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Colletotrichum gloeosporioides: Apparent continuous spore rain may hide local disparities and iterative disease dynamics

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Crop diseases are often considered as episodic events associated with specific environmental and weather conditions, but little is known about disease development when conditions for epidemics are sustained in time, as often occurs in the tropics. *Colletotrichum gloeosporioides* (anthracnose) presence on guava trees was monitored for 45 weeks. Results showed that spore prevalence varied but was consistently present over the period and was greater during the dry than during the rainy season. Secondly, while the general pattern was that of continuous presence of the disease throughout the study area, local patterns on individual trees presented casual peaks that were only partially concomitant, thus suggesting that apparent continuous fungal propagule rain observed in the fields results from distinct repetitive local spore pulses, potentially with asymmetrical contribution from the surrounding vegetation. Local disease dynamics in wild vegetation adjacent to the fields should therefore be more closely investigated in order to clarify its role in crop disease at greater scales such as landscape levels.

Keywords: *Colletotrichum gloeosporioides*, anthracnose, field edges, guava trees, *Psidium guajava*

The nature of crop disease is often described as recurrent local bursts merging into sustained epidemics at regional scales (Stone et al. 2007). Anticipating disease consequences is often lead by monitoring efforts within (Newlands 2018) and across agricultural regions (Nagarajan et al. 2014) to prevent disasters and to try to manage risk and decrease impacts on crops. Many plant diseases result from specialist plant-pathogens interactions, and monitoring requirements are often reliably predicted at local emergence of symptoms (Rumpf et al. 2010), based on regional history of those diseases (Meyer et al. 2021; Velasco et al. 2020) and sometimes knowledge of the various plant species and varieties within the landscape (Papaix et al. 2011). Some plant diseases nevertheless originate from generalist pathogens with diverse sources of inocula (Doyle et al. 2013), especially fungal diseases with explosive spore outbursts when favourable conditions occur (Chakraborty et al. 2004). Eventually, the collective view of plant diseases may be impacted by their casual nature, sudden appearance, yet periodic recurrence (Mailleret et al. 2012), typically exemplified by temperate pathogens which

initiate seasonal disease epidemics. There might be many times though, including under tropical settings (Stanley et al. 2011), where there is the potential for regularly encountered favourable conditions which cause pathogens to multiply and spread rapidly in the environment (Rivera-Mariani et al. 2020), so that disease risk can then manifest as a continuous risk factor for crops.

Such is the case with the fungus *Colletotrichum gloeosporioides*, a worldwide and widespread species complex causing anthracnose disease on a very broad spectrum of hosts (Cannon et al. 2012; Lu et al. 2004), including many fruit crops and vegetables. In the Caribbean, this fungus attacks many commercial and staple crops, including yam (*Dioscorea alata*) (Sweetmore et al. 1994; Green and Simons 1994), and has been the focus of many research efforts for disease management and control in the past decades (McDonald et al. 1998). Unpredictability of the disease triggered many farmers into withdrawing from yam cultivation or shifting toward growing more resistant yam species (Penet et al. 2016b), despite the many control practices thought to be effective (Penet et al.

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2016a), and the creation of resistant varieties (Petro et al. 2011). The fungus relies both on wind and rains for dispersal, though wind promotes long-distance migration and rain drives local epidemics within fields (Penet et al. 2014), and epidemics typically are strongest in October/November on yam. Strain diversity of *C. gloeosporioides* is demonstrably quite high and most often localised, suggesting local origins (Frézal et al. 2018). Several studies have documented a high prevalence of *C. gloeosporioides* in hedge vegetation (Dentika et al. 2022) and locally common weed species (Dentika et al. 2021; Frare et al. 2016; Raid and Pennypacker 1987); and weeds infected with this fungus are known to be involved in anthracnose disease onset on yam in the fields (Dentika et al. 2021).

Thus, the presence of *C. gloeosporioides* on guava (*Psidium guajava*) trees was investigated and fungal infection was monitored weekly. Guava was chosen as a focal species because it is a fruit tree often grown at field margins, either as a complementary food product or for farmers direct food use. Hedges growing spontaneously at field margins might offer temporary protection of crops from winds and also may trap pathogenic spores. However, once certain fungi become established on hedge vegetation, they might also contribute to disease spread in field margins.

Materials and methods

For 45 weeks from February to mid-December 2018, three mature guava trees located at field margins or near buildings were sampled, each being at a distance of 100 - 300 m apart from each other, at INRAE-Centre Antilles-Guyane (study tree locations: 16°12'13.2"N, 61°39'46.2"W; 16°12'12.9"N, 61°39'43.4"W and 16°12'11.4"N, 61°39'42.5"W). Every week, one leaf was removed from the top, middle and base of the canopy of each tree, with the aim of collecting both older and younger leaves. None of the leaves collected

showed any symptoms of *C. gloeosporioides* infection.

