

Development of Yield Loss Models in Relation to Reductions of Components of Soybean Infected with *Phakopsora pachyrhizi*

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ABSTRACT

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Epidemics of soybean rust (*Phakopsora pachyrhizi*) were manipulated by applying protectant fungicides at weekly intervals to different plant growth stages. Effects of disease on plant growth and yield components were monitored at different growth stages. Reduction of shoot weights was different among the cultivars. The number of pods per plant measured at soybean growth stage R6 was reduced as much as 40% in the diseased plants, but the number of seeds per pod was not affected, indicating that disease affected the attainable yield by reducing pod set. From growth stages R6 to R7 (beginning maturity), percentage of pod abortion was high for severely diseased plants, although pods per plant already had

been reduced at R6. Seed growth rate (grams per day) from R4 to R7 was reduced by 40–80% in diseased plants in 1986 and was negatively correlated with relative area under the disease progress curve. The time for diseased plants to growth from R4 to R7 was reduced by as many as 16 days compared with protected plants and was significantly correlated with the disease. A general yield loss model was modified to analyze the coefficients of empirical yield loss models. Slopes of simple linear yield loss models could be represented by the sum of reduction slopes of seed growth rate and seed growth period and were validated by actual data.

Additional keywords: foreign disease, *Glycine max*.

Yield loss models have a very important role in developing a disease data base for disease impact assessment. Yield loss models often lack conceptual meaning because their coefficients

are from empirical yield loss experiments that vary from location to location. Additional information about the components and mechanism of yield loss will help interpret the empirical yield loss models (13). A general yield loss model has been developed for potato with a biological explanation (11). Information on yield loss of leguminous crops affected by foliar diseases is comparatively scarce, partly because of the complicated yield buildup

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mechanisms for these crops (5). A conceptual approach in leguminous crop modeling may be of assistance in understanding yield loss physiology. Soybean rust (caused by *Phakopsora pachyrhizi* Syd.), as a foliar disease of a leguminous crop, provides a good example for such a study.

Soybean rust occurs in both the eastern and western hemispheres and is a major disease of tropical and subtropical areas (2,3,12,14). The disease causes considerable yield loss in many Asian countries (2); losses as high as 40% have been reported in Japan (7). The disease is not known to occur in the United States but is considered a potential threat to U.S. soybean production (1,6,8). Through a long-term study, researchers at the USDA Foreign Disease-Weed Science Research Unit are attempting to couple a soybean growth simulation model with a disease model to assess the potential impact of soybean rust to U.S. agriculture (19,20). Information regarding disease effects on crop development and growth will help improve the research. However, previous yield loss studies do not provide such information because they focus primarily on variation of final yield (2,7,9,17). This paper reports results of a cooperation between the Asian Vegetable Research and Development Center and the USDA Foreign Disease-Weed Science Research Unit to assess the risk of soybean rust to the U.S. soybean production (19,20). Part of this effort is to understand the effect of soybean rust on yield buildup/accumulation and the biological explanation of empirical yield loss models.

MATERIALS AND METHODS

Planting and treatments. Soybeans were planted on 2 October 1986 and 27 February 1987 at the farm of the Asian Vegetable Research and Development Center. For each year, a split-split plot design was established. There were four main plots for replication and each was divided into four subplots for treatment with sizes of 15 × 15 m in 1986 and 11 × 12 m in 1987. To create different disease effects on various yield components, four treatments were established by applying fungicide weekly until inoculation of plants at different growth stages (4). The fungicide was mancozeb (80% Dithane M-45, Rohm and Haas Company, Philadelphia) applied at a rate of 2.4 kg/ha. At designated soybean growth stages, fresh spores were collected from diseased leaves to make a suspension of 2 × 10⁴ spores per milliliter. Plants were inoculated uniformly with a pressurized sprayer set at 1.5 × 10⁵ Pa until runoff after a 10-min overhead irrigation at night-fall. The treatments were 1) inoculation at V4 with no application of fungicide, 2) application of fungicide until inoculation at R1, 3) application of fungicide until inoculation at R4, and 4) application of fungicide to 50% leaf yellow (R7). The effect of fungicide on host physiology was assumed to be insignificant. Corn strips 2 m wide were planted between subplots and main plots to reduce interplot interference. The subplots were split into six and four sub-subplots for cultivar in 1986 and 1987, respectively. Sub-subplots were 4 × 6 m in 1986 and 4 × 5 m in 1987 with a 1-m working path. Cultivars AGS 129, AGS 181 (1986 only), G 38 (1986 only), SRE-B-15C (SREB), SRE-D-14B (SRED), and TK 5 were used. SREB and SRED had shown some tolerance to soybean rust in previous studies (14). Soybeans were planted by hand at a density of three seeds per hill, with 10-cm distance between hills and 50-cm row spacing. Plots were thinned to 20 plants per meter after seedling emergence. Overhead irrigation was supplied whenever necessary.

