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ORIGINAL PAPER

The powdery mildew disease of rubber (*Oidium heveae*) is jointly controlled by the winter temperature and host phenology

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Abstract

Rubber powdery mildew disease (*Oidium heveae)* is a serious threat to natural rubber production (*Hevea brasiliensis*) in some rubber developing regions of the world. Both phenological- and meteorological-related factors have been reported influencing the powdery mildew disease. However, few studies have investigated the effects of both phenological- and meteorological-related factors on the disease. The objective of this study is to quantify the contributions of phenological- and meteorological-related factors to affect the disease. We used the partial least squares (PLS) regression method to comprehensively quantify the effects of thirty-five phenological related factors and six meteorological factors on the infection level of powdery mildew of rubber trees over 9-year records (2003–2011). The relative contributions of significant factors were further investigated by the variation partition analysis. We found that the most influential variables were the mean temperature during winter and the duration of leaf development to maturation which explained 32 and 26% of the variations in the infection level. We found the controlling role of winter mean temperature, for the first time, on the infection level of powdery mildew. The controlling role of winter temperature may have directly increase the infection level when winter temperature is high and indirectly increase the infection level through prolonging the duration of leaf development to maturation, although the duration itself had smaller influences. We detected a warming trend of the winter temperatures from 2003 to 2011, which indicates that the infection level of powdery mildew will be increased if the winter warming continues.

Keywords Rubber plantation · *Oidium heveae* · Partial least square (PLS) regression · Winter warming · Phenology

Introduction

Rubber tree (*Hevea brasiliensis*) is an important industrial crop that produces more than 98% of the world's natural rubber production (Bowers 1990). Natural rubber is an essential and critical raw material to industries, including transportation, medicine, and defense. The growing demands for natural rubber have stimulated the expansion of rubber plantations outside its traditional habitats in Amazon regions, especially in Southeast Asia countries, which produce more than 90% of global natural rubber (Li and Fox 2012; Warren-Thomas et al. 2015; Warren-Thomas et al. 2018). However, the production of rubber is often affected by leaf diseases, e.g., the South American leaf blight (SALB) disease in Amazon region

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(Guyot and Le Guen 2018), Corynespora (Liyanage et al. 1986), Colletotrichum (Guyot et al. 2001; Liu et al. 2018), Pestalotiopsis (Pornsuriya et al. 2020), and powdery mildew disease in Southeast Asia countries (Priyadarshan et al. 2005). Powdery mildew disease of rubber, caused by the *Oidium heveae*, is a major threat to rubber plantations in tropical China (Liyanage et al. 2018). This disease mainly affects immature leaves, flowers, and other immature tissues of rubber trees in the refoliation season, and the disease could result in up to 45% losses of rubber latex production (Liyanage et al. 2018). The outbreaks of this disease have affected the livelihoods of the involved farmers by two aspects: one is the economic loss caused by the powdery mildew through rubber latex reduction and purchasing chemical fungicides, and the other is using of chemical fungicides and the ecological consequences to the environment (Li et al. 2016). Therefore, the infection level of powdery mildew has become an important index for estimating rubber latex production.

To minimize economic losses caused by the powdery mildew, experience-based monitoring and assessments are mainly adopted before applying chemical fungicides to control this disease (Liyanage et al. 2018; PPRI 1985; Yu et al. 1985). Applying chemical fungicides (normally through spraying sulfur) is mainly depended on the monitoring and assessments of the disease, and the decision on when to spray is often made by the experienced workers through monitoring both the phenology of rubber trees and local meteorology, based on the assumption that these two are the main factors influencing the infection of powdery mildew (PPRI 1985; Yu et al. 1985). Therefore, phenology of rubber trees and local meteorology during the refoliation period are frequently monitored to forecast the infection of powdery mildew (PPRI 1985; Yu et al. 1985). The government in the main rubber cultivation region of Xishuangbanna (Yunnan province) has even developed an agro-meteorological service to forecast the powdery mildew based on the monitoring of rubber phenology and local meteorology during the refoliation periods of rubber trees (http://www.cma.gov.cn/2011xwzx/2011xqxxw/2011xjctz/201902/t20190226_515594.html). However, until now, it is difficult to find studies investigating the influence of both rubber phenology and meteorological factors on the rubber powdery mildew disease. Identifying the influencing factors is important and necessary for forecasting this disease.

A recent study investigating the responses of infection level of powdery mildew to the daily climatic variables has demonstrated that temperatures during both defoliation and refoliation periods are important (Zhai et al. 2020). That research indicated the importance of leaf phenology to the infection level of powdery mildew (Zhai et al. 2020). In another research, we found that the timing of rubber phenology was influenced by monthly climatic variables (Zhai et al. 2019). The phenology of rubber trees can be described by five phenological stages in the refoliation season: budburst, copper brown (emergence of leaves), color changing (starting of the expansion phase, hanging leaves), light green (full expansion phase, still hanging), and leaf aging (leaf thickening and straightening) (Fig. 1) (Shao and Hu 1984; Xiao 2010; Zhang et al. 2009, Zhai et al. 2019). These five phenological stages were also named as B1, B2a, B2b, C, and D in previous international studies (Hallé and Martin 1968; Guyot et al. 2008).

The leaves are more easily infected by the powdery mildew disease from copper brown to light green stages (Shao and Hu 1984). However, it is still unclear how the powdery mildew disease responds to the timing of these phenological stages. Additionally, other studies found that shorter duration from budburst to leaf aging could decrease the leaf susceptibility to powdery mildew (Xiao 2010; Yu et al. 1980; Zhang et al. 2009).

Therefore, to clarify the influencing factors on the disease, it is necessary to include the climatic factors in both defoliation and refoliation periods together with the timing and duration of the phenological stages. Any studies focusing on a single factor to predict the powdery mildew infection may not be accurate enough.

Therefore, we hypothesize that the timing of the phenological stages, the duration of leaf development (or leaf development duration), and climatic variables have a joint effect on the infection level of powdery mildew. Following this hypothesis, we ask and try to answer the following three questions: (1) which factors (e.g., timing of phenological stages, leaf development duration, and climatic variables) affect the infection level of powdery mildew; (2) which factors are more important to explain the variations of infection level; (3) whether and how are the effects of the above-identified influencing factors on the infection level of powdery mildew dependent upon each other?

