# Analysis of Epidemics of Rhizoctonia Aerial Blight of Soybean in Louisiana

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## ABSTRACT

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Frequency of primary infections, disease focus establishment, expansion of disease foci, and seasonal progress of soybean aerial blight caused by *Rhizoctonia solani* were studied from 1986 to 1988. Primary infections from natural inoculum were quantified by counting and then removing diseased leaves at 3- to 5-day intervals. High numbers of primary infections were found early in the season. The correlation between average number of primary infections per day and average daily rainfall was highly significant. The relationship between plant growth stage and the establishment and expansion of disease foci was studied in fields without a history of aerial blight by periodically inoculating 10 leaves at the center of each of 10 subplots. Establishment ratios of disease foci were low before soybean stages V7 and V4 in 1986 and 1988, respectively. In 1987, high establishment ratios in early plant growth stages were associated with heavy and frequent rainfall. Significant expansion of disease foci occurred only after canopy closure in all three seasons. Development of disease was correlated with rainfall and soybean growth stage ($R^2$ ranges from 0.73 to 0.96 for different year × row spacing combinations). Expansion of disease foci was predicted using the number of rain days after inoculation and the soybean growth stages at inoculation. Disease in fields with natural inoculum progressed erratically, and correlation coefficients among disease incidences rated at different soybean growth stages were significantly reduced as the time span increased. The epidemiology of aerial blight may be divided into two phases, one before and one after canopy closure. The first phase is soilborne and determines the number of potential disease foci in the crop canopy. The second phase is leafborne and is important to the expansion of disease foci.

Rhizoctonia aerial blight of soybean is a destructive foliar disease caused by *Rhizoctonia solani* Kühn, anastomosis group 1, IA intraspecific group (13,15,24). The disease causes rapid defoliation of soybean plants (*Glycine max* (L.) Merrill) in warm, humid regions and has been reported worldwide (17). In Louisiana, aerial blight was first reported in 1954 (21); it now occurs in most soybean production areas of the state (13) and causes up to 30% loss of yield (10). Yield losses of up to 50% have been reported in research plots (13). In the southern United States, the aerial blight pathogen also causes rice sheath blight. The increase of rice sheath blight in Louisiana and Texas is considered to be a result of soybean-rice rotation (3,15).

Although the type of inoculum responsible for primary aerial blight infection has not been confirmed (17), seedling infection caused by soilborne inoculum of aerial blight has been reported (25). Rain-splashed debris containing mycelium and sclerotia from the soil has been reported as the inoculum for Rhizoctonia web blight of bean (6,7); plants are first infected on lower portions (1,15). The importance of host growth stage in aerial blight progress has been reported (13,15,19,24). On soybean, the mycelium begins to grow along the stems and infects the upper parts of the plants during the flowering stages (1,13,15). The disease spreads by means of aerial mycelia growing from leaf to leaf and plant to plant, forming distinct disease foci within the canopy (13,15,24). Rainfall during the flowering stages may encourage an outbreak of the disease (13,22,23). Baker and Martinson (2) postulated that the development of foliar blights caused by *R. solani* depends on certain combinations of environmental conditions.

Quantitative information on disease epidemics that rely on soilborne inoculum and interplant growth of mycelium (20) is lacking. Examples of diseases similar to aerial blight include Sclerotinia wilt of sunflower (11), southern blight of processing carrot caused by *Sclerotium rolfsii* Sacc. (20), and diseases caused by *R. solani* in other crops (5,6,18). It is necessary to know how to quantify the epidemics of this type of disease.

The objectives of this study were to better understand the epidemiology of aerial blight by quantifying the effect of rainfall and plant growth stage on primary infection, the establishment and expansion of disease foci, and disease progress.

## MATERIALS AND METHODS

**Location and planting.** Simultaneous experiments were conducted during 1986–1988 at two sites located 7 km apart at

Baton Rouge, LA. The experimental site at the Burden Research Plantation had a 10-yr history of aerial blight. Experiments to study primary infection and natural disease progress were conducted at this location. A 20- × 20-m plot with 25-cm row spacing and two plots 40 × 40 m with 75-cm row spacing were planted on 1 June 1986, 4 June 1987, and 4 June 1988. At the Ben Hur Farm location, which had no previous history of aerial blight, an experiment to study the establishment and enlargement of disease foci was conducted. Two plots, each 30 × 40 m with 25-cm row spacing (except during 1986) or 75-cm row spacing, were planted on 18 May 1986, 30 May 1987, and 30 May 1988. Distance between plants (within rows) was 3–5 cm. The soybean cultivar Davis, which is highly susceptible to aerial blight, was used in all experiments.

Daily rainfall, maximum temperature, and minimum temperature were obtained from Bench Mark weather stations located at each experimental site. Ten plants were randomly sampled from each location at 3- to 4-day intervals to determine the soybean growth stage (4).

**Primary infections.** At the Burden site, 20 subplots of 1.5 × 3 m were randomly selected from the plot with 25-cm row spacing. After seedling emergence, the foliar lesions of aerial blight in each subplot were counted at 3- to 5-day intervals. One lesion was considered as one primary infection. If a plant had only one infected leaf, the leaf was removed. If a plant had more than a single infected leaf or infections in other parts, the plant was removed. The mean of primary infections per subplot and associated standard deviation was determined for each sampling.

