The Nature of Bean Yield Reduction by Bean Yellow and Bean Common Mosaic Viruses

R. O. Hampton

Research Plant Pathologist, Agricultural Research Service, U. S. Department of Agriculture, and Department of Botany and Plant Pathology, Oregon State University, Corvallis 97331.

Cooperative investigations of the Western Region, Agricultural Research Service, U. S. Department of Agriculture, and the Oregon Agricultural Experiment Station.

Technical Paper No. 3962 of the Oregon Agricultural Experiment Station, Corvallis.

Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture, and does not imply its approval to the exclusion of other products that may also be suitable.

Accepted for publication 17 June 1975.

ABSTRACT

Naturally infected field bean (*Phaseolus vulgaris* 'Red Mexican U.I. 34') (RM34) plants were selected for typical symptoms of either bean yellow mosaic virus (BYMV) or bean common mosaic virus (BCMV), hand-harvested, and analyzed for disease-induced effects on the components of seed yield. Bean yellow mosaic caused a 33% reduction in the number of pods per plant and a 41% reduction in seed yield, relative to healthy control plants. Moderate and severe bean common mosaic caused 50% and 64% reductions in the number of pods per plant, respectively, and 53% and 68% reductions in seed yield. Path analysis of yield component relationships revealed that certain indirect effects on yield of BCMV-infected plants were greater than the direct effects of individual yield components. BCMV-infected plants with fewer pods per plant than normal also tended to produce fewer than normal seeds per pod, although plants selected for uniformity of BCM symptoms varied significantly with regard to this yield-component relationship. The qualitative effects of BYM and BCM on RM34 bean plants were similar.

Phytopathology 65:1342-1346

Additional key words: yield components, disease-induced yield loss, virus-induced yield loss, path coefficient analysis.

Bean yellow mosaic (BYM) and bean common mosaic (BCM) have been widely regarded as the most ubiquitous and generally destructive virus-induced diseases of *Phaseolus vulgaris* L. Persistant stands of forage legumes are the principal reservoirs from which BYMV is spread by aphids to bean (10, 11, 22). Plants from infected seed (14) comprise the primary source from which BCM is aphid-transmitted to other bean plants (20, 24).

Losses due to these viruses often have been stated in terms of percentages of infected plants (12, 18, 21), affected acreage (5, 16), or estimated yield reduction (13, 19, 21). No effective statistical basis has been available for estimating the direct effect of BYMV or BCMV infection on bean seed yield.

Heavy reliance upon *P. vulgaris* seed as a high-quality food source in several regions of the world, and the increasing world demand for high-protein foods, now draw attention to the necessity of minimizing disease-induced yield losses and require a greater understanding of the precise nature of these yield losses. Supplementary to the task of developing specific genes for disease resistance, plant breeders and pathologists may be increasingly called upon to investigate morphological (7) and physiological plant characteristics providing protective tolerance against disease-induced yield losses.

This paper analyzes the effects of BYM and BCM on seed yield components of Red Mexican U.I. 34 field bean and on the interactions of these components. It also elucidates the effects of disease severity on individual plant responses, and provides a basis for assessing and interpreting seed yield losses induced by these viruses.

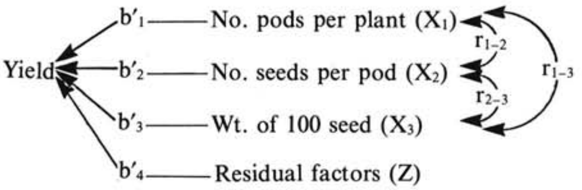
MATERIALS AND METHODS.—The field bean (cultivar Red Mexican U.I. 34) RM34 was suitable for this study because it is susceptible to strains of BYMV and BCMV indigenous to Pacific Northwest bean-growing areas, thus permitting comparison of the yield-reducing effects of these two related viruses on a single cultivar. Also, the dry-seed weight yield criterion normal for field beans was preferred to the fresh pod yield of snap beans cultivars, since seed weight registers cumulative plant responses to virus infection over the entire growing season.

