

Influence of Climatic Factors on the Development of Cashew Powdery Mildew

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Abstract

Influence of Climatic Factors on the Development of Cashew Powdery Mildew

Cashew powdery mildew, caused by *Erysiphe quercicola*, is the major disease affecting cashew cultivation in Northeastern Brazil, primarily infecting young tissues and significantly reducing crop productivity. This study evaluated the effects of different climatic factors and inoculum sources on key stages of the pathogen's life cycle. Inflorescences, young leaves, immature nuts, and mature nuts were exposed to five relative humidity levels, with no significant effect on conidial germination. Viability differed among inoculum sources, with inflorescences exhibiting the highest rates and mature nuts the lowest. Conidia derived from inflorescences were subsequently subjected to combinations of temperature, light spectra, and photoperiod. A temperature of 23°C favored both germination and appressorium formation; green and red light promoted fungal development, whereas blue light exerted an inhibitory effect. A 12 h photoperiod resulted in the highest values for the evaluated parameters. Under controlled conditions, low light intensity increased disease severity and sporulation. These findings demonstrate that temperature and light modulate critical stages of the *E. quercicola* life cycle, providing valuable insights for improving disease management strategies.

INTRODUCTION

Cashew (*Anacardium occidentale* L.) is one of the most important fruit crops in Northeastern Brazil, making a significant contribution to the regional economy through the production of nuts and peduncles destined for agro-industrial processing and export markets (Freire et al., 2022). Among the main phytosanitary constraints affecting cashew cultivation, powdery mildew stands out as a widely distributed disease in tropical regions, characterized by high aggressiveness, rapid spread, and a strong capacity to damage young plant organs. Young leaves, inflorescences, peduncles, and immature fruits represent the primary infection sites and are frequently associated with substantial yield losses and the premature abscission of reproductive structures (Martins et al., 2020).

Taxonomic and molecular studies have demonstrated that *Erysiphe quercicola* is the predominant etiological agent of cashew powdery mildew in Brazil, exhibiting a stronger affinity for young tissues when compared with *E. necator*, whose occurrence is sporadic and largely restricted to mature leaves (Liberato et al., 2020; Ferreira et al., 2019; Takamatsu et al., 2015). This physiological preference confers a high capacity for colonization and sporulation, thereby promoting rapid disease dissemination under favorable environmental conditions.

The development of powdery mildews is strongly influenced by environmental factors. Classical studies indicate that conidial germination occurs over a wide range of relative humidity levels, demonstrating the group's relative tolerance to dry environments (Yarwood, 1957). In contrast, temperature and light play decisive roles in conidial germination, appressorium formation, and sporulation (Jarvis, 1964). Studies on tropical *Erysiphe* species have shown optimal performance under moderate temperature ranges and low irradiance, conditions that reduce photochemical stress and favor host colonization (Heintz & Blaise,

2019; Suthaparan et al., 2010). Blue radiation, in particular, has been associated with suppressive effects on powdery mildew development due to its higher energy potential and the induction of inhibitory responses (Suthaparan et al., 2010). Inoculum sources also play a decisive role in powdery mildew epidemiology. Inflorescences and young fruits are highly susceptible structures and frequently harbor high conidial loads, thereby facilitating pathogen establishment and the rapid amplification of secondary inoculum (Martins et al., 2020; Suthaparan et al., 2010).

Despite advances in the characterization of *E. quercicola*, studies integrating multiple environmental factors and comparing the viability of different inoculum sources remain scarce. Therefore, this study comprehensively evaluated how inoculum sources, in association with controlled conditions of relative humidity, temperature, light spectrum, photoperiod, and light intensity, influence key stages of the pathogen's life cycle, aiming to broaden the understanding of the environmental determinants underlying the epidemiology of cashew powdery mildew.

MATERIALS AND METHODS

1. Viability of *E. quercicola* conidia obtained from different inoculum sources of dwarf cashew under varying environmental conditions

Fungal inoculum was obtained from inflorescences, immature nuts (length < 1.7 cm), mature nuts (length > 1.7 cm), necrotic nuts, and young leaves of the dwarf cashew clone 'BRS 189', cultivated at the Experimental Field of Embrapa Agroindústria Tropical in Pacajus, Ceará State, Brazil. The collected inoculum sources were placed in plastic bags and insulated containers and immediately transported to the Plant Pathology Laboratory of Embrapa Agroindústria Tropical in Fortaleza, Ceará, Brazil, for immediate use.

Five relative humidity (RH) levels were used: 0%, 35%, 50%, 85%, and 100%, according to Martins et al. (2020). RH values were monitored using LogTag sensors (model Haxo-8) with an LT/USB interface and LogTag Analyser 2.9 software. The different RH levels were established using saturated salt solutions, with 85% obtained using NaCl, 50% using CaCl₂, and 35% using MgCl₂·6H₂O (Bendek et al., 2007). Twenty treatments were arranged in a completely randomized design (CRD) using a factorial scheme consisting of five relative humidity levels (0%, 35%, 50%, 85%, and 100%) × four inoculum sources (young leaves, inflorescences, mature nuts, and immature nuts), with four replicates. Treatments were allocated in Petri dishes containing filter paper moistened with 2 mL of the corresponding salt solution, and microscope slides bearing conidia extracted from each inoculum source using a fine brush. The treatments were incubated in a BOD chamber at 23°C for 24 h, under 15 W fluorescent lamps providing a mean irradiance of 0.59 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

For each treatment, 100 conidia per replicate were evaluated, recording the presence or absence of germ tube and appressorium formation (Fig. 1A and 1B). The resulting data were subjected to analysis of variance (ANOVA), and mean percentages of germination and appressorium formation were compared using Tukey's test at the 5% significance level, employing RStudio software version 4.3.1 with the

packages *easynova* and *ExpDes.pt*. Each treatment consisted of 4 replicates, and measurements were performed in duplicate (technical replicates).

3.2 Evaluation of *E. quercicola* germination and appressorium formation under varying temperature and light conditions.

Based on the results of the first experiment, 35% RH and the inflorescence inoculum source yielded the highest levels of germination and appressorium formation. Therefore, conidia originating from inflorescences of the clone 'BRS 189', under 35% RH, were subsequently exposed to different temperature and light conditions.

To evaluate the effect of light spectrum, colored plastic *insulfilm* filters in red, green, and blue were used, corresponding to wavelength ranges of 620–740 nm, 500–565 nm, and 440–485 nm, respectively, in addition to white light. Fungal responses were also assessed under five photoperiod regimes (0, 7, 12, 17, and 24 h) in a BOD chamber equipped with 15 W fluorescent lamps providing a mean irradiance of $0.59 \mu\text{mol m}^{-2} \text{s}^{-1}$.

The experiment was conducted in a completely randomized design using a triple factorial arrangement ($4 \times 5 \times 2$) with three replicates. The factors evaluated were light color (four levels: green, red, blue, and white), photoperiod (five levels: 0, 7, 12, 17, and 24 h), and temperature (two levels: 17°C and 23°C), following the methodology and evaluation procedures described above. Each treatment consisted of 3 replicates, and measurements were performed in duplicate (technical replicates).

3.3 Evaluation of climatic effects on the development of cashew powdery mildew under laboratory conditions

Leaf discs (18 mm in diameter) were obtained from young leaves and surface-disinfested by immersion in 70% ethanol for 30 s, followed by 1.5% sodium hypochlorite for 3 min, and then rinsed three times with autoclaved distilled water. Inoculation was performed by direct contact using field-collected inoculum. Young leaves were used, and a 1 cm² fragment of symptomatic tissue was applied, corresponding to an average of 1,760 conidia per square centimeter.

A completely randomized design was used in a factorial scheme consisting of five photoperiods (12, 7, 17, 24, and 0 h) × two temperatures (17°C and 23°C), with five replicates. The plates were incubated in the same BOD chambers used in the previous experiment.

For the evaluation of light spectrum, the same methodology used in the conidial behavior experiment was adopted. However, in this assay, the interaction among photoperiod and temperature associated with light spectrum was evaluated. The experiment was conducted in a completely randomized design using a triple factorial arrangement consisting of three light colors (red, green, and blue) × three photoperiods (7, 12, and 17 h) × two temperatures (17°C and 23°C), with three replicates per treatment.

The plates were then incubated in BOD chambers. Each treatment consisted of 5 replicates, and measurements were performed in duplicate (technical replicates).

Conidial quantification was performed using the quadrant method. Transparent adhesive tape was placed over the sporulating area of the leaf disc and then mounted on a microscope slide divided into four 1 cm² sections. Two quadrants were randomly selected and evaluated, with three fields of view assessed per quadrant. The mean number of conidia per field was calculated, followed by the mean of the two quadrants, representing the number of conidia per cm² of the sample. Counts were performed under a microscope at 10× magnification; each field of view was photographed and subsequently analyzed using ImageJ software for conidial quantification.

1. Evaluation of the effect of different light intensities on the development of disease severity and sporulation of cashew powdery mildew under field conditions.

Considering that the experiments were conducted in BOD chambers under low light intensity (mean of 0.59 $\mu\text{mol m}^{-2} \text{s}^{-1}$) provided by 15 W fluorescent lamps, it is necessary to evaluate disease development under field conditions, where plants are exposed to realistic light environments.

