Quantitative Aspects of the Spread of Asian Soybean Rust in the Southeastern United States, 2005 to 2006

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ABSTRACT

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The regional dynamics of soybean rust, caused by *Phakopsora pachyrhizi*, in six southeastern states (Florida, Georgia, Alabama, South Carolina, North Carolina, and Virginia) in 2005 and 2006 were analyzed based on disease records collected as part of U.S. Department of Agriculture's soybean rust surveillance and monitoring program. The season-long rate of temporal disease progress averaged ≈ 0.5 new cases day⁻¹ and was higher in nonsentinel soybean (*Glycine max*) plots than in sentinel soybean plots and kudzu (*Pueraria lobata*) plots. Despite the early detection of rust on kudzu in January and/or February each year (representing the final phase of the previous year's epidemic), the disease developed slowly during the spring and early summer on this host species and did not enter its exponential phase until late August, more than 1 month after it did so on soybean. On soybean, cases occurred very sporadically before the beginning of July, after which their number increased rapidly. Thus, while kudzu likely provides the initial inoculum for epidemics on soybean, the

rapid increase in disease prevalence on kudzu toward the end of the season appears to be driven by inoculum produced on soybean. Of 112 soybean cases with growth stage data, only one occurred during vegetative crop development while $\approx 75\%$ occurred at stage R6 (full seed) or higher. The median nearest-neighbor distance of spread among cases was ≈ 70 km in both years, with 10% of the distances each being below ≈ 30 km and above ≈ 200 km. Considering only the epidemic on soybean, the disease expanded at an average rate of 8.8 and 10.4 km day⁻¹ in 2005 and 2006, respectively. These rates are at the lower range of those reported for the annual spread of tobacco blue mold from the Caribbean Basin through the southeastern United States. Regional spread of soybean rust may be limited by the slow disease progress on kudzu during the first half of the year combined with the short period available for disease establishment on soybean during the vulnerable phase of host reproductive development, although low inoculum availability in 2005 and dry conditions in 2006 also may have reduced epidemic potential.

Additional keywords: epidemic velocity.

Asian soybean rust, caused by *Phakopsora pachyrhizi*, is among the most damaging diseases of soybean (*Glycine max*) worldwide. In the absence of control measures, yield reductions up to 80% have been reported from countries in Asia where the pathogen is endemic (35). Losses of similar magnitude can occur in production areas in Africa and in South America (6,23,36) where soybean rust was introduced within the past decade. In the continental United States, prior to the first detection of the disease in November 2004 (30,33), model-derived yield loss estimates ranged from 11 to 30% for the main soybean-producing areas in the midwestern United States and up to 50% for the southern states (34). That significant yield reductions due to *P. pachyrhizi* can occur in United States soybean production areas is evident from fungicide trials in Georgia in 2005, where yield reductions of up to 33% have been documented in untreated control plots (20,31). However, to what extent such losses will be realized on a regional scale across the United States soybean belt is highly uncertain.

Overwinter survival of *P. pachyrhizi* in the United States is dependent on moderate temperatures and the presence of a living alternative host, such as kudzu (*Pueraria lobata*), during the soybean-free period. Based on climate matching of frost-free areas and the geographical distribution of kudzu, Pivonia and Yang (27) and Pivonia et al. (28) identified the Gulf Coast region of the southern United States (especially southern Texas and southern

and central Florida) as the most likely overwintering areas for the pathogen. The suitability of these regions for survival was subsequently confirmed by the U.S. Department of Agriculture's (USDA) soybean rust surveillance and monitoring program during the winters of 2005 and 2006 (13,17,31). Thus, whether or not yield losses of the magnitude cited above will be experienced in the United States depends largely on the seasonal potential for spread of *P. pachyrhizi* from these overwintering sites to the major soybean production regions in the midwestern states. While this potential is being assessed theoretically with atmospheric transport models (18,26), quantitative information on regional rates of spread of soybean rust in the United States is currently lacking. In the absence of such information, the potential for pathogen spread from overwintering areas remains the most uncertain component within a framework for predicting epidemic potential of soybean rust in the United States (28). This is especially true since regional disease spread tends to be curtailed more often by limited opportunities for pathogen establishment (i.e., absence of a host at a susceptible stage) than by atmospheric transport of inoculum (4). Thus, the objective of this study was to quantify regional patterns of temporal increase and spatial spread of soybean rust in the southeastern United States in 2005 and 2006, the first two growing seasons after the introduction of the disease into the continental United States.

