Modeling Leaf Age-Related Susceptibility and Rust Eruption Dynamics in Peanut

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ABSTRACT

To improve simulation of epidemics of peanut rust, information on the effects of leaf age and pustule eruption dynamics is needed. An analysis was made of the change of leaf susceptibility of rust with leaf aging using plants exposed to field inoculum. The youngest leaf was most susceptible to rust infection. As leaves aged, susceptibility decreased quickly. The relationship of infection frequency (Y, relative number of pustules) to leaf age (X, leaf position downward on the main stem) was described by a mathematical model $Y = 2.17X^{(-0.83)}$. The dynamics of pustule eruption also was studied using artificial inoculation. Analysis showed that after inoculation, pustule eruption over time was distributed in a logistic pattern. Rust eruption began at 130 and reach a peek at 250 rust degree days—that is, between 7 and 15 d after inoculation. Mathematical models of leaf age-related susceptibility and rust eruption dynamics will be incorporated into simulation model of rust epidemics.

Key Words: *Arachis hypogaea*, groundnut, *Puccinia arachidis*.

Since the development of the simulation model EPIDEM for tomato early blight (16), several simulation models have been developed for forecasting and management of plant disease epidemics (2, 13, 15, 19, 22). Computer-based models can simulate disease progress in a plant population as influenced by host growth dynamics, environmental conditions, or a combination of these variables. By simulation of disease epidemics under various crop management regimes, recommendations for disease control can be selected with greater efficiency (7, 22).

Host growth is considered a main factor in the development of epidemics for some diseases (4, 14). The main effects of host growth are an increase in the number of new infection sites and, conversely, a dilution effect on disease incidence (2, 14, 19, 21). Another important factor is that host susceptibility may change with aging, here termed age-related susceptibility (10). Susceptibility of a host to disease may increase and/or decrease with aging, or fluctuate with time (8). Even at a given growth-stage, different organs (e.g., leaves and stems) on the same plant may show different levels of disease susceptibility (10). Therefore, age-related susceptibility of the host must be considered in epidemiological studies of certain plant disease systems.

Another important factor in disease development is the latent period, defined as the period between the start of host infection and the time when lesions or pustules sporulate (2, 14). For peanut rust, this is the period between inoculation and eruption of uredinia (5). Latent period is considered a constant in simple disease progress models (16). However, host and pathogen factors, and environmental conditions can influence the duration of the latent period. Because of the influences from multiple factors, pustules from a single infection event probably never develop synchronously. Thus, pustule eruption may be distributed over a time span in a certain pattern. Simulators that employ a constant latent period use the mean, median, or modal value of the latent period, but not the dynamics of eruption. Therefore, Shaner and Hess (11) proposed a concept of daily appearance rate in their research of slow leaf-rusting of wheat.

Temperature affects pathogen development within the host and thus affects the duration of latent period (6). It is well known that an organism can develop only when the temperature is above its biological base (effective temperature). Therefore, the dynamics of disease appearance (pustule eruption in the case of peanut rust) should be related to the effective temperature.

Peanut rust (*Puccinia arachidis* Speg.) is one of the most important constraints to peanut (*Arachis hypogaea* L.) production in the world (6, 9, 17, 21), and many studies have been conducted on development of the disease (6, 9, 19). In studying host resistance, Cook (3) reported that rust susceptibility was correlated with leaf wettability, which was probably affected by leaf age. However, no further work has been reported on the simulation of age-related susceptibility of the host and rust eruption dynamics of infection of the disease.

Wang and Lin (19) developed a computer simulator for peanut rust (CSGR-1) with good validation results. However, while host growth affected disease progress, the simulator did not account for the influence of changing susceptibility with leaf aging on disease development. Latent period also was considered in sub-models of disease increase as a constant time span in CSGR-1. Additional research has not been done to improve the model. To obtain a better understanding of rust epidemics, work is needed on these two epidemiological events. Therefore, the objective of the present study was to quantify age-related susceptibility and rust eruption dynamics of peanut rust using infectivity experiments.

Materials and Methods

Age-Related Susceptibility. The peanut cultivar used was Guangdong-oil 551-116 (*Arachis hypogaea* subsp. *fastigiata*, an upright cultivar) which is a widely grown peanut in South China. Two crops are grown per year, usually from March or April to August (about 125 d to maturity) and from August to December (about 120 d to maturity). Seeds were sown in pots (22 cm diam. and 20 cm height) with several seeds per

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pot and five pots per experiment. Plants were grown outside the greenhouse on the campus of South China Agric. Univ. Possible sources of pathogen inoculum were located at lest 4 km from the study site. When the plants had six fully expanded leaves on the main stem, they were taken to a peanut field and subjected to field inoculum for 12 hr from 6 PM to 6 AM, with the top leaf tagged for identification. After exposure to field inoculum, the plants were returned to the greenhouse. Eighteen days after inoculation, the pustules on all leaflets on the main stems of all 25 plants were counted. The experiment was repeated 15 times

