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Modelling in vitro mycelial growth, sporulation, and spore germination of *Mycosphaerella musicola* under different levels of illuminance

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ABSTRACT

This study aimed to evaluate the effect of light on mycelial growth, sporulation, and germination in vitro of the causal agent of Yellow Sigatoka. For mycelial growth, 10 colonies were transferred to Petri dishes, and their weight (mg) was evaluated at 0, 15, 21, 28, 35, and 42 days of cultivation under different levels of illuminance. Under the same conditions, the sporulation was also quantified at 5, 7, 11, 13, and 14 days. For the germination assay, equal volumes of a spore suspension were dispensed into small glass containers, which were then placed inside shading structures with different illuminance intensities. Hourly, lactophenol was added to a container from each environment to halt development, and illuminance was measured simultaneously using a light meter. The data obtained from sporulation (positive linear relationship) and germination (positive exponential behavior) were significant across the tested illuminance levels. Mycelial growth fitted a linear model only partially at high illuminance levels. In contrast, sporulation increased significantly with greater light intensity, being best described by a linear regression that accounted for 97% of the observed variation. Spore germination followed an exponential pattern, with higher percentages under elevated illuminance. It is concluded that although mycelial growth is not light-dependent, fungal reproduction and the onset of infection are strongly stimulated by higher light intensities.
Keywords: Banana, Pseudocercospora, Infection, Light, Mathematical models.

Modelagem matemática do crescimento micelial, esporulação e germinação de esporos de *Mycosphaerella musicola* sob diferentes níveis de iluminância

RESUMO

O objetivo deste estudo foi avaliar a influência de diferentes níveis de iluminância no crescimento micelial, na esporulação e na germinação in vitro do agente causal da Sigatoka-amarela. Para a avaliação do crescimento micelial, dez colônias foram transferidas para placas de Petri, e sua massa (em mg) foi determinada aos 0, 15, 21, 28, 35 e 42 dias de cultivo. Sob as mesmas condições, a esporulação foi quantificada aos 5, 7, 11, 13 e 14 dias. Para a germinação, alíquotas de uma suspensão de esporos foram plaqueadas em pequenos frascos de vidro, os quais foram dispostos em diferentes ambientes de sombreamento. A cada hora, lactofenol era adicionado aos frascos para interromper o crescimento, enquanto a iluminância era medida com um luxímetro. Os dados revelaram que a esporulação, que apresentou uma relação linear positiva, e a germinação, que exibiu um comportamento exponencial positivo, foram significativamente influenciadas pelos níveis de iluminância testados. O crescimento micelial ajustou-se parcialmente ao modelo linear em altos níveis de iluminância. Em contraste, a esporulação aumentou significativamente com maior iluminância, sendo melhor descrita por regressão linear, explicando 97% da variação observada. A germinação mostrou comportamento exponencial, com maiores percentuais sob iluminância elevada. Conclui-se que, embora o crescimento micelial não dependa da luz, a reprodução e o início da infecção são fortemente estimulados por maiores intensidades luminosas.
Palavras-chaves: Banana, *Pseudocercospora*, Infecção, Luz, Modelos matemáticos.

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Modelado matemático del crecimiento micelial, la esporulación y la germinación de esporos de *Mycosphaerella musicola* bajo diferentes niveles de iluminancia

RESUMEN

El objetivo de este estudio fue evaluar la influencia de diferentes niveles de iluminancia en el crecimiento micelial, la esporulación y la germinación in vitro del agente causal de la Sigatoka amarilla. Para evaluar el crecimiento micelial, se transfirieron diez colonias a placas de Petri y se determinó su masa (en mg) a los 0, 15, 21, 28, 35 y 42 días de cultivo. Bajo las mismas condiciones, se cuantificó la esporulación a los 5, 7, 11, 13 y 14 días. Para la germinación, se sembraron alícuotas de una suspensión de esporos en pequeños frascos de vidrio, los cuales se dispusieron en diferentes ambientes de sombreado. Cada hora, se añadía lactofenol a los frascos para detener el crecimiento, mientras se medía la iluminancia con un luxómetro. Los datos revelaron que la esporulación, que mostró una relación lineal positiva, y la germinación, que exhibió un comportamiento exponencial positivo, se vieron significativamente influenciadas por los niveles de iluminancia evaluados. El crecimiento micelial se ajustó parcialmente al modelo lineal en niveles elevados de iluminancia. En contraste, la esporulación aumentó significativamente con mayor iluminancia, describiéndose mejor mediante una regresión lineal que explicó el 97% de la variación observada. La germinación mostró un comportamiento exponencial, con mayores porcentajes bajo iluminancia elevada. Se concluye que, aunque el crecimiento micelial no depende de la luz, la reproducción y el inicio de la infección son fuertemente estimulados por intensidades lumínicas más altas.