The relationship between the number of primary infections and the amount of daily rainfall was determined. For a given season, primary infections per day per subplot for the $i$th interval ($N_i$) was calculated as

$$N_i = \frac{1}{20} \sum_{j=1}^{20} X_{ij} / t_i \tag{1}$$

where $X_{ij}$ is the primary infections in $j$th subplot at $i$th rating, $t_i$ is days from the day after $(i-1)$-th rating to the day of $i$th rating. Average daily amount of rainfall for $i$th interval ($M_i$) was calculated as

$$M_i = \sum_{t=1}^{n_i} R_{it} / t_i \tag{2}$$

where $n_i$ equals $t_i$, $R_{it}$ is amount of daily rainfall at $t$th day in $i$th interval. Since disease symptoms do not appear for 36 hr after inoculation (24), the time for calculation of primary infection was lagged 1 day in correspondence with the time for calculation of rainfall. Correlation coefficients were calculated between the $N_i$ and $M_i$ for each season.

**Establishment and enlargement of disease foci.** At the Ben Hur site, plots with both 25- and 75-cm row spacing were divided into 10 blocks, each 3 × 40 m. Blocks were 3.5 m apart, with a 1.5-m unplanted strip. Each block was divided into 10 subplots

TABLE 1. Mean diameters (cm) of disease foci following inoculation with *R. solani* at different soybean growth stages (GS) for the 1986, 1987, and 1988 growing seasons in plots with 75-cm row spacing at the Ben Hur Research Farm, Baton Rouge, LA

| Inoculation | | Disease focus diameter measured at different GS | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Date (1986) | GS | 6/4 V1 | 6/11 V3 | 6/17 V4 | 6/22 V7 | 6/28 V8 | 7/2 V9 | 7/6 V11 | 7/13 V14 | 8/1 R2 |
| 6/4 | V1 | 8.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6/10 | V3 | ... | 10.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6/17 | V4 | ... | ... | 8.5 | 8.6 | 0 | 0 | 0 | 0 | 0 |
| 6/22 | V7 | ... | ... | ... | 10.5 | 10.0 | 10.0 | 23.5 | 45.0 | ND[a] |
| 6/28 | V8 | ... | ... | ... | ... | 8.5 | 9.5 | 22.5 | 41.1 | ND |
| 7/2 | V9 | ... | ... | ... | ... | ... | 11.0 | 30.0 | 55.5 | ND |
| 7/6 | V11 | ... | ... | ... | ... | ... | ... | 30.0 | 38.8 | 44.0 |
| 7/13 | V14 | ... | ... | ... | ... | ... | ... | ... | 20.0 | 25.6 |
| 7/24 | R2 | ... | ... | ... | ... | ... | ... | ... | ... | 23.5 |

| Date (1987) | GS | 6/18 V2 | 6/26 V3 | 7/10 V7 | 7/29 V12 | 8/12 R3 |
|---|---|---|---|---|---|---|
| 6/11 | VC | 10 | 10 | 11.3 | 22.9 | 81.9 |
| 6/15 | V1 | 10 | 10 | 9.3 | 23.6 | 62.7 |
| 6/19 | V2 | ... | 10 | 7.1 | 21.1 | 67.5 |
| 6/23 | V2 | ... | 10 | 11.8 | 21.0 | 79.3 |
| 6/27 | V3 | ... | ... | 6.9 | 20.5 | 47.5 |
| 7/01 | V4 | ... | ... | 7.7 | 20.8 | 57.9 |
| 7/06 | V6 | ... | ... | 8.3 | 23.9 | 55.5 |
| 7/11 | V8 | ... | ... | ... | 10.0 | 45.5 |
| 7/15 | V9 | ... | ... | ... | 18.5 | 68.7 |
| 7/21 | V10 | ... | ... | ... | 19.2 | 66.5 |
| 7/27 | V12 | ... | ... | ... | ... | 30.5 |

| Date (1988) | GS | 6/22 V3 | 6/28 V5 | 7/5 V7 | 7/15 V9 | 8/1 V14 | 8/22 R3 |
|---|---|---|---|---|---|---|---|
| 6/14 | V1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6/17 | V2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6/22 | V3 | ... | 10.0 | 10.5 | 10.3 | 46.6 | 120.6 |
| 6/25 | V4 | ... | 10.0 | 12.6 | 13.6 | 59.4 | 138.3 |
| 6/28 | V5 | ... | ... | 10.0 | 10.3 | 26.3 | 116.7 |
| 7/05 | V7 | ... | ... | ... | 10.0 | 57.2 | 147.2 |
| 7/10 | V8 | ... | ... | ... | 10.0 | 53.5 | 126.7 |
| 7/15 | V9 | ... | ... | ... | ... | 56.1 | 112.5 |
| 7/20 | V10 | ... | ... | ... | ... | 10.7 | 93.5 |
| 7/25 | V11 | ... | ... | ... | ... | 12.9 | 101.0 |
| 7/29 | V12 | ... | ... | ... | ... | 10.0 | 54.4 |
| 8/3 | V14 | ... | ... | ... | ... | ... | 45.0 |
| 8/8 | R2 | ... | ... | ... | ... | ... | 46.5 |
| 8/15 | R3 | ... | ... | ... | ... | ... | 10.0 |

[a] ND = no data collected.

of 3 × 4 m. The treatments consisted of sequential inoculations at different soybean stages (Table 1). At each inoculation, one subplot was selected from each block. Inoculum consisted of a suspension of *R. solani* AG-1, IA intraspecific group, isolated from diseased plants at the Burden location and cultured on potato-dextrose agar plates (10 cm in diameter). The inoculum suspension was made by stirring a 2-wk-old potato-dextrose agar culture with 200 ml of distilled water and was applied at the rate of 100 ml per subplot. Fifteen leaves were inoculated within 10 cm of a row at the center of each subplot. After 24–48 hr, each inoculated area was examined and selectively thinned to 10 infected leaves. Aerial blight was rated at nine, five, and six different soybean growth stages for 1986, 1987, and 1988, respectively (Table 1).