The cages were constructed using mesh materials that controlled internal irradiance at 30%, 50%, and 70%, in addition to 0%, achieved using opaque black plastic bags, and 100%, in which plants were fully exposed to sunlight. Measurements obtained with a lux meter indicated that, at 0% light, intensity ranged from 0 to 0.27 lux (0.0014–0.0049 $\mu\text{mol m}^{-2} \text{s}^{-1}$); at 30%, from 0.5 to 332 lux (2.30–6.12 $\mu\text{mol m}^{-2} \text{s}^{-1}$); at 50%, from 0.86 to 756 lux (3.04–13.94 $\mu\text{mol m}^{-2} \text{s}^{-1}$); at 70%, from 0.56 to 710 lux (5.22–13.09 $\mu\text{mol m}^{-2} \text{s}^{-1}$); and at 100%, from 146 to 1135 lux (12.29–20.92 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Forty-day-old young seedlings were used and inoculated by contact using the application of a 1 cm² fragment of symptomatic tissue. After inoculation, the seedlings were maintained in an inoculation room at 26°C until the third day after inoculation (DAI), when they were transferred to the cages. Each cage contained five juvenile seedlings of the clone BRS-189.

Evaluations were performed at 4 and 20 days after inoculation to assess disease severity and to quantify sporulation. The experiment was conducted in a completely randomized design using a factorial scheme with five light intensity levels.

Disease severity was assessed digitally using a computer-based image analysis approach. For each treatment, photographs of randomly selected symptomatic leaves were taken to generate an image database. Images were then segmented to separate pixels corresponding to healthy tissue, pathogen-infected tissue, and the image background, resulting in three color palettes representing each component. The images were subsequently analyzed in RStudio using the *pliman* package, which provided the percentage of disease severity for each analyzed leaf (Fig. 3).

Conidial quantification values were obtained using ImageJ software with the quadrant method, while powdery mildew severity on leaves was assessed in RStudio using the *pliman* and *EBImage* packages.

Data were subjected to analysis of variance (ANOVA), and the F-test was applied at the 1% significance level. When significant effects were detected, treatment means were compared using Tukey's test at the 5% significance level, employing RStudio software version 4.3.1 with the *easyanova* and *ExpDes.pt* packages.

Statistical analysis

Data were subjected to analysis of variance (ANOVA), and means were compared by Tukey's test at the 5% significance level for qualitative factors. Data normality and homogeneity of variances were verified using the Shapiro–Wilk test. All statistical analyses were performed in RStudio version 4.3.1 using the packages *ExpDes.pt*, *easyanova*, *pliman*, and *EBImage*.

All experiments were performed twice over time as independent experimental repetitions. Since no significant differences were observed between repetitions, data from both experimental runs were pooled for statistical analysis.

RESULTS

1. Viability of *E. quercicola* conidia obtained from different inoculum sources of dwarf cashew under varying environmental conditions

The evaluation of *E. quercicola* conidial viability obtained from different inoculum sources and subjected to distinct relative humidity levels revealed no significant interaction between inoculum source and humidity. Relative humidity levels also had no significant effect on germination or appressorium formation, indicating that, within the tested range, humidity was not a determining factor for conidial viability. In contrast, significant differences were observed among inoculum sources. Conidia derived from inflorescences exhibited the highest mean germination rate (77%) and differed significantly from the other sources according to Tukey's test ($p \leq 0.05$).

The mature nuts, young *maturi*, and young leaf inoculum sources did not differ significantly from one another, although mature nuts exhibited the lowest absolute mean germination. A similar pattern was observed for appressorium formation: conidia originating from inflorescences showed the highest percentage of appressoria formed (67%), whereas young leaf and immature nuts presented statistically similar values. In contrast, mature nuts stood out as the least efficient inoculum source, with only 15% of conidia forming appressoria, differing significantly from the other sources. These results indicate that, although relative humidity did not influence conidial viability under the evaluated conditions, the type of host tissue from which the inoculum is obtained plays a decisive role in the germination capacity and infective potential of *E. quercicola*, with inflorescences representing the most favorable source for the initial infection process (Fig. 4A and 4B).

4.2) Evaluation of *E. quercicola* germination and appressorium formation under varying temperature and

light conditions

Analysis of variance indicated significant effects of photoperiod and temperature on *Erysiphe quercicola* conidial germination. Photoperiod showed an F value of 7.55 ($p < 0.001$), and temperature an F value of 28.23 ($p < 0.001$), demonstrating that both factors significantly influenced the response variable. Light spectrum had no significant effect ($p = 0.9301$). Among the evaluated interactions, only the Spectrum $\times$ Temperature interaction was significant ($p = 0.0487$), whereas Photoperiod $\times$ Spectrum, Photoperiod $\times$ Temperature, and Photoperiod $\times$ Spectrum $\times$ Temperature interactions were not statistically significant. The coefficient of variation (CV = 29.68%) was within an acceptable range for this type of assessment, and the Shapiro–Wilk test confirmed the normality of residuals ($p = 0.6218$) (Table 1).

Table 1
Comparison of means for the spectrum $\times$ temperature interaction on the percentage of conidial germination of *E. quercicola*.

Spectrum x Temperature		
Spectrum	17°C	23°C
Black	40 aB	67 aA
Blue	58 aA	58 aA
Green	42 aB	71 aA
White lighth	46 aA	57 aA
Red	40 aB	70 aA

Means followed by the same lowercase letter within rows do not differ from each other, and means followed by the same uppercase letter within columns do not differ from each other, according to Tukey’s test.

Appressorium formation in germinated *E. quercicola* conidia was significantly influenced by the evaluated environmental factors (Table 1). Analysis of variance revealed highly significant effects of photoperiod ($p < 0.01$) and temperature ($p < 0.01$) on the response variable. In contrast, the main effect of light spectrum was not significant ($p = 0.6677$). A significant second-order interaction between light spectrum and temperature was observed ($p = 0.0205$). The remaining interactions photoperiod $\times$ spectrum, photoperiod $\times$ temperature, and the three-way interaction among all factors were not statistically significant. The assumptions of the analysis were met, as model residuals exhibited a normal distribution, as confirmed by the Shapiro–Wilk test ($W = 0.741$; $p > 0.05$). The coefficient of variation for the experiment was 34.43% (Table 2).

Table 2
Comparison of means for the spectrum × temperature interaction on the percentage of appressorium formation in conidia of *E. quercicola*.

Spectrum x Temperature		
Spectrum	17°C	23°C
Blue	45.5 aA	45.8 aA
Green	32.2 aB	61 aA
White light	33 aB	52 aA
Red	31.3 aB	60 aA

Means followed by the same lowercase letter within rows do not differ from each other, and means followed by the same uppercase letter within columns do not differ from each other, according to Tukey's test.

4.3 Evaluation of climatic effects on the development of cashew powdery mildew under laboratory conditions

4.3.1 Effect of photoperiod and temperature

Analysis of variance indicated significant effects of the evaluated factors on *E. quercicola* conidial production. Photoperiod had the greatest impact on the response variable, with significant differences among the tested levels ($F = 433.73$; $p < 0.001$). Temperature also affected conidial production, although to a lesser extent ($F = 7.69$; $p = 0.0084$). In addition, a significant interaction between photoperiod and temperature was observed ($F = 22.62$; $p < 0.001$), indicating that the fungal response varied according to the combination of these factors. The coefficient of variation of the experiment was 23.57%.

The interaction between photoperiod and temperature resulted in significant differences in *E. quercicola* sporulation. At 17°C, conidial production ranged from zero under continuous darkness to 239 conidia at a 7 h photoperiod, reaching intermediate values at 12 h (209.4 conidia) and peaking at 17 h (2,886.6 conidia). Under continuous light (24 h), sporulation decreased to 802.8 conidia. At 23°C, sporulation was higher than at 17°C for most photoperiods, with values ranging from 87.6 conidia in continuous darkness to 299.2 conidia at 7 h, 537.6 conidia at 12 h, and a maximum of 3,972.2 conidia at 17 h. However, under continuous light, conidial production declined sharply to 84.2 conidia. Overall, a 17 h photoperiod promoted the highest sporulation at both temperatures, whereas continuous darkness and continuous light resulted in the lowest values (Fig. 4).

4.3.2 Effect of photoperiod, temperature, and light spectrum

Conidial production and germination of *E. quercicola* were significantly influenced by photoperiod, temperature, and light spectrum. Temperature exerted the strongest effect on sporulation ($p < 0.0001$), followed by light spectrum ($p = 0.0002$) and photoperiod ($p = 0.0274$). Among the interactions, significant effects were detected for temperature $\times$ spectrum ($p = 0.0014$) and for the three-way interaction photoperiod $\times$ temperature $\times$ spectrum ($p = 0.0493$), whereas the remaining interactions were not statistically significant ($p > 0.05$).

Germination was consistently higher at 23°C across all evaluated photoperiods and light spectra, whereas values at 17°C remained low. Under a 12 h photoperiod, the highest values were recorded under green (3,285.3 conidia) and red (2,722.3 conidia) spectra, followed by white (2,648.0 conidia) and blue (1,953.6 conidia). Under a 17 h photoperiod, a similar pattern was observed, with red (3,580.3 conidia) and green (2,964.4 conidia) spectra showing the highest values at 23°C. At a 7 h photoperiod, the highest means were again observed under green (3,197.4 conidia), white (2,869.4 conidia), and red (2,858.6 conidia) spectra at 23°C, whereas blue light resulted in the lowest germination at this photoperiod (158.6 conidia). At 17°C, mean values remained low and statistically similar across treatments (Table 3).