BYM plots were arrayed in a commercial field of RM34 bean as six 0.2-hectare (ha) areas from each of which three paired samples of 24 infected and 24 healthy plants were obtained. The bean field was located adjacent to and downwind from a red clover (*Trifolium pratense* L.) seed field from which BYMV had been spread to beans by aphid vectors. Representative samples of BYMV-infected and healthy plants were marked in each plot at the late bloom stage and hand-harvested when seeds contained approximately 20% moisture.

BCMV-infected and healthy plants were selected and harvested from a commercial RM34 bean field into which BCMV had been introduced as infected seed and spread by aphid vectors. Fifty bean plants showing severe BCM symptoms, 50 plants showing moderate BCM symptoms, and 100 healthy plants were harvested within a selected 1.21-ha experimental area. Twelve severely affected and two moderately affected plants bore no pods. Data from these plants were eliminated to make possible the necessary statistical analyses.

No BCMV-infected plants were found in the field selected for determining yield effects induced by BYMV, and no BYMV-infected plants were found in the field selected for determining yield effects induced by BCMV. Plants marked for harvest in the one group showed symptoms entirely characteristic for BYM (22, 23) and, in the other group, symptoms entirely characteristic for BCM (22, 23).

All harvested plants were brought to uniform dryness (8-10% moisture), after which the number of pods per plant (X_1), average number of seeds per pod (X_2), weight (g) per 100 seed (X_3), and total seed weight (Y, yield) were determined for each plant. The components comprise yield according to the relationship, $X_1 \cdot X_2 \cdot X_3 = Y$. Infection-induced yield reduction was expressed subtractively upon each component of yield. The mechanism by which virus infection caused yield reduction was interpreted in relation to the yield concepts of Wright (17) and Grafius (9). Direct and indirect effects of yield components on seed yield of healthy and infected plants were examined by path coefficient (b'_{1-3}) analysis, the significance and methodology of which was effectively presented by Dewey and Lu (8). Paths of relationships presented in this paper are illustrated in the following diagram:



where b'_{1-3} are the standardized partial regression coefficients (15) and r_{1-3} are the correlation coefficients for yield components X_{1-3}.

The symbol of each statistical term in the text is identified by subscripts "h" and "i" for healthy and BYMV-infected plants, and "h," "m," and "s" for healthy, moderately BCM-, and severely BCM-infected plants, and of 1, 2, and 3 for the above yield components.

The terms "infection-induced" or "disease-induced" were preferred to "virus-induced" for yield reduction, since the effects measured in this study resulted from the combined effects of virus infection and subsequent disease processes.

RESULTS.—*Yield reduction induced by bean yellow mosaic virus infection.*—BYMV-infected plants produced 41.4% less seed than did healthy plants (Table 1). Most of the yield loss was attributable to the lower number of pods borne by infected plants (−32.9%), although pods of infected plants also contained fewer and smaller seeds than did pods of healthy plants. The theoretical relative yielding ability of infected plants (56.5% the yield of healthy plants), assuming zero interaction among yield components, closely approximated the actual mean yield by those plants (58.6%). There was, therefore, little net influence of yield-component interactions.

Standard error terms, and related confidence intervals, indicated that all infection-induced yield component declensions were significant, $P = 0.05$.

The direct contribution to yield by *seed weight* was slightly greater for BYMV-infected than for healthy plants (Table 2), while the direct contributions by *number of pods per plant* and *number of seeds per pod* were slightly less for BYMV-infected than healthy plants. The indirect effects of yield components were small for both infected and healthy plants. There was some tendency, however, for infected plants with fewer pods than normal to also produce fewer than the normal numbers of seed per pod. This tendency was expressed through the path relationship of $(r_{1-2}b'_1)\ i = 0.112$, in which the contribution to yield by *number of pods per plant* was influenced by the positive correlation between *number of pods per plant* and *number of seeds per pod*. This path relationship for healthy plants was negative $(r_{1-2}b'_1)\ h = -0.034$, as would be expected.

The sum of direct and indirect contribution to yield for each yield component (correlation coefficient with yield) was greater in infected than healthy plants.

Yield reduction induced by bean common mosaic virus infection.—Among BCMV-infected plants yielding at least a single seed, moderate infection reduced yield by 52.8% (Table 3) and severe infection reduced yield by 67.6%. Inclusive of plants bearing no pods, severe BCM reduced yield by 75.0%.

