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Article

Effect of High Temperature on the Growth and Disease Development of *Erysiphe quercicola* on Rubber Trees

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Abstract: Powdery mildew is a serious disease of rubber tree (*Hevea brasiliensis*) worldwide. Temperature is the main climatic factor that influences the development of this disease. In this study, the effects of five high temperatures (30, 32, 34, 36, and 38°C) at each of six exposure durations (0.5, 1, 3, 6, 12, and 24 h) were measured for the pathogen at 0, 3, 12, and 48 hr post-inoculation (hpi), which represented four life stages of the fungus (conidia, conidial germination, infection, and hyphal growth). The results indicated that the germination, infection and disease severity was reduced with the increasing temperature and exposure duration. Temperature and exposure duration also significantly interacted to affect all life stages ($P < 0.001$). The relationships of inhibition rate of conidial germination, infection and disease severity with duration of exposure time (*et*) and high temperature (*T*) were described by logistic equations with the percentage variance accounted for above 68%. Ungerminated conidia were found to be the most resistant stage to high-temperature for *E. quercicola* from rubber tree out of the four stages tested in this study. Only controlled-environmental experiments were conducted and field studies are needed to enhance disease forecasting of rubber tree powdery mildew.

Keywords: *Hevea brasiliensis*; rubber tree powdery mildew; high temperature effect; germination; infection; disease severity

1. Introduction

Natural rubber is an essential industrial raw material, which is primarily derived from the rubber tree (*Hevea brasiliensis*) [1]. Although the rubber tree is native to the Amazon basin, it is now mainly planted in Southeast Asia, which produces more than 90% of the global supply of natural rubber [2].Powdery mildew occurs in all rubber-growing regions, especially with a high incidence in sub-optimal regions for rubber cultivation [3]. The causal agent of the disease was first described as *Oidium heveae*. However, recent studies demonstrated that *O. heveae* is the asexual morph of *Erysiphe quercicola* on rubber tree [4-6], although its teleomorph has not been reported on rubber tree yet. The pathogen is an obligate biotrophic fungus and only infects young tender rubber leaves, buds, inflorescences and shoots; therefore, the disease mainly occurs in spring, when trees refoliate after the winter, resulting in a reduction of latex yields of up to 45% [2].

Rubber cultivation regions in China, mainly in Hainan, Yunnan, and Guangdong provinces, are all located in sub-optimal rubber cultivation regions. The environmental conditions in these regions including low temperature, higher altitude and dry weather are more stressful to rubber and the rubber clones planted in China have been adapted to these stresses [7]. Also, these locations provide favorable conditions for the epidemic of some diseases, such as powdery mildew, which is the most serious leaf disease of rubber tree in these regions [8]. The disease occurs mainly from February to May in China. None of the popular commercial rubber tree clones are resistant to powdery mildew [3], so current control of rubber powdery mildew still relies on fungicide applications, primarily sulfur dust [9-10].

Weather conditions play a crucial role in the development of powdery mildew diseases [11]. The main climatic factor that has been reported to influence the development of rubber tree powdery mildew is temperature [12-13]. The favorable temperature for conidial germination ranges from 16 to 22°C and from 15 to 25°C for infection, colonisation and sporulation [14]. The effects of constant temperature and leaf age on conidial germination and disease development of rubber tree powdery mildew were studied in a previous study [15]. Temperature affected germination and post-germination growth of rubber tree powdery mildew while leaf age primarily affected post-germination growth of the pathogen. The estimated optimal temperature for conidial germination of *E. quercicola* was 23.2°C. No visible symptoms were observed at a constant temperature above 30°C. Also in field conditions, it was noted that rubber tree powdery mildew development declines when the daily maximum temperature is >32°C [12]. A more recent study also indicated that the infection level of rubber powdery mildew decreased by 8% per 1 °C rise of the daily maximum temperature above the optimum in the refoliation season [13]. These previous reports indicated that high temperature has adverse effects on the development of rubber tree powdery mildew. However, with global climate change, daytime temperatures frequently reach >32°C in spring in the rubber-production regions in China. Therefore, it is necessary to understand the effects of high temperature on the development of rubber tree powdery mildew.

