causing typical symptoms in Salinas Valley lettuce fields. The symptoms he described indicate that these were relatively mild isolates and not a necrotic or virulent variant.

In our study, 'Gallega' became systemically infected with LMV-L inoculated at 4 stages of growth. The sequence of symptom development and severity of symptoms in 'Gallega' were similar to those observed on 'Imperial 410' and 'Calmar'. The resistance in 'Gallega' appears to be somewhat effective against the typical seed-borne LMV isolates, but not against the more virulent isolate.

Genes for LMV resistance are of value in a lettuce breeding program as long as they confer resistance to the prevalent strains of the virus. The success of the mosaic-free seed program in controlling the typical seed-borne isolates indicates the need for resistance to the more virulent isolates that occur in wild hosts.

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The Influence of Flower Removal on Growth and Seed Yield of *Phaseolus vulgaris* L.[1]

H. C. Wien[2], R. F. Sandsted, and D. H. Wallace

Abstract. Dry beans (*Phaseolus vulgaris* cvs. Red Kidney and Great Northern) were grown in the cool season in the lowland tropics at Los Banos, Philippines. Manual removal of flowers for 11 days from first bloom resulted in increased wt of vegetative parts and no change in rate of total dry wt gain. New branches, roots, and leaves provided efficient alternate sinks for assimilates, so that leaf area was increased and maintained longer, and more branches formed. Although temporary flower removal increased pod set compared to control plants, pod and seed abortion prevented a significant yield increase. This resulted in lower ratios of seed wt to total dry wt, and decreased pod wt production per unit leaf area.

Dry edible beans (*Phaseolus vulgaris* L.) can be grown during the cool months of November to February under lowland tropical conditions at Los Banos, Philippines. However, the period from emergence to maturity was only 59 days, compared to 99 days at Ithaca, New York. Seed yields were proportionately lower, being 1978 kg/ha at Los Banos and 3177 kg/ha at Ithaca, corresponding to production rates of about 33 kg/ha/day for both locations[3]. Several workers report delay in senescence of plants by removal of flowers or immature pods (9, 13, 16). Ojehomon (16) found when opening flowers of cowpea were removed for up to 12 days, seed yields were not significantly affected, or decreased only slightly. Lyons (11) showed that the gametocide Mendok (2,3-dichloroisobutyrate) temporarily prevented fruit set of tomatoes but increased the amount of fruit set per plant at a later date, increasing single-harvest yields.

This experiment was conducted to determine if early flower removal in dry beans would prolong growth, increase fruit set, and produce higher seed yields. By temporarily altering the major sink for assimilates, and determining effects on vegetative and reproductive growth by growth analysis and light interception measurements, we hoped to better understand source-sink relationships. Since bean cultivars differ greatly in days to first flower (3), the results may have implications in breeding for yield.

Materials and Methods

The experiment was conducted on a well-drained Lipa clay loam soil (1) fertilized by banding 65-28-54 kg/ha (N-P-K) in rows 73 cm apart and 15.2 cm deep. Granular nematocide Nemagon (dibromochloropropane) was mixed with the fertilizer at 10 kg/ha active ingredient. Preplant incorporation of 1 kg/ha of trifluralin provided good weed control. Seeds were hand planted Nov. 14, 1969, about 10 cm above and to the side of

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[3] Wien, H. C. 1971. The influence of spacing on light interception, growth and seed yield of *Phaseolus vulgaris* L. under temperate and tropical conditions. Ph.D. Thesis, Cornell University, Ithaca, New York.

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the fertilizer, in plots 5m long and 8 rows wide, separated by 1m borders. Seeds were placed 2 per hill with 10 cm spacing between hills in the row. Plants were thinned to 1 per hill, and missing plants replaced by transplanting within 10 days after emergence. Insects and diseases were controlled with weekly applications of insecticides and fungicides. Irrigation by overhead sprinkler was necessary only once about 10 days before plant senescence.

Two cultivar and 2 flower removal treatments were used in a factorial design with 6 replications. The cultivars were 'California Light Red Kidney' and 'Great Northern U.I. 61'. Treatments were manual flower removal, beginning at first bloom and continuing 10 days for 'Great Northern' and 12 for 'Red Kidney', and a control.

