Effect of *Cowpea severe mosaic virus* on Crop Growth Characteristics and Yield of Cowpea

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ABSTRACT

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Field experiments were carried out in St. Augustine, Trinidad & Tobago, West Indies to determine the effects of time of inoculation of *Cowpea severe mosaic virus* (CPSMV) and cultivar on crop growth and yield in cowpea (*Vigna unguiculata*). Crop growth and yield loss were investigated through growth analysis and yield component analysis on three cultivars in two seasons (wet and dry). Time of inoculation had the most profound impact on yield. Inoculations during the early log phase (seedling stage), 12 days after seeding (DAS), consistently had the greatest impact (50 to 85% yield loss) compared with those inoculated during the exponential growth phase (24 DAS; 22 to 66% yield loss) or linear growth phase (35 DAS; 2 to 36% yield loss). The effects were particularly pronounced in the dry season and in the more determinate cultivar, H8-8-27. Reduction in maximum leaf area index, leaf area duration, or maximum vegetative dry matter explained reductions in yield. Yield reductions resulted primarily from reduced pod number per plant and, to a lesser extent, from reduced average pod dry weight. The results show that CPSMV control measures should be aimed at delaying infection by CPSMV to minimize the impact on cowpea yield.

Additional keywords: resistance

Cowpea (*Vigna unguiculata*) is an important legume grown as a grain, vegetable, fiber, or fodder crop in the tropical and subtropical world. In the Caribbean, farmers cultivate both grain and vegetable cowpea (7). Vegetable-type cowpea, known as "bodi" or "bora" and grown for its tender, green, immature pods, is particularly important in Trinidad and Guyana. For instance, in Trinidad, 90% of the production area is under bodi (24).

Cowpea severe mosaic virus (CPSMV), a comovirus, is considered the most important virus of cowpea in the Caribbean (22). It is a major problem in El Salvador, Venezuela (4), Costa Rica (25), and Northeast Brazil (12), and also occurs in Peru, Surinam, and the United States (5). CPSMV causes crinkling and severe mottling of newly emerging leaves and, in severe cases, results in the overall stunting of the plant (24). CPSMV is transmitted by chrysomelid beetles, primarily *Cerotoma arcuata* (17).

Although dwarf vegetable cowpea cultivars resistant to CPSMV have been developed (23) and released in Trinidad and Tobago, farmers continue to grow indeterminate climbing cultivars of vegetable cowpea as well as grain cowpea, which are highly susceptible to CPSMV. Producers prefer the long pods that can be obtained from these indeterminate cultivars. Published reports of the physiological impact of CPSMV infection on crop development and yield are limited and inconclusive (4,21,26).

This study investigates the effects of CPSMV infection over two seasons (wet and dry) at various stages of growth on crop phenology, vegetative and reproductive development, and yield in three susceptible cowpea cultivars differing in growth habit.

MATERIALS AND METHODS

Experiments were conducted at the University Field Station, Valsayn, Trinidad in the wet (Jun to August 2000) and dry (January to March 2001) seasons. The soil type at the field station belongs to the River Estate Series classified in the subgroup Fluventic Eutropepts. It is a flat, deep, alluvial, sandy-loam with free internal drainage (3).

The cultivars used were H8-8-27 a dwarf, compact black-eyed cowpea cultivar obtained from the University of California, Riverside; Los Banos Bush Sitao #1, a dwarf, bushy vegetable-type cultivar which originated in the Philippines; and Green Arrow, a climbing vegetable-type cultivar originating from Taiwan and commonly grown in Trinidad for its yard-long bean. All the cultivars are highly susceptible to CPSMV but vary in their determinacy, with H8-8-27 being the most determinate and Green Arrow the most indeterminate.

The field experiments were established on cambered beds, with each plot consisting of five rows, 6.5 m long, interrow spacing of 60 cm, and intrarow spacing of 15 cm. Three seeds were planted per hill and the seedlings later thinned to one per hill. Plants of the climbing cv. Green Arrow were tied individually to 2-m wooden stakes, 21 days after seeding (DAS). Granular compound fertilizer Blaukorn for chloride-sensitive crops (12% N, 12% P_2O_5, 17% K_2O, 2% MgO, 6% S, 5% CaO, 0.2% Fe, 0.02% B, 0.01% Zn, plus traces of Mg, Cu, and Mb) was spread manually along rows at a rate of 200 kg ha^{-1} during molding at 14 DAS. Plots were sprayed every 10 days during the study period, 14 to 62 DAS, with the following pesticides: a synthetic-pyrethriod, Cypermethrin (Control flowable 500SC, Proficol, Bogota, Columbia), applied at 0.05 kg a.i. ha^{-1} to reduce vector transmission of CPSMV; and a prophylactic fungicide, copper hydroxide (Kocide; Griffin Corp., Valdosta, GA, USA), applied at 2.5 kg ha^{-1} to control Cercospora leaf spot (*Pseudocercospora cruenta* and *Cercospora apii*). Another insect growth inhibitor, Cyromazine (Trigard, Syngenta Ltd., Cali, Columbia), applied at 0.16 kg ha^{-1}, was used on the crop to reduce leaf miner damage to seedling plants caused by *Liriomyza* spp. Adequate crop moisture was maintained during the dry season by overhead irrigation applied twice weekly until field capacity.

