Evaluation and Modeling of Rate-Reducing Resistance of Soybean Seedlings to *Phytophthora sojae*

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ABSTRACT

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Lesion length and rate of lesion expansion on taproots of aeroponically grown soybeans infected with *Phytophthora sojae* provided an accurate assessment of rate-reducing resistance. Four days after inoculation with race 3 of *P. sojae* (1,000 zoospores/plant), mean lesion lengths for the cultivars Corsoy, Sloan, Cumberland, Williams, Asgrow 3127, Agripro 26, and Asgrow 2575 were 8.7, 8.6, 7.0, 7.0, 7.7, 5.2, and 4.0 cm, respectively ($LSD_{0.05} = 0.84$). Linear spline regression models consisting of two intersecting straight lines with slopes B_1 and B_2 were used to describe lesion expansion over a 14-day period for each cultivar. Coefficients of determination (R^2) for the selected models ranged from 0.98 to 0.99. Estimates of B_1 among the cultivars did not differ significantly. Estimates of B_2 for the seven cultivars were 1.2, 1.1, 0.9, 0.8, 0.6, 0.4, and 0.1 cm/day, respectively ($LSD_{0.05} = 0.29$). Estimates of B_2 provided an accurate description of rate-reducing resistance. The points where the two lines intersect (join points) for the seven cultivars occurred at 2.1, 2.0, 1.8, 1.7, 2.2, 1.1, and 1.3 days after inoculation, respectively ($LSD_{0.05} = 0.67$).

Additional keywords: aeroponics, linear splines.

Phytophthora root and stem rot of soybeans (*Glycine max* (L.) Merr.) is caused by the fungus *Phytophthora sojae*. Control of the disease has focused on breeding resistant cultivars. Two types of resistance have been recognized in soybean: single-gene resistance and rate-reducing resistance.

Single-gene resistance is conferred by dominant genes (*Rps*) and is characterized by a hypersensitive response following an incompatible interaction between the plant and the fungus (14,15). No *Rps* gene confers resistance to all of the 27 reported races of *P. sojae* (21). The development of compatible races limits the potential of *Rps* genes to provide long-term control.

Rate-reducing resistance is quantitatively inherited and is characterized by a reduced rate of lesion expansion and subsequent smaller lesion size following a compatible interaction (17,24). Synonyms of rate-reducing resistance in soybean include tolerance and field resistance (6,14). Rate-reducing resistance may offer more consistent long-term control than single-gene resistance because it is supposedly race-nonspecific (6,16,17).

Rapid and precise methods to evaluate rate-reducing resistance are needed if this resistance is to be utilized in breeding programs (16). Resistance to *P. sojae* was effectively evaluated on the taproots of soybeans grown in aeroponic culture (22). The system provided easy access to the taproots of soybeans for direct application of inoculum and repeated nondestructive measurements of lesion length. The distinctive borders of the lesions that resulted from infection allowed precise measurements of lesion length. Cultivars were evaluated for single-gene resistance or rate-reducing resistance based on lesion length. The rate of lesion expansion on the soybean taproot could provide a more accurate assessment of rate-reducing resistance.

Disease development on taproots of soybeans grown in aeroponic culture was reported to occur in two distinct phases: an initial phase in which the rate of lesion expansion was very rapid, and a subsequent phase in which the rate of lesion expansion slowed (22). The first phase of disease development occurred within 3 days after inoculation with *P. sojae*. Graphic displays of lesion length on taproots plotted over time indicated that the relationship could be accurately described by models consisting of two straight lines (linear splines) with a common point of intersection (3,4). The first and second lines describe the first and second phases of disease development, respectively. The point of intersection identifies the time of transition from the first phase to the second phase of disease development.

In this paper, soybean cultivars were evaluated for rate-reducing resistance to *P. sojae* on the basis of lesion length and the rate

of lesion expansion on the taproot of aeroponically grown plants. Linear spline models were developed that described disease development. Components of the models were evaluated for their description of rate-reducing resistance.

