Relating Epidemic Progress from a General Disease Model to Seasonal Appearance Time of Rusts in the United States: Implications for Soybean Rust

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ABSTRACT

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Soybean rust, *Phakopsora pachyrhizi*, has been considered a threat to the production of the U.S. soybean, *Glycine max*. During the past decade, this disease gradually spread to Africa, South America, and recently to the United States. Previous soybean rust risk assessments with an assumption of availability of spores early in a season showed that weather conditions (dew and temperature) during a growing season, in general, are suitable for disease development in U.S. soybean-growing regions. Predicting the time of rust appearance in a field is critical to determining the destructive potential of rusts, including soybean rust. In this study, comparative epidemiology was used to assess likely rust incipient time in four locations within the U.S. Soybean Belt from south to north: Baton Rouge, LA; Charlotte, NC; Indianapolis, IN; and Minneapolis, MN. Temperature

effects on the infection cycle of five rusts occurring in the Midwest were evaluated using a general disease model. The likely incipient times were examined with the modeling results. Among the rusts studied, early-appearing rusts had suitable conditions for development earlier in a season. However, a lag period of several weeks to more than 3 months was found from the time when conditions are suitable for a rust to develop or when hosts are available to the time when the rust was detected in fields. Length of the lag period differed among the rust species examined. If nature of long-distance dispersal is not significantly different among the rusts, implications of our study to the expected seasonal soybean rust incipience in fields lead to two possible scenarios: (i) average appearance time of soybean rust across the Soybean Belt should be somewhere between appearance times of common corn rust and southern corn rust, and (ii) with late appearance of the disease, late-planted soybean in the south has greater risk.

Soybean rust, caused by *Phakopsora pachyrhizi*, has been considered a threat to the U.S. soybean production (1). During the past decade, soybean rust has gradually spread from the eastern hemisphere to Hawaii (13), Africa (12), and South America (48), and in late 2004, to the United States. A quantitative computer simulation model predicted considerable yield losses in many soybean-growing areas of the United States (45). The model assumed that rust urediniospores are available early in a growing season. In the United States, *Phakopsora pachyrhizi* is likely to overwinter in parts of Florida, southern Texas, and neighboring countries further south (27). Rust infections in most U.S. soybean-growing regions would depend on northward seasonal dispersal from overwintering regions. The time of initial rust appearance in fields throughout the Soybean Belt will be critical to its negative effects on soybeans. The earlier the disease occurs in a soybean field, the greater the potential impacts on yield. The dates of initial occurrence for rust diseases in several crops are characterized by a gradual onward shift as the latitude increases from south to north in the United States. The time of rust appearance in a region changes from year to year. However, in a long-term perspective, some rusts appear earlier in a year than others. Annual incipient time of rusts in non-overwintering regions depends on biotic and abiotic components and is complex to predict, even with well-studied rusts. Assessment of epidemiological factors

(e.g., infection efficiency, latent period, spore production, and infectious period) is needed for the prediction of epidemic progress (41). Controlled experiments have been widely used to assess epidemic components for rust fungi. Simulation of a polycyclic disease progress by using monocycle processes and avoiding the complexity of natural conditions has led to a better understanding of fungal population dynamics (32). Analysis of the prevailing conditions for epidemic development for rusts currently occurring in the United States, and its relation to the expected rusts appearance time according to historical data might gain a better understanding on processes related to the rusts incipience time. As soybean rust has established in North America only recently, analogies to other rusts behavior might aid prediction of the expected timeframe of its incipience in different locations. In the current study, we attempt to determine a relationship between disease progress as affected by temperature and its incipience. The effects of temperature on the infection cycle of several rust diseases on crops important in the United States were evaluated and incorporated into a general disease model. The relationships between modeling results and the likely incipient times of rusts at different locations were examined for a possible pattern that might aid prediction of seasonal incipience timeframe of recently introduced rust. The implications to the range of soybean rust incipient times at different locations of the U.S. soybean production region are discussed.

