# How do hedgerow characteristics alter the dispersal of Pseudocercospora fijiensis propagules? 

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#### Abstract

BACKGROUND: Hedgerows represent an agroecological lever for pest management. To date, few studies have shown that they can be used as a lever for the control of aerial fungal diseases, especially as a barrier to dispersal. On banana production, the main disease is black leaf streak disease (BLSD), which is a fungal disease caused by Pseudocercospora fijiensis. This pathogen disperses through two types of spores: ascospore and conidia. The aim of this study was to observe and to quantify the effect of hedgerows on BLSD dispersal. Trap plants were placed at the same distance to an artificial source of inoculum with a hedgerow on one side. Lesions were counted to establish the daily lesion density of each trap plant. The combination of hedgerow characteristics such as height, width, and optical porosity were used to evaluate its potential capacity to intercept spores. RESULTS: When ascospores were used as a source of inoculum, the lesion density on traps plant decreased up to 50\% between the hedgerow with the lowest interception capacities and the one with the highest interception capacities. For conidia, hedgerow height and side of the trap plants (with or without hedgerow between them and the source) were not significant, but low porosity of the hedgerow reduced the lesion density. On the contrary, for ascospore, the hedgerow effect was anisotropic; the trap plants on hedgerow side had less lesions.

CONCLUSION: Our study is the first experimental proof of the effect of hedgerows on P. fijiensis dispersion, both on conidia and ascospore. We showed that hedgerow characteristics impact the capacity of interception of the hedgerow. © 2023 Society of Chemical Industry.


Supporting information may be found in the online version of this article.
Keywords: Musa spp.; Pseudocercospora fijiensis; black leaf streak disease; hedgerow; barrier effect; sporulation; Martinique

## 1 INTRODUCTION

Studies have now confirmed that biodiversity and complex landscapes tend to reduce pest damages ${ }^{1,2}$ both by hosting predators and by limiting the spread of the pest. Very scarce knowledge is available on the effect of landscape composition and landscape structures on the regulation of disease dynamics. However, landscape elements have shown efficient potential mechanisms of regulation of their inoculum as having a direct or indirect barrier effect. For instance, the presence of natural or semi-natural areas can reduce pathogen dispersal since their disposition and structure can either form corridors or barriers. ${ }^{3,4}$ An indirect barrier effect of tree stratum on the production of inoculum is typically the modification they induce on the microclimate. As shown in agroforestry systems, hedgerows help to limit temperature variations and therefore reduce dew on the leaves, which reduces the infection of leaves by spores and the production of spores themselves. ${ }^{5-7}$ Another benefit of the agroforestry system is to reduce air movement and the dissemination of spores. ${ }^{7}$ In certain cases, allelopathic effects might reduce spore production even if this remains poorly studied. ${ }^{8}$
The direct barrier effect would function as a physical barrier against dissemination of propagules, for example, non-host plants capture
spores before contaminating susceptible plants. Such aspects have been mainly studied in the case of intercropping systems. The effectiveness of a barrier is expected to vary with diseases and especially with their characteristics of dispersal. The two main modes of the spread of fungal diseases are wind or water splash (rain). For waterborne pathogens, the architecture of the plant and the spatial arrangement is an important factor that can alter the dispersal of spores. For example, Vidal, ${ }^{9}$ reported that the barrier effect against

[^0]Septoria in wheat was improved by alternating susceptible with resistant varieties thus increasing the Leaf Area Index (LAI) and density of plants in the rows. This intercropping design reduced the susceptible tissue proportion and trapped spores on non-sensitive plants.
For airborne diseases, alternating rows of resistant or other species with susceptible cultivars is also a way to reduce disease through spore interception by resistant plants. ${ }^{8-12}$ The size of the barrier appears to be a key characteristic that contributes to its effectiveness, for example, the wider the non-host or resistant crop, the more efficient it is for limiting the spread of disease. ${ }^{13}$ The rate of disease reduction depends on the associated species. ${ }^{14}$ Fernández-Aparicio et al. ${ }^{15}$ also demonstrated differential effects of the density of intercropped plants, low densities limiting horizontal dispersion of Mycosphaerella pinodes severity on pea plant, while high density alters its vertical dispersion. Similar effects on disease epidemics have also been observed comparing a reduction of host density with intercropping, ${ }^{16}$ because increasing distances between susceptible plants also alters disease spread. ${ }^{17}$