CPSMV-infected plants of Los Banos Bush Sitao #1 were maintained at the University of the West Indies in an insect-protected enclosure to reduce the possibility of insects colonizing plants. The isolate of CPSMV was confirmed by serology and host range tests (22). Newly expanding leaves were collected from these plants and macerated in phosphate buffer, pH 7 (10:1 wt/wt), using a blender, and the macerate filtered through cheesecloth. Mechanical transmission was done by dusting emerging leaves with Carborundum dust (600 mesh) and wiping the leaves with a piece of cotton wool soaked in inoculum. Inoculations were performed manually in the late afternoon between 4:00 and 6:00 P.M.

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All the plants of the three inner rows of each plot were either left uninoculated (control) or inoculated with CPSMV at 12 DAS (early lag growth stage to first trifoliolate stage), 24 DAS (vegetative log growth phase), or 35 DAS (linear phase). The 12 treatment combinations (cultivars-by-inoculation treatment) were replicated three times following a randomized complete block design. In each experiment, the three blocks were sown at 3-day intervals.

All field observations and plant samples were obtained from the three innermost rows. Five arbitrarily selected plants were harvested from each plot at 20, 30, 40, 50, and 65 DAS and separated into leaf and stem, dried in an oven at 80°C for 72 h, and weighed. Crop growth rate (CGR) was calculated as average dry matter increase (g) per day. The leaf area of a single plant sample per plot was measured using a ΔT area meter (Hitachi Denshi Ltd., Tokyo, Japan). The leaf samples were dried and weighed as before and the specific leaf area (SLA) (leaf weight/leaf area) was determined on a per plot basis. The leaf area of the others plant samples from the plot was estimated using SLA as a conversion factor. Leaf area index (LAI) per plot was calculated from the average leaf area obtained from five plants per plot divided by the ground area for each harvest. Leaf area duration (LAD) and accumulated vegetative dry matter (VDM) were calculated from the area under the LAI and VDM curves, respectively, on a plot basis. The area of the resulting trapezoid was calculated as follows: $A = (LAI_1 \text{ or } VDM_1 + LAI_2 \text{ or } VDM_2)/2 \times T$, where A = area under the curve, LAI_1 or VDM_1 = measurement at harvest-1, LAI_2 or VDM_2 = measurement at harvest-2, and T = number of days between destructive harvests.

Canopy light (photosynthetically active radiation; PAR) interception was measured at 49 DAS (late linear phase) for each plot at solar noon ± 1 h, when above-canopy irradiance levels measured greater than 1,000 µm PAR m^{-2} s^{-1}. A meter-long quantum line sensor (LICOR, Lincoln, NE) extending from plant to plant between two rows was used to measure transmitted irradiance (I_t) and a quantum point sensor probe (LICOR) held level on top of the canopy was used to measure above-canopy irradiance (I_o). Canopy absorption for each plot was estimated from four measurements. Percentage absorbed irradiance (I_a) was calculated using the formula $I_a = (1 - I_t/I_o) \times 100\%$ (11).

Dry pods were harvested at crop maturity (indicated by pod yellowing and appearance of marked indentations on the pod) from the two center rows of each plot, approximately 1 month after flowering. The pods were counted and then dried for 72 h at approximately 40°C, and total pod dry weight and seed dry weight were recorded. The number of seed per pod and 100-seed weight were based on 30 pods arbitrarily selected per plot. Harvest index was calculated as either seed weight/total dry weight or pod dry weight/total dry weight.

Analysis of variance of data and regression analysis were done using the statistical software MINITAB (Minitab Inc, State College, PA). Growth analysis and yield component analysis were carried out according to general linear model and regression analysis, respectively. Means were separated using protected least significant difference (LSD).