MATERIALS AND METHODS

The model. A mathematical model developed by Gumpert et al. (8) to describe the epidemic development of airborne foliar fungal diseases was used to compare the temperature effects on

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different rusts occurring in the regions in the east of the Rocky Mountains. The model, a generalization of Vanderplank's discontinuous model (42), describes the daily increase in the number of infections on host plants during the exponential phase of a disease. The number of infections at day t was calculated with the following equation: $Y(t) - Y(t-1) = IE \times D \times SP[Y(t-LP) - Y(t-LP-IP)]$. Giving the initial conditions, $Y(t) = 0$ at $-(LP + IP) < t < 0$ and $Y(t) = IE \times I$ at $t = 0$, where $Y(t)$ is the number of infections at day t ; IE is infection efficiency; D is the proportion of spores that are deposited on a potential infection site; SP is the number of spores production per lesion per day; LP is latent period in days; IP is the infectious period in days; and I is the initial influx number of spores from an external source to the field. The measure $\rho = Y(t)/Y(t-1)$ represents the factor by which the number of infections is multiplied every day, after the initial wave has dumped. As the epidemic turns from the simple interest phase to the compound interest phase, the ρ value is stabilized. Detailed information on the model and its assumptions can be found in Gumpert (7) and Gumpert et al. (8).

We used monthly temperature normals during a growing season to compare monthly modeling results of five rusts in four selected locations within the U.S. Soybean Belt from south to north: Baton Rouge, LA; Charlotte, NC; Indianapolis, IN; and Minneapolis, MN. The rust fungi compared were *Puccinia triticina*, causal agent of wheat (*Triticum aestivum*) leaf rust; *Puccinia arachidis*, causal agent of groundnut (*Arachis hypogaea*) rust; *Puccinia polysora*, causal agent of southern corn (*Zea mays*) rust; *Puccinia sorghi*, causal agent of common corn rust; and *Phakopsora pachyrhizi*, causal agent of soybean rust. The selected locations are representative of the Soybean Belt for a possible gradual south to north expansion or appearance time of rusts during a growing season. Temperature normals (30-year averages) of all locations are provided in Table 1.

Many factors affect the disease cycle processes in a pathosystem, including environment-related factors (temperature, leaf wetness duration, and radiation), host-related factors (plant age, leaf age, and plant stage), and pathogen-related factors (urediniospore age, spore density, uredinia age, lesion age, and lesion size). Unless otherwise noted, values of all disease components were taken from reported experiments conducted in constant temperatures with young susceptible plants and virulent pathogens; this

was an attempt to keep hosts and pathogens effects and environmental effects other than temperature uniform.

In a model run, 100 spores were assumed successfully infecting the host plants ($Y(t) = IE \times I = 100$ at $t = 0$). After disease initiation, development continues according to the average temperature conditions of the month examined, whereas leaf wetness duration was not considered a limiting factor for disease development. The effect of temperature on each of the disease components was evaluated for all rusts.

Evaluating infection efficiency. The effect of temperature on the infection efficiency of the rusts was assumed to follow a classical response curve for biological systems with three cardinal temperatures: optimum (T_{opt}), maximum (T_{max}), and minimum (T_{min}). The following equation was used to calculate the curve (2,29): $Y = \alpha(T - T_{min})(T_{max} - T)^\beta$, where $\alpha = Y_{max}/[(T_{opt} - T_{min})(T_{max} - T_{opt})^\beta]$ and $\beta = (T_{max} - T_{opt})/(T_{opt} - T_{min})$.

Y is the infection index and $Y_{max} = 1$ when wetness conditions are optimal. Values of infection efficiency at optimum conditions and cardinal temperatures for the different rusts were determined based on literature values (Table 2). Chances for infections in a field are usually higher during the night and early morning than daytime because relative humidity is higher and leaf wetness duration is longer in the night than in daytime. Therefore, the average infection index for each month was determined using mean nighttime temperatures. Mean nighttime temperature was estimated by averaging the mean and the minimum monthly temperatures (Table 1).

Melching (21) showed for southern corn rust that the infection efficiency is affected by spore density on leaf surface. Analyzing the results presented by Melching (21) suggests a significant negative correlation between the natural logarithm values of spore density and infection efficiency ($R^2 = 0.99$). In the current model, if not otherwise noted, infection efficiency values chosen for the different rusts are for medium-to-low densities of ≤ 200 spores per cm^2 . Multiplying infection efficiency at optimal conditions (Y_{max}) and infection index (Y) gave the infection efficiency value for each temperature.

