Soybean Rust Development and the Quantitative Relationship Between Rust Severity and Soybean Yield

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ABSTRACT

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Phakopsora pachyrhizi was inoculated on two soybean (*Glycine max*) genotypes at three different reproductive growth stages (GS) in four trials. Leaf rust was more severe on Taita Kaohsiung No. 5 (TK 5), a commercial cultivar, than on SRE-B15-A (B15 A), a genotype selected for tolerance to leaf rust. At GS R6, the percentage of leaf area infected ranged from 14 to 95% for TK 5 and from 0 to 34% for B15 A. Values for area under disease progress curve (AUDPC) were significantly greater for TK 5 than B15 A. Yields in fungicide-protected plots ranged from 2,312 to 3,546 kg/ha and were not significantly different between the genotypes. Average yields of plants inoculated at GS R1 were reduced by 62 and 22% and seed weights by 35 and 14% for TK 5 and B15 A, respectively, compared with fungicide-protected plots. Regressions of yield percentage of fungicide-protected plants on disease severity assessments at GS R6, AUDPC, and area under the green leaf area curve were significant for both genotypes.

Additional keywords: yield loss

Soybeans (*Glycine max* (L.) Merr.) are grown from temperate to tropical regions of the world. Production is greatest in the United States, Brazil, and the People's Republic of China, and it is increasing in tropical and subtropical regions because greater emphasis has been placed on breeding soybeans suitable for tropical environments (7).

There are numerous constraints to soybean production in the tropics, including problems related to adaptation, diseases, insect pests, poor nodulation, and seed longevity. In the Eastern Hemisphere, soybean yields have been reduced consistently by leaf rust, caused by *Phakopsora pachyrhizi* Syd. & P. Syd., which is endemic to most of the region (2). Yield losses ranging from 5 to 95% have been reported from experimental trials in Australia, Japan, the Republic of China, and the Philippines (1,5,6,12,16,22,24,28,30,32). The pathogen is prevelant in other regions of the world, such as Brazil, Puerto Rico, and parts of Africa, but it causes less damage, and isolates have been reported to be less aggressive than isolates from the Eastern Hemisphere (2). Bromfield (2) has reviewed the importance of leaf rust in countries where the disease occurs. Sinclair (21) recently reviewed the potential threat of leaf rust to soybean production in the tropics.

Severity of soybean leaf rust greatly increases during pod-filling stages (25). Late-maturing genotypes were found to be as susceptible as earlier maturing genotypes when compared at similar growth stages (23). The magnitude of yield loss and adverse effects on yield components have been correlated with the onset of the disease in relation to growth stage (16).

Rate-reducing and race-specific resistance to leaf rust has been reported (3,4,10,11,14), but no cultivars with acceptable resistance to all strains of *P. pachyrhizi* have been developed. The difficulties associated with the identification and quantification of rate-reducing resistance and the ineffectiveness of race-specific resistance have led to the use of selecting genotypes tolerant to *P. pachyrhizi* (24).

Tolerance to *P. pachyrhizi* was defined as the relative yielding ability of soybean cultivars grown under severe rust stress; tolerance has been identified and used to minimize yield losses (24). In experimental plots at the Asian Vegetable Research and Development Center (AVRDC) in Taiwan, yield reduction in commercial cultivars attributable to leaf rust ranged from 48 to 91% and from 58 to 90% in trials conducted from March to June (spring season) and from September to November (fall season), respectively. Lines developed for tolerance to rust at AVRDC yielded 30–60% more than commercial cultivars (26). Tolerance has also been used in reference to cultivars that have susceptible reactions and an equivalent level of infection and reproduction of the pathogen but have significantly greater yields than other susceptible cultivars (18,19).

Yield loss studies have shown the impact of leaf rust on soybean yield, but there is a lack of information regarding the relationship of leaf rust severity to yield and its components in genotypes that have been developed for leaf rust tolerance. The objectives of this study were to quantify the effect of soybean leaf rust severity on yield and yield components and to compare the effect of leaf rust on a susceptible tolerant genotype with a susceptible intolerant cultivar.

