X. Li

Iowa State University, Ames, IA 50011

P. D. Esker

University of Wisconsin-Madison, Madison, WI 53706

Z. Pan

St. Louis University, St. Louis, MO 63108

A. P. Dias

Monsanto Company, St. Louis, MO 63167

L. Xue

St. Louis University, St. Louis, MO 63108

X. B. Yang

Iowa State University, Ames, IA 50011

Asian soybean rust (SBR) is caused by *Phakopsora pachyrhizi* Syd. & P. Syd. This disease results in substantial annual economic losses. Researchers in various Asian, South American, and African countries have reported that soybean (*Glycine max* (L.) Merr.) yield losses due to SBR could be as high as 40 to 80% in a field (7,25,26,33,61,71,73). SBR has drawn a great deal of attention and interest from agricultural scientists in the United States since it was reported in South America in 2001 (53,73). This disease is significant in two distinctive ways. First, SBR causes significant yield loss; and second, it is epidemiologically important because of the unique characteristics that define its ecology and risk assessment.

In the past few years, there have been significant increases in our understanding of this pathosystem. The goals of this article are to summarize several aspects of our current knowledge of the different attributes of this pathosystem that may drive epidemics of SBR and to discuss how this research has been integrated across regions.

Uniqueness of the SBR Pathosystem and Its Scientific Value

The SBR pathosystem is interesting and different in several ways. First is the large scale of its geographic distribution. Soybean originated in ancient China and today is one of the most important agricultural commodities in the Western Hemisphere (3,25). It is the world's fourth largest crop by planting area, estimated at 94.9 million hectares in 2007 (Food and Agriculture Organization of the United Nations [FAO]). The disease range of SBR covers the major soybean producing countries (Fig. 1) across very different climatic conditions including tropical, subtropical, and temperate climates on different continents. Most notably, three soybean production regions, China, North America, and South America, all have comparably large soybean production areas encompassing various ge-

ographies. Characteristics of the pathosystem of SBR on these continents can be more specifically addressed in terms of regional configurations of factors such as host distribution, terrain features, and climate that work together to drive SBR epidemics in these regions.

Other factors serve to distinguish SBR from other similar airborne foliar diseases as well. First, the lack of resistance in commercial soybean cultivars and the differences in regions and environments associated with SBR provide researchers with a valuable model system to study how regional conditions affect the dynamics of an airborne disease. The geographic range of both soybean and soybean rust rapidly expanded recently; for example, there have been dramatic increases in soybean hectareage in South America and the movement of *P. pachyrhizi* into this continent. SBR offers researchers opportunities to observe the adaptation of a pathogen in new environments, a valuable example for disease ecology, evolution, and risk assessment. Understanding such aspects of this special model system is not only the key to risk assessment and disease management of SBR, but also benefits researchers working with similar diseases, particularly exotic diseases caused by invasive pests.

In this article, we will emphasize three important aspects of the SBR pathosystem: (i) the characteristics or, in other words, the unique interactions of the pathosystem on different continents; (ii) the importance of SBR in the development of the framework of plant disease risk assessment; and (iii) new ideas and novel techniques applied in the research and management of SBR.

Global Distribution, Economic Importance, and Epidemiology of SBR

SBR was first discovered in Japan, and then identified throughout tropical and subtropical Asia and Oceania in the early twentieth century (7,61). Over several ensuing decades, SBR spread across the globe and was reported in other regions (Fig. 1) (7,10,31,33, 38,44,56,72,73). It was believed that Hurricane Ivan carried *P. pachyrhizi* spores from South America into the United States (29) before it was first detected by Schneider et al. (58) in November 2004.

Corresponding author: X. Li, Iowa State University, Ames, IA 50011;
E-mail: linuslee@iastate.edu

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Historical Reports of Soybean Rust and 2007 Major Soybean Production Countries

Countries with >1,000 kHa soybean area: United States: 30,562; Brazil: 20,638; Argentina: 16,100; China: 8,900; India: 8,550; Paraguay: 2,200; Canada: 1,169

Fig. 1. Soybean planting areas in the world's major soybean producing countries and historical reports of soybean rust caused by *Phakopsora pachyrhizi*.

In the tropical and subtropical areas of southern China where soybean is only a minor crop, SBR has caused severe yield losses (61). For example, the yield losses were at least 10^5 metric tons and 0.2 to 0.3 billion Chinese yuan, about US\$20 to 30 million per year during the 1990s (61).

Soybean is the largest crop by planting area in South America. Production is centered in Brazil, Argentina, and Paraguay (Fig. 2). The Brazilian Cerrado, a savanna-like region, is the world's largest tropical soybean production region. The impact of SBR in South America is well documented even though the disease has only a short history there (31,57,73). SBR has been observed in most of the Cerrado soybean areas with variable epidemic intensities (20,73). In 2003, economic losses in the states of Mato Grosso and Bahia alone were US\$487.3 million, and about 80% of the soybean fields were sprayed twice that year with fungicides costing US\$544 million (73).

Although SBR had been reported in 20 U.S. states, Ontario in Canada (Table 1), and in Mexico (10) by the end of 2009, yield losses in commercial soybean fields in North America have been considered minimal (67). Nevertheless, the annual total number of counties with SBR reports increased steadily over the past 5 years (Table 1). For the Soybean Belt in North America, there are remaining concerns about SBR outbreaks.

Only five resistance genes (*Rpp1*, *Rpp2*, *Rpp3*, *Rpp4*, and *rpp5*) have been identified since the 1980s (4,7,9,18,24). Commercial cultivars resistant to *P. pachyrhizi* are not yet available on the market, and no soybean cultivars with complete resistance to this fungus have been reported. *P. pachyrhizi* infects soybean leaves at any growth stage by urediniospores (Fig. 3), typically resulting in yellowish or brown lesions approximately 1 to 3 mm in size. The lesions can turn into volcano-shaped pustules, mostly on the lower leaf surface during infectious periods (Fig. 4). Dispersal of *P. pachyrhizi* urediniospores produced in the pustules is favored by strong winds, particularly the rapid low-level airflows that transport spores over long distances (29,47,48,51). Severe infections cause premature defoliation in the field, leading to significant yield losses (Fig. 5).

Infection by *P. pachyrhizi* requires a temperature range of 10 to 27°C (optimal 22 to 23°C) and free moisture for more than 6 h

Fig. 2. Soybean plants with heavy infections of soybean rust in a field (left) in contrast to plants that received fungicide protection before infection (right).

from rainfall or dew. Disease development in soybean is favored by temperatures from 17 to 27°C and is suppressed when temperatures exceed 30°C (7,61).