MATERIALS AND METHODS

Soybean rust database. The website of the USDA's Pest Information Platform for Extension and Information (PIPE), available to registered users online (19), served as the primary database for

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this study. Records of the chronology of positive detections (i.e., confirmed cases of soybean rust occurrence), collected as part of the soybean rust sentinel plot monitoring network (2,14), were obtained from the PIPE website for six states (Florida, Georgia, Alabama, South Carolina, North Carolina, and Virginia) in the southeastern United States in 2005 and 2006. These states were selected for detailed analysis because they appeared to form a contiguous epidemic unit based on the general pattern of disease progression in the 2 years. In contrast, the Mississippi Basin (from Texas and Louisiana to Illinois and Indiana) was likely subject to a separate epidemic in 2006. The anticyclonic and southerly air flow patterns that typically prevail during the summer over the Southeast and the Mississippi Basin, respectively (5,16), tend to restrict inoculum exchange between the two regions.

There were 147 and 160 unique soybean rust cases for the six southeastern states in 2005 and 2006, respectively. The following variables contained within the database were retained for analysis: (i) date (day of the year), (ii) state, (iii) county, (iv) host (soybean, kudzu, or other), and (v) plot type (categorized as sentinel plot or nonsentinel plot). Sentinel plots were fixed plots, generally planted early and designated a priori for regular surveillance within the soybean rust monitoring program, while nonsentinel plots consisted of “mobile” plots or commercial fields that were monitored only after regional surveys indicated the presence of disease there (2).

In addition to these variables, the latitude and longitude associated with each case was obtained from the Custom Disease Report section of the PIPE website. For cases in which no such information was available, latitude and longitude values corresponding to the county centroid (extracted from U.S. Census Bureau 1990 Gazetteer Files) were used as an approximation.

Temporal progress. Variables related to the regional-scale temporal progress of soybean rust included the total number of cases, the total number of affected counties, the total duration of the epidemic (i.e., the time between the first and the last case each year), and the season-long average rate of increase in disease prevalence (calculated by dividing the total number of cases by the corresponding duration of the epidemic). These variables were considered separately for each state and for the six states combined. In addition, the rate of increase in disease prevalence was computed separately for kudzu plots, sentinel soybean plots, and nonsentinel soybean plots, based on the corresponding epidemic durations.

Spatial spread. For each year, the maximum spatial extent of the epidemic was calculated as the largest linear distance (in kilometers) between two cases that occurred in that year, regardless of when these two cases occurred relative to each other. These distance calculations were based on latitude-longitude information for each case. In addition, we determined nearest-neighbor distances of spread for all cases each year (10,11). These

computations rested on the assumption that each new case originated from the closest previously recorded case, as long as the previously recorded case serving as inoculum source was at least 10 days old. The latter restriction was applied to account for an average latent period of 10 days (1,21,22). Affected plots were assumed to remain infectious for 60 days based on the fact that rust does not usually appear in soybean until the crop enters reproductive development (data below), leaving ≤ 2 months until crop senescence. Preliminary results showed that calculated distances of spread were relatively insensitive to the choice of these two time periods.

All distance calculations were carried out using Excel 2002 software (Microsoft, Redmond, WA). Frequency distributions of nearest-neighbor distances of spread were obtained using PROC UNIVARIATE in SAS (version 9.1; SAS Institute, Cary, NC).

RESULTS

General description of the epidemic. The overall extent of the soybean rust epidemic in the southeastern United States, including the number of cases, the number of affected counties, the maximum distance between cases, and the total duration of the epidemic, was $\approx 10\%$ greater in 2006 than 2005 (Table 1). For example, the maximum distance between affected counties was 1,257 km in 2005 (between Mobile County, AL, and Tyrrell County, NC) and 1,418 km in 2006 (between Miami-Dade County, FL, and Accomack County, VA). Despite the larger number of cases in 2006 (160 versus 147), the longer duration of the epidemic (332 versus 301 days) in that year resulted in the season-long average rate of temporal disease increase being essentially identical in the 2 years (0.49 and 0.48 cases day⁻¹ in 2005 and 2006, respectively). The rate of temporal disease progress was greater in the northern-tier states (the Carolinas and Virginia) than in Florida, Georgia, and Alabama, mainly because of the shorter epidemic duration in the former states.