MATERIALS AND METHODS

A soybean line, SRE-B15-A (B15 A), selected for tolerance to leaf rust at AVRDC (1980–1987), and an intolerant commercial cultivar, Taita Kaohsiung No. 5 (TK 5), were planted on 3 October 1986, 2 March and 21 September 1987, and 3 March 1988. These trials will be referred to as trials 1, 2, 3, and 4, from the earliest to the latest date of planting, respectively. Both B15 A and TK 5 mature between 90 and 105 days in the spring and fall seasons in Taiwan.

Experimental plots measured 4 × 6 m each and were spaced 2 m apart. Seeds were planted in eight rows, 50 cm apart with 4×10^5 plants per hectare, i.e., 10 cm between hills with two seeds per hill. The four trials were conducted at AVRDC in sandy loam soil. *Crotalaria* sp. was grown in the field between the spring and summer seasons, and the field was fallow between the fall and spring seasons.

Trials were arranged as split plots in a randomized complete block design with four replications of the main plots, line B15 A and cultivar TK 5. Subplots included four treatments: inoculation with *P. pachyrhizi* at GS R1, R3, or R5 (8) and a fungicide-protected treatment. Dithane M-45 (80%) (maneb) was applied weekly at 1.92 kg a.i./ha to all plants from GS V7 up to 1 wk before inoculation. The fungicide-protected treatment was sprayed every 7 days until GS R7.

Urediniospores used for inoculation were collected from infected leaves of TK 5 grown in a field separate from the experimental plot. Collected leaves were placed in polyethylene bags overnight at room temperature. The next day, leaves were soaked and rinsed in water for 5–10 min. The washing solution of uredin-

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iospores was filtered through cheesecloth or a nylon net and diluted to 2×10^4 spores per milliliter. Plants were inoculated by spraying the suspension on leaves with a pressurized sprayer set at $9.8\text{–}14.7 \times 10^4$ Pa. Plots were furrow-irrigated initially and then overhead-irrigated for 10 min two to three times per week starting at the time of inoculation of the first plots (R1).

Leaf rust severity, defoliation, and growth stage were rated every 7 days from 38, 47, 51, and 57 days after planting in trials 1–4, respectively, until harvest at GS R8. The percentage of leaf area infected was estimated based on a visual observation of plants on a whole plot basis. Defoliation was determined by counting the number of defoliated nodes on 10 randomly selected plants per plot. The percentage of defoliation was calculated as follows: (number of nodes without leaves/total number of nodes) × 100. Area under the disease progress curve (AUDPC) was calculated according to the formula presented by Shaner and Finney (20). The percentage of green leaf area was estimated as follows: (100 − percentage of defoliation) − [percentage of leaf area infected × (100 − percentage of defoliation)]. The percentage of green leaf area in the protected plots was 100 − percentage of defoliation. The area under the percent green leaf area curve (AUGLAC) was calculated with the same formula as AUDPC (20).

Before harvest, the height of 10 randomly selected plants per plot was measured, and the number of pods and branches were counted. The number of seeds per pod was calculated by dividing the total number of seeds by the total number of pods. Yield was measured from a 3 × 5 m area in the center of each plot, weight of 100 seeds was recorded in grams, and both weights were adjusted to 13% seed moisture. Reduction in yield and seed weight was expressed as a percentage of the yield from plants in fungicide-protected plots within each replication.

Data were analyzed by analysis of variance. Fisher's least significant difference values were calculated ($P \leq 0.05$) for genotype, treatment, genotypes within the same treatment, and treatments within the same genotype. Seed weight and yield data for each plot were correlated with percentage of leaf area infected, defoliation, percentage of green leaf area, AUDPC, and AUGLAC. Regressions of percentage of leaf area infected, defoliation, and percentage of green leaf area on days after planting were obtained for each genotype in the four trials. Regressions of yields on percentage of leaf area infected, defoliation, and percentage of green leaf area were computed for each genotype and trial. *F* statistics were examined to determine the overall significance of each model and the significance of polynomial terms.