As was true for BYM-induced effects, the greatest determinant of BCM-induced yield reduction was decreased numbers of pods per plant. Infection-induced yield reduction at both levels of BCM severity, in fact, approximated the reduction in numbers of pods per plant. Seed-size variability, $s_{\bar{x}}$, = 0.471 (h), 0.792 (m), 1.65 (s), increased with increasing severity of BCM. Severely BCM-affected plants produced larger seeds than either healthy or moderately BCM-affected plants.

The theoretical relative yielding ability of BCMV-infected plants (moderate BCM, $YC_m = 46.7\%$; severe BCM, $YC_s = 31.4\%$) closely approximated the actual mean yield of BCM-affected plants ($Y_m = 47.2\%$ and $Y_s = 32.4\%$). Agreement between these results and those

TABLE 1. Influence of bean yellow mosaic virus (BYMV) infection on the yield of Red Mexican U.I. 34 bean plants

Yield component	Healthy plants[a]	BYMV-infected plants[a]	Decrease due to BYMV infection (%)[b]
No. pods/plant	27.66 0.571	18.55 0.496	32.9
No. seeds/pod	3.95 0.048	3.67 0.040	7.1
Wt. (g)/100 seeds	23.71 0.573	21.49 0.349	9.4
Wt. (g) seed/plant (yield)	24.96 0.564	14.62 0.454	41.4[c]

[a]Upper number, mean value respectively for 428 healthy plants and 425 BYMV-infected plants; lower number, standard error.

[b]The theoretical relative yielding capacity of BYMV-infected plants (expressed relative to the yield of healthy plants), based on the direct contribution of yield components, was calculated as $YC_v = (100 - 32.9)(100 - 7.1)(100 - 9.4)/10{,}000 = 56.5\%$.

[c]The actual yield of BYMV-infected plants, relative to that of healthy plants, was $Y_v = (100 - 41.4) = 58.6\%$.

TABLE 2. Path coefficient analysis of yield components of healthy and bean yellow mosaic virus infected Red Mexican U.I. 34 bean plants (n = 432 healthy, 432 infected)

Relationships of yield and:	Healthy plants	Infected plants
No. pods/plant (X_1)		
Direct effect (b'_1)	0.881[a]	0.860
Indirect effect via no. seeds/pod ($r_{1-2}b'_2$)	−0.013	0.034
Indirect effect via wt of seed ($r_{1-3}b'_3$)	0.006	−0.003
Correlation with yield (r_{1y})	0.874[b]	0.891
No. seeds/pod (X_2)		
Direct effect (b'_2)	0.328	0.260
Indirect effect via no. pods/plant ($r_{1-2}b'_1$)	−0.034	0.112
Indirect effect via wt of seed ($r_{2-3}b'_3$)	−0.055	−0.033
Correlation with yield (r_{2y})	0.239	0.339
Wt of seed (X_3)		
Direct effect (b'_3)	0.186	0.257
Indirect effect via no. pods/plant ($r_{1-3}b'_1$)	0.029	−0.011
Indirect effect via no. seeds/pod ($r_{2-3}b'_2$)	−0.097	−0.034
Correlation with yield (r_{3y})	0.118	0.212
Residual factors (Z)	0.129	0.096

[a]Standardized partial regression coefficients (15).
[b]Correlation coefficients among the three yield components were r_{1-2}, −0.039 (healthy-h) and 0.130 (infected-i); r_{1-3}, 0.033 (h) and −0.013 (i); r_{2-3}, −0.297 (h) and −0.129 (i).

TABLE 3. Influence of bean common mosaic virus infection on the yield of Red Mexican U.I. 34 bean plants

Component	Healthy plants[a]	Moderately BCMV-infected plants[a]	Severely BCMV-infected plants[a]	Decrease (%) due to infection	
				Moderate[b]	Severe[b]
No. pods/plant	31.72 1.34	16.00 1.98	11.47 1.79	49.6	63.8
No. seeds/pod	3.94 0.054	3.97 0.104	3.08 0.117	0	21.8
Wt (g)/100 seeds	42.17 0.471	38.31 0.792	46.82 1.65	9.2	(11.0)
Wt (g) seed/plant (yield)	51.96 2.18	24.50 3.10	16.84 2.68	52.8[c]	67.6[c]