Evaluating latent period. The definition of latent period used is in accordance with Vanderplank (42), the time between inoculation and uredinium eruption. The basic parameter values used to calculate the effect of temperature on the latent period of the

TABLE 1. Monthly temperature normal for the period of 1971 to 2000 in four locations in the U.S. Soybean Belt

Location	March	April	May	June	July	August	September
Baton Rouge, LA (30.5 N, 91.1 W, altitude = 20 m)							
Maximum	21.7	25.2	28.9	31.8	32.6	32.7	30.8
Mean	15.7	19.2	23.3	26.5	27.6	27.4	25.3
Minimum	9.8	13.2	17.8	21.2	22.6	22.2	19.7
Mean night ^a	12.8	16.2	20.6	23.9	25.1	24.8	22.5
Charlotte, NC (35.2 N, 80.9 W, altitude = 240 m)							
Maximum	17.8	22.7	26.5	30.3	32.3	31.3	27.6
Mean	11.6	16.1	20.6	24.7	26.8	26.1	22.6
Minimum	5.3	9.5	14.6	19.2	21.4	20.7	17.2
Mean night ^a	8.4	12.8	17.6	21.9	24.1	23.4	19.9
Indianapolis, IN (39.7 N, 86.3 W, altitude = 241 m)							
Maximum	...	17.2	23.1	27.8	29.8	28.7	25.2
Mean	...	11.1	17.0	22.1	24.1	23.1	19.1
Minimum	...	5.1	11.0	16.3	18.4	17.4	12.9
Mean night ^a	...	8.1	14.0	19.2	21.3	20.2	16.0
Minneapolis, MN (44.9 N, 93.2 W, altitude = 260 m)							
Maximum	...	13.9	21.2	26.1	28.5	26.9	21.7
Mean	...	8.1	15.2	20.2	22.9	21.4	16.1
Minimum	...	2.3	9.2	14.3	17.2	16.0	10.4
Mean night ^a	...	5.2	12.2	17.3	20.1	18.7	13.3

^a Mean night temperature is estimated as the average of the mean and minimum temperatures.

different rusts were from reported experiments (Table 3) conducted under constant temperature with young plants, except for soybean rust, where the latent period was evaluated under uncontrolled temperatures from which the average air temperature was calculated (15).

The following procedure was used to calculate the average latent period for a given temperature: latent period was a function of physiological days (PD) of the rusts. PD_i can be a linear function of temperature as described previously (11,46):

$$PD_i = \begin{cases} (T_i - T_{min}) / (T_{opt} - T_{min}), & \text{if } T_{min} \leq T_i < T_{opt} \\ (T_{max} - T_i) / (T_{max} - T_{opt}), & \text{if } T_{max} \geq T_i > T_{opt} \end{cases}$$

T_{opt} is the temperature where latent period was found or estimated the shortest. Values of T_{max} and T_{min} were chosen that fit the literature results best, with minimal standard deviation of the multiplication of the observed latent period and the calculated physiological day (Table 3). T_i is the mean temperature normal (Table 1). The average latent period during a given month was calculated using the following equation: $LP \text{ (at } T_i) = LP \text{ (at } T_{opt}) / PD_i$.

Evaluating infectious period and daily spore production. The infectious period is the time between the beginning and cessation of spore production of uredinium or lesion. Daily spore production is the average daily spore production at that time. The effect of temperature on the infectious period was interpolated from published data (23,25,31,33,47). If the effect of temperature was minor in temperature range relevant to the current study, or data were available only for a certain temperature (usually close to optimum conditions), the infectious period was set constant; otherwise a linear relation was estimated between each two adjacent temperatures and the infectious period or daily spore production. The infectious period chosen for southern corn rust was set according to Nishi et al. (23) data for *Puccinia polysora* (isolate Ku-9604) as 3, 9, and 8 days at 16, 26, and 28°C, respectively. The infectious period chosen for groundnut rust was set at 15, 26, and 21 days at 18, 27, and 28.5°C, respectively (33). Infectious periods of soybean rust (47) and common corn rust (25) were set as a constant of 28 days due to data availability. The infectious period of wheat leaf rust was set as a constant of 10 days (31), because it was found to be stable on several wheat cultivars in the

