



# Contrasted effects of temperature during defoliation vs. refoliation periods on the infection of rubber powdery mildew (*Oidium heveae*) in Xishuangbanna, China

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## Abstract

Rubber powdery mildew caused by the foliar fungi *Oidium heveae* is one of the main diseases affecting rubber plantations (*Hevea brasiliensis*) worldwide. It is particularly serious in sub-optimal growing areas, such as Xishuangbanna in SW China. To prevent and control this disease, fungicides causing serious environmental problems are widely used. Strong correlations between the infection level and the temperature variables were reported previously, but they were related to monthly data that did not allow unraveling the patterns during the entire sensitive period. We correlated the infection level of powdery mildew of rubber trees recorded over 2003–2011 with antecedent 365 days daily temperature variables using partial least squares (PLS) regression. Our PLS regression results showed that the infection level of powdery mildew responded differently to the temperature variables of the defoliation and refoliation periods. Further analysis with Kriging interpolation showed that the infection level increased by 20% and 11%, respectively, per 1 °C rise of the daily maximum and mean temperature in the defoliation season, while it decreased by 8% and 10%, respectively, per 1 °C rise of the daily maximum and temperature difference in the refoliation season. This pattern was likely linked to the effects of temperature on leaf phenology. It seems highly possible that the infection level of powdery mildew increases, as increasing trends of maximum temperature and mean temperature during the defoliation continue.

**Keywords** Rubber plantation · *Hevea brasiliensis* · Partial least squares (PLS) regression · Phenology · Xishuangbanna

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## Introduction

Powdery mildew disease, caused by *Oidium heveae*, is a major disease affecting rubber trees in almost all rubber-growing countries, especially in Southeast Asia, which accounts for 93% of the natural rubber production in the global market (Liyanage et al. 2018; Priyadarshan 2011). Most rubber plantations are monospecific and plots are monoclonal, making them particularly sensitive to leaf diseases such as powdery mildew (Liyanage et al. 2016). The powdery mildew disease mainly infects the immature leaves, flowers, and other immature tissues of rubber trees during refoliation season after annual wintering. It is particularly serious in the sub-optimal cultivating habitats, like Xishuangbanna in SW China, where the rubber trees have distinct phenology for annual leaf shedding (wintering) and leaf flushing (refoliation) (Liyanage et al. 2018; Priyadarshan 2011; Zhai et al. 2019).

The epidemic duration of *Oidium heveae* in natural conditions is only 40 days, and climatic variables directly affect the development of the pathogen (Paris and Cohen 2002; Shao and Hu 1984; Shao et al. 1996). Copper sulfate powder, one of the cheapest and most effective pesticides, is widely used to prevent and control this disease; however, it causes decrease in soil pH, changes the soil bacterial composition and diversity, and affects biogeochemical cycling (Lan et al. 2018; Li et al. 2016). The climatic factors have been reported seriously influencing the infection incidence and being critical for forecasting and estimating the infection of this disease (SCATCS 1959; SCATCS 1983; Shao and Hu 1984; Yu and Wang 1988; Yu et al. 1980; YITC 1981; Zhou 1982). Therefore, to estimate the powdery mildew infection incidence and to guide disease control, people have paid great attention to the impact of climatic variables, especially in critical periods (Paris and Cohen 2002; SCATCS, 1983 1985; Shao and Hu 1984; Shao et al. 1996). The Chinese government supported strongly investigations into the powdery mildew disease in the 1960s–1980s, during which most of the rubber trees were managed by state farms (Xu et al. 2009). During that time, studies have been conducted to identify the determining climatic factors that affect the powdery mildew infection (SCATCS 1959; SCATCS 1983; Shao and Hu 1984; Yu and Wang 1988; Yu et al. 1980; YITC 1981; Zhou 1982). Most of these studies have identified temperature as the main factor and mainly focused on the response of the infection level to monthly temperature data during the refoliation phase. The powdery mildew infection appears to respond differently to temperature in the defoliation and refoliation seasons of rubber trees. For example, a high mean temperature in December–January could increase the powdery mildew infection level (Yu et al. 1980; YITC 1981). Conversely, high mean temperature in spring, during the refoliation season, decreases the infection level (PPRI, SCATCS 1983; Shao and Hu 1984; Shao et al. 1996; Yu et al. 1980; YITC 1981). However, the monthly

climatic data used in the previous studies might overlook the effects of climatic variables on the dynamics of powdery mildew infection in critical periods. Hence, they are not precise enough to analyze the effects of ongoing and future impacts of climate changes on the disease in rubber plantations. Moreover, they considered only the infection period, whereas the full annual climatic conditions, especially winter climatic conditions, may have an influence (Luedeling and Gassner 2012; Yu et al. 1980).

Therefore, long-term and detailed observation data is critical to understand and predict the impacts of climatic condition on the disease. In this study, we collected 9-year long observation data from 2003 to 2011 to investigate the impacts of climatic variables at a daily resolution on the powdery mildew infection. In 2011, state farms implemented reforms for rubber plantations involving contracting work out to certain households; accordingly, monitoring, measurements, and other related research were terminated. We used partial least squares regression to better identify the critical periods influencing the infection level. Our site-based disease observation data and the daily meteorological data provided a unique opportunity for exploring the responses of this disease to climate change. Our findings will provide a new understanding for how rubber powdery mildew may respond to projected long-term climate change.