Data collection. Days from planting to each soybean growth stage were recorded for every sub-subplot during the growing season. Each sub-subplot was divided into four equal sections for rust rating. Rust severity, defined as percentage of diseased leaf area, was rated for every section at every growth stage from R1 to R7 (beginning maturity) for 1986, and at R1, R4, R6 (seed full size), and R7 for 1987. Mean values of sub-subplot were calculated using data from the four sections.

Ten plants for 1986 and five for 1987 were randomly sampled from each sub-subplot at soybean growth stages R1, R4, R6, and R7 by cutting stems at ground level. Means of every variable

were calculated from total plants sampled. Leaf area (in square centimeters) per plant was measured with a portable area meter (Li-Cor, Inc., Lincoln, NE). Plants then were divided into leaf, shoot, seed, and pod skin when those components were present. Numbers of seeds per plant and pods per plant were counted at R6 and R7. Each part was completely dried in ovens at 50 C for 24 h. Leaf and shoot weights at R1, R4, R6, and R7, and seed weight at R6 and R7, were measured. Seed weight at R4 was recorded as zero because seed initiated at the R4 stage.

Data analysis. Analysis of variance was used to determine effects of main plot (replication), fungicide treatment (subplot), and cultivar (sub-subplot) on leaf area, shoot weight, pods per plant, seeds per pod at R6, seed weight per plant at R7, pod abortion, and partitions between seed and vegetative parts of the plant from R4 to R6 and R6 to R7 (see below). The error terms used for fungicide treatment and cultivar were variances of replication-treatment interaction and replication-treatment-cultivar interaction, respectively. To examine disease effects on vegetative parts, shoot weights of different treatments were plotted against successive growth stages. Data for TK 5 and SRED are presented graphically as representatives.

Because the maximum number of pods per plant or seeds per pod was reached at growth stage R6, pods per plant and seeds per pod at R6 were compared among treatments as an indication of disease effect on the attainable yield. Reduction of pod set (*LP*) was calculated for each cultivar-treatment combination at growth stage R6 as

$$LP(\%) = 100 (P_h - P_d) / P_h \quad (1)$$

in which P_h and P_d were the means of pods per plant of fully protected (treatment 4) and diseased plants, respectively.

Percentage of pod abortion (*PA*) from plant growth stages R6 to R7 was calculated for each cultivar-treatment combination as

$$PA(\%) = 100 (N_6 - N_7) / N_6 \quad (2)$$

in which N_6 and N_7 were the total pods per plant at growth stages R6 and R7, respectively.

Disease effects on plant partition were examined by use of ratios between the weight increases of seeds and shoot plus pod during the growth stages R4 to R6 and R6 to R7 for each cultivar-treatment combination as

$$Z = (w_j - w_i) / (W_j - W_i) \quad (3)$$

in which w and W were seed dry weight and shoot plus pod weight, respectively, at soybean growth stages R4 and R6 or R6 and R7.