RESULTS

Leaf rust pustules were visible 10–14 days after inoculation. No disease was observed on plants in uninoculated, fungicide-protected plots. The percentage of leaf area infected did not significantly differ between the two genotypes at the initial rating (GS R2) in any of the trials. At GS R6, the percentage of leaf area infected was significantly different for genotypes, treatments, and the genotype × treatment interaction. Among means of percentage of leaf area infected for TK 5, treatments differed significantly for all trials (Table 1). B15 A had significantly lower values for percentage of leaf area infected within each of the inoculated treatments compared with TK 5 for all trials (Table 1). Leaf rust development was more rapid and severe for TK 5 than B15 A for plants inoculated at GS R1 in all trials (Fig. 1). Regressions of percentage of leaf area infected over time were fit by quadratic equations, except for TK 5 in trials 1 and 2 (Fig. 1).

Values for AUDPC and AUGLAC differed significantly for genotypes, treatments, and the genotype × treatment interaction. TK 5 had significantly higher AUDPC values than B15 A within each of the inoculated treatments for all trials (Table 1). In most trials, the AUDPC values for B15 A and TK 5 increased significantly at each earlier time of inoculation. The AUGLAC was significantly lower for TK 5 than B15 A within each inoculated treatment (Table 1). Within TK 5, the AUGLAC increased as inoculations were delayed. Within B15 A, the range of AUGLAC values was not as great as for TK 5, and there were less significant differences between treatments as compared with TK 5 (Table 1).

The percentage of defoliation of plants inoculated at GS R1 was not significantly different between TK 5 and B15 A until the last two ratings in trials 1 and 3 (Fig. 1). Defoliation increased at a similar rate for both entries. Quadratic models were significant and best explained the percentage of defoliation for both the entries in 12 of 16 cases, and four cases were fit by linear models. The percentage of green leaf area was reduced as plants matured, and it was significantly lower for TK 5 than for B15 A after the third rating for plants inoculated at GS R1 in all trials (Fig. 2). The percentage of green leaf area significantly decreased in each entry for each trial, and variation in the data was best explained by a quadratic model, except in two cases.

No consistent significant differences occurred between height of plants, seeds per pod, or in the number of branches and nodes within B15 A or TK 5 in any of the trials. The number of pods and seeds from plants in fungicide-protected plots and in plots inoculated at GS R5 increased significantly compared with plots inoculated at GS R1 in trials 2 and 4 (Table 2). No significant differences occurred between the number of pods

Table 1. Percentage of leaf area infected at growth stage (GS) R6, area under disease progress curve (AUDPC), and area under green leaf area curve (AUGLAC) for two soybean genotypes inoculated with *Phakopsora pachyrhizi* at three growth stages

		Leaf area infected (%)		AUDPC[a]		AUGLAC[a]	
Trial	Growth stage	TK 5	B15 A	TK 5	B15 A	TK 5	B15 A
1	R1	69	3	2,573	356	2,056	4,071
	R3	46	1	1,993	191	2,599	4,348
	R5	14	0	769	43	3,830	4,676
FLSD ($P > 0.05$)[b]		6.6		189		199	
FLSD ($P > 0.05$)[c]		10.5		240		349	
2	R1	95	25	2,159	567	1,758	2,948
	R3	80	10	1,507	228	2,286	3,456
	R5	68	7	1,174	171	2,702	3,635
FLSD ($P > 0.05$)[b]		5.0		87		156	
FLSD ($P > 0.05$)[c]		7.4		202		160	
3	R1	89	31	1,335	423	1,925	2,775
	R3	74	20	1,040	279	2,212	3,062
	R5	29	3	491	42	2,857	3,380
FLSD ($P > 0.05$)[b]		4.2		57		91	
FLSD ($P > 0.05$)[c]		4.2		64		172	
4	R1	83	34	2,496	1,052	1,280	2,383
	R3	60	20	1,572	606	2,162	3,024
	R5	30	7	925	258	2,956	3,614
FLSD ($P > 0.05$)[b]		9.4		139		135	
FLSD ($P > 0.05$)[c]		8.2		122		121	

[a] Values determined with the formula given by Shaner and Finney (20).