Table 3
Number of conidia of *E. quercicola* under different combinations of photoperiod, light spectrum and temperature.

Photoperiod 12 h		
Spectrum	17°C	23°C
Blue	154.6 bBa	1953.6 aAa
Green	726 bBa	3285.3 aAa
White Ligth	2461.3 aAa	2648.0 aAa
Red	630.3 bBa	2722.3 aAa
Photoperiod 17 h		
Spectrum	17°C	23°C
Blue	243 bAa	2105.6 aABa
Green	105.3 bAa	2964.4 aABa
White Ligth	370 bAa	1876.6 aBa
Red	105.3 bAa	3580.3 aAa
Photoperiod 7 h		
Spectrum	17°C	23°C
Blue	134.3 aAa	158.6 aBb
Green	217.3 aAa	3197.4 aAa
White light	370.6 aAb	2869.4 aAa
Red	288.3 aAa	2858.6 aAa

Values followed by the same lowercase letter in the row do not differ from each other by the LSD test ($p \leq 0.05$). Uppercase letters compare columns within each spectrum. Lowercase letters in italics compare photoperiods.

Overall, the highest germination levels were observed under the combination of 23°C with green and red light spectra, whereas the lowest means were recorded at 17°C, regardless of photoperiod or light spectrum. These patterns are consistent with the significant temperature $\times$ spectrum interaction and the significant three-way interaction identified by the ANOVA.

1. Evaluation of the effect of different light intensities on disease severity and sporulation of cashew powdery mildew under field conditions

4.4.1 Evaluation of disease severity

Image analysis performed in RStudio allowed the determination of the percentage of symptomatic and healthy leaf area for each leaf (Fig. 6 and Fig. 7).

Figure 6. Symptoms of cashew powdery mildew on leaves subjected to different levels of shading (0%, 30%, 50%, 70%, and 100%) at 20 days after inoculation (DAI). On the left, representative leaves from each treatment; on the right, respective percentages of damaged leaf area quantified by image analysis.

The experiment was conducted in a completely randomized design to evaluate the effect of different light intensities on the severity of cashew powdery mildew under field conditions. Disease severity data were subjected to analysis of variance (ANOVA), considering light intensity levels and days after inoculation (DAI) as sources of variation. Data normality and homogeneity of variances were verified using the Shapiro–Wilk test. All analyses were performed in RStudio version 4.3.1 using the packages ExpDes.pt, easyanova, pliman, and EBImage.

4.4.1 Evaluation of disease severity

Analysis of variance revealed a significant effect of illuminance ($p = 0.00004$) and a significant interaction between illuminance and evaluation days ($p = 0.00001$). The main effect of evaluation days was not significant ($p = 0.56592$). Due to the significant interaction, the effect of illuminance was interpreted separately for each evaluation day by analyzing the simple effects of the interaction.

Analysis of variance revealed a significant interaction between illuminance and evaluation time ($p < 0.001$), indicating that the effect of illuminance on disease severity varied over the evaluation period. At 4 days after inoculation, disease severity was significantly higher under 70% illuminance than under the other illuminance levels, which did not differ from one another. At 20 days after inoculation, the highest disease severity was observed under 0% illuminance, whereas the 30% illuminance treatment showed an intermediate response, not differing significantly from either 0% or the remaining illuminance levels. The 50%, 70%, and 100% illuminance treatments exhibited the lowest disease severity at this evaluation.

Analysis of the effect of evaluation time within each illuminance level showed a significant increase in disease severity from 4 to 20 days only under 0% illuminance. In contrast, under 70% illuminance, disease severity was significantly higher at 4 days than at 20 days after inoculation. No significant differences between evaluation times were observed under 30%, 50%, or 100% illuminance. These results demonstrate that disease progression was dependent on illuminance conditions, with distinct temporal responses according to light intensity (Fig. 7).

4.4.2 Evaluation of sporulation

The sporulation of *E. quercicola* was significantly influenced by the factors days after inoculation, illuminance levels, and the interaction between these factors ($p < 0.001$). The factor “days” showed the greatest effect ($F = 48.8896$), followed by illuminance ($F = 12.4566$). The interaction between days ×

illuminance was also significant ($F = 8.4001$), indicating that the effect of illuminance varied over time. The coefficient of variation was 42.24%. Conidial count data were square-root transformed $\sqrt{x}$ prior to analysis to stabilize variances. Normality and homogeneity of variances were verified using the Shapiro–Wilk test. All statistical analyses were performed using the transformed data, and non-transformed means are shown for presentation purposes. The Shapiro–Wilk test indicated normality of the residuals at the 5% significance level.

The number of conidia of *E. quercicola* varied significantly among the illuminance levels and across the evaluation periods. At 4 days after inoculation, the highest values were observed at 70% illuminance (2950.3), followed by 30% (2232.0) and 50% (1849.8), whereas the lowest number of conidia occurred at 100% illuminance (333.6). The means differed from one another as indicated by the lowercase letters within the columns. At 20 days, a marked increase in sporulation was observed under all illuminance conditions, particularly at 0% (11,140.3) and 70% (7361.3), which showed the highest values, while 100% illuminance remained with the lowest mean (51.3). Comparisons among illuminance levels within each time point revealed statistically significant differences, as indicated by the uppercase letters within the row (Fig. 8).

Figure 8. Means followed by the same lowercase letter do not differ significantly among light intensity levels within each evaluation time (4 or 20 days after inoculation). Means followed by the same uppercase letter do not differ significantly between evaluation times within each light intensity level, according to Tukey's test ($p \leq 0.05$)

Overall, the regression analyses demonstrated that reduced light availability favored the sporulation of *E. quercicola*, whereas higher light intensities markedly suppressed fungal reproduction. These findings reinforce the importance of illuminance as a major environmental factor affecting the epidemiology and inoculum production of cashew powdery mildew under field conditions.

DISCUSSION

The germination and appressorium formation of *E. quercicola* were not influenced by relative humidity, indicating a broad tolerance of the fungus to different RH conditions, as previously reported for other powdery mildews (Shomari & Kennedy, 1999). Although the 35% and 50% levels showed numerically higher values, only temperature exerted a significant effect, corroborating Martins et al. (2020), who emphasized the greater importance of this factor in the early development of the pathogen.

The inoculum source had a marked effect: inflorescences, as young tissues, yielded the highest mean values for germination and appressorium formation, whereas older, mature tissue showed the lowest values. The greater viability of conidia originating from immature tissues suggests a higher efficiency of *E. quercicola* in colonizing new shoots of dwarf cashew, promoting intense secondary cycles and rapid sporulation, key factors underlying the epidemiological success of powdery mildews.

Temperature once again stood out as a decisive variable. Ranges between 20–23°C favored germination, germ tube growth, and appressorium formation, reinforcing the predominance of temperature over relative humidity (Martins et al., 2020; Honorato et al., 2016). Regarding light, the green and red spectra promoted higher mean germination rates, whereas blue light and darkness resulted in the lowest values. This response, which contrasts with the pattern observed in temperate-climate species (Sempio & Castori, 1952), likely reflects ecological adaptations of *E. quercicola* to tropical environments.

Nevertheless, spectral variations did not show a significant overall effect on germination and appressorium formation in the analysis as a whole. Previous studies indicate that shorter-wavelength radiation, such as UV-B and UV-C, has a germicidal effect and can suppress the progress of powdery mildews (Suthaparan et al., 2014; Gadoury et al., 2019), although these wavelengths were not evaluated in the present study.

A 12-h photoperiod favored germination and appressorium formation, whereas continuous light or continuous darkness reduced these responses, in partial agreement with Carver et al. (1994). However, the absence of a significant difference among 0 h, 24 h, 12 h, and 7 h photoperiods for appressorium formation suggests that this stage is less sensitive to photoperiod. The relatively high variability observed in some in vitro assays is inherent to conidial germination and sporulation processes under controlled conditions.

In the severity assessments conducted on leaf discs, a strong interaction was observed among temperature, light, and photoperiod. At 23°C, a 17-h photoperiod promoted the highest production of conidia per cm², whereas 0 h and 24 h resulted in the lowest values, a pattern similar to that described by Carver et al. (1994). However, at 17°C, a continuously illuminated environment led to greater sporulation, demonstrating that the fungal response to photoperiod depends on temperature and, possibly, light intensity.

Light quality also modulated sporulation: white light promoted higher mean values under specific conditions, as reported for *E. pisi* var. *pisii* (Ayres et al., 1983). The blue spectrum consistently resulted in the lowest mean values, corroborating Edwards (1993), who demonstrated its negative effect on the development of *E. graminis* f. sp. *hordei*.

In experiments conducted under different illuminance levels, shaded conditions (0–30%) resulted in greater disease severity and sporulation, whereas full light (100%) significantly reduced disease progress. Similar findings have been reported for *O. neolycopersici* (Miesrolova et al., 2010) and for oak powdery mildew (Schnathorst, 1965; Leibovich et al., 1996; Willocquet et al., 1996). Under high light intensities, there is evidence of an extended latent period and reduced sporulation (Aust & Hoyningen-Huene, 1986).