## Materials and methods

### Study area

Xishuangbanna, one of the two main rubber-producing regions in China, is located at the northern edge of the Asian tropical zone (Zhu et al. 2006). It is a sub-optimal region for rubber cultivation (Yu et al. 2014) (Fig. 1), for its colder and drier climate compared with the humid tropics, the optimal environment of rubber trees (Priyadarshan 2011; Yu et al. 2014). The mean annual temperature is 22.6 °C, and annual precipitation is 1130 mm (Zhai et al. 2019) (Fig. 2). Xishuangbanna has two seasons (Cao et al. 2006; Zhang and Cao 1995): dry season (from November to April) and rainy season (from May to October). The dry season is further divided into a cool-dry season (from November to February) and a hot-dry season (from March to April) (Cao et al. 2006). The cool-dry season is distinct, with a 17 °C mean temperature and dense fog during the night and in the morning and little rain. This is when the rubber trees shed leaves (wintering, from early December to the middle of January) and refoliated (from the end of January to the end of March) (Zhou et al. 2008). The hot-dry season (end of March to May) is distinct with dry and hot weather in the afternoon and dense fog in the morning only but still little rain (Cao et al. 2006). During this season, the leaves continue to develop

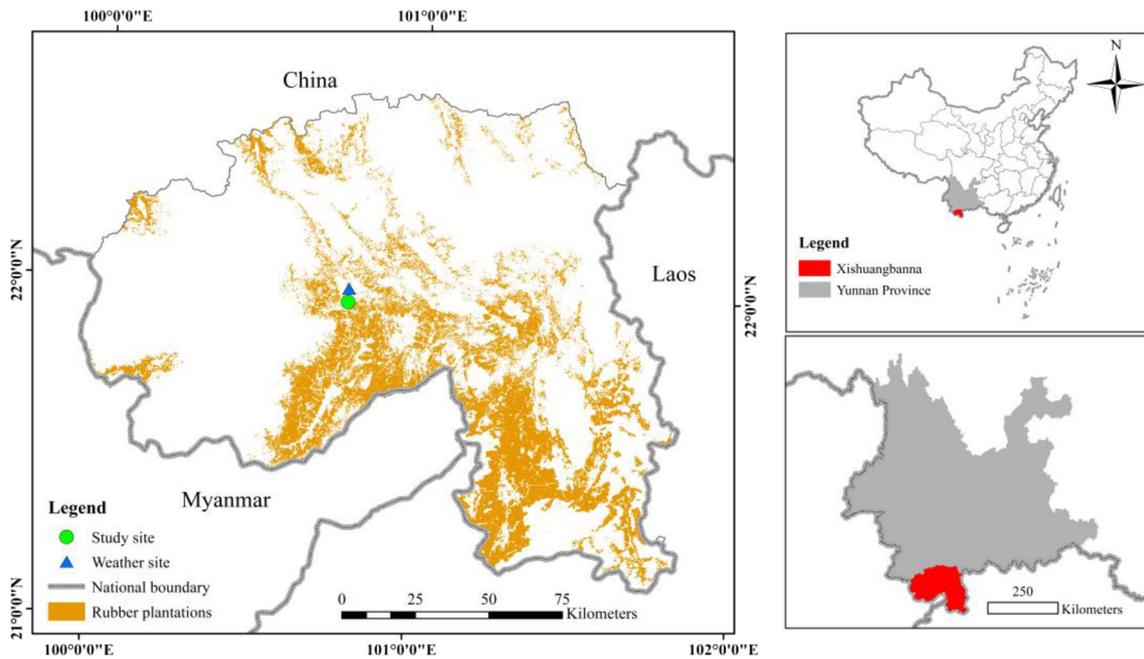


Fig. 1 The location of study site

(Liyanage et al. 2019). The rainy season, from May to October, accounts for 87% of the annual rainfall in this region. The rubber trees are tapped in the rainy season until the cool-dry season.

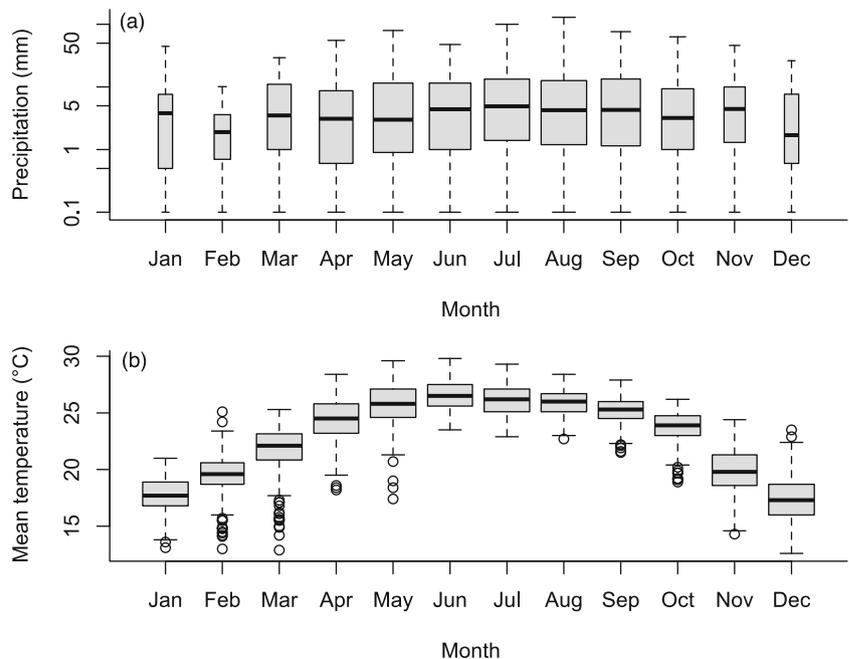
We studied the powdery mildew disease of rubber trees in a state-owned farm (the sixth branch of Jinghong Farm) located near Jinghong City, Xishuangbanna Prefecture, Yunnan Province (21° 48 N, 100° 46 E). There are 1813 ha of rubber plantations in this farm. The major clones of rubber trees are RRIM600, GT1, PR107, and YUNYAN1. GT1 and PR107

are less resistant to powdery mildew than RRIM600 and YUNYAN1 (Zhang et al. 2009).