MATERIALS AND METHODS

Cultivar selection. Seven cultivars reported to have different levels of rate-reducing resistance were selected (6,8,17,23). Reported resistance ratings were low for Corsoy and Sloan; intermediate for Asgrow 3127, Williams, and Cumberland; and high for Agripro 26 and Asgrow 2575. In addition, Corsoy and possibly Cumberland contain *Rps7*; and Agripro 26 and Asgrow 2575 contain *Rps1*. There are no reported *Rps* genes in the other cultivars. Seeds of the different cultivars were supplied by R. L. Bernard (USDA, University of Illinois, Urbana), Asgrow Seed Co. (Ames, IA), and Agripro Seed Co. (Kalamazoo, MI).

Plant culture. Seven 3-day-old plants of each cultivar were transplanted from vermiculite to an aeroponics system. The plants were randomly arranged in the root-misting chamber of the aeroponics system. Plant roots were misted at 5-min intervals for 1 sec with a nutrient solution (0.5× Hogland and Arnon). The nutrient solution was not recirculated. Specific details of the aeroponics system have been reported (22).

The aeroponics system was housed in an environmental growth chamber. Temperature in the chamber was set at 22.5 C (± 2.5 C) and irradiance was 192 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Plants were exposed to light for 12 h of a 24-h cycle.

Fungal culture and inoculation. A culture of race 3 of *P. sojae* from five successive single-zoospore transfers was maintained on 0.25× lima bean agar (5.75 g of lima bean agar (Difco) and 15 g of Bacto-Agar (Difco) in 1 L of deionized, distilled water). The interactions between race 3 of *P. sojae* and the seven cultivars included in this study were compatible following hypocotyl inoculation (7).

Plants were inoculated 48 h after transplantation by submerging the root tip approximately 0.5 cm into 0.5 ml of a solution containing 1,000 zoospores for 20 min (22).

Model selection. Lesion length on taproots of cultivars was measured exactly at 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 7.0, 10.0, and 14.0 days after inoculation (DAI). Mean lesion length (cm) for each cultivar was plotted against DAI, and lesion length for individual replicates of each cultivar was plotted against DAI. Linear spline models consisting of two straight line segments that intersect at a common point (join point) between 1 and 4 DAI, inclusively, were constructed following the procedure for use of dummy variables to fit time trends described by Draper and Smith (4).

Thirteen linear spline models were constructed for each cultivar. Models were constructed with join points (*JP*) forced at 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, and 4.0 DAI (designated *JP*1.0 through *JP*4.0, respectively); or with join points calculated by the model to occur between 1.0 and 1.5, 1.5 and 2.0, 2.0 and 2.5, 2.5 and 3.0, 3.0 and 3.5, and 3.5 and 4.0 DAI (designated *JP*1.0–1.5 through *JP*3.5–4.0, respectively). Each of the linear spline models have a Y intercept equal to 0, since lesion length at the time of inoculation (0 DAI) was 0 cm. The models *JP*1.0 through *JP*4.0 are described by the equation:

$$Y = B_1X_1 + B_2X_2$$

The models *JP*1.0–1.5 through *JP*3.5–4.0 are described by the equation:

$$Y = B_1X_1 + B_2X_2 + B_3X_3.$$

These models were selected on the basis of repeated experiments that indicated that the *JP* of the seven cultivars would occur at a time interval between 1 and 4 DAI.

The data from each cultivar also were fit to a second-degree polynomial (*P2*) and a second-degree polynomial with a Y intercept equal to 0 (*P2I0*). The polynomial models were compared to the *JP* models to determine which provided a better description of disease development on soybean taproots. This was accomplished by comparing the coefficients of determination (R^2) of the models.

Dummy X variables were used in the regression analyses to calculate the slopes (B_1 and B_2) of the two intersecting line segments and the join point. Values of the dummy variables for five representative linear spline models are listed in Table 1. Models with calculated join points require an additional X variable in the equation to estimate B_3. The coefficient B_3 is used to estimate the join point. A model is acceptable only if it produces a negative B_3 value. This requirement is necessary to satisfy the mathematical assumptions underlying the models as outlined by Draper and Smith (4) for models where $0 < B_2 < B_1$.