One critical area of SBR research that is not yet well understood is the effects of light on epidemics. Negative phototropism of germ tubes of *P. pachyrhizi* urediniospores and the growth of pustules on the adaxial surface of leaves suggest that light may be adverse to the pathogen (7,34). Urediniospores of *P. pachyrhizi* can be decimated by ultraviolet radiation when they are exposed to solar radiation (28). Dias (14) recently examined disease occurrence in soybeans exposed to different daylight conditions in Florida as well as the relationship between the regional disease level and cloudiness in Brazil and South Africa. Their results indicated that both shorter daylight length and increased cloudiness can significantly favor disease occurrence in the field (14). Field observations in southern China by Tan et al. (61) indicated that the disease was more commonly severe in valleys of mountainous areas, where plants re-

Table 1. Summary of soybean rust occurrence^a in the United States and Canada since the 2005 growing season sorted by the average percentage of counties reporting soybean rust in a state each year

States	County number	2005 ^b	2006	2007	2008	2009	Average ^c	Frequency ^d
Alabama	67	49.3	38.8	59.7	83.6	100.0	66.3	5
Arkansas	75		37.3	44.0	88.0	97.3	53.3	4
Mississippi	82	2.4	11.0	31.7	96.3	100.0	48.3	5
Louisiana	64	3.1	40.6	32.8	51.6	89.1	43.4	5
Georgia	159	22.0	10.7	32.7	47.2	86.2	39.7	5
Florida	67	34.3	35.8	35.8	35.8	34.3	35.2	5
South Carolina	46	50.0	45.7	15.2	34.8	26.1	34.3	5
North Carolina	100	18.0	42.0	6.0	5.0	11.0	16.4	5
Tennessee	95		20.0	7.4	5.3	46.3	15.8	4
Missouri	115		4.3	32.2	0.9	7.8	9.0	4
Virginia	134		13.4	6.7	9.0	11.2	8.1	4
Kentucky	120	0.8	15.0	2.5	3.3	10.8	6.5	5
Illinois	102		7.8	3.9	3.9	18.6	6.9	4
Oklahoma	77			15.6	1.3	7.8	4.9	3
Texas	254	0.4	2.8	10.2	2.0	2.4	3.5	5
Iowa	99			14.1			2.8	1
Kansas	105			8.6		1.0	1.9	2
Indiana	92		6.5	1.1		1.1	1.7	3
Nebraska	93			4.3			0.9	1
Maryland	24				4.2		0.8	1
Total U.S. ^e		138	274	335	387	576		
Ontario, Canada	50			2			0.4	1

^a Data from the United States Department of Agriculture PIPE (<http://sbr.ipmPIPE.org>).

^b Percentage of counties with soybean rust (SBR) reports in that state.

^c Average numbers of counties reporting SBR occurrence in each year.

^d Frequency of SBR occurrences in this state in 2005 to 2009.

^e Total numbers of counties with SBR reports in the United States in that year.

Fig. 3. Morphology and illustration of germination of urediniospores of *Phakopsora pachyrhizi* under a compound microscope. **A**, Germ tube growth after 2 h. **B**, Germ tube growth and differentiation of appressorium of the same urediniospores after 8 h.

ceived less direct sunlight (Fig. 6). Furthermore, in higher-latitude regions where summer daylight is long until late in the season, as in northern China and the northern United States, SBR was usually reported after August (23,40,64). It appears that long daylength and strong solar radiation are not favorable to SBR.

Overwintering of *P. pachyrhizi* requires living hosts and temperatures greater than 4°C (7,61), although the urediniospores can survive short freeze/thaw cycles (32). The pathogen may overwinter in soybean or in alternative hosts, especially kudzu (*Pueraria lobata* (Willd.) Ohwi), as *P. pachyrhizi* can infect many plants in the family Fabaceae (8,46,55,59,61).

Kudzu is primarily a wild plant species native to tropical and subtropical Asia. It is also cultivated in China as an indigenous vegetable and an herbal medicine (Fig. 7). Although it was initially introduced as an ornamental plant and was later used for erosion control, kudzu has now spread across approximately 0.8 million hectares in the southern United States (2). The fast, perennial growth of kudzu and its characteristic dense canopies make it an

Fig. 4. Soybean rust symptoms on a soybean leaflet from a field in Mato Grosso, Brazil.

ideal overwintering host in Argentina, China, and the United States and a very important source of initial inoculum (Fig. 8) (22,31,61).

On a landscape scale, host connectivity refers to the functional linkage of host patches with pathogen dispersal capability, which may have a significant impact on SBR epidemics as well (43,65). In this article, we will give only qualitative descriptions of host connectivity in each region, as more detailed research linking host connectivity to SBR occurrence and spread is yet to be done.

Uniqueness of the SBR Pathosystem on Each Continent

The SBR pathosystems are similar in China, South America, and North America, in that the occurrence of SBR in high latitudes in these regions depends on the source of inoculum in overwintering areas in low latitude tropical zones. Africa and Australia are not

Fig. 5. A soybean field in Mato Grosso, Brazil, showing premature defoliation of plants caused by severe infection with *Phakopsora pachyrhizi*.

compared here because the disease can overwinter throughout soybean production areas on these two continents (49), and the planting areas are very small compared with those on the other three continents.

The basic characteristics of the SBR pathosystem in each region, including soybean distribution, overwintering areas, and regional climates, are summarized in Figures 9 to 11, respectively. Overwintering areas are based on the assessment by Pivonia and Yang (49), who used a general climatic favorability index to estimate the climatic conditions that would enable year-round establishment of SBR. This provided a mechanism to divide each continent into two regions: an overwintering region and a non-overwintering region, as shown by the orange lines (Figs. 9 to 11). Additional detailed discussions differentiating the SBR pathosystem on each continent were then based on the major SBR epidemic-related factors, such as availability and connectivity of major hosts, temperature, rainfall, wind pattern, and solar radiation. The variation of each regional SBR epidemic is characterized not only by each factor, but also by synergistic effects.

Each regional SBR pathosystem has its own features; none is identical to any other. For a quantitatively comparative vision, we synthesized the information of each of these factors within a region to derive a quantified favorability for the disease epidemics (scored on a scale of 1 to 5) based on the authors' experience and understanding of SBR. These scores in Table 2 may help readers compare the regional epidemic potential of SBR and understand its distinctive points on each continent.

China. The majority of soybean fields are on the plains (North China Plain and Northeast China Plain) in northern and northeastern China with highly concentrated planting areas, indicating high connectivity of the host (Fig. 9). In contrast, soybean is a minor crop in central and southern China, where it is planted in patchy fields. These small soybean fields and scattered kudzu patches in the wilderness or in vegetable fields result in localized SBR host connectivity.