seedling stage under the temperature range 15.6 to 26.7°C (40). Daily spore production of groundnut rust under different temperature was interpolated from published data (33). Spore production rate of groundnut rust was 160, 1,600, and 530 spores per lesion per day at 18, 27, and 28.5°C, respectively. Daily spore production chosen for wheat leaf rust was considered a constant at 300 (31), due to a quite stable spore production under a wide temperature range (40). For soybean rust, common corn rust, and southern corn rust, spore production rate was 420 (47), 250 (25), and 1,500 (3), respectively, due to data limitations on the effect of temperature on spore production, although experimental results for common corn rust (43) suggest that 20°C is the optimum temperature for spore production. These simplifications due to data constraints tend to overestimate p values when temperatures are far from the optimum for spore production or infectious period. However, at lower temperatures, the longer latent periods and/or the low infec-

Fig. 1. Relative amounts of infections (the infection index) for soybean rust (SBR), wheat leaf rust (WLR), groundnut rust (GNR), common corn rust (CCR), and southern corn rust (SCR) in relation to temperature when leaf wetness is not a limiting factor. Cardinal temperatures used to calculate the curves are given in Table 2.

TABLE 2. Maximum infection efficiencies, cardinal temperatures, and calculated parameters used to evaluate the relative amount of infections (the infection index) under temperature effects for five rust diseases

Rust	IE	T_{opt}	T_{max}	T_{min}	α	β	Sources
Soybean	0.06	22.5	27.5	10	0.0420	0.40	Marchetti et al. (19) (for temperatures) Melching et al. (22) (for infection efficiencies)
Groundnut	0.15	22	30	8	0.0218	0.57	Butler and Jadhav (2) (for temperatures) Savary (33) (for infection efficiencies)
Common corn	0.13	16	30	7	0.0018	1.56	Webber (44) and Vitty et al. (43) (for temperatures) Mahindapala (18) (for infection efficiencies)
Wheat leaf	0.17	15	30	2	0.0034	1.15	Sache and de Vallavieille-Pope (31) (for temperatures and infection efficiencies)
Southern corn	0.07	23	32	10	0.0168	0.69	Godoy et al. (6) (for temperatures) Melching (21) (for infection efficiencies)

TABLE 3. Estimated cardinal temperatures used to calculate rust latent period (LP) under the effects of temperature, in which LP was related to physiological days (PD) of the rusts, and average $LP \times PD$ was considered the latent period at optimum temperature

Rust	T_{opt}	T_{min}	T_{max}	$PD \times LP$ (average)	SD ^a	Source data
Soybean	26	5	42	5.7	0.69	Kitani and Inoue (15)
Groundnut	27	14	40	7.9	0.15	Savary (33)
Common corn	27	3	42	4.8	0.19	Mahindapala (18)
Wheat leaf	27	0	40	4.9	0.13	Tollenaar (39)
Southern corn	26	12	42	8.7	0.72	Nishi et al. (23)

^a Standard deviation (SD) of the calculated $PD \times LP$ values for the LP values under different temperatures, which were from literature. Lower SD suggests a better fit to the published data.

tion indexes values tend to dictate low ρ values and minimize overestimations.

Deposition frequency. The proportion of produced spores that are deposited on a potential infected site can be influenced by many factors, including crop geometry, uredinia location on the leaf, and meteorological conditions. Shaner and Hess (35) calculated a value of 0.02 for the deposition frequency in wheat leaf rust. Gumpert (7) used an upper limit of 0.1 for this parameter. In the current study, a constant of 0.05 was used for all rusts.

