Phenotypic Response of Six Soybean Cultivars To Bean Pod Mottle Virus Infection

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ABSTRACT

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Response of six soybean cultivars to infection by bean pod mottle virus was monitored during two growing seasons for chlorotic leaf area, leaf rugosity, and canopy width and height reduction. Symptoms were most severe on the cultivars Centennial and/or Forrest and mildest on Davis. Yield losses ranged from 3–13% and 4–10% in 1981 and 1982, respectively. Yield reductions were correlated ($P = 0.05$) with both chlorotic leaf area and leaf rugosity ($r = 0.998$ and 0.961 in 1981, and $r = 0.910$ and 0.928 in 1982, respectively). Bean pod mottle virus-inoculated cultivars Ransom and Centennial had greater leaf chlorophyll concentrations after flowering than uninoculated plants, whereas chlorophyll concentrations in Davis did not vary between inoculated and uninoculated plants. Plants inoculated at the two-leaf stage (V2) developed the most severe symptoms, whereas the mildest symptoms developed in plants inoculated at the V9 growth stage. Degree of symptom expression of inoculated, greenhouse-grown plants during the winter differed from that of the characteristic symptoms developed by plants of the same cultivars when field grown.

Soybeans (*Glycine max* (L.)Merr.) infected with bean pod mottle virus (BPMV) are commonly found in eastern North Carolina where high populations of the beetle vector (*Cerotoma trifurcata* Forst.) prevail; disease incidence in some fields may approach 100%. Symptoms of this disease range from a mild chlorotic mottle to a severe mosaic with the most obvious symptoms appearing on younger leaves (8,15). Schwenk and Nickell (13) stated that the disease was capable of killing plants of some genotypes and causing terminal necrosis in others.

Although yield losses due to BPMV infection have been reported from tests conducted under greenhouse conditions (3,13), in hill plots, or with widely-spaced plants (3,6,14), these conditions are not comparable to those under which commercial soybean production is reduced since plant densities are dissimilar. In other investigations, soybean mosaic virus (SMV) infection in both control and BPMV-inoculated treatments may have confounded the interpretation of results (8,9).

The stage of plant growth at the time of inoculation influences the amount of yield loss due to BPMV (9). In North Carolina, plants inoculated at the V1 or V2 stage (2), first trifoliate leaf stage, had a mean yield loss of 28% while plants inoculated 5 wk later had a yield loss of 5%. Yield losses were decreased from 26 to 15% by delaying inoculation from the primary leaf stage to the prebloom stage in Arkansas (15).

The investigations reported here examine the effect of BPMV infection of soybean with respect to the percentage of virus-related yield reduction in several cultivars, the type and sequence of foliar symptoms, relationship of stage of plant development at time of infection to yield loss, and correlation of yield loss with different symptoms.

MATERIALS AND METHODS

Field experiments were conducted at the Tidewater Research Station near Plymouth, NC. The soybean cultivars that were used have a determinant growth habit: Centennial and Forrest are resistant to race 1 of the soybean cyst nematode (*Heterodera glycines* Ichinohe 1952); and cultivars Davis, Ransom, and York are resistant to soybean mosaic virus (SMV). Cultivar NC-PMR is resistant to both the cyst nematode and SMV (11). Cultivar reactions to BPMV were unknown. Seeding dates were 14 May 1981 and 12 May 1982 with a planting density of 23 seeds per meter of row. Adjacent paired inoculated and uninoculated plots each consisted of three rows (5.5 m long and 0.96 m apart). Four rows of soybeans (Ransom) were planted between every sixth plot row and were used as a path for a high clearance sprayer that was used to apply 0.83 kg a.i./ha of Sevin 80 WP (carbaryl, Union Carbide, Research Triangle Park, NC 27709) to the entire field biweekly to control beetle vectors. Prior to planting in 1982, the systemic insecticide DiSyston (disulfoton, Mobay Chem Corp., Kansas City, MO 64120) was applied in the furrows at a rate of 1.1 kg a.i./ha.