**Rubber powdery mildew data and climate data**

Rubber powdery mildew monitoring and measurements were conducted from the end of January to the end of March with a 3-day interval from 2003 to 2011. The observation sites were chosen to represent the whole area of the plantation with mature (tapped) trees. Following the guidelines and standards of

Fig. 2 Monthly mean precipitation (a) and temperature (b) in 2003–2011. The precipitation has been log<sub>10</sub> transformed. The tall and narrow bars indicated intense storms that occurs infrequently, while the border bars indicated less intense rainfall events occurring more frequently



the Bureau of China State Farm, twenty trees were selected and marked in each of the 15 observation sites representing the whole plantation (total 300 trees). The sampling proportion—about 5% of the trees in each observation site—was similar to that of published studies on leaf diseases in rubber trees (Shao et al. 1996; Chen and Li, 2002; Rivano et al. 2013; Cardoso et al. 2014). Although the infection sensitivity to powdery mildew disease is different according to clones, this does not influence infection variabilities in years and plots (Shao et al. 1996). Therefore, we did not record the data based on clones. One leaf whorl, corresponding to one growth unit, was collected from each of the twenty trees (Shao and Hu 1984). We collected 15–60 leaves from each whorl, which led to 300–1200 leaves per observation site. The number of leaves infected by powdery mildew was recorded on each observation site. The infection level of the powdery mildew was then calculated for each observation site following the Eq. (1).

Infection level(%)

$$= \frac{\text{Number of infected leaves}}{\text{total number of sampled leaves}} \times 100\% \quad (1)$$

In this study, we mainly focused on the impacts of temperatures on the powdery mildew infection, mainly due to the findings that the temperature is the main environmental factor influencing sporulation of powdery mildew disease (Liyanage et al. 2016). Additionally, in a local study, researchers found the monthly mean temperature in January as one of the two indicators for powdery mildew infection forecasting (YITC 1981). They also found that the epidemic rate of powdery mildew infection is determined by minimum and maximum temperatures (Shao et al. 1996). Therefore, we used daily maximum, minimum, and mean temperatures between 2003 and 2011, which were collected from Jinghong weather station of the National Meteorological Information Center of China (<http://data.cma.cn/>). The daily temperature difference (TD) was the difference between daily maximum and minimum temperatures. We have checked that there was no missing values and null value before further processing. The climatic variables have been processed by a 15-day running mean approach before correlating it to powdery mildew by the partial least squares (PLS) regression (Luedeling and Gassner 2012). After the running mean processing, all the daily climatic data were replaced by the mean value of a period of 15 days, which started 7 days before and ended 7 days after the date.

## Statistical analysis

PLS regression was used to analyze the responses of the infection level of powdery mildew to climatic variables on a daily resolution. We correlated the average powdery mildew

infection level to the climatic variables of the smoothed daily mean climatic variables of antecedent period, i.e., from Apr 01 of year N-1 to Mar 31 of year N, which meant during the preceding summer, fall, winter, and current spring in this study. PLS regression is a reliable and suitable regression method for this study as the independent variables (in this case, climatic variables) are highly correlated and the number of independent variables exceeds the number of dependent variables (the infection level of powdery mildew) (Guo et al. 2013; Luedeling and Gassner 2012). PLS could reduce the number of independent variables using the principal component analysis and canonical correlation analysis. The PLS method produces two major outputs: the variable importance in the projection (VIP) statistic and the standardized model coefficients (Luedeling and Gassner 2012). The VIP values reflect the importance of all climatic variables in explaining the variations of the infection level of powdery mildew. Standardized model coefficients and their 95% confidence interval indicate the strength and direction of the impacts of climatic variables in the PLS model (Luedeling and Gassner 2012). The climatic variables with  $VIP \geq 0.8$  and standardized coefficient confidence intervals significantly different from 0 were considered important to explain the infection level of powdery mildew (Guo et al. 2013; Luedeling and Gassner 2012). Positive value of the model coefficients and  $VIP \geq 0.8$  indicated an increase in infection level while rising of temperature variables. Conversely, negative model coefficients and  $VIP \geq 0.8$  were correlated with a decrease in infection level. The accuracy of the PLS model was evaluated with the root mean square error (RMSE) of the regression analyses. The PLS analysis was mainly based on the “pls” and “chillR” package in R programming language (Luedeling 2017; Luedeling and Gassner 2012; Mevik et al. 2016).

Based on the VIP and model coefficients of the PLS, we identified periods of time that significantly influenced the infection level of powdery mildew. To investigate further the relationship between the infection level and the climatic variable (Tmax, Tmean, and TD) during two identified critical periods, we used a three-dimensional response map derived from the Kriging technique. Kriging is often used in spatial statistics to estimate values at locations between measured points; however, it can also be used for response maps and using factor values as coordinates instead of spatial coordinates (Guo et al. 2017; Luedeling et al. 2013). In this study, we substituted the spatial coordinates with temperature variables during the two identified critical periods. Default settings of the Kriging technique in the R package “field” were adopted (Nychka et al. 2017).