Materials and methods

Study area

Xishuangbanna, one of the sub-optimal regions for rubber cultivation in Southeast Asia, is located at the northern edge of the Asian tropical zone (Yu et al. 2014; Zhu et al. 2006) (Fig. S1). Compared with the optimal environment of rubber cultivation regions in the humid tropics, the climate in Xishuangbanna is cooler and drier (Priyadarshan 2011; Yu et al. 2014). Xishuangbanna has two seasons: the rainy season (May–October) and the dry season (November–April) which is further divided into the cool-dry season (November–February) and the hot-dry season (March–April) (Cao et al. 2006; Zhang and Cao 1995). The cool-dry season is featured for the lowest temperature in a year and little rainfall. During the cool-dry season, the rubber trees experience leaf

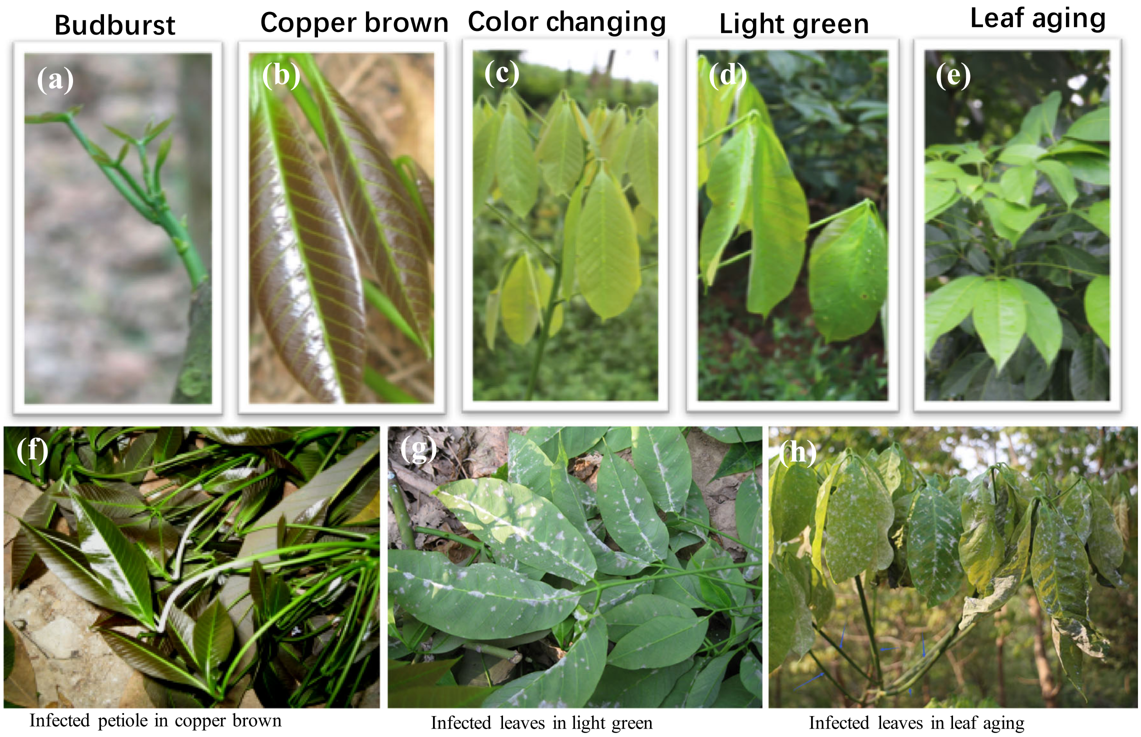

Fig. 1 The five phenological phases of rubber trees in the refoliation season (a-d), and the leaves infected by powdery mildew disease

defoliation (or wintering, from early December to the middle of January) and refoliation (from the end of January to the end of March) (Zhai et al. 2019). The hot-dry season is featured with dry and hot weather during the afternoon, and the rubber trees during this season start to be tapped for latex production and are also fruiting. More than 80% of the rainfall is from the rainy season, during when rubber trees are tapped and fruits mature. Our research site was located in a state-owned farm (the sixth branch of Jinghong Farm) located near Jinghong City, Xishuangbanna Prefecture, Yunnan Province (21°48 N, 100°46E). This state farm has 1813 hectares of rubber plantations, and the major clones are RRIM600, GT1, PR107, and YUNYAN1.

Data collections

From 2003 to 2011, the rubber powdery mildew infection level was observed with an interval of 3 days from the end of January to the end of March during the refoliation stage. The phenology of the rubber trees was also observed from mid-January to mid-April with an interval of 3 days. Following the guidelines and standards of the Bureau of China State Farm, 20 trees were selected and marked in each of the 15 observation sites representing the whole plantation (total 300 trees). We recorded both phenology and powdery mildew disease at the observation sites. One leaf whorl of rubber trees was randomly collected from each of these 20 trees, and 15–60 leaves were collected from each whorl, which led to 300–1200 leaves in each sub-observation site. The infection level of the powdery mildew was then calculated in each observation site (Xiao 2010). We used the same equation (1) of the infection level of the powdery mildew of each observation site as Zhai et al. (2020). More detailed information on phenology monitoring and powdery mildew infection monitoring was inferred from Zhai et al. (2019) and Zhai et al. (2020) respectively. The study covered the whole area of the state farm, planted with clones RRIM600, GT1, PR107, and YUNYAN1. Sample plots were chosen to represent the landscape of the plantation without considering clones as a factor, since Shao et al. (1996) showed that the clone did not influence the level of powdery mildew disease in the local conditions, although GT1 and PR107 are considered less resistant to powdery mildew than RRIM600 and YUNYAN1. The observation stopped in 2011, when state farms implemented reforms for contracting rubber plantations out to certain households.

$$Infection\ level(\%) = \frac{Number\ of\ infected\ leaves}{total\ number\ of\ sampled\ leaves} \times 100\% \qquad (1)$$

The refoliation of rubber trees was characterized by 5 stages: budburst (bb), copper brown (cb), color changing (cc), light green (lg), and leaf aging (la). The timing of each phenological stage was divided into 4 periods according to the percentage of leaves in each stage: 5%, 10%, 20%, and peak showing the highest percentage of leaves in each stage (i.e., bb_5, bb_10, bb_20, bb_peak). Duration of leaf development was assessed by (1) the duration between phenological stages (i.e., length_bb_cb, length_bb_cc), referring to the days required from 5% of a preceding stage (i.e., budburst) to the peak of a subsequent phenological stage (i.e. copper brown, color changing), and assessed by (2) the duration of a given stage, which was measured as the days required from 5% to the peak of each stage (i.e. length_bb, length_cb).