The results confirm that illuminance plays a determining role in the pathogen's sporulation, directly modulating the quantity of conidia over time. The high sporulation observed under 0% illuminance at 20

days after inoculation suggests that environments without light incidence favor fungal reproduction, possibly by reducing photobiological stress and maintaining more stable microclimatic conditions for conidiophore development. A similar pattern has been reported for radiation-sensitive fungi, whose sporulation tends to increase under shaded conditions (Rotem, 1994; Suthaparan et al., 2012).

In contrast, the marked reduction in conidial production under 100% illuminance indicates that full light exposure inhibits sporulation, possibly by affecting physiological processes related to conidiophore differentiation or by creating microenvironments with lower moisture retention, a condition critical for the sporulation process (Agrios, 2005; Yarwood, 1950). The lack of increase in sporulation between 4 and 20 days under this treatment reinforces the persistence of this inhibitory effect.

The similarity among the intermediate treatments (30%, 50%, and 70% illuminance) suggests that the fungus tolerates a broad range of light levels, maintaining relatively stable conidial production. However, the consistent increase observed at 20 days indicates that, although light is not strongly limiting within these ranges, the duration of colonization is a determining factor, as reported for other biotrophic pathogens (Jarvis et al., 2002; Nair et al., 1990).

The significant interaction between illuminance and evaluation period reinforces that the effect of light depends on the pathogen's developmental stage. Under agricultural conditions, naturally shaded environments, such as dense canopies or prolonged periods of cloudiness, may intensify inoculum production, whereas greater light incidence tends to reduce it (Rotem & Aust, 1991). Therefore, management strategies that modify the microclimate, such as pruning or adjustments in plant spacing, may directly influence sporulation dynamics in the field.

Overall, the results demonstrate that environmental factors decisively modulate key stages of the *E. quercicola* life cycle. Relative humidity did not influence the initial phases of infection, whereas inoculum source, a temperature of 23°C, light quality, and photoperiod determined marked variations in germination, appressorium formation, and sporulation. Under field conditions, the greater severity observed under shaded environments and the pronounced reduction under high illuminance highlight the central role of light in the progression of powdery mildew in dwarf cashew seedlings.

These findings broaden the understanding of the pathogen's ecology and provide a basis for cultural management practices, particularly regarding planting layout, pruning, and microclimate modulation. Field studies conducted at different times of the year are recommended to integrate these factors into the epidemiological dynamics of commercial production systems.

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Declarations

Conflict of interest

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Authors contribution

Conceptualization: AFPH, MVVM, and WLF. Methodology, formal analysis, and investigation: AFPH, MECMG, and MVVM. Writing—original draft preparation: AFPH and MVVM. Writing—review, and editing: AFPH and MVVM. Funding acquisition and supervision: MVVM and WLF. All authors approved the final manuscript.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request, and in the EMBRAPA Research Data Repository.

References

1. Agrios GN (2005) Plant pathology, 5th edn. Elsevier Academic, San Diego
2. Aust HJ, von Hoyningen-Huene J (1986) Effects of various light intensities on development of powdery mildew on barley. J Phytopathol 115:140–148

3. Ayres PG, Press MC, Spencer-Phillips PTN (1983) Effects of light quality and intensity on powdery mildew of pea (*Erysiphe pisi*). *Physiol Plant Pathol* 22:187–200
4. Bendek M, Cordeiro MRT, Baldissera T (2007) Soluções salinas saturadas utilizadas para gerar umidade relativa controlada. Embrapa Clima Temperado. Circular Técnica 69
5. Carver TLW, Ingerson-Morris SM, Thomas BJ (1994) Light quality and light quantity effects on development of cereal powdery mildews. *Plant Pathol* 43:234–244
6. Edwards MC (1993) The effects of light quality on infection of barley by *Erysiphe graminis* f. sp. *hordei*. *Physiol Mol Plant Pathol* 42:255–269
7. Ferreira MFS, Santos Filho L, Pereira O, Liberato JR (2019) Identificação molecular de oídios associados ao cajueiro no Brasil. *Trop Plant Pathol* 44:213–221
8. Freire KCS, Albuquerque TB, Ximenes E et al (2022) Cashew production in the Brazilian Northeast: challenges and phytosanitary constraints. *Revista Brasileira de Fruticultura* 44:e-013
9. Gadoury DM et al (2019) Ultraviolet radiation suppresses powdery mildew development. *Plant Dis* 103:1857–1866
10. Heintz C, Blaise P (2019) Environmental modulation of tropical powdery mildew pathogens. *Mycological Progress* 18:987–998
11. Honorato JF, Santos F, Câmara MPS (2016) Temperature-dependent development of *Erysiphe quercicola*. *Trop Plant Pathol* 41:159–167
12. Jarvis WR (1964) The development of powdery mildew in relation to environmental factors. *Annu Rev Phytopathol* 2:49–68
13. Jarvis WR, Gubler WD, Grove GG (2002) Epidemiology of powdery mildews in agricultural pathosystems. In: Bélanger R, Bushnell WR, Dik AJ, Carver TLW (eds) *The powdery mildews: a comprehensive treatise*. APS, St. Paul, pp 169–199
14. Leibovich B, Yarwood CE (1966) Effects of light intensity on powdery mildew of oak. *Phytopathology* 56:1047–1051
15. Liberato JR, Arriel NHC, Ferreira MFS (2020) Taxonomic delimitation of powdery mildew species in Anacardiaceae. *Mycologia* 112:344–356
16. Martins MVV, Santos AA, Araújo L et al (2020) Environmental factors associated with the development of cashew powdery mildew. *Trop Plant Pathol* 45:312–321
17. Miesrolova A, Gjærum HB, Suthaparan A (2010) Influence of shading on the severity of tomato powdery mildew (*Oidium neolycopersici*). *J Plant Dis Prot* 117:165–171
18. Nair NG, Allen RN, Elgar GJ (1990) Environmental factors influencing sporulation of *Uncinula necator*. *Phytopathology* 80:63–66
19. Rotem J (1994) The genus *Alternaria*: biology, epidemiology and pathogenicity. APS, St. Paul
20. Rotem J, Aust HJ (1991) The effect of light on sporulation of fungi. *Annu Rev Phytopathol* 29:397–426

21. Schnathorst WC (1965) Effect of light intensity on the powdery mildew of oak. *Phytopathology* 55:323–328
22. Sempio A, Castori P (1952) Influenza della luce sui funghi oidi. *Phytopathologia Mediterranea* 1:45–52
23. Shomari SH, Kennedy R (1999) Environmental influences on conidial germination in powdery mildews. *Eur J Plant Pathol* 105:493–500
24. Suthaparan A, Stensvand A, Gislerød HR et al (2014) UV-induced defense responses against powdery mildew. *Environ Exp Bot* 105:40–48
25. Suthaparan A, Stensvand A, Solhaug KA et al (2010) Suppression of powdery mildew by UV-B radiation. *Plant Dis* 94:475–482
26. Suthaparan A, Solhaug KA, Stensvand A, Torre S (2012) Effects of UV radiation on the biology of *Podosphaera pannosa*, the rose powdery mildew fungus. *J Phytopathol* 160:167–174
27. Takamatsu S, Matsuda S, Grum-Grzhimaylo AA (2015) Molecular phylogeny of the genus *Erysiphe*: implications for host specificity. *Mycoscience* 56:73–81
28. Willocquet L, Clerjeau M, Savary S (1996) Effect of light intensity on powdery mildew epidemics. *Plant Pathol* 45:99–107
29. Yarwood CE (1950) The influence of light on fungal reproduction. *Bot Rev* 16:1–2

Unsectioned Paragraphs

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Supplementary Information

Figures

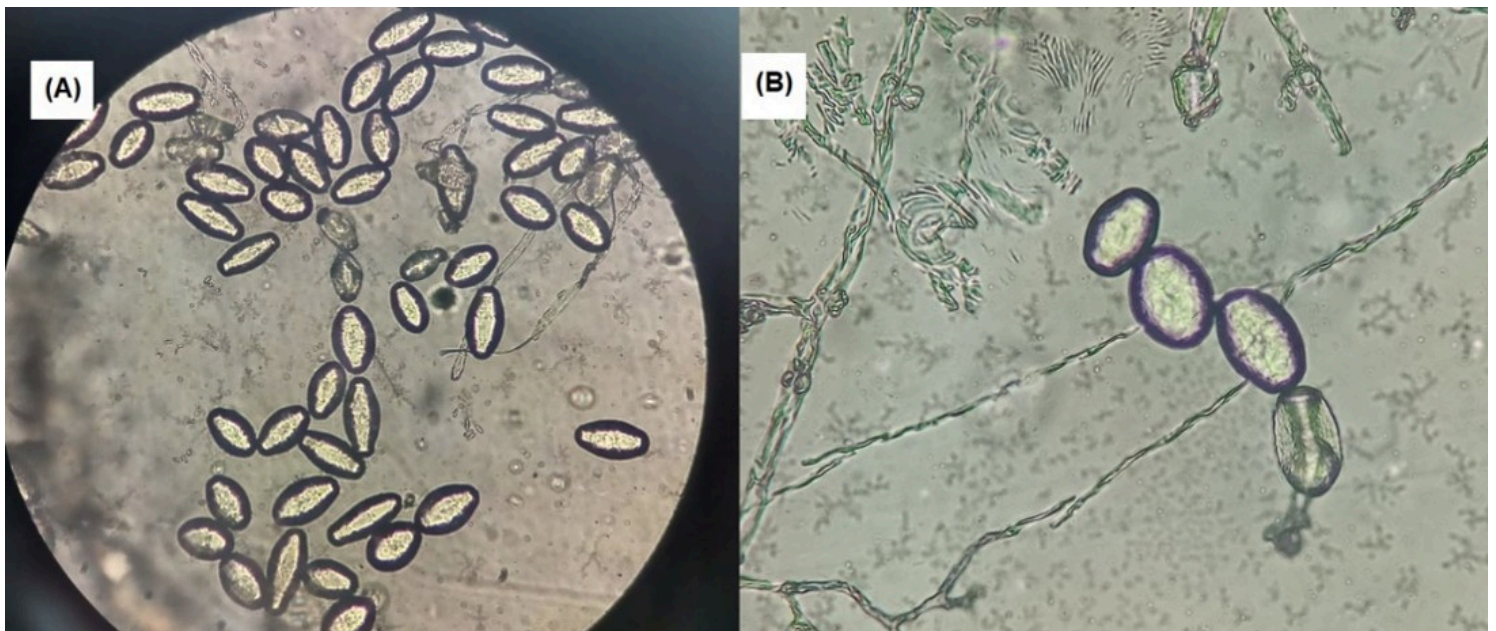


Figure 1

(A) *E. quercicola* conidia; (B) conidia in chains with appressorium formation.