The objectives of this study were to (a) assess the effects of high temperature and exposure duration on *E. quercicola* infection and development on rubber tree; and (b) develop models to describe the observed effects. This knowledge will increase our ability to develop effective management programs for rubber tree powdery mildew, including a rubber powdery mildew forecaster.

2. Materials and Methods

2.1. Plant Materials and Inoculum Preparation

A susceptible rubber tree clone CATAS7-33-97 [16] was used in this study. Seedlings of rubber tree were produced by tissue culture provided by the Rubber Research Institute, Chinese Academy of Tropical Agricultural Science. Mildew-free seedlings were planted in plastic pots (15 cm diameter) with coconut coir compost. Seedlings with the youngest leaves at the copper bronze stage were used. Plants selected for inoculation had three leaves that were at the same phenological stage. All experiments were done from March to April, 2022, which coincides with disease epidemics in Haikou. Each full experiment comprising investigations of five temperatures for each of six exposure times on each of four pathogen stages: conidia, germinating conidia, infection and hyphal growth, took over ten days, not including initial growth of the plants.

2.2. Inoculation Procedure

A field population of *E. quercicola* collected from rubber tree plantations in Haikou in March, 2022 was used in this study, similarly to the use of field populations on other powdery mildew studies, e.g. on *Podosphaera macularis* [17]. The pathogen was first identified based on molecular data (ITS and 28S rDNA region sequence) and maintained in growth chambers with a 12-h day length at 25°C through successive transfers onto rubber tree seedlings (CATAS7-33-97) with leaves at the copper bronze stage. The conidia on these leaves at 10 days postinoculation (dpi) were used for inoculation by surface contact (dusting/tapping). All plants after inoculation were maintained at 25°C prior to and after heat treatment. All experiments were done from March to April 2022, which is when rubber powdery mildew epidemics occur in Haikou.

2.3. Experiment Design

The experiment was arranged as a factorial design with an additional control, factors being temperature and exposure time, for each pathogen stage. Each seedling was considered as a replicate and there were three replicates for each treatment.

Previous work identified the timing of pathogen growth on rubber tree leaves at 0, 3, 12, and 48 hr postinoculation (hpi) representing four life stages of the fungus (conidia, conidial germination, infection, and hyphal growth) when grown at 25°C [14].The effects of five high temperatures (30, 32, 34, 36, and 38°C) at each of six exposure durations (0.5, 1, 3, 6, 12, and 24 h) were measured were measured at 0, 3, 12, and 48 hpi. Therefore, there were 31 treatments including a control for each life stage. Inoculated plants kept at 25°C throughout the experiment were used as controls for reference. Three seedlings, each with three leaves at the copper bronze stage were used for each treatment. Previous pilot studies for conidial germination and infection were conducted in advance as small separate experiments to develop the methods used and their results agreed with our main experiments, confirming the results reported below.

2.4. Effect of High Temperature on Growth and Disease Severity

For the pathogen at the conidium stage (0 hpi) when exposed to high temperature, a leaf segment (half of an inoculated leaf) was selected at random and cut from one seedling at 24 hpi for conidial germination assessment by microscope. The other half was removed at 48 hpi for infection assessment by microscope. The remaining two leaves for each seedling were used for disease severity assessment. The cut leaf segments were cleared by immersion in glacial acetic acid for 24 hr and washed with sterile distilled water for 2 min. Then the segments were stained in 1% aniline blue for 10 min, rinsed in distilled water, and mounted in glycerol on glass slides. Then these leaf segments were examined with a digital microscope (Eclipse 80i; Nikon Corporation, Tokyo, Japan). Conidial germination was assessed at 24 hpi as percentage of conidia that produced germ tubes (Fig. 1a). Infection was assessed at 48 hpi as percentage of conidia that produced at least one hypha extending from an appressorium (Fig. 1b). At least fifty conidia were examined for each cut leaf segment. The disease severity (the percentage of the number of lesion pixels divided by the number of whole leaf region pixels) was assessed 10 days after inoculation, where the number of pixels was obtained using Adobe Photoshop 2022 software (Adobe Systems Incorporated, San Jose, CA, USA), as used previously for in plant diseases [18-19].