Palabras clave: Banano, Pseudocercospora, Infección, Luz, Modelos matemáticos.

INTRODUCTION

Brazil is one of the world's largest banana producers (FAO, 2011). However, despite its prominent position in global production, the country still faces serious challenges in phytosanitary management (Cordeiro; Matos; Kimati, 2005).

Yellow Sigatoka is one of the primary diseases affecting banana crops in regions where environmental conditions favor its development, and it occurs in virtually all banana-producing areas, with few exceptions (Cordeiro; Matos, 2001; 2003). The pathogen adapts well to cooler regions, especially at altitudes above 1,200 meters (Jácome, 2002). Damage caused by both Yellow and Black Sigatoka can be severe in plantations without proper management, reaching 100% under favorable microclimatic conditions, and resulting in fruit with no commercial value (Cordeiro; Matos; Meissner-Filho, 2004).

Based on its origin, semi-shaded environments are considered the most suitable for banana cultivation (Favreto; Model; Tonietto, 2007). The low incidence and reduced severity of Black Sigatoka in areas with limited light availability support this hypothesis (Silva *et al.*, 2025). In environments with only 30% light incidence, there is a significant delay in Yellow Sigatoka infestation, characterized by only a few necrotic leaves, and the disease development period is extended by about 4 days compared with environments receiving approximately 70% light. Nevertheless, the first lesions appear simultaneously under both light conditions (Dold *et al*., 2008).

The effects of light can be either direct or indirect, with greater damage reported in treatments exposed to higher luminosity levels for Black Sigatoka (Norgrove *et al*., 2012). In

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high-density planting systems, incidence is unaffected, however, disease severity is reduced by 18% (Emebiri; Obiefuna, 1992).

Agroforestry systems have significantly reduced the severity of both Yellow and Black Sigatoka by decreasing UV radiation, which is essential for sporulation and the release of fungal spores (Schrotz *et al*., 2000).

Remarkable results showed the effect of light on cereal fungal pathogens (Cerón-Bustamante *et al*., 2023a). For Abreu (2000) sporulation begins three days after cultivation and may fluctuate over time for *M. musicola*. The number of *M. fijiensis* colonies is lower in the dark when the plates remain sealed for 21 or 14 days (Etebu *et al*., 2005). Some studies on interactions between banana plants and *M. fijiensis* indicate that toxin production is associated with light exposure (Lepoivre *et al*., 2002). Other studies show that ultraviolet (UV) radiation is a limiting factor for the production of *M. musicola* ascospores, which explains the low sporulation rates (Jones, 2002).

According to some authors, shading reduces cercosporin activity, a compound involved in pathogenesis and dependent on photosensitization (Daub; Ehrenshalf, 2000; Daub *et al.*, 2005). However, other studies report that the pigments present in the mycelium and secreted into the culture medium of *M. fijiensis* are melanins that absorb visible light and act as photosensitizers, potentially generating O_2. This finding suggests that the role of these pigments should be further investigated as a potentially important factor contributing to the progression of Sigatoka disease, and the new molecular approaches could be the solution (Santana-Filho, 2024).

Chemical and morphological differences have been identified among three fungal species within the *Mycosphaerella* complex. Preliminary data indicated a toxin-production pathway, with only minor chemical variations among the fungi (Stierle *et al.*, 1991).

Plants grown under shading systems present low disease severity. This may be explained by reduced dew formation and decreased light incidence (Cordeiro; Matos; Kimati, 2005). The shade produced by dominant extracts is an essential reducer of the damage caused by Yellow Sigatoka (Vivan, 2002).

This study aimed to investigate the behaviour of the pre-penetration parameters of the fungus under different illuminance levels. This independent variable in this study refers to the limit of the ratio of the luminous flux received by the surface surrounding a point, considered over the surface area, as it approaches zero. The illuminance is not uniformly distributed across all points within a given space; average values are commonly used to determine whether lighting conditions are suitable for specific activities (Bormann, 2003). The hypothesis tested

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was that higher illuminance intensities induce greater mycelial growth, sporulation, and germination of the pathogen's conidia.