To investigate the temporal trend of maximum temperature (Tmax), mean temperature (Tmean), and temperature difference (TD) in the two identified critical periods, we used a linear regression model to analyze the changes of the three temperatures in the past 30 years. The statistical significance

was tested using the  $t$  test. All analyses were implemented in the R programming language (R Core Team 2017).

## Results

### Responses of rubber powdery mildew to the temperatures

During 2003–2011, the mean infection level increased slowly from Jan 16 to Jan 30 and faster from Jan 31 to Mar 30 (Fig. 3a), with significant variations between years (Fig. 3b). The 2003–2010 average annual infection level was 22.7% and was much higher in 2008 than in other years (Fig. 2c). Tmax, Tmean, and TD had a clear positive effect in the defoliation season and negative effects in the refoliation season (Fig. 4). However, there was no clear pattern for the precipitation, especially during the defoliation and refoliation (Fig. S1). Therefore, the 365 daily temperatures of Tmax, Tmean, and TD between previous April (year N-1) and March (year N) were used as independent variables for the PLS regression, while the average annual infection level of powdery mildew worked as the dependent variable. The RMSE for the PLS models was 1.77% for Tmax, 2.52% for Tmean, and 2.04% for temperature difference, which indicated that the models were well suited for the data. From the VIP and standardized model coefficients of the PLS regression models, we identified the critical periods, during which temperatures showed significant effects on the infection level of powdery mildew.

Several candidate periods of at least 7 days with VIP values  $> 0.8$  were identified. Much higher VIP scores, up to 2.0, during defoliation and refoliation period (from December to March) compared with the growth season of rubber trees (especially from August to November), indicated that the temperatures during the defoliation and refoliation periods had a stronger influence on powdery mildew than climatic variations during the previous growth-season. Therefore, we focused on the temperatures during the defoliation and

refoliation months with VIP scores  $> 0.8$  as the critical periods that influence the powdery mildew disease.

Model coefficients for the daily Tmax were mostly positive and VIP values mostly exceeded 0.8 between Dec 10 and Jan 21, indicating that a higher Tmax during this period was correlated to a higher infection level (Fig. 4). Conversely, significant negative effects of Tmax on the infection level of powdery mildew were detected between Feb 7 and Mar 15, which indicated that a higher Tmax during this period was related to a lower infection level. As the pattern was clear and consistent, with VIP value  $> 0.8$ , we considered Dec 10–Jan 21 and Feb 7–Mar 15 as two critical phases for the responses of the infection level of powdery mildew to Tmax (Fig. 4).

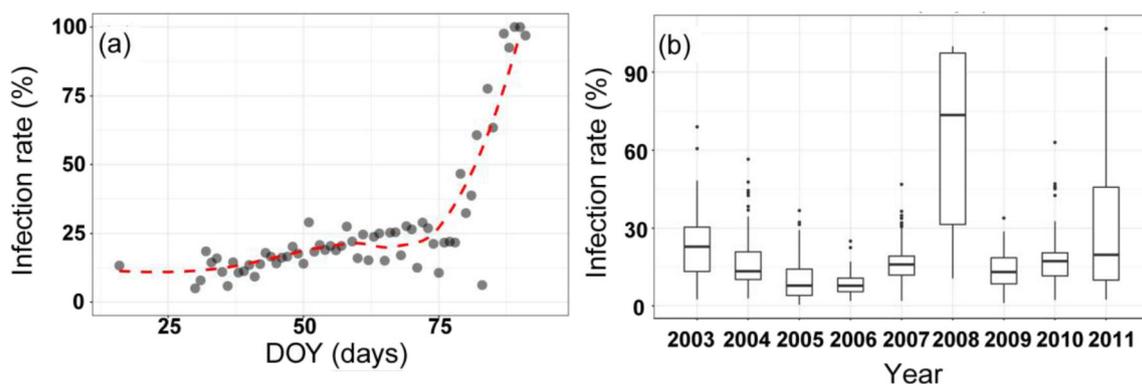
The response pattern of the infection level to the daily Tmean showed a similar pattern as that of Tmax: the significant positive effects were between Dec 11 and Jan 24, and the significant negative effects were between Feb 8 and Mar 10 (Fig. 4). We, therefore, regarded Dec 11–Jan 24 and Feb 8–Mar 10 as two critical phases for the responses of the infection level of powdery mildew to the daily mean temperature.

The temperature difference had a shorter positive effect period from Dec 6 to Jan 11 and a longer negative effect period from Jan 23 to Mar 30 (Fig. 4).