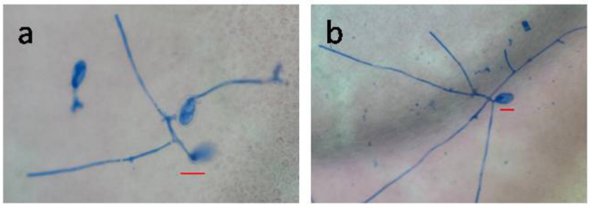

Figure 1. Conidial germination and infection of *Erysiphe quercicola* inoculated on rubber tree leaves at copper bronze stage at 25°C. a, observed at 24 hr postinoculation (hpi); b, observed at 48 hpi. Scale bars = 20 µm.

Similarly, for the pathogen at conidial germination stage (3 hpi) when first exposed to high temperature, one leaf from each seedling was cut at 48 hpi for infection assessment by microscopy. The remaining leaves were used for disease severity assessment.

For the pathogen at infection (12hpi) and hyphal growth (48hpi) stages, all three leaves for each seedling were used for disease severity assessment.

2.5. Data Analysis

To evaluate the effects of high temperature, exposure duration and their interaction on the growth and disease severity of rubber tree powdery mildew, an analysis of two- factor repeated-measures ANOVA was conducted [20] using the generalized linear model (GLM) in SPSS v. 21 (SPSS Inc.).

Inhibition rate (IR) was calculated by (1−germination, infection or disease severity in treatment temperature/germination, infection or disease severity at 25°C) × 100%. The relationship of inhibition rate with duration of exposure time (*et*) and high temperature (*T*) was regressed by the following logistic equation [21]:

$$IR=1-EXP(a+bet(c-T))/(1+ EXP(a+bet(c-T)))$$

where the equation parameters a, b and c were estimated with the nonlinear regression procedure of SPSS v. 21 (SPSS Inc.).

The time to 50% survival (LT_{50}) was calculated by

$$t=-a/b/(c-T).$$

3. Results

3.1. Effect of High Temperature and Exposure Duration on Erysiphe Quercicola Conidia (0 hpi Onset)

High temperature, exposure duration, and their interaction significantly affected conidial germination, infection, and disease severity when *E. quercicola* conidia (0 hpi Onset) were exposed to high temperature ($P< 0.001$). At each temperature evaluated, exposure duration had significant effects on conidial germination although the effect of exposure duration was more marked at 36 and 38°C (Fig. 2a). The germination rate was still higher than 50% (of the total number of conidia assessed) when the spores were exposed to 30, 32 and 34 °C for 24 h. Even at 36 and 38 °C, the germination was higher than 50% when conidia were exposed to these high temperatures for 6 and 3 h, respectively. No conidia germinated when they were exposed to 38 °C for 24 h and the germination was below 6% at 36°C for 24 h.

High temperatures commencing at the spore stage (0 hpi) also caused the amount of infection and disease severity to decline with increasing temperature and exposureduration. This effect was more marked with longer exposure durations at all tested temperatures, 30 to 38°C (Fig. 2b and 2c). The amount of infection was below 20% when conidia were exposed to 30, 32 and 34°C for 24h, or exposed to 36 or 38°Cfor only 12 h. The disease severity was below 5% for conidia exposed to 30, 32 and 34°C for 24 h while the disease severity was below 10% and 5% for conidia exposed to 36 and 38°C for 12 h and 6 h, respectively.

For conidia treated with high temperatures, logistic models satisfactorily described the relationship of inhibition rate (IR) of germination, infection and disease severity of rubber tree powdery mildew with duration of exposure time (*et*) and high temperature (*T*) with the percentage variance accounted for at 89.5, 92.6 and 82.0%, respectively (Table 1). The LT_{50} values (time duration to inhibit 50% germination, infection or disease severity at a given high temperature) for germination were more than 7 hours even for the conidia exposed to 38 °C. LT_{50} values for infection and disease severity ranged from 3.7 to 10.5 h and 3.6 to 14.4 h for conidia exposed to 38 to 30°C, respectively (Table 2).

