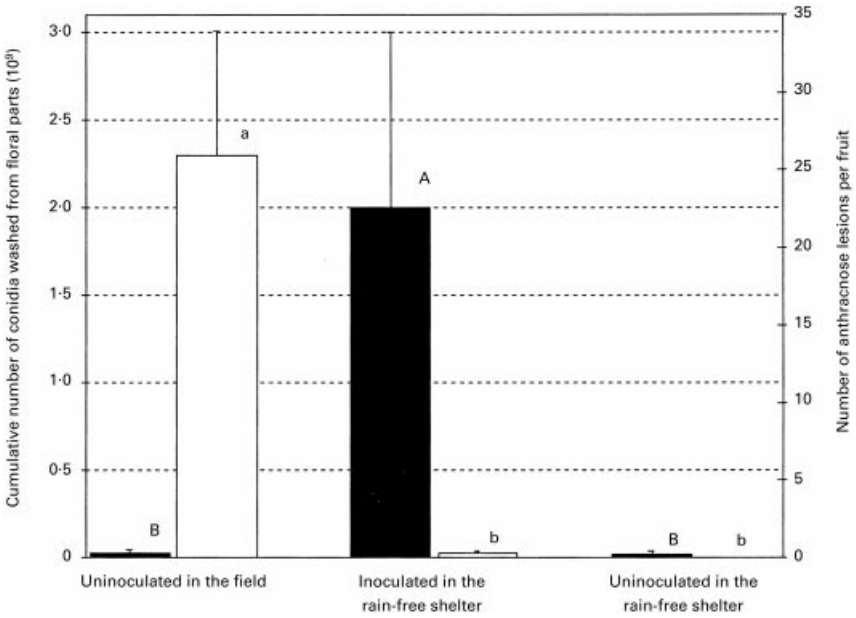


Figure 3 Cumulative number of conidia of *C. musae* recovered from floral parts of banana plants (black bars), from flowering until harvest, on eight banana plants in the open field; five plants under plastic shelters whose floral parts were inoculated at flowering; and five plants under plastic shelter whose floral parts were not inoculated. The number of lesions per fruit (white bars), observed on all the fruit of the bunches under consideration, is represented on the right-hand axis. Bars represent the means calculated for bunches of different treatments, and their standard errors are shown above. Means marked with the same letter do not differ significantly according to the Newman–Keuls test at 5% probability (upper case letters for amounts of inoculum; lower case for numbers of lesions).

Several hypotheses could explain the *C. musae* dynamics on floral parts and other organs. The substrate on which the fungus develops could become progressively unfavourable; or the progressive appearance of other, more competitive or antagonistic fungal species could lead to the disappearance of *C. musae*. In this connection it is interesting to note that in the course of the two isolation experiments, there was a progressive appearance of colonies of the genus *Cephalosporium*, which became preponderant until harvest.

The results show clearly that the floral parts and the bunch bract constitute the main sources of inoculum for spore infestation of fruit. This confirms the conclusions from earlier studies made using spore traps that provided evidence of this auto-inoculum (de Lapeyre de Bellaire & Mourichon, 1997). The similarity between the dynamics of the inoculum reaching the bunches, observed by spore trapping, and the dynamics of *C. musae* populations on floral parts, suggests very strongly that these organs are the most important source of inoculum. This is in contrast to the conclusions of Simmonds & Mitchell (1940), who considered that senescent leaves were the main source of inoculum. In practice senescent leaves are often removed, but they probably contribute to allo-inoculum. This allo-inoculum, although less important than the auto-inoculum that develops on the floral parts and the bunch bract is, however, not negligible. The good correlation observed between the severity measured on fruit from which the sources of auto-inoculum had been removed and on fruit from which they had not suggests that this auto-inoculum is dependent on an external source. Thus it becomes evident that any effect on allo-inoculum (such as removal of dead leaves or weather conditions) will affect the secondary development of auto-inoculum. This could explain the sanitation practices of the banana plantations being the primary factor accounting for very high levels of fruit contamination measured in earlier surveys (Simmonds & Mitchell, 1940; Chillet *et al*., 1998).

The importance of the role of water in spore dispersal and fruit infestation is clearly demonstrated. First, a strong relationship was noted between rainfall and the severity of anthracnose. Such relationships are mentioned by various authors for other fruit anthracnoses (Denham & Waller, 1981; Dodd *et al*., 1992; Waller, 1992), although in the case of pawpaw anthracnose, for which the role of the airborne teleomorph (*Glomerella cingulata*) in the disease cycle has been suggested, the relation between rainfall and the severity of the disease was not clearly shown (Hunter & Buddenhagen, 1972; Duran & Mora, 1988). In the case of banana, placing a perforated plastic sleeve around the bunches has the effect of limiting the circulation of rainwater and reduces the levels of fruit contamination by >82%, although this practice did not affect inoculum production on the floral parts. Similarly, a reduction of anthracnose and stem-end rot severity was reported when bagging mango fruit on the tree with paper bags for more than 56 days (Hofman *et al*., 1997). Finally, it

is shown that in the absence of rain, and even in the presence of a high level of inoculum on the floral parts, the dispersal of conidia is unlikely because the levels of fruit contamination observed were zero. Similarly, no anthracnose development was reported on mango trees covered with rain-out shelters (Fitzell & Peak, 1984).

The results of this study have important applications in the control of banana anthracnose. They reveal real possibilities for avoiding chemical control by reducing the levels of fruit contamination in the field. It is clear that placing a plastic sleeve around the banana bunches reduces the levels of fruit contamination very markedly, by acting directly on the occurrence and amount of rain water. This sleeve effect has never been shown before. Sleeving was developed primarily to accelerate fruit growth (Berril, 1956; Turner & Rippon, 1973; Ganry, 1975) and as a protection against thrips attacks (Lachenaud, 1972). However, this effect on the level of anthracnose occurs only if sleeving is done early. This practice alone appears to be more effective than the removal of the floral parts and the bunch bract, which are labour-intensive operations. Although the combination of the two practices leads to a very satisfactory reduction in the severity of the disease, it is probable that sleeving alone could suffice to maintain the levels of fruit contamination at an acceptable threshold without recourse to chemical control. Work is currently in progress to test this technique on a large scale, and to define economic thresholds in terms of the acceptable number of anthracnose lesions per fruit.

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