The climatic data between 2003 and 2011, including daily maximum, minimum, and mean temperatures, were downloaded from the National Meteorological Information Center of China (http://data.cma.cn/). We then calculated the daily temperature difference (TD) from daily maximum and minimum temperatures.

Our previous study of Zhai et al. (2020) showed that the mean temperature from 10 December to 21 January (recorded as Tmean1) and from 7 Feb to 15 Mar (Tmean2), maximum temperature from 10 December to 21 January (Tmax1) and from 7 Feb to 15 Mar (Tmax2), and temperature difference from 6 December to 11 January (TD1) and from 23 Jan to 30 Mar (TD2) significantly affected the infection level. Therefore, these six climatic variables were also used as independent factors (Zhai et al. 2020).

Statistical analysis

Partial least square (PLS) regression was employed to analyze the responses of the infection level of powdery mildew disease to both phenology-related variables (including twenty factors related to the timing of phenological stages and fifteen factors related to the duration of leaf development) and climatic variables (including six climatic variables).

We employed the PLS regression method as it is suitable for our data with highly correlated independent variables and more independent variables than the dependent variables (Guo et al. 2013; Luedeling and Gassner 2012). The variable importance in the projection (VIP) statistic and standardized model coefficients, the two main outputs, were used to explain the importance and the strength and direction of the impacts of independent variables on the dependent (the infection level of powdery mildew) (Luedeling and Gassner 2012). Independent variables with VIP $\geq$ 0.8 and standardized coefficient confidence intervals significantly different from zero were considered important for explaining the infection level of powdery mildew disease (Luedeling and Gassner 2012; Yu et al. 2014). The positive value of the model coefficients and VIP $\geq$ 0.8 was correlated to the increase of infection level of powdery mildew while the independent variables increased. Negative model coefficient and VIP $\geq$ 0.8 was correlated to the decrease of infection level of the powdery mildew while the independent increased. The accuracy of the PLS model was evaluated with the root mean square error (RMSE) of the regression analyses.

Based on the VIP and model coefficients, we identified 23 factors that significantly influenced the infection level of powdery mildew. To assess the relative contributions of the above 23 factors to the infection level of powdery mildew, these factors have been classified into three groups: climatic variables, the timing of phenological stages, and duration of leaf development. To decompose the variation of the infection level of powdery mildew into fractions explained by the climatic variables, the timing of phenological stages, and duration of leaf development, we conducted a variance partitioning analysis based on redundancy analysis. The PLS regression has also been employed to analyze the responses of the identified critical factor (i.e., length_cb_la) to daily climatical variables after the variation partitioning analysis. We have checked before further processing that there were no missing values and Null value in the climatic data. The climatic variables have been processed by a 15-day running mean approach before correlating it to the identified critical factor (Duration of copper brown to leaf aging) by the partial least square (PLS) regression (Luedeling and Gassner 2012). With this 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.

To investigate further the relationship between the critical factors identified by the variance partitioning analysis (Length_cb_la) and climatic variable (Tmean1, Tmean2, and TD1) during identified critical periods, we used a three-dimensional response map derived from the Kriging technique. We used the Kriging by substituting the spatial coordinates with temperature variables during the two identified critical periods (e.g. Tmean1 and Tmean2). The Kriging technique could be used for response maps (Guo et al. 2017; Luedeling et al. 2013). We used the default settings of the Kriging technique in the R package “field” (Nychka et al. 2017).

All analyses were implemented in the R programming language (R Core Team 2017). PLS analysis was mainly based on the “pls” and “chillR” package (Luedeling 2017; Luedeling and Gassner 2012; Mevik et al. 2016). The variation partitioning analysis was conducted using the “varpart” function in the R package “vegan” (Dixon 2003). We also used the R package “rdacca.hp” (https://github.com/laijiangshan/rdacca.hp) of the canonical correlation analysis to analyze the individual contribution of each variable to the total variations after the variation partitioning analysis.

Results

Factors affecting the infection level of powdery mildew

We identified 23 factors that significantly affected the infection level of powdery mildew (Fig. 2). Among these 23 factors, there were 3 factors related to the timing of phenological stages, 14 factors related to the duration between phenological stages, and 6 factors related to climatic variables.

Among the four developing levels of each stage, only three variables had significant effects: the timing of 5% level of