Relationships between disease and seed growth rate (*R*), and disease and seed growth period (*P*), were examined. The relative area under the disease progress curve (RAUDPC; 11,21) from growth stages R1 to R6 was calculated using disease severity (X_i) and days after planting (t_i) as

$$RAUDPC = \left[\sum_{i=1}^{n-1} (X_i + X_{i+1}) (t_{i+1} - t_i) \right] / [100 (t_n - t_1)] \quad (4)$$

The growth rate of seeds (grams per day) from R4 to R7 was calculated for each cultivar-treatment combination as:

$$R = (w_7 - w_4) / t \quad (5)$$

in which w_4 and w_7 were seed dry weight at growth stages R4 and R7, respectively, and t was number of days from R4 to R7 of plants in each sub-subplot. Both rate and days of seed growth from R4 to R7 were plotted against the RAUDPC. To relate *R* and *P* to coefficients of yield loss models, a general yield loss model from Shtienberg et al (11) was modified. Their model is

TABLE 1. Analysis of variance *F* tests and significance ($P > F$) for the effects of replication (main plot), fungicide treatment (subplot), and cultivar (sub-subplot) on leaf area (cm²/plant), shoot weight (g/plant), pods/plant, and seeds/pod at soybean growth stage R6, seed weight/plant at R7, pod abortion, and partition of plants infected with *Phakopsora pachyrhizi*

Variable	Replication		Fungicide		Cultivar		Fungicide × cultivar	
	<i>F</i>	<i>P</i> > <i>F</i>	<i>F</i>	<i>P</i> > <i>F</i>	<i>F</i>	<i>P</i> > <i>F</i>	<i>F</i>	<i>P</i> > <i>F</i>
1986								
Leaf area	0.41	0.753	3.38	0.068	6.38	0.0001	2.09	0.023
Shoot weight	0.14	0.930	39.92	0.0001	10.53	0.0001	4.01	0.0001
Pods/plant	0.70	0.575	3.77	0.053	20.77	0.0001	2.03	0.0272
Pod abortion ^a	1.63	0.251	4.30	0.038	1.94	0.101	1.99	0.031
Seeds/pod	0.82	0.487	0.22	0.883	137.74	0.0001	1.61	0.097
Seed weight	0.09	0.965	43.78	0.0001	12.59	0.0001	3.69	0.0002
Partition ^b A	2.39	0.078	1.64	0.190	6.26	0.0001	0.79	0.682
B	3.39	0.023	13.00	0.0001	1.08	0.388	2.00	0.092
1987								
Leaf area	0.92	0.470	2.20	0.157	10.01	0.0001	0.62	0.770
Shoot weight	0.20	0.896	10.23	0.003	3.09	0.039	1.23	0.307
Pods/plant	0.81	0.521	0.310	0.815	6.03	0.002	1.36	0.241
Pod abortion	0.09	0.96	0.172	0.910	0.80	0.500	2.10	0.054
Seeds/pod	1.10	0.363	1.09	0.366	414.14	0.0001	1.35	0.245
Seed weight	0.57	0.647	7.44	0.008	5.26	0.004	1.48	0.194
Partition A	0.51	0.680	0.69	0.565	14.74	0.0001	0.24	0.985
B	0.30	0.824	5.80	0.002	15.72	0.0001	1.72	0.120

^a Pod abortion (*PA*) was calculated as $PA (\%) = 100 (N_6 - N_7)/N_6$, in which N_6 and N_7 were number of pods per plant at growth stages R6 and R7, respectively.

^b Ratio between increases of seed weight and shoot plus pod weight during soybean growth. A is for the period of R4 and R6 and B is for the period of R6 to R7.