Join points, estimates of B_1 and B_2, and R^2 values for the *JP* models were obtained for each cultivar using the SAS GLM procedure for the regression of cultivar means on the appropriate dummy variables (13). Regression coefficients and R^2 values for the second-degree polynomial models (*P2* and *P2I0*) also were obtained for each cultivar using the SAS GLM procedure. Because the *JP* and *P2I0* models lacked a calculated Y intercept, their R^2 values were calculated from the equation:

$$R^2 = 1 - RSS/CSS$$

where R^2 is the coefficient of determination, *RSS* is the residual sum of squares from the model, and *CSS* is the corrected total

TABLE 1. Values of dummy X variables for five representative regression models with linear splines evaluated for describing the relationship between lesion length formed on taproots of soybean cultivars infected with *Phytophthora sojae* and time in days after inoculation (DAI)[a]

Model *JP*1.0			Model *JP*1.0–1.5 and *JP*1.5				Model *JP*3.5–4.0 and *JP*4.0			
DAI	*X*1	*X*2	DAI	*X*1	*X*2	*X*3[b]	DAI	*X*1	*X*2	*X*3[b]
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1.0	1.0	0.0	1.0	1.0	0.0	0.0	1.0	1.0	0.0	0.0
1.5	1.0	0.5	1.5	1.5	0.0	1.0	1.5	1.5	0.0	0.0
2.0	1.0	1.0	2.0	1.5	0.5	1.0	2.0	2.0	0.0	0.0
2.5	1.0	1.5	2.5	1.5	1.0	1.0	2.5	2.5	0.0	0.0
3.0	1.0	2.0	3.0	1.5	1.5	1.0	3.0	3.0	0.0	0.0
3.5	1.0	2.5	3.5	1.5	2.0	1.0	3.5	3.5	0.0	0.0
4.0	1.0	3.0	4.0	1.5	2.5	1.0	4.0	4.0	0.0	1.0
7.0	1.0	6.0	7.0	1.5	5.5	1.0	7.0	4.0	3.0	1.0
10.0	1.0	9.0	10.0	1.5	8.5	1.0	10.0	4.0	6.0	1.0
14.0	1.0	13.0	14.0	1.5	12.5	1.0	14.0	4.0	10.0	1.0

[a] DAI and *JP* are abbreviations for days after inoculation and join point, respectively. Models *JP*1.0, *JP*1.5, and *JP*4.0 have a forced *JP* and are described by the equation, $Y = B_1X_1 + B_2X_2$. Models *JP*1.0–1.5 and *JP*3.5–4.0 have a calculated *JP* and are described by the equation, $Y = B_1X_1 + B_2X_2 + B_3X_3$.

[b] Values for dummy X variables were assigned as follows: X_1 = DAI from 0 DAI to JP_{max} (JP_{max} is the largest attainable *JP* for a given model), and then X_1 = 1 from JP_{max} to 14 DAI; X_2 = DAI − X_1; and X_3 = 0 from 0 DAI to JP_{max}, and then X_3 = 1 from JP_{max} to 14 DAI. X_3 is not used in *JP*1.0, *JP*1.5, and *JP*4.0 because the join point is forced at 1.0, 1.5, and 4.0 DAI, respectively.

TABLE 2. Mean lesion length formed on taproots of cultivars infected with *Phytophthora sojae* at different days after inoculation[a]

Cultivar	Days after inoculation									
	1.0	1.5	2.0	2.5	3.0	3.5	4.0	7.0	10.0	14.0
Corsoy	2.6	4.9	6.6	6.9	7.6	7.9	8.7	11.7	17.8	20.6
Sloan	2.3	5.2	5.9	6.9	7.3	8.0	8.6	12.1	14.5	20.2
Cumberland	3.0	4.3	5.5	5.7	6.1	6.6	7.0	10.9	12.5	15.8
Williams	3.5	4.8	5.8	5.9	6.6	6.8	7.0	11.5	13.1	15.1
Asgrow 3127	2.9	4.5	5.3	5.9	6.3	6.9	7.7	10.4	11.1	13.0
Agripro 26	3.6	3.7	4.3	4.4	4.9	5.0	5.1	6.4	8.4	8.8
Asgrow 2575	2.9	3.4	3.8	3.9	4.0	4.0	4.0	4.2	4.2	4.6
$LSD_{0.05}$	1.03	0.67	0.84	0.69	0.71	0.76	0.84	1.89	2.90	3.54
CV	32.0	14.1	14.7	11.3	10.7	11.0	11.3	18.2	23.8	23.4

[a] Lesion length is measured in centimeters and data are the mean of seven replicates. LSD ($P = 0.05$) values based on univariate analysis of variance for a specific day after inoculation.

sum of squares from model *P2* (2).