Sampled guava leaves were immediately taken to the laboratory to isolate *C. gloeosporioides*. The leaves were washed briefly and successively in diluted bleach solution (sodium hypochlorite at 10%), distilled water, 70% methanol and water to disinfect the surfaces. Small disks of 1 cm were then removed from the apical middle and basal regions of each leaf, using methanol-disinfected hole-punchers, under sterile air conditions in a laminar flow cabinet (model LRF 48). Each leaf disk was then placed in a petri dish with agar based S medium to promote the growth and detection of the fungus *C. gloeosporioides* (Dentika et al. 2021). Petri dishes were sealed with parafilm tape and left to incubate for 4 - 5 days on a shelf and subjected to 12 h light and 12h dark (with Osram T8 L 36 W/865 Lumilux Daylight G13 neons, with lumen intensity close to natural daylight), at room temperature (22 – 28°C). Fungi growing from the leaf disks were then mounted on microscope slides and their conidia were investigated under light microscopy for species identification based on spore morphology (Von Arx 1957), to estimate the weekly prevalence of *C. gloeosporioides* on sampled trees. Prevalence was calculated for each individual tree (three leaves per tree and three disks from each leaf) and estimated by the proportion of leaf discs from which *C. gloeosporioides* had been isolated out of the total leaf disc sample. Weekly sample size was thus 27 (nine disks from each of three trees). Over the whole monitoring period of 45 weeks, there were 405 disks from each tree and 1215 disks in total.

Results

C. gloeosporioides was detected continuously and the degree of leaf infection fluctuated with the seasons (Figure 1). The level of detection was high early in the year, during the dry (Lent) season, and lower in the later months during the rainy season. Despite fluctuations,

the baseline prevalence was always non-null as the fungus was always detected. Patterns of *C. gloeosporioides* prevalence on individual trees nevertheless showed a fairly different view of the infection dynamics (Figure 2), and a much broader variation than was apparent from pooled results: one of the trees had higher prevalence throughout the whole sampling campaign (Figure 2A), another was intermediate and demonstrated more

constancy in weekly prevalence rates (Figure 2B), and the third had globally lower prevalence but wider variation of prevalence peaks (Figure 2C). The range of prevalence peaks (7 - 9 over the study period) also varied from trees to trees and while some were coincidental, some others were shifting in time when comparing the different trees. The peaks were nevertheless not directly correlated to any clearcut recorded weather conditions.

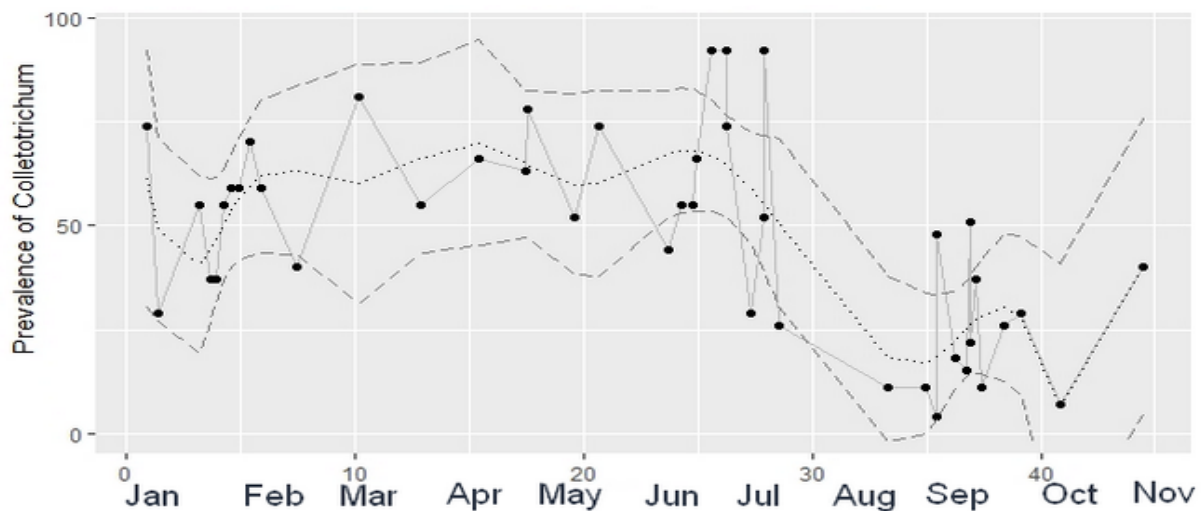


Figure 1: Prevalence of *C. gloeosporioides* over 45 weeks, all trees combined; observed prevalence: solid grey line connecting black dots; black dotted line, average function of prevalence curve (estimated as samples with *Colletotrichum*/total sample ratio); dark grey dash lines, 95% confidence interval