[b] Fisher's least significance differences between treatment means for the same genotype.

[c] Fisher's least significance differences between treatment means for different genotypes.

or seeds per plant between the two genotypes, except in trial 1, when TK 5 had a significantly higher number of pods and seeds than B15 A.

Differences in yield and 100-seed weight data for genotypes, treatments, and genotypes × treatments were significant. The yield of B15 A was significantly higher than that of TK 5 for all inoculated treatments except for the late inoculation at GS R5 in trials 1 and 3 (Table 3). In the fungicide-protected plots, yields of B15 A and TK 5 did not differ significantly. The lowest yields for B15 A and TK 5 were obtained from plots inoculated at GS R1. Yields increased as the inoculation date was delayed. In all trials, yields of TK 5 inoculated at GS R1 were significantly lower than yields of plants inoculated at GS R5 or from fungicide-protected plots. Yield reductions averaged over four trials from plants inoculated at GS R1, R3, and R5 were 63, 53, and 34% for TK 5 and 23, 16, and 7% for B15 A when compared with yields of fungicide-protected plants.

The 100-seed weight of B15 A was greater than TK 5 for each treatment in all trials (Table 3). Seed weights for both genotypes increased as inoculations were delayed. The range of differences within B15 A was less than TK 5, although in all trials, the seed weights from fungicide-protected plots were significantly more than those from plots inoculated at GS R1. Seed weight reductions in the four trials averaged 37, 32, and 20% for TK 5 and 14, 11, and 5% for B15 A when inoculated at GS R1, R3, and R5, respectively.

The percentage of yield of fungicide-protected plants of TK 5 was reduced significantly as the percentage of leaf area infected increased in all trials (Fig. 3). The yield of B15 A decreased significantly as the percentage of leaf area infected increased in two of the four trials, however, the magnitude of decrease was significantly less than that of TK 5. The percentage of yield of B15 A was never less than 60% when fungicide protected, whereas the percentage of leaf area infected was greater than 60%. Seed weight was also reduced with an increase in the percentage of leaf area infected, although the coefficient of determination values were lower and the differences were not as great as for percentage of yield. The range of values of seed weights were, by comparison, not as great as yields based on percentages from fungicide-protected plants.

Slopes of regression lines of yield percentages decreased as the AUDPC values increased; yield of TK 5 was better correlated to AUDPC values than was yield of B15 A (Fig. 4). A quadratic model accounted for 66–83% of the variation, and only in trial 1 was a second-degree polynomial not significant. With an increase in the values of AUGLAC, the yields increased (Fig. 4). Plants with an AUGLAC of 3,000 or greater had 80% of the yield of plants from protected plots for B15 A, whereas AUGLAC for TK 5 did not reach 3,000, and yields were mostly less than 80% of fungicide-protected plants.