In 1981, a test was conducted using cultivars Centennial, Davis, and Ransom to examine symptoms of plants inoculated at either the V2 (11 June) or V6 (25 June) growth stages (2). In a second yield test, these three cultivars plus Forrest and York were grown to determine the effects on yield of inoculating plants at the V2 growth stage. A randomized complete block design with eight replications was used for each test. In 1982, similar tests were conducted except the yield test had 10 replications and also included NC-PMR; in the date-of-inoculation study, V2 and V6 inoculations were conducted on 8 and 21 June, respectively; Davis was deleted; and a V9-growth-stage-at-inoculation treatment (6 July) was added.

Original inoculum was derived from individual local lesions produced on Kentucky Wonder pole bean (*Phaseolus vulgaris* L.) leaves inoculated with purifed BPMV. Excised subepidermal local lesions were used to inoculate greenhouse-grown Ransom soybean seedlings. Inocula used for field tests were obtained by macerating young, symptomatic Ransom leaves 1:10 (w/v) in 0.05 M phosphate buffer, pH 6.9. Inoculations were performed with a pad inoculator (10) except for the inoculations at the V9 growth stage in 1982 which were done by rubbing the leaves with a gauze pad soaked in inoculum containing 600-mesh carborundum (Fisher Scientific Co, Pittsburgh, PA 15219).

Chlorotic leaf area (CLA) was estimated by using a modified Horsfall-Barratt scale (4) (Fig. 1), and ratings were converted to percent leaf area by using the conversion tables developed by Redman et al (7). In 1981, CLA data were collected prior to and after flowering on all leaflets at the top four nodes (youngest leaf =

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no. 1 node) of ten randomly selected plants in the center row of each inoculated plot of Centennial, Davis, and Ransom (inoculated on 11 June). In 1982, percent CLA of the above cultivars plus Forrest, NC-PMR, and York was measured on only one leaflet of each of the top four nodes of 10 randomly-selected plants from the center row of each inoculated plot (inoculated on 8 June).

Canopy widths and heights were measured at three random points in each center row in 1981 (8 and 11 July) and in 1982 (6 and 29 June and 20 and 27 July). Plant height was also measured at maturity.

Leaf rugosity was estimated on a scale from 1, for flat leaves, to 5 for severely crinkled leaves. The center row of each inoculated plot was evaluated on 3, 11, 19, and 27 July 1981. Rugosity data were collected on 29 June, 20 and 27 July, 4 and 18 August, and 1 September 1982.

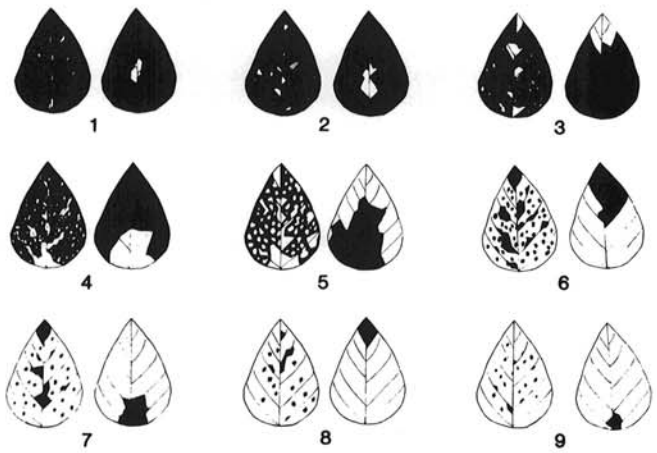

Fig. 1. Modified Horsfall-Barratt scale used for estimating chlorosis. Scores 1–9 represent 3, 6, 12, 25, 50, 75, 88, 94, and 97% chlorotic leaf area, respectively.

TABLE 1. Percent chlorotic leaf area of six soybean cultivars infected with bean pod mottle virus