Join points were calculated from the equation:

$$JP = JP_{max} + (B_3 / (B_1 - B_2))$$

where *JP* is the join point, JP_{max} is the largest attainable *JP* value for a given model (e.g., 2.0 is the largest attainable *JP* value for the model *JP*1.5–2.0), and B_1, B_2, and B_3 are regression coefficients (4). For each cultivar, the *JP* model with the highest R^2 value was selected.

Univariate, completely randomized design analyses of variance were performed on lesion lengths observed at each of the 10 measurement times. Since there was some evidence of heterogeneity of error variance as a function of DAI, join points and estimates of B_1 and B_2 were computed for each individual replicate of each cultivar using all 13 of the linear spline models. For each replicate, the *JP* model with the highest R^2 value was selected. These values were then subjected to completely randomized design analyses of variance to obtain estimates of the error variances of the join points and slopes (B_1 and B_2) computed from the regression analyses of cultivar means. These error variances were used as the basis for computing least significant differences (LSD [$P = 0.05$]) for comparisons of B_1, B_2, and *JP* among cultivars (1).

RESULTS

Evaluation of rate-reducing resistance. The lesions that formed on the taproots of the seven cultivars were brown and water-soaked and similar in appearance. A dark band formed between the zone of healthy and diseased tissue on the cultivar Asgrow 2575 at 4 DAI. A similar but more diffuse band also was observed on Agripro 26.

Four groups of cultivars had significantly different mean taproot lesion lengths at 14 DAI (Table 2). The groups, in order of decreasing lesion length, were as follows: Corsoy and Sloan; Cumberland, Williams, and Asgrow 3127; Agripro 26; and Asgrow 2575. The same groups of cultivars had significantly different mean taproot lesion lengths at 3.5 and 4.0 DAI. Similar groupings were apparent at all other measurement times except 1.0 DAI; however, differences between some cultivars from the different groups were not always significant.

Lesions were longest on taproots of Agripro 26 and shortest on taproots of Corsoy and Sloan at 1.0 DAI. At 1.5 DAI, lesions were longest on taproots of Corsoy and Sloan and shortest on taproots of Agripro 26 and Asgrow 2575.

Mean lesion length for Asgrow 2575 was significantly different from the other cultivars, except Agripro 26, from 1.5 to 14.0 DAI. Asgrow 2575 and Agripro 26 were significantly different from each other from 3.0 to 14.0 DAI. Mean lesion length was not significantly different for the cultivars Asgrow 3127, Cumberland, and Williams at any measurement time. Corsoy and Sloan were significantly different from each other only at 10 DAI. The group Cumberland, Williams, and Asgrow 3127 and the group Corsoy and Sloan were not significantly different at 7.0 DAI.

TABLE 3. Regression estimates from linear spline models of lesion expansion over a 14-day period for means of cultivars infected with *Phytophthora sojae*[a]

Cultivar	B_1	B_2	*JP*	Model
Corsoy	3.0	1.2	2.1	*JP*2.0–2.5
Sloan	3.1	1.1	2.0	*JP*2.0
Cumberland	2.9	0.9	1.8	*JP*1.5–2.0
Williams	3.3	0.8	1.7	*JP*1.5–2.0
Asgrow 3127	2.8	0.6	2.2	*JP*2.0–2.5
Agripro 26	3.6	0.4	1.1	*JP*1.0–1.5
Asgrow 2575	2.9	0.1	1.3	*JP*1.0–1.5
$LSD_{0.05}$		0.29	0.67	

[a] B_1, B_2, and *JP* are the first slope, second slope, and point of intersection (join point) of the two straight lines, respectively. Units for B_1 and B_2 are in cm/day; units for *JP* are in days after inoculation. Regression analyses were performed on means of seven replicates.

Williams and Cumberland were not significantly different from Sloan or Corsoy at 1.5, 2.0, 7.0, and 10.0 DAI. Mean lesion length for Sloan and Corsoy was greater than Williams, Cumberland, and Asgrow 3127 from 1.5 to 14 DAI.