Mountains (1,000 to 2,000 m elevation) and hills dominate southern China. Mountain ranges along Guizhou, Hunan, Jiangxi, and Zhejiang provinces protect the south from freezing temperatures by blocking cold surges from Siberia and providing a natural division for the SBR overwintering and non-overwintering regions in China (Fig. 9).

Fig. 6. A typical soybean field in a mountainous area in Yunnan in southern China, where a field usually receives less sunlight due to blocking of ridges than fields on the open plains.

Fig. 7. Cultivated kudzu plants in Guangxi in southern China. Roots are harvested as an indigenous vegetable. Moderate soybean rust infection was detected in this field; however, it was not a problem for these plants.

Tan et al. (61) summarized historical information on SBR in China and outlined three types of regions where SBR occurred either occasionally, frequently, or severely. The regions with frequent and severe occurrences are featured by climate types Cw (subtropical summer rain) and Cr (subtropical wet) (Fig. 9). Overall, these regions are warm with abundant rainfall in the growing season. In the Cr climate region, summers may often be too hot for *P. pachyrhizi* to infect soybean, but they generally allow year-round establishment of SBR, especially development in the early growing season in the overwintering region. For example, in Wuhan (Cr climate region in Figure 9) in early July with mean temperatures reaching 25.5 to 32.8°C, little SBR can occur (61). In Yunnan in the Cw climate region, the maximum monthly mean temperature is 19 to 22°C due to its high elevation, and SBR develops fairly well here except in winter (61). This Cw region is important as an alternative inoculum source in summer because of its cooler weather and ample rainfall brought by moist air from the oceans, as well as its upstream position relative to the prevailing winds (52,61). When weather in the adjacent areas in southern China with Cr climate is unfavorably warm for SBR, this Cw region acts as a reservoir to continuously provide urediniospores for regional SBR epidemics.

In central to northern China with Dc (temperate continental) climate, SBR can be established in summer, but temperature favorability decreases toward the north as local temperatures decrease (52,54). The overall temperature favorability for SBR during the growing season in China is generally high, especially in both the overwintering region and the southern part of the non-overwintering region (areas around Wuhan in Figure 9) (Table 2).

The rainfall pattern in eastern China is dominated by the East Asia monsoon (15), which normally results in a large amount of temporally (2 to 3 months) and spatially concentrated rainfall (Fig.

Fig. 8. A, Young kudzu leaflets with severe soybean rust infections found in a hilly area in Alabama. B, A large kudzu patch in Natchez, MI.

Fig. 9. Distribution of soybean planting areas (45) in China and major climate types with four representative locations over major soybean production regions. The pathogen *Phakopsora pachyrhizi* overwinters in the south. Climate regions are based on W. Rudloff and World Agricultural Outlook Board of the United States Department of Agriculture (54,66).

Fig. 10. Distribution of soybean planting areas (45) in South America and major climate types with three representative locations over major soybean production regions. The pathogen *Phakopsora pachyrhizi* overwinters in the north. Climate regions are based on W. Rudloff and World Agricultural Outlook Board of the United States Department of Agriculture (54,66).

9). The driving forces of the monsoon are high pressures in the oceans which shift seasonally (15). The oceans provide moist air for intensive rainfall, forming a rain belt usually beginning in April or May in southern China. The rain belt then moves northward during summer until it reaches northern China (e.g., Shenyang in

Figure 9). Meanwhile, it weakens due to diminishing moist airflows. Using summarized historical disease information from various locations in southern China, Tan et al. (61) postulated that 150 mm or more of rainfall and 10 to 15 rain days in 1 month may provide the right environment for SBR epidemics, if there is suffi-

Fig. 11. Distribution of soybean planting areas (45) in North America and major climate types with three representative locations over major soybean production regions. The pathogen *Phakopsora pachyrhizi* overwinters in the south. Climate regions are based on W. Rudloff and World Agricultural Outlook Board of the United States Department of Agriculture (54,66).

Table 2. Host availability and environmental favorability^a for soybean rust epidemics in each major soybean production region

Region	Temperature		Rainfall	Light	Dispersal	Overwintering hosts ^b , connectivity	Growing season hosts, connectivity
	Growing season	Winter					
South America – north	4	3	5	4	4	Localized	Connected
South America – south	3	2	3	2	3	Isolated	Connected
North America – south	3	2	3	3	4	Isolated	Localized
North America – north	3	1	2	2	4	N/A	Connected
China – north ^c	3	1	3	2	2	N/A	Connected
China – south	4	3	5	4	2	Isolated	Localized

^a Scale of 1 to 5. High scores represent high favorability: 1, Unfavorable, against disease occurrence in general. 2, Less favorable, allowing disease occurrence at a low level. 3, Moderately favorable, allowing disease occurrence at a moderate level. 4, Favorable, allowing disease occurrence at a high level. 5, Very favorable, allowing disease occurrence at a high level frequently.

^b Including soybean and kudzu, a between-season bridging host. Connected: planted in large areas as a major crop. Localized: planted in small areas locally as a minor crop. Isolated: planted in isolated patchy areas.

^c China – north region has a very large latitude range (25°–48°N). Scores can be considered averaged values over this latitude range. Generally, favorability of the five environmental factors is higher in the south (central China) and lower in the north (northern and northeastern China) of this region.

cient initial inoculum. Such a rainfall condition is quite common in southern to central China during the rainy season, as shown in Figure 9. However, it is not uncommon that after the rain belt moves out, the dominating high pressures may cause summer droughts, which may persist for weeks. This spell of dry and hot weather may hamper the disease progress of SBR (61).

In China, prevailing winds during the growing season are from the south. Typhoons can occur frequently in summer in southern China. They cause strong turbulence in the canopy, which en-

hances the escape and dispersal of airborne pathogens. While these winds do have the potential to facilitate rapid inoculum movement from the south to central and northern China, two factors may limit the inter-regional dispersal of *P. pachyrhizi*: (i) the role of the mountains in blocking inoculum-carrying airflows and (ii) the rain belt. Pan et al. (47) suggested that low-level airflows around 1,000 m in height are very important for spore dispersal of *P. pachyrhizi* based on their meteorological model simulations. These low-level airflows can be blocked by the mountains in southern China, par-

ticularly those in an east-west orientation. Thus, the mountain ranges act as a barrier against inter-regional spore dispersal as they keep cold air masses separated into regions. Although there is no direct evidence, the fact that SBR usually is observed in central China after the monsoon peak (Wuhan in Figure 9; 61) implies that the spatially concentrated rain belt may act like a filter reducing inter-regional spore dispersal. Rainfall removes fungal spores from the air efficiently (21,41). Recent work by Li et al. (41) showed that 10 min of rainfall at a rate of 5 mm/h was able to remove 50% of SBR urediniospores much faster than dry deposition. Overall, the synergy of the geographic features and monsoon weather are not favorable for a rapid inter-regional epidemic of SBR in China; gradual or localized epidemics are more the norm.