MATERIALS AND METHODS

The experiments were conducted in the Plant Pathology Laboratory at Embrapa Cassava and Fruits (Cruz das Almas, Bahia). The growth parameters of colonies, sporulation, and germination of the fungus *Mycosphaerella musicola* were evaluated under different illuminance levels.

Isolate collection and sporulation induction

The fungus was isolated from the leaves of the banana cultivar 'Pacovan' that exhibited characteristic symptoms of Yellow Sigatoka. Samples were collected in June 2010, in the town of Laranjeiras (Muritiba, Bahia). Both the collection and the sporulation procedures followed the methodology described by Cordeiro, Rocha and Araújo (2011). Symptomatic leaves were placed in a moist chamber until sporodochia emerged. These structures were examined under a microscope and subsequently transferred to agar media. After several days, the resulting colonies were selected and transferred to malt medium. Following growth, the colonies were macerated and cultured in V8 medium to induce sporulation.

In vitro mycelial growth

In this experiment, in vitro mycelial growth was evaluated as a function of the illuminance, measured with a light meter. Thirty-six plates were prepared with V8 culture medium, and 10 *Mycosphaerella musicola* colonies were placed per plate, selected for the highest possible uniformity. The treatments were four levels of illuminance: 5383 Lux, 110 Lux, 10.2 Lux, and 2 Lux. At time zero (control), 80 colonies (2 plates per treatment) were weighed on precision scales to obtain the green weight. The average green weight across all treatments at that time point. The other assessments were made at 15, 21, 28, 36, and 42 days of fungus cultivation, when one plate from each treatment was removed, and shortly afterwards, the 10 colonies were weighed on precision scales. The weight of the colonies was evaluated at four illuminance levels, at 25°C, and under a 12-hour photoperiod.

In vitro Sporulation

The experiment consisted of four treatments with three replications each, and each plate constituted one replication. The treatments were conducted at different illuminance levels (3,380, 250, 30, and 1 lux), with a 12-hour photoperiod on the plates. Light levels were obtained by placing the plates under boxes manufactured with several types of shade meshes. Evaluations were performed at 5, 7, 11, 13, and 14 days after the suspension was sown. Spores were released

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following the methodology proposed by Cordeiro, Rocha and Araújo (2011). Using a Pasteur pipette, two slides were prepared in Neubauer chambers for each treatment, and the slides were examined under a stereomicroscope to quantify the number of spores per milliliter. Two fields were counted on each slide, totalling four observed fields.

Spore germination

In this experiment, a 5 ml volume of a homogenized suspension, prepared according to the methodology described by Cordeiro, Rocha and Araújo (2011), was placed into glass jars containing penicillin. The jars were distributed within a miniature shade structure made with the following screen types: full clarity (58.976 lx), 25% shade (44.373 lx), 50% shade (27.328 lx), 75% shade (24.673 lx), and a structure covered with three layers of 75% shade (4.181 lx). Six jars were placed in each structure, for a total of 30 jars containing the spore suspension. Every hour, one jar from each treatment was removed and taken to the laboratory to inhibit fungal germination with lactophenol. At the same time, after each removal, illuminance inside the miniature structures was measured. Twenty measurements were taken with the light meter, yielding the illuminance values presented above for each treatment. The jars were stored under refrigeration until microscopic evaluation of the number of germinated spores as a function of the illuminance levels tested. For counting, 4 slides were prepared and placed under the stereomicroscope. The germination percentage was determined by counting 100 spores per slide.

Statistics

The data were analyzed using simple linear and exponential regression, which estimate the value of a dependent variable (Y) from an independent variable (X) under the assumption that the data follow the given model. The program BioStat 5.0 was used in all three analyses, in which colony growth, sporulation, and fungus germination were the dependent variables, and illuminance was the independent variable. The dependent variables were, respectively, colony weight (mg), number of spores ml-1, and percentage of spore germination. For the sporulation variable, the data were log-transformed because they were multiplicative in nature.

RESULTS

Colony growth

The linear regression model was significantly adjusted to data obtained under high illuminance in incubator conditions, as shown in Table 1. However, for low values (as 10.2 and 2 lx), no model has been satisfactorily adjusted. Comparing the regression in both cases there

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was no significant difference, indicating that the linear model best describes mycelial growth. However, the equation for 5383 lx accounts for 86% of the data, whereas the equation for 110 lx accounts for about 70%.