Black Leaf Streak Disease (BLSD) also known as black Sigatoka, caused by the fungus Pseudocercospora fijiensis, ${ }^{18,19}$ is a foliar disease of Musa spp. that provokes leaf necrosis which inhibits photosynthesis, leading to a decrease of yield and reduction of green life of fruit, compromising its quality. ${ }^{18}$ BLSD has the most important economic impact on banana production. ${ }^{20}$ This disease is the reason for the main use of pesticides in this crop leading to important fungicide applications and to an active ingredient load approaching 70 kg per hectare per year. ${ }^{20,21}$ To make production more ecologically friendly, new agroecological levers need to be developed. Pseudocercospora fijiensis produces two types of propagules: ascospores by sexual reproduction and conidia by asexual reproduction. ${ }^{22}$ Conidia are produced in the early stages of the disease and are dispersed only a few meters away, while ascospores are produced in the necrotic stages (stage 6) and spread over hundreds of meters. ${ }^{23}$ Even if dispersal is a key component in disease epidemiology, there is still a lack of knowledge on the effect of different landscape structures on the dispersion of fungal diseases in general ${ }^{4}$ and in particular for BLSD.
In agroforestry systems, a reduction of lesion density and spore abundance has been observed for BLSD. ${ }^{24}$ Additionally, the presence of trees is likely to act as barriers to the dispersal of propagules. ${ }^{7,24,25}$ On the other hand, using a large BLSD monitoring data and the modelling of landscape effects on disease dynamics in Martinique, we have highlighted that hedgerow might alter

BLSD epidemics. ${ }^{26}$ Indeed a review of hedgerows effect on the dispersal of fungal propagules, suggests that windbreak hedgerows reduce propagule dispersal from infested to healthy fields. ${ }^{25}$ However, to date, no experimental studies have been carried to demonstrate such hedgerows effects, particularly for the dispersal of spores of $P$. fijiensis.

The goal of this study was to assess potential direct barrier effects of hedgerows on the dispersion of ascospore and conidia of $P$. fijiensis. We have used hedgerows with different characteristics to see how they could influence this barrier effect. To this end, we carried out 20 experiments on seven hedgerows, using a controlled source of spores and trap plants to measure the influence of hedgerows on the dispersal of $P$. fijiensis spores.

## 2 MATERIALS AND METHODS

In this work, we carried out two experiments to determine the capacity of regulation of the hedgerow on each type propagule dispersal: ascospore and conidia. These studies included a total of 20 experiments, 11 with artificial sources of ascospore and nine9 with artificial sources of conidia. These experiments were performed in Martinique, using seven hedgerows with different characteristics (Table 1), four being used for the study of barrier effects using ascospore sources and three for the study of barrier effects using sources of conidia. We located trap plants on each side of hedgerows at equal distances to the artificial source of inoculum to measure abundance of spores. We collected wind data during the experiments for evaluating potential anisotropic effects of hedgerows on BLSD dispersal.

### 2.1 Hedgerows

Two criteria were used for the selection of hedgerows used for our studies: (i) they had to be far enough ( $>400 \mathrm{~m}$ ) from any banana plants in order to limit the influence of other sources of spores, ${ }^{23}$ and (ii) hedgerows had to be at least 10 m long and homogenous. We selected contrasted hedgerows covering a wide range of characteristics (Fig. 1, Table 1).
These characteristics included their shape that is, height (at 1.5 m high and at the canopy), width and their optical porosity (Table 1) which could influence spore interception. As banana plants are 5 m high, hedgerow's height had to be equal or superior to 5 m . With a laser rangefinder, we measured the height and width at three points on the length of each hedgerow and calculated the average. For optical porosity, we used the same method as Lazzaro. ${ }^{27}$ The principle is to calculate the percentage