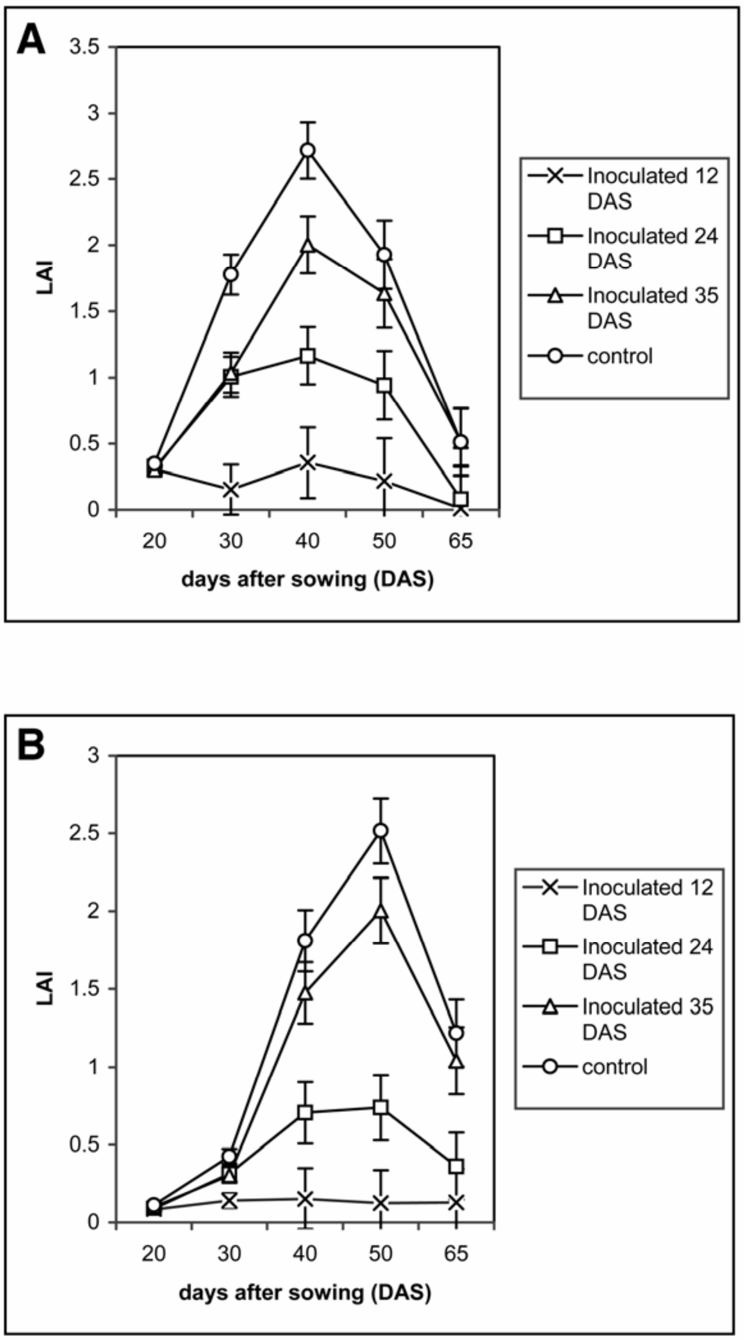

Fig. 1. Effect of time of inoculation (12, 24, and 35 days after sowing [DAS], control) with *Cowpea severe mosaic virus* on canopy development (leaf area index, [LAI]) in cowpea during the **A,** wet season and **B,** dry season trials. Bars represent standard error of the mean.

RESULTS

Monthly sunshine hours ranged between 6.6 and 7 h day^{-1} during the wet season study and from 7.5 to 9.5 h day^{-1} during the dry season study. Monthly mean temperatures ranged from a maximum of 31.4 to 32.1°C to a minimum 22.5 to 22.9°C in the wet season study and from a maximum of 30.3 to 31.1°C to a minimum of 20.0 to 20.2°C in the dry season study. Average relative humidity during the wet and dry seasons was 76 and 67%, respectively. Average monthly precipitation was 176 and 14 mm during the wet and dry season study periods, respectively.

Crop phenology and canopy development. The number of days to first flowering varied between cultivars and occurred at 35, 37 to 38, and 43 DAS for cvs. H8-8-27, Los Banos Bush Sitao #1, and Green Arrow, respectively, and was not significantly ($P > 0.05$) affected by inoculation with CPSMV (*data not presented*). There was a significant ($P = 0.003$) but small influence of season on time to flowering, which occurred 5 days earlier in the wet season than in the dry season (*data not presented*). Similarly, the time to achievement of maximum LAI was not significantly ($P > 0.05$) influenced by inoculation with CPSMV. For all cultivars in the warmer wet season, maximum LAI was achieved earlier in the wet than in the dry season (results shown only for pureline H8-8-27; Fig. 1).

