# Alleviation of Restricted Systemic Spread of Pepper Mottle Potyvirus in *Capsicum annuum* cv. Avelar by Coinfection with a Cucumovirus

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## ABSTRACT

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In the resistant *Capsicum annuum* 'Avelar,' pepper mottle potyvirus (PepMoV) antigen accumulated in inoculated leaves but not in uninoculated leaves by 21 days postinoculation (dpi). The amount of PepMoV antigen in the inoculated leaves of Avelar was significantly less than that in comparable leaves from the susceptible control, *C. annuum* cv. NuMex R Naky. The accumulation and movement of PepMoV were examined using immuno-tissue blot analysis. PepMoV antigen was detected at 4 dpi in both genotypes in the inoculated central zone of the first two true leaves; however, PepMoV antigen was detected much sooner and at much higher concentrations in the uninoculated leaves of NuMex R Naky compared with Avelar. PepMoV was not detected in the first pair of uninoculated leaves by 25 dpi, although viral antigen was detected in the stem below the inoculated leaves and in the first internode above the inoculated leaves. When Avelar plants were coinfected with PepMoV and cucumber mosaic cucumovirus, PepMoV antigen accumulation was no longer restricted temporally or spatially within at least 50% of the Avelar plants.

Potyviruses are among the most destructive plant pathogens in *Capsicum* spp., with potato virus Y, pepper mottle virus (PepMoV), and tobacco etch virus commonly identified in pepper crops in the United States (29). Sources of resistance or tolerance in *Capsicum* to these viruses have been described, with much of the work focusing on genotypes that contain monogenic recessive factors that confer resistance or tolerance to the pathogen (9,29). *C. annuum* L. 'Avelar' was reported to have a monogenic recessive factor that conferred tolerance to PepMoV (30). Plants of this genotype and a cultivar derived from Avelar, Delray Bell, remained symptomless for approximately 4 wk postinoculation, after which a mild mottle appeared on inoculated and older uninoculated leaves (30). Uninoculated leaves, four to five leaves above the inoculated leaves, did not become symptomatic, and no virus was detected by immunodiffusion assays (26). In this report, we show that Avelar restricts systemic infection by PepMoV by what appears to be a restriction of cell-to-cell and/or long-distance spread of the virus.

Coinfection of a single plant by two related or unrelated plant viruses can result in various interactions between the viruses. Coinfection may enhance replication and/or movement of one or both viruses. Interactions may be synergistic, resulting in extremely severe disease symptoms, for example cowpea stunt disease, which results from coinfection of cowpea with blackeye cowpea mosaic potyvirus and cucumber mosaic cucumovirus (CMV) (22). In other cases, a virus that is restricted in its cell-to-cell and/or long-distance movement in some host species may no longer be restricted when the host is infected by a second virus (1,2,6,16,27,28). Under natural conditions, coinfection of a single plant by two or more viruses is not unusual; thus, there is potential for significant yield loss due to such interactions. In addition to examining the response of the resistant genotype Avelar and the susceptible genotype *C. annuum* 'NuMex R Naky' (R Naky) to inoculation with PepMoV, we examined the response of these genotypes to coinfection with PepMoV and CMV. CMV was chosen for its potential to enhance PepMoV systemic spread in the resistant genotype Avelar because of its ubiquitous nature, the lack of resistance to CMV in *Capsicum*, and the precedence for CMV-potyvirus interactions (4,23,24).

## MATERIALS AND METHODS

**Plant growth conditions and virus isolates.** Seeds were surface-sterilized by soaking in 10% sodium hypochlorite for 8 min followed by three rinses in double-distilled water (approximately 200 ml per rinse). Seeds were germinated on moistened filter paper in petri plates at room temperature (22 C) until radicle emergence, when seedlings were transplanted to a modified Cornell mix and maintained in a temperature-controlled greenhouse with metal halide illumination. Seeds of *C. annuum* R Naky (susceptible genotype) were obtained from F. Loaiza-Figueroa (Asgrow Seed Co., San Juan Bautista, CA.), and seeds of Avelar (resistant genotype) were obtained from R. Heisey (Asgrow).

PepMoV (strain V-1182) was provided by T. A. Zitter (Cornell University, Ithaca, NY) and was maintained in R Naky. CMV-PPRC-V27 (CMV-V27), isolated from *C. annuum* in California, was obtained from Asgrow and was maintained in *Cucurbita pepo* L. 'Caserta.'