Weekly samples of 1 m of a single row were taken to determine leaf area, and dry weights of leaves, stems, roots and pods. For leaf area measurements, 1 leaf disk per trifoliate leaf (disk area = 3.98 cm^2) was taken with a leaf punch (6). After drying leaf laminae and leaf disks, the area was calculated using the relationship: leaf area = leaf dry wt x disk area/disk dry wt. Leaf area duration was calculated by adding the weekly average leaf area indices (leaf area per unit ground area) for the growing season. Roots in the upper 15 cm were dug out with a spading fork, washed, and included in the dry wt sample. Systematic sampling began 17 days after emergence in a randomly selected corner of each plot, with a min of 50 cm of row left at the end of each sample as a border, and alternate sampling of rows. The first 2 samples were taken only from control plots, the next 4 from both, and the last 2 only from deflowered plots. At final harvest, seed yields were obtained from duplicate samples of 2 rows, each 1 m long. Yield components were measured from duplicate single row samples also 1 m long.

Light interception was measured at 4-day intervals, using the light-sensitive paper method of Friend (5) with the paper in clear plexiglass boxes as described by Francis (4). Three boxes were mounted on a plywood strip 40 cm long, with 2 strips per plot placed on leveled platforms perpendicular to the row so that duplicate meters were situated at the base of the plants, and 1 quarter and halfway between rows. Readings were converted to $cals/cm^2/day$ with a calibration curve constructed with an Eppley pyrheliometer. They were averaged for each plot and converted to percent light intercepted by comparing with incident light energy obtained from meters placed above the crop canopy.

Results and Discussion

Dry matter accumulation followed a sigmoid curve, with 'Great Northern' showing lower weights at all sampling dates (Fig. 1). The similar rate of dry wt increase for deflowered and control treatments for both cultivars indicates that the assimilates were efficiently diverted to alternate sinks. This is supported by altered partitioning of dry matter; flower removal caused increased wt of stems and dead leaves, roots, and to a lesser extent, green leaves (Fig. 2). Similar results were reported by Nosberger and Thorne (15) with barley after floret removal, and by Cockshull and Hughes (2) with *Chrysanthemum.* In contrast, Nosberger and Humphries (14) found that continued removal of developing white potato tubers reduced net assimilation rate and total wt. Leaf number and specific leaf wt (wt per unit leaf area) increased as a result of the treatments, and they theorized that lack of mobilizing growth substances prevented distribution of photosynthate to branches, thus providing less efficient storage for available carbohydrates than tubers. Our results suggest that in beans, the stems, leaves and roots collectively function as efficiently as sinks for photosynthates as developing pods.

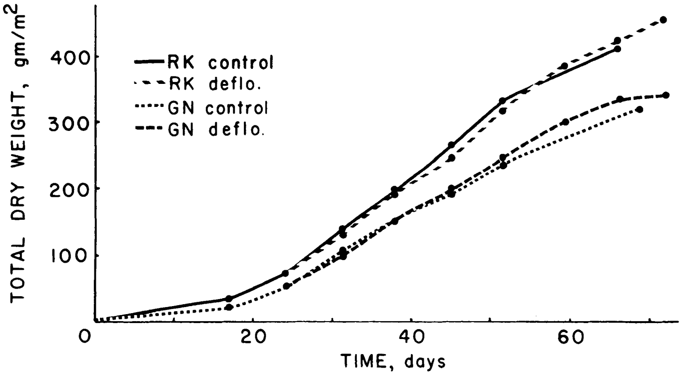

Fig. 1. Total dry wt accumulated with time for 'Red Kidney' and 'Great Northern' with and without deflowering.

For both control and deflowered plants, wt increase of vegetative plant parts essentially stopped 1 week after pod setting started (Fig. 2). This suggests that pod growth is largely sustained by photosynthate produced during the reproductive period, as also reported for cereal grains by Thorne (18) and for peas by Meadley and Milborn (12), rather than by translocation of dry matter previously accumulated in the vegetative tissue. Possibly the wt decrease of vegetative tissue at the end of the growing season (Fig. 2B) resulted from translocation of carbohydrates to the pods. The partitioning pattern for 'Great Northern' was similar to that of 'Red Kidney', although 'Great Northern' has indeterminate growth habit, while 'Red Kidney' is determinate.

Flower removal caused slightly higher leaf area indices (leaf area per unit ground area) and maintenance of leaf area for a longer period (Fig. 3). In contrast to findings with potato tuber removal (14), specific leaf wt was not significantly different between cultivars or between flower removal treatments. No treatment differences in net assimilation rate or crop growth rate were detected for any of the weekly sampling intervals. This again suggests that vegetative and reproductive tissue provided alternate sinks of equal efficiency.