Governed by the solar declination, summer daylight length in southern China is shorter than it is in the north, and light intensity is often weakened by cloudy skies in the Inter-Tropical Convergence Zone (ITCZ). The ITCZ shifts from north to south following seasonal changes in solar declination and is characterized most notably by cloud cover year-round as viewed by satellite imagery (52). This cloudy zone provides favorable light conditions for SBR occurrence. The major soybean production regions in northern and northeastern China naturally have more unfavorable light conditions because of longer daylight length and less cloudy conditions.

South America. As soybean is the largest crop by planting area in South America, host connectivity is very high (Fig. 10). The majority of the Cerrado region, in which most of Brazil's soybeans are produced, is on the Brazilian central plateau, stretching into Paraguay as well, with altitudes ranging from 200 to 1,300 m. Argentina's soybean production region is also dominated by plains with high host connectivity during the growing season.

The climates are Aw (tropical wet and dry) in most Brazilian tropical regions; Cr in southern Brazil, northeastern Argentina, and Paraguay; and BS (steppe) in central Argentina (Fig. 10). Being in the tropical zone, the Cerrado region has only small temperature variations across seasons (illustrated for Goiania in Figure 10), and soybean can grow in winter (June to August). The average winter temperature is approximately 20°C, which is relatively favorable for *P. pachyrhizi* infection; thus, SBR can overwinter either in commercial fields or on volunteer plants. The areas or regions around southern Brazil and Paraguay, as shown by the temperature pattern in Puerto Stroessner, also have a mild winter, favoring year-round occurrence of SBR.

In Argentina, temperatures are much less favorable for either *P. pachyrhizi* overwintering or disease development in summer because of cooler weather (illustrated by Rosario in Figure 10). Thus, the overall temperature favorability for regional epidemics of SBR in the overwintering and non-overwintering regions in South America is high and moderate, respectively (Table 2).

Rainfall in the Cerrado region is dominated by the ITCZ. In austral summer (December to February), abundant rainfall persists along latitude 15°S in the central Cerrado (19,52). Such cloudy and rainy weather favors SBR development. In the Cerrado in the winter, there is a very dry period due to descending airflows when the ITCZ shifts to the north. This dry period is unfavorable for SBR epidemics. In contrast, in southern Brazil, the rainfall pattern is relatively uniform (e.g., a wetter winter in Puerto Stroessner in Figure 10), and also the amount of rainfall in summer is generally favorable for disease epidemics according to the proposed favorable condition of >150 mm rainfall in 1 month in China (61). Thus, with synergistic favorability of both temperature and rainfall in this region, SBR outbreaks could be severe (73). As the temperatures are generally in a relatively favorable range for SBR in Brazil, availability of rainfall seemed more important given the dry season in some areas of the Cerrado. Del Ponte et al. (13) examined the severity of SBR associated with monthly rainfall during the growing season in Brazil and developed an SBR forecast model using rainfall as the predictive factor. In total, rainfall during the growing seasons in Brazil's SBR overwintering region is highly favorable for disease epidemics. In contrast to Brazil, in Argentina's non-overwintering region of SBR, e.g., the rainfall pattern in Rosario,

there is much less rainfall in summer, which is not favorable for SBR epidemics (scored 3 in Table 2).

The winds in South America also shift following the ITCZ. In January, winds of moderate intensity from the northeast prevail between the equator and 30°S in eastern South America (19,52). Without blockage by mountains, the South American geographical features (31,47,73) seem to provide more opportunities for inter-regional spore dispersal of *P. pachyrhizi* than those in southern China.

Summer daylight length in Brazil is generally short compared to that in high-latitude regions in Argentina. Considering the extensive cloudiness in the ITCZ that further reduces solar radiation, light conditions in Brazil, which are similar to those in southern China, should be relatively favorable for SBR. Thus, the prevailing winds and cloudiness further increase the risks of SBR outbreaks in Brazil. As latitude increases, summer daylight length is much longer in Argentina, leading to unfavorable conditions for SBR.

North America. The North American SBR pathosystem also has an overwintering and a non-overwintering region (Fig. 11). However, this overwintering region is much smaller than those in South America and China (Figs. 9 and 10). In spite of this difference, similarities are found between North America and China in deployment of soybean production (i.e., major soybean production areas are in the north in both regions), availability of the major nonsoybean host, kudzu, and climates.

First, host connectivity in the North American Soybean Belt is undoubtedly high. Recent quantitative analysis of the connectivity of soybean in the United States by Margosian et al. (43) using graph theory and geographical information system techniques further confirmed this. Along the lower Mississippi River Valley, there are highly concentrated soybean planting areas. However, most of the other areas in the southern United States and Mexico have only localized soybean planting areas. It would follow that these localized soybean fields probably provide only limited bridging sources of the inoculum. Some localized kudzu patches enable overwintering of *P. pachyrhizi* in various locations in Alabama, Florida, and Louisiana (USDA data on <http://sbr.ipmPIPE.org/>; 32).

The climate type in the southern United States east of the Rocky Mountains is Cr, which is the same as that in southeastern China. In the north, climate type is Dc, which matches the climate type of northern China. A substantial difference between China and North America in terms of climate regions is the absence of a Cw climate region in the latter.

High temperatures in the southern United States and Mexico may enable early occurrence of SBR in wild hosts before soybean is planted. However, hot weather (e.g., Lafayette in June in Figure 11) may impede disease development in early summer. The Cw region in China acts as an alternative spore source during summer when disease development is limited due to high temperatures in adjacent areas, whereas in North America, there is no large alternative region to provide inoculum. Therefore, SBR development in the southern United States and Mexico may be more sensitive to hot weather, reducing the available inoculum that could spread northward. Temperatures in the northern United States and Canada are generally too low to allow rapid development of SBR until June even if a considerable amount of *P. pachyrhizi* inoculum is available. The combination of temporal-spatial patterns of temperatures in North America is relatively less favorable for inter-regional epidemics of SBR compared to China and South America (Fig. 11 and Table 2).