On a state-by-state basis, the main difference between the 2 years was the lower number of cases in Georgia (by almost 50%), the larger number of cases in North Carolina (more than double), and the appearance of cases in Virginia for the first time in 2006 (Table 1). In 2005, the disease records were dominated by the southern-tier states (Florida, Georgia, and Alabama), while in 2006, cases were distributed equally between the two subregions. The numbers of cases and affected counties in Florida, the presumed main overwintering region of *P. pachyrhizi* in the Southeast, were very similar in the 2 years.

Temporal progress. In both years, the soybean rust epidemic started early (in January or February) but slowly (Fig. 1A). Indeed, rapid increases in the number of cases were not observed until mid-July in 2005 and late August in 2006. After late September, the disease progress curves for the 2 years were very similar. The epidemic leveled off in mid-November in both years.

TABLE 1. Summary statistics for the regional spread of Asian soybean rust in the southeastern United States in 2005 and 2006

State	2005					2006				
	Number of		Duration of epidemic (days) ^a	Rate of temporal progress (cases day ⁻¹) ^b	Max. distance between cases (km)	Number of		Duration of epidemic (days) ^a	Rate of temporal progress (cases day ⁻¹) ^b	Max. distance between cases (km)
	Cases	Affected counties				Cases	Affected counties			
Florida	30	23	294	0.10	879	28	24	309	0.09	908
Georgia	38	35	209	0.18	476	20	17	302	0.07	419
Alabama	35	33	176	0.20	454	29	26	330	0.09	483
South Carolina	25	24	95	0.26	377	21	21	49	0.43	314
North Carolina	19	18	20	0.95	459	44	42	56	0.79	411
Virginia	0	0	...	...	...	18	18	28	0.64	253
All six states	147	133	301	0.49	1,257	160	148	332	0.48	1,418

^a Time between first and last case.

^b Calculated by dividing the total number of cases by the corresponding duration of the epidemic.

In the early part of the epidemic (before mid-June), soybean rust was restricted almost entirely to kudzu plots (Fig. 1B). In 2005, disease increase on kudzu was gradual until late August, after which the number of cases increased rapidly. In 2006, a relatively large number of cases were recorded in January and February (representing the final phase of the 2005 epidemic), followed by a long period of inactivity until late August, after which the increase in disease prevalence was rapid, as in the previous year.

In soybean plots in both years, cases occurred very sporadically before the beginning of July (Fig. 1C). Thereafter, the number of new cases increased rapidly. The earliest cases on soybean were recorded consistently in sentinel plots (Fig. 1D), with the lag period between the first detection in sentinel soybean plots and nonsentinel soybean plots being 1 month in 2005 and almost 4 months in 2006 (Fig. 1E). Disease increase in the latter plots was very rapid as soon as the first case was recorded. This rapid development of disease prevalence in nonsentinel plots is also reflected in the average rates of temporal disease increase, which were consistently greater for nonsentinel soybean compared with kudzu and sentinel soybean (Table 2).

Of 112 soybean cases for which crop growth stage data were available in the 2 years, only one occurred during late vegetative crop development while $\approx 75\%$ occurred at stage R6 (full seed) or higher (Table 3). The most common soybean growth stage at the time of disease detection was R8 (pods mature) in 2005 and R7 (pods yellowing) in 2006.

Spatial spread. Consistently in both years, the most common nearest-neighbor distance of spread between soybean rust cases was in the range of 30 to 60 km, followed by 60 to 90, 0 to 30, and 90 to 120 km, in that order (Fig. 2). The maximum nearest-neighbor distance was much larger in 2006 (902 km between Martin County, FL, and Baldwin County, AL) than in 2005 (307 km between Jefferson County, FL, and Baldwin County, AL). Nevertheless, within the 10th to 90th percentile, calculated distances of spread were very similar between the 2 years (Table 4). For example, the median nearest-neighbor distance of spread was

TABLE 2. Average rate of temporal progress of Asian soybean rust in the southeastern United States in 2005 and 2006

Host	Number of cases ^a		Rate of increase in disease prevalence (cases day ⁻¹) ^b	
	2005	2006	2005	2006
All hosts	147	160	0.49	0.48
Kudzu	37	49	0.12	0.15
Sentinel soybean plots	19	29	0.16	0.28
Nonsentinel soybean plots	60	42	0.58	0.68

^a The sum of the number of kudzu, sentinel soybean, and nonsentinel soybean cases is lower than the total number of cases because some records in the disease database lacked sufficient plot type information.

^b Calculated by dividing the total number of cases by the corresponding duration of the epidemic.