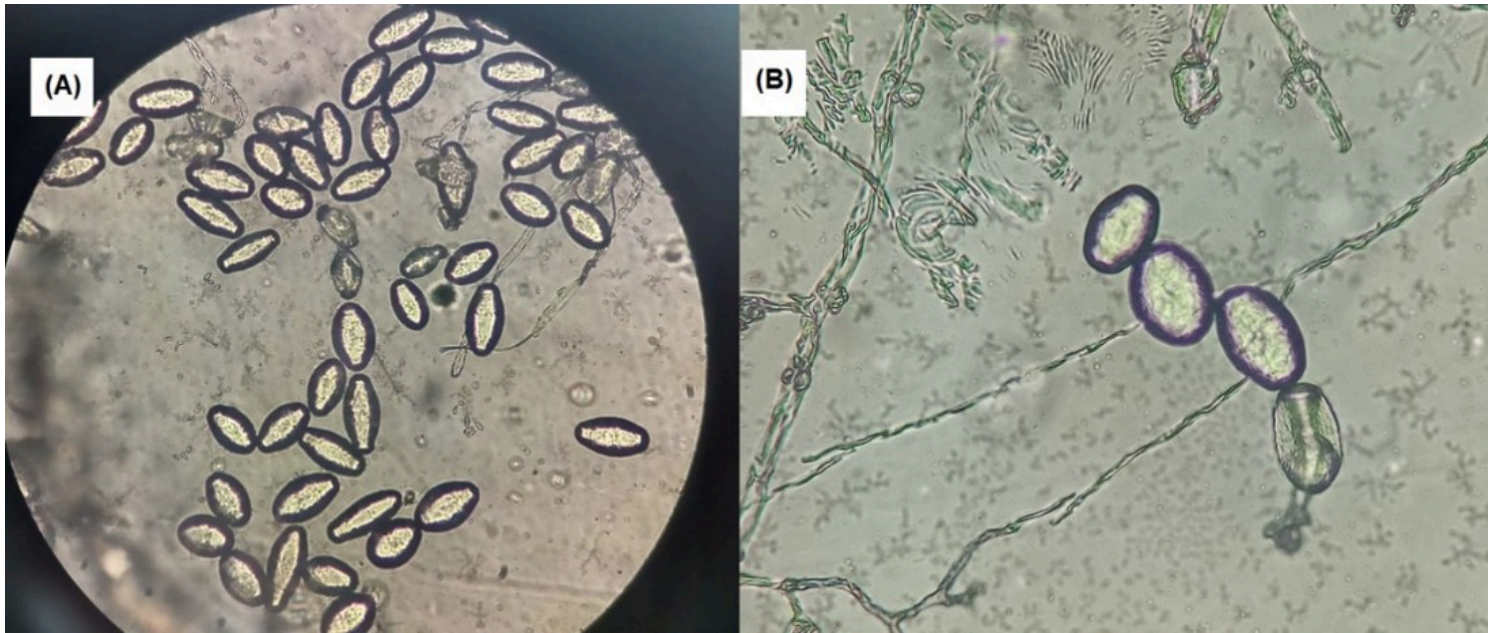


Figure 1

(A) *E. quercicola* conidia; (B) conidia in chains with appressorium formation.

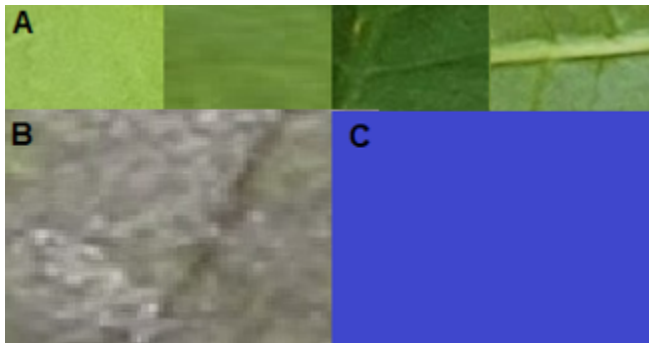


Figure 2

Color palettes corresponding to the pixels of each component. A: healthy tissue; B: symptomatic tissue; and C: background.

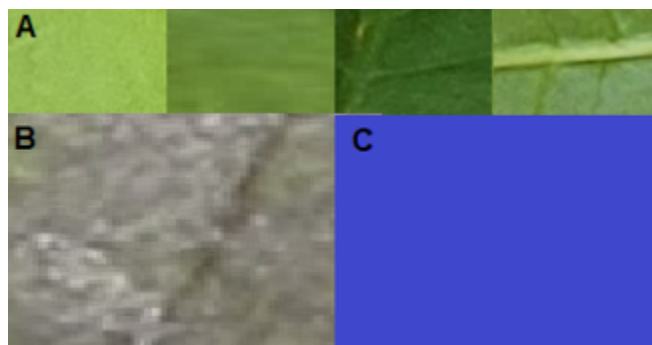


Figure 2

Color palettes corresponding to the pixels of each component. A: healthy tissue; B: symptomatic tissue; and C: background.

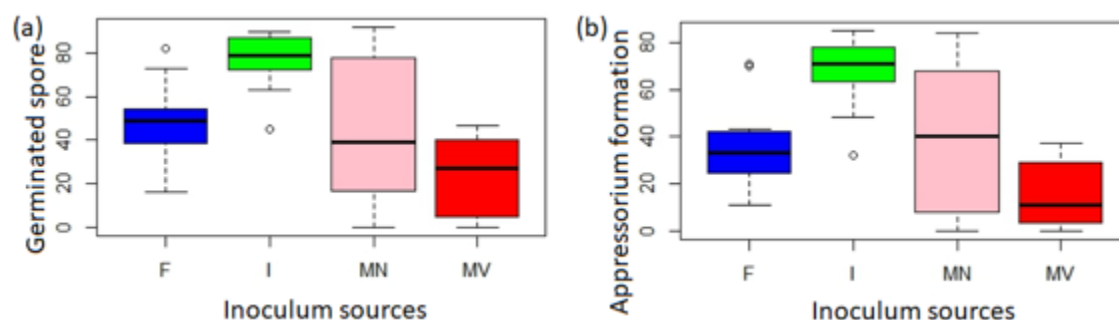


Figure 3

Boxplot of the percentage of germinated conidia from different inoculum sources (A); boxplot of the percentage of conidia forming appressoria (B). Means followed by the same letter do not differ significantly according to Tukey's test ($P \leq 0.05$). F: Young leaf; I: Inflorescence; MN: Young "maturi"; MV: Old "maturi". Germinated conidia (CV = 42.60%); appressorium formation (CV = 51.11%).

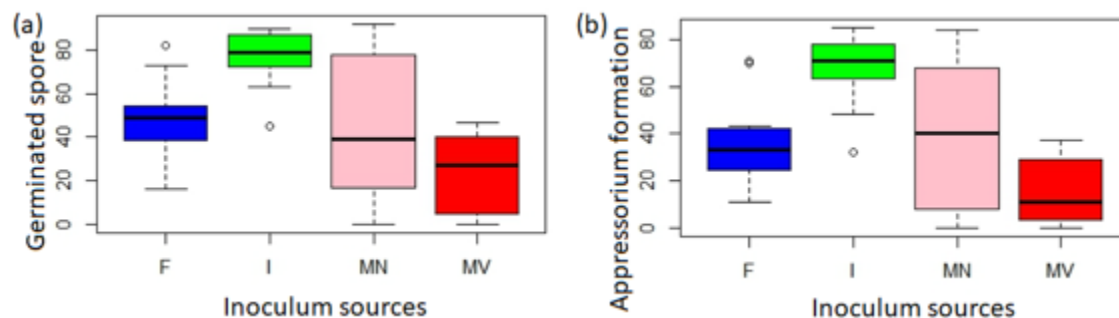


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Boxplot of the percentage of germinated conidia from different inoculum sources (A); boxplot of the percentage of conidia forming appressoria (B). Means followed by the same letter do not differ significantly according to Tukey's test ($P \leq 0.05$). F: Young leaf; I: Inflorescence; MN: Young "maturi"; MV: Old "maturi". Germinated conidia (CV = 42.60%); appressorium formation (CV = 51.11%).