North America differs from China in rainfall patterns as shown in Figure 11. There is no dominating monsoon system as strong as the East Asia monsoon in eastern North America. Generally, the amount of rainfall decreases from east to west and south to north (52). Although North American summers usually have more rainfall than other seasons, it is not as concentrated as in China (Fig. 9), leading to lower probabilities of favorable monthly rainfall conditions (>150 mm). Even though summer temperatures in southern China may be as high as the temperatures in the southern United States and Mexico, a 1- or 2-week continuous rainfall during monsoon season can provide tremendous relief of the high

summer temperatures impeding SBR and can favor local disease development (61), which is a less-frequent condition in North America. Using an empirical disease model based on monthly rainfall and rain days in various locations in central China (61), Li (39) estimated the frequency of the years (1951 to 2000) in which June or July had favorable monthly rainfall conditions for SBR in the United States. Over this 50-year period, only a limited region in the southeastern United States (Florida and part of Georgia, Alabama, South Carolina, and Mississippi) had 20 to 30 years of favorable rainfall conditions in June or July (39). The Soybean Belt only had about 10 to 15 favorable years (39). North America, particularly the Soybean Belt, seems to have lower rainfall favorability compared with China, including its northern region and extending to South America. The other source of free moisture for *P. pachyrhizi* infection, dew, is common in fields during the growing season and should help disease development (7,61,70). No solid information is available to show the essential effects of dew on regional SBR epidemics. Further precise measurement of dew in a field is still problematic.

Geographical features present another major difference between North America and China. In contrast to mountainous southern China, the plains east of the Rocky Mountains provide a smooth underlying surface, which favors the low-level airflows carrying fungal spores to reach the inland regions (5,51). It has been well documented that this geographical feature and the prevailing winds in the summer have been responsible for long-distance dissemination of many airborne pathogens, e.g., the wheat rusts (17). Pan et al. (47,48) and Isard et al. (29) have pointed out this favorability for SBR as well.

In the northern soybean production areas of North America, SBR usually has been observed in late season since 2005 (23,35,40,64). Even in the southeastern United States, the disease has not increased exponentially until late August (11). Recently, Barnes et al. (1) reported that SBR spores were collected in rainfall from all the states across the Midwest and the eastern United States in 2005 and 2006. The numbers of spores had a bimodal pattern with two peaks in May and August in both years (1). According to the climate data in Figure 11, temperatures in the Soybean Belt in June and July can reach a level generally favorable for SBR establishment. Given the fact that the summer daylight length is long in the high-latitude regions of North America, if neither temperature nor spore dispersal limit SBR spread, such late-season SBR increases may be associated with suppression of the disease by long daylight length in June and July, similar to the field observations in northern China and Argentina (31,61).

SBR and Plant Disease Risk Assessment

Over the past few decades, risk assessment of SBR has received a great amount of attention, making it a potentially important model system for risk assessment of airborne plant diseases (6,16,37,48,62,68,69). The earliest research on the risk of SBR to the U.S. soybean industry can be traced back to the 1970s, when the International Working Group on Soybean Rust was formed to deal with the possibility of global SBR spread. In 1984, Kuchler et al. (37) estimated that the possible overall economic losses due to severe SBR epidemics in the United States might be up to \$7.2 billion/year. In the 1980s and 1990s, many Asian plant pathologists initiated ongoing research focused on critical components of the biology, pathology, epidemiology, and disease management of SBR, which has provided valuable information for subsequent research (60,61).

More information on this topic was made available when SBR was found in the Western Hemisphere. In the United States, researchers warned of the possibility of its arrival in the early 2000s (44,47,49). Right before SBR reached the continental United States, possible *P. pachyrhizi* spore routes were examined, which identified the possibility of SBR introduction into this region by hurricanes (47). Pivonia and Yang (49) identified the possible permanent SBR establishment region on this continent using general climatic favorability.

Because *P. pachyrhizi* has been observed to overwinter in southern North America since 2005, dispersal of the pathogen's initial inoculum to the north received much attention from several research groups that used meteorological models such as the regional climate model (MM5) and the particle dispersion model (HYbrid Single Particle Lagrangian Integrated Trajectory, HYSPLIT) (29,36,48). Pivonia and Yang (50) used a generalized disease model to compare SBR with five other rusts, including common corn rust (causal pathogen *Puccinia sorghum*) and southern corn rust (causal pathogen *Puccinia polysora*), based on their temperature attributes and climatic data from representative locations in the Midwest. They suggested that the seasonal appearance time of SBR might be between that of common corn rust and southern corn rust (50). Li (39) and Li and Yang (42) continued to assess the overall risk of SBR outbreaks in the United States based on comparisons of two aspects: (i) SBR compared with other soybean fungal diseases according to ecological and biological attributes; and (ii) SBR compared with other rusts in the United States using their temperature attributes and regional climatic temperatures. Their work suggested that the disease range of SBR may reach farther north into Minnesota and Wisconsin in years with favorable weather conditions, but the possibility of a severe outbreak in the north-central region is low. However, the disease may cause significant yield losses in the southeastern United States when weather is ideal for epidemics (39,42). Today, the risk of SBR seems to be less than people previously thought before the disease was first detected in 2004 in Louisiana, but an uncertainty exists because of the changing climates and possible adaptation of the pathogen to North American environments.

New Management Techniques in the United States

Two new SBR management techniques in the United States are remarkable and promising for the future: (i) the PIPE (Pest Information Platform for Extension and Education); and (ii) inter-regional pathogen dispersal and real-time disease risk forecast. The PIPE was established in 2006 in coordination with a nationwide SBR monitoring program (30). Because coordinated teams across many states working on SBR scouting, diagnosis, extension, and forecast have made this system a success, information on other pests such as soybean aphids has been recently incorporated. With future expansion, this system may provide a prototype for development of a more general and powerful pest management information system.

Another remarkable technological improvement in SBR management has been the development of long-distance spore dispersal and disease risk forecasts on the basis of modern aerobiological models and mesoscale weather forecasts. Assessing the long-distance dispersal of *P. pachyrhizi* is a key component of understanding the risk of SBR epidemics in the north. Given a source location where *P. pachyrhizi* spores are produced, their long-distance dispersal process can be modeled by the HYSPLIT model with input of either regional observational weather data or forecast data from a mesoscale weather modeling system (29,48). Driven by high-resolution weather data, the modeling of long-distance dispersal of *P. pachyrhizi* enables us to further assess the risk of disease occurrence in particular counties where the spores may land. Because weather is the primary environmental condition driving the local epidemics, the risk of SBR can be addressed by spore dispersal in conjunction with weather favorability for disease development. This approach to SBR forecast has been deployed since 2005 and was found to successfully predict disease occurrence in Iowa in 2007 (13,40).

Summary and Future Challenges

There have been substantial gains in our knowledge of the risk of SBR across continents after decades of work. Collectively, we can classify SBR as a tropical disease with a seasonal range extending into temperate zones. The pathogen, *P. pachyrhizi*, may have co-evolved with soybean, as well as kudzu, which both originated in tropical regions of Asia (63). The disease adapts to a tropi-

cal environment where there is little distinct temperature difference between summer and winter (53).