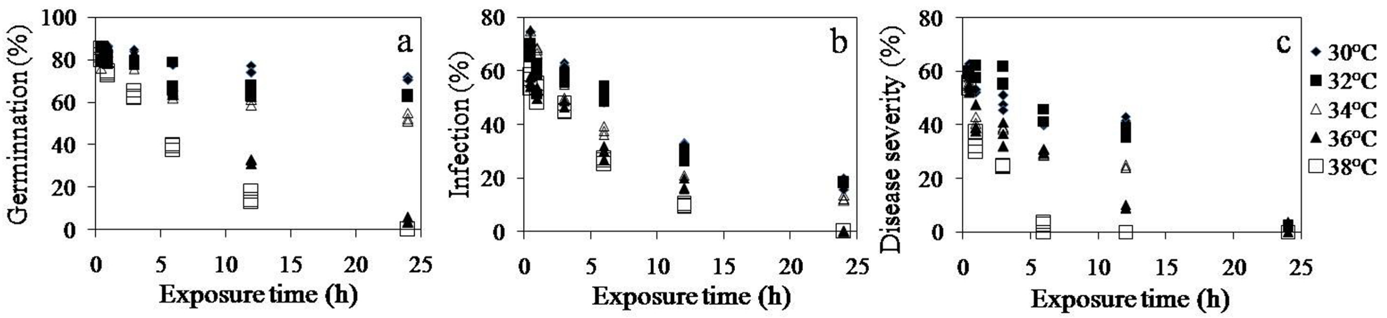

Figure 2. Effects of five different high temperatures (30, 32, 34, 36 and 38°C) and six exposure duration times (0.5, 1, 3, 6, 12 and 24 h) on conidial germination (a), infection (b) and disease severity (c) of *Erysiphe quercicola* on rubber tree leaves when high temperatures commenced immediately at inoculation (0 hpi). Inoculated leaves were subsequently incubated at 25°C. Inoculated plants kept at 25°C throughout the experiment were used as controls for reference with conidial germination, infection and disease severity at 86.64%, 82.26% and 65.06%, respectively. High temperature, exposure duration, and their interactions significantly affected conidial germination, infection, and disease severity ($P< 0.001$).

Table 1. Parameter estimates for the model IR=1-EXP(a+bet(c-T))/(1+ EXP(a+bet(c-T))) describing the relationship of inhibition rate (IR) with duration of exposure time (*et*) and high temperature (*T*) of *Erysiphe quercicola* from rubber tree at different life stages (exposure stages) when exposed to high temperatures.

Exposure stage	Influence stage	a	b	c	Percentage variance accounted for
Conidium	Germination	2.192±0.121	0.046±0.004	31.321±0.278	89.5
	Infection	0.967±0.051	0.021±0.002	25.620±0.665	92.6
	Disease severity	1.452±0.135	0.037±0.006	27.304±0.625	82.0
Germination	Infection	0.530±0.072	0.036±0.004	29.348±0.279	80.9
	Disease severity	1.400±0.154	0.087±0.014	27.632±0.553	82.4
Infection	Disease severity	1.067±0.149	0.049±0.008	29.847±0.391	68.2
Hyphal growth	Disease severity	0.681±0.069	0.037±0.004	28.592±0.309	84.5

Table 2. Predicted LT_{50} (time to 50% survival) of *Erysiphe quercicola* from rubber tree at different life stages (exposure stages) when exposed to high temperatures.

Exposure stage	Influence stage	30°C	32°C	34°C	36°C	38°C
Conidium	Germination	>24	>24	20.0	10.9	7.5
	Infection	10.5	7.2	5.5	4.4	3.7
	Disease severity	14.4	8.3	5.8	4.5	3.6
Germination	Infection	22.4	5.5	3.1	2.2	1.7
	Disease severity	6.8	3.7	2.5	1.9	1.6
Infection	Disease severity	>24	10.1	5.2	3.5	2.7
Hyphal growth	Disease severity	13.2	5.4	3.4	2.5	2.0