Fig. 1. Temporal progress of Asian soybean rust on A, all hosts, B, kudzu, C, all soybean plots, D, sentinel soybean plots, and E, nonsentinel soybean plots in the southeastern United States in 2005 (●) and 2006 (○). The earliest cases in A and B in 2006 represent the final phase of the 2005 epidemic on kudzu. The sum of the number of kudzu, sentinel soybean, and nonsentinel soybean cases is lower than the total number of cases because some records in the disease database lacked sufficient plot type information.

≈70 km, with 10% of the distances each being below ≈30 km and above ≈200 km.

Across the southeastern United States, the season-long average rate of spatial spread of soybean rust, calculated by dividing the maximum distance between cases by the total duration of the epidemic (Table 1), was 4.2 and 4.3 km day⁻¹ in 2005 and 2006, respectively. However, when the analysis was restricted to soybean only (where maximum distances of 1,223 and 1,378 km were covered in 139 and 132 days in 2005 and 2006, respectively), higher rates of 8.8 and 10.4 km day⁻¹ were obtained for the 2 years.

DISCUSSION

Knowledge of the early temporal and spatial dynamics of newly introduced exotic species is important to be able to predict future spread and damage potential in their new habitat (15). Our analysis of the temporal increase and spatial spread of soybean rust in the southeastern United States in the first two growing seasons after the introduction of *P. pachyrhizi* into the continental United States was based on disease records collected as part of the USDA's soybean rust surveillance and monitoring program. This database was considered ideal for such epidemiological analyses because of its dense network of fixed-site sentinel plots and mobile survey plots across the soybean belt, the frequent and coordinated monitoring conducted in these plots, and the consistent methodology used to ascertain the presence of soybean rust (2,14).

Prior to mid-June, soybean rust in the southeastern United States was restricted almost entirely to kudzu. Kudzu is generally considered the main overwintering host for *P. pachyrhizi* in the United States, especially in the largely frost-free areas of southern and central Florida where the plant remains evergreen year-round (13,27,28,31). In other areas in the Southeast where kudzu is prevalent but dies back during the winter, the species resumes its vegetative growth between March and May, generally before soybeans are planted and considerably earlier than when commercial soybeans attain their reproductive stages when disease is more likely to occur (7,23,25).

In both years, the first cases of soybean rust on kudzu were reported from old-growth patches during January and/or February. The low temperatures during this period and the associated prolonged incubation periods suggest that the corresponding infections likely occurred toward the end of the previous year and did not manifest themselves until later. Alves et al. (1), working with soybean, showed that the disease can develop at temperatures as low as 10°C, but the incubation period was 29 days. In conditions of lower average temperatures and on the less susceptible host kudzu (13; M. R. Bonde and H. Edwards, unpublished data), new cases reported early in the year may have originated several months previously.

Despite the early detection of soybean rust on overwintered kudzu in late winter, the disease developed slowly during the

spring and early summer on this host species. This long phase of relative inactivity may have been due to several factors, particularly the slow regreening of kudzu in areas where it dies back during the winter as well as the lower (compared with soybean and other hosts) susceptibility to infection and reduced potential for sporulation from rust pustules on kudzu (M. R. Bonde and H. Edwards, unpublished data). The lower susceptibility of kudzu to soybean rust in the field is clearly reflected in the fact that the disease on kudzu did not enter its exponential phase until late August in both years, more than 1 month after it did so on soybean. Thus, while kudzu likely provides the initial inoculum for epidemics on soybean, the rapid increase in disease prevalence on kudzu toward the end of the season appears to be driven by inoculum produced on soybean. Indeed, in a research plot in north Florida where 90% of soybean plants were affected by soybean rust, 25% of kudzu leaves near the plots showed rust symptoms, and disease severity on kudzu was 65% lower than on soybean (13).

In soybean, the first cases of the disease were reported from early-planted sentinel plots. The lag period between the first detection in sentinel plots and that in nonsentinel plots was 1 month in 2005 and almost 4 months in 2006. Although not constant between years, this lag period is sufficiently long to serve as an early warning for commercial soybean fields in the area (29). The advance warning afforded by the sentinel soybean plots is especially important considering the fact that the increase in disease prevalence across nonsentinel plots (which includes

TABLE 4. Frequency distribution of nearest-neighbor distances of spread of Asian soybean rust in the southeastern United States in 2005 and 2006

Percentile	Distance (km) ^a	
	2005	2006
5	20.5	20.6
10	28.8	28.7
25	39.8	37.2
50	68.8	69.8
75	106.5	124.4
90	215.8	198.0
95	309.9	240.7

^a Based on the assumption that each new case originated from the closest previously recorded case, with the restriction that the previously recorded case serving as inoculum source had to be between 10 and 70 days old.