[a]Upper number, mean value respectively for 99 healthy, 48 moderately infected, and 38 severely infected plants; lower number, standard error.
[b]Theoretical relative yielding ability of moderately and severely BCM-affected plants, respectively, were:
$YC_m = (100 - 49.6)(100 - 0)(100 - 9.2)/10{,}000 = 45.8\%$
$YC_s = (100 - 63.8)(100 - 21.8)(100 + 11.0)/10{,}000 = 31.4\%$ (see Table 1).
Parentheses indicate that seeds from severely BCM-affected plants were larger than those from healthy plants.
[c]Actual mean yield of moderately and severely BCM-affected plants, respectively, were:
$Y_m = (100 - 52.8) = 47.2\%$ and
$Y_s = (100 - 67.6) = 32.4\%$ (see Table 1).

obtained for BYM-affected plants, demonstrates that yield-component interactions exerted little net influence on the yielding characteristics of infected plants.

Two degrees of BCM severity provided the opportunity to examine a gradient of infection-induced effects on paths of yield-component relationships (Table 4).

The direct contribution of *number of seeds per pod* to seed yield ($b'_{2h} = 0.335$) was reduced by moderate or severe BCM ($b'_{2m} = 0.121$; $b'_{2s} = 0.156$). At the same time, BCM-affected plants with fewer *pods per plant* than normal produced larger-than-normal seeds, an effect expressed through the path relationships, $r_{1-3}b'_{1h} = 0.060$; $r_{1-3}b'_{1m} = -0.061$; $r_{1-3}b'_{1s} = -0.110$. This response represents simple compensation between two competitive yield components (1) and also is characteristic of healthy plants. However, an opposite trend in yield component relationships resulted with increased BCM symptoms severity; namely, infected plants with fewer *pods per plant* than normal produced fewer *seeds per pod* than normal. This effect is expressed through the path relationships, $4_{1-2}b'_{1h} = 0.128$; $r_{1-2}b'_{1m} = 0.142$; $r_{1-2}b'_{1s} = 0.287$.

An examination of this relationship in the appropriate bivariate distribution for severely BCM-affected plants (Fig. 1) suggested behavioral heterogeneity among plants, relative to these two yield components (see Discussion).

DISCUSSION.—RM34 bean plants infected with

TABLE 4. Path coefficient analysis of yield components of healthy and bean common mosaic virus-infected Red Mexican U.I. 34 bean plants n = 99 (healthy), 48 (moderate), 38 (severe)

Relationships of yield and:	Healthy plants	Infected plants	
		Moderate	Severe
No. pods/plant (X_1)			
Direct effect (b'_1)	0.994[a]	0.971	0.936
Indirect effect via no. seeds/pod ($r_{1\text{-}2}b'_2$)	−0.043	0.018	0.048
Indirect effect via wt of seed ($r_{1\text{-}3}b'_3$)	0.014	−0.004	−0.020
Correlation with yield (r_{1y})	0.965[b]	0.985	0.964
No. seeds/pod (X_2)			
Direct effect (b'_2)	0.335	0.121	0.156
Indirect effect via no. pods/plant ($r_{1\text{-}2}b'_1$)	−0.128	0.142	0.287
Indirect effect via wt of seed ($r_{2\text{-}3}b'_3$)	−0.153	−0.022	−0.123
Correlation with yield (r_{2y})	0.054	0.241	0.320
Wt of seed (X_3)			
Direct effect (b'_3)	0.230	0.073	0.169
Indirect effect via no. pods/plant ($r_{1\text{-}3}b'_1$)	0.060	−0.061	−0.110
Indirect effect via no. seeds/pod ($r_{2\text{-}3}b'_2$)	−0.223	−0.037	−0.114
Correlation with yield (r_{3y})	0.067	−0.025	−0.055
Residual factors (Z)	0.010	0.016	0.013

[a]Standardized partial regression coefficients (15).
[b]Correlation coefficients among the three yield components were $r_{1\text{-}2}$, −0.129 (healthy–h), 0.146 (moderate–m), and 0.307 (severe–s); $r_{1\text{-}3}$, 0.060 (h), −0.063 (m), and −0.118 (s); $r_{2\text{-}3}$, −0.677 (h), −0.303 (m), and −0.728 (s).

either BYMV or BCMV expressed nearly identical yield reduction responses; i.e., reduction in seed yield was due principally to reduction in numbers of pods per plants. Minor effects produced by these viruses upon yield component relationships also were similar. Similarities in plant responses to these viruses might be expected, since both are members of the potato virus Y group (6) and are serologically related (3, 4). Only BCMV, however, is seed transmitted in *Phaseolus* sp. at significant frequencies (22) and genetic sources of resistance to these viruses in *Phaseolus* sp. are independent (2).