3.2. Effect of High Temperature and Exposure Duration on Erysiphe quercicola at Germination Stage (3hpi Onset)

High temperature, exposure duration and their interaction significantly affected infection and disease severity when *E. quercicola* at germination stage (3 hpi onset) were exposed to high temperature (*P*< 0.001). Conidia at the germination stage at 30 to 32°C only experienced a gradual decline in infection with increasing duration of heat exposure but declines were much more dramatic when exposed to 36 to 38°C (Fig. 3a).Infection percentage (% conidia producing at least one hypha extending from an appressorium) was higher than 25% and 20% respectively when the treatment temperatures were 30 and 32°C for 24 h at the conidial germination stage, however, the infection percentage was below 13%, 9% and 6% when the treatment temperatures were 34, 36 and 38°C for 12, 12 and 6 h, respectively.

The disease severity declined sharply with increasing exposure durations at all five high temperatures applied at the germination stage (3 hpi) (Fig. 3b). Disease severity was below 10% when exposed to 30, 32 and 34°C for 12 h, and it was below 10% when exposed to 36 and 38°C for 12h and 1 h, respectively. Logistic models were applied to describe the the relationship of inhibition rate (IR)of infection and disease severity of rubber tree powdery mildew with *et* and *T* for the conidia at the germination stage with the percentage variance accounted for at 80.9 and 82.4%, respectively

(Table 1). LT_{50} values were estimated based on parameters of the logistic models for infection and disease severity ranged from 1.7 to 22.4 h and 1.6 to 6.8 h for conidia at the germination stage exposed to 38 to 30°C, respectively (Table 2).

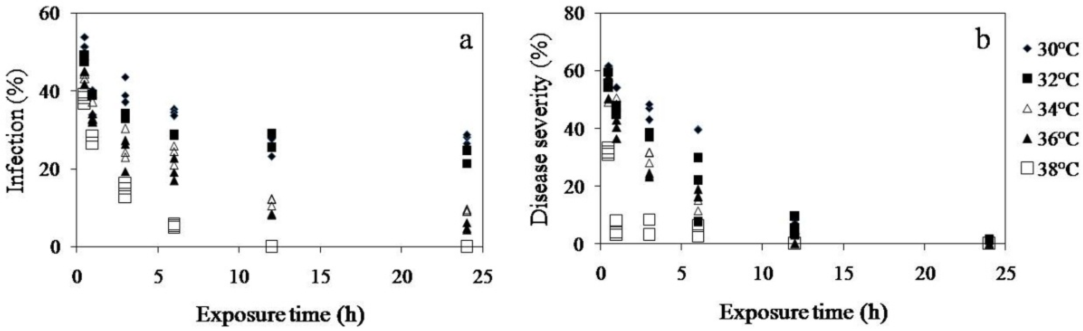

Figure 3. Effects of five different high temperatures (30, 32, 34, 36 and 38°C) and six exposure duration times (0.5, 1, 3, 6, 12 and 24 h) on infection (a) and disease severity (b) of *Erysiphe quercicola* on rubber tree leaves, when high temperatures commenced at the conidial germination stage (3 hpi). Inoculated leaves were otherwise kept at 25°C. Inoculated plants kept at 25°C throughout the experiment were used as controls for reference with infection and disease severity at 62.48% and 63.00%, respectively. High temperature, exposure duration and their interaction significantly affected infection by conidia, and disease severity (P< 0.001).

3.3. Effect of High Temperature and Exposure Duration on Erysiphe quercicola at Infection (12 hpi onset) and Hyphal Growth Stage (48 hpi Onset)

High temperature, exposure duration and their interaction significantly reduced disease severity when *E. quercicola* at infection (12 hpi onset) and hyphal growth stage (48 hpi onset) were exposed to high temperature (P< 0.001). When the pathogen was exposed to high temperature at the infection stage, the disease severity subsequently declined especially after exposure to 38 °C. Disease severity was below 11% when the pathogen had been exposed to 38°C for 1h while the disease severity was higher than 35% for the other 4 temperatures applied for 1h. Disease severity was also below 11% when the pathogen was exposed at 34 and 36 °C for 24 and 12 h, respectively. However, disease severity was above 16% and 20% when exposed to 32 and 30°C for 24 h (Fig. 4a).