| Hedgerow number | Experiment | Latitude | Longitude | Spore type | Height (m) | Width (m) | Optical porosity | Hedgerow interception surface (HIS) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | A4, A6, A8 | 14.691293 | -61.007434 | Ascospores | 4.8 | 1.0 | 0.62 | 3.36 |
| 2 | C7, C8, C9 | 14.657885 | -60.918078 | Conidia | 4.7 | 3.8 | 0.95 | 16.74 |
| 3 | C1, C5, C6 | 14.566732 | -60.974873 | Conidia | 7.3 | 3.1 | 0.81 | 18.40 |
| 4 | $\begin{gathered} \mathrm{A} 1, \mathrm{~A} 2, \mathrm{~A} 3 \\ \mathrm{~A} 5 \end{gathered}$ | 14.720637 | -60.995838 | Ascospores | 9.2 | 2.8 | 0.88 | 24.90 |
| 5 | C2, C3, C4 | 14.695125 | -60.917391 | Conidia | 9.0 | 3.0 | 0.95 | 25.42 |
| 6 | $\begin{gathered} \text { A10, A11, } \\ \text { A12 } \end{gathered}$ | 14.694566 | -60.917806 | Ascospores | 6.6 | 8.3 | 0.92 | 50.40 |
| 7 | A7, A9 | 14.780155 | -61.007303 | Ascospores | 8.1 | 11.6 | 0.94 | 93.96 |



Figure 1. Photos of hedgerows used during experiments: (A) hedgerow 1 (Hedgerow Interception Surface $=3.36$ ) and $(B)$ hedgerow 7 (Hedgerow Interception Surface $=93.96$ ).
of light that can pass through the hedgerow. We took a photo of each hedgerow from top to bottom, converting the image to 1-bit black and white and the percentages of each were calculated. ${ }^{27}$ The percentage of hedgerow pixels (black pixels) was assumed to be a predictor of the surface that could intercept spores and was the variable used as optical porosity in our calculations. The optical porosity varied between 0 (transparent) to 1 (opaque). Then for each hedgerow, we calculated the potential hedgerow interception surface (HIS) using all hedgerow characteristics (height, width, optical porosity) (Eqn (1), Table 1), HIS being putatively linked to the capacity of the hedgerow to intercept fungal spores. We sorted the hedgerows per HIS, hedgerow 1 having the lowest HIS and hedgerow 7 the highest HIS (Table 1, Fig. 1).

$$
\begin{equation*}
\text { HIS }=\text { height } \times \text { width } \times \text { optical porosity } \tag{1}
\end{equation*}
$$

### 2.2 Artificial sources of fungal spores

In our experiment, we used two types of sources of spores, one with ascospores (experiments A, Table 1) and the other with conidia (experiments C, Table 1). For ascospore, we built an artificial banana plant architecture with six leaves made of PVC hose, iron wire and mosquito net (Fig. S1(A)). We concentrated necrotic banana leaf pieces on these artificial leaves representing
approximately $1.5 \mathrm{~m}^{2}$ necrotic surface as an important source of ascospore. Indeed, according to Burt's calculation, ${ }^{28}$ the size of this source could be estimated to about 6 million ascospores. To provoke ascospore discharge, necrotic leaves were watered every day with about 10 L of distilled water. ${ }^{29}$ For sources of conidia, we collected five infected banana plants in a field with leaf length between 1 and 1.5 m , we potted them and we removed all necrotic parts of the leaves during the experiment, to have only conidia sporulation (Fig. S1(B)).

### 2.3 Trap plants

We used trap plants (young banana plants from in vitro micropropagation) to determine spore dispersal from the artificial source. ${ }^{23,24}$ Trap plants with new leaves unfurled, were exposed in the field from 9 to 12 days, allowing for the unfurled leaves to be totally unrolled. Then, they were placed in a greenhouse under a plastic bag to maintain humidity at $100 \%$. Temperature ranged between 25 and $29^{\circ} \mathrm{C}$ for optimal development of lesions during incubation. ${ }^{6,30}$ Lesions were counted after twice the incubation time minus 2 days ${ }^{23}$ and the daily density (DD) of lesions was calculated (Eqn (2)) with the number of lesions divided by leaf area (Eqn (3)) and number of days of exposure.

$$
\begin{align*}
& \text { DD }=\frac{\text { number of lesions }}{\text { Leaf area } \times \text { number of day of exposure }}  \tag{2}\\
& \text { Leaf area }=\text { Leaf length } \times \text { Leaf width } \times 0.83 \tag{3}
\end{align*}
$$