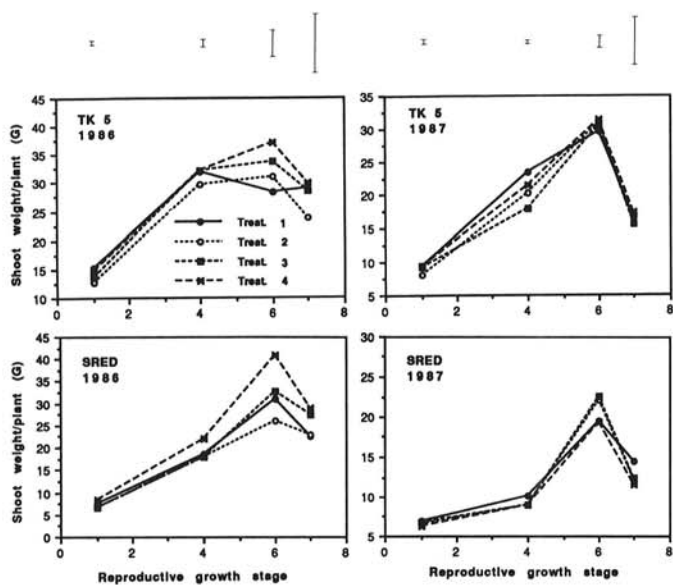


Fig. 1. Shoot growth of soybean cultivars TK 5 and SRED infected with rust (*Phakopsora pachyrhizi*) during the 1986 and 1987 growing seasons in Taiwan. Treatment 1 = inoculation at V4 with no application of fungicide; treatment 2 = application of fungicide until inoculation at R1; treatment 3 = application of fungicide until inoculation at R4; treatment 4 = application of fungicide to maturity. Bars = $LSD_{0.05}$ for each growth stage.

$$YL (\%) = 100 - (1 - a \cdot A/R) ((P_{dmax} - P'_{tg}) / (P_{cb} - P_{tg})) 100$$

where *A* is disease intensity (RAUDPC) and *a* is reduction of bulking rate induced by one unit of disease intensity. Other variables are date of tuber growth initiation (P'_{tg} and P_{tg}) and date for cession of bulking (P_{dmax} and P_{cb}) under diseased and nondiseased conditions, respectively. Those dates were calculated by a potato simulation model. We modified their model by relating *A* to seed growth period so that the coefficients of the yield loss model could be partitioned. The modification was

$$YL = 1 - [R(1 - B_1 \cdot A)] [P(1 - B_2 \cdot A)] / R \cdot P,$$

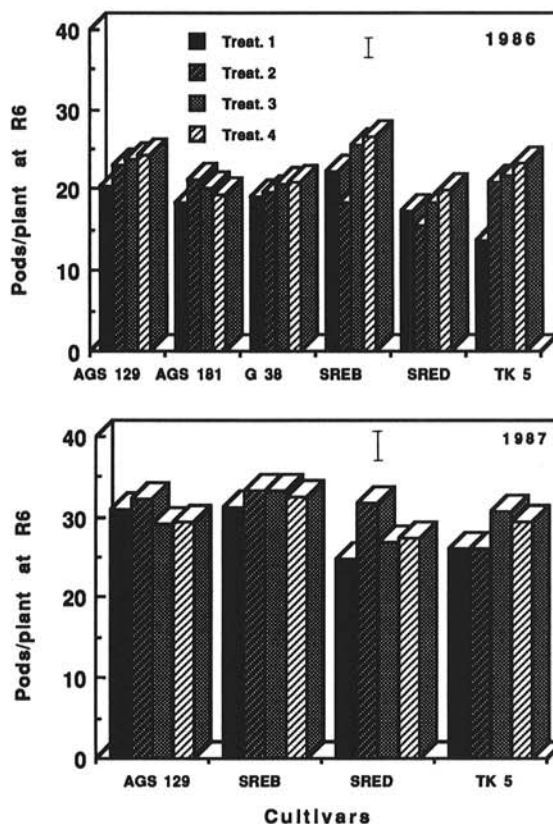


Fig. 2. Effect of rust (*Phakopsora pachyrhizi*) on pod set of soybean cultivars at growth stage R6. Treatment 1 = inoculation at V4 with no application of fungicide; treatment 2 = application of fungicide until inoculation at R1; treatment 3 = application of fungicide until inoculation at R4; treatment 4 = application of fungicide to maturity. Bars = $LSD_{0.05}$.

which can be simplified to

$$YL = (B_1 + B_2) \cdot A - B_1 \cdot B_2 \cdot A^2 \quad (6)$$

where B_1 and B_2 are relative reductions (0–1.0) of seed growth rate and seed growth period induced by one unit of disease in-

tensity, respectively. B_1 and B_2 were obtained by regressing relative reduction of R and P against the RAUDPC.