Maximum LAI and maximum VDM achieved were significantly ($P < 0.0001$) reduced by CPSMV infection, especially in plots infected at the seedling stage (Fig. 1). The season–inoculation time and season–cultivar–inoculation time interaction effects were significant ($P < 0.0001$; Fig. 2) for both maximum LAI and LAD (but smaller in magnitude than the main effect of time to inoculation). Accumulated VDM (Fig. 3) showed a similar trend to maximum LAI and LAD. The proportional reductions in maximum LAI in response to inoculation time (80, 50, and 20% for 12, 24, and 35 DAS) were very similar to reductions in LAD. As observed for maximum LAI, the effect of inoculation time on LAD was more severe in the dry season than in the wet season (Fig. 2). Green Arrow, overall, had a much smaller LAD during the dry season, reflecting its early senescence in that season.

Average CGRs were generally higher in the wet season (average 3.67 g m^{-2} day^{-1}) than in the dry season (average 2.12 g m^{-2} day^{-1}). Time of inoculation with CPSMV had a significant ($P < 0.001$) influence on average CGR, which was greater in the dry (77, 51, and 34% at 12, 24, and 35 DAS, respectively) than in the wet season (66, 27 and 4% at 12, 24, and 35 DAS respectively).

Time of inoculation with CPSMV had a significant ($P < 0.0001$) effect on canopy absorption, with 48, 73, and 92% of the PAR absorbed by plants inoculated at 12, 24, and 35 DAS, respectively, compared with the uninoculated control. The season–inoculation time interaction was significant ($P = 0.02$; Fig. 4). Canopy extinction coefficient varied between 0.75 and 1.12 and was only significantly ($P = 0.002$) higher at the 12-day inoculation.

Partitioning of dry matter into reproductive parts. Cultivar had a significant ($P < 0.0001$) effect on partitioning into reproductive parts, measured as harvest index, and was highest in Los Banos Bush Sitao #1 (0.63), followed by H8-8-27 (0.41) and Green Arrow (0.37). The season–time of inoculation interaction effect also was significant ($P = 0.017$) but smaller in magnitude than the cultivar main effect. Harvest index, which decreased with later inoculations in the dry season, increased in the wet season (Table 1), but was significantly different from the control only in the early inoculation treatments. For instance, harvest index was significantly lower in plots inoculated at 12 DAS in the wet season, but was increased in plots inoculated at 12 and 24 DAS in the dry season.

Yield and components of yield. Seed and pod yield were highly correlated ($R^2 \geq 0.98$) in the dry season for all three cultivars. In the wet season, pod and seed yield were highly correlated for Los Banos Bush Sitao #1 ($R^2 = 0.86$) and H8-8-27 ($R^2 = 0.99$) and moderately associated for Green Arrow ($R^2 = 0.62$). Pod yield was significantly influenced ($P < 0.0001$) by time of inoculation and season–time of inoculation and cultivar–time of inoculation interaction effects. Although the pod yield of control plots was 40% higher in the dry (1,707 kg ha^{-1}) than in the wet season (1,231 kg ha^{-1}), the yields of CPSMV-infected plots were lower in the dry (630 kg ha^{-1}) than in the wet (940 kg ha^{-1}) season (Table 1). Inoculation with CPSMV at 35 DAS did not significantly affect yield in the wet season, but resulted in a 36% reduction in yield in the dry season. Among the cultivars tested (Table 2), yield reductions were most dramatic in H8-8-27 (average yield loss 65%), intermediate in Green Arrow (average yield loss 50%), and relatively low in Los Banos Bush Sitao #1 (average yield loss 32%).

CPSMV significantly ($P < 0.0001$) and negatively impacted every component of dry pod yield pod number $plant^{-1}$, dry pod weight, seed size, and seed number pod^{-1} (Table 3). Yield component analysis showed that variation in dry pod yield can be explained by pod number $plant^{-1}$ (76%), dry pod weight (16.7%), 100-seed weight (<1%), and seed per pod (<1%). Overall, the average reduction in dry pod yield over all inoculation times was approximately 48%, while those for pod number per plant

