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Infection of *Phytophthora capsici* on pepper—Models and affecting factors

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Abstract Under controlled conditions in a growth chamber, we studied the mortality of pepper seedlings caused by *Phytophthora capsici*. The results showed that soil temperature and soil water content were important factors affecting their infection with *P. capsici* and the optimum condition for infection was found to be a soil temperature of 22°C–28°C and a soil water content of 40%. The relationships of pepper seedling mortality caused by *P. capsici* along with soil temperature, soil water content and their interactions can be described by mathematical models. Field observations suggested that the Gompertz model was the best one for describing the epidemiological dynamics of the disease. The incidence of pepper phytophthora blight was significantly related to the initial incidence of pepper phytophthora blight, soil temperature, soil water content and air temperature. A forecasting model for pepper phytophthora blight in the field was developed.

Keywords *Phytophthora capsici*, pepper phytophthora blight, mortality, soil temperature, soil water content, epidemic dynamic

the mortality of the plants ranges between 30% to 40%, which when severe, could be more than 50% and even up to 100% (Lü et al., 2001; Wang, 2002; Liu et al., 2004b; Sun et al., 2006). The pathogen overwinters in soil and diseased plant residue and seeds by oospores and chlamydospores. It infects host by sporangium and zoospores and is dispersed in the fields by air and through the soil. The disease caused by the soil-borne pathogen is the most serious. Pepper phytophthora blight is the result of interaction among host plants, pathogen and the environment. Soil temperature and soil water content are two major factors that affect the infectivity of pathogen (Bowers and Mitchell, 1990; Bowers et al., 1990; Liu et al., 2004a). Quantitative analysis of the environmental factors affecting the infection of pathogen is the basis of estimating disease development dynamics and aids in laying down scientific control tactics (Ristaino et al., 1993; Ristaino et al., 1994; Li et al., 1995; Niu et al., 2005; Yan et al., 2005). So, under the controlled conditions in a climatic chamber, the authors analyzed the influence of soil temperature and soil water content on the infection of *P. capsici* to provide basic data for the forecast and control of pepper phytophthora blight.

1 Introduction

The phytophthora blight, caused by *P. capsici* Leonian, is a destructive disease for peppers. Under normal conditions,

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2 Materials and methods

2.1 Materials

In this study, pepper cultivar Longjiao 4(881) was used. The isolate of *P. capsici* was obtained from the diseased pepper plant in Harbin and identified by the method used by Zheng (1997). Then, the pure strain was maintained on potato dextrose agar (PDA) culture medium in the tube and transferred once per month.

2.2 Methods

2.2.1 Seeding and plant transplanting

Pepper seeds were sown in the uninfected soil layer in growing plates and transplanted into 9-cm-diameter

plastic pots with 200 g of dry soil per pot as the 6th true leaf began to expand with one plant per pot and 20 pots in one group. During the test, the plants were watered to maintain a constant soil water content level measured by the alcohol burning method (Zhu, 1983).

2.2.2 Preparation of inoculums and inoculation

The tested isolate was inoculated on to carrot agar (CA) plates and cultured for 5 days in the dark chamber at a constant temperature of 25°C. Mycelium pieces were prepared using a 5-mm-diameter aseptic punch on the fringe of colony and were placed in the aseptic plates (Φ 9 cm) with 10 mL non-bacterial water. These were cultured for 36–48 h at 25°C (light intensity: 9000 lx) with the side of mycelium upwards and thereafter filtrated by 4 layers gauze to obtain sporangial suspension for the inoculation (Chang et al., 1995; Liu et al., 1999). The concentration of sporangial suspension was measured before inoculation and then the sporangial suspension was made at the required concentration for the test. Finally, pepper plants were inoculated using the soil inoculation method: selecting the seedlings transplanted for one week followed by the addition of a fixed amount of sporangial suspension into the soil in the pots with pre-weighted dry soil and mixing it thoroughly to make the final concentration of 50 sporangia per gram dry soil (Liu et al., 2004a).

2.2.3 Experiment on soil temperature and water content

In this experiment, we established a total of 10 levels of soil temperature at 10°C, 13°C, 16°C, 19°C, 20°C, 25°C, 28°C, 31°C, 34°C and 37°C, respectively. We also established a total of 9 levels of soil water content at 60%, 50%, 45%, 40%, 35%, 30%, 25%, 20% and 15%, respectively, and a total of 90 treatment combinations, with 20 plants per treatment and 3 repetitions. After being inoculated by using the method noted in 2.2.2, the plants were moisturized for 2 d in a climatic chamber with a photoperiodic regime of 12 h light (9000 lx) and 12 h darkness as a designed experimental condition and then were removed to the growth chamber with 25°C and 40% soil water content. In the third day after inoculation, we started the study of the diseased plants up until the seventh day when no new diseased plant were noted with a single plant as a unit to record the number of diseased plants and calculated the final mortality in each treatment (%).