Equation 6 is equivalent to a quadratic yield loss model

$$YL = b_1 \cdot A + b_2 \cdot A^2 \quad (7)$$

where b_1 and b_2 are regression coefficients and equal to $(B_1 + B_2)$ and $B_1 \cdot B_2$ of equation 6, respectively. Equation 6 means that R and P are related each other additively ($B_1 + B_2$) in linear term and related each other interactively ($B_1 \cdot B_2$) in quadratic term. If b_2 is not significant, $(B_1 + B_2)$ is expected to equal or close to equal the slope of a simple linear yield loss model. The above assumption was examined by regressing yield loss (YL) against the RAUDPC (A) with option of no intercept. All calculations were made using an SAS package (10).

RESULTS

Except for the partition in the first year, there was no significant effect of replication in either year (Table 1). Cultivars were significantly different ($P = 0.001$) for every plant growth variable in both years except for late partition and pod abortion. Shoot weight, pods per plant, seed weight, and dry matter partition from R6 to R7 were significantly different among the fungicide treatments in each year. Pod abortion in 1987 was not significant. Leaf area per plant reached a maximum at growth stage R6 for every cultivar. Leaf area per plant at R6 was not significantly different among the fungicide treatments at $P = 0.068$. Leaf area per plant was significantly different among treatments by cultivar interactions for 1986 ($P = 0.023$) but not for 1987 ($P = 0.77$) (Table 1).