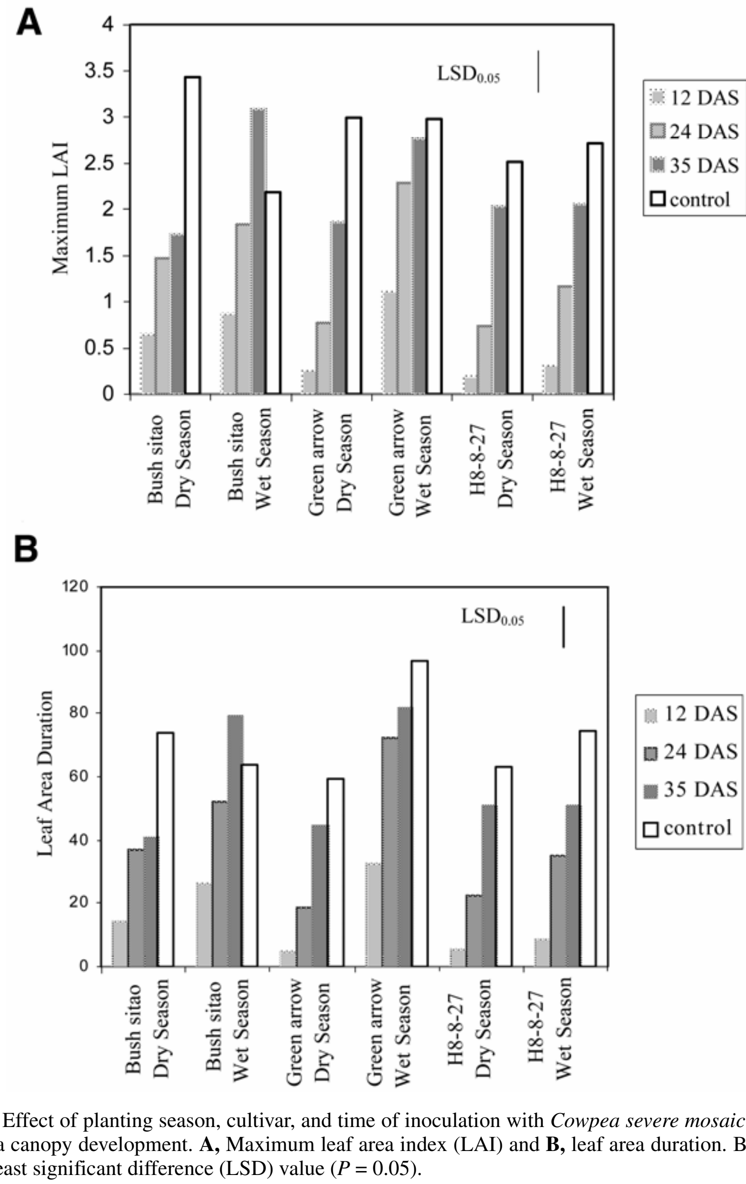

Fig. 2. Effect of planting season, cultivar, and time of inoculation with *Cowpea severe mosaic virus* on cowpea canopy development. **A,** Maximum leaf area index (LAI) and **B,** leaf area duration. Bar represents least significant difference (LSD) value ($P = 0.05$).

and average dry pod weight were 42 and 20%, respectively. The reduction in pod number m^{-2} (Table 3), the main yield component, was significantly (P = 0.001) greater in the dry compared with the wet season and in cv. H8-8-27 compared with Green Arrow and Los Banos Bush Sitao #1 (Table 2). Of the components of dry pod weight, seed number was affected to a larger extent by CPSMV compared with 100-seed weight. For instance, average reduction in seed number due to CPSMV infection was about 12.5% compared with that in 100-seed weight, which was only 5% (Table 3).

Pod dry weight not only was affected by time of inoculation with CPSMV but also showed a highly significant (P < 0.0001) cultivar–time of inoculation interaction. Whereas Green Arrow and H8-8-27 showed reductions in pod dry weight in response to inoculation at 12, 24, and 35 DAS, Los Banos Bush Sitao #1 behaved differently, accounting for the interaction. For example, Los Banos Bush Sitao #1 inoculated at 12 and 24 DAS resulted in lower pod dry weights compared with the control, whereas plots inoculated at 35 DAS showed an increase in pod weight (*data not presented*).

Across cultivars, seed number and size were reduced significantly only in plots inoculated at 12 and 24 DAS but not in those inoculated at 35 DAS (Table 3). However, the reduction in seed number pod^{-1} from CPSMV infection was apparent only in H8-8-27 and Green Arrow, but not evident in Los Banos Bush Sitao #1 (*data not presented*), accounting for the cultivar–inoculation time interaction.