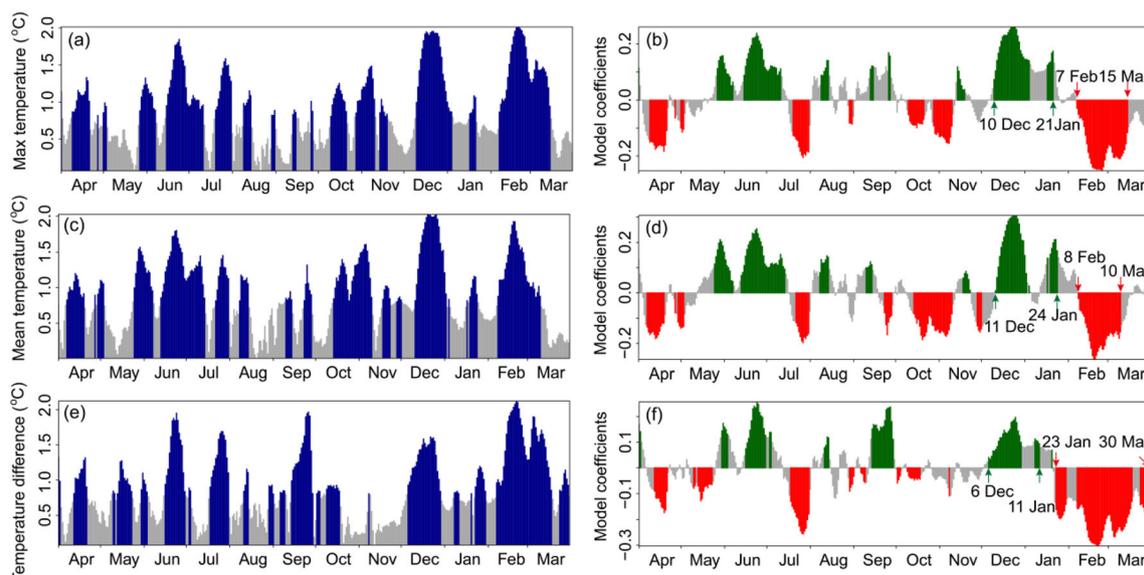
Combining the above results, we found positive effects of daily Tmax, Tmean, and TD on the infection level of powdery mildew in the defoliation season. Conversely, negative effects of Tmax, Tmean, and TD were recorded during refoliation season.

### Specific responses of rubber powdery mildew infection to temperature

To illustrate the relative influence of the two critical phases on the resultant infection level, we plotted the infection level as a function of the three temperature variables during the two critical phases together and interpolated the response by Kriging method (Fig. 5). The trends of the infection level to



**Fig. 3** Infection level of powdery mildew of each observation site (15 points per year) with day of the year (DOY) (a) and with years (b)



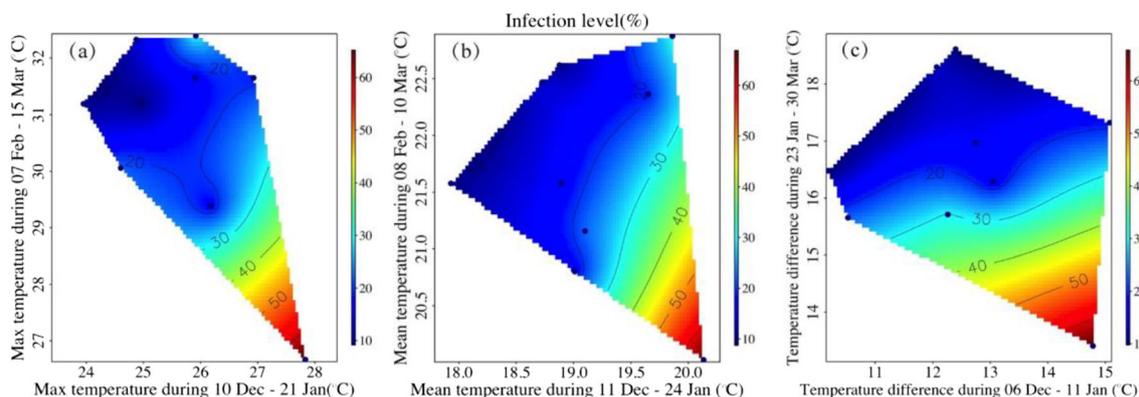
**Fig. 4** Results of partial least squares (PLS) regression correlating infection level of powdery mildew during 2003–2011 with 15-day running means of (a), (b) daily maximum temperature, (c), (d) daily mean temperature, and (e), (f) daily temperature difference from previous April to March. The effects of variables are considered important when the confidence intervals of model coefficients (b, d, f) are significantly different

from 0, and very important for projection (VIP) values are greater than 0.8. The blue bars in the left panel stand for the VIP scores of the daily maximum, mean temperature, and mean temperature difference. Red bars in the right panel correspond to important negative effects of climate variables on powdery mildew infection, while green bars indicate important positive effects. Gray bars indicate non-significant effects

temperature variables were indicated by contour lines in the respective Kriging figures.

The average slope of the contour lines from the Tmax was around 45°, indicating that both periods had about the same importance on the infection level: an increasing effect of Tmax during Dec 10–Jan 21 of the defoliation season and a depressing effect of Tmax during Feb 07–Mar 15 of the refoliation season (Fig. 5). The infection level of powdery mildew was expected to be greater than 40%, when the maximum temperature during Dec 10–Jan 21 was above 26 °C or the maximum temperature during Feb 07–Mar 15 was lower than 29 °C. When a higher maximum temperature during