An established disease focus was defined as a diseased plant or plants that became an inoculum source to the healthy plants during the remainder of the season. If the disease from the initial inoculation site could no longer be found, this site was considered an unestablished disease focus. The establishment ratio at each inoculation was calculated by dividing the number of subplots in which the disease developed by the 10 subplots inoculated at each time.

The diameter of each established disease focus was measured at each reading. The focus diameter was defined as the distance between the two farthest diseased leaves across the inoculation area. Measurements were made down and across the rows. The mean of the two measurements was taken as the focus diameter.

The relationship of disease focus expansion to rainfall and soybean growth stage was determined. A numerical soybean growth stage was modified from Fehr's scales (4) by assigning VC–V14 with values 0–14 and R1–R5 with values 15–19. Using rainfall and crop canopy density as the key determinants for aerial blight development (13,15,18,19,24), a full model for disease focus expansion was written as

$$Y_{ij} = B_0 + B_1 X1_{ij} + B_2 X2_{ij} + B_3 X3_i + B_4 X4_{ij} + E_{ij} \quad (3)$$

where $Y_{ij}$ was the disease focus diameter for the *i*th inoculation at *j*th rating. $B_0$, $B_1$, $B_2$, $B_3$, and $B_4$ were the partial regression coefficients. $X1_{ij}$ and $X2_{ij}$, respectively, were accumulated rain days and accumulated amount of rainfall from the day after *i*th inoculation to the day before the *j*th rating. $X3_i$ and $X4_{ij}$ were the soybean growth stages at *i*th inoculation and at *j*th rating, respectively. Near-colinearity between the independent variables was diagnosed using standard statistical techniques (14). If near-colinearity presented reduced models (in which one variable from a colinear group was dropped) among the independent variables, they would be written with different combinations to determine the optimum model variables. Reduced models of regression were selected by aptness of residual plot, $R^2$, $F$ value, and $P>F$ and lack of colinearity.

**Disease progress.** At the Burden site, development of aerial blight was monitored in the two plots with 75-cm row spacing. From each plot, 35 subplots of 75 × 100 cm were randomly selected. Disease incidence (percentage of diseased leaves) for each subplot was rated at soybean growth stage V4-V5, V9-V10, V12-V13, and R4. Mean and standard deviation of disease incidence was plotted against number of days after planting to examine the disease progress. For each plot, correlation coefficients were calculated among disease incidences rated at the four growth stages. Autocorrelation of a disease progress was examined with the correlation coefficients between sequential disease readings ($r_{ij}$). The higher the autocorrelation was, the greater the value of $r_{ij}$ would be.

All computations were done with SAS statistical package (16).

## RESULTS

**Weather and primary infection at Burden.** Because natural seedling infection caused by the aerial blight agent was not confirmed until 1987 (25), primary infection before 27 days after planting was not evaluated in 1986. Before canopy closure, maximum primary infections per subplot were 4.2, 5.5, and 2.5 for 1986, 1987, and 1988, respectively. The coefficient of variation for primary infections per subplot at each evaluation was always greater than 50%.

Fluctuations in rainfall paralleled fluctuation in primary infection numbers (Fig. 1). In 1986, more infections occurred during the early soybean growth stages than during the late growth stages. In June 1987, the heavy rainfall at early plant growth stages was followed by a high number of infections. During mid-July 1987, a period of relatively low rainfall was followed by a low number of primary infections. About 60% of the primary infections occurred within 40 days after planting for both 1986 and 1987. In 1988, less rainfall occurred in the early season, and less than 40% of primary infections occurred within 40 days after planting. Correlation coefficients between primary infections per day per subplot ($N_i$) and average daily rainfall ($M_i$) were 0.92 ($P \leq 0.002$), 0.71 ($P \leq 0.01$), and 0.59 ($P \leq 0.01$) for 1986, 1987, and 1988, respectively.