Physiological determinants of yield. There was a strong linear relationship (R^2 = 0.71 to 0.95) between seed yield and maximum VDM in the dry season for all three cultivars investigated. In contrast, the relationships between maximum VDM and seed yield were poor in the wet season for both H8-8-27 (R^2 = 0.56) and Green Arrow (R^2 = 0.28), but continued to be strong and linear in Los Banos Bush Sitao #1 (R^2 = 0.90). Similar trends were observed with pod yield and accumulated VDM (*data not presented*).

There was a linear relationship (P < 0.05) between maximum LAI and average CGR for all three cultivars in the dry season (*data not presented*). Thus, the optimum LAI was not achieved in the three cultivars. The maximum LAI recorded for Los Banos Bush Sitao #1, Green Arrow, and H8-8-27 in the dry season were 4.0, 3.3, and 3.1, respectively. In the wet season, a linear relationship (maximum LAI versus average CGR) was obtained only for Los Banos Bush Sitao #1 (maximum LAI = 3.45), whereas an asymptotic, logarithmic relationship was observed for both Green Arrow and H8-8-27. The ceiling LAIs for Green Arrow and H8-8-27 were 2.84 and 2.2, respectively. The poor relationship between maximum VDM and pod yield in Green Arrow and H8-8-27 in the wet season was indicated by the nonlinear relationship between LAI and CGR obtained for these cultivars (*data not presented*). The relationships between average CGR and LAD were similar (*data not presented*).

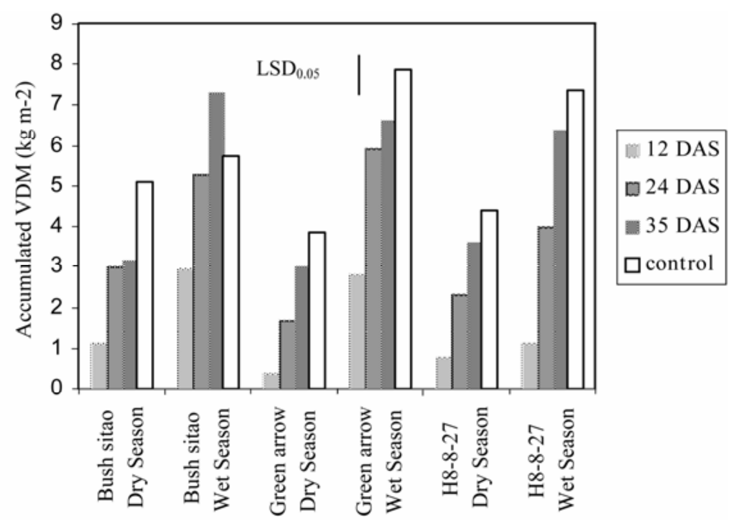

Fig. 3. Effect of planting season, cultivar, and time of inoculation with *Cowpea severe mosaic virus* on cowpea accumulated vegetative dry matter (VDM). Bar represents least significant difference (LSD) value (P = 0.05).

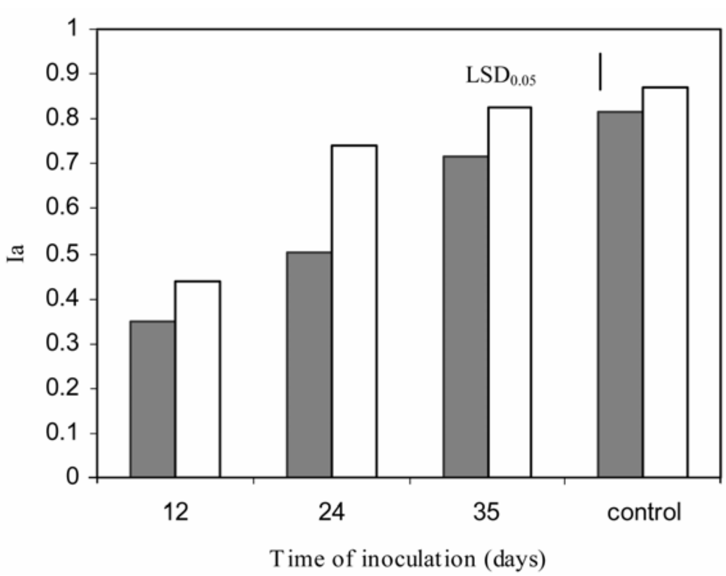

Fig. 4. Effect of planting season and inoculation with *Cowpea severe mosaic virus* on canopy light interception (I_a) in cowpea. Bar represents least significant difference (LSD) value (P = 0.05). Clear columns represent the wet season and shaded columns the dry season.