Data collected	Node	Chlorotic leaf area (%)[x]					
		Centennial	Ransom	Davis	Forrest	NC-PMR	York
1981[y]							
16 July	1	42 a	24 b	21 b			
	2	42 a	15 b	5 c			
	3	24 a	11 b	2 c			
	4	10 a	4 b	2 b			
28 July	1	48 a	26 b	17 b			
	2	23 a	15 b	6 c			
	3	20 a	5 b	2 b			
	4	10 a	4 b	1 b			
1982[z]							
29 June	2	45 a	8 d	4 d	30 b	15 c	4 d
20 July	1	33 a	35 a	27 a			
	2	29 a	13 b	5 c	24 a	30 a	7 bc
	3	12 a	4 b	2 b			
	4	4 a	2 b	1 c			
27 July	1	49 a	49 a	26 b			
	2	37 a	20 b	4 c	31 a	23 b	3 c
	3	15 a	4 b	2 b			
	4	4 a	2 b	1 b			
4 August	1	30 a	14 b	12 b			
	2	13 a	5 b	3 b			
	3	6 a	2 b	2 b			
	4	3 a	1 b	1 c			

[x] For each row, means followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's new multiple range test.
[y] Plants inoculated at the V2-V3 growth stage on 8 June.
[z] Plants inoculated at the V2-V3 growth stage on 11 June.

Chlorophyll *a* and *b* content was determined (16) from leaf samples taken on 18 August 1982 from the top seven nodes of 10 BPMV-infected plants (inoculated at V2 growth stage) and 10 uninoculated plants of Centennial, Davis, and Ransom; one plant from each treatment in each replication was sampled. Leaf samples were packed in ice and transported to the laboratory. A composite of leaf tissue from each plant was obtained by cutting disks from each of the leaflets with a 0.5-cm-diameter cork borer.

Center rows of plots were trimmed to 4.9 m before harvest and threshed similarly in both years. Seed were cleaned and weighed after uniform seed moisture (approximately 10%) was obtained.

The symptomatology of greenhouse-grown, BPMV-infected Centennial, Davis, and Ransom plants were observed in eight plants of each cultivar, grown one plant per 15-cm-diameter pot, seeded on 24 September and mechanically inoculated with BPMV at the V2 growth stage. Plants were grown under long-day photoperiods until 3 November, fertilized with VPH (Miller Chemical and Fertilizer Corp, Hanover, PA 17331), and treated with Temik (aldicarb, Union Carbide, Research Triangle Park, NC 27709) to control spider mites. CLA was measured according to the modified Horsfall-Barratt scale every other week for 5 wk starting on 8 November.

Data were analyzed by using an analysis of variance procedure (PROC GLM) of the Statistical Analysis System (SAS) (12). Mean separation tests were performed according to Duncan's new multiple range test (1). Paired *t*-tests were also used when appropriate.

RESULTS

Some plants in the uninoculated plots became infected with BPMV in 1981, presumably due to the transmission of BPMV by bean leaf beetles. Appoximately 12% (range 0–33%) of plants in control plots were symptomatic by 1 August; 99% of the inoculated plants were symptomatic. In 1982, 0.1% (range 0–3%) of the plants in uninoculated plots were symptomatic on July 1; 94% (range 70–100%) of the inoculated plants had symptoms.

Chlorotic leaf area (CLA). The CLA of cultivars differed significantly on 16 and 28 July 1981; the greatest differences among cultivars were expressed in second-node leaflet data (Table 1). Although percent CLA was observed to decline as leaves aged in all cultivars, the change was most obvious between nodes one and two in plants of cultivar Davis. Centennial had the highest amount of chlorotic area in leaflets at the top four nodes. Differences in percent CLA among leaflets at any node for any cultivar were not significant ($P = 0.05$).

In 1982, ratings of CLA from the second node of cultivars Centennial, Forrest, NC-PMR, and Ransom were greater than those for Davis and York (Table 1). A decline in CLA again was noted in Centennial, Davis, and Ransom as leaves aged; Davis had the sharpest decline in CLA between the first and second node. Chlorotic leaf symptoms of Centennial were more severe than those of the other cultivars at all nodes on 29 June and 4 August.

Rugosity. In 1981, rugosity symptoms of BPMV-infected Centennial were most severe, and those of Davis were the mildest (Fig. 2A). Leaf rugosity decreased after flowering in all cultivars except Ransom, and was least noticeable on Davis which was the only cultivar with less rugosity on 27 July than on 3 July.

In 1982, genotypes also could be separated into groups based on rugosity scores (Fig 2B). Centennial had higher rugosity scores than other cultivars on 29 June, and by 20 and 27 July, a highly rugose group (Centennial, Forrest, and NC-PMR) was significantly different from a slightly rugose group (Ransom, York, and Davis). Cultivars could be separated into three groups on 1 September based on rugosity: severe (Centennial, Ransom, and Forrest), moderate (NC-PMR and York), and mild (Davis).