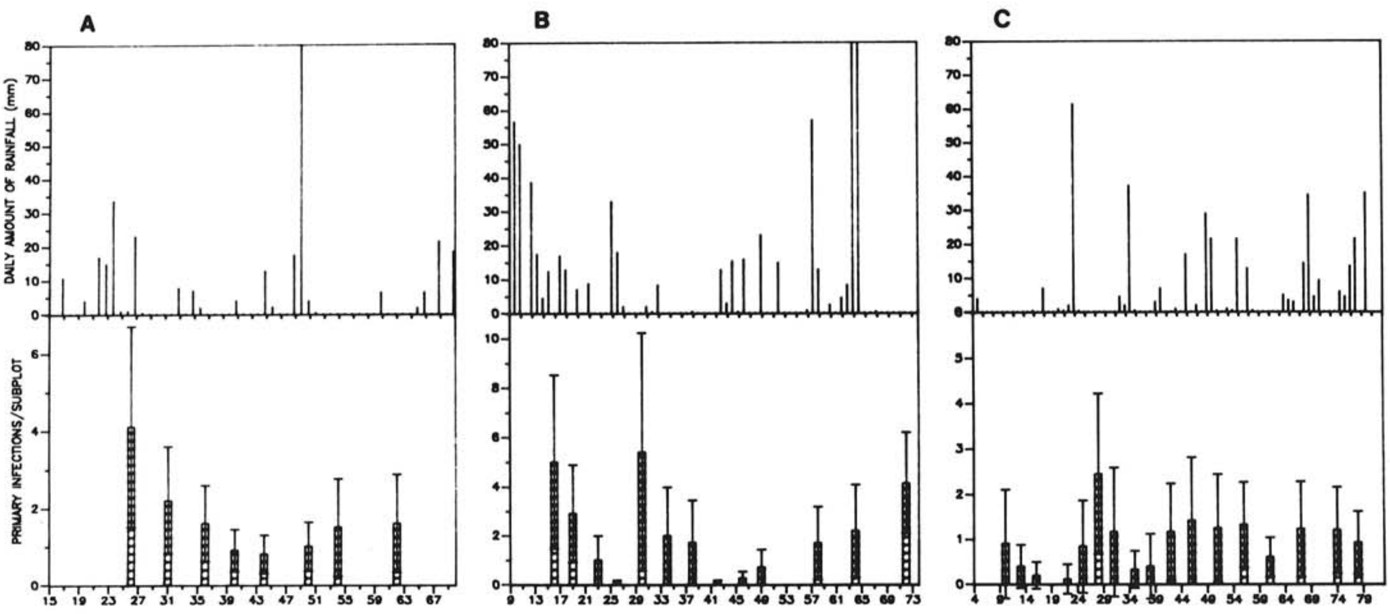


**Fig. 1.** Number of primary infections of Rhizoctonia aerial blight of soybean observed per subplot of 1.5 × 3 m and the corresponding rainfall at Burden during the 1986 (**A**), 1987 (**B**), and 1988 (**C**) growing seasons.

**Weather and establishment and enlargement of disease foci at Ben Hur.** Rainfall records from 15 May to 16 September 1986, 1987, and 1988 at the Ben Hur Research Farm are given in Figure 2. Rainfall patterns were different each year. In 1986, rainfall was frequent in the early season; there was less rain late in the season. In 1987, unusually frequent and heavy rainfall was distributed throughout the recorded period. For 1988, the early season was relatively dry; later in the season, rainfall was frequent but not heavy. For the period of 1 June to 31 August (the primary time for aerial blight development in Louisiana [13,15]), the difference in rainfall from year to year was significant. From 1 June (about planting time) to 15 July (about growth stage V10-V11), the number of rain days and accumulated amount of rainfall were 23 days and 233.17 mm, 23 days and 399.03 mm, and 16 days and 122.68 mm for 1986, 1987, and 1988, respectively. From 16 July (canopy closure) to August 30, the number of rain days and accumulated amount of rainfall were 16 days and 186.69 mm, 23 days and 379.0 mm, and 30 days and 225.55 mm for 1986, 1987, and 1988, respectively.

In 1986, no disease foci resulted from inoculations before V7, and the establishment ratio increased as the growth stage at inoculation increased (Fig. 3). In 1987, the high establishment number resulted from inoculations at all growth stages in both row spacings (Fig. 3), indicating the influence of early-season rainfall on focus establishment. In 1988, no foci were formed from inoculation before V4 at either row spacing, but establishment ratios were high from inoculations at late growth stages (Fig. 3).

For the plots with 75-cm row spacing in 1986 and 1988, rapid expansion of established disease foci did not occur until after growth stage V9 (2 July 1986 and 15 July 1988) (Table 1). In 1987, significant expansion of foci was not observed at V7 (10 July), and rapid expansion of foci occurred at V12 (29 July). Rates of focus expansion were greatest between the last two observation dates in 1987 and 1988 and were highest for disease foci in 1988 (Table 1).