DISCUSSION

This study supports previous studies (4,12,21,26) showing that CPSMV can have a significant and important effect on cowpea yields. The present study demonstrated that yield losses associated with CPSMV infections can vary from as little as 2% to as much as 85%, compared with the control, depending on the time of inoculation, season, and cultivar. This may help to explain discrepancies in yield losses reported in the earlier studies.

Our results show that, of the parameters we measured, physiological age of plants at the time of CPSMV infection is by far the most important variable affecting the extent of yield loss. Inoculation during the early lag phase (12 DAS; seedling stage) consistently had the greatest impact on yield (48 to 84% reductions) compared with plants inoculated during the exponential growth phase (24 DAS, 22 to 66% yield loss) or linear growth phase (35 DAS, 2 to 36% yield loss). Interestingly, the lower and upper limits of yield loss associated with inoculations at any particular stage corresponded to the wet and dry seasons, respectively. This indicates that the yield impact in cowpea by CPSMV may be greater in the dry seasons than in wet seasons. At any given time of inoculation, yield losses were much higher during the dry season for the determinate H8-8-27

(48 to 88%), depending on the time of inoculation, compared with the indeterminate climbing cv. Green Arrow (21 to 72%) or the semi-determinate, bushy cv. Los Banos Bush Sitao #1 (3 to 57%). Overall, the determinate cv. H8-8-27 had a greater yield loss when inoculated early in its life cycle than the other cultivars. Umaharan (22) found that genotypes showing a faster growth rate masked symptoms of CPSMV due to their vining tendency. Similar interactions due to fast growth rate have been reported in barley with respect to barley yellow dwarf disease (10).

In this study, phenology was not influenced by CPSMV. In previous studies, the vegetative growth phase of cowpea was shown to be extended when plants were placed under extreme stress conditions such, as waterlogged soils (22) or extreme temperatures (20,28). It is possible that delaying flowering provides some opportunity for recovery growth. The relatively constant days to flowering and days to maximum LAI in this study suggest that CPSMV did not produce an extension of the vegetative growth phase, regardless of the time of inoculation. Hence, the possible recovery growth in the more determinate cv. H8-8-27 in both the wet and dry seasons may have been compromised. Although the indeterminate climbing cv. Green Arrow did not show vegetative recovery in the dry season (and, consequently, was severely affected by CPSMV), it showed considerable plasticity and recovery in the wet season. The results suggest that the warmer and wetter conditions that exist during the wet season may allow recovery growth, especially in the less determinate cultivars, and minimize the yield impact of CPSMV.

Our results suggest that maximum VDM (or accumulated VDM) may be a good predictor of pod and seed yields, particularly in the dry season (R^2 = 71 to 95%). Generally, clear skies and resulting greater incident irradiance in the dry season crop in this study resulted in a linear response for LAI with yield, even at LAIs as high as 4.0. Hence, inoculation treatments (12, 24, and 35 DAS) that affected LAI and VDM resulted in yield losses in proportion to the reduction in VDM. In cowpea, carbon and proteins needed for fruit during seed filling originate from the breakdown of vegetative organs, especially leaves (15); therefore, plant size at flowering is important, especially for determinate cultivars which have limited capacity to continue growth once apices become reproductive (16).

By comparison, in the wet season, the relationship between maximum VDM and yield was variable and not as strong overall (R^2 = 28 to 56%), except in Los Banos Bush Sitao #1 (R^2 = 90%). The skies during the wet season were cloudy and the conditions warm. As a result, the uninoculated controls recorded supra-optimal LAI and the yield of uninoculated controls was approximately 40% less in the wet season than in the dry season. Interestingly, due to apparent better recovery growth, the yields of inoculated plots were better in the wet than in the dry season. Littleton et al. (13) showed that, for a determinate cowpea cultivar grown in the humid tropics, maximum interception of irradiance is obtained at an LAI of 3, as was found in this study. Wein (27) opined that LAIs higher than 3 would, however, be required under conditions of greater insolation, as observed in the dry season in this study.

Partitioning of dry matter into reproductive organs is normally relatively constant in the absence of severe stress, such as drought or disease (9). In this study, harvest index was relatively constant, but increased slightly under the severely stressed conditions experienced in the 12-day inoculation treatment, especially in the dry season. The increase in harvest index exhibited in this study may reflect some degree of compensation for the severely compromised vegetative development.