Soil temperature, soil water content and their interactions were taken as independent variables, with Ln (M), Gompit (M), Logit (M) and $SQRT$ (M), as dependent variables. A stepwise regression analysis was done using SYSTAT software with the optimum models selected on the principle of the largest related coefficient (R) and the smallest standard error (SE) as the relative formulae

among mortality, soil temperature and soil water content.

2.2.4 Test of environmental factors in field

The test was done in a network chamber to protect against insects. At the end of May, pepper seedlings in the greenhouse were transplanted into the chamber for ridge culture. Four test plots were established, with about 30 m² per plot. When flower buds occurred in the middle of July, one pepper plant was randomly selected in the centers of Plots 1–3, respectively. These plants were inoculated using the method described in 2.2.2 to simulate soil dispersal with a commensurate quantity of inoculum. Plot 4 was not inoculated as CK. Plots 1, 2 and 3 were irrigated once every 12 d, 8 d and 4 d, respectively, in the furrows, reaching to 2/3 height of the ridge while Plot 4 was irrigated in the same way as Plot 1, which lasted 3 years.

After inoculation, air temperature and relative humidity were measured by using an auto-recorder for temperature and moisture at 7-day intervals with soil temperature 10 cm under the soil surface measured using a geothermometer at 2:00, 8:00, 14:00 and 20:00 so as to calculate the daily average soil temperature. The soil samples 6 cm under the soil surface were taken using a 5-spot sampling method at 2:00, 8:00, 14:00 and 20:00 to detect and calculate daily average soil water content. In the meantime, the disease incidence of pepper phytophthora blight of each plot was observed daily.

Based on the daily average air temperature, the daily average relative humidity, the daily average soil temperature, the daily average soil water content, the initial incidence and their interactions as independent variables, and Ln (I), Gompit (I) and Logit (I), as dependent variables, respectively, a stepwise regression analysis was carried out to choose the optimum model among the incidence of pepper blight and all factors.

3 Results and analysis

3.1 Effect of soil temperature and soil water content on mortality of pepper plants caused by *P. capsici*

3.1.1 Mortality of pepper plants caused by phytophthora blight in different treatments

The results after inoculation in the controlled chamber show that the pepper plants died 20 hours after inoculation, therefore, in this study we investigated diseased plants by the unit of a single plant. One diseased plant was regarded as one infection. In the condition of large inoculum density, multiple infection occurred and the percentage of mortality (y) was rectified by using

Gregory's formula: $m = -\ln(1 - y)$ (Zeng and Yang, 1986). The investigation of mortality started 7 days after inoculation and was transformed to real mortality (Table 1).

Table 1 Influence of soil temperature and soil water content on mortality of pepper plants caused by *P. capsici*

soil water content/%	soil temperature/°C									
	10	13	16	19	22	25	28	31	34	37
15	0.04	0.10	0.20	0.30	0.42	0.55	0.51	0.30	0.15	0.00
20	0.08	0.15	0.33	0.38	0.55	0.61	0.55	0.31	0.21	0.01
25	0.10	0.20	0.41	0.40	0.61	0.68	0.65	0.38	0.26	0.02
30	0.15	0.23	0.45	0.55	0.72	0.75	0.75	0.46	0.28	0.05
40	0.28	0.38	0.50	0.56	0.95	0.99	0.99	0.60	0.31	0.07
45	0.25	0.28	0.31	0.51	0.91	0.94	0.84	0.54	0.26	0.05
50	0.15	0.25	0.27	0.46	0.81	0.85	0.45	0.48	0.20	0.00
60	0.10	0.35	0.40	0.42	0.65	0.70	0.40	0.31	0.13	0.00

Table 1 shows that under the same soil water content, the mortality of pepper plants caused by phytophthora blight increased with increasing the soil temperature up to 28°C and thereafter decreased. The optimum soil temperature for the infection of pathogen was between 22°C–28°C. At the same soil temperature, the mortality of pepper plants increased with increasing soil water content up to 40% (close to saturation), and thereafter declined. The optimum soil water content for the infection of pathogen was close to saturation. Over-saturation and over-drying were not beneficial to the disease.