Discussion

The monitoring showed a continuous presence of *C. gloeosporioides* among leaves of guava during the study period, with more or less regular peaks of high prevalence, sometimes superimposed or occurring quite closely. These peaks are indicative of a pulse in fungal dispersal instalment, reflecting sporadic important spore clouds in the environment. Contrary to expectations of fungus development, prevalence peaks were generally higher during the drier study period (0-60%, January to June) compared to the rainy season (60-100%, August to November). However this pattern matched with earlier

historical reports of increased anthracnose risk early during the year (Degras 1986), compared to current more impacting epidemics which more often occur during October/November (Penet et al. 2016a). Recent modes of cropping have evolved toward planting later in the year, to better fit local market expectations of yam harvest at the end of the year, which also allows growing of yams at a more favourable period of rain occurrence. Another consequence of current cropping with late plantation is thus avoiding growth during the dry season, which could translate as decreased anthracnose risk provided a low inoculation of the vegetation nearby fields.

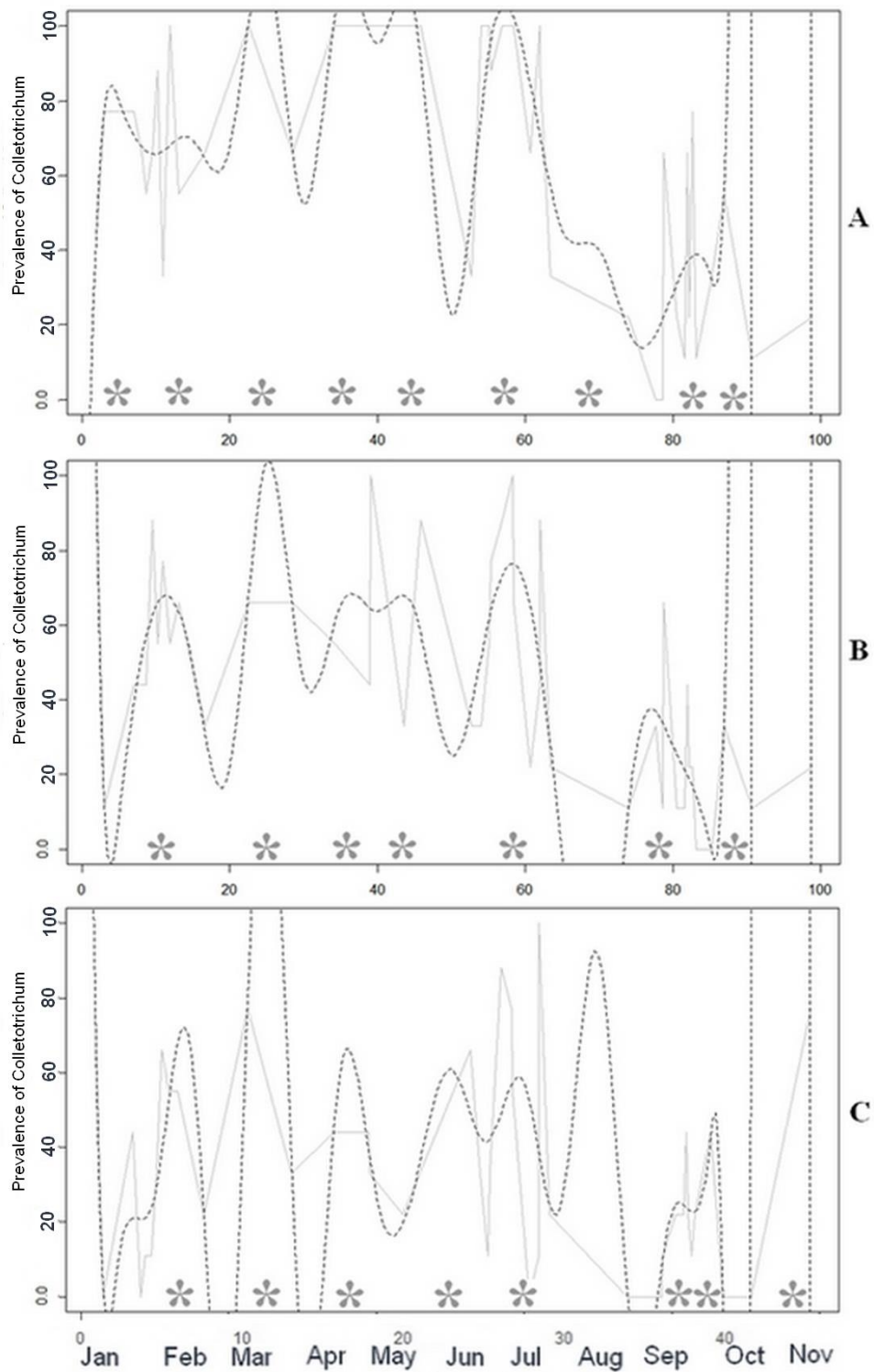


Figure 2. Prevalence of *C. gloeosporioides* over 45 weeks, individual trees (A, B and C); grey lines: total observed prevalence; dashed black lines, naive smoothing estimate of prevalence; the asterisks indicate potential inoculation peaks. Sampling period expressed as % of campaign (A, B) and corresponding equivalence in weeks and month (C).

Individual tree monitoring revealed variation in both intensity of peaks and baseline presence of the fungus demonstrating firstly that the local environment may be more or less receptive of spore bursts and more or less conducive of dispersal, and secondly that shift in peaks might indicate varying contributions of local vegetation to spore clouds throughout the year. As a result, while the overall prevalence pattern is sustained, local effects might exhibit greater variation ranges. A further consequence of local variation is differential timing contributions to spore clouds. Thus, the overall environmental presence of disease is actually hiding periodic pulses from diverse origins and iterative contributions of landscape vegetation to spore clouds. It would be interesting to test whether these also correlate to genetic diversity in strains affecting crops throughout the growing season, as *C. gloeosporioides* is known to be especially diverse in the wild (Lu et al. 2004) and even at very local sampling levels in crops (Frézal et al. 2018). Overall, prevalence was not demonstrating marked canopy effects at either time of monitoring campaign, in contrast to other studies that detected initial contamination from lower canopy (possibly due to inoculation from the ground) and faster progress of infection at the top of the tree (Hamada et al. 2019), but Dentika et al. (2022) found that the top of canopy was less contaminated on average.