Data obtained in this study reflected the end result of virus infection processes upon RM34 plants. They do not reveal the mechanism by which the number of pods per plant was reduced by infection. This mechanism was the subject of a separate study completed in this laboratory.

The majority (approximately 75%) of severely BCM-affected plants produced fewer *seeds per pod* as the yield-restrictive effects of BCMV caused fewer *pods per plant* to be produced, resulting in a positive regression line (Fig. 1). At the same time, approximately 25% of these plants were distributed along a theoretical, negative regression line. Such plants produced fewer *seeds per pod* as *number of pods per plant* increased, as would be expected for healthy plants. Indeed, this negative regression line, fitted by the method of least squares, approximated the computed regression line for healthy plants. Thus, although all plants in this population were selected at late-bloom stage for uniformly severe BCM symptoms, a minority of the plants produced yield responses similar to those of healthy plants.

Production of larger seeds by severely BCM-affected plants than by either healthy or moderately BCM-affected plants suggests that infection-related reduction in the number of pods and seeds was disproportionate to the supportive ability of these plants. Therefore, adequate photosynthate is presumed to have been available to the remaining developing seed.

Finally, the direct contribution of yield components to RM34 seed yield was substantially greater than indirect effects, for both healthy and virus-infected plants. This

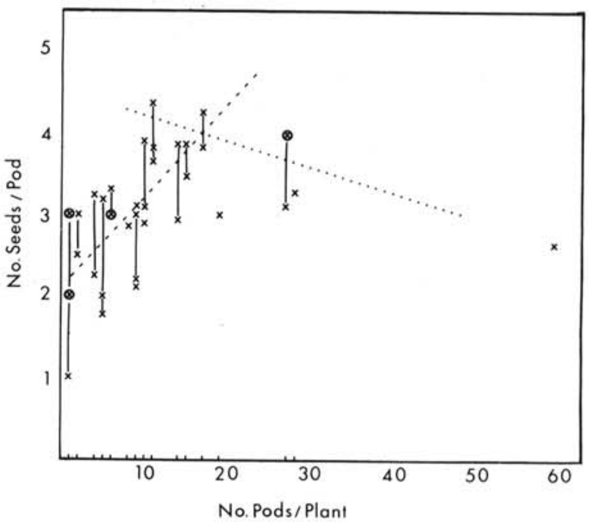


Fig. 1. Relationship of the number of seeds per pod and the *number of pods per plant*, among plants of bean cultivar RM34 (Red Mexican U.I. 34) selected for uniformly severe bean common mosaic symptoms. Legend:---= regression line representing plants (75% of the population) that produced fewer seeds per pod as fewer than average pods per plant were produced. ······ = regression line representing plants (25% of the population) that produced more seeds per pod as fewer than average pods per plant were produced; ×=datum representing a single plant, ⊗=two plants with identical data. Connective lines illustrate the range in numbers of seed per pod for plants with a given number of pods.

relatively minor role of yield component path relationships in bean seed yield seems to reconcile the "geometric" (9) and "regression" (8) concepts of yield component relationships. In essence, the former ignores paths of relationships among yield components, whereas the latter contends that important effects may be hidden in simple correlations. Paths of yield component relationships were examined in the present study and thereby subtle effects exerted by BYMV or BCMV on yield components were discerned.

The extent to which BYMV or BCMV reduces yield in other *P. vulgaris* genotypes by limiting the numbers of pods per plant is unknown. Information from the present study, however, suggests that breeding programs directed toward development of virus resistance might profitably evaluate plant responses to virus infection in terms of specific yield components, particularly on a population (50-to-100 plant) basis. Such an approach would appear particularly appropriate for BYMV, since tolerance to this virus is more frequently found than resistance or immunity.