Rusts incipience times. Corn is usually planted after the second weeks of March and April in Louisiana and Indiana, respectively. Common corn rust is usually first detected in Louisiana cornfields from mid- to late May, and in the U.S. Corn Belt, arrival of urediniospores and initial infection occurs usually in mid-June to mid-July (26). In a 4-year survey to track its first appearance in Indiana, the rust was found between 18 June and 24 July (34). Southern corn rust appears much later in the season. It normally occurs in Mississippi in late July (14). In Indiana, in a 4-year survey, the incipient dates ranged between 21 August and 27 September (34). Groundnut rust appearance times resemble that of southern corn rust, normally it is not observed before late July or early August in southern Texas (10) and even later in Georgia (38). In North Carolina, groundnut rust showed up in four out of seven seasons surveyed and always late in the season (9).

Model components results: Infection efficiency. Optimum infection index for wheat leaf rust and common corn rust have a lower temperature range than that of the other rusts (Fig. 1). The maximum infection efficiency obtained from literature for soybean rust (22) was relatively low compared with the other rusts (Table 2). The relatively low infection efficiency value might be due to the high spore densities used in experiment. However, for wheat leaf rust, spore densities used in experiments to obtain infection efficiency values were >300 urediniospores per cm^2 (31).

Latent period. Latent periods calculated with physiological day had a good fit to those from literature, which report the temperature effects on the latent period of the five rusts (Fig. 2; Table 3). The optimum and maximum temperatures calculated for all rusts are within the same range, 26 to 27°C and 40 to 42°C, respectively (Table 3). The minimum temperatures affecting the latent period vary over a wide range from 0°C for wheat leaf rust to 14°C for groundnut rust. In Baton Rouge, LA for instance, in March and April, the latent periods of groundnut rust and southern corn rust are probably too long to sustain the progress of a disease, and the latent period for all rusts is the shortest during June and July (Fig. 2). The parameters for calculation of latent period of soybean rust were from an experiment conducted in Japan (15). Latent period ranged from 13 days at 15.4°C to 6 days at 28°C of average temperatures. In another experiment conducted in Australia by Kochman (16), the latent period ranged between 14 days at 12°C to 9 days at 22°C. At 27°C, the latent period was lengthened to 11 days.

RESULTS

The calculated rates of increase, ρ , of the rusts during different months of a growing season in five locations are presented in Table 4. Based on ρ values, temperature conditions in Baton Rouge, are suitable for the development of wheat leaf rust and common corn rust from March. During April, conditions are more suitable for wheat leaf rust and common corn rust, less suitable for southern corn rust and groundnut rust, and intermediate for soybean rust (Table 4; Fig. 3A). In May, temperature conditions are suitable for all rusts. In June and July temperature, conditions gradually become less suitable for common corn rust, mainly due to a reduction in its infection efficiency (Table 4; Fig. 3B). In Indianapolis, ρ values suggest that conditions are suitable for wheat leaf rust and common corn rust from May to September, and for soy-

bean rust and southern corn rust from June to August (Table 4; Fig. 4A and B). Wheat leaf rust has a broad suitability from spring to fall in all U.S. locations checked. Common corn rust also shows a broad suitability, except in Baton Rouge where summer temperatures might retard its development. In general, U.S. temperature conditions for soybean rust epidemics are not suitable early in the soybean-growing season (Table 4; Fig. 5). Soybean rust ρ values for Baton Rouge and Indianapolis also were calculated using possible scenarios of an increase in urediniospores mortality due to pre-exposure of spores to high temperatures and latent period values according to Kochman (16) (Table 5). At low pre-exposure temperatures for 8 h (24.5°C and below), spore germination percentage was stable. At pre-exposure temperatures of 28.5°C and higher, spore germination percentage continued declining. Mean daytime temperature was estimated by averaging the maximum and the mean monthly temperatures. Average daytime temperatures in Baton Rouge exceed 28.5°C between June and August, indicating long daily exposure periods to temperatures $\geq 28.5^\circ\text{C}$. When using latent period values according to Kochman (16), the soybean rust shortest latent period is increased from 6 to 8 days, and consequently, overall ρ values are reduced. The reduction affects mainly the results in Baton Rouge (Table 5), wherein the optimal month for reproduction is changed from June

Fig. 2. Fitted curves for published data on latent period as a function of temperature for A, soybean rust (SBR), wheat leaf rust (WLR), and common corn rust (CCR); and B, southern corn rust (SCR) and groundnut rust (GNR).

to May, and the time with about optimal conditions for reproduction narrows to around May and again in September. In Indianapolis (Table 5), conditions remain suitable between June and August.