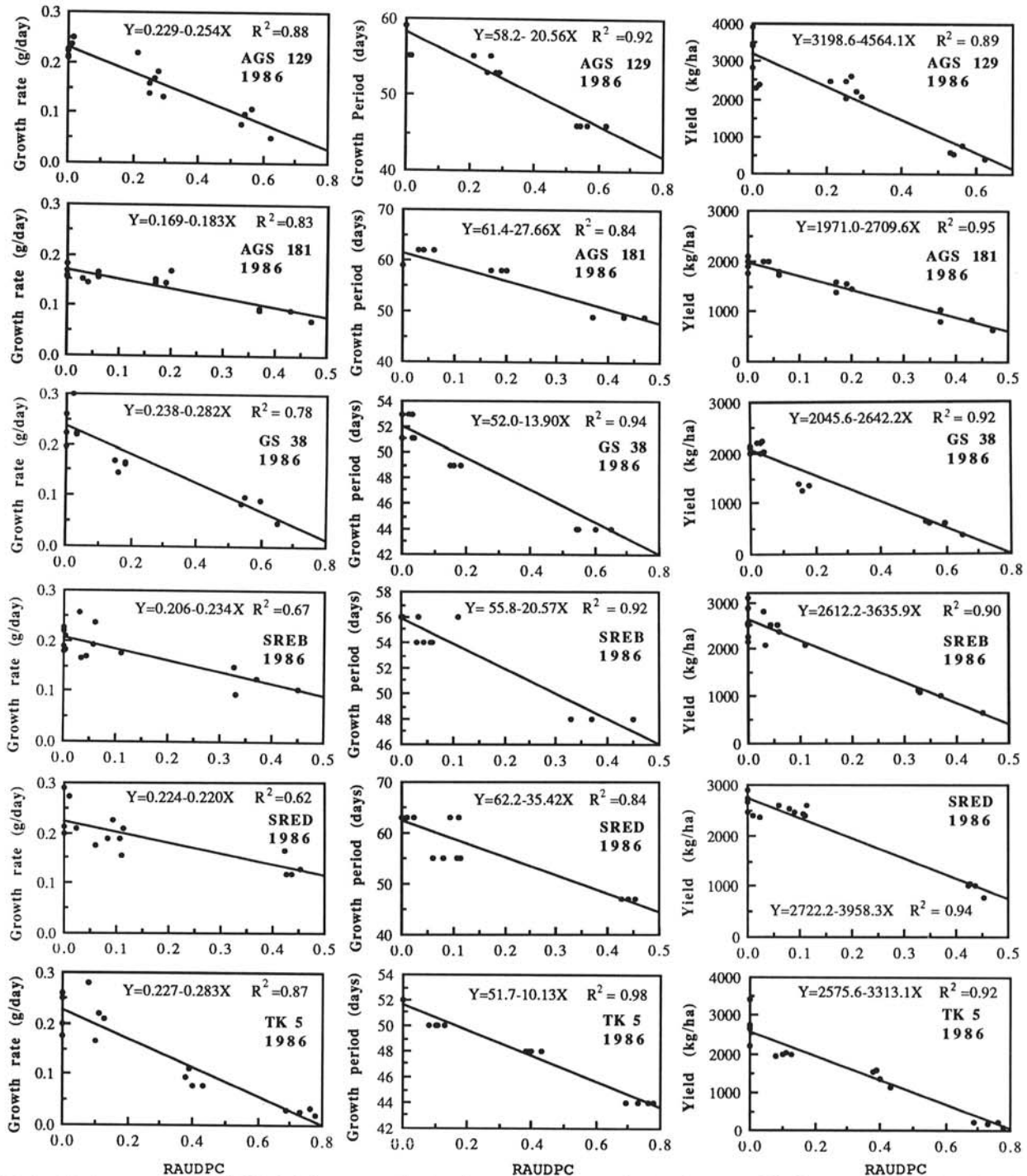


Fig. 3. Relationship between the RAUDPC (relative area under the disease progress curve) of soybean rust (*Phakopsora pachyrhizi*) and seed growth rate, seed growth periods from R4 to R7, and yield on soybean cultivars for the 1986 growing season.

Disease effects on vegetative growth. Shoot weight reached the maximum at soybean growth stage R6 and then dropped rapidly for all cultivars, represented by the results of TK 5 and SRED (Fig. 1). At growth stage R6, shoot weight was about 20% lower in diseased treatments compared with fully protected plants (treatment 4) in 1986 (Fig. 1). For TK 5 in 1986, the shoot weight in severely diseased plants (treatment 1) stopped increasing before growth stage R6 (Fig. 1).

Disease effects on attainable yield. The maximum number of seeds per pod at R6 was not different among fungicide treatments (Table 1). However, the number of pods per plant at R6 in treatment 4 (fully protected) was 10% more than in treatment 1 (no fungicide) for every cultivar in 1986 (Fig. 2). Reduction of pods per plant for treatment 1 was 40% for TK 5 in 1986 compared with treatment 4. Pod abortion from R6 to R7 occurred in every treatment of every cultivar in 1986. The percentage of pod abortion in treatment 1 was significantly higher than in other treatments although pod number was already lower in treatment 1 at R6.

Disease effect on the growth of yield components. The ratio between increases of seed weight and shoot plus pod weight was not significantly different among the treatments for the period R4 to R6 for both years (Table 1). For the period R6 to R7, the ratio increased as disease severity increased in both years.

Seed growth rate (grams per day) was significantly reduced by the rust disease and was linearly correlated with RAUDPC (Figs. 3 and 4). Compared with treatment 4, seed growth rate of diseased plants was reduced 40–80% in 1986. In 1987, the reduction also was significant except for SREB.

Seed growth period also was significantly correlated to

RAUDPC (Figs. 3 and 4). Duration from R4 to R7 was decreased by 16 days (out of 63) for SRED and 8 days (out of 52) for TK 5 in severely diseased plants—reductions of approximately 23 and 15%, respectively, compared with the period of no disease treatments. In 1987, there was no significant reduction in growth period for SREB and SRED due to the light disease severity.

Regression of RAUDPC to yield (Figs. 3 and 4) or yield loss (Table 2) produced simple linear relationships. The quadratic term of equation 7 was not significant for each case. For TK 5 and AGS 129 in 1987, the quadratic equation had a greater r^2 than that of simple linear regression, but both b_1 and b_2 were insignificant. Therefore, simple linear regression was used (Fig. 4 and Table 2). Slopes of simple yield loss equations were close to the sum of reduction slopes of seed growth rate and growth period (Table 2). The reduction slopes of the two components were different for different cultivars. Slopes between the 2 yr were very close (Table 2) except for those of SREB and SRED, on which disease was not severe in 1987. Generally, the relationship of disease to seed growth rate, seed growth period, and yield had higher r^2 in 1986 (Fig. 3) than in 1987 (Fig. 4) because of lower disease severity in 1987.