The coefficient of variation was smallest between 2.5 and 4.0 DAI, inclusively. Variation was greatest at 1.0, 10.0, and 14.0 DAI.

Model selection. The *JP* model selected for the cultivar Sloan had a forced join point at 2.0 DAI (Table 3 and Fig. 1). Models selected for the other cultivars had calculated join points between 1.0 and 1.5, 1.5 and 2.0, or 2.0 and 2.5 DAI. Join points ranged from 1.1 DAI for Agripro 26 to 2.2 DAI for Asgrow 3127. Join point values for Agripro 26 and Asgrow 2575 were significantly smaller than Asgrow 3127, Corsoy, and Sloan.

Estimates of B_1 ranged from 2.8 cm/day for Asgrow 3127 to 3.6 cm/day for Agripro 26 and were not significantly different among the seven cultivars. Estimates of B_2 ranged from 0.1 cm/day for Asgrow 2575 to 1.2 cm/day for Corsoy and were significantly different among the cultivars.

Coefficients of determination, R^2, were higher for the *JP* models than for the *P2* or *P2I0* models (Table 4). Values for R^2 ranged from 0.98 to 0.99, 0.62 to 0.98, and 0.15 to 0.97 for the *JP*, *P2*, and *P2I0* models, respectively.

DISCUSSION

Rate-reducing resistance to *P. sojae* was accurately evaluated on soybean taproots grown in aeroponic culture. Corsoy and Sloan; Cumberland, Williams, and Asgrow 3127; Agripro 26; and Asgrow 2575 expressed relatively low, moderate, high, and very high levels of rate-reducing resistance, respectively, based on lesion length at 14 DAI. These rankings are consistent with previous reports (6,8,17,23).

The aeroponics system affords greater precision in detecting differences between cultivars with high levels of resistance and cultivars with intermediate or low levels of resistance than it does between cultivars with intermediate levels of resistance and culti-

vars with low levels of resistance. This sensitivity would be useful if this system were employed for breeding resistant cultivars, since it is the progeny with superior resistance that are of interest. Jimenez and Lockwood (6) also reported that differences between cultivars with intermediate and low levels of resistance were not always discernible following inoculation of soil-grown soybean plants with zoospores.

Although differences between cultivars with intermediate and low levels of resistance were not always significant at earlier measurement times, we are confident that ratings made at 14 DAI will consistently discriminate between the two groups. Differences between the two groups at 14 DAI were the greatest