3.1.2 Model of relationship among the mortality of pepper plants caused by phytophthora blight, soil temperature and soil water content

The soil temperature (*ST*), soil water content (*SW*) and their interactions were taken as independent variables, with Ln (*M*), Gompit (*I*), Logit (*M*) and *SQRT* (*M*) as dependent variables, respectively, and a stepwise regression analysis was carried out with SYSTAT software so as to select the optimum model with the largest *R* and the smallest *SE* as a relation formula among mortality, soil temperature and soil water content, which is as follows:

$$\begin{aligned}
 SQRT(M) = & -1.4304 - 3.107 \times 10^{-2} \times SW + 0.1467 \times ST \\
 & - 3.112 \times 10^{-3} \times ST^2 - 3.614 \times 10^{-4} \times SW^2 \\
 & - 5.1 \times 10^{-8} \times ST^2 \times SW^2 \\
 (R = & 0.940, SE = 0.08478, F = 120.436)
 \end{aligned}$$

where *M* is mortality percentage, *ST* is soil temperature (°C), *SW* is soil water content (%). Its function is to describe the changing law of mortality of pepper plants caused by the blight with an increase in soil temperature

and soil water content (*ST* = 10°C–37°C, *SW* = 15%–60%). The estimated value of relationship among mortality percentage, soil temperature and soil water content was calculated based on this model (Fig. 1). Figure 2 shows the relationship between mortality percentage, soil temperature and soil water content.

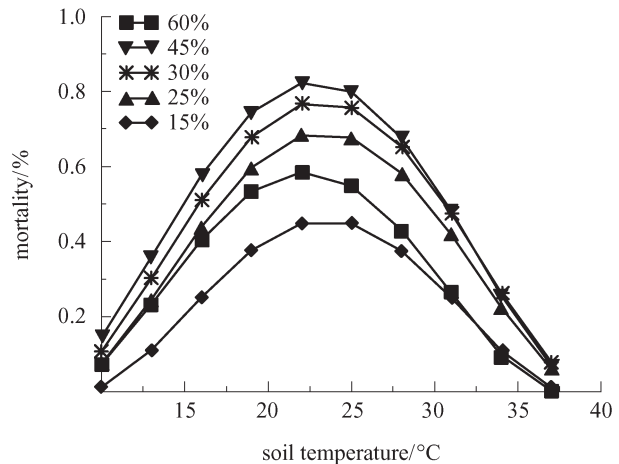


Fig. 1 Influence of soil temperature and soil water content on mortality percentage of pepper caused by *P. capsici* (estimated value)

3.2 The relationship between incidence of pepper phytophthora blight and environmental factors in fields

3.2.1 Epidemic dynamic model of pepper phytophthora blight in fields

The daily incidence was studied after inoculation in the field and a point figure of relationship between the incidence and the study time was drawn. We found that the incidence of pepper phytophthora blight in fields showed an S-shape change with the passage of time. In order to accurately reflect the epidemic process of pepper phytophthora blight in the field, we selected "S" curve models such as Gompertz, Weibull, Richard and Exponential equations (Zeng and Yang, 1986; Campbell and Madden, 1990) and so on, and adapted a fitting test with SYSTAT software by using the Marquardt method and determining the optimum formula of the Gompertz model by comparison regression coefficient of determination (*R*²) and residual square sum (*SQ*), as follows:

$$I = \exp[-4.7810 \times \exp(-0.0221 \times D)]$$

$$(R^2 = 0.9814, SQ = 0.008203, F = 720.3333)$$

where *I* is the incidence and *D* is the disease epidemic days. Figure 3 shows the result of changes of incidence of pepper phytophthora blight with disease epidemic time.