### 2.4 Experimental settings

We placed the source of spores on one side of the hedgerow. Then, all trap plants were placed in lines of five plants on each side of the hedgerow at equal distances to the artificial source of spores. The distance between the spore source and the trap plants were established according to their dispersal ability. For experiments with a source of ascospore, trap plants were placed at 10, 20, 30, 40 and 50 m from the source (Fig. 2(A)). For experiments with a source of conidia, trap plants were placed at 3,7 , and 11 m from the source because of shorter distance of disper$\operatorname{sion}^{23}$ (Fig. 2(B)). To guarantee no competition between the trap plants on the line, we spaced them 1.5 m apart. Finally, the trap plants were installed on poles at 1.7 m above the ground to benefit from the same climatic conditions as a banana plant.

### 2.5 Wind data

We used a weather station (FROGGIT ${ }^{\circledR}$ WS1800) placed on the plot to collect direction $\left({ }^{\circ}\right)$ and wind speed $\left(\mathrm{km} \cdot \mathrm{h}^{-1}\right)$ every 10 min during exposure of the trap plants. The direction was given in $22.5^{\circ}$ sections, and we kept that value in our calculations. We placed the compass rose center on the source of spores to associate each trap plant to the section corresponding to the wind direction coming from the spore source. We considered that winds directed from the source to the trap plant were the most efficient to disperse spores. All recorded wind speeds were added (by sections of $22.5^{\circ}$ ). For each trap plant, we associated the wind speed sum (WSS) oriented from the source to this trap plant.

### 2.6 Statistics

To define how characteristics of the hedgerows impacted the dispersal of BLSD spores, we modelled the daily density (DD) of each trap plant using Generalized linear model (GLM) including the following variables as predictors: the side of the trap plant (side
(A)






(B)



Figure 2. Experimental designs: (A) testing barrier effect of hedgerows on ascospores dispersal, (B) testing barrier effect of hedgerows on conidial dispersal.
protected by the hedgerow or the side exposed directly to the inoculum source), the distance to the source, the WSS, the hedgerow height, the hedgerow width, the hedgerow optical porosity, and the HIS. After testing these variables following a backwardforward selection procedure, we only kept the significant predictors. All statistical analyses were performed with R 4.1.1. ${ }^{31}$

## 3 RESULTS

### 3.1 Effect of hedgerows on the dispersal of ascospores

The patterns of DD on each trap plant for the ascospore experiments are presented in Fig. 3, ranging between 0 and 0.18 lesions. $\mathrm{cm}^{-2}$.day ${ }^{-1}$. DD was significantly different between the two sides of the hedgerow, with higher lesion densities on the source side (Table 2; $P<0.01$, estimate $=0.01509$ ). The DD decreased with the distance to the source and was contrasted for the four tested hedgerows (Fig. 4), and this decrease was significant (Table 2; $P<0.0001$, estimate $=0.52648$ ). Either hedgerow characteristics (height, width, and optical porosity) ( $P<0.05, P<0.0001$, and $P<0.01$, respectively) or HIS had a
significant effect on DD ( $P<0.0001$ ). We chose to keep HIS as a predictor of DD because it is a variable that integrates all hedgerow characteristics and it was strongly significant in the model (Table 2; $P<0.0001$, estimate $=-0.00072$ ). With stronger wind [log(WSS)], less inoculum is trapped on the trap plant ( $P<0.0001$, estimate $=-0.00371$ ) (Table 2). Overall, the linear model explained $23.9 \%$ of the variance of $D D\left(R^{2}=0.2392\right)$.
Using the model presented in Table 2, we predicted DD for the four hedgerow characteristics used and in a case without hedgerow. This prediction was made for two strengths of wind blowing equilaterally (light and strong). Lesion densities decreased with distance to the source and with the rise of HIS (Fig. 5). The source side trap plants had higher average DD. Strong winds (corresponding to the maximum average wind in all experiments) led to lower contaminations than light wind (corresponding to the minimum average wind in all experiments). The highest regulation was observed with hedgerow 7 in light wind, which reduced lesion densities by $\sim 65 \%$ at 30 m distance to the source compared to the case without hedgerow.