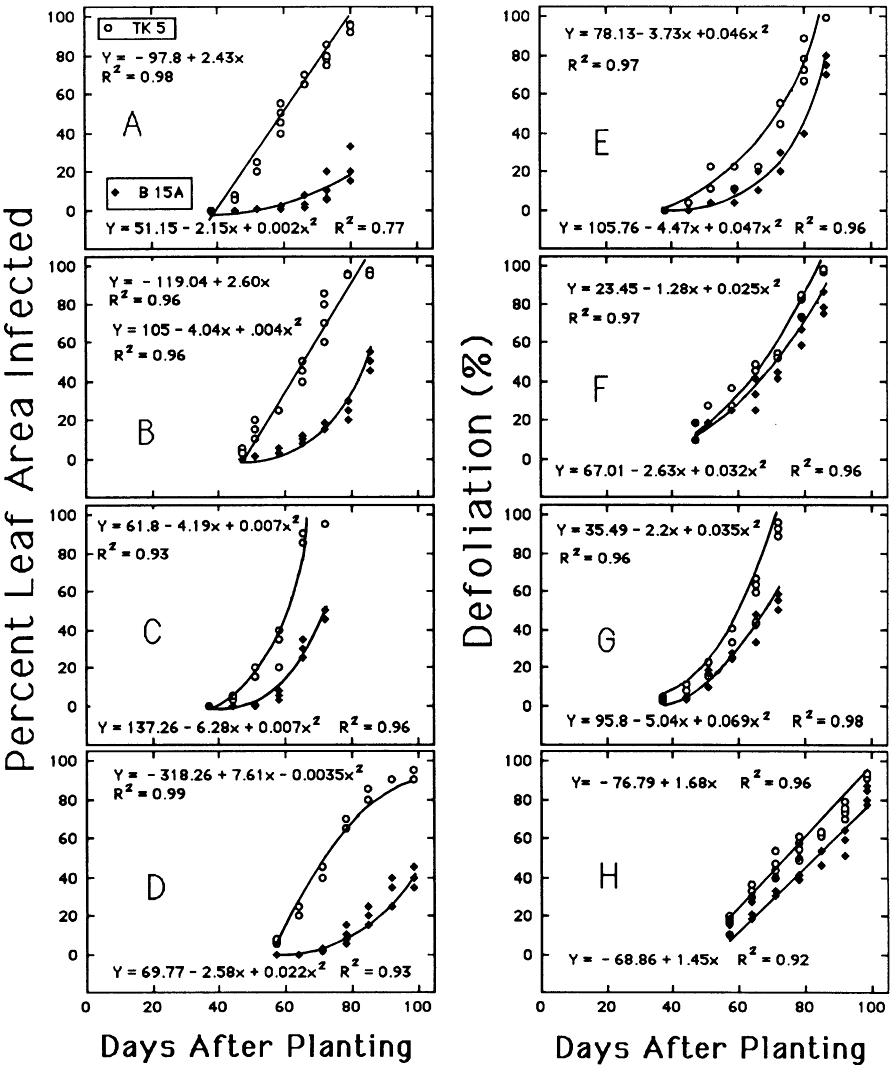

Fig. 1. Percentage of leaf area infected in **(A)** trial 1, **(B)** trial 2, **(C)** trial 3, and **(D)** trial 4 and defoliation in **(E)** trial 1, **(F)** trial 2, **(G)** trial 3, and **(H)** trial 4 of two soybean genotypes (B15 A and TK 5) inoculated at growth stage R1.

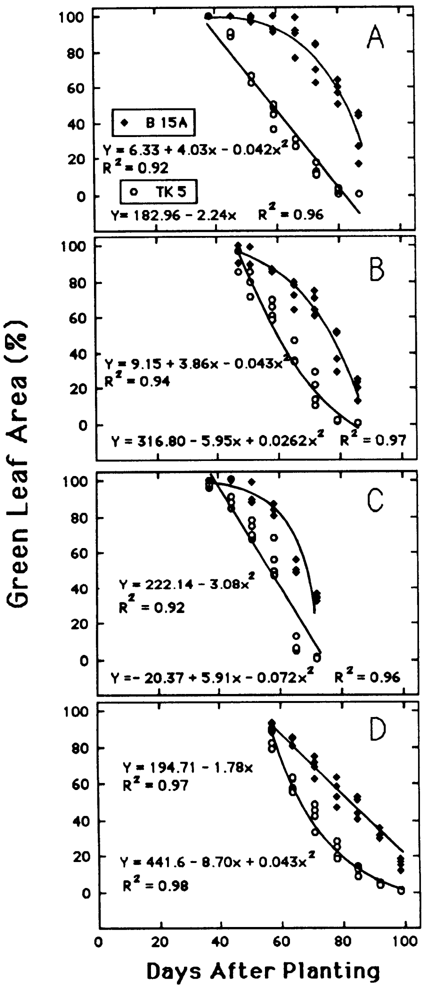

Fig. 2. Percentage of green leaf area of two soybean genotypes (B15 A and TK 5) inoculated at growth stage R1 in **(A)** trial 1, **(B)** trial 2, **(C)** trial 3, and **(D)** trial 4.