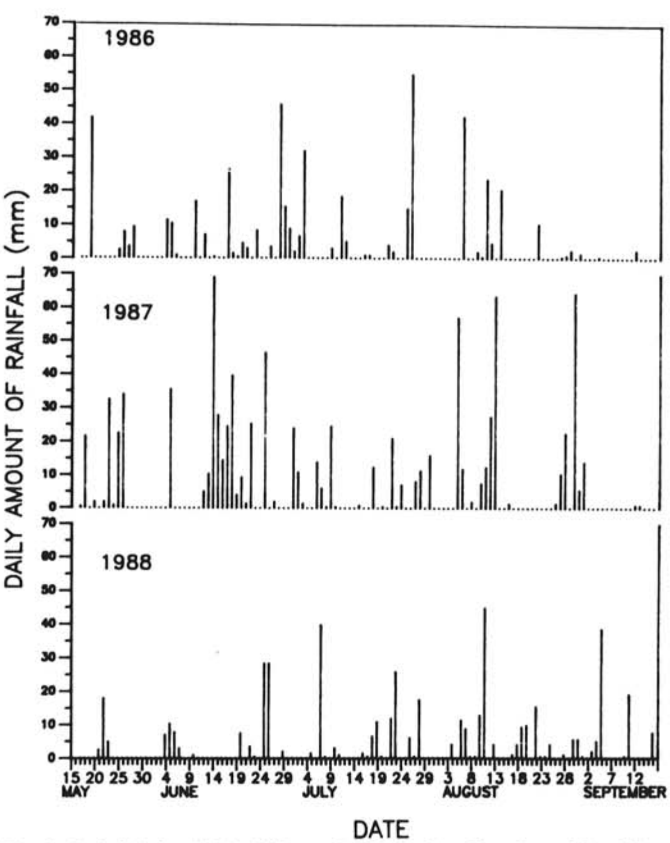


**Fig. 2.** Rainfall for 1986, 1987, and 1988 at Ben Hur from May 15 to September 16.

Since the disease spreads by means of mycelial growth from leaf to leaf and plant to plant, the onset of focus expansion was earlier in plots with 25-cm row spacing than in plots with 75-cm row spacing (Tables 1 and 2). In 1987, for example, disease foci in the plots with 25-cm row spacing had average diameters of 37.5, 45.8, and 28.2 cm for the first, second, and third inoculations at the V7 growth stage. In the plots with 75-cm row spacing, the diameter did not begin to expand at V7 (Table 1). In 1988, disease focus expansion began at V8 in plots with 25-cm row spacing, approximately 15 days earlier than in plots with 75-cm row spacing (Tables 1 and 2).

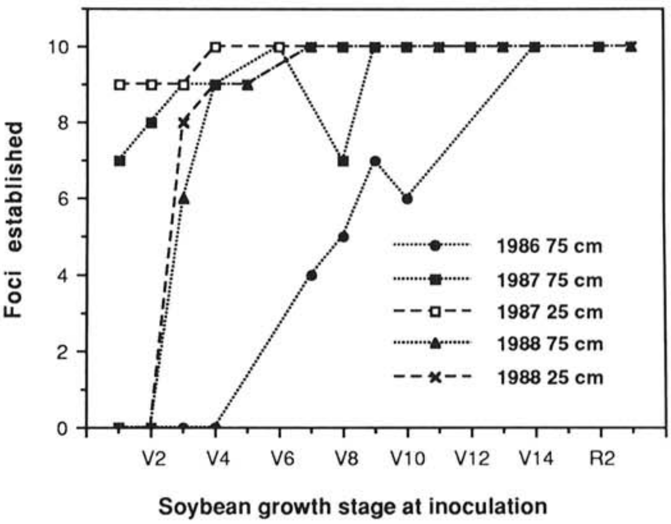


**Fig. 3.** Number of disease foci of Rhizoctonia aerial blight resulting from inoculation at different soybean growth stages during the 1986, 1987, and 1988 growing seasons.

TABLE 2. Mean diameter (cm) of disease foci following inoculation with *R. solani* at different soybean growth stages (GS) for the 1987 and 1988 growing seasons in plots with 25-cm row spacing at the Ben Hur Research Farm, Baton Rouge, LA

| Inoculation | | Disease focus diameter measured at different GS | | | | |
|---|---|---|---|---|---|---|
| Date (1987) | GS | 6/18 V2 | 6/26 V3 | 7/10 V7 | 7/29 V12 | 8/12 R3 |
| 6/11 | VC | 10 | 10 | 37.5 | 63.6 | 186.3 |
| 6/15 | V1 | 10 | 10 | 45.8 | 94.5 | 195.5 |
| 6/19 | V2 | ··· | 10 | 28.2 | 91.4 | 182.0 |
| 6/23 | V2 | ··· | 10 | 21.0 | 95.0 | 188.5 |
| 6/27 | V3 | ··· | ··· | 18.0 | 80.0 | 190.0 |
| 7/01 | V4 | ··· | ··· | 18.8 | 67.3 | 186.0 |
| 7/06 | V6 | ··· | ··· | 16.8 | 67.0 | 174.0 |
| 7/11 | V8 | ··· | ··· | ··· | 47.5 | 155.0 |
| 7/15 | V9 | ··· | ··· | ··· | 44.4 | 145.0 |
| 7/21 | V10 | ··· | ··· | ··· | 21.1 | 68.5 |
| 7/27 | V12 | ··· | ··· | ··· | ··· | 50.3 |

| Date (1988) | GS | 6/22 V3 | 6/28 V5 | 7/5 V7 | 7/15 V9 | 8/1 V14 | 8/22 R3 |
|---|---|---|---|---|---|---|---|
| 6/14 | V1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6/17 | V2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6/22 | V3 | ··· | 10.0 | 10.0 | 20.5 | 41.2 | 121.2 |
| 6/25 | V4 | ··· | 10.0 | 10.8 | 26.7 | 55.6 | 119.4 |
| 6/28 | V5 | ··· | ··· | 10.0 | 16.0 | 47.5 | 117.9 |
| 7/05 | V7 | ··· | ··· | ··· | 20.0 | 64.5 | 118.1 |
| 7/10 | V8 | ··· | ··· | ··· | 18.9 | 49.4 | 89.5 |
| 7/15 | V9 | ··· | ··· | ··· | ··· | 38.6 | 98.3 |
| 7/20 | V10 | ··· | ··· | ··· | ··· | 14.4 | 84.4 |
| 7/25 | V11 | ··· | ··· | ··· | ··· | 18.3 | 98.3 |
| 7/29 | V12 | ··· | ··· | ··· | ··· | 10.0 | 77.5 |
| 8/3 | V14 | ··· | ··· | ··· | ··· | ··· | 60.0 |
| 8/8 | R2 | ··· | ··· | ··· | ··· | ··· | 57.2 |
| 8/15 | R3 | ··· | ··· | ··· | ··· | ··· | 26.1 |