Figure 3. Lesion density by trap plant (lesion. $\mathrm{cm}^{-2}$. day $^{-1}$ ) in the ascospores experiments. The red squares show the sources of ascospores. The green rectangles show the hedgerows [the surface and color depend on their HIS (Hedgerow Interception Surface) and their optical porosity, respectively]. The blue circular bar plots show the wind speed sum [wind speed sum (WSS) in $\mathrm{km} \cdot \mathrm{h}^{-1}$ ] according to the direction. Missing points correspond to dead plants.

Table 2. Equation, description of the variables and results from the linear model of lesion densities during experiments with an inoculum source of ascospores

| Equation <br> Variables | $\mathrm{DD}=\log ($ WSS $)+\frac{1}{\text { distance }}+$ HIS |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Unit | Description | Df | Estimates | AIC | $\delta$ AIC | P |
| Log(WSS) | $10 \mathrm{Km} \cdot \mathrm{h}^{-1}$ | Logarithm of Wind Speed Sum during exposure in a cardinal direction | 1 | -0.00371 | -2756.1 | 7.9 | 0.00178 |
| HIS | - | Hedgerow interception surface $=$ Height $\times$ width $\times$ optical porosity | 1 | -0.00073 | -2699.1 | 64.816 | <0.0001 |
| 1/distance | $\mathrm{m}^{-1}$ | Inverse of the distance to the source ( $10,20,30,40,50 \mathrm{~m}$ ) | 1 | 0.52648 | -2733.1 | 30.795 | <0.0001 |
| Side | - | Side of the trap plant (the side exposing directly to the inoculum source) | 1 | 0.01509 | -2758.2 | 5.747 | 0.00565 |
| AIC, Akaike information criterion; df, degrees of freedom; $P, P$-value; $\delta$ AIC, variation of AIC explained by the predictor. |  |  |  |  |  |  |  |



Figure 4. Mean and standard deviation of lesion densities (lesion. $\mathrm{cm}^{-2}$. day $^{-1}$ ) observed in experiments with ascospore sources on four hedgerows and their HIS (Hedgerow Interception Surface), related to the distance $(\mathrm{m})$ to the spore source and of the side of the hedgerow. The right side in green shows trap plants that were separated from the source by the hedgerow; the left side in white shows the trap plants that were not separated from the source by the hedgerow.


Figure 5. Prediction of the daily lesion density on trap plants according to the distance from the source of ascospores; on the right side in green, trap plants were separated from the source by the hedgerow while on the left in the white area trap plant are on the same side as the ascospore source. The type of hedgerow is defined by their HIS (Hedgerow Interception Surface), and the two wind forces (light and strong) correspond, respectively, to the minimal ( $11.98 \mathrm{~km} . \mathrm{h}^{-1}$ ) and maximal ( $203.54 \mathrm{~km} . \mathrm{h}^{-1}$ ) WSS (Wind Speed Sum) observed on average per experiment in ascospore experiments.


Figure 6. Lesion density by trap plant (lesion. $\mathrm{cm}^{-2}$. $\mathrm{day}^{-1}$ ) in the conidia experiments. The red squares show the sources of conidia. The green rectangles show the hedgerows [the surface and color depend on their HIS (Hedgerow Interception Surface) and their optical porosity, respectively]. The blue circular bar plots show the wind speed sum [wind speed sum (WSS) in $\mathrm{km} . \mathrm{h}^{-1}$ ] according to the direction. Missing points correspond to dead plants.

### 3.2 Effect of hedgerows on the dispersal of conidia

In conidia experiments (Fig. 6), we observed lower lesion densities ranging between 0 and 0.037 lesions. $\mathrm{cm}^{-2}$. day $^{-1}$, according to the tested hedgerows. These DD did not depend significantly on the side of the hedgerow ( $P=0.9041$ ) unlike ascospore experiments, or distance from the source of conidia ( $P=0.9599$ ) (Fig. 7), but mostly by porosity of the hedgerow. DD was not significantly altered by the height of the hedgerow, so we did not use HIS as a descriptor of the hedgerow but only the optical porosity which had a strong significance. After selection of the significant variables in the model, DD was significantly predicted by
the optical porosity (linear regression $P<0.0001$, estimate $=$ -0.39747 ), the wind $[\log (\mathrm{WSS})](P<0.05$, estimate $=0.03573)$, and their interaction (linear regression $P<0.05$, estimate $=$ -0.03844 ) (Table 3).
Our model predicted that hedgerows with high optical porosity (close to 1 , i.e., opaque) led to lower DD compared to hedgerows with low optical porosity (Fig. 8). Interestingly, the interaction between the optical porosity of hedgerows and wind suggests that the hedgerow does not have the same effect with light wind or strong wind. A hedgerow with high porosity tends to increase DD when the wind increases, and inversely low porosity