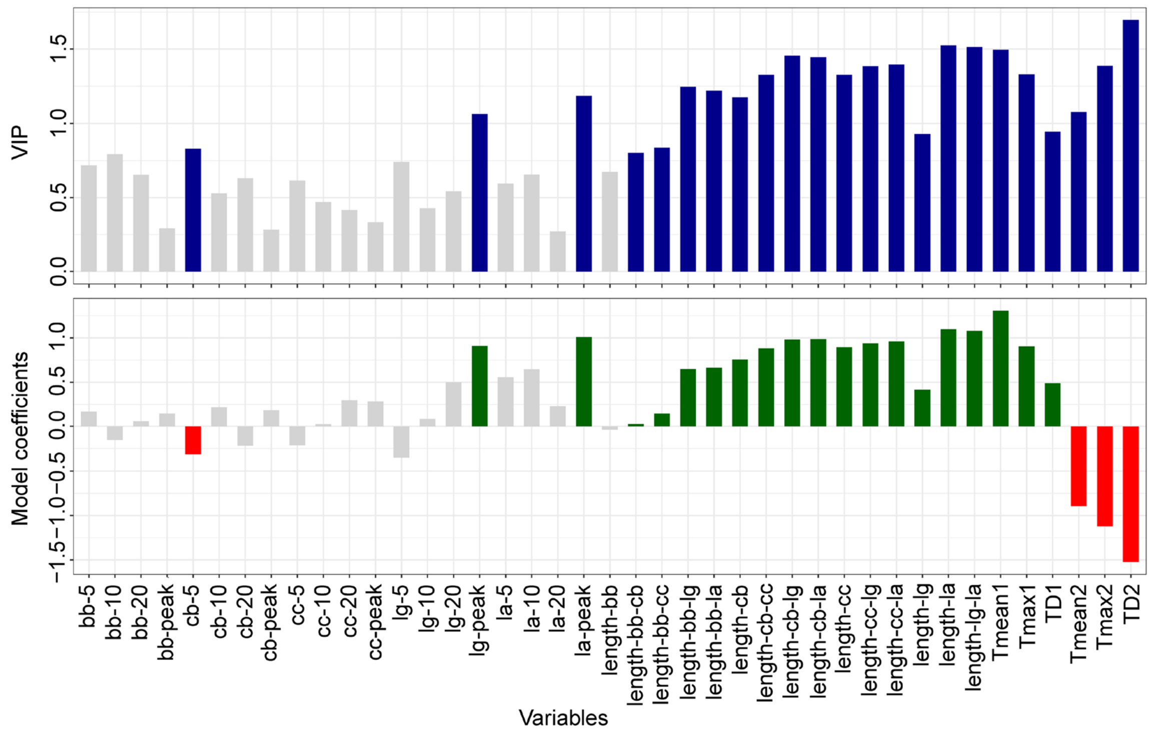

Fig. 2 Results of Partial Least Squares (PLS) regression correlating infection level of powdery mildew during 2003–2011 to fourty-one factors in three groups of the timing of phenologies, the duration of leaf development, and the climatic variables. In the upper panel, blue bars mean that VIP is above 0.8, the threshold for variable importance. In the under panel, red bars correspond to important and negative model coefficients and VIP values are greater than 0.8, while green bars indicate important positive relationships between infection level of powdery mildew and the gray bars indicate no statistical significance

copper brown and the timing of peak level of light green and leaf aging (Fig. 2). Later start of the copper brown phase (later emergence of the leaves) resulted in a lower infection level. Conversely, later peak of the light green and leaf aging phases (later growth and maturation peaks) resulted in higher infection levels (Fig. 2).

The PLS results demonstrated that almost all the factors related to the duration between phenological stages (e.g., length_cb, length_cb_la) had a positive effect on the infection level. This indicated that increasing the number of days required for leaf development would increase the infection level.

The climatic variables (Tmean1, Tmax1, and TD1) in the defoliation season had a positive effect, while the climatic variables in the refoliation season had a negative effect. This indicated that increasing temperature in the defoliation period would increase the infection level of powdery mildew, while increasing temperature in the refoliation period would decrease the infection level of powdery mildew (Fig. 2).

Overall effects of the temperature variables and the duration of leaf development to maturation on the infection level of powdery mildew

The variations identified by the PLS were grouped into three groups for the variation partitioning analysis. The variation partitioning analysis showed that the combination of the temperature variables (including Tmean1, Tmean2, and TD1) and the duration of leaf development to maturation (duration from copper brown to leaf aging, indicating the number of days required from copper brown stage to leaf maturation), were the two most important influential factors on the variation of the infection level of powdery mildew among the forty-one studied variables (Fig. 2 and Fig. 3). The temperature variables and the duration of leaf development to maturation could jointly explain 54% of the observed variation in the infection level (Fig. 3a). We have then further disentangled the joint effects and estimated the percentage of total variation explained by each variable (Fig. 3b). The mean temperature during winter (Tmean1, 32%) explained the highest percentage of the total variation, followed by the duration of leaf development to maturation (length_cb_la, 26%). The temperature difference during winter (TD1) explained only 3% of the variation.

Therefore, the joint effects of temperature variables and the duration of leaf development to maturation were the main factor influencing the infection level of powdery mildew, with the duration of leaf development to maturation playing a lesser significant role.

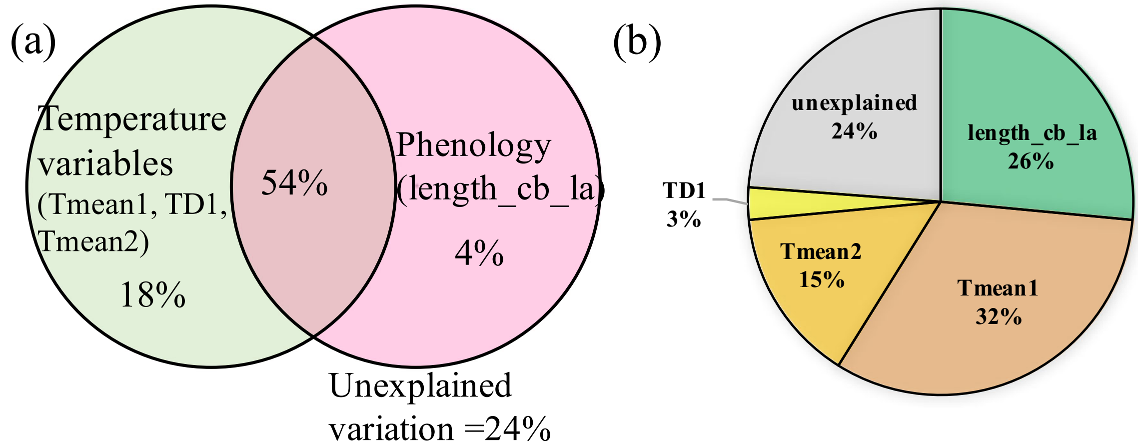

Fig. 3 Variation partition analysis of the effects of timing of phenologies, duration of leaf development, and the climatic variables on the infection level of powdery mildew (**a**) and the percentage of each factors on total variation (**b**):length_cb_la is the duration from copper brown to leaf aging, Tmean1 is the mean temperature from 10 December to 21 January, Tmean2 is the mean temperature from 7 Feb to 15 Mar, and TD1 is the temperature difference from 6 December to 11 January