Rugosity symptoms after flowering were less apparent in Davis and NC-PMR, more severe in Forrest and York, and remained constant in Centennial compared with preflowering symptoms. Although chlorotic symptoms in Ransom decreased after flowering, rugosity increased late in the season and was the highest on 1 September.

Canopy width and height. Inoculations of all genotypes at the V2 growth stage caused a "shock reaction," resulting in stunted plants. Average canopy width and height reductions 6 days after inoculation were 9 and 11%, respectively, in 1981 and 19 and 18%, respectively, in 1982. Growth rate of inoculated plants after this initial reaction was similar to that of uninoculated plants. Inoculated plants were 6 and 8% shorter, respectively, than uninoculated plants at the end of the 1981 and 1982 seasons. Significant differences in canopy width and height and final plant height were usually observed between inoculated and noninoculated plants and differences were similar in magnitude, with few exceptions, for all genotypes tested.

Chlorophyll concentration. Most chlorotic symptoms had faded by 18 August 1982, and BPMV-infected foliage of Centennial and Ransom was noticeably greener than foliage of uninoculated plants. This reaction was not observed in Davis. Concentration (mg/g of leaf tissue) of chlorophyll *a* in inoculated and uninoculated leaves of Centennial, Davis, and Ransom were 2.2 and 1.8, 1.8 and 1.8, and 2.4 and 1.8, respectively. Concentrations of chlorophyll *b* in infected and noninfected leaves of these cultivars were 0.8 and 0.65, 0.7 and 0.7, and 0.8 and 0.7, respectively.

Effect of growth stage at inoculation on symptom expression. Centennial and Ransom displayed less CLA both years when inoculated at growth stage V6 than when inoculated at growth stage V2 (Fig. 3). Differences in chlorosis between plants inoculated at different growth stages were greater on 27 July 1982 than on 28 July 1981. Percent CLA of Davis plants inoculated at the V2 and V6 growth stage averaged only 7 and 3% on 15 July 1981, and 4 and 3% on 28 July 1981, respectively.

On 15 July 1981 (Centennial, Davis, and Ransom flowered 19, 20, and 25 July, respectively), Centennial and Ransom had significantly more rugosity when inoculated at V2 than when inoculated at V6; differences after flowering were not significant (Fig. 4). Time of inoculation did not significantly affect rugosity scores for Davis.

Centennial and Ransom inoculated at the V2 growth stage in 1982 exhibited significantly more rugosity throughout the season than when inoculated at later growth stages. Although plants inoculated at V6 were more rugose than plants inoculated at V9 growth stage, the difference was not always statistically significant.

Yield loss. Inoculated plants of all cultivars except Davis yielded significantly less than did uninoculated plants (Table 2). Forrest exhibited the greatest yield loss each year.

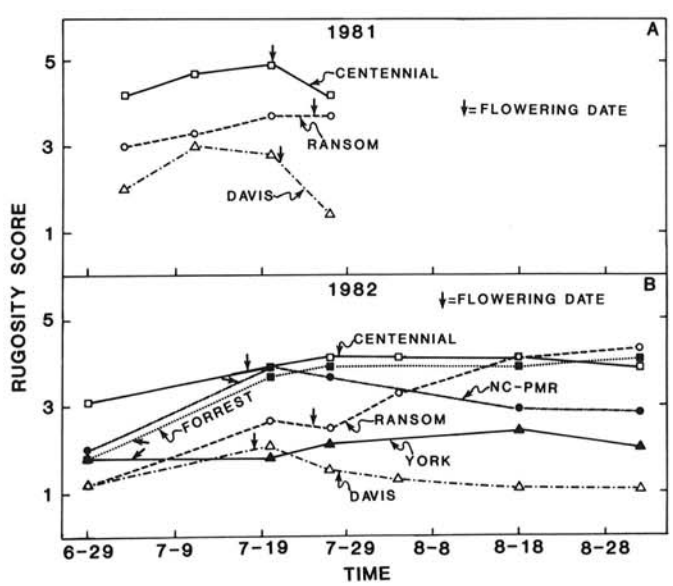

Fig 2. Progression of rugosity symptoms of soybean cultivars inoculated with bean pod mottle virus at the V2 growth stage **A,** in 1981 and **B,** in 1982. The rugosity scale ranged from 1 (flat leaves) to 5 (severely crinkled leaves).