The age of a leaf was determined according to its position on the main stem—that is, the youngest fully expanded leaf was designated age 1, the second leaf as age 2, etc. For each replication of the experiment, the mean numbers of pustules per leaflet, X_{ij}, was calculated with data from plants in the same replication as:

$$X_{ij} = \frac{1}{m}\sum_{k=1}^{m} N_{ijk} \qquad \text{[Eq. 1]}$$

where N_{ijk} was the number of pustules of an i^{th} age leaflet in k^{th} plant in j^{th} replication, averaged over four leaflets per leaf; m was the number of plants per replication; and X_{ij} was the mean number of pustules of an i^{th} age leaflet in j^{th} replication.

To remove variation resulting from different amounts of infection in each replication of the experiment, the mean numbers of pustules per leaflet were transformed into Y_{ij}, the relative number of pustules per leaflet, based on a mean number of one pustule per leaflet as:

$$Y_{ij} = \frac{X_{ij}}{\frac{1}{n_j}\sum_{i=1}^{n_j} X_{ij}} \qquad \text{[Eq. 2]}$$

where X_{ij} was the mean number of pustules for the i^{th} leaflet in the j^{th} replication, and n_j was the number of different leaf ages in the j^{th} replication of the experiment.

The relative number of pustules per leaflet (Y_i) could be obtained from the data of Y_{ij}:

$$Y_i = \frac{1}{n_i}\sum_{j=1}^{n_i} Y_{ij} \qquad \text{[Eq. 3]}$$

where n_i was the number of Y_{ij} of i^{th} age leaflets. The epidemiological meaning of Y_i was the amount of infections occurring in each i^{th} age leaflet (relative number of pustules per leaflet) when the mean pustules for each leaflet was one in the field.

With relative number of pustules and leaf ages known, a mathematical model was developed to describe the relationships of susceptibility and leaf-age, using least square regression. To test the fitness of the model, determination coefficient (R^2) and the F value were calculated and validated.

Two experiments using artificial inoculation with uredospore suspensions were conducted to validate the age-related resistance model. Artificial inoculation was accomplished by spraying a uredospore suspension that was prepared by using field-collected uredospores and distilled water. The density of uredospores in the suspesion was about 2-3 × 10^5 uredospores/mL. Eighteen days after inoculation, the pustules on all leaflets on the main stems of all plants in the experiment were counted. Observations were transformed into the relative number of pustules as described before. Comparison was made of the calculated values of the model and experiment data.

To estimate the accuracy of the model, the proportion of accuracy (PA) was calculated by comparing actual data (Y) from the two artificial infection experiments and predicted values (YE) (20) as follows:

$$PA = (1 - |Y - YE| / Y) \times 100 \qquad \text{[Eq. 4]}$$

where $|Y - YE|$ was the absolute difference between actual observations and predicted values.

Rust Eruption Dynamics. Peanut seeds were sown in pots as described previously with three seeds per pot and 10 pots for each of two replications in the experiment. When plants had six to seven fully expanded leaves on the main stem (about 30 d old), they were inoculated by spraying with a uredospore suspension as previously described. When the first uredinia was observed, pustules were counted daily on all leaflets of the main stem until the numbers of pustules did not increase. Daily temperature was recorded continuously over the course of each experiment by a temperature data-logger (Guangzhou Weather Instrument Corp. Guangzhou, People's Republic of China). A daily mean temperature was calculated from the temperature recordings at 2, 7, 13, and 20 hr each day.

A logistic model was used to characterize the dynamics of disease appearance as:

$$N_i = \frac{k}{1 + \exp[-(a + bT_i)]} \qquad \text{[Eq. 5]}$$

where N_i was the numbers of pustules per leaflet at time T_i (days); k was the asymptote of the curve, the maximum number of pustules per leaflet; and a and b were estimated parameters related to the number of pustules at $t = 0$, and the rate of pustule increase, respectively.

Parameter k was calculated by the two-paired points method (18) using pustule counts. According to the method, a group of four observations arranged in two pairs with a same time interval was used to estimate k, series of all of such groups in the observation series were used to estimate many k values, and then the mean of these estimated values was used as the final estimate of k. The equation for estimating k was as follows:

$$k = \frac{N_j N_m (N_i + N_n) - N_i N_n (N_j + N_m)}{N_j N_m - N_i N_n} \qquad \text{[Eq. 6]}$$

where: $t_j - t_i = t_n - t_m \neq 0, i < j, m < n, i \neq m$.

After the final k was obtained, the probability of daily rust eruption P_i was calculated as the ratio of N_i to k.