Detailed effects of temperature variables on the duration of leaf development and relationships with the infection level of powdery mildew

We found that both the duration of leaf development to maturation and the infection level of powdery mildew were affected by the mean temperatures (Tmean) and temperature differences (TD) of same periods, through investigating the relationship between the two temperature variables and the duration of leaf development to maturation, and also the relationship between the two temperature variables and the infection level of powdery mildew by the PLS regression. We conducted the PLS regression on the daily climatic variables of mean temperatures (Tmean) and temperature differences (TD) between previous April and current March to the average duration of leaf development to maturation which worked as the dependent variable. The root means square error (RMSE) for the PLS models were 1.81% for Tmean and 2.04% for temperature difference, which indicated that the models fitted well for the data ($n = 9$ years).

The PLS results of the two temperature variables and the duration of leaf development to maturation showed that mean temperature and daily temperature difference had a similar effect on the duration of leaf development to maturation. From the VIP and standardized model coefficients of the PLS regression results, we found that defoliation and refoliation period (from November to March) had higher VIP scores, up to 2.0, which indicated that the temperatures during the defoliation and refoliation periods had a stronger influence on the duration of leaf development to maturation (Fig. 4a and Fig. 4b) and the powdery mildew infection (Fig. 4c and Fig. 4d) than climatic variations during the previous growth-season (Jun–July and Oct–Nov). We found that the daily mean temperature during 14 Dec–30 Dec had a significant positive effect, while the daily mean temperature during 11 Feb–13 Mar had a significant negative effect on the duration of leaf development to maturation (Fig. 4a). That means that higher temperatures during the defoliation period slowed down subsequent leaf growth, whereas high temperatures during refoliation accelerated it. Results were similar for the daily temperature difference, but with a longer period of influence during defoliation (23 Nov–20 Jan) and a slight delay in the influence period at refoliation (13 Feb–15 Mar) (Fig. 4b).

We found higher mean temperature during 11 Dec–24 Jan and higher temperature differences during 6 Dec–11 Jan resulted in a higher infection level of powdery mildew, while higher mean temperature during 6 Feb–10 Mar and higher temperature differences during 23 Jan–30 Mar resulted in a lower infection level (Fig. 2c and 2d). We found the mean temperature during 14 Dec–30 Dec and during 11 Feb–10 Mar and the temperature differences during 6 Dec–20 Dec and during 13 Feb–15 Mar significantly affected both the duration of leaf development to maturation and infection level of powdery mildew (Fig. 4). However, we did not keep the temperature differences during 13 Feb–15 Mar as the critical periods for the infection level as the variation partitioning analysis did not show that the temperature differences in spring significantly affected the infection level of powdery mildew (Fig. 3 and Fig. 4).

We then further plotted the duration of leaf development to maturation (the duration from copper brown to leaf aging) as a function of mean temperature during the two identified periods (during 14 Dec–30 Dec and during 11 Feb–10 Mar) and also as a function of mean temperature during 14 Dec–30 Dec and temperature difference during 6 Dec–20 Dec with the Kriging interpolation (Fig. 5 and Fig.