DISCUSSION

In our study, leaf rust epidemics on soybeans were initiated at different reproductive growth stages by inoculation with *P. pachyrhizi.* Yields of B15 A and TK 5 were similar when fungicide protected, but at equal levels of disease severity, B15 A had higher yields than TK 5. In trials 1 and 3, with lower yields and rust severity (fall season), yields of B15 A were similar in all treatments. This indicated that B15 A had tolerance to leaf rust.

Yield components, including seed weight, number of pods per plant, and number of seeds per pod, have been reported to decrease when soybeans are infected with *P. pachyrhizi* (16). For other fungal foliar diseases of soybean, such as brown spot (*Septoria glycines* Hemmi) and red leaf blotch (*Dactuliochaeta glycines* (R. B. Stewart) Hartman & Sinclair), reduction in seed size was shown to be a primary component of yield loss (9,13,17,29). Under controlled conditions, leaf rust was shown to reduce the number of filled pods, seeds per pod, and mean seed weight (15). In our study, the number of pods and seeds per plant from inoculated plants differed significantly from fungicide-protected plants only when the yields were high, i.e., in the two spring seasons. The reduction in seed weight was greater in TK 5 than B15 A, which equated with yield reduction. The reduction in the number of pods, seeds, and seed weights was more pronounced in TK 5 than in B15 A.

Specific and rate-reducing resistance to *P. pachyrhizi* is not routinely used in the development of commercial cultivars, partly because of the lack of resistance to all isolates and because of the difficulty in breeding for rate-reducing resistance (2). Selecting and breeding for high-yielding lines that are tolerant to rust have had only limited success. Yield losses in international screening trials ranged from 1 to 47% in tolerant lines, compared with 20 to 87% for intolerant lines (27).

Our study showed that B15 A had partial resistance to *P. pachyrhizi* compared with TK 5 because of the lower range of severity values. Partial resistance to *P. pachyrhizi* based on latent period and the number of uredinia per lesion or slow-rusting lines has been described (31,33), but in the case of B15

Table 2. Production of pods and seeds of soybeans inoculated with *Phakopsora pachyrhizi* at three growth stages (GS) and under fungicide protection

	Trial 1		Trial 2		Trial 3		Trial 4	
Growth stage[a]	**Pods**[b] **(no.)**	**Seeds**[c] **(no.)**	**Pods**[b] **(no.)**	**Seeds**[c] **(no.)**	**Pods**[b] **(no.)**	**Seeds**[c] **(no.)**	**Pods**[b] **(no.)**	**Seeds**[c] **(no.)**
R1	26	49	23	47	25	49	20	42
R3	24	47	26	53	25	50	23	50
R5	27	52	29	56	25	51	26	57
Protected	25	48	32	63	27	53	29	60
FLSD ($P > 0.05$)[d]	NS[e]	NS	3.5	7.0	NS	NS	4.7	8.9

[a] Inoculated with *P. pachyrhizi* or protected with Dithane M-45 (80%) (maneb) (1.92 kg a.i./ha) 2.4 kg/ha) sprayed at 7-day intervals.

[b] Average count of pods from 10 plants per plot for two soybean genotypes (B15 A and TK 5).

[c] Average count of seeds per plant from 10 plants per plot for two soybean genotypes (B15 A and TK 5).

[d] Fisher's least significant difference.

[e] Not significant.