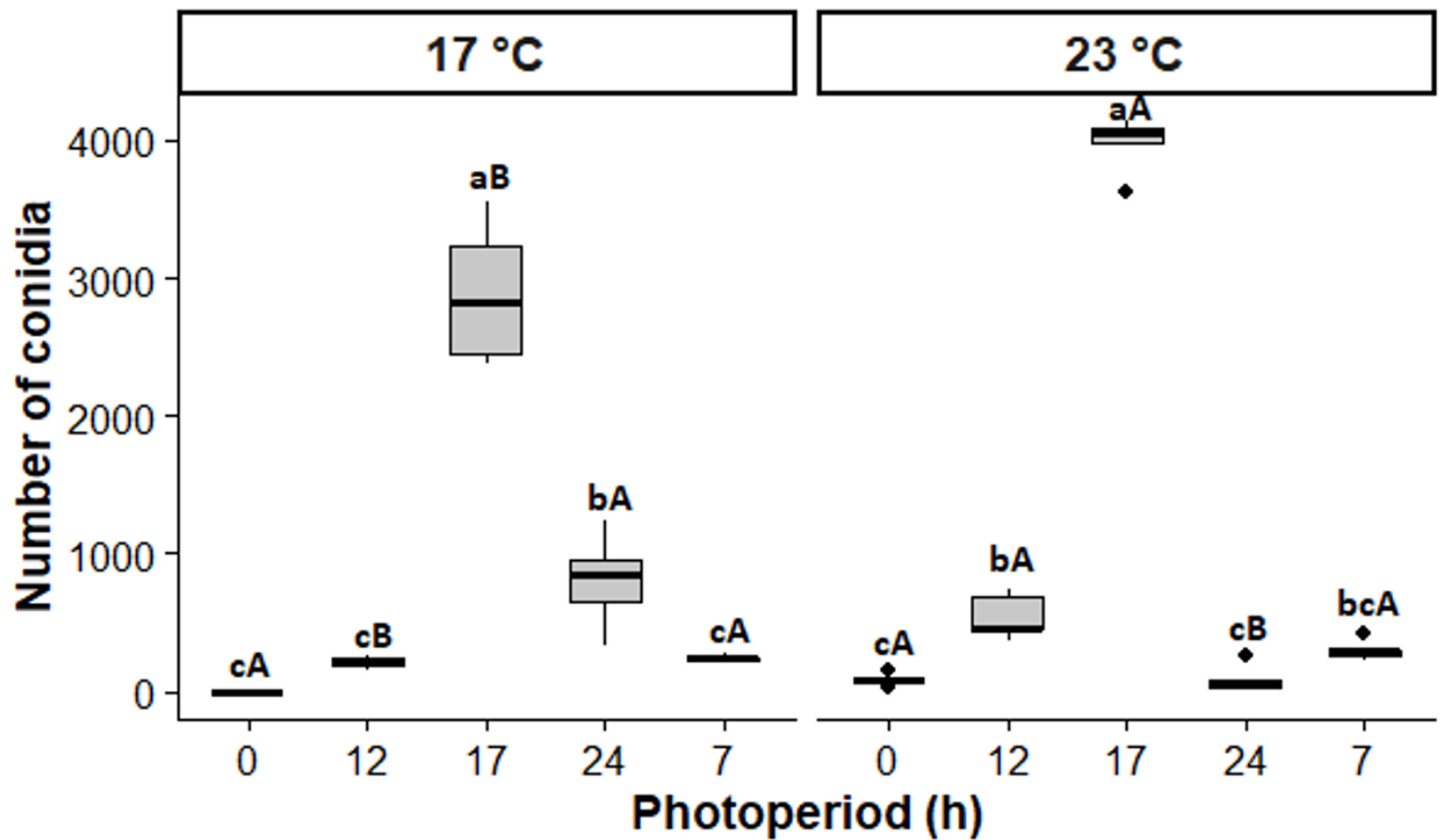


Figure 4

Means followed by the same lowercase letter do not differ significantly among photoperiods within each temperature. Means followed by the same uppercase letter do not differ significantly between temperatures within each photoperiod, according to Tukey's test ($p \leq 0.05$).

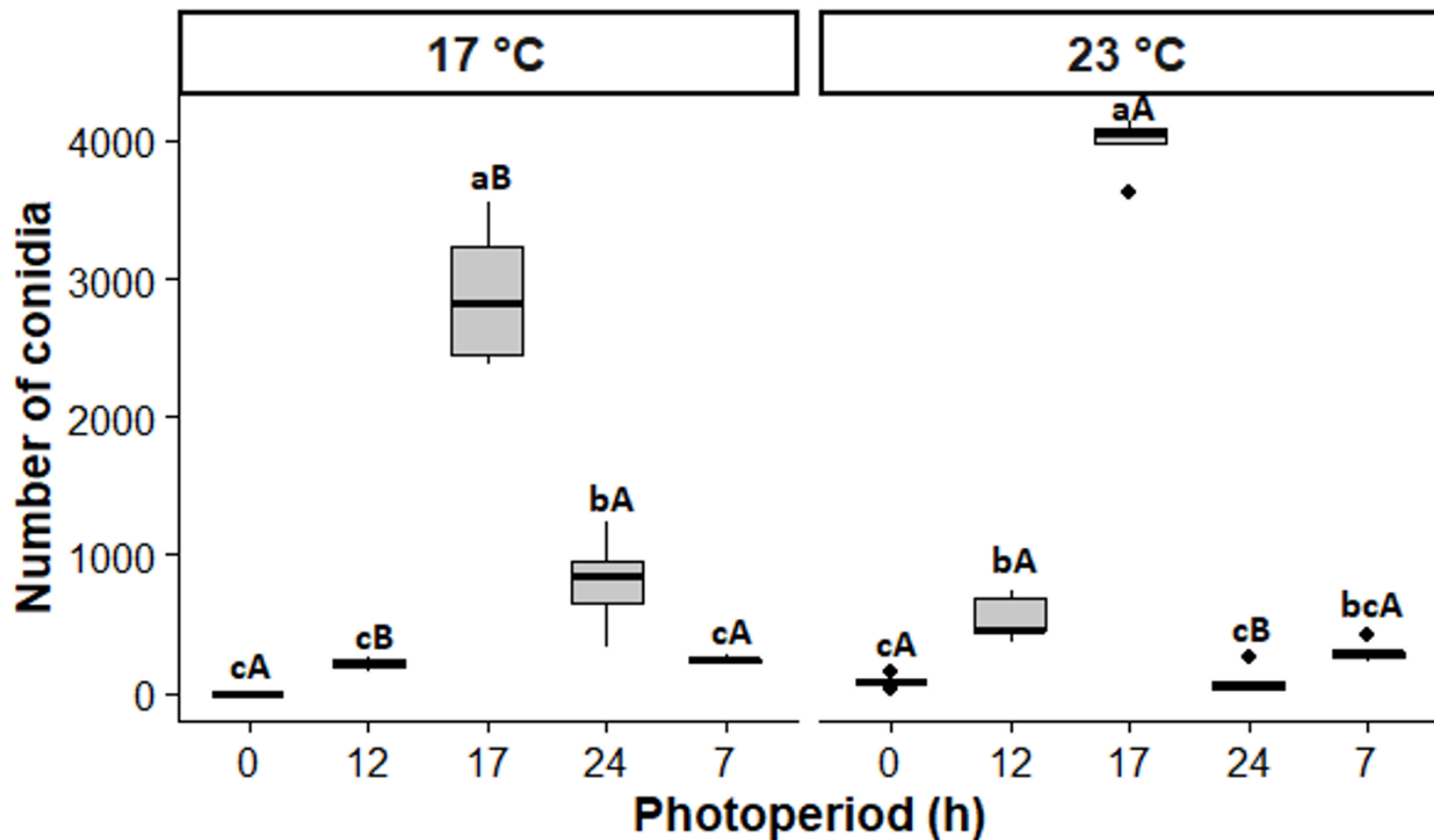


Figure 4

Means followed by the same lowercase letter do not differ significantly among photoperiods within each temperature. Means followed by the same uppercase letter do not differ significantly between temperatures within each photoperiod, according to Tukey's test ($p \leq 0.05$).