As expected, percent light interception (Fig. 4) paralleled

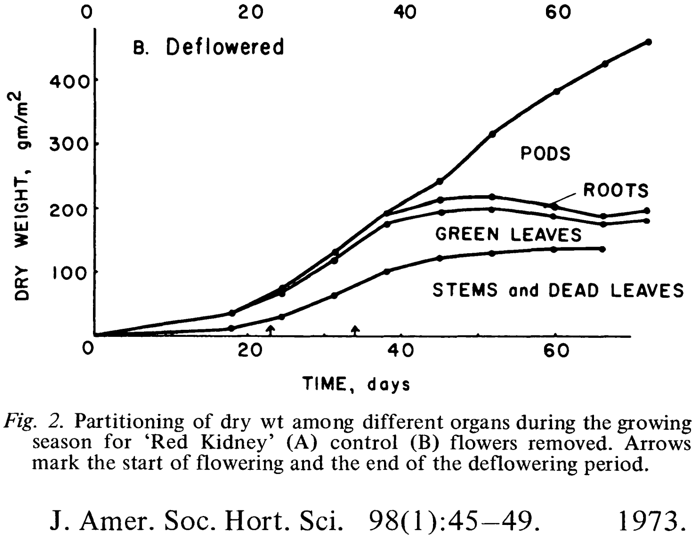

Fig. 2. Partitioning of dry wt among different organs during the growing season for 'Red Kidney' (A) control (B) flowers removed. Arrows mark the start of flowering and the end of the deflowering period.

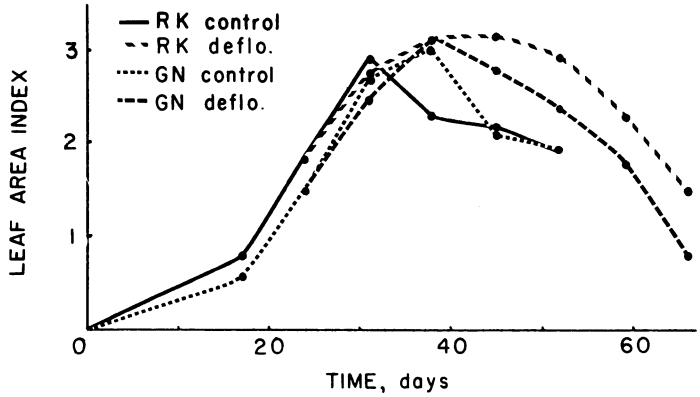

Fig. 3. Leaf area index during the growing season for 'Red Kidney' and 'Great Northern' with and without deflowering.

leaf area index (Fig. 3). Deflowering prolonged high level light interception, particularly for 'Red Kidney'. Deflowered plots intercepted more than 85% of the light for 28 days compared to only 20 days for control plots of this cultivar. A leaf area index of about 3.0 was required for 90% light interception.

In 'Red Kidney', flowers are borne mainly at the termini of main and branch stems. Continuous flower removal for 12 days left no flower buds on these first-formed terminal racemes. Instead of forming more buds on these racemes, the plants produced new axillary branches at lower nodes with flowers in their terminal axes, so that by day 45 after emergence, control and deflowered plants respectively had 6.9 and 10.4 branches per plant. In 'Great Northern', which normally bears flowers in the axils of upper main stem leaves and branches, branch number showed no increase by day 45, being 4.4 and 4.9 for control and deflowered plants. Flower removal resulted in pod-setting at later nodes on the main stem and branches; it probably stimulated growth of additional nodes, but counts were not made.

After cessation of flower removal, both cultivars set pods at the same time, with 'Great Northern' setting more than 'Red Kidney'. The total number of pods produced was higher for deflowered than control plots but declined with time due to pod abscission and seed abortion.

Experiments of Martinez Rodas[4] indicate that increased competition for substrates may cause some developing pods to stop growing. This was shown to involve no failure of the pod wall and seed components *per se* during development. Meadley and Milbourn (12) found that shading of pea plants during reproductive growth resulted in 36% abscission of flowers and pods, in contrast to 7.5% for controls. These results suggest that the pod abscission and flat pod formation on deflowered plants of our experiment may have resulted from increased competition for carbohydrates by the large number of developing pods.