Centennial inoculated in the V2, V6, or V9 growth stage yielded 7, 3, and −3% less, respectively, than uninoculated controls, whereas these values for Ransom were 6, 3, and 3%; only plants inoculated at the V2 growth stage sustained significant yield reductions.

Significant correlations calculated between yield reduction caused by BPMV and plant response variables are given in Table 3. Correlations between rugosity and yield loss were greatest on 19 July 1981 and 27 July 1982. Correlations between CLA and yield reduction improved until flowering, after which they became insignificant.

Greenhouse study. BPMV-infected Centennial had the least, and Ransom the most, CLA when grown under greenhouse conditions (Table 4). The youngest leaf on all cultivars always had more chlorosis than older leaves, and the sharp drop in percent CLA between the first and second nodes of Davis, observed in the field,

TABLE 2. Effect of bean pod mottle virus infection on yields of selected soybean cultivars inoculated at the V2-3 growth stage

	1981			1982		
Cultivar	Inoculated (q/ha)	Uninoculated (q/ha)	Loss (%)	Inoculated (q/ha)	Uninoculated (q/ha)	Loss (%)
Centennial	28.0	30.6	9*[a]	25.5	27.9*	9*
Davis	29.9	30.9	3	28.3	29.4	4
Forrest	37.8	43.4	13*	32.2	35.8	10*
NC-PMR	...	...	...	22.1	23.9	6*
Ransom	26.4	28.3	7*	27.0	28.9	6*
York	38.2	40.	6*	28.0	30.2	7*

[a]Asterisks indicate the percent yield loss was significant based on paired *t*-tests ($P = 0.05$).

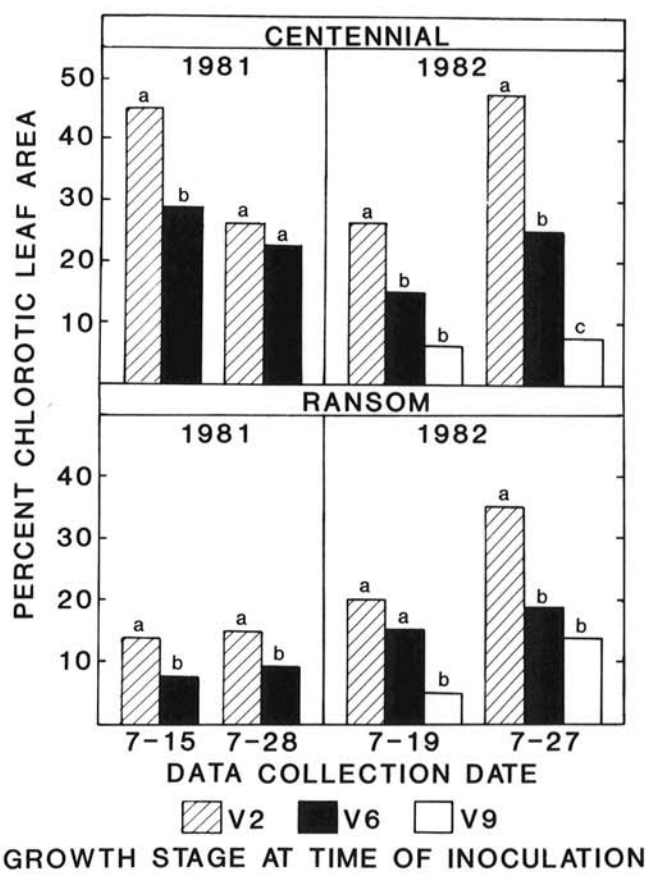

Fig. 3. Effects of growth stage of soybeans at date of inoculation with BPMV on percent chlorotic leaf area at the second node. For each data collection date, columns with different letters differ significantly according to Duncan's new multiple range test ($P = 0.05$).

was also observed on 8 and 22 November in the greenhouse test. BPMV-infected plants of all cultivars did not develop rugosity symptoms, and infected Centennial and Ransom plants did not turn darker green after flowering.