When compared with the rusts incipience times in the fields, modeling results predict that in general, conditions for disease development in a location are suitable long before the actual appearance of the rusts. As documented rusts appearance times in a location are usually very general in literature, the use of monthly means to obtain model components is a simplification suitable to the current work, which is aimed at examining general relations between the environment and rusts incipience. Calculation using means of shorter time intervals or historical temperature data together with other environmental effects for a location would refine model results. Results from such calculation should be accompanied by more accurate data on rusts incipience in different years and might improve our interpretation of modeling results for rusts appearance times.

DISCUSSION

Among the rusts compared in this study, wheat leaf rust and common corn rust generally appear in fields earlier during a year than southern corn rust and groundnut rust. Winter wheat is planted earliest, in fall. Wheat leaf rust can survive winter, usually up to latitude 40 in the United States (5,30); and the fall-planted wheat provides an extensive potential host area for the rust to overwinter. Current modeling results suggest that temperatures are suitable for pathogen development from spring to fall in all locations examined. In Baton Rouge, winter temperatures are suitable for wheat leaf rust maintenance, but they are too low for disease increase (36). Fast disease increase started in March and was not related to inoculation date. When environmental conditions for disease development are conducive in a season, initial disease levels (X_0), or in other words, amount of overwintered inoculum in the local field, would be the most important component influencing final disease and damage for wheat leaf rust (4), as well as for wheat stripe rust, *Puccinia striiformis* (17). Throughout the overwintering regions, wheat leaf rust has the potential to

Fig. 3. Calculated infection progress curves of hypothetical epidemics, staying in the exponential phase, of soybean rust (SBR), wheat leaf rust (WLR), groundnut rust (GNR), common corn rust (CCR), and southern corn rust (SCR), under **A**, April and **B**, June temperature conditions in Baton Rouge, LA.

TABLE 4. Rates of disease increase (ρ), for different months at five different locations as affected by temperatures, during the exponential phase of the different rusts, where higher ρ values represent more suitable conditions for the rusts reproduction

Location/rust	March	April	May	June	July	August	September
Baton Rouge, LA (30.5 N, 91.1 W, altitude = 20 m)							
Soybean	1.12	1.20	1.28	1.31	1.30	1.31	1.32
Groundnut	1.00	1.15	1.37	1.54	1.47	1.50	1.47
Common corn	1.25	1.31	1.37	1.26	1.23	1.24	1.29
Wheat leaf	1.31	1.39	1.42	1.42	1.38	1.39	1.45
Southern corn	1.00	1.17	1.31	1.38	1.33	1.33	1.38
Charlotte, NC (35.2 N, 80.9 W, altitude = 240 m)							
Soybean	1.00	1.13	1.23	1.32	1.31	1.32	1.27
Groundnut	1.00	1.06	1.22	1.42	1.54	1.48	1.33
Common corn	1.12	1.25	1.31	1.35	1.29	1.31	1.33
Wheat leaf	1.22	1.34	1.38	1.47	1.41	1.43	1.42
Southern corn	1.00	1.00	1.17	1.33	1.38	1.38	1.25
Indianapolis, IN (39.7 N, 86.3 W, altitude = 241 m)							
Soybean	...	1.00	1.16	1.27	1.32	1.28	1.20
Common corn	...	1.10	1.28	1.34	1.36	1.33	1.31
Wheat leaf	...	1.22	1.35	1.43	1.41	1.42	1.39
Southern corn	...	1.00	1.08	1.26	1.34	1.31	1.18
Minneapolis, MN (44.9 N, 93.2 W, altitude = 260 m)							
Soybean	...	1.00	1.11	1.23	1.28	1.27	1.14
Common corn	...	1.00	1.28	1.32	1.33	1.35	1.31
Wheat leaf	...	1.13	1.31	1.39	1.42	1.43	1.34
Southern corn	...	1.00	1.04	1.21	1.30	1.25	1.06

Fig. 4. Calculated infection progress curves of hypothetical epidemics, staying in the exponential phase, of soybean rust (SBR), wheat leaf rust (WLR), common corn rust (CCR), and southern corn rust (SCR), under **A**, May and **B**, July temperature conditions in Indianapolis, IN.

start its buildup in the field according to the rise in temperature from south to north.