Table 3. Yield and 100-seed weight of two soybean genotypes inoculated with *Phakopsora pachyrhizi* at three growth stages (GS) and under fungicide protection

		Yield (kg/ha)		100-seed weight	
Trial	**Growth stage**[a]	**TK5**	**B15 A**	**TK 5**	**B15 A**
1	R1	1,192	2,074	11.6	17.6
	R3	1,475	2,095	12.9	18.3
	R5	2,051	2,299	15.2	19.1
	Protected	2,318	2,312	17.3	19.2
FLSD ($P < 0.05$)[b]		156		1.1	
FLSD ($P < 0.05$)[c]		314		1.3	
2	R1	1,196	2,717	11.2	17.5
	R3	1,744	3,149	11.9	18.4
	R5	1,855	3,164	12.7	18.8
	Protected	3,639	3,546	17.4	20.0
FLSD ($P < 0.05$)[b]		165		0.9	
FLSD ($P < 0.05$)[c]		388		1.3	
3	R1	1,008	1,802	8.5	13.5
	R3	1,121	1,880	9.1	13.6
	R5	2,138	2,222	13.6	15.5
	Protected	2,343	2,239	13.8	15.6
FLSD ($P < 0.05$)[b]		137		0.6	
FLSD ($P < 0.05$)[c]		161		1.2	
4	R1	890	2,249	11.0	15.8
	R3	1,128	2,538	11.4	16.1
	R5	1,613	2,984	12.2	17.7
	Protected	3,282	3,383	18.2	19.8
FLSD ($P < 0.05$)[b]		508		1.1	
FLSD ($P < 0.05$)[c]		586		1.2	

[a] Inoculated with *P. pachyrhizi* protected with Dithane M-45 (80%) (maneb) (1.92 kg a.i./ha) sprayed at 7-day intervals.

[b] Fisher's least significant differences between treatment means for the same genotype.

[c] Fisher's least significant differences between treatment means for different genotypes.

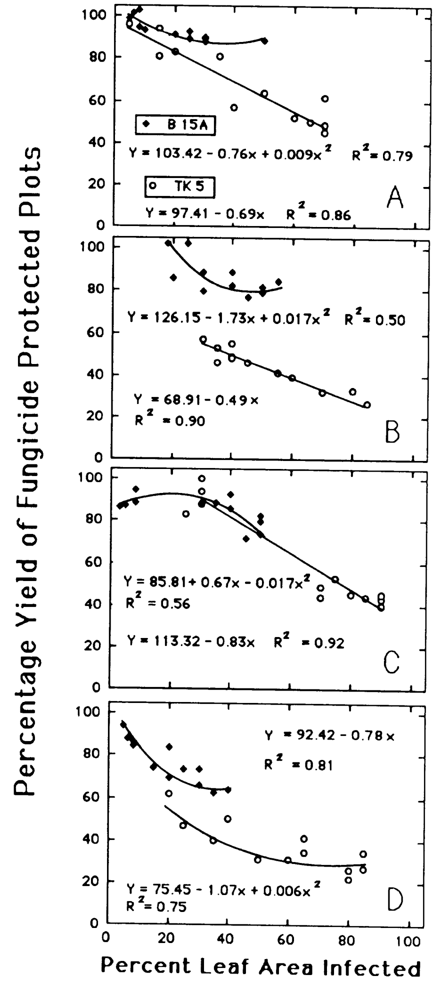

Fig. 3. Percentage of yield of fungicide-protected plants of two soybean genotypes (B15 A and TK 5) on percentage of leaf area infected in **(A)** trial 1, **(B)** trial 2, **(C)** trial 3, and **(D)** trial 4.