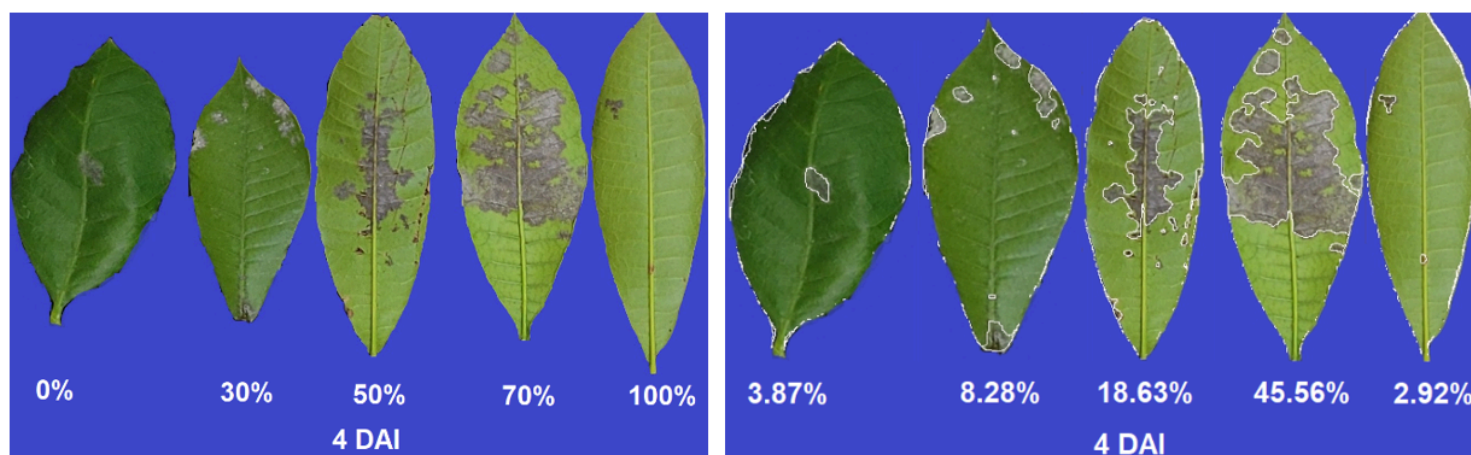


Figure 5

Symptoms of cashew powdery mildew on leaves subjected to different levels of shading (0%, 30%, 50%, 70%, and 100%) at 4 days after inoculation (DAI). On the left, representative leaves from each treatment;

on the right, respective percentages of damaged leaf area quantified by image analysis.

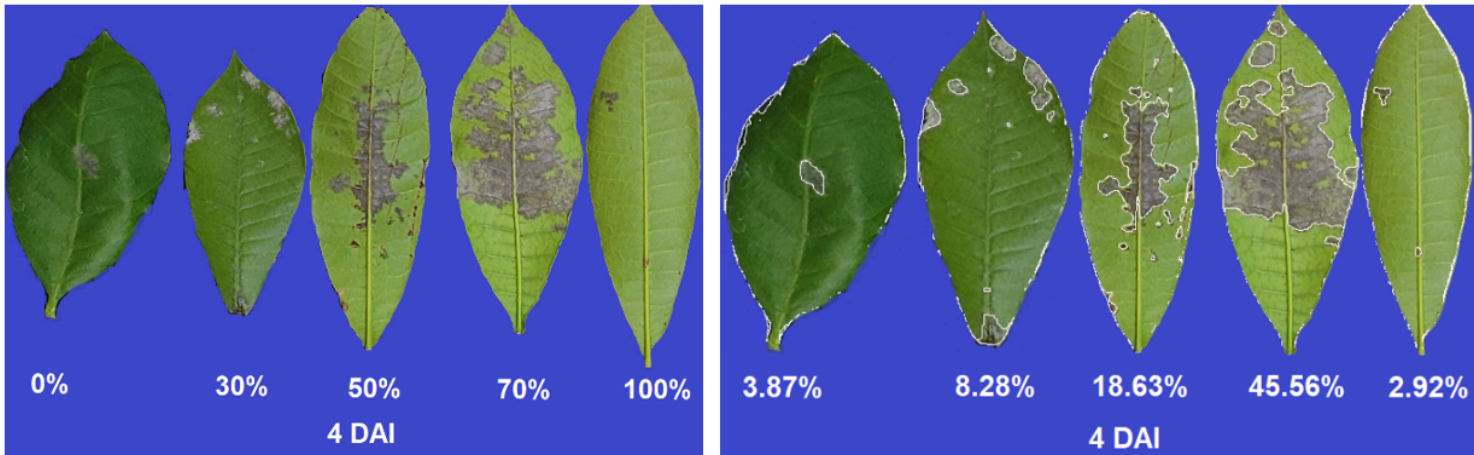


Figure 5

Symptoms of cashew powdery mildew on leaves subjected to different levels of shading (0%, 30%, 50%, 70%, and 100%) at 4 days after inoculation (DAI). On the left, representative leaves from each treatment; on the right, respective percentages of damaged leaf area quantified by image analysis.

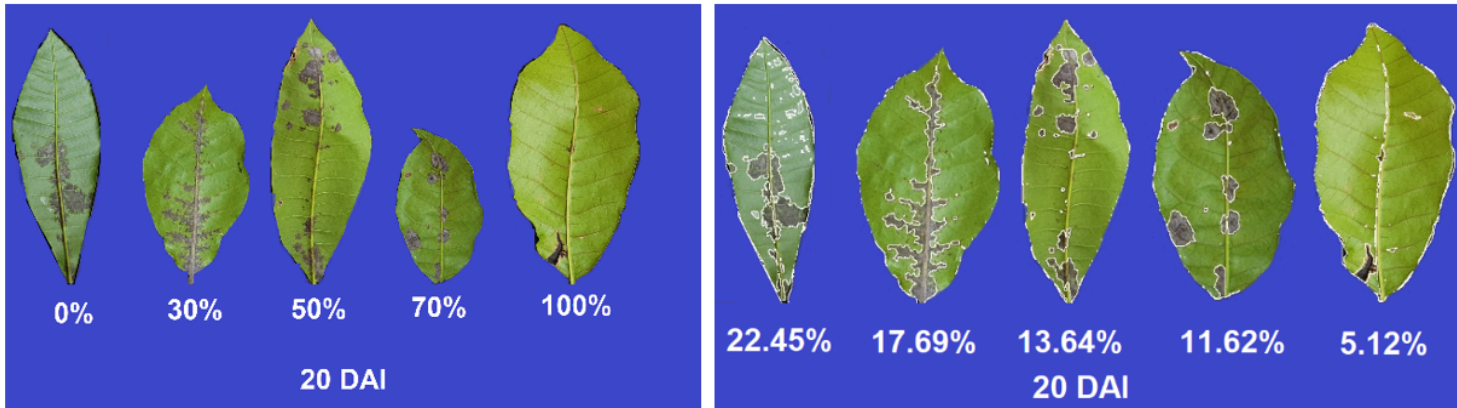


Figure 6

Symptoms of cashew powdery mildew on leaves subjected to different levels of shading (0%, 30%, 50%, 70%, and 100%) at 20 days after inoculation (DAI). On the left, representative leaves from each treatment; on the right, respective percentages of damaged leaf area quantified by image analysis.

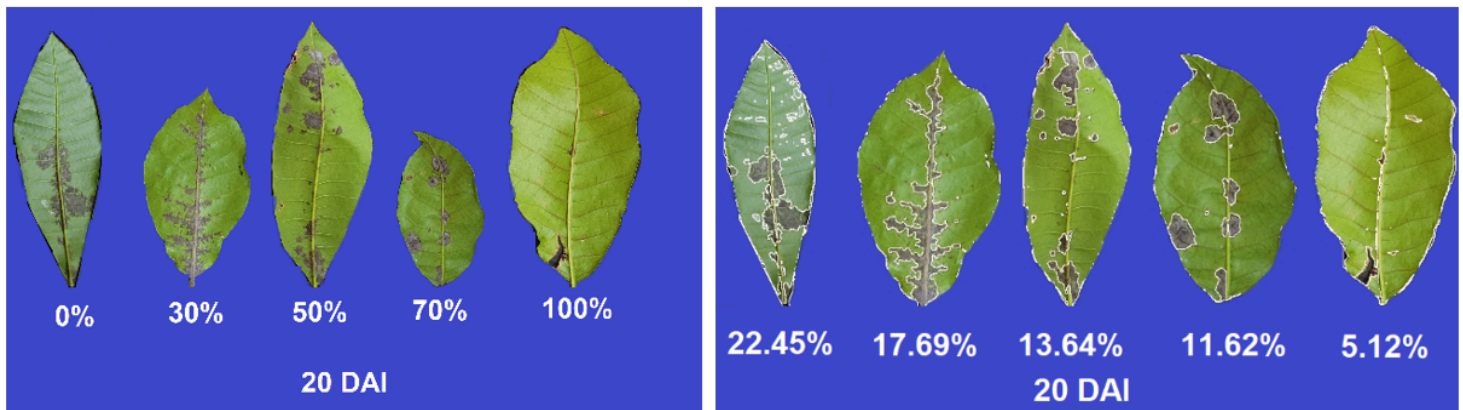


Figure 6

Symptoms of cashew powdery mildew on leaves subjected to different levels of shading (0%, 30%, 50%, 70%, and 100%) at 20 days after inoculation (DAI). On the left, representative leaves from each treatment; on the right, respective percentages of damaged leaf area quantified by image analysis.