DISCUSSION

Gaunt (5) recently suggested categorizing disease effects into effect on plant development and effect on plant growth to understand the complicated loss mechanism in leguminous crops. van Bruggen (15,16) showed the two types of effects of *Rhizoctonia solani* on dry bean. The effect on plant development was a delay of the periods of plant flowering and pod set. The effect on plant

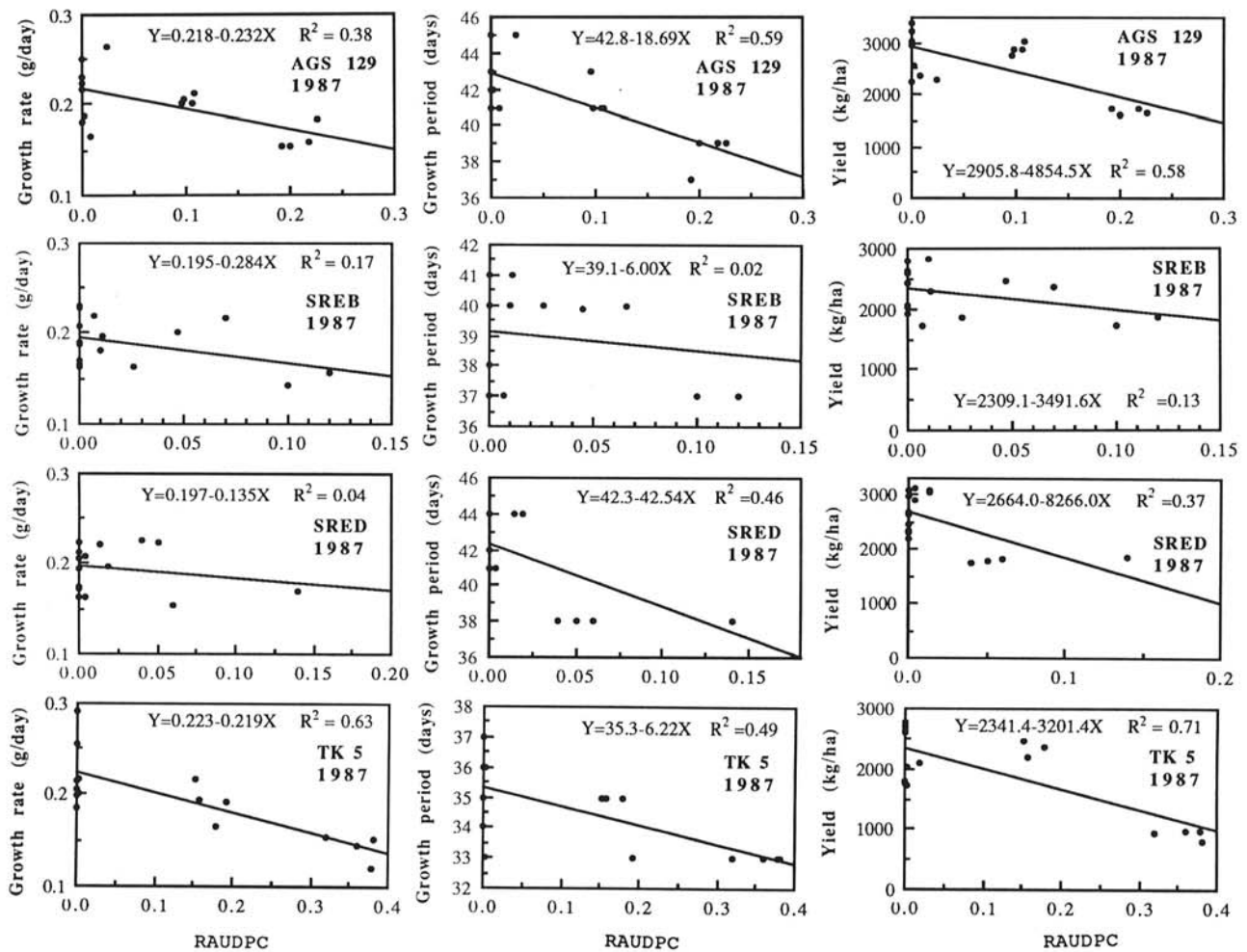


Fig. 4. Relationship between the RAUDPC (relative area under the disease progress curve) of soybean rust (*Phakopsora pachyrhizi*) and seed growth rate, seed growth period from R4 to R7, and yield on soybean cultivars for the 1987 growing season.