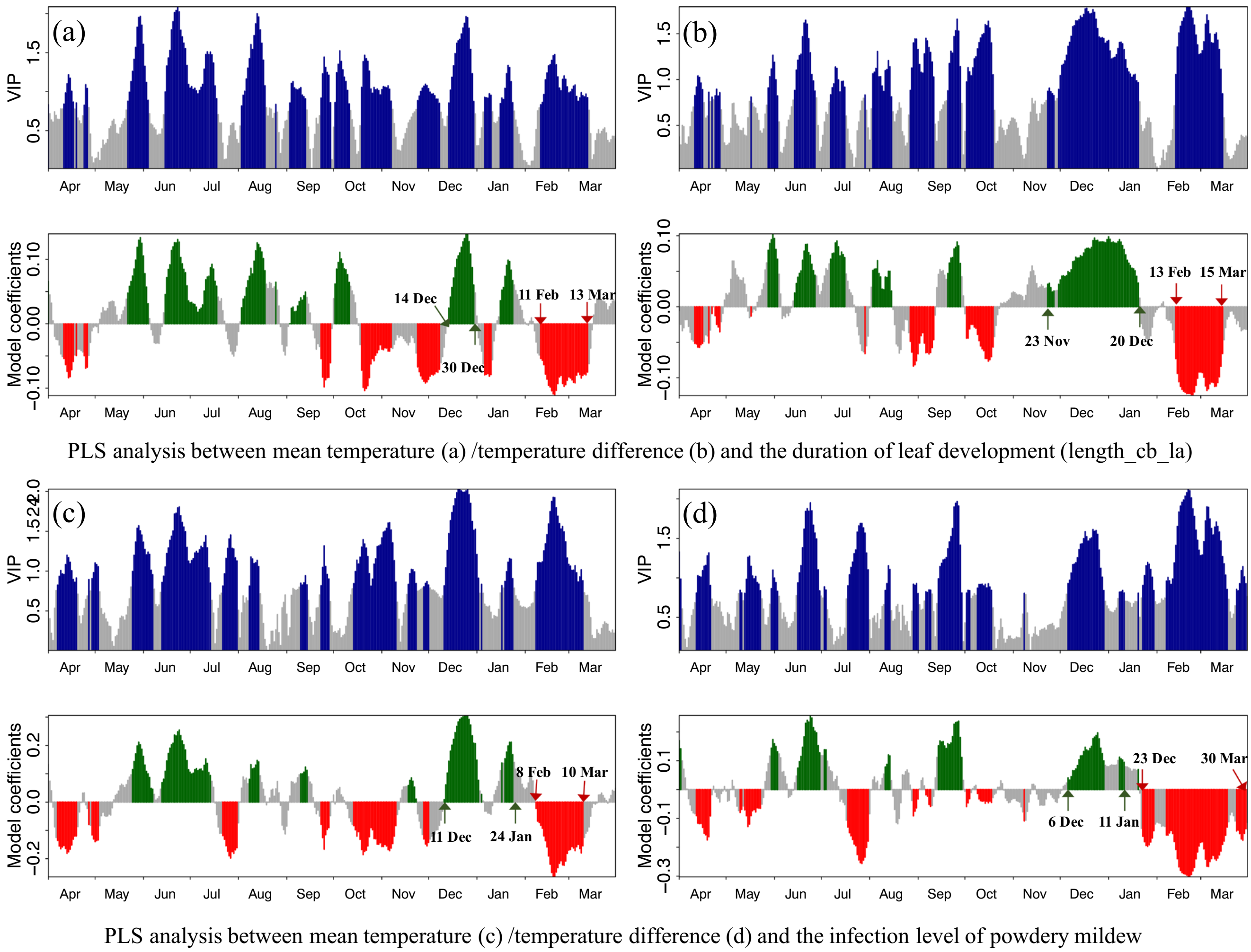

Fig. 4 The PLS regression analysis between (**a**) daily mean temperature, and (**b**) daily temperature difference from previous April to March and the duration of leaf development (from copper brown to leaf aging (length_cb_la)), and also the PLS regression analysis between (**c**) daily mean temperature, and (**d**) daily temperature difference and infection level of powdery mildew during 2003–2011. See the caption of Fig. 2 for a full explanation of PLS results

S2). That clearly showed that the longer duration of leaf development to maturation was mainly responding to the higher mean temperatures during winter (Fig. 5 and Fig. S2). Warming during 14 Dec–30 Dec lengthened the duration of leaf development to maturation by 4.6 days/°C (p =0.05, Fig. 6a), although the warming trend of mean temperature during 14 Dec–30 Dec during 2003–2011 was not significant (p = 0.16) and increasing trend of the duration of leaf development to maturation was also not significant (p = 0.38, Fig. S3). The positive relationship between the duration of leaf development to maturation and the mean temperature during 14 Dec–30 Dec was consistent with our findings from the Kriging interpolation (Fig. 5). The increase of the duration of leaf development to maturation increased the infection level of powdery mildew by 1.5% per day, which agreed with the PLS results in Fig. 2 (p < 0.01, Fig. 6b).

Discussion

Climate and phenology jointly affected powdery mildew disease

This study built on previous results identifying critical influencing temperature periods in both the leaf defoliation and refoliation stages as drivers of subsequent powdery mildew infection level of rubber leaves (Zhai et al. 2020). We went further by providing a most comprehensive quantification of all the relevant factors to investigate the relationships between phenological, climatic factors and the powdery mildew infection by the PLS approach. Our results clearly showed that the powdery mildew infection was mainly affected by the extrinsic factor of winter temperature and intrinsic factor of the duration of leaf development to maturation. Most of the previous studies on the forecasting of powdery mildew

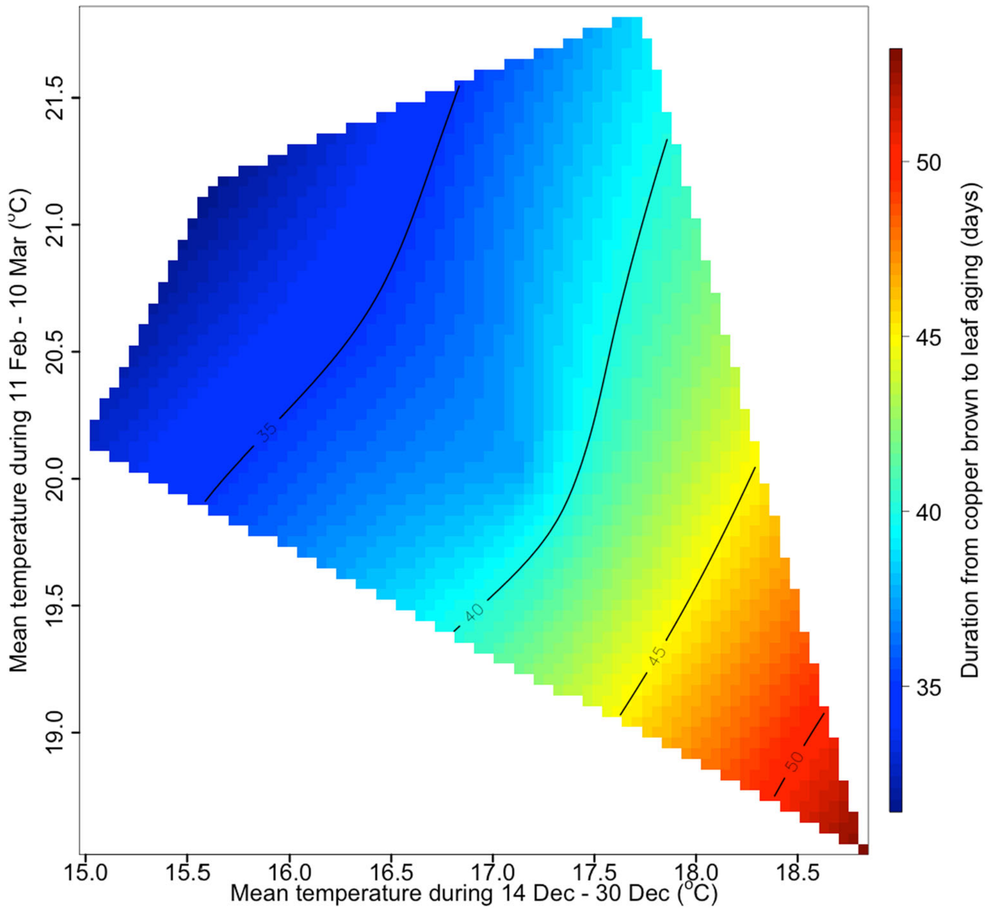

Fig. 5 Response of duration from copper brown to leaf aging to the mean temperature during 14 Dec-30 Dec and during 11 Feb – 10 Mar. Variation in color reflects variation in the duration from copper brown to leaf aging during 2003–2011. The slopes of the contour lines show the relative importance of impacts of temperature increases during 14 Dec- 30 Dec and during 11 Feb – 10 Mar on the duration from copper brown to leaf aging