Our results show that the impact of CPSMV on yield is primarily through

Table 1. Effect of planting season and time of inoculation (days after sowing [DAS]) with *Cowpea severe mosaic virus* on harvest index and yield in cowpea[a]

	Harvest index (g m^2)[b]		Yield (kg ha^{-1})		
Season, DAS	**PDM/TDM**	**SW/TDM**	**Seed**	**Dry pod**	**Pod no. m^{-2}**
Dry					
12	0.31	0.21	175 (84)	250 (85)	24 (78)
24	0.49	0.32	385 (66)	574 (66)	38 (64)
35	0.49	0.33	723 (36)	1089 (36)	55 (47)
Control	0.45	0.28	1,128	1,707	105
Wet					
12	0.46	0.33	359 (48)	643 (48)	46 (42)
24	0.49	0.33	609 (22)	966 (22)	68 (14)
35	0.39	0.23	717 (2)	1,211 (2)	78 (2)
Control	0.37	0.24	750	1,231	79
LSD (0.05)[c]	0.09	0.06	111	177	11

[a] Numbers in parenthesis refer to the percentage reduction in yield compared with the control.
[b] PDM = pod dry matter, TDM = total dry matter, and SW = seed weight.
[c] LSD = least significant difference.

Table 2. Effect of cultivar and time of inoculation (days after sowing [DAS]) with *Cowpea severe mosaic virus* on yield and its components in cowpea[a]

	Yield (mt ha^{-1})		
Cultivar, DAS	**Seed**	**Dry pod**	**Pod no. m^{-2}**
Los Banos Bush Sitao #1			
12	0.521 (57)	0.808 (57)	60 (54)
24	0.816 (33)	1.218 (34)	87 (33)
35	1.180 (3)	1.787 (4)	100 (23)
Control	1.219	1.86	130
Green Arrow			
12	0.155 (72)	0.375 (70)	22 (61)
24	0.235 (58)	0.527 (57)	29 (47)
35	0.438 (21)	0.955 (22)	48 (15)
Control	0.554	1.23	56
H8-8-27			
12	0.125 (88)	0.157 (88)	22 (75)
24	0.440 (58)	0.565 (57)	42 (53)
35	0.541 (48)	0.708 (46)	52 (43)
Control	1.04	1.32	91
LSD (0.05)[b]	0.133	0.214	13

[a] Numbers in parenthesis refer to the percentage reductions compared with the control.
[b] LSD = least significant difference.

Table 3. The effect of time of inoculation (days after sowing [DAS]) with *Cowpea severe mosaic virus* on yield components in cowpea[a]

DAS	Pod no. per plant	Dry pod weight per pod (g)	100-seed weight (g)	Seed no. per pod
12	3.7 (54)	1.28 (32)	12.58 (9)	7.29 (22)
24	5.2 (44)	1.54 (18)	13.05 (5)	8.17 (12)
35	6.4 (30)	1.68 (10)	13.58 (1.5)	8.95 (4)
Control	9.2	1.87	13.78	9.26
LSD (0.05)[b]	0.9	0.13	0.31	0.31

[a] Numbers in parenthesis refer to the percentage reductions compared with the control.
[b] LSD = least significant difference.

reduction in pod number. Similarly, other studies have shown that the number of pods per plant is the major yield determinant in cowpea (6,19) and the most sensitive to stresses (2,8). The average pod weight also was affected by CPSMV inoculation, mostly due to a reduction of seed number per pod (average reduction of 12.5%) but also due to reduction in 100-seed weight (average reduction of 5%). The results of this study confirm the findings of Littleton et al. (14) that sink size, which is determined by fruit set, never limits yield development in cowpea. The inability of the set pods to fill, as indicated by lower seed number and seed weight under stressed conditions (such as when plants are infected by CPSMV), suggests that source size may be the major limiting factor (1).

Rajnauth et al. (18) recommended that control strategies should aim at reducing initial inoculum level by planting disease-free seed away from CPSMV-affected fields, by reducing the rate of CPSMV infection by removal of infected plants, and by reduction of vector populations early in the crop's lifecycle. The results of this study support these findings, because late infections did not significantly reduce yields.

This study also shows that irrigated, dry season conditions of greater insolation are more conducive to increased production of cowpea if CPSMV infections are controlled or CPSMV-resistant cultivars are planted. In addition, this study suggests that, in the absence of resistant cultivars, the use of less determinate genotypes may allow recovery growth, especially in the wet season and, hence, reduce the impact of CPSMV on yields.

Further field experiments with isogenic lines differing in level of resistance to CPSMV would provide information about the effect of severity levels of the disease on yield loss, which would be useful in cowpea breeding programs aimed at combining the necessary level of CPSMV resistance with desirable production traits.

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