DISCUSSION

The percent CLA and the rate at which chlorosis was masked were influenced more by genotype than by environment, since the relative amounts of chlorosis were similar for genotypes in 1981 and 1982 and locations (each year's test was in a different field). The sharp drop in CLA between the first and second node of virus-infected Davis may have been responsible for it being the only cultivar not manifesting significant yield losses.

The modified Horsfall-Barratt scale, which was used in this study to estimate percent CLA in grading soybean lines for BPMV resistance, was practical and can be used for routine evaluation of soybean lines. Data taken from one leaflet at the second node from each of 10 plants in each replication sufficed since the greatest difference between cultivars for percent CLA occurred at the second node and differences among leaflets on each leaf were not significant. The quantitative nature of the data would make evaluation of genotypes for BPMV resistance more uniform when comparing data from different years or data taken by different evaluators.

Rugosity data also were useful in separating genotypes for BPMV resistance (as expressed by seed yields) since cultivar rankings for rugosity were similar in 1981 and 1982. In 1982, however, rugosity scores were more variable (noticeably so for Ransom) than were second-node CLA data; hence, environment and/or plant age probably had a greater effect on rugosity than on chlorosis. The association of low rugosity scores with low percentage of CLA, indicates that the amount of chlorosis in young leaves may predetermine the degree of rugosity as the leaf ages and that both symptoms may be related.

The reductions in canopy width and plant height of BPMV-infected plants were in agreement with the previous observations of Ross (8) that BPMV-infected soybeans were stunted. These parameters were not useful in predicting the yield response of genotypes since all cultivars were affected similarly.

Since infection of young plants (V2) caused significantly more severe foliar symptoms, stunting, and yield reduction than did later infections, estimations of BPMV resistance or disease loss should consider the stage of plant development at time of infection. Yield loss from plants infected at an early growth stage (V2) should be maximum, whereas yield loss from plants at later growth stages would be considerably less.

The 12% incidence of BPMV in plots of uninoculated plants (4 August 1981) may have had some influence on yields; however, since infections at the V6 or later growth stages did not appreciably affect yields in 1982, this natural virus spread in 1981 probably occurred too late to significantly reduce yields. This is also supported by the similarity in 1981 and 1982 of percent yield losses caused by BPMV infection of the various cultivars since natural virus spread to the uninoculated plots in 1982 was negligible.

Since inoculations at the V2-3 growth stage caused average yield losses of about 7.5%, BPMV is potentially an important soybean disease in eastern North Carolina due to its periodic widespread occurrence. Uniform infection between V2 and V4 leaf stages would be unlikely to occur in fields planted in May, however, crops planted later in June or July near an earlier-planted field of soybeans with many viruliferous beetle vectors could sustain a significant yield loss.

TABLE 3. Correlations (r) on various dates between leaf rugosity or chlorotic leaf area (CLA) and percent yield reduction of soybeans inoculated with bean pod mottle virus at the V2 growth stage

	1981		1982		
Variable	Data collected (day/mo)	Centennial, Davis, and Ransom (r)[b]	Data collected (day/mo)	Centennial, Davis, and Ransom (r)[b]	All cultivars[a] (r)[b]
Rugosity	11 July	0.857	29 June	0.953	0.698
	19 July	0.961	27 July	0.999	0.928
	27 July	0.908	1 Sept.	0.901	0.780
CLA	15 July	0.960	20 July	0.997	0.840
	28 July	0.998	27 July	0.943	0.910

[a] Centennial, Davis, Forrest, NC-PMR, Ransom, and York.
[b] All correlations were significant ($P = 0.05$).