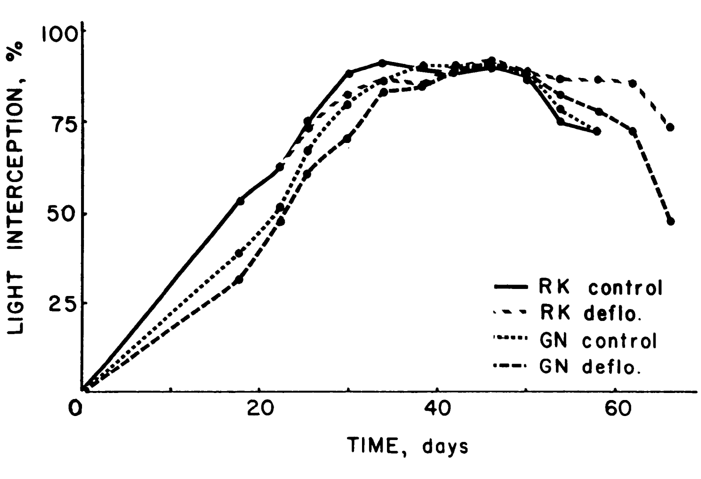

Fig. 4. Percent light interception during the growing season for 'Red Kidney' and 'Great Northern' with and without deflowering.

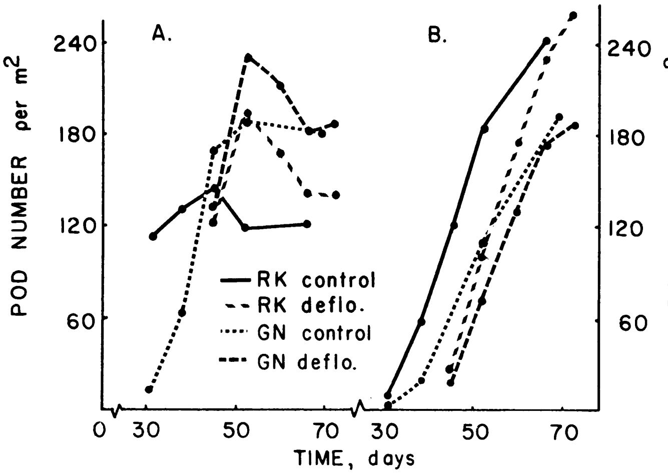

Fig. 5. Changes in pod number per m^2 (A) and pod wt per m^2 (B) with time for 'Red Kidney' and 'Great Northern' with and without deflowering.

Environmental factors that may have contributed to this reduction in reproductive growth late in the season include a 14-day period without rain or irrigation ending on day 56. Cloudy weather probably lessened the stress in this period, but the accompanying low solar radiation, averaging 141 cals/cm^2/day (400-700 mm), could also have restricted pod set and development. Air temp averaged 25.7°C during the growing season, with a mean max of 29°C, and were, therefore, not likely limiting.

Figure 5B indicates that pod loss was more than compensated by the wt gain of individual pods, so that pod wt per m^2 increased until final harvest. Rate of pod wt increase was greater for deflowered than for control plants, due largely to greater pod number. For 'Red Kidney', the higher rate for deflowered than control plants was sustained long enough that pod weights at final harvest were greater; for 'Great Northern' seed maturity was only delayed 3 days so that final harvest pod weights were similar.

Seed yields showed similar trends (Table 1). 'Red Kidney' had higher yield in both large and small yield samples than 'Great Northern', and flower removal caused a slight, and non-significant increase over controls. This was evident in the 2-row yield sample of both cultivars but only with 'Red Kidney' in the 1-row yield sample. The slightly higher seed yields of deflowered plots resulted from higher pod numbers. Flower removal decreased number of seeds per pod in 'Great Northern' but not in 'Red Kidney'. Deflowering reduced seed size (g/100 seeds). The decrease was more for 'Red Kidney' than 'Great Northern', giving a significant cultivar x treatment interaction.

Leaf area duration for 'Red Kidney' in the reproductive period was higher for deflowered plots (Table 2). Pod and seed wt produced per unit leaf area during reproductive growth (pod-leaf ratio) was decreased by deflowering, indicating inefficient use of the additional leaf area. Pod-leaf ratio of 'Red Kidney' was greater than that of 'Great Northern', as was the leaf area duration.