Table 1. Results of the regression analysis for mycelial growth, sporulation, and spore germination of *Mycosphaerella musicola* in vitro for different levels of illuminance.

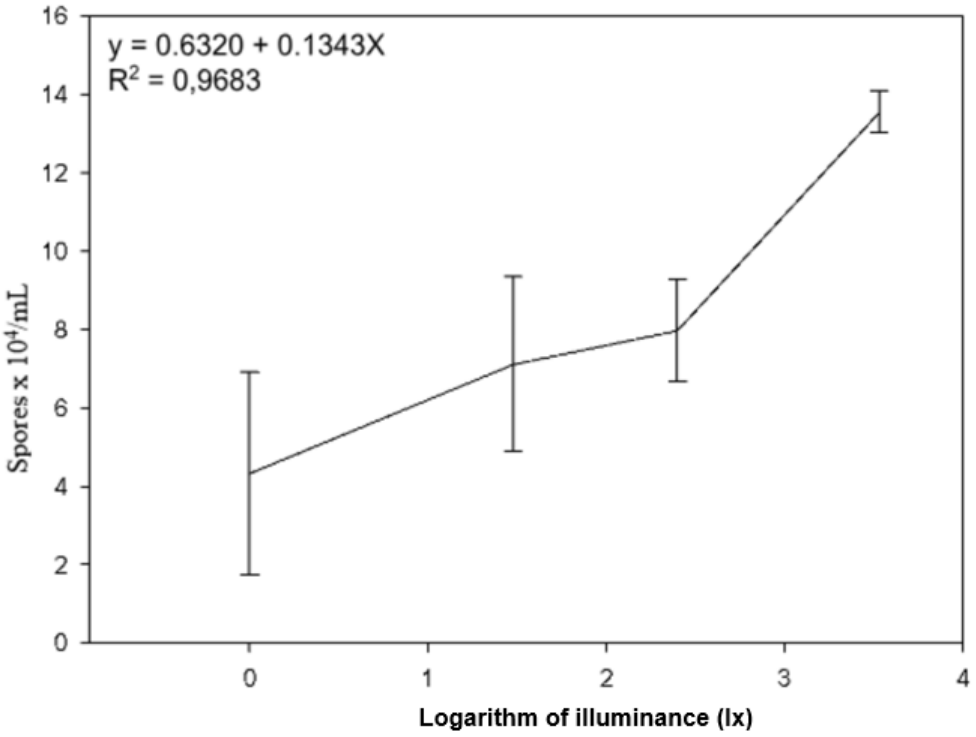
Variable	Equation	r^2	Regression model
Mycelial growth	Y′= 3.9897 + 0.0531X	0.696	Linear
Sporulation	Y′= 0.6320 + 0.1343X	0.968	Linear
Germination	Y = 4.014 + 0.0848*exp.(-lux/-13688,6)	0.971	Exponential

Fonte: elaborado pelos autores, 2024.

Sporulation

Illuminance levels significantly affected pathogen sporulation (p = 0.0127). Thus, sporulation increases with increasing light levels (Figure 01). 97% of the data analyzed can be explained and adjusted by the linear regression model. The best sporulation averages were obtained at 3380 lx, which was significantly different from the others. The treatment at 250 lx was substantially different from the treatment at 1 lx, but there was no significant difference between the treatments at 30 lx and 250 lx.

Figure 01. Number of spores per milliliter of spore suspension prepared with the fungus *Mycosphaerella musicola*, grown in petri plates under illuminances at 3380 lx, 250 lx, 30 lx, and 1lx. The data were logarithmically transformed because they are multiplicative; thus, Log 3380 lx = 3.53, Log 250 lx = 2.40, Log 30 lx = 1.48, Log 1lx = 0.00. The equation was obtained using a linear regression model in the program BioStat 5.0.



Fonte: elaborado pelos autores, 2025.