Figure 7. Mean and standard deviation of lesion densities (lesion. $\mathrm{cm}^{-2}$. $\mathrm{day}^{-1}$ ) observed in experiments with conidia according to the distance ( m ) from the spore source on three hedgerows and their porosities. On the right, in the green area, trap plants are separated from the source by the hedgerow while in the white area trap plants are on the same side as the source.

| Equation <br> Variables | $\mathrm{DD}=\log (\mathrm{WSS}) \times$ porosity |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Unit | Description | Df | Estimates | AIC | $\delta$ AIC | P |
| Log(WSS) | $10 \mathrm{Km} . \mathrm{h}^{-1}$ | Logarithm of Wind Speed Sum during exposure in a cardinal direction | 1 | 0.03573 | -1578.3 | 2.2 | 0.02749 |
| Optical porosity | - | Hedgerow optical porosity included between 0 (no hedgerow) and 1 (opaque hedgerow) | 1 | -0.39747 | -1516.0 | 137.2 | <0.0001 |
| Log(WSS):Optical porosity | - | Interaction between logarithm of Wind Speed Sum and optical porosity | 1 | -0.03844 | -1578.7 | 2.5 | 0.03467 |
| AIC, Akaike information criterion; df, degrees of freedom; $P, P$-value; $\delta$ AIC, variation of AIC explained by the predictor. |  |  |  |  |  |  |  |

hedgerows tend to be more effective at reducing DD when the wind increases (Fig. 8).

## 4 DISCUSSION

Our experiments aimed at determining how hedgerows impact the dispersion of ascospores and conidia of $P$. fijensis. Here, we have shown that hedgerows limit the dispersal of both propagules and have evidenced a differential effect of a gradient of hedgerows. To our knowledge, this is the first experimental study that highlights
the effect of hedgerows in spore dispersal for this pathosystem, a domain also poorly studied for other airborne diseases.
Our method intended to be as close as possible to a field situation. By using trap plants, we only measured infectious spores contrary to Burkard trap ${ }^{5}$ or Rotorod sampler. ${ }^{32}$ Indeed, using spore traps, it is not possible to distinguish spores alive or dead. Trap plants are poorly used in dispersion studies because it is much more complex to manipulate living organisms like plants and also because it requires much work. However, this method allows to detect efficient inoculum which is more relevant for epidemiological studies. This is