Of the total dry wt accumulated, 44.1 and 46.7%, for 'Red Kidney' and 'Great Northern', respectively, represented seed wt. These harvest indices were slightly reduced by flower removal because extra vegetative tissue was not matched by proportionate increase in seed wt. Although deflowering

Table 1. Seed yields and yield components for 'Red Kidney' and 'Great Northern' with and without deflowering and their interactions.[z]

	Seed yields, kg/ha		Seed yield components		
Cultivar	Large sample	Small sample	Full pod no./m^2	Seed no./pod	100 seed weight, gm.
Red Kidney	1861	1900	130.5	3.02	49.77
Great Northern	1622**	1528**	184.8**	3.30**	27.27**
Control	1697	1675	151.7	3.20	39.65
Deflowered	1786^{ns}	1753^{ns}	163.7^{ns}	3.12^{ns}	37.39**
Red Kidney Control	1820 a	1803 a	120.6 c	3.01 c	51.72 a
Red Kidney Deflowered	1902 a	1997 a	140.4 b	3.04 c	47.83 b
Great Northern Control	1574 b	1548 b	182.7 a	3.40 a	27.58 c
Great Northern Deflowered	1669 b	1509 b	187.0 a	3.20 b	26.95 c
Interaction	ns	ns	ns	*	**

[z]Means not sharing the same letter within columns are significantly different at the 5% level. * and ** means significantly different at 5% and 1% levels; ns, means differences not significant.

increased branch number of 'Red Kidney', the percentage of branches with pods decreased from 71 to 56%.

Seed wt comprised 71.2 and 76.5% of the total dry wt accumulated between flowering and harvest for 'Red Kidney' and 'Great Northern', showing a cultivar trend similar to harvest index. In both cultivars, this conversion efficiency (8) was 14% larger with flower removal. The greater pod number of deflowered plants may have "mobilized" more of the dry matter to developing pods. Conversion efficiency would thus be a measure of "sink strength," as suggested by Loach (10) for sugarbeets. Since there was no change in wt of vegetative tissue for most of the reproductive period (Fig. 2), conversion efficiency was determined just after flowering when leaf and stem weights were still increasing, and just before final harvest, when leaf, stem, and root weights declined. Since pod numbers were nearly equal for controls and deflowered plants in the latter period, sink strength effects due to larger pod numbers must have arisen just after flowering. Although this is not shown in Fig. 5 because only pods longer than 2.5 cm were counted, a large number of pods set on deflowered plants after flower removal ceased. A similar pattern was observed by Ojehomon (16) with cowpea. The assimilate demands of more reproductive tissue presumably brought about more rapid termination of vegetative growth in deflowered plants.

Table 2. Leaf area duration after flowering, pod-leaf ratio, conversion efficiency, and harvest index of 'Red Kidney' and 'Great Northern' with and without deflowering and their interactions.[z]

	Leaf area duration after flowering, weeks	Pod-leaf ratio[y]	Conversion efficiency, percent[x]	Harvest index, percent
Red Kidney	10.38	24.77	71.22	44.11
Great Northern	9.62*	19.97**	76.51*	46.70*
Control	9.24	23.83	69.07	46.22
Deflowered	10.76**	20.95*	78.66**	44.29*
Red Kidney Control	8.80 b	27.61 a	66.49 c	44.36 b
Red Kidney Deflowered	11.96 a	21.92 b	75.94 ab	43.86 b
Great Northern Control	9.68 b	20.05 b	71.65 bc	48.09 a
Great Northern Deflowered	9.56 b	19.89 b	81.37 a	44.71 b
Interaction	**	*	ns	ns

[z]Means not sharing the same letter within columns are significantly different at the 5% level. * and ** means significantly different at 5% and 1% levels; ns, mean differences not significant.

[y]Pod-leaf ratio = $\frac{\text{Pod + seed wt}}{\text{Leaf area duration after flowering}}$

[x]Conversion efficiency = $\frac{\text{Seed wt}}{\text{Dry wt produced after flowering}} \times 100$

Our results appear to contradict Smith and Prior (17), who demonstrated that bean yields were reduced by blossom and early pod drop caused by high temp. Podset is seldom completely inhibited by such conditions, however, so that the plants still develop a few pods. These may mobilize dry matter partitioning sufficiently to prevent further podset. Experiments with partial flower removal will have to be conducted to test this contention.

Flower removal increased conversion efficiency but decreased harvest index. This indicates that harvest index differences due to flower removal were determined largely by growth in the prolonged vegetative period.