When the pathogen was exposed to high temperature at the hyphal growth stage, the disease severity was below 4% when high temperature exposure duration exceeded 6h at 38°C, however, it was higher than 15% when exposed to 38°C for only 3 h. Disease severity was below 10% for treatments exposed to 34 and 36°C, for 24 h and 12 h, respectively, while disease severity exceeded 13% for treatments exposed to 32 and 30°C for 24 h (Fig. 4b).

Based on the logistic models describing the the relationship between inhibition rate (IR) of disease severity of rubber tree powdery mildew with *et* and *T* for the pathogen at the infection or hyphal growth stage, the percentage variance accounted for was 68.2 and 84.5%, respectively (Table 1), LT_{50} values ranged from 2.7 h to over 24 h for the pathogen at the infection stage for temperatures ranging from 38 to 30°C, while for the hyphal growth stage, LT_{50} values ranged from 2 h to 13.2 h for temperatures ranging from 38 to 30°C (Table 2).

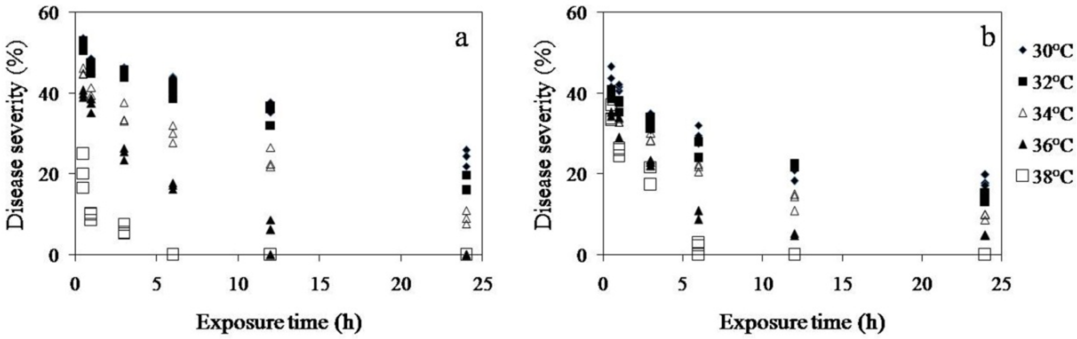

Figure 4. Effects of five different high temperatures (30, 32, 34, 36 and 38°C) and six exposure duration times (0.5, 1, 3, 6, 12 and 24 h) on disease severity caused by *Erysiphe quercicola* on rubber tree leaves when high temperatures commenced at infection (a) (12 hpi) or the hyphal growth stage (b) (48 hpi). Inoculated leaves were otherwise kept at 25°C. Inoculated plants kept at 25°C throughout the experiment were used as controls for reference with disease severity at 54.62% and 55.49% for infection and the hyphal growth stage, respectively. High temperature and exposure duration significantly affected disease severity ($P < 0.001$).

4. Discussion

The present study investigated the effects of high temperature on the rubber tree powdery mildew pathogen, *E. quercicola*. The results indicated that the conidial germination, infection and disease severity was reduced with increasing temperature and exposure duration, although the declines were much more dramatic at 36 or 38°C. This was consistent with previous studies using field data indicating a negative effect of daily maximum temperature on the infection severity of powdery mildew during the refoliation season [13].

When the conidia inoculated onto rubber tree leaves were exposed to high temperature, the percentage germination was still above 50% even when conidia were exposed to 30, 32 and 34 °C for 24 h, which is consistent with a former study showing that conidia still germinated under a constant temperature of 35 °C [15]. However, the germination was below 6% and there was a total loss of conidium viability when conidia were exposed to 36 and 38°C for 24 h, respectively.

Disease severity was above 35% when conidia were exposed to 36°C for 3 h immediately at inoculation (0 hpi). However, disease severity was below 25% when the pathogen was exposed to 36°C for 3 h at the other three later growth stages (3, 12 and 48 hpi onset). These results indicated that the effects of high temperature on *E. quercicola* from rubber tree were different among different life stages of the pathogen (conidia, conidial germination, infection and hyphal growth). Similar results were also reported for *E. necator* and *Blumeria graminis* f. sp. *tritici*, which are the pathogens causing grape powdery mildew and wheat powdery mildew, respectively [20, 22].