Unlike wheat, other crops in this study are usually planted during spring and early summer and harvested in late summer and fall. For such crops, rusts' X_0 values on the newly emerged plants are expected to be zero. However, the time for disease development is much longer compared with winter wheat, harvested from June. Corn is usually planted as early as mid-March in the southern United States. The model suggests that temperature conditions are suitable for common corn rust development in March and are optimum in April and May in Baton Rouge. But, despite the seemingly suitable conditions, common corn rust is usually first detected in the Mississippi delta states from mid- to late May, and in the U.S. Corn Belt, initial epidemic occurs usually in mid-June to mid-July. The southern United States and vicinity is usually suggested as a source region for common corn rust dispersal northward, and the rust infects, during winter, sweet corn grown in southern Florida (28). In both locations, Baton Rouge, a possible common corn rust overwintering area, and Indianapolis, a possible area where rust development is dependent upon urediniospores reaching from the south, a general lag period of 6 weeks and more is found between the time when temperature conditions for development are suitable or when leaf is available to the appearance of the rust in fields. Common corn rust is rarely found very early in the season in northern regions such as in Ontario, Canada, where the rust was observed in 1951 as early as 11 June (20). Regardless of whether the inoculum source for such early incidence is endogenous (through overwintered urediniospores or through aeciospores) or exogenous, common corn rust is normally detected much later in a growing season. However, most corn varieties grown in the Corn Belt have broad-spectrum resistance to common corn rust. This resistance might retard disease development and the time elapsed to a detectable disease incidence. This is not the case with southern corn rust and groundnut rust. Most corn or groundnut varieties grown in the United States are not resistant to the rust of each crop. Nevertheless, a longer lag period was found between time with suitable conditions and southern corn rust comparing to common corn rust in appearance. Model results suggest that average temperature conditions are suitable for southern corn rust from June and optimal in July in Indianapo-

Fig. 5. Calculated soybean rust infection progress curves of hypothetical epidemics, staying in the exponential phase, in four different locations throughout the U.S. soybean-growing region, under temperature conditions of several months during the soybean-growing season. x axis represents days after inoculation and y axis represents the number of infections.

TABLE 5. Rates of disease increase (ρ), for different months at two different locations as affected by temperatures, during the exponential phase of soybean rust under the conditions of two different reports on the effects of temperature on the latent periods (LP) and on increased spores mortality

	May	June	July	August	September
Baton Rouge, LA					
LP according to Kitani and Inoue (15)	1.28	1.31	1.30	1.31	1.32
LP according to Kochman (16)	1.25	1.21	1.18	1.19	1.23
Germination reduced by half when daytime temperatures ^a are $\geq 28.5^{\circ}\text{C}$	1.28	1.22	1.19	1.20	1.32
Both ^b	1.25	1.16	1.14	1.15	1.23
Indianapolis, IN					
LP according to Kitani and Inoue (15)	1.16	1.27	1.32	1.28	1.20
LP according to Kochman (16)	1.14	1.23	1.24	1.23	1.17

^a Mean daytime temperature is estimated as the average of the mean and maximum temperatures.

^b LP values used were from Kochman (16) and spore germination was reduced by half when average monthly daytime temperatures were $\geq 28.5^{\circ}\text{C}$. In Baton Rouge, average monthly daytime temperatures are above 28.5°C between June and August. In Indianapolis, average monthly daytime temperatures are lower than 28.5°C .

lis. Actually, by the time it was first detected, late August and onward in Indiana (34), the conditions are already less suitable for disease development. Like with southern corn rust, modeling results for groundnut rust in Charlotte suggest suitable conditions for the rust from June and optimal conditions in July; however, rust incipience is late in the season, if at all. Both pathogens, although appearing every year, are usually not considered a production problem for early-planted fields in the south, but crop losses might occur in mid- to late-planted fields. Further north, throughout the Corn Belt or in peanut production regions in Georgia and North Carolina, these rusts are not frequently a crop problem.