Efforts by many are directed toward quantification and modeling of the soybean rust pathosystem with consideration of different environmental and meteorological factors (11,50,61,70). Del Ponte and Esker (12) recently integrated published research to develop a system-based approach for risk assessment of SBR based on environmental factors. On a continental scale, it is still problematic to model a regional soybean rust pathosystem with incorporation of all factors and to compare these factors to each other.

In spite of the significant progress toward better understanding of SBR, there is still a lack of information on how the canopy affects disease development, including temperature variability within the canopy, aerobiological aspects of spore release, long-distance dispersal, and effects of dew in SBR forecasting (12). It may be reasonable to hypothesize that conditions for long-distance dispersal of *P. pachyrhizi* in North America are more favorable than conditions in China, but quantitative comparisons are needed. These are not necessarily new discussions, as many of these components have been recognized as important for some time (21). Therefore, further integration of different meteorological and physical approaches is needed.

The earth has been experiencing a warming stage since the 1970s, especially in high-latitude regions during the night (27). Rainfall also has increased in the northern United States (27). Changes in both temperatures and rainfall seem to lead toward a possible increase of SBR in the North American soybean production regions. Late-season occurrences of SBR in the Soybean Belt have limited potential to cause yield losses; however, if the temperatures are warmer in the early growing season, e.g., May, the strong low-level airflows carrying urediniospores of *P. pachyrhizi* may lead to an early establishment of SBR in this region. With the foreseeable impacts from global warming, our present understanding of SBR risks needs to be updated to face future challenges. Systematic research on this pathosystem should continue to help us better understand the epidemiology, ecology, and risk assessment of SBR in warming climates.

Literature Cited

- Barnes, C. W., Szabo, L. J., and Bowersox, V. C. 2009. Identifying and quantifying *Phakopsora pachyrhizi* spores in rain. *Phytopathology* 99:328-338.
- Blaustein, R. J. 2001. Kudzu's invasion into southern United States life and culture. Pages 55-62 in: *The Great Reshuffling: Human Dimensions of Invasive Species*. J. A. McNeely, ed. The World Conservation Union, IUCN, Gland, Switzerland and Cambridge, UK.
- Boerma, H. R., and Specht, J. E., eds. 2004. *Soybeans: Improvement, Production, and Uses*. 3rd ed. American Society of Agronomy, Inc.; Crop Science Society of America, Inc.; Soil Science Society of America, Inc., Madison, WI.
- Bonde, M. R., Nester, S. E., Austin, C. N., Stone, C. L., Frederick, R. D., Hartman, G. L., and Miles, M. R. 2006. Evaluation of virulence of *Phakopsora pachyrhizi* and *P. meibomia* isolates. *Plant Dis.* 90:708-716.
- Borchert, J. R. 1950. The climate of the central North American grassland. *Ann. Assoc. Am. Geographers* 40:1-39.
- Bromfield, K. R. 1980. Soybean rust - Some considerations relevant to threat analysis. *Prot. Ecol.* 2:251-257.
- Bromfield, K. R. 1984. Soybean Rust. Monogr. No. 11. American Phytopathological Society, St. Paul, MN.
- CAB International. 2008. *Crop Protection Compendium*. CABI. Online publication.
- Calvo, É. S., de Souza Kiihl, R. A., Garcia, A., Harada, A., and Hiromoto, D. M. 2008. Two major recessive soybean genes conferring soybean rust resistance. *Crop Sci.* 48:1350-1354.
- Cárcano Rodríguez, A., Aguilar Rios, J., and Hernández, J. R. 2006. First report of Asian soybean rust caused by *Phakopsora pachyrhizi* from Mexico. *Plant Dis.* 90:1260.
- Christiano, R. S. C., and Scherm, H. 2007. Quantitative aspects of the spread of Asian soybean rust in the southeastern United States, 2005 to 2006. *Phytopathology* 97:1428-1433.
- Del Ponte, E. M., and Esker, P. D. 2008. Meteorological factors and Asian soybean rust epidemics - A systems approach and implications for risk assessment. *Sci. Agric.* 65:88-97.
- Del Ponte, E. M., Godoy, C. V., Li, X., and Yang, X. B. 2006. Predicting severity of Asian soybean rust epidemics with empirical rainfall models. *Phytopathology* 96:797-803.
- Dias, A. P. S. 2007. Epidemiological studies of shading effects on Asian soybean rust. Ph.D. thesis. Iowa State University, Ames.
- Ding, Y. H., Wang, H. J., and Wang, B. 2005. East Asian monsoon: East Asia. In: *The Global Monsoon System: Research and Forecast*. Rep. Int. Comm. 3rd Int. Workshop Monsoons (IWM-III), Hangzhou, China. WMO/TD No. 1266 (TMRP Report No. 70). C. P. Chang, B. Wang, and N. C. G. Lau, eds. Secretariat of the World Meteorological Organization, Geneva, Switzerland.
- Dowler, W. M., and Bromfield, K. R. 1983. Potential disease problems for United States agriculture - Soybean rust. *Phytopathology* 73:782.
- Eversmeyer, M. G., and Karmer, C. L. 2000. Epidemiology of wheat leaf and stem rust in the central great plains of the USA. *Annu. Rev. Phytopathol.* 38:491-513.
- García, A., Calvo, É. S., de Souza Kiihl, R. A., Harada, A., Hiromoto, D. M., and Vieira, L. G. E. 2008. Molecular mapping of soybean rust (*Phakopsora pachyrhizi*) resistance genes: Discovery of a novel locus and alleles. *Theor. Appl. Genet.* 117:545-553.
- García, N. O. 1994. South American climatology. *Quaternary Int.* 21:7-27.
- Godoy, C. V., Yorinori, J. T., and Paiva, W. M. 2006. Overview of soybean rust in South America during 2005-2006. In: *Proc. 2006 Nat. Soybean Rust Sympos.* American Phytopathological Society, St. Paul, MN.
- Gregory, P. H. 1973. *The Microbiology of the Atmosphere*. John Wiley & Sons, New York.
- Harmon, P. F., Momol, M. T., Marois, J. J., Dankers, H., and Harmon, C. L. 2005. Asian soybean rust caused by *Phakopsora pachyrhizi* on soybean and kudzu in Florida. *Plant Health Progress* 2005:1-4.
- Hartman, G. L., Hines, R. A., Faulkner, C. D., Lynch, T. N., and Pataky, N. 2007. Late season occurrence of soybean rust caused by *Phakopsora pachyrhizi* on soybean in Illinois. *Plant Dis.* 91:466.
- Hartman, G. L., Miles, M. R., and Frederick, R. D. 2005. Breeding for resistance to soybean rust. *Plant Dis.* 89:664-666.
- Hartman, G. L., Sinclair, J. B., and Rupe, J. C., eds. 1999. *Compendium of Soybean Diseases*. 4th ed. American Phytopathological Society, St. Paul, MN.
- Hartman, G. L., Wang, T. C., and Tschanz, A. T. 1991. Soybean rust development and the quantitative relationship between rust severity and soybean yield. *Plant Dis.* 75:596-600.
- IPCC. 2007. Summary for policymakers. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the 4th Assessment Report of the Intergovernmental Panel on Climate Change*. S. D. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, eds. Cambridge University Press. Cambridge, UK.
- Isard, S. A., Dufault, N. S., Miles, M. R., Hartman, G. L., Russo, J. M., De Wolf, E. D., and Morel, W. 2006. The effect of solar irradiance on the mortality of *Phakopsora pachyrhizi* urediniospores. *Plant Dis.* 90:941-945.
- Isard, S. A., Gage, S. H., Comtois, P., and Russo, J. M. 2005. Principles of the atmospheric pathway for invasive species applied to soybean rust. *BioScience* 55:851-861.
- Isard, S. A., Russo, J. M., and DeWolf, E. D. 2006. The establishment of a national Pest Information Platform for Extension and Education. *Plant Health Progress* 2006:1-4.
- Ivanovich, A. 2005. Soybean rust in Argentina. *Plant Dis.* 89:667-668.
- Jurick, W. M., II, Narvaez, D. F., Brennan, M. M., Harmon, C. L., Marois, J. J., Wright, D. L., and Harmon, P. F. 2008. Winter survival of the soybean rust pathogen, *Phakopsora pachyrhizi*, in Florida. *Plant Dis.* 92:1551-1558.
- Kawuki, R. S., Adipala, E., and Tukamuhawa, P. 2003. Yield loss associated with soybean rust (*Phakopsora pachyrhizi* Syd.) in Uganda. *J. Phytopathol.* 151:7-12.
- Koch, E., and Hoppe, H. H. 1987. Effect of light on uredospore germination and germ tube growth of soybean rust (*Phakopsora pachyrhizi* Syd.). *J. Phytopathol.* 119:64-74.
- Koenning, S. R., Frye, J. W., Butler, S. C., and Creswell, T. C. 2007. First report of *Phakopsora pachyrhizi* on kudzu (*Pueraria montana* var. *lobata*) in North Carolina and increased incidence of soybean rust on soybean in 2006. *Plant Dis.* 91:637.
- Krupa, S., Bowersox, V., Claybrooke, R., Barnes, C. W., Szabo, L., Harlin, K., and Kurl, J. 2006. Introduction of Asian soybean rust urediniospores into the Midwestern United States—A case study. *Plant Dis.* 90:1254-1259.
- Kuchler, F., Duffy, M., Shrum, R. D., and Dowler, W. M. 1984. Potential economic consequences of the entry of an exotic fungal pest: The case of soybean rust. *Phytopathology* 74:916-920.
- Levy, C. 2005. Epidemiology and chemical control of soybean rust in Southern Africa. *Plant Dis.* 89:669-674.
- Li, X. 2007. Soybean rust in the United States: Assess its potential epidemic ranges and frequency based on disease limiting factors, disease attributes, and comparative epidemiology. Ph.D. thesis. Iowa State University, Ames.
- Li, X., Engelbrecht, C. J., Mueller, D. S., and Yang, X. B. 2008. First report of soybean rust caused by *Phakopsora pachyrhizi* in Iowa and its statewide occurrence. *Plant Dis.* 92:975.
- Li, X., Mo, J. Y., Guo, T. X., and Yang, X. B. 2009. Estimation of soybean