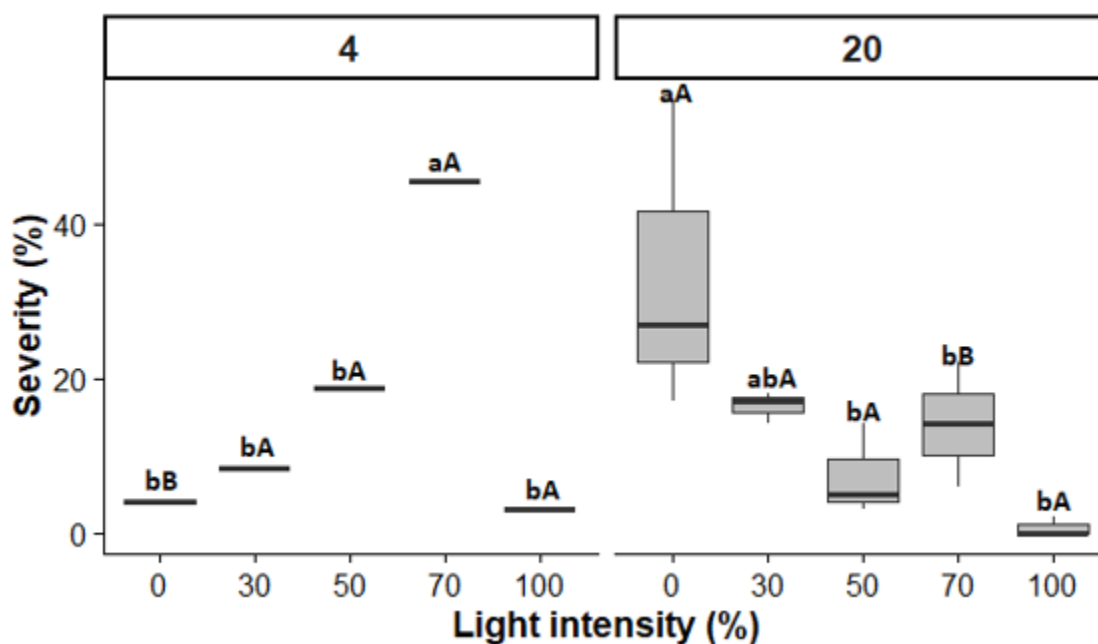


Figure 7

Means followed by the same lowercase letter do not differ significantly among light intensity levels within each evaluation time (4 or 20 days after inoculation). Means followed by the same uppercase letter do not differ significantly between evaluation times within each light intensity level, according to Tukey's test ($p \leq 0.05$).

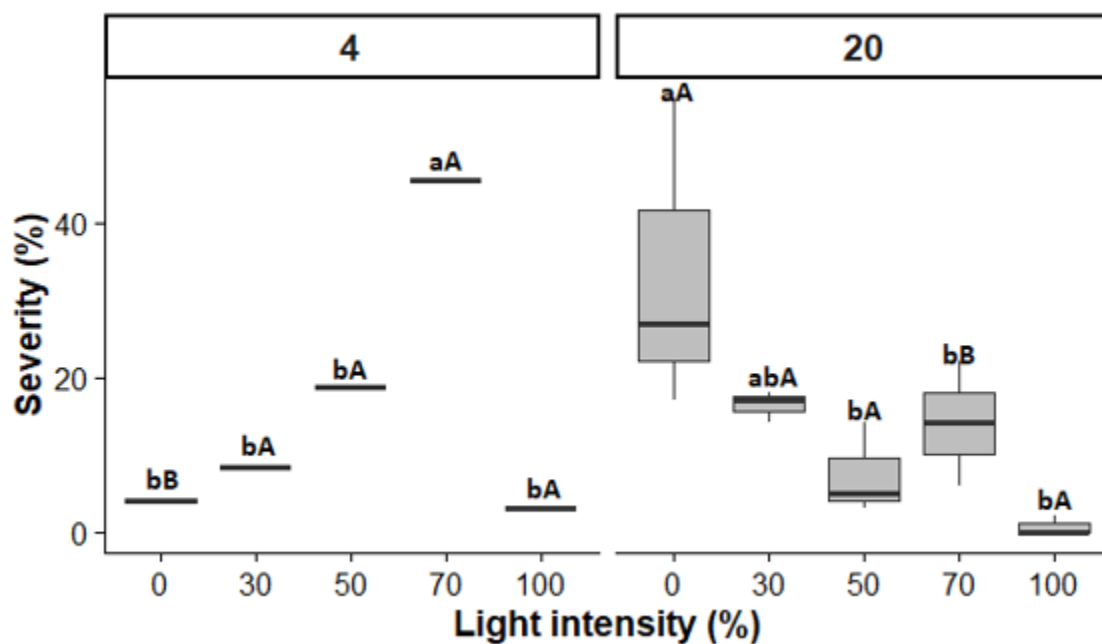


Figure 7

Means followed by the same lowercase letter do not differ significantly among light intensity levels within each evaluation time (4 or 20 days after inoculation). Means followed by the same uppercase letter do not differ significantly between evaluation times within each light intensity level, according to Tukey's test ($p \leq 0.05$).

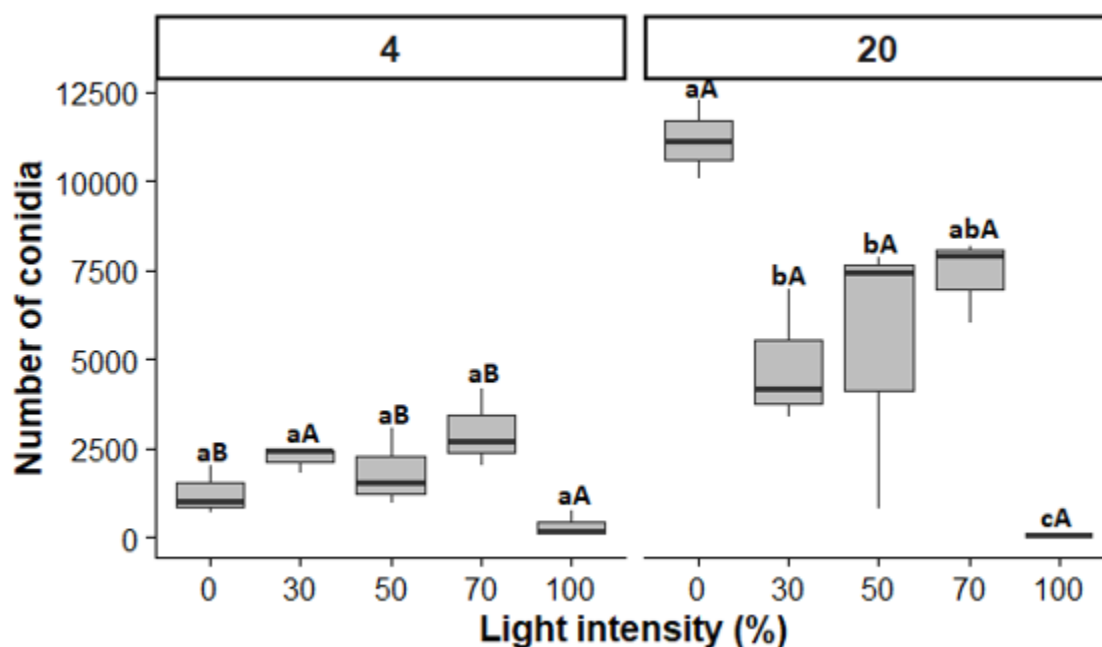


Figure 8

Means followed by the same lowercase letter do not differ significantly among light intensity levels within each evaluation time (4 or 20 days after inoculation). Means followed by the same uppercase letter do not differ significantly between evaluation times within each light intensity level, according to Tukey's test ($p \leq 0.05$).

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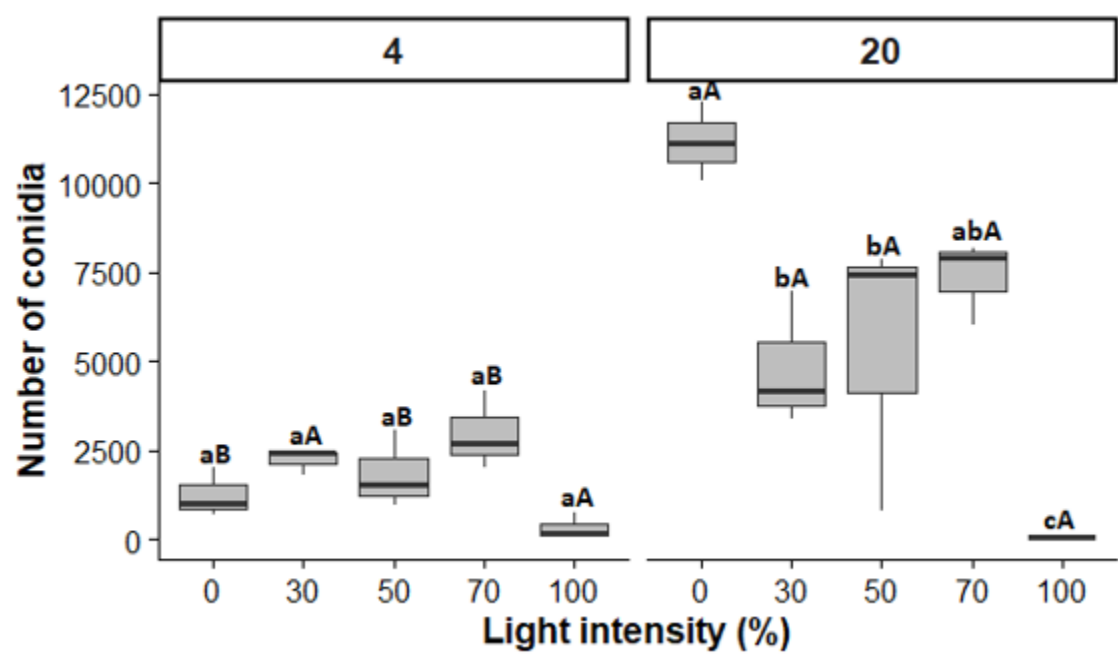


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Means followed by the same lowercase letter do not differ significantly among light intensity levels within each evaluation time (4 or 20 days after inoculation). Means followed by the same uppercase letter do not differ significantly between evaluation times within each light intensity level, according to Tukey's test ($p \leq 0.05$)