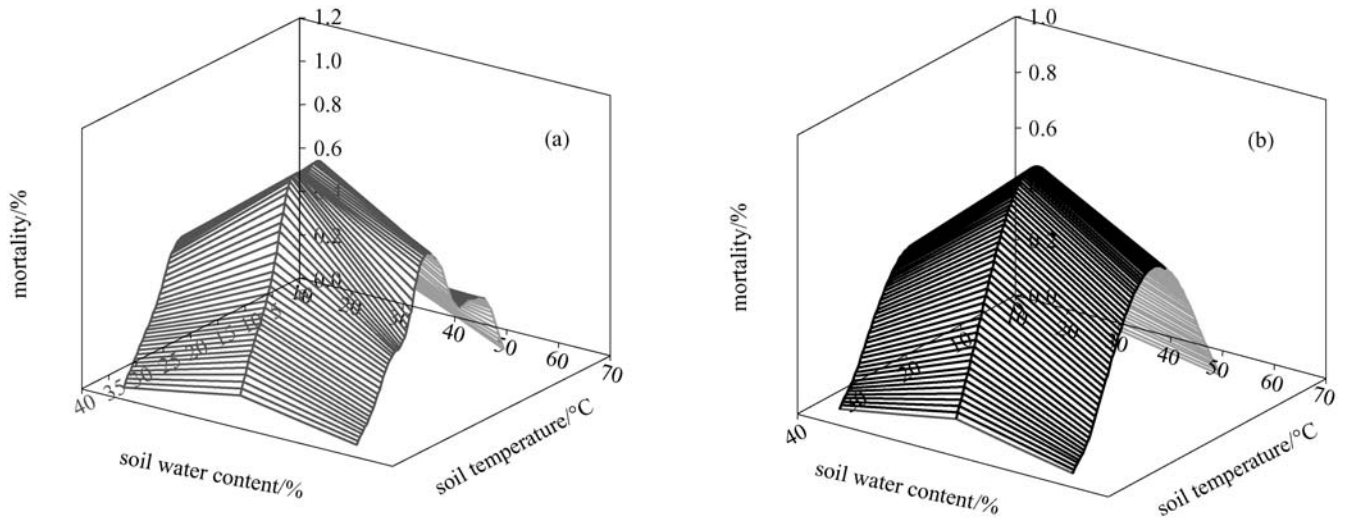


Fig. 2 Relationship among mortality percentage of pepper caused by phytophthora blight, soil temperature and soil water content
 Note: (a) shows observed values; (b) estimated values

3.2.2 The relationship between incidence of pepper phytophthora blight and environmental factors in the fields

Analysis of the interaction between incidence of pepper phytophthora blight, air temperature, air relative humidity, soil temperature and soil water content shows that from July 15 to September 25, the daily average temperature declined from 34°C to 10°C and the daily average relative humidity was in the range of 50%–96% which remained high and changed very little from late July to early September. Besides, the daily average soil temperature decreased from 28°C to 11°C, and the daily average soil water content of three plots was in the range of 18%–31%, 19%–31% and 23%–31%, respectively, with final incidences being 17.91%, 18.57% and 22.86% respectively, which indicated that the plot with the high

irrigation frequency and high soil water content would have a high incidence.

The daily average air temperature, the daily average air relative humidity, the daily average soil temperature, the daily average soil water content, the initial incidence and their interactions were taken as independent variables, with Ln (*I*), Gompit (*I*) and Logit (*I*) as dependent variables, respectively, and the stepwise regression analysis was carried out using SYSTAT software, and an optimum model with the largest *R* and the smallest *SQ* was selected as follows:

$$\begin{aligned} \text{Gompit}(I) = & 0.357 + 0.845 \times \text{ompit}(I_0) + 9.0 \times 10^{-3} \times T \\ & - 0.025 \times SW - 4.53 \times 10^{-5} \times SW \times ST^2 \\ & + 4.303 \times 10^{-5} \times SW^2 \times ST \\ & (R=0.987, SQ=0.05, F=139.972), \end{aligned}$$

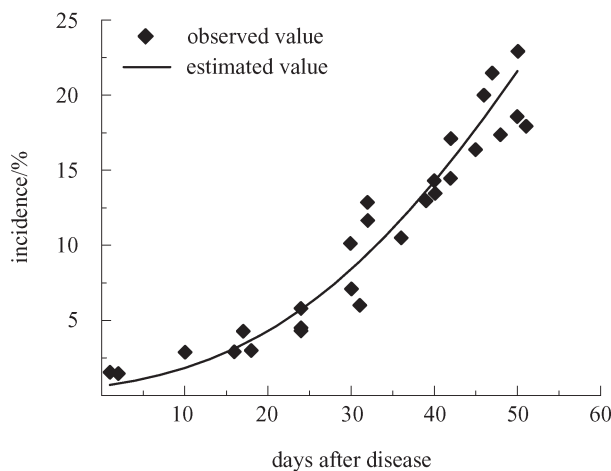


Fig. 3 Epidemic curve of pepper phytophthora blight in the fields

where *I* is the final incidence of pepper phytophthora blight, and *ST*, *SW*, *T* and *I*₀ represent soil temperature, soil water content, air temperature, and initial incidence, respectively. This model describes the pattern of the Gompertz value of incidence changing with the environmental factors in the fields, indicating that *ST*, *SW*, *T* and *I*₀ are the most important factors for the incidence of pepper phytophthora blight in the field, with little influence of air relative humidity on it.