The minimum temperature for the growth of the pathogen was assumed to be 8 C, based on germination of uredospores (1). The rust degree days (*RDD*) was calculated as follows:

$$RDD_i = \sum_{j=1}^{i}(T_j - 8) \qquad \text{[Eq. 7]}$$

where T_j was the daily mean temperature (C) of j^{th} day, calculated as described previously, and RDD_i was the *RDD* in i^{th} day. To estimate the relationship between rust eruption probability (P) and *RDD*, the logistic model was rewritten by dividing each side of the equation by k and replacing

t with RDD. Least squares method was used to estimate parameters a and b for the following equation:

$$P = \frac{1}{1+\exp[-(a+bRDD)]} \quad \text{[Eq. 8]}$$

Results

Age-Related Susceptibility. The relative numbers of pustules per leaflet, based on a mean number of one pustule/leaflet, were 1.9365, 1.4921, 0.8827, 0.6456, 0.5757, and 0.4675 for 1, 2, 3, 4, 5, and 6th age. The corresponding standard deviations were 0.0664, 0.1277, 0.0762, 0.0638, 0.0665 and 0.0739. The relative number of pustules per leaflet showed that infection declined with leaf aging.

With the least square method, a power function was selected with the highest coefficient of determination (R^2):

$$Y = 2.17X^{(0.83)} \quad \text{[Eq. 9]}$$

where X was leaf age, and Y was relative number of pustules/leaflet. For this equation, R^2 = 0.9622, F = 101.82 [$F_{0.01}(1,4)$ = 21.2].

A comparison of results from artificial inoculations and that calculated by the equation is made in Fig. 1. The mean proportion of accuracy of the prediction was 93%.

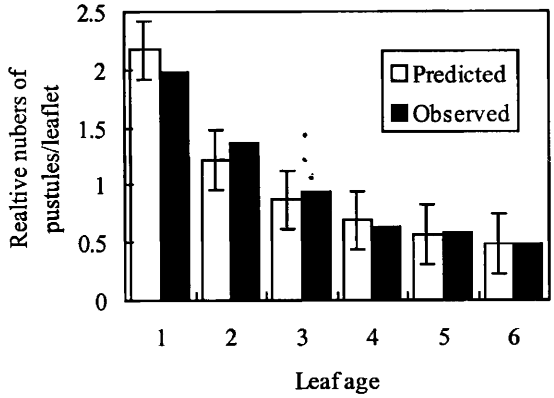

Fig. 1. Relationship between leaf age and susceptibility to peanut rust. Leaf age refers to the leaf position on main stem—i.e., the youngest fully expanded leaf is designated age 1; the second, age 2; etc. Relative number of pustules/leaflet, supposed mean pustules for each leaflet is 1. Observed values are the mean number of pustules from 50 plants by artificial inoculation. Predicted values are calculated from the age-related susceptibility model: $Y = 2.17X^{(-0.83)}$ where X refers to leaf age and Y relative number of pustules/leaflet.

Rust Eruption Dynamics. From the data it was evident that the pustule eruption over time was sigmoidal (Fig. 2) and that the logistic equation could be used to describe such progress. Values of k estimated for each experiment were 98 and 157 pustules per leaflet, respectively. To describe the relationship between rust eruption dynamics and rust degree days, the logistic model was rewritten by dividing both sides of the equation by k and replacing t with RDD. The following equation was obtained for the eruption dynamics of peanut rust (Fig. 3).

$$P = \frac{1}{1+\exp(15.9333-0.06578RDD)} \quad \text{[Eq. 10]}$$

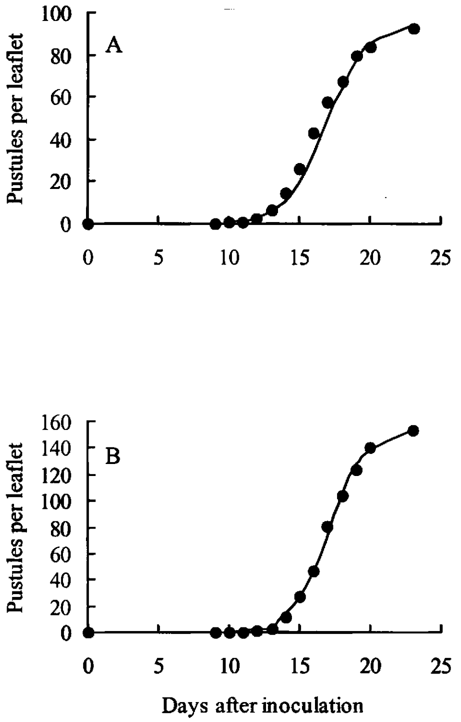

Fig. 2. Pustule eruption dynamics of peanut rust over time. Dots are observations and lines are fitted logistic curves. A and B refer to different experiments.