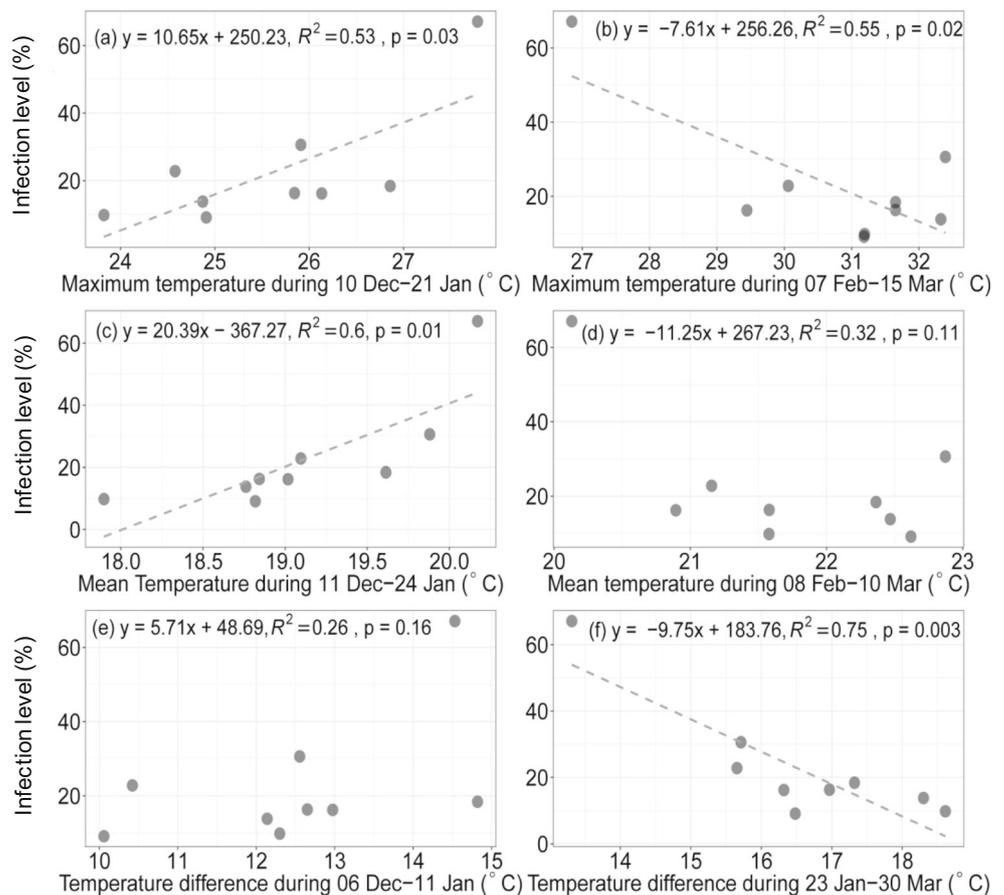
Dec 10–Jan 21 was followed by a lower maximum temperature during Feb 07–Mar 15, a higher infection level would be expected in that year. Conversely, when a lower maximum temperature during Dec 10–Jan 21 was followed by a higher maximum temperature during Feb 07–Mar 15, a lower infection level would be expected. The relationships between infection level and daily Tmax during the two periods were further analyzed. The results from the linear model were consistent with the results from the Kriging interpolation analysis. The infection level increased by 11% per 1 °C rise of Tmax during the defoliation season (Dec 10–Jan 21;  $P < 0.05$ ; Fig. 6), while the infection level decreased by 8% per 1 °C



**Fig. 5** Response of infection level of powdery mildew to daily maximum temperature (a), mean temperature (b), and temperature difference (c) during the defoliation season (x-axis) and the refoliation season (y-axis). Variation in color reflects variation in infection level, while the black dots

indicate the mean infection level of each year during 2003–2011. The slopes of the contour lines show the relative importance of impacts of temperature during the defoliation and the refoliation season

**Fig. 6** Relationships between infection level of powdery mildew and daily maximum temperature during defoliation (a) and refoliation (b), mean temperature during defoliation (c) and refoliation (d), and temperature difference during defoliation (e) and refoliation (f). Each point represents the annual average level from 2003 to 2011. Trends are significant with  $P < 0.05$



rise of  $T_{\text{max}}$  during the refoliation season (Feb 07–Mar 15;  $P < 0.05$ ; Fig. 6).

Regarding daily mean temperature, the steep slope of the contour lines indicated that the infection level was mainly determined by the variation of mean temperature during the defoliation season (Fig. 5). Although a depressing effect of high mean temperature was detected during the refoliation season, the infection level was more sensitive to the higher mean temperature during the defoliation season. When a higher mean temperature during Dec 11–Jan 24 was followed by a lower mean temperature during Feb 08–Mar 10, a higher infection level would be expected. Conversely, when a lower mean temperature during Dec 11–Jan 24 was followed by a higher mean temperature during Feb 08–Mar 10, a lower infection level would be expected. During the defoliation season,  $1^{\circ}\text{C}$  rise of mean temperature increased the infection level by 20% ( $P < 0.1$ ; Fig. 6). Once the mean temperature during the defoliation season was above  $19.5^{\circ}\text{C}$ , the infection level of powdery mildew was expected to reach 40% and it would increase to 60% when the temperature rose to  $20^{\circ}\text{C}$ . From Feb 08–March 10, higher daily mean temperature reduced the infection level, which was less than 30% when the mean temperature was above  $22^{\circ}\text{C}$  during this period. The mean temperature during the refoliation season had a negative

effect on the infection level; however, the effect was not statistically significant ( $P = 0.15$ ).

Regarding daily temperature difference (TD), the low slope of the contour lines indicated that the infection level of powdery mildew was almost entirely determined by the variation of temperature difference during Jan 23–Mar 30, i.e., the refoliation season, which is also the main epidemic period of powdery mildew in Xishuangbanna. Further analysis of the relationships between infection level and temperature difference during the two periods showed that during Jan 23–Mar 30 of the refoliation season, the infection level of powdery mildew decreased by 10% per  $1^{\circ}\text{C}$  rise of temperature difference ( $P < 0.05$ ; Fig. 4). Therefore, the infection level was expected to be lower than 30% when the temperature difference during the refoliation period was above  $16^{\circ}\text{C}$ .