TABLE 4. Development of chlorotic leaf area of three greenhouse grown soybean cultivars inoculated with bean pod mottle virus at the V2 growth stage on 24/9/82

Data 1982	Node	Chlorotic leaf area (%)[x]		
		Ransom[y]	Centennial	Davis
8 November	1[z]	51 a	11 b	19 b
	2	11 a	4 b	3 b
	3	16 a	1 b	1 b
	4	6 a	<1 b	<1 b
22 November	1	30 a	2 b	27 a
	2	28 a	4 b	2 b
	3	20 a	2 b	1 b
	4	14 a	2 b	<1 b
6 December	1	11 a	4 b	2 b
	2	12 a	2 b	1 b
	3	11 a	1 b	<1 b
	4	5 a	1 b	0 b

[x] For each node, means followed by same letter do not differ significantly ($P = 0.05$) according to Duncan's new multiple range test.
[y] Flowering dates for Ransom, Centennial, and Davis were 10, 12, and 19 of November, respectively.
[z] Node number 1 is youngest.

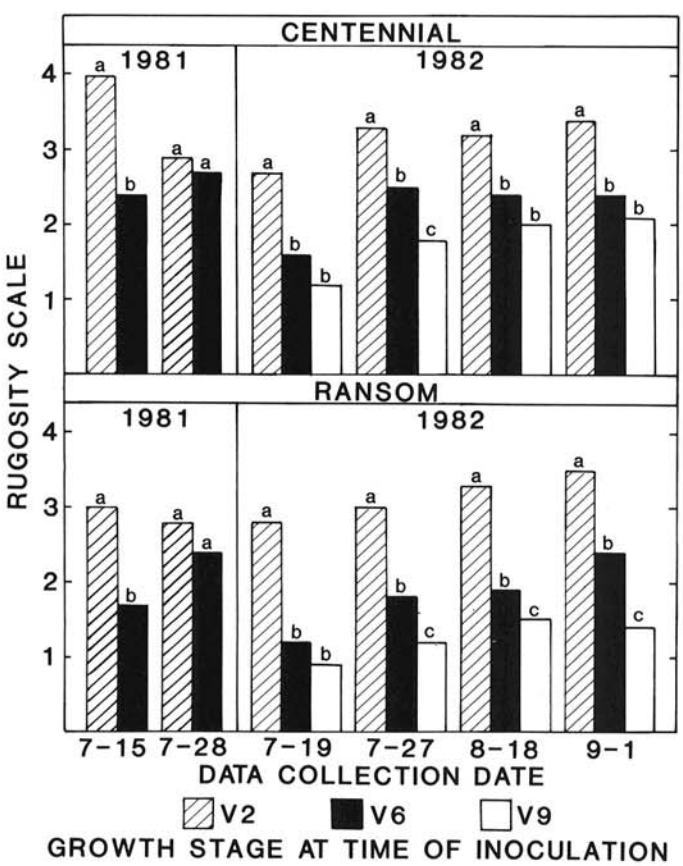

Fig. 4. Effect of growth stage of soybean plants at date of inoculation with BPMV on leaf rugosity. For each data collection date, columns with different letters differ significantly according to Duncan's new multiple range test ($P = 0.05$).

The high correlation of percent CLA before and during flowering with yield losses in both seasons provides meaningful support for selection during this period of resistant genotypes that could be used as parents for crosses during the current season. Consideration of the amount of yield loss caused by BPMV is important and should be considered in cultivar development. Since maximum yield loss occurred when infection was early, the advantage of mechanically inoculating plants with BPMV at the V2 to V3 growth stage resides in obtaining nearly uniform infection during the same day early in the season when beetle transmissions are sporadic.

Since the symptomatic leaves are limited to the canopy that develops after infection, soybean plants inoculated with BPMV in the V9 growth stage developed fewer symptomatic leaves than those inoculated at the V2 growth stage. Johnston and Pendleton (5) showed that the middle third of the canopy was most important for yield and this may partially explain why yield loss is minimal when infection occurs at later vegetative growth stages. The longer period of vegetative growth of Ransom between inoculation at V9 and flowering may explain why Ransom sustained more yield loss than Centennial in the time-of-inoculation studies in 1982.

Even though the pattern of percent CLA for various nodes of Davis was similar in both field and greenhouse studies, the large discrepancies in type and intensity of symptoms between field- and greenhouse-grown BPMV-infected plants of Centennial and Ransom indicate that symptom-based evaluation of soybean lines for BPMV resistance in the greenhouse is of questionable value. With the current state of knowledge, the most reliable evaluations are based on data collected from field-grown plants.

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