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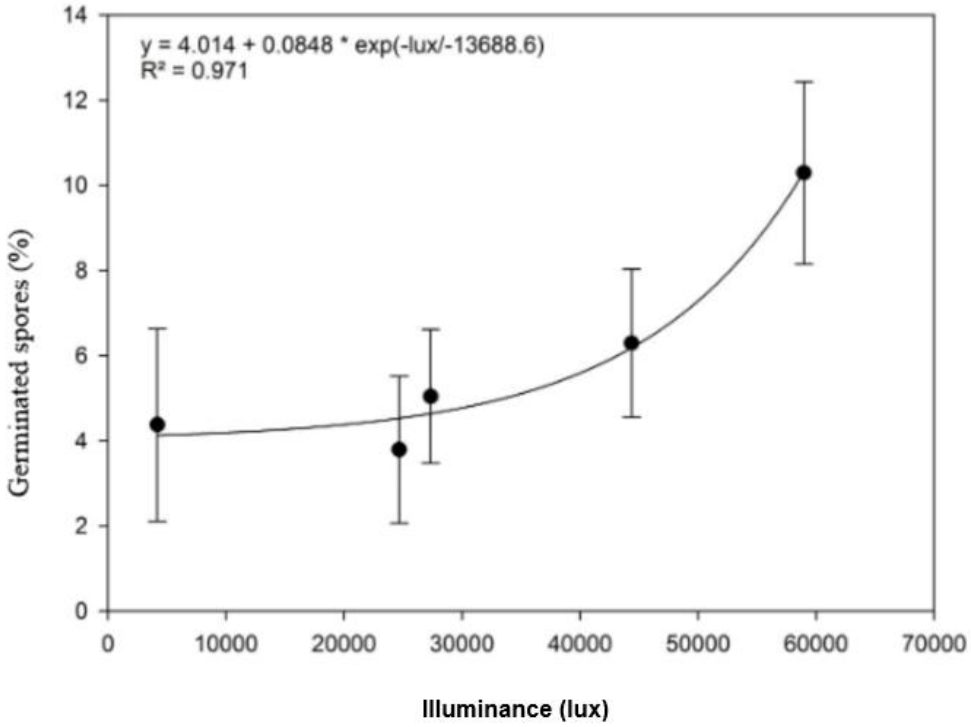
Germination

The nonlinear model best fit the germination data and was significant at 5% level. There is an exponential relationship between the variables, and the positive effect of the variable on germination is evident from its equation. The highest germination percentage was obtained when the spore suspension was under conditions with an average luminance of 58.975,53 lx (Figure 02). It can also be observed that the germination percentage at 6h is around 10%, indicating that the fungus's germination may take longer than that observed in this experiment.

Figure 2. Percentage of spores of *Mycosphaerella musicola* germinated in vitro under levels of illuminance: 4181.20 lx; 24672.67 lx; 27327.49 lx; 44373.49 lx, and 58975.52 lx. The chart presents the model's equation, an exponential function of three parameters, adjusted by nonlinear regression using the program TableCurve 2D v5.01.



Fonte: elaborado pelos autores, 2025.

DISCUSSION

Colony growth

The results show no evidence that illuminance levels affect the mass growth of *Mycosphaerella musicola* colonies. This contrasts with the findings of Montarroyos *et al.* (2007), who reported greater radial growth of *M. musicola* colonies under continuous darkness and reduced growth under constant light. However, their study assessed colony diameter, whereas the present work evaluated colony mass, a more appropriate metric for this species, whose mycelium develops also in a vertical pattern. Rosa and Menezes (2001) likewise

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quantified mycelial diameter of different isolates under varied media and pH levels (12 h light/12 h dark), showing growth induction at pH 4.5, though again using diameter as the primary variable.

Given these methodological differences, it can be inferred that light does not interfere with the vegetative growth (biomass accumulation) of *M. musicola*. More detailed physiological studies on light perception and its regulation of fungal development may further clarify the independence between vegetative growth and photobiological responses for this pathogen.

Recent evidence supporting this interpretation shows that *Zymoseptoria tritici* develops smaller leaf areas with spotting symptoms in bread wheat when exposed to shorter wavelengths, which also reduce mycelial biomass under these conditions (Cerón-Bustamante *et al*., 2023b). However, the findings of this manuscript reinforce the hypothesis that colony mass growth in *Mycosphaerella musicola* is not coupled to light-regulated developmental processes.

Sporulation

Unlike the pattern observed for colony growth, illuminance had a marked effect on the sporulation of *M. musicola*. Sporulation increased proportionally with light availability, with peak values occurring around the 10th day after induction under the highest illuminance levels.