According to the predicted LT_{50} values, conidia at the germination stage appear to be the most sensitive to high-temperature exposure among the four life-cycle stages investigated in this study. For *B. graminis* f. sp. *tritici*, haustoria formation was the key infection stage affected by heat stress in high-temperature-resistant isolates [22]. In contrast, among three life-cycle stages (conidial germination, conidial production, and colony growth) investigated, conidial production was found to be the most sensitive to high-temperature for *E. necator* [20]. Ungerminated conidia may be the most resistant stage to high-temperature stress for *E. quercicola* from rubber tree. This was also the most resistant stage to high-temperature stress for *E. necator* and *B. graminis* f. sp. *tritici* [20, 22]. However, disease severity was still above 20% for all four stages exposed to 30, 32, 34 and 36°C for 3 h and for the conidia and hyphal growth stages when exposed to 38°C for 3 h. Commencement of high temperature exposure at a range of successive pathogen stages allowed normal pathogen development to occur up to the onset of that high-temperature exposure, so that effects of the high temperature could be quantified separately for those different pathogen stages. Overall, it was shown that the pathogen can resist high temperatures for a short duration i.e. 3 h when the temperature was below 38°C. This can explain why the disease is still common and serious in locations where the daily maximum temperature exceeds 32°C, which is common where the disease occurs in China.

The disease severity was below 4% when high temperature treatments began at 0 or 3 hpi (conidia and conidial germination stage) for high temperatures of 30, 32 and 34°C for a duration of 24 h, but disease severity was above 8% when exposed to high temperatures at later onset times (12 and 48 hpi corresponding to infection and hyphal growth stages). At the conidia and conidial germination stages with exposure duration for 24 h, the high temperature not only affected the present stage, but decreases in spore germination resulted in reductions in subsequent disease severity compared to controls. It is not clear whether the lower rate of conidial germination under high temperatures was the result of conidial mortality or whether they could germinate later when suitable conditions resumed but nevertheless, the lower germination rate resulted in lower disease severity after 10 days. It was reported that *E. quercicola* conidia began to germinate and infect within 24 h even at 35°C [15].

Except for direct effects on the pathogen, it was reported that high temperature also affected the susceptibility of host plants to pathogen e.g. hop leaves to *P. macularis* [16]. This may be caused by changes in the cuticle and epidermal cell walls under high-temperature conditions as the infection of *P. macularis* on strawberry was related to a combination of cuticle and cell wall thickness [23]. Whether high temperature has effect on the susceptibility of rubber tree leaves to *E. quercicola* needs future study. Also as only controlled-environmental experiments were conducted in this study, additional field studies are needed to enhance forecasting of rubber tree powdery mildew infections.

5. Conclusions

This study has demonstrated high temperature (≥30°C), exposure duration and their interaction significantly affected conidial germination, infection of *E. quercicola* from rubber tree as well as disease severity. More importantly, the relationships of inhibition rate of conidial germination, infection and disease severity with duration of exposure time (*et*) and high temperature (*T*) were described by logistic equations and the time to 50% survival (LT_{50}) was calculated based on the parameters of logistic equations. Among the four stages tested in this study, ungerminated conidia were found to be the most resistant stage to high-temperature for *E. quercicola* from rubber tree. The results of this study can be used to explain why the disease is still common and serious in locations where the daily maximum temperature exceeds 32°C, which is common where the disease occurs in China. Although only controlled-environmental experiments were conducted in this study, the results also provide basic data for disease forecasting of rubber tree powdery mildew.

Author Contributions: Conceptualization, Xueren Cao; Funding acquisition, Jonathan S. West and Xueren Cao; Investigation, Yongxiang He and Ying Xiao; Methodology, Yongxiang He and Ying Xiao; Validation, Yongxiang He and Ying Xiao; Writing – original draft, Xueren Cao; Writing – review & editing, Jonathan S. West. All authors have read and agreed to the published version of the manuscript.

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