- rust uredospore terminal velocity, dry deposition, and the wet deposition associated with rainfall. *Eur. J. Plant Pathol.* 123:377-386.
42. Li, X., and Yang, X. B. 2009. Similarity, pattern, and grouping of soybean fungal diseases in the United States: Implications for the risk of soybean rust. *Plant Dis.* 93:162-169.
 43. Margosian, M. L., Garrett, K. A., Hutchinson, J. M. S., and With, K. A. 2009. Connectivity of the American agricultural landscape: Assessing the national risk of crop pest and disease spread. *BioScience* 59:141-151.
 44. Miles, M. R., Frederick, R. D., and Hartman, G. L. 2003. Soybean rust: Is the U.S. soybean crop at risk. American Phytopathological Society. Online publication.
 45. Monfreda, C., Ramankutty, N., and Foley, J. A. 2008. Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global biogeochemical cycles* 22:GB1022, doi:10.1029/2007GB002947.
 46. Ono, Y., Buriticá, P., and Hennen, J. F. 1992. Delimitation of *Phakopsora*, *Physopella* and *Cerotelium* and their species on *Leguminosae*. *Mycol. Res.* 96:825-850.
 47. Pan, Z., Pivonia, S., Pasken, R., Pietrowicz, J., and Yang, X. B. 2004. Simulation of airborne dispersal potentials of soybean rust from Africa to South America and from South America to North America. (Abstr.) *Phytopathology* 94:S80.
 48. Pan, Z., Yang, X. B., Pivonia, S., Xue, L., Pasken, R., and Roads, J. 2006. Long-term prediction of soybean rust entry into the continental United States. *Plant Dis.* 90:840-846.
 49. Pivonia, S., and Yang, X. B. 2004. Assessment of the potential year-round establishment of soybean rust throughout the world. *Plant Dis.* 88:523-529.
 50. Pivonia, S., and Yang, X. B. 2006. Relating epidemic progress from a general disease model to seasonal appearance time of rusts in the United States: Implications for soybean rust. *Phytopathology* 96:400-407.
 51. Pivonia, S., Yang, X. B., and Pan, Z. 2005. Assessment of epidemic potential of soybean rust in the United States. *Plant Dis.* 89:678-682.
 52. Robinson, P. J., and Henderson-Sellers, A. 1999. *Contemporary Climatology*. 2nd ed. Pearson Education Limited, New York.
 53. Rossi, R. L. 2003. First report of *Phakopsora pachyrhizi*, the causal organism of soybean rust in the Province of Misiones, Argentina. *Plant Dis.* 87:102.
 54. Rudloff, W. 1981. *World-climates*. Wissenschaftliche Verlagsgesellschaft, Stuttgart, Germany.
 55. Rytter, J. L., Dowler, W. M., and Bromfield, K. R. 1984. Additional alternative hosts of *Phakopsora pachyrhizi*, causal agent of soybean rust. *Plant Dis.* 68:818-819.
 56. Sathe, A. V. 1972. Identity and nomenclature of soybean rust from India. *Curr. Sci.* 41:264-265.
 57. Scherm, H., Christiano, R. S. C., Del Ponte, E. M., Esker, P. D., and Godoy, C. V. 2007. Meta-analysis of fungicide efficacy trials against Asian soybean rust in Brazil. In: *Proc. 2007 Nat. Soybean Rust Sympos.* American Phytopathological Society. Online publication.
 58. Schneider, R. W., Hollier, C. A., Whitman, H. K., Palm, M. E., McKemy, J. M., Hernandez, J. R., Levy, L., and DeVries-Paterson, R. 2005. First report of soybean rust caused by *Phakopsora pachyrhizi* in the continental United States. *Plant Dis.* 89:774.