disease have focused on the single effects of either the timing of phenological stages, duration of leaf development between the phenological stages, or the climatic variables (PPRI 1985; Shao and Hu 1984; Yu et al. 1980; Yu et al. 1985; Zhang et al. 2009). Our results clearly quantified that the joint effects of the two most important factors explained more than 50% of the variations in the infection level of powdery mildew (Fig. 3). The highly joint and mixed effects of temperature variables and duration of leaf development to maturation indicated that the powdery mildew infection is strongly influenced by both extrinsic and intrinsic factors, as that found for oak trees which are highly affected by the winter temperature and phenology (Marcais and Desprez-Loustau 2014; Marcais et al. 2017). Studies on rubber trees showed that the infection of powdery mildew varied with rubber clones (Fang et al. 2013; Liyanage et al. 2019), and the species dependence of oak trees to the

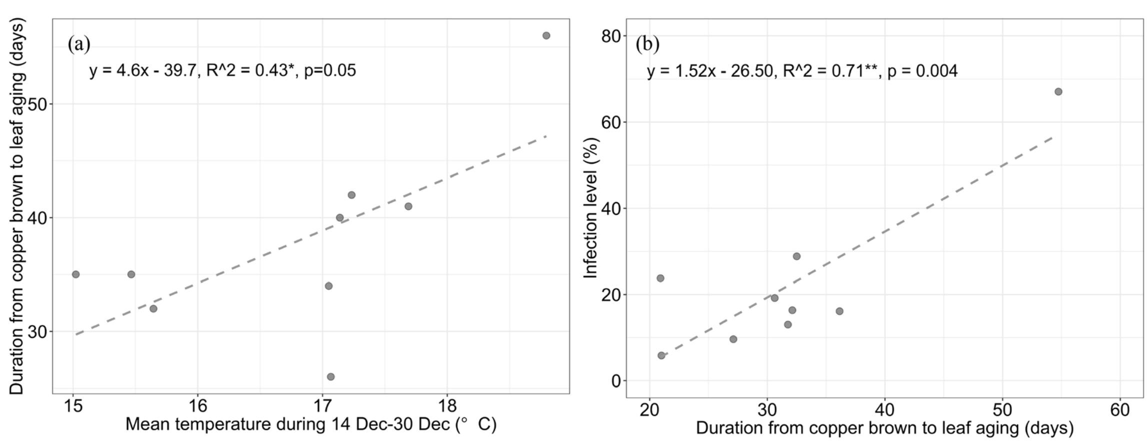

Fig. 6 Relationship between the duration from copper brown to leaf aging and mean temperature during 14 Dec- 30 Dec (**a**), and relationship between infection level of powdery mildew and the duration from copper brown to leaf aging (**b**). Trends are significant with $^*p < 0.05$, $^{**}p < 0.01$

infection of powdery mildew was also detected (Marcais and Desprez-Loustau 2014; Marcais et al. 2017). We assumed that the response variations between rubber clones might relate to rubber phenology (both defoliation and refoliation phenological stages), with different sensitivity to winter temperature (Fig. 5 & Fig. 6c). Therefore, the temperature during 14 Dec -30 Dec is highly recommended to be monitored as an early warning for the powdery mildew disease.

About one fourth of the variation in the infection level of powdery mildew was left unexplained which could be related to the duration of defoliation, which positively affected the powdery mildew infection (Yu et al. 1980). However, due to the lack of data on the defoliation dynamics, we could not test it directly in this study. Yu et al. (1980) and Yu et al. (1985) showed that warmer winter temperature increased the duration of defoliation, leaving more overwinter leaves which can be the sources of inoculum of next spring (Yu and Wang 1988). Moreover, as the warmer winter delayed the refoliation, this could result in incomplete defoliation leading to a longer time for refoliation and consequently a higher infection level similarly to observations on C*olletotrichum* (Guyot et al. 2001). To control the rubber leaf disease of C*olletotrichum* and reduce the inoculum on the overwinter leaves, Guyot et al. (2001) recommended using artificial defoliation, which has also been highly recommended to control the powdery mildew disease in China (Yu and Wang 1988; Yu et al. 1980; Yu et al. 1985).

There were some periods outside the defoliation-refoliation with significant effects, which indicated that there might be different influencing phases of mean temperature on the rubber leaf flushing phenology and also on the infection level of powdery mildew. Such effects may relate to the 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). So far, there was no research investigating along a year, and the effects of temperature on the rubber leaf flushing phenology or the infection level of powdery mildew along a year would be interesting.

The phenological information is critical for forecasting powdery mildew infection

Our results in this study provided the most comprehensive evaluations of all phenology-related factors on the infection level of powdery mildew. In the current research, based on more precise daily data, we found that a delay of the leaf emergence (5% leaves at the copper brown stage) decreased the infection level of powdery mildew. Conversely, the delay of the peak of leaf expansion (light green stage) and the peak of leaf aging increased the infection level, and almost all the duration of leaf development showed a significant positive effect on the infection level (Fig. 2). These explained the large differences recorded in previous researches, which considered limited factors (PPRI 1983; Shao and Hu 1984; Yu et al. 1980). Our PLS results indicated that the duration of leaf development was more important than the timing of each phenological stage. This was confirmed by the variation partitioning analysis and the canonical correlation analysis, which showed that the duration from copper brown to leaf aging explained 26% of the total variation of the infection level. Such results of the importance of the duration of leaf development were also found by Yu et al. (1980) on powdery mildew and by Guyot et al. (2008) on another important rubber leaf disease, the South American Leaf Blight (Guyot et al. 2008). The prolonged duration of leaf development meant a slower leaf maturation making them more vulnerable to be infected (Pearse and Karban 2013). The year of 2008 with the severest powdery mildew infection had a higher mean temperature during defoliation (14–30 December) that resulted in a longer duration of leaf development to maturation (Fig. 6), although the leaf flushed earlier compared to other years (Zhai et al. 2019). This particular year confirmed that the timing of budburst is not as important as the leaf development rate. Less than 40 days of duration from copper brown to leaf aging would lead to an infection level lower than 35% (Fig. 5), which indicates that the duration of leaf development to maturation (from copper brown to leaf aging) could be used as an indicator for forecasting the powdery mildew infection. Although the temperature difference during Feb 13–15 Mar was not an influencing factor to the infection level of powdery mildew based on the VPA (Fig. 3), we found it significant to the infection level based on the PLS and the linear model (Fig. 3c and Fig. 7a). We also found that the temperature difference during Feb 13–15 Mar was significant to the duration of leaf aging which was consistent with that of the linear model (Fig. 4e and Fig. 7a). Therefore, to warning the infection level, it is necessary to monitor the temperature difference during Feb 13–15 Mar, during when every 1 °C decrease will increase the duration of leaf aging by 2.5 days, which will lead a 3.8% increase in infection level (Fig. 6b and Fig. 7).