TABLE 3. Frequency distribution of soybean growth stage at the time of first detection of Asian soybean rust in the southeastern United States in 2005 and 2006

Soybean growth stage ^a		Frequency of cases	
Code	Description	2005	2006
V8	Eighth trifoliate	1	0
R1	Beginning bloom	0	1
R3	Beginning pod	4	1
R4	Full pod	1	2
R5	Beginning seed	7	12
R6	Full seed	9	17
R7	Pods yellowing	2	22
R8	Pods mature	17	16

^a Fehr et al. (9).

Fig. 2. Frequency distribution of nearest-neighbor distances of spread of Asian soybean rust in the southeastern United States in 2005 and 2006. Distances calculated based on the assumption that each new case originated from the closest previously recorded case, with the restriction that the previously recorded case serving as inoculum source had to be between 10 and 70 days old. Not shown are two extreme values of 635 and 902 km recorded in 2006.

commercial fields planted at regular times) was very rapid as soon as the first case was recorded in these plots.

The considerable delay of disease onset in nonsentinel soybean plots in 2006 (early September) compared with 2005 (late July) may have been weather-related. For example, large parts of Georgia and Alabama were affected by a moderate to severe drought during the summer of 2006 (3), and the hurricane season was calmer than in 2005 (32). Regardless of the reasons for the delay in disease onset, the average rate of temporal progress of soybean rust prevalence in nonsentinel plots was very similar in the 2 years.

The season-long average rate of spatial spread of soybean rust on soybean was 8.8 and 10.4 km day⁻¹ in the southeastern United States in 2005 and 2006, respectively. When a similar analysis was carried out for the states in the Mississippi Basin (Texas, Louisiana, Mississippi, Arkansas, Tennessee, Kentucky, Missouri, Illinois, and Indiana) in 2006 (Christiano and Scherm, *unpublished data*), a total of 120 soybean cases covering a maximum distance of 1,885 km (between Hidalgo County, TX, and Tippecanoe County, IN) were recorded in a 104-day period, resulting in an average rate of spread of 18.1 km day⁻¹. The higher epidemic velocity in the Mississippi Basin is not surprising, given that this region is part of the North American *Puccinia* path in which long-distance disease spread is greatly facilitated owing to the prevailing southerly winds (24). In contrast, the anticyclonic airflow patterns that typically prevail over the Southeast are less favorable for North-South inoculum dissemination.

Our calculated rate of spread of soybean rust in the southeastern United States is at the lower end of the 9 to 18 km day⁻¹ range reported for the annual spread of tobacco blue mold, caused by *Peronospora tabacina*, from the Caribbean Basin through the southeastern United States and along the Eastern Seaboard (4,8). Similarly, the rate of spread of soybean rust in the Mississippi Basin is at the lower end of the 17 to 76 km day⁻¹ range reported for wheat stem rust, caused by *Puccinia graminis* f. sp. *tritici*, in the same region (4,12). Although the databases and methods with which rates of spread for the three diseases were calculated are different, a general comparison of the magnitude of spread is possible. The lower rate of spread of soybean rust may be the result of the shorter time period available for effective disease establishment on soybean. Tobacco and wheat can be affected by blue mold and stem rust, respectively, during most stages of plant development. This allows the respective pathogens to leap-frog northward at approximately the same rate as new plantings of their hosts are established at successively higher latitudes as the season progresses (4). In contrast, soybean rust generally does not occur in the field until plants reach their reproductive stage of development, as documented in the present study (Table 3) and in field studies in other production areas (7,23,25). Based on various issues of the *Weekly Weather and Crop Bulletin*, issued jointly by the U.S. Department of Commerce and the USDA, soybean bloom typically commences in mid-June in southern states and in early July in northern states. In both regions, soybean harvest is well underway by early October. In effect, this leaves the disease no more than 3 months to spread from soybean fields in the South to those in the North. The short window of opportunity for disease establishment during reproductive development of soybean, together with the slow progress of the disease on kudzu during the first half of the year, may limit the damage potential of soybean rust in the United States, although low inoculum availability in 2005 and dry conditions in 2006 also may have reduced regional spread.

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