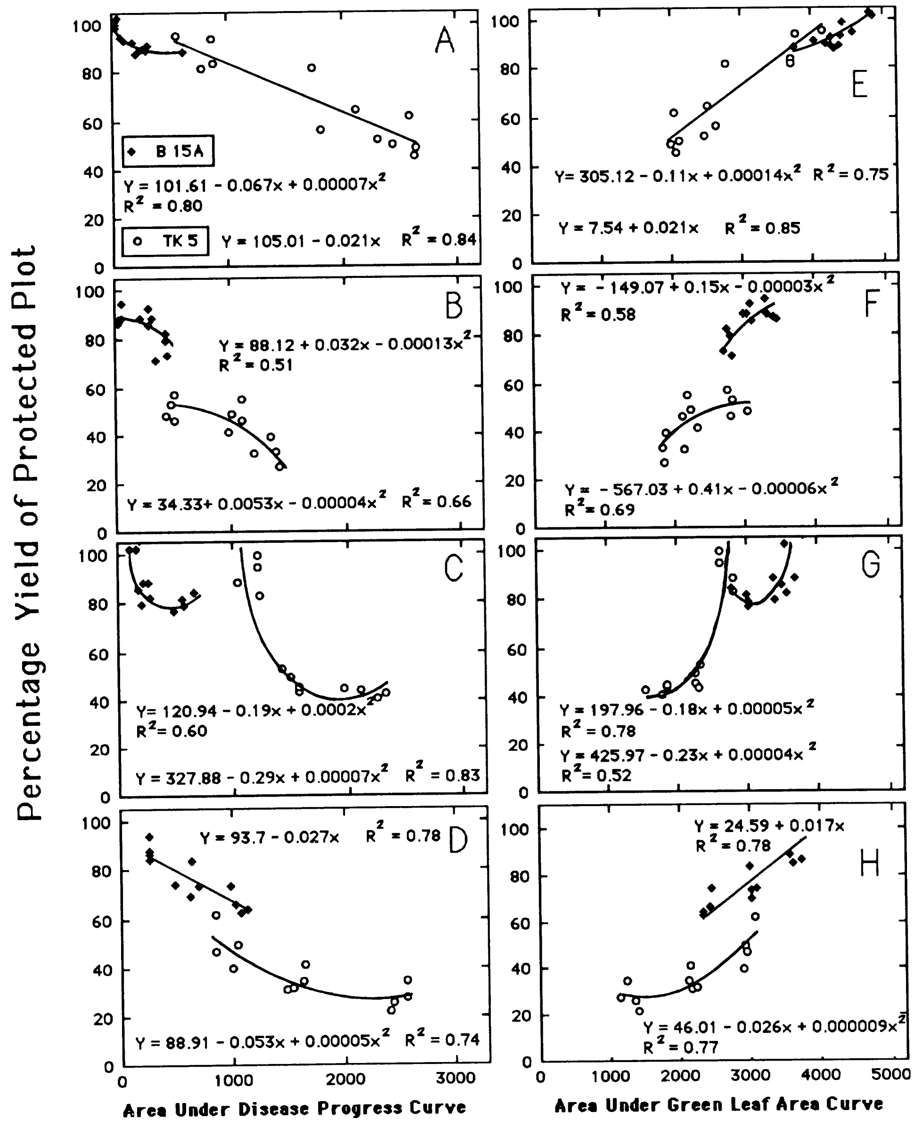

Fig. 4. Percentage of yield of fungicide-protected plants for two soybean entries (B15 A and TK 5) on area under disease progress curve in **(A)** trial 1, **(B)** trial 2, **(C)** trial 3, and **(D)** trial 4 and on area under green leaf area curve in **(E)** trial 1, **(F)** trial 2, **(G)** trial 3, and **(H)** trial 4.

A, expression of partial resistance to leaf rust has not been determined. The use of tolerance and/or genotypes with partial resistance, combined with the timely application of fungicides, can minimize the effects of leaf rust. To date, there have been no recommendations to indicate the most appropriate times for applying fungicides based on a forecasting system and an economic analysis of costs. Future research to assess lines with partial resistance and tolerance over a wide range of environments and a forecasting system to maximize the economic usefulness of fungicides are needed to offset the yield losses in soybeans caused by *P. pachyrhizi.*

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