TABLE 2. Comparison of slopes from simple regressive yield loss model and slopes calculated from relative reductions of seed growth period (B_1 in eq 6) and seed growth rate (B_2 in eq 6) caused by *Phakopsora pachyrhizi* on different cultivars during the 1986 and 1987 growing seasons in Taiwan

Cultivar	Reduction slopes ^a				Calculated slope $B_1 + B_2$	Regression ^b		
	Period		Rate			$b_1 \pm SD$	$b_2 \pm SD$	r^2
	$B_1 \pm SD^c$	r^2	$B_2 \pm SD$	r^2				
1986								
AGS 129	0.353 (0.03)	0.92	1.114 (0.12)	0.88	1.468	1.553 (0.12)	NS ^d	0.95
AGS 181	0.441 (0.05)	0.84	1.080 (0.13)	0.84	1.531	1.366 (0.10)	NS	0.95
G 38	0.265 (0.06)	0.95	1.085 (0.12)	0.85	1.432	1.300 (0.09)	NS	0.93
SREB	0.367 (0.03)	0.92	1.113 (0.43)	0.33	1.379	1.372 (0.10)	NS	0.91
SRED	0.569 (0.06)	0.84	0.918 (0.21)	0.62	1.551	1.370 (0.12)	NS	0.91
TK 5	0.196 (0.01)	0.98	1.248 (0.13)	0.87	1.457	1.294 (0.08)	NS	0.95
1987								
AGS 129	0.421 (0.09)	0.58	1.073 (0.30)	0.38	1.495	1.574 (0.34)	NS	0.60
SREB	1.053 (0.45)	0.28	2.276 (1.87)	0.07	3.382	2.175 (1.04)	NS	0.24
SRED	1.000 (0.29)	0.48	1.00 (1.20)	0.02	1.680	1.331 (1.03)	NS	0.11
TK 5	0.146 (0.07)	0.49	0.982 (0.21)	0.63	1.158	1.301 (0.17)	NS	0.81

^a Reduction slopes were relative reductions of seed growth rate and seed growth period, respectively, caused by one unit of the relative area under the disease progress curve (RAUDPC), see eq 6 in text. The slopes were regression coefficients of the relative reduction of seed growth rate or period against RAUDPC.

^b Regression between RAUDPC and relative yield losses. The quadratic terms were insignificant and b_1 is expected to be equal to $(B_1 + B_2)$.

^c Standard deviation.

^d Not significant.

growth was a reduction of stem and root weight. Our results on soybean rust also distinguish the two types of effects. For example, effects on plant development were demonstrated as a reduction of attainable number of pods per plant (Fig. 2) and earlier maturation with increasing disease intensity (Fig. 3). Disease effects on plant growth included abortion of pods and reductions of photosynthetic area, seed growth rate, partition, and shoot weight (Table 1).

Information of plant response to various disease organisms is essential for a valid assessment of potential threats from foreign pathogens. Such information can be used to integrate a rust simulation model with a soybean growth simulation model (19). Our study has delineated some of the information needed for model development and integration in assessing the potential for soybean rust impact. Our results emphasize the need for a host model that simulates plant growth and measures disease effect as a function of photosynthetic area. For example, SOYGRO (18) can readily integrate the disease effect on photosynthetic area through its interface of pest defoliation. The disease effect on potential yield, seed growth rate, and growth period can be reflected in SOYGRO because these variables are demonstrated as functions of photosynthetic area.

Coefficients of yield loss models are important parts in the disease data base. Because the coefficients are from empirical yield loss models, application of these coefficients for yield loss assessment is limited. Shtienberg et al (11) proposed a general yield loss model that calculates disease effects on yield in terms of bulking rate. Our work partitions the slope of a yield loss model into parts related to the physiology of yield development. It is not clear from this study if the insignificance of the quadratic term in equation 7 relating yield loss to RAUDPC is due to the experiment error or to the complicated interaction between seed growth rate and growth period. Nevertheless, this study has provided an opportunity to delineate the effects of disease on various plant growth stages and the subsequent effects on yield components. Such information can be used to develop a more reliable crop development-disease loss model.

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