Considering the significant effects of the  $T_{\text{max}}$  during both defoliation and refoliation seasons,  $T_{\text{mean}}$  during the defoliation season, and the temperature difference during the refoliation season on the infection level of powdery mildew, we investigated the changes of the above temperature variables in the last 30 years from 1981 to 2011. The maximum and mean temperature during the defoliation season had a significant increasing pattern with years. In the past 30 years, the  $T_{\text{max}}$  during the defoliation season increased by  $1.65^{\circ}\text{C}$ ,

with the rate of  $0.55\text{ }^{\circ}\text{C}$  per decade (Fig. 7). The mean temperature during the defoliation season increased by  $1.44\text{ }^{\circ}\text{C}$  during the past 30 years, with the rate of  $0.48\text{ }^{\circ}\text{C}$  per decade (Fig. 7). The Tmax and TD during the refoliation season also presented an increasing pattern, but this was not statistically significant ( $P = 0.16$  for Tmax and  $P = 0.5$  for TD).

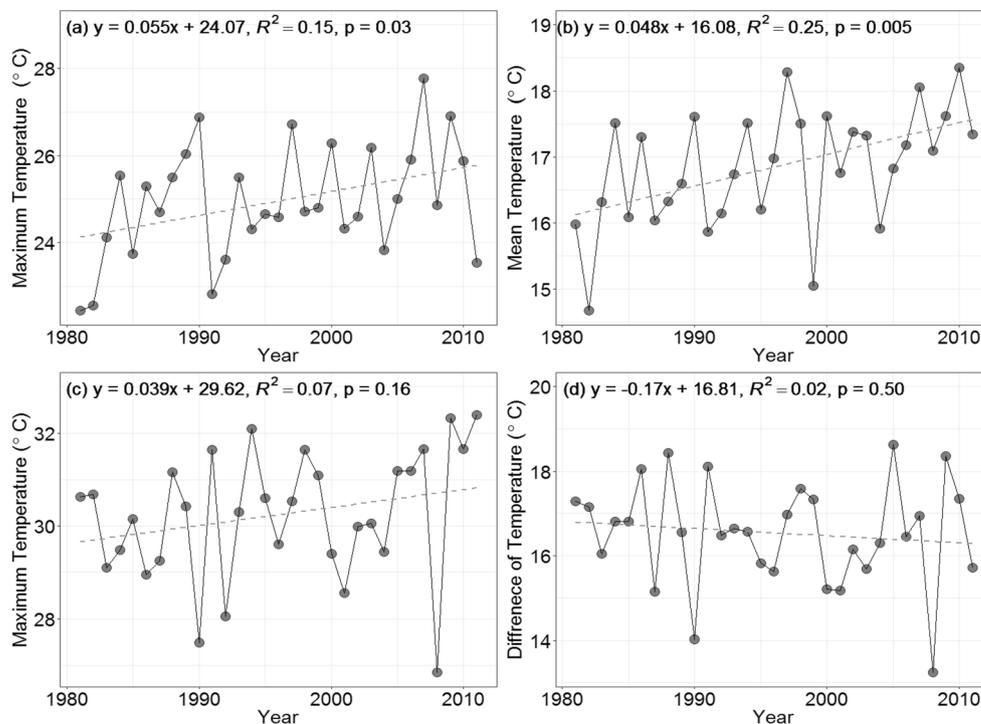
## Discussion

### Contrasted effects of temperatures in the two phenological stages on the powdery mildew infection

There are few publications evaluating the responses of the rubber powdery mildew infection to temperatures in both defoliation and refoliation periods. The positive response of powdery mildew infection to the daily mean temperature during defoliation season detected in our research matched previous observations: higher mean temperatures in winter always related to a higher infection level of powdery mildew based on a short-term field observation (Shi 2012; Zhang et al. 2009). This is consistent to the reported effects of winter mean temperature on the epidemiology of oak powdery mildew in Europe (Desprez-Loustau et al. 2011; Marcais and Desprez-Loustau 2014). However, our results demonstrated that the infection level of powdery mildew responded differently to temperatures (the mean temperature, maximum temperature, and temperature difference) in the defoliation and refoliation periods (Figs. 4 and 5). Such differences could be related either to the development of the fungi itself or to the sensitivity

of the trees. In fact, the development of rubber powdery mildew occurs on a wide range of temperature ( $16\text{--}32\text{ }^{\circ}\text{C}$ ) (Lu et al. 1982); therefore, the observed pattern might rather relate to the phenology of rubber trees during these periods. It is known that during the defoliation season, higher maximum and mean temperature can delay the leaf shedding (YITC 1981; Zhou 1982), then also delaying refoliation. If new leaf develops later, they may be in their most sensitive phase when rain restarts. Such conditions have been shown favorable to the development of several fungal leaf diseases in rubber trees (Guyot et al. 2010, 2005, 2001). Moreover, the higher temperature in the defoliation season could sustain more overwintering fungi by keeping more overwinter leaves, thus increasing the source of parasitism of next spring (PPRI, SCATCS 1983; Yu et al. 1980; Yu et al. 1985). In contrast, the higher temperature during the refoliation season can accelerate the development of leaves from budburst (Yu and Wang 1988; Zhai et al. 2019), thereby shortening the disease sensitive period. A slower leaf development and longer duration of leaf development to maturation, as when temperature is low in refoliation season like in year 2008, also indicates a wider window of opportunities for the powdery mildew fungi to parasitize the leaf tissues (PPRI, SCATCS 1983; Yu et al. 1980). This is consistent with three recently published studies showing that relatively low temperature in February–March increased the infection level of powdery mildew in Yunnan (Cai et al. 2018; Chen et al. 2019; Su et al. 2015). A case study from Hainan, the other large rubber cropping region in China, found that high temperature during defoliation stage caused the prolong of leaf shedding period and then a high infection

**Fig. 7** The trends of the (a) daily maximum temperature during Dec 10–Jan 21 and (c) during Feb 7–Mar 15, (b) mean temperature during Dec 11–Jan 24, and (d) temperature difference during Jan 23–Mar 30 over 30 years. Trends are significant with  $P < 0.05$



level has been observed in 2017 (Wen et al. 2018). As a whole, our results underline the importance of rubber phenology for powdery mildew infection research (PPRI, SCATCS 1983; Yu et al. 1980).