These results suggest continuous diffusion of spores in the environment, as variation in prevalence is important both overall and for individual trees and reflects variation in dispersal. Two alternative processes might nevertheless account for high *C. gloeosporioides* presence in the vegetation: quiescence, i.e. when fungi seemingly stop growth, and local inoculation pool, when infections lead to local spore contaminations. Quiescence in *C. gloeosporioides* is indeed a major post-harvest issue in tropical fruits e.g. avocado (Beno-Moualem and Prusky 2000), banana (de Bellaire et al. 2000), mango (Kamle

and Kumar 2016), though the phenomenon is understood as a strategy to dodge antifungal compounds in non-mature fruits (Adikaram et al. 2015) and infections restart as soon as fruits ripen. Infections in vegetative parts of plants are nevertheless not known to result in quiescence (Adikaram et al. 2015). The effects of bursts of local inoculation/infection burst may also produce high variation in prevalence and may not be easily distinguished from the effect of long distance dispersal. Both local and external dispersal probably occur, but the hallmark of a local inoculation burst is a locally prevalence sustained in time. In this study individual trees demonstrated peaks that might sometimes match with local inoculation bursts. Prevalence peaks with dramatic fluctuation occurred frequently and can only result from long distance dispersal of spores. Further studies involving either aerial sampling (estimating spore load) or genotyping of strains would ascertain respective contributions of local vs. long distance dispersal and their impact on disease dynamics.

Conclusion

C. gloeosporioides fungi had varying but pervasive prevalence on guava throughout the year and had prevalence peaks reflecting local bursts in spore clouds across vegetation. These bursts appear sometimes coincidental, sometimes delayed between local trees, indicating that a continuous presence of the pathogen is subjected to iterative pulses locally. Interestingly, while anthracnose is a disease more frequently expressed by crops during the rainy season, the pathogen occurred earlier in the year during the dry season and prevalence was highest during this period, suggesting higher loads of *C. gloeosporioides* spores in the environment and more heavy natural inoculation of the vegetation. The nature of iterative bursts should be investigated regarding genetic composition and aggressiveness of strains, in order to understand its consequences on disease onset in crops, especially yams.

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Statements and declarations

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Competing interests

The authors declare that the research was conducted in the absence of any personal, commercial or financial relationships that could be construed as a potential conflicts of interest.

Data transparency

Data are available from the corresponding author on request. "THIS CAR"

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