Disease focus expansion was highly dependent on rainfall and plant growth stage. Determination coefficients of the full model (eq. 3) for each year and row spacing ranged from 0.733 to 0.957 with $P < 0.0001$ (Table 3), indicating that about 90% of the variation of disease focus expansion was determined by plant growth stages and rainfall. Intercepts were negative or insignificant in some cases. In the full models, negative partial regression coefficients were observed inconsistently in every year (Table 3), indicating an instability of sign in the model. In some cases, values of partial regression coefficients and standard errors were very high. VIF and eigenvalue analysis indicated near-colinearity between the soybean growth stage at inoculation (*X3*) and the growth stage at prediction (*X4*) and between accumulated rain days after inoculation (*X1*) and accumulated amount of rainfall after inoculation (*X2*). After dropping variables *X4* and *X2* from the full model, no significant colinearity existed. Selection of reduced models suggested that the best combination was with variables *X1* (accumulated rain days after inoculation) and *X2* (soybean growth stage at inoculation). $R^2$ in reduced models ranged from 0.615 to 0.930 with $P < 0.0001$ (Table 3). The values of partial regression coefficients differed from year to year and between the different row spacings (Table 3).

**Natural disease progress at Burden.** Before canopy closure, at soybean growth stage V10–V12 or until 55 days after planting, disease progress was mostly limited to individual plants. Plant-to-plant spread was confined within rows. Disease incidence before growth stage V10–V12 was less than 5% in each field (Fig. 4). The slopes of disease curves for each year increased after the second rating (Fig. 4). Final percentages of diseased leaves for the two plots were 9 and 15% for 1986, 30 and 30% for 1987, and 15 and 31% for 1988. Standard deviations at different ratings were greater than 65% of the means.

Correlation coefficients among disease incidences rated at different growth stages were significant in most cases (Table 4). Significance was usually high when the time between two ratings was close but tended to decrease as the interval between ratings increased. Correlation coefficients were relatively consistent during 1987. Two negative values, −0.259 and −0.096, occurred in 1988. The relatively low values of correlation coefficients among the disease incidences at different growth stages indicates the low autocorrelation within the disease progress.

## DISCUSSION

Rhizoctonia aerial blight epidemics appear to be divided into two phases. The first phase is the initiation of disease foci, during which aerial blight progresses as a soilborne disease. The second phase is after canopy closure, and aerial blight then progresses as a leafborne disease. During the growing season, patterns of rainfall between the two phases is an important determinant of the development of aerial blight.

The first phase in an epidemic of aerial blight is important in determining the number of primary infections. Approximately 60% of the primary infections occurred before canopy closure in 1986 and 1987 (Fig. 1). Before canopy closure, rain hits the ground directly, and this may distribute the inoculum from soil to foliage. This is what happens in the case of Rhizoctonia web blight of bean, in which rain-splashed sclerotia and mycelia from soil are the major primary inocula (6,7).

Rainfall before canopy closure is critical to the establishment of disease foci, but rapid expansion of disease foci does not occur. Disease focus expansion was insignificant during this period, although rainfall was frequent, for instance following the early inoculations in 1987 (Tables 1 and 2). The disease primarily progressed upward on individual plants rather than horizontally across plants. This lack of horizontal growth might be attributable to low free moisture in the open canopy and less chance for leaves to come into contact (24).

TABLE 3. Regression analysis for disease focus diameter of aerial blight to rainfall measurements and soybean growth stage, showing percent variation determined by full models and the improvement of regression coefficients in reduced models