4 Discussion

Analysis of the factors affecting the infection of a pathogen is an important basis for disease forecasting and control (Li et al., 1995). The pepper phytophthora blight spreads by air and soil. When roots and stems are

infected with *P. capsici* from the soil, the damage can lead to the death of the plants (Yi et al., 2002; Liu et al., 2004b). In the past, there were two shortcomings in the studies concerning the epidemic of pepper blight. First, the studies were not systematic. Most of these had qualitative descriptions but lacked quantitative analysis; The other shortcoming is that many of these studies paid too much attention to factors of air temperature, rainfall and irrigation, but neglected the important effects of soil factors which includes soil temperature and soil water status on the development of pepper phytophthora blight (Kuan and Erwin, 1982; Ristaino, 1991; Ristaino et al., 1992; Café-Filho and Duniway, 1995; 1996; Lü et al., 2001). In this study, most of the important factors, including soil temperature and soil water content that affected the incidence of pepper phytophthora blight were simulated under the controlled conditions to analyze their quantitative relationship to the infection of the pathogen.

In the condition of combining certain cultivars with the isolate, soil temperature and soil water status are the most important factors affecting the successful infection of *P. capsici*. In this experiment, we found that the soil temperature ranging from 22°C to 28°C was optimum for the infectivity of sporangia of *P. capsici* which was in accordance with the optimum mycelium growth temperature which ranged from 24°C to 26°C (Zheng, 1997). The field results also show that the pepper phytophthora blight was the worst in the years when moderate temperatures ranged from 22°C to 28°C in close coordination with the rainfall (Bowers and Mitchell, 1990) because the soil temperature was beneficial to the infection of *P. capsici*. In the meantime, the soil water status was a factor for restriction of the disease. Generally, the soil water status could be described by the soil water content and soil water matric potential (Ψ_m). In the range of suitable temperature and soil water content of 40%, or when Ψ_m value is close to 0 and soil is close to saturation, the sporangia are most likely to be infectious. If soil is too wet or too dry, it will not be suitable for the infection (Scherm and Yang, 1996). The past results have shown that when Ψ_m value is 0 to -1 kPa, zoospores of *P. capsici* will be released and when the temperature is suitable, with Ψ_m value close to 0, it will benefit the survival of *P. capsici*. Conversely, if the soil is over-saturated or too dry, it will be detrimental to the survival of *P. capsici* (Hord and Ristaino, 1992). In Heilongjiang Province, the worst pepper phytophthora blight usually appears during the rainy season around July and August, when the temperature is suitable and the high soil water content after rainfall becomes an important factor. In addition, high soil water content after irrigation may also result in a high incidence of pepper phytophthora blight in a greenhouse.

The penetration of a pathogen is very important in an infection chain. The soil temperature and soil water

status significantly affect the infection probability of *P. capsici*, and there exists obvious interactions in these factors (Zeng and Yang, 1986; Campbell and Madden, 1990). So in disease forecasting in the field, besides considering cultivars and culture factors, we should attach importance to soil temperature and soil water status so that we can accurately estimate the infection probability of pathogen and can make a definitive scientific forecast on the disease progress probability.

The test of relationship between pepper phytophthora blight incidence and environmental factors was carried out in the network to prevent the infection of a foreign pathogen during the disease progress. So besides initial incidence, air temperature, air relative humidity, soil temperature and soil water content are most important factors in the disease epidemic. Analysis of all the above factors indicated that relative humidity always remained at a high level throughout the whole experiment, which could meet the criteria for an epidemic. The change in the ranges in the air temperature, soil temperature and soil water content was large enough that it could restrict pathogen infection and epidemiology of the disease. According to the analysis of the relationship between incidence and all the factors, we established a forecasting model for pepper blight incidence in the field.

No foreign report on pathogen infection simulation has been published. The forecasting model of *P. capsici* pathogen infection was established in the controlled condition of a growth chamber which still needs further testing and corrections to make a relatively accurate forecast of the disease progress in the field. The results obtained in the experiment can provide both basic data for forecasting diseases and for the establishment of a systematic simulation model of disease and forms a base and method for continuous research work.

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