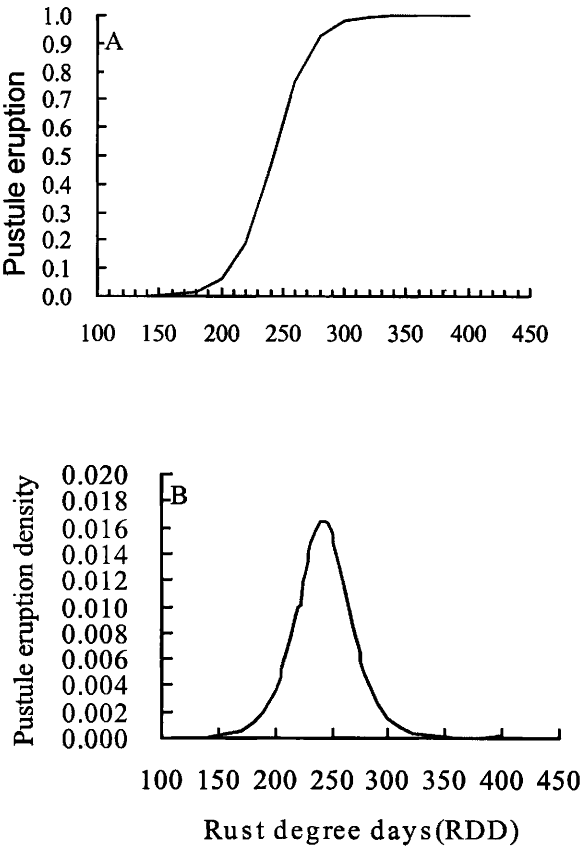

Fig. 3. Rust eruption dynamics of peanut rust over rust degree days. A) Pustule eruption refers to total pustules accumulated, and B) eruption density refers to daily pustules eruption. Rust degree days are the accumulated temperatures above 8 C.

For this equation, $R^2 = 0.9832$, $F = 1346.07$ ($F_{0.01} = 7.82$).

By differentiating the equation, rust eruption probability density (p) was obtained (Fig. 3).

$$p = \frac{0.06578\exp(15.9333 - 0.06578RDD)}{[1 + \exp(15.9333 - 0.06578RDD)]^2} \quad \text{[Eq. 11]}$$

Pustule appearance occurred at 7 d after inoculation (*RDD* is about 130) and reaches a peak after 15 d, when *RDD* was about 250.

Discussion

The resistance of peanut leaves to rust was related to the age of leaves and increased with leaf aging (i.e., the infection amount decreases with leaf aging) as reported by Cook (3). In Cook's experiment, the susceptibility of leaves was shown to have a positive correlation with their wettability, which decreases with leaf aging. Cook (3) also found that, regardless of plant age, a similar positive relationship reported for leaf susceptibility with wettability for all nonphysiologically resistant cultivars studied. Although the plants used in our study were relatively young, the results could still be used as reference in disease simulation or in other related studies of older plants because the relative process of leaf aging would be similar. In a study on the susceptibility of rice to blast (*Pyricularia oryzae*), Roumen *et al.* (10) found that the susceptibility of leaves declined rapidly with increasing age. This decline in susceptibility tended to follow the same pattern in rice cultivars with different levels of resistance. These observations indicate that age-related leaf susceptibility to certain diseases may be related to structure and/or physiology of aged leaves.

In a study of rust resistance with several peanut cultivars, Subrahmanyam *et al.* (12) found that uredospores could germinate and invade both resistant and susceptible cultivars. However, fungal growth was restricted by the host plant in resistant genotypes. It is believed that the susceptibility of peanut to rust is mostly based on the host physiology, and appears to have little relation with the morphological structure of the plant.

In this study, the age of a leaf was determined by its position on the main stem. This certainly is not an exact measure of age compared with that of actual time (e.g., days). However, it is convenient for simulation studies because in population dynamics it is difficult to calculate the actual age of every single leaflet in large population. Use of leaflet position on the main stem as leaf age is a simplified measure of aging because the time interval between two leaves growth is relatively constant for a given cultivar. For Guangdong-oil 551-116 this is about 5 d. Although temperature has an effect on peanut growth (19), the daily mean temperature often is relatively stable during the growing seasons in South China.

In the present study, rust eruption dynamics influenced by effective accumulated temperatures (*RDD*) was conducted and showed good fitness to the experimental data. The eruption of pustules following simultaneous inoculations was a dynamic process over a relatively long time interval. Using the rust eruption dynamics with *RDD* to simulate disease rust eruption dynamics would be more helpful in simulation of rust epidemics than that with a predetermined latent period based on regular time.

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