| | Partial regression coefficients and standard error (in parentheses)[a] | | | | | | |
|---|---|---|---|---|---|---|---|
| Year | Intercept | *X1* | *X2* | *X3* | *X4* | $R^2$ | $P>F$ |
| Full models | | | | | | | |
| 1986 75 cm | −5.779 | −3.402 | 1.628 | −8.091 | 9.886 | 0.935 | 0.0001 |
| | (4.551) | (1.171) | (1.928) | (0.977) | (0.943) | | |
| 1987 75 cm | −5.381 | −3.954 | 4.019 | −4.936 | 7.237 | 0.879 | 0.0001 |
| | (4.508) | (0.985) | (0.747) | (1.747) | (1.413) | | |
| 1988 75 cm | 6.432 | 8.111 | −2.987 | 7.254 | −7.220 | 0.929 | 0.0001 |
| | (7.727) | (1.822) | (4.086) | (1.845) | (2.197) | | |
| 1987 25 cm | −15.966 | −13.424 | 8.438 | −29.829 | 32.843 | 0.872 | 0.0001 |
| | (18.155) | (3.830) | (2.958) | (6.588) | (5.316) | | |
| 1988 25 cm | 1.856 | 3.639 | 5.575 | 5.082 | −4.172 | 0.957 | 0.0001 |
| | (5.203) | (1.227) | (2.751) | (1.243) | (1.479) | | |
| 75 cm[b] | −17.031 | 5.025 | −3.876 | 3.312 | −0.374 | 0.733 | 0.0001 |
| | (5.417) | (0.783) | (0.924) | (1.433) | (1.410) | | |
| 25 cm | −18.837 | −5.734 | 9.113 | −12.349 | 17.725 | 0.812 | 0.0001 |
| | (10.345) | (1.518) | (1.711) | (2.744) | (2.719) | | |
| Reduced models | | | | | | | |
| 1986 75 cm | 2.101 | 2.746 | | 1.150 | | 0.696 | 0.0001 |
| | (2.771) | (0.903) | | (1.160) | | | |
| 1987 75 cm | −15.635 | 2.086 | | 3.393 | | 0.696 | 0.0001 |
| | (5.927) | (0.267) | | (0.704) | | | |
| 1988 75 cm | −11.818 | 4.395 | | 1.576 | | 0.903 | 0.0001 |
| | (6.178) | (0.255) | | (0.418) | | | |
| 1987 25 cm | −15.034 | 6.790 | | 8.921 | | 0.701 | 0.0001 |
| | (13.481) | (1.043) | | (2.800) | | | |
| 1988 25 cm | −10.231 | 3.846 | | 2.474 | | 0.930 | 0.0001 |
| | (4.548) | (0.188) | | (0.473) | | | |
| 75 cm | −15.203 | 3.175 | | 3.524 | | 0.674 | 0.0001 |
| | (5.628) | (0.245) | | (0.558) | | | |
| 25 cm | −15.567 | 6.175 | | 2.388 | | 0.615 | 0.0001 |
| | (10.925) | (0.608) | | (0.452) | | | |

[a] *X1* = Accumulated rain days from the day after inoculation to the day of prediction. *X2* = Amount of rainfall from the day after inoculation to the day of prediction. *X3* = Soybean growth stage at inoculation. *X4* = Soybean growth stage at prediction.
[b] Pooled data from the same row spacing of each year.

During the second phase, although primary infections caused by soil inoculum still occur, canopy closure might prevent the direct impact of rain against the ground and therefore reduce inoculum dispersal. In Rhizoctonia web blight of beans, mulching has been reported to effectively reduce disease severity (6). Activity of the fungus in this phase consists of focus expansion within the canopy. The disease rapidly increases through interplant mycelial growth (13,15). During this phase, the number of rain days is more important than the amount of rainfall, as indicated by this study. Frequent rainfall might affect the interplant mycelial growth by maintaining leaf wetness and might also disperse the aerial mycelium. Growth of the soybean canopy is in the log phase during the period of canopy closure (9). Many new, young leaves are generated in a short period of time and may be more susceptible to the disease.

Our study partly explains the results of a previous study (13), in which the progress and final severity of aerial blight decreased as the row spacing increased. In 1987, at the 75-cm row spacing, expansion of established disease foci occurred within and across rows at growth stages V10–V13. At the 25-cm row spacing, focus expansion started at growth stage V7 (approximately 15 days earlier than that of the 75-cm row spacing). A similar situation was observed in 1988. The closed canopy may increase moisture and the chance of leaf contact, both of which are necessary for mycelial development within and between rows.