In summary, temporary removal of flowers diverted assimilates to vegetative organs without reducing dry matter production rates, showing that these tissues are efficient alternate sinks. More pods were set on deflowered plants, and vegetative growth was more abruptly terminated as reflected in higher conversion efficiencies, i.e. partitioning of a higher percentage of current photosynthate to the fruit. Although deflowered plants had greater leaf area duration and more light interception in the reproductive period, a greater proportion of pods abscised. The decline in pod numbers may have been caused by insufficient assimilates brought about by limiting light and moisture. As a result, seed yields were not affected by flower removal, but harvest index and pod-leaf ratio were decreased.

The experiment indicates that the benefits of larger initial pod number derived from a prolonged vegetative period requires optimal growing conditions in the reproductive period to translate this advantage into higher seed yields. This illustrates the importance of the reproductive period for seed production, as shown by Meadley and Milbourn (12) with peas, and Hartman and Brun (7) with soybean.

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Inheritance and Linkage of Turnip Mosaic Virus and Downy Mildew (*Bremia lactucae*) Reaction in *Lactuca serriola*[1]

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Abstract. Data for resistance in *Lactuca serriola* L. to turnip mosaic virus (TuMV) and downy mildew were obtained from 5 F_2 progenies of crosses between TuMV-susceptible, mildew-resistant, and TuMV-resistant, mildew-susceptible parents. The F_1 progeny were TuMV and mildew-resistant. Of 1,103 F_2 plants assayed 823 were TuMV-resistant and 280 TuMV-susceptible. A total of 834 mildew-resistant plants were observed, and 269 mildew-susceptible. Resistance to TuMV and mildew are each controlled by a single dominant allele, designated *Tu* and *Dm,* respectively. The TuMV gene, *Tu tu,* is linked with the mildew gene, *Dm dm.* In the repulsion phase, the crossover value was 12.0% ± 2.9. F_2 progenies of crosses between TuMV-susceptible, mildew-resistant *L. serriola* and TuMV-susceptible, mildew-resistant *L. sativa* cv. 'Calmar' or 'Imperial 410', and crosses among cv. 'Calmar', 'Imperial 410', and 'E-4', indicated they possessed the same dominant allele for mildew-resistance, and the same recessive allele for TuMV-susceptibility.

Downy mildew-resistant *Lactuca sativa* L. crisphead cultivars currently grown in the United States are turnip mosaic virus (TuMV)-susceptible (9, 11). Zink and Duffus (9, 10) have reported circumstantial evidence which indicates that TuMV-susceptibility in *L. sativa* cvs. Calicel, Calmar, Imperial 410, Valrio, Valtemp, and Valverde is associated with mildew-resistant progenies derived from a *Lactuca serriola* L. collection (P.I. 91532)[4] from Russia (5, 8). In a survey of *L. serriola* growing in noncultivated areas in the Santa Clara and Salinas Valleys of California the populations fell into 3 classes: a) TuMV-resistant, mildew-resistant; b) TuMV-resistant, mildew-susceptible, and c) TuMV-susceptible, mildew-resistant (9). From this collection several lines were selected which were homozygous TuMV-susceptible, mildew-resistant.

The purpose of this paper is to report: a) the nature of inheritance of TuMV-susceptibility and mildew-resistance in *L. serriola;* b) the linkage relation of TuMV and mildew reaction; and c) new information concerning the inheritance of mildew-resistance in *L. sativa.*

Materials and Methods

Crosses were made between the homozygous TuMV-resistant, mildew-susceptible 'Great Lakes 118' and the homozygous TuMV-susceptible, mildew-resistant *L. serriola* lines to study the inheritance of TuMV-susceptibility, mildew-resistance, and the linkage of the TuMV gene with the mildew gene. In each cross, the *L. serriola* line was used as the pollen parent.

A second series of crosses were made between homozygous TuMV-susceptible, mildew-resistant *L. serriola* lines and homozygous TuMV-susceptible, mildew-resistant cvs. Calmar, and Imperial 410 to determine if the genes for mildew and TuMV reaction are the same in *L. serriola* lines and *L. sativa* cultivars. In each cross, *L. serriola* was used as the pollen parent. Crosses were also made among the homozygous TuMV-susceptible, mildew-resistant cvs. Calmar, Imperial 410, and E-4, to test for identity of the alleles for resistance to mildew and susceptibility to TuMV.

Seed for plants to be assayed for disease reaction was

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