Figure 8. Prediction of the daily lesion density (lesion. $\mathrm{cm}^{-2}$. day $^{-1}$ ) caused by conidia sources on trap plants as a function of the Wind Speed Sum [log (WSS) $\mathrm{km} \cdot \mathrm{h}^{-1}$ )], and for two hedgerows tested in the conidia experiments (Hedgerows 2,3 with optical porosities of $81 \%, 95 \%$, respectively) and a simulation of experiment with no hedgerow (with a porosity of $0 \%$ ).
all the more important that survival of spores can be affected by UV radiation. ${ }^{33}$ In former studies we used a fungicide resistant artificial inoculum source, which could not be possible in Martinique because such strains of $P$. fijiensis are not present. ${ }^{23}$ Then, in order to limit contaminations from other sources than the source implemented in the experimental design, our experiments were located more than 400 m away from any banana plant and inoculum source. Based on our knowledge, this was sufficient to limit important contaminations from other sources. ${ }^{6}$
Our results showed that these effects differed according to the type of propagules (conidia or ascospore). In both cases, hedgerows are efficient to reduce the dispersal of fungal propagules. For ascospores, the inoculum collected on trap plants was lower on the opposite side from the source of inoculum, suggesting possible spore interception by hedgerows. For conidia, we did not observe any unilateral effect but rather a global effect of the hedgerow on the inoculum trapped. We did not observe an effect of distance from the source either but maybe the distance gradient tested is not wide enough. Several characteristics of hedgerows, height, width, and optical porosity were significant to limit ascospore dispersal, while only their optical porosity explained the reduction of conidial dispersion. The wind also influenced spore dispersal in interaction with hedgerows, but differentially for both propagules.
The height of the hedgerow can affect the spread of airborne diseases, depending on the dispersal height of the pathogen. ${ }^{34}$ Our results in conidial dispersion showed that hedgerow height does not appear to affect the efficiency of the tested hedgerows (ranging between 4.7 and 9.0 m height). This might be linked to the aerologic properties of the pluricellular filamentous conidia that tend to fall more than fly, contrary to fusiform bicellular ascospores. ${ }^{35}$ Indeed, conidia are not trapped 2 m above banana plants. ${ }^{35}$ In the case of ascospore dispersion, several properties of hedgerows, the height, width, and optical porosity altered the inoculum trapped, as well as combined in an indicator of HIS. The higher the HIS, the higher the surface of nonsusceptible surfaces that participate in intercepting spores. ${ }^{7}$
Hedgerows also impact the aerology by functioning like a barrier, disrupting the airflow. ${ }^{36}$ They might act like a windbreaker
and limit wind strength, and then probably reduce the release of spores in the air. Hedgerows also change wind dynamics and thus the spore pathway potentially protecting susceptible crops from contamination. Here we have found that hedgerows with a low porosity strongly reduced conidia dispersal and this might be a windbreak effect. Indeed, since conidia of $P$. fijiensis are released by wind, ${ }^{37}$ modifying its strength could impact the quantity of propagules in the air because less conidia might be released when wind speed is too low. For hedgerows with a low porosity, conidia trapped were lower with strong winds than with light wind. This might be linked to important turbulences of wind that might transport conidia out of the experimental design. These turbulences around hedgerows might also explain that ascospores are also less numerous for strong winds. Ascospores are lighter and because of that the wind strength necessary for their dispersal and flight will be lower. This difference of importance of the wind was observed earlier in spore trapping studies. ${ }^{35}$ The main influence of hedgerows for reducing ascospore dispersal might be by intercepting the spores in the canopy; the higher the HIS, more ascospores can be caught.

Therefore, hedgerows could provide multiple roles in the management of BLSD: limiting external contamination by intercepting spores but also reducing auto-contamination by wind-breaking and changing aerology in the field. In earlier experiments, Rieux et al., ${ }^{23}$ observed an exponential decrease of ascospores dispersed from an inoculum source in an open field, with a very sharp decrease after 100 m . We observed such pattern with the less efficient hedgerows (low HIS) (Fig. 4, Hedgerow 1). However, for hedgerows having a higher HIS (Fig. 4, hedgerow 7), less ascospores were trapped and their decrease was slower.
A similar experimental design including the same type of inoculum sources has been used to better understand the dispersal of $P$. fijiensis propagules. ${ }^{23}$ Interestingly, the maximum lesion densities per day in an ascospore experiment was similar to the maximum measured ( 0.18 lesion.cm ${ }^{-2}$.day ${ }^{-1}$ ) in this former study in an open field. ${ }^{23}$ However, in our experiments the level of inoculum collected from trap plants varied between experiments at
the same site. This was likely due to the amount of inoculum available in the source, depending on where and when necrotic leaves were collected. On another hand, UV radiation might have also affected the viability of ascospores trapped on leaves and cause variations in infection efficiency between experiments. ${ }^{33}$
In future studies, it would be interesting to model how the disposition of hedgerows could improve the regulation of BLSD in a field to establish which hedgerow patterns would provide the best control. Such a modelling approach would certainly be useful to explore how hedgerows surrounding banana fields protect them from long distance dispersal ${ }^{34}$ and how tree lines between banana plant rows, can protect them from field autocontamination as in agroforestry systems. ${ }^{24,38}$

## 5 CONCLUSION

In this work, we conducted two experiments to study how hedgerows alter dispersal of conidia and ascospores of $P$. fijiensis. With our experiments, we were able to determine which characteristics of the hedgerow enhanced their barrier effect depending on the propagules and hedgerow characteristics. We also highlighted that the barrier effect of hedgerows depends on wind speed. Our results show that hedgerow might be an efficient lever to control BLSD and should be integrated in IDM strategy. However, field experiments should be done to adjust such arrangements as an efficient lever for BLSD control.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## CONFLICT OF INTEREST STATEMENT

Authors declare no conflict of interest.

## SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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