These results are consistent with classical studies on *Mycosphaerella* and *Pseudocercospora species*. Both *M. Mycosphaerella* and *M. musicola* sporulate more abundantly under high-light conditions and produce few or no conidia in continuous darkness (Hanada; Gasparotto; Pereira, 2002; Etebu *et al.*, 2005; Albuquerque, 1993; Jones, 2002; Lepoivre *et al.,* 2002). Similarly, Sepúlveda *et al*. (2009) reported maximal conidial production under continuous light, intermediate levels under a 12-hour photoperiod, and minimal production in darkness.

The present results indicate that illuminance regulates the reproductive capacity of *M. musicola*. Reduced sporulation under low light limits inoculum availability, which in turn diminishes secondary disease cycles and the likelihood of new infections. The reduced number of spores on plates with low illuminance directly reflects this inhibitory effect.

Recent advances in fungal photobiology further support these observations. Cerón-Bustamante *et al.* (2023a) demonstrated that light regulates key aspects of the fungal life cycle and pathogenicity, influencing development, reproduction, and virulence in phytopathogenic fungi. These findings reinforce that sporulation is one of the fungal developmental processes most strongly regulated by light intensity, aligning with the responses observed for *M. musicola* in this study.

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Germination

For the germination variable, the statistical analysis indicated that the three-parameter exponential model provided the best fit to the data. Illuminance clearly influenced germination and, consequently, the initial stages of infection. However, the overall low germination percentages suggest that the evaluation period may not have been ideal, and that the methodology used should be refined for future studies. Preliminary and still unpublished observations in shaded plants support the idea that reduced light lowers the number of lesions on leaves, which may be linked to both the reduced sporulation under low illuminance and the smaller stomatal density found in plants acclimated to shade (Santana-Filho, 2012).

Most earlier studies on related pathogens focused on temperature or leaf wetness as the main drivers of conidial and ascospore germination in *M. fijiensis* (Jacome *et al.*, 2002) and information specifically addressing the effect of illuminance on *M. musicola* remained limited. Research on *M. citri* suggested sensitivity to photoperiod through its influence on pseudothecial formation (Mondal; Timmer, 2002), hinting that light-regulated processes may be conserved within this group.

More recently, Silva *et al.* (2024) demonstrated that light does not interfere with conidial germination or appressorium formation in *Phyllosticta citricarpa*, reinforcing the essential role of temperature and moisture in these processes for this pathogen. However, the results of the present study show that, in *Mycosphaerella musicola*, illuminance plays a fundamental role.

Additional evidence has emerged that further clarifies how light influences pre-penetration events, indicating that illuminance interacts with molecular and ecological determinants of pathogenicity in *Pseudocercospora spp.* High-resolution transcriptomic studies of *P. fijiensis* reveal that conidial germination is dominated by pathogenicity factors and effectors that facilitate rapid adaptation to illuminated leaf surfaces (Carreón-Anguiano *et al.*, 2023). Similarly, infection by *P. musae* triggers early reprogramming of *Musa paradisiaca* defense pathways, demonstrating that light-exposed tissues induce complex molecular responses during the initial host-pathogen interaction (Borah; Bora; Bhorali, 2022). New insights from next-generation sequencing approaches further show that illumination shapes microbial community dynamics and regulates gene expression involved in fungal development and infection processes (Santana-Filho, 2024). Taken together, these findings reinforce that pre-penetration steps, including germination, signalling, and early host colonization, are tightly modulated by illuminance and associated transcriptional plasticity in closely related Sigatoka pathogens.

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CONCLUSIONS

Our results establish predictive models for colony growth, sporulation, and conidial germination of *M. musicola*, the causal agent of Sigatoka disease. Additional information on the physiology of this fungus and related species is still required to clarify how and to what extent light interferes with these pre-penetration processes. Furthermore, the application of mathematical modelling to the behaviour of this pathosystem will contribute to the development of precision agriculture.

This study offers an innovative contribution by integrating distinct mathematical approaches to describe three fundamental physiological stages of the pathogen quantitatively and comparatively: mycelial growth, spore production, and germination. Demonstrating the specific effects of illuminance on each of these processes represents a conceptual advance that remains scarcely explored in the literature. This functional differentiation reveals new dimensions of the pathogen's ecology and strengthens the understanding of its epidemiological behaviour. Moreover, the linear and exponential models applied here provide unprecedented parameters for the epidemiological modelling of Yellow Sigatoka, supporting more robust predictions and the development of advanced integrated management strategies, particularly in production systems that differ in shading, canopy architecture, and light intensity.

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