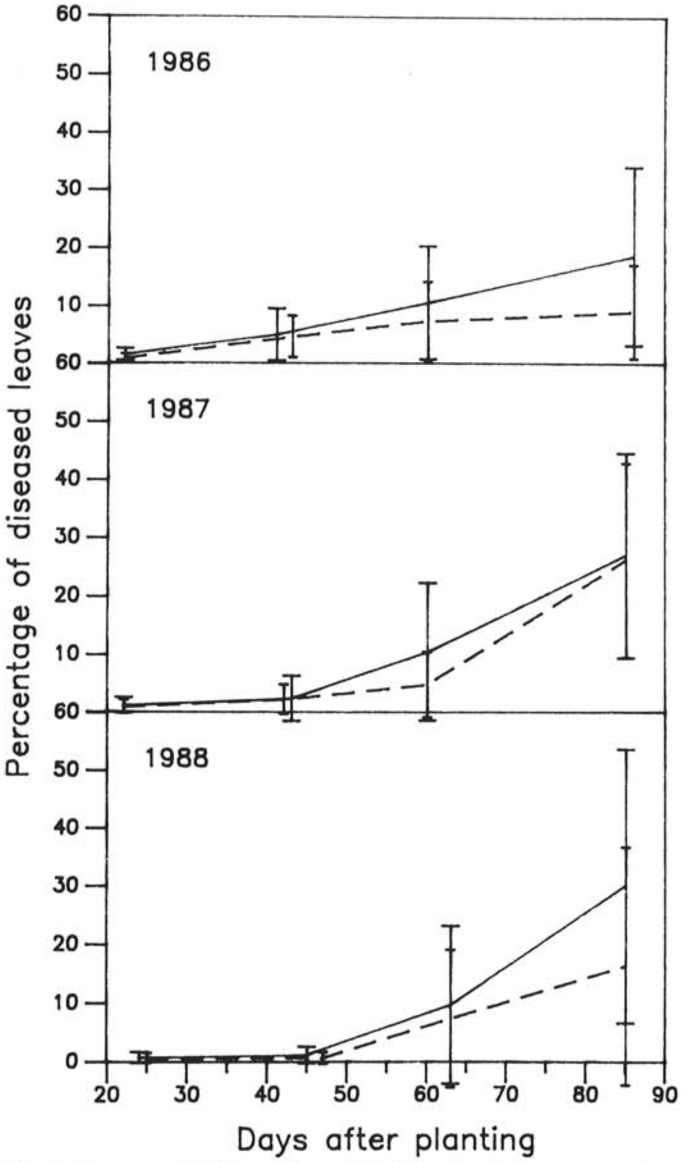


**Fig. 4.** Progress of Rhizoctonia aerial blight of soybean measured as percentage of diseased leaves in subplots of 0.75 × 1.0 m after planting during the 1986, 1987, and 1988 growing seasons. Dashed and solid lines represent data of field one and field two, respectively. Vertical bars are standard deviation of observations.

One reason for the difficulty in quantifying aerial blight is that no delimited diseased individual can be counted as a basic modeling unit. Spread of disease by means of aerial mycelium results in an unclear boundary between diseased and healthy individuals. Erratic development of the disease may be another reason for the difficulty in quantifying the disease. Autocorrelation within the disease progress was not high, especially over long time spans (Table 4). Autocorrelation may be low because of the high dependence of aerial blight development on free moisture. A large amount of plant tissues became diseased in a short period when environmental conditions were favorable, but diseased leaves dropped quickly during dry weather. Since the fungal mycelium is present on plant parts, the disease could develop rapidly during the next period of favorable environmental conditions. Finally, vigorous regeneration of leaves from diseased plants masks the diseased portion and affects the disease rating, which increases the difficulty in disease quantification.

The lack of quantitative information on Rhizoctonia foliar blights may also be because of the complex nature of the diseases. The soilborne phase of *R. solani* is present at the beginning of the season and is the main source of inoculum for primary

TABLE 4. Matrices of correlation coefficients among percentage of diseased leaves at different soybean growth stages (GS) in two fields during the 1986, 1987, and 1988 growing seasons

| | | 1986 field 1 | | |
|---|---|---|---|---|
| GS | V4 | V9 | V12 | R4 |
| V4 | 1.000 | 0.852[a] | 0.523 | 0.588 |
| V9 | | 1.000 | 0.588 | 0.517 |
| V12 | | | 1.000 | 0.877 |
| R4 | | | | 1.000 |
| | | 1986 field 2 | | |
| GS | V4 | V9 | V12 | R4 |
| V4 | 1.000 | 0.591 | 0.268 | 0.172 |
| V9 | | 1.000 | 0.437 | 0.393 |
| V12 | | | 1.000 | 0.895 |
| R4 | | | | 1.000 |
| | | 1987 field 1 | | |
| GS | V4 | V9 | V12 | R4 |
| V4 | 1.000 | 0.601 | 0.533 | 0.467 |
| V9 | | 1.000 | 0.621 | 0.462 |
| V12 | | | 1.000 | 0.584 |
| R4 | | | | 1.000 |
| | | 1987 field 2 | | |
| GS | V4 | V9 | V12 | R4 |
| V4 | 1.000 | 0.851 | 0.693 | 0.537 |
| V9 | | 1.000 | 0.915 | 0.682 |
| V12 | | | 1.000 | 0.758 |
| R4 | | | | 1.000 |
| | | 1988 field 1 | | |
| GS | V5 | V10 | V13 | R4 |
| V5 | 1.000 | 0.488 | 0.752 | 0.435 |
| V10 | | 1.000 | 0.063 | −0.096 |
| V13 | | | 1.000 | 0.624 |
| R4 | | | | 1.000 |
| | | 1988 field 2 | | |
| GS | V5 | V10 | V13 | R4 |
| V5 | 1.000 | 0.202 | −0.259 | 0.069 |
| V10 | | 1.000 | 0.255 | 0.531 |
| V13 | | | 1.000 | 0.567 |
| R4 | | | | 1.000 |

[a]Significance level $r = 0.337$ for $P = 0.05$ and $r = 0.433$ for $P = 0.01$ ($n = 35$).

infections (2,6,7). During the season, disease development is via leafborne mycelium. Currently, no mathematic model has been developed to describe a disease, such as aerial blight, that has both soilborne and leafborne phases. However, models have been developed in root diseases where pathogens also have limited mobility (8). The progress curves of root diseases are often sigmoidal, or S-shaped. This fact was considered explainable by the typical sigmoidal curve of root growth because the disease incidence should parallel curves for root growth if the probability of root contact with the pathogen is determined principally by root growth (12). Gilligan (8) further considered the effect of root growth on disease development in two aspects: the rate of host growth limits the rate of primary infection, and the geometry of root growth influences the rate of secondary infection. Models describing these relationships were developed (8), and models in root diseases may provide an approach to model soybean aerial blight.

Aerial blight relies on both infection rate and level of primary inoculum. The significant correlation between rainfall and the number of primary infections during the season indicates the possibility of predicting the primary infection if soil inoculum data is available. The further development of these primary infections can be described using the disease focus as a basic quantitative unit for aerial blight. Similarly, Smith et al suggested that quantitative evaluation of epidemics of southern blight of processing carrot may be possible by rating disease foci rather than disease severity (20). The results of our experiments suggest that development of a single aerial blight focus can be predicted by the combination of plant growth stages and rainfall patterns (Table 3).

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