Other climatic factors could also have a strong influence on leaf fungal disease in rubber tree. For example, Guyot et al. (2010) showed that air humidity was the most important factor, followed by rainfall, for South American Leaf Blight incidence in Brazil. However, in their conditions, temperatures did not vary much during the year. Higher rainfall during refoliation tends to increase powdery mildew incidence in China (PPRI, SCATCS 1983; Yu et al. 1980 in Hainan; YITC 1981 in Xishuangbanna) and we found the same (Fig. S1). But the influence was likely indirect, by decreasing temperature (PPRI, SCATCS 1983; Yu et al. 1980; YITC 1981). In practice, the control of the disease by spraying copper sulfate is guided by the temperatures (Chen et al. 2019; Tan and Wang 2003; Tan et al. 2001).

### The critical period for powdery mildew infection

In this study, we identified both defoliation and refoliation seasons as critical periods for the infection level of powdery mildew using the PLS method. The significant effects of the temperatures in the defoliation season were overlooked in previous studies, while that of the refoliation season were highlighted (PPRI, SCATCS 1983, 1985; Yu et al. 1980; YITC 1981). Here, we found that the temperatures in both defoliation season and refoliation season significantly affect the infection level of powdery mildew in Xishuangbanna. In contrast, previous short-term observation or experience-based method, which was commonly applied to identify critical periods for the powdery mildew infection (Paris and Cohen 2002; PPRI, SCATCS 1983, 1985; Yu and Wang 1988; YITC 1981), might overestimate or underestimate the duration of critical periods. A research team in Xishuangbanna identified the period of January–March as the critical period (YITC 1981), while Zhou (1982) found December–January as the critical period. The studies from other regions identified the season of winter–spring (PPRI, SCATCS 1983, 1985) or only the refoliation season (Paris and Cohen 2002) as the critical period.

Moreover, most previous studies used monthly data in certain months to relate the infection level of powdery mildew to climatic factors, while many processes of plants have been found to respond to daily temperatures (Guo et al. 2013; Guo et al. 2015). The use of monthly climate data might not be able to identify the patterns as detailed as the daily climate data (Guo et al. 2017; Guo et al. 2013; Guo et al. 2015). Our results and findings proved that the PLS regression method was an effective approach to identify the detailed responding pattern of daily climate variables on the infection level of powdery mildew. This method has been proved effective in

analyzing the relationship between daily temperatures and plants' phenology, chilling and heating requirements of plants, and productivity of grasslands (Guo et al. 2017, 2013, 2015). All these findings will further improve our ability to explain the variation in the infection level of powdery mildew and show great potential for future disease monitoring and forecasting.

The PLS results showed also some positive relationships between temperatures from the end of May to the middle of July and infection level and negative relationship between temperatures from April to May and the infection level. Some significant effects also occurred during the rainy season. This may relate to the flowering (March to April), fruiting (Middle of April to September), and new leaf flushing that occur 2 or 3 times during the year (Priyadarshan 2011). That could also relate to the fungi development, as conidia could spread during the rainy season to complete the disease cycle (Yu and Wang 1988).

### Implications for forecasting powdery mildew disease based on temperatures

Our results indicated that daily maximum temperature, mean temperature, and temperature difference during both defoliation (December to January) and refoliation (January to March) are critical for forecasting powdery mildew disease. Any studies based on only one season will overlook the important influences of the other one. Therefore, to predict the infection level of powdery mildew of next spring, the temperatures during defoliation and refoliation season are all crucial. During the defoliation season, when the daily maximum temperature during the defoliation season is lower than 26 °C or the mean temperature lower than 19.3 °C, the infection level of powdery mildew is expected to be less than 30%. However, to predict the infection level of powdery mildew while it occurs and makes a control decision, we should pay more attention to the temperatures during the refoliation season. During that season, if temperature difference is lower than 15 °C or maximum temperature lower than 29 °C, the infection level of powdery mildew is expected to be higher than 40%.

Although our study relies on data collected up to 2011, the observed relationships would likely be still valid today. Actually, in the last 30 years, warming trends of the daily maximum temperature and mean temperature have been observed during the defoliation period, but not during the refoliation one. If such warming trends continue in the future, as expected from climatic scenarios downscaled to Xishuangbanna region (Zomer et al. 2014), more severe powdery mildew infection will likely occur, which will cause great economic losses and have serious environmental consequences with more fungicide used.

## Conclusion

In this study, we used partial least squares regression to correlate the infection level of powdery mildew to daily temperatures. This method has been shown to be effective in identifying the critical periods and in presenting how the temperatures in the critical periods affected the infection level of powdery mildew in Xishuangbanna. Our results indicated that to forecast the infection level of powdery mildew, we should monitor the daily maximum and mean temperature during the defoliation season, while the decision-making for powdery mildew disease control during the refoliation season should pay more attention to the daily maximum temperature and temperature difference. The findings from our study show great potential applications for the early warning system of rubber powdery mildew.

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