When environmental conditions are favorable for airborne disease development on a susceptible host, a delay in disease onset is probably due to lack of inoculum. In other words, spore concentration is below a threshold for disease onset. The threshold level should not be a constant value but a variable depending on environmental conditions and the plants growth stage. In our study, only the temperature effect was evaluated, which may have addressed suitability for disease onset early in a season. Future studies to include more factors into a disease simulation model might reduce difference between model predictions and actual disease onset. However, inclusion of leaf wetness duration should not change the modeling results dramatically. At optimum temperatures, the minimal duration of leaf wetness for infection are 4, 3 to 4, 8, 4, and 6 h for wheat leaf rust, common corn rust, southern corn rust, groundnut rust, and soybean rust, respectively (2,6, 18,19,31). In southeastern United States, where rust incipience is expected to be earlier in a season than that in northern regions, and in many other areas across the Corn Belt, relative humidity is usually rather high. For a normal year, the number of days with leaf wetness sufficient for rust infections should be high enough in a crop season for disease development. In North America, soybean rust is predicted to overwinter in parts of Florida, southern Texas, and further south (27). Soybean rust, like southern corn rust and groundnut rust, does not have a known aecial stage. Initial sources for seasonal rust inoculations in the Soybean Belt are expected to be exogenous, presumably like that for southern corn rust and groundnut rust. Accordingly, the gap between the time with highly suitable conditions and incipience in the field is expected to resemble more that of the southern corn rust and groundnut rust than that of common corn rust. The infection index pattern suggested for soybean rust (Fig. 1) resembles more that of southern corn rust and groundnut rust. However, latent period of soybean rust at the beginning of the growing season is much shorter than that of southern corn rust and groundnut rust. Direct implication of model ρ results would suggest that soybean rust will appear in soybean fields in the different regions sometime after common corn rust and before southern corn rust and groundnut rust if the nature of long-distance dispersal is not significantly different. However, more experimental efforts are needed to fur-

ther evaluate the infection efficiency, latent period, and the other components of the monocycle of soybean rust development. If the latent period of the rust established in North America resembles more the results found by Kochman (16), the time with more suitable conditions in the south will narrow to be around May and part of June and again in September, a shorter period for establishment than any of the other rusts compared herein. Moreover, exposure of soybean rust urediniospores to high temperatures, common in southern United States during summer, for several hours may reduce its germination percentage (16) and consequently its infection efficiency. The effect of a narrow window of suitable conditions for the disease in the south on its development in north regions may hinder early rust establishment in the south and consequently its northward spread. In such a scenario, soybean rust in the United States would mainly have a potential to impact yields of late-planted soybean in the south. Evidence from China proposed that soybean rust development would be minimal or cease when daily average temperatures are $\geq 27^{\circ}\text{C}$ (37), and results of Kochman (16) support such a scenario.

The highest ρ value for soybean rust is relatively lower than values for the other rusts examined, in agreement with Sache and Zadoks (32), who calculated lower maximum relative growth rate ($r_{\max}$) to *Phakopsora pachyrhizi* compared with other legume rusts, among them *Puccinia arachidis*. The implication of lower reproduction rate ρ is longer time for the disease to move from zero or trace to a detectable level. The low ρ value is mainly due to the low infection efficiency in this rust (22), and because of its relatively low daily spore production. However, albeit the relatively low ρ values, premature soybeans' leaf defoliation imposed by soybean rust infections at low disease severities (24) and the current lack of resistance or tolerance in commercial varieties emphasizes the destructive potential of that disease.

In summary, despite its simplicity, the general disease model used in our study provides a tool to compare suitability of environmental conditions to the development of different rusts in time over crop a production region in the United States. Our modeling results addressed the potential lag period from a time when conditions are highly suitable for the development of a rust disease to its detection in a field. Such lag periods suggest that when using a general disease model or other disease models, we should take into account the incipience time in a growing season as well as dispersal dynamics to obtain the most likely risk for an airborne disease.

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