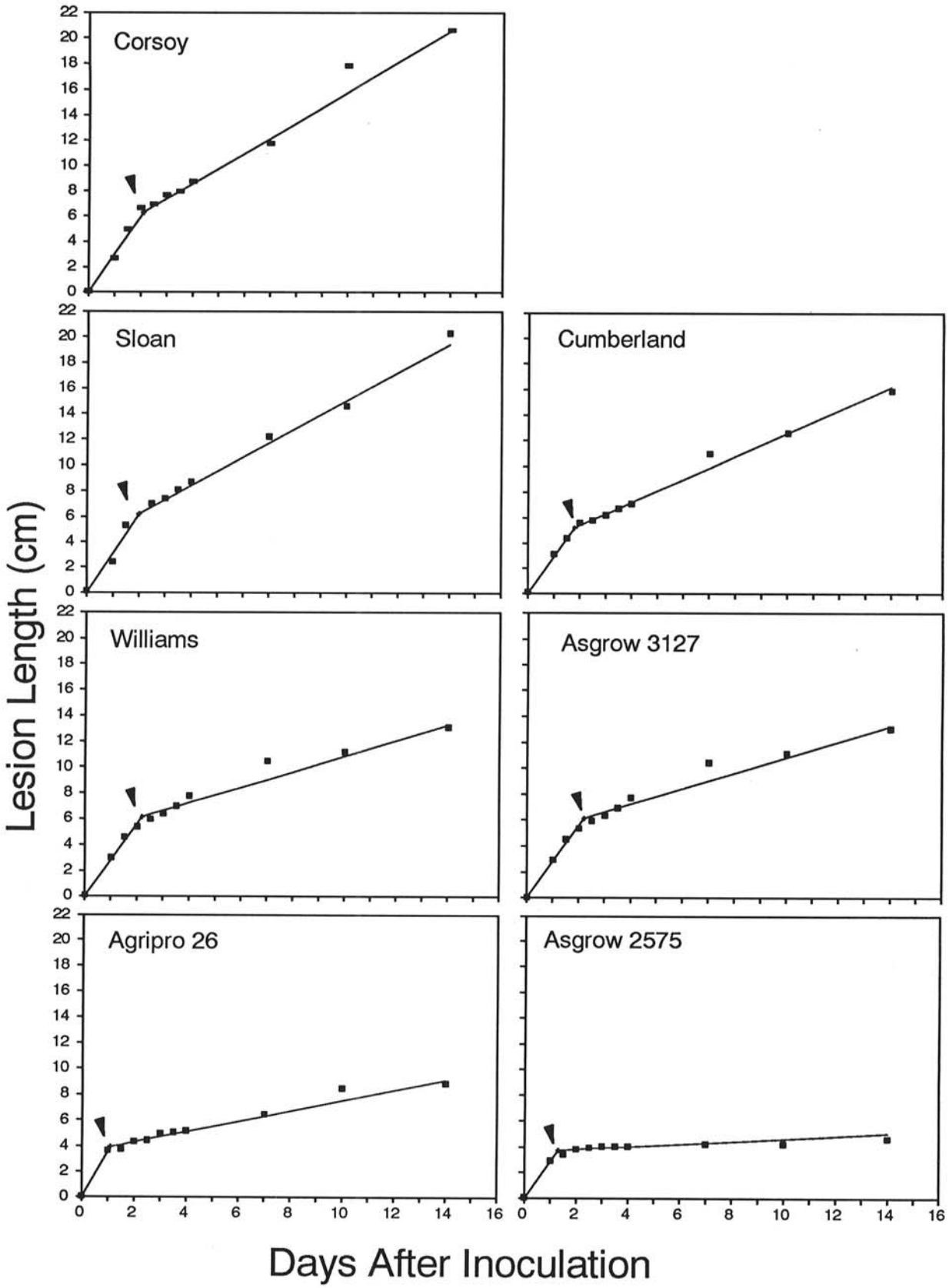

Fig. 1. Estimated values and join points (arrow) for linear spline models with slopes B_1 and B_2 and mean observed values (■) of lesion length on taproots of soybean cultivars over a 14-day period after inoculation with *Phytophthora sojae*.

of any measurement time, and this divergent trend continued resulting in more apparent differences at later observation times (data not presented). For example, the lesion on the cultivar of the group Sloan and Corsoy expanded beyond the hypocotyl-root junction reaching the cotyledon as previously reported (22), while the lesions on the cultivars Cumberland, Williams, and Asgrow 3127 remained below the hypocotyl-root junction. Olah et al (10) reported also that lesion progress was impeded at the hypocotyl-root junction. The importance of this transition zone in resistance warrants further investigation.

Linear measurements were not made past the hypocotyl-root junction because the lesion on the hypocotyl was less discernible than on the taproot. Such imprecise measurements would have contributed excess variation to the linear spline models. In addition, lesion measurements on the hypocotyl were not accurate indicators of disease progress, since internal necrosis often extended beyond the margins of the visible expanding lesion. Internal necrosis was not observed in advance of the lesion on the taproot.

The *JP* models provided a better fit to the data than did the polynomial models (*P2* and *P2I0*), particularly for the cultivars Agripro 26 and Asgrow 2575. The models also provided an accurate description of disease development. The slope of the first segment, B_1, described the first phase of disease development when the rate of lesion expansion was very rapid. During this phase, the lesion expanded in two directions from the infection site; toward the root tip and toward the cotyledon. The first phase of disease development ended when the lesion extended to the root tip and root-tip growth ceased, which was indicated by the join point.