LITERATURE CITED

1. ADAMS, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean Phaseolus vulgaris. Crop Science 7:505-510.
2. BAGGETT, J. R., W. A. FRAZIER, and F. P. MC WHORTER. 1966. Sources of virus resistance in beans. Plant Dis. Rep. 50:532-536.
3. BEEMSTER, A. B. R., and J. P. H. VAN DER WANT. 1951. Serological investigations on the Phaseolus viruses 1 and 2. Antonie van Leeuwenhoek. J. Microbiol. and Serol. 17:285-296.
4. BERCKS, R. 1960. Serologische Untersuchungen zur differenzierung von Isolaten des Phaseolus-virus 2 und ihrer Verwandtschaft mit Phaseolus-virus 1. Phytopathol. Z. 39:120-128.
5. BLOOD, H. L. 1947. An unusually heavy infection of yellow bean mosaic destroys the Cache Valley bean crop. Plant Dis. Rep. 31:384.
6. BRANDES, J., and R. BERCKS. 1965. Gross morphology and serology as a basis for classification of elongated plant viruses. Adv. Virus Res. 11:1-24.
7. COYNE, D. P., J. R. STEADMAN, and F. N. ANDERSON. 1974. Effect of modified plant architecture of Great Northern dry bean varieties (Phaseolus vulgaris) on white mold severity, and components of yield. Plant Dis. Rep. 58:379-382.
8. DEWEY, D. R., and K. H. LU. 1959. A correlation and path-coefficient analysis of components of crested wheatgrass seed production. Agron. J. 51:515-518.
9. GRAFIUS, J. E. 1964. A geometry for plant breeding. Crop Sci. 4:241-246.
10. HAGEL, G. T., and R. O. HAMPTON. 1970. Dispersal of aphids and leafhoppers from red clover to Red Mexican beans, and the spread of bean yellow mosaic by aphids. J. Econ. Entomol. 63:1057-1060.
11. HAMPTON, R. O. 1967. Natural spread of viruses infectious to beans. Phytopathology 57:476-481.
12. HARTER, L. L. 1927. Bean diseases in the West. Plant Dis. Rep. 11:148-149.
13. HORSFALL, J. G. 1930. Diseases of canning crops. Plant Dis. Rep. Suppl. 76:83-89.
14. REDDICK, D., and V. B. STEWART. 1919. Transmission of the virus of bean mosaic in seed and observations on thermal death-point of seed and virus. Phytopathology 9:445-450.
15. STEEL, R. G. D., and J. H. TORRIE. 1960. Multiple and partial regression and correlation. Pages 277-304 *in* R. G. D. Steel and J. H. Torrie, Principles and procedures of statistics. McGraw-Hill, New York. 481 p.
16. STEWART, V. B., and D. REDDICK. 1917. Bean mosaic. Phytopathology 7:61 (Abstr.).
17. WRIGHT, S. 1921. Correlation and causation. J. Agric. Res. 20:557-585.
18. ZAUMEYER, W. J. 1930. Bean diseases in the western United States in 1929. Plant Dis. Rep. 14:38-43.
19. ZAUMEYER, W. J. 1946. Bean diseases in some of the intermountain states in 1945. U.S. Bur. Plant Ind., Soils, and Agric. Eng. Plant Dis. Rep. 30:97-105.
20. ZAUMEYER, W. J., and C. W. KEARNS. 1936. The relation of aphids to the transmission of bean mosaic. Phytopathology 26:614-629.
21. ZAUMEYER, W. J., and R. H. THOMAS. 1947. Bean diseases in some of the mountain states in 1947. Plant Dis. Rep. 31:432-442.
22. ZAUMEYER, W. J., and R. H. THOMAS. 1957. A monographic study of bean diseases and methods for their control. U.S. Dept. Agric. Tech. Bull. 868. 255 p.
23. ZAUMEYER, W. J., and B. L. WADE. 1935. The relationship of certain legume mosaics to bean. J. Agric. Res. 51:715-749.
24. ZETTLER, W. J. 1967. A comparison of species of Aphididae with species of three other aphid families regarding virus transmission and probe behavior. Phytopathology 57:398-400.