X. Li

P. D. Esker

Z. Pan

A. P. Dias

L. Xue

X. B. Yang

Dr. Li received bachelor's and master's degrees in plant pathology in 1997 and 2000 from China Agricultural University. He joined Dr. X. B. Yang's lab at Iowa State University in 2002 and received his Ph.D. in 2007. Since 2004, he has been working on the risk assessment, disease scouting, and forecast of soybean rust in the United States. He is currently a postdoctoral research associate in Dr. Yang's lab working in interdisciplinary areas such as disease evolution driven by climate changes, forecast of pathogen long-distance dissemination, and disease ecology.

Dr. Esker is an assistant professor and extension field crops plant pathologist within the Department of Plant Pathology at the University of Wisconsin in Madison. Dr. Esker received a degree in genetics and bacteriology from the University of Wisconsin, and a master of science degree from Iowa State University in plant pathology. He received his Ph.D. from Iowa State University with a co-major in plant pathology and statistics. His program emphasizes increasing the understanding of how plant pathogens affect field crop production through a systems approach.

Dr. Z. Pan is an associate professor in atmospheric science at the Department of Earth and Atmospheric Sciences, Saint Louis University. He received his Ph.D. in water resources/atmospheric science in 1996 from Iowa State University, where he continued to work as a postdoctoral researcher before joining Saint Louis University in 2003. His main research interests include regional climate change, aerial pathogen transport, and land surface-atmosphere interactions.

Dr. Dias is currently the lead scientist of the Northern Corn Pathology program at Monsanto. She received a Ph.D. in

plant pathology with a minor in statistics at Iowa State University, working on extensive research of light effects on soybean rust in 2007. Her studies were on the keys to understanding the negative impact of solar light on soybean rust development. Her previous degrees were received from Universidade Federal de Viçosa in Brazil, on agricultural meteorology (M.S.) and agronomy (B.S.). Dr. Dias's major interest has been epidemiology and modeling of plant diseases, particularly the relationships among host, pathogen, and climate, in order to explain epidemic development.

Dr. Xue obtained his Ph.D. in meteorology from Saint Louis University in September 2009. He is currently a postdoctoral fellow in the advanced study program at the National Center for Atmospheric Research. He joined Dr. Pan's group in 2004 and started working on soybean rust forecasting in 2005. His research interests cover the long-term and long-range transport and dispersion of airborne particles, the interaction between biogenic aerosols and clouds, and cloud microphysics.

Dr. Yang is a professor at Iowa State University in plant pathology. He obtained his B.A. and M.S. degrees from China Agricultural University and his Ph.D. in plant pathology in 1989 from Louisiana State University. Dr. Yang is a pioneer in plant disease risk assessment, the impact of climate change on plant diseases, and large-scale patterns of disease occurrence in time and space. His program is mainly focused on the research and extension of major soybean diseases such as sudden death syndrome, frogeye leaf spot, white mold, Rhizoctonia root rot, charcoal rot, and soybean rust and their management. He is a Fellow of the American Phytopathological Society.

59. Slaminko, T. L., Miles, M. R., Frederick, R. D., Bonde, M. R., and Hartman, G. L. 2008. New legume hosts of *Phakopsora pachyrhizi* based on greenhouse evaluations. *Plant Dis.* 92:767-771.
60. Tan, Y. J., Wang, Y. T., Yang, Y. D., and Yu, Z. L., eds. 1994. The Advance of Soybean Rust Research. Hubei Science and Technology Press, Wuhan, China.
61. Tan, Y. J., Yu, Z. L., and Yang, C. Y. 1996. Soybean Rust. China Agriculture Press, Beijing, China.
62. Teng, P. S., and Yang, X. B. 1993. Biological impact and risk assessment in plant pathology. *Annu. Rev. Phytopathol.* 31:495-521.
63. Wang, J. L., ed. 1982. Soybean. Heilongjiang Science and Technology Press, Haerbin, China.
64. Watson, S. R., Giesler, L. J., Ziemas, A. D., and Brovont, T. E. 2008. First report of soybean rust caused by *Phakopsora pachyrhizi* in Nebraska. *Plant Dis.* 92:1588.
65. With, K. A., Gardner, R. H., and Turner, M. G. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78:159-169.
66. World Agricultural Outlook Board. 1994. Major World Crop Areas and Climatic Profiles. U.S. Dep. Agric. Agric. Handb. No. 664.
67. Wrather, J. A., and Koenning, S. R. 2006. Estimates of disease effects on soybean yields in the United States 2003 to 2005. *J. Nematol.* 38:173-180.
68. Yang, X. B. 2006. Framework development in plant disease risk assessment and its application. *Eur. J. Plant Pathol.* 11:25-34.
69. Yang, X. B., Dowler, W. M., and Royer, M. H. 1991. Assessing the risk and potential impact of an exotic plant disease. *Plant Dis.* 75:976-982.
70. Yang, X. B., Dowler, W. M., and Tschanz, A. T. 1991. A simulation model for assessing soybean rust epidemics. *J. Phytopathol.* 133:187-200.
71. Yeh, C. C., and Yang, C. Y. 1975. Yield loss caused by soybean rust, *Phakopsora pachyrhizi*. *Plant Prot. Bull. [Taiwan]* 17:7-8.
72. Yorinori, J. T. 2004. Soybean rust: General overview. In: Proceedings of VII World Soybean Research Conference, IV International Soybean Processing and Utilization Conference, III Congresso Brasileiro de Soja (Brazilian Soybean Congress), Foz do Iguaçu, PR, Brazil.
73. Yorinori, J. T., Paiva, W. M., Frederick, R. D., Costamilan, L. M., Bertagnolli, P. F., Hartman, G. E., Godoy, C. V., and Nunes-Jr., J. 2005. Epidemics of soybean rust (*Phakopsora pachyrhizi*) in Brazil and Paraguay from 2001 to 2003. *Plant Dis.* 89:675-677.