The slope of the second segment, B_2, described the second phase of disease development when the rate of lesion expansion was slower. As the relative resistances of the cultivars increased, corresponding estimates of B_2 decreased. The estimate of B_2 provided an accurate description of rate-reducing resistance. A similar trend occurred for the join point values, with the exception of Asgrow 3127. As resistance increased, join point values decreased. If B_2 describes the magnitude of rate-reducing resistance, then the join point also could describe the time it requires for host resistance to become effective following infection by *P. sojae*. Incompatible interactions between cultivars with the *Rps2* or *Rps3* gene and *P. sojae* were characterized also by a rapidly expanding lesion that abruptly terminated taproot growth (22). If linear spline models had been employed to describe disease development on these cultivars, the calculated *JP* values also would have been low.

Estimates of B_1 were not significantly different among the seven cultivars. Variation in early measurements was high, which probably reflects the complexity of disease development in the early stages of pathogenesis. For example, cell necrosis due to the hypersensitive response, rather than to fungal parasitism, could be responsible for the rapid rate of lesion expansion and the abrupt termination of root tip growth expressed by cultivars with effective *Rps* genes (22). Stössel et al (15) reported that lesions that had formed on soybean hypocotyls after incompatible interactions were composed primarily of nonpenetrated, necrotic cells. Similarly, a rapid resistant response by cultivars with high levels of rate-reducing resistance also could cause a high level of induced cell necrosis that subsequently terminates root tip growth. In contrast, cultivars slower to respond to fungal invasion would have a higher proportion of the cells parasitized, and the rate of lesion expansion and the termination of root tip growth would be more dependent upon the rate of fungal colonization. Estimates of B_1 for more aggressive isolates of *P. sojae* were significantly greater than estimates of B_1 for less aggressive isolates when compared on Williams or Asgrow 3127 (20).

Lesion development as described by B_1 is complicated further by differences in cell age and tissue differentiation in the taproot. Both decrease from the initial infection site toward the root tip but increase from the point of infection toward the hypocotyl-root junction.

The linear spline models permitted the detection of subtle differences in disease development among cultivars. Constructing the models to fit the data, rather then forcing the data to fit a given model, expanded biological inference. For example, an individual *JP* model could have produced an acceptable R^2 value for all seven cultivars. However, comparisons would have been limited to estimates of B_2, and the potential biological information provided by the *JP* would have been obscured.

It is likely that rate-reducing resistance is complex and caused by several biochemical mechanisms. These mechanisms could be effective during different stages of pathogenesis. Resistant responses to infection by *P. sojae* include phytoalexin accumulation, apposition production, and cell necrosis (5,15). Signaling that activates resistance also could be involved (12). Variation in the rate of development for any of the resistance responses could be responsible for the different levels of rate-reducing resistance. Such variation could be expressed among cultivars as difference in estimates of B_2 and *JP* values. Histological and biochemical studies comparing cultivars with different estimates of B_2 and *JP* values may reveal the mechanisms responsible for rate-reducing resistance.

Graphic displays of lesion length plotted over time and estimates of B_2 from the linear spline models suggest that the mechanism(s) responsible for this resistance decreases the rate of lesion expansion. Tooley and Grau (17) reported a slow rate of lesion expansion on cotyledons of resistant plants inoculated with encysted zoospores of *P. sojae*. Olah and Schmitthenner (9) and Olah et al (10) also reported small lesions on hypocotyls of some cultivars inoculated with mycelia of *P. sojae*, but referred to these cultivars as tolerant. Apparently, rate-reducing resistance is an active response by the host that impedes pathogen invasion of the taproot, which subsequently slows the rate of epidemic development in the field (18,19). Since disease progress is slowed on an individual plant and a field population basis, referring to this resistance as rate reducing provides a more accurate and comprehensive description of the host response to infection than the terms tolerance or field resistance (11).

TABLE 4. Coefficients of determination for three models describing lesion expansion over a 14-day period for cultivars infected with *Phytophthora sojae*[a]

Cultivar	*JP*	*P2*	*P2I0*
Corsoy	0.99	0.98	0.97
Sloan	0.99	0.97	0.95
Cumberland	0.99	0.98	0.96
Williams	0.98	0.98	0.95
Asgrow 3127	0.98	0.97	0.94
Agripro 26	0.98	0.91	0.80
Asgrow 2575	0.99	0.62	0.15

[a] R^2 values for linear spline (*JP*), second-degree polynomial (*P2*), and second-degree polynomial with intercept forced at 0 (*P2I0*).

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