The importance of daily data for powdery mildew study

Most previous studies related to infection of powdery mildew to monthly climatic data, while the powdery mildew developed and spreaded fast in days (Shao and Hu 1984; Yu and Wang 1988). It is not enough to capture and identify the response pattern of powdery mildew to climatic variables. A recently published study used the daily temperature to forecast the infection index of powdery mildew clearly showed the importance of daily temperature, which is the main reason for high variations between the findings of previous studies (Chen et al. 2019). Our study and the model developed by

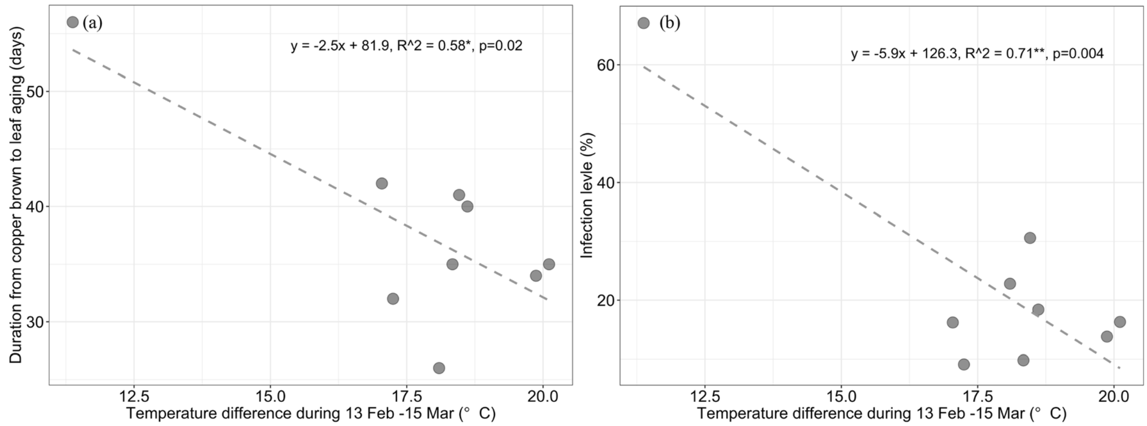

Fig. 7 Relationship between the duration from copper brown to leaf aging and temperature temperature during 13 Feb -15 Mar (**a**), and relationship between infection level and temperature temperature during 13 Feb -15 Mar (**b**). Trends are significant with $^*p < 0.05$, $^{**}p < 0.01$

Chen et al. (2019) indicated that the rubber powdery mildew should respond significantly on a daily resolution. However, we found a significant influence of mean temperature, which was different from Chen et al. (2019), who developed the forecasting model mainly based on the maximum and minimum temperature during the infection period (1 Feb–15 Mar. for Jinghong site) and also the maximum temperature during leaf flushing phenological stages. However, the critical factors and periods were not based on their findings but the results from different studies with inconsistent methodologies and analysis. In our study, we clearly identified the influencing periods of temperatures by using daily climatic data. The daily climatic data seems then necessary and is recommended for future powdery mildew studies.

Implications for forecasting powdery mildew disease based on temperatures and phenology

Our results showed great potentials to forecasting powdery mildew disease based on temperatures and phenology, especially for temperatures, which makes sense from the recent study to develop forecasting models based on temperatures (Chen et al. 2019). However, this research lacked phenology information and only focused on the temperature during the refoliation period. Our results showed the controlling role of winter temperature on the infection level of powdery mildew and the role of rubber phenology, therefore adding winter temperature and phenology to the forecast model would improve its accuracy.

Based on our results, we recommend combining the winter temperature and temperature difference in the refoliation period to forecast the powdery mildew. Although the winter temperature showed the controlling role, the temperature difference in the refoliation period which is easier to monitor than that of the duration of leaf aging showed great potentials as a monitoring indicator.

Our results indicated that the growers in the marginal rubber growing region will experience increasing infection levels of powdery mildew if the winter warming is significant in the future, as forecasted by several climate models (Zomer et al. 2014). That may reduce the planters' incomes and also induce higher inputs of fungicide which may be detrimental for the environment. Therefore, rubber clones with a faster leaf development rate would be highly recommended for future cultivar breeding and rubber industry sustainability.

Conclusions

From this study, our understanding of the complex factors influencing the infection level of powdery mildew of rubber trees is significantly improved. We found that winter temperature had a controlling influence on the infection level of powdery mildew. The second most important factor was the duration of leaf development to maturation. Both the extrinsic factor of winter temperature and intrinsic factor of the duration of leaf development to maturation were jointly influencing the powdery mildew infection. Future studies on the winter phenology (leaf fall dynamics) and subsequent powdery mildew infection will improve our understandings of the epidemiological features of the powdery mildew disease in tropical China and provide scientific knowledge if it is introduced to other rubber development regions. These efforts can also help us to predict rubber powdery mildew in response to climate changes now and in the future, as well as predicting the future ecological and economic consequences.

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