**Inoculations.** In all experiments, plants were inoculated when the third pair of true leaves had just begun to expand. Hereafter, leaf positions will be designated as inoculated leaves, which represent the first two true leaves, and pairs of uninoculated leaves designated as the first, second, third, etc., pairs of uninoculated leaves above the inoculated leaves, with the first pair of uninoculated leaves being the next younger leaves above the inoculated leaves. In the experiments designed to examine PepMoV antigen accumulation in inoculated and uninoculated leaves, virus was applied to the first two true leaves (the inoculated leaves) by rub-inoculation. Inoculum consisted of two to three young, severely symptomatic PepMoV-infected leaves of R Naky ground

in 3 ml of 50 mM potassium phosphate buffer, pH 8.0. PepMoV antigen accumulation was determined in the inoculated leaves and in the second pair of uninoculated leaves using enzyme-linked immunosorbent assay (ELISA) at 21 days postinoculation (dpi).

The accumulation and spread of PepMoV antigen were examined through time at several positions within the inoculated leaf, in uninoculated leaves, and in stem sections. Immuno-tissue blot analyses were used to detect PepMoV antigen accumulation in the various tissues. PepMoV inoculum was applied to the middle portion (designated as the inoculated central zone) of the first two true leaves with a cotton swab. At specific times postinoculation, blots were made from tissue taken from the following positions: the inoculated central zone, the base of the inoculated leaf, and one leaf of each pair of uninoculated leaves. Leaf blots were made by rolling leaves transversely into a tight circle and making a single cut across the rolled leaf using a razor blade; the cut surface was pressed onto nitrocellulose for approximately 20 s. The presence of PepMoV antigen in stem sections was determined at each internode; the first internode was below the inoculated leaves, and internodes two to four were above the inoculated leaves. The tissue blots were stored at 4 C through the course of the experiment and were analyzed for the presence of viral antigen at one time under the same conditions.

In studies that examined the interaction of PepMoV and CMV-V27, Avelar and R Naky plants were inoculated with either PepMoV, CMV-V27, or a mixed inoculum of PepMoV and CMV-V27. Inoculum consisted of two to three young, severely symptomatic leaves of PepMoV-infected R Naky or CMV-V27-infected Caserta squash ground in 3 ml of 50 mM potassium phosphate buffer, pH 7.0. Mixed inoculum consisted of two symptomatic leaves of PepMoV-infected R Naky and two leaves of CMV-V27–infected Caserta squash ground together in 5 ml of buffer. Inoculum was applied to the first two true leaves, and virus accumulation was determined serologically by either ELISA or immuno-tissue blot analysis. For ELISA, the second pair of uninoculated leaves was tested at 21 dpi for the presence of PepMoV and CMV-V27 antigen. For immuno-tissue blot analysis, various tissues from plants inoculated with either single or mixed inocula were blotted twice to generate duplicate blots, each of which then was reacted with either anti-PepMoV or -CMV immunoglobulin (Ig). Leaf and stem blots were made at 21 dpi, as described above, and included an inoculated leaf and one leaf each of the first and second pairs of uninoculated leaves and sections through the stem at internodes one and two, which were below and above the inoculated leaves, respectively. All blots were analyzed at one time under the same conditions.

**Serological procedures.** Viral antigen was detected by direct double-antibody sandwich-ELISA, essentially according to Clark and Adams (3). Microtiter plates (Corning Glass Works, Corning, NY) were coated with Ig made against purified preparations of PepMoV virions (provided by T. A. Zitter) or CMV virions (D. Gonsalves, Cornell University, Geneva, NY) diluted in 50 mM carbonate buffer, pH 9.6, and incubated for 12–16 h at 4 C. Igs were purified from antiserum as described by McLaughlin et al (17) and conjugated to alkaline phosphatase as recommended by the manufacturer (Type VII T alkaline phosphatase, Sigma Chemical Co., St. Louis). Sap was expressed from leaf samples using two motorized metal rolling pins with the addition of 1.0 ml of phosphate buffered saline containing 0.5% Tween 20 (PBS-T). The expressed sap was collected and centrifuged at 10,000 rpm for 10 min in a microcentrifuge. The supernatant (antigen) was diluted 1:1 with PBS-T, added to the microtiter plate, and incubated at 35 C for 3 h or at 4 C for 12–16 h. Alkaline phosphatase-conjugated Ig was diluted in PBS-T, and reactions were incubated for 12–16 h at 4 C. Substrate reactions (*p*-nitrophenyl phosphate at 1 mg/ml diluted in 10% diethanolamine, pH 9.8) developed at room temperature, and absorbance values (405 nm) were determined using a Bio-Rad 2550 EIA reader (Bio-Rad Laboratories, Richmond, CA).

Immuno-tissue blots were made on nitrocellulose membrane (Schleicher & Schuell, Keene, NH) that was treated prior to blotting according to Holt and Beachy (10). Membranes were incubated in 50 mM Tris-HCl, pH 7.4, 200 mM sodium chloride (TBS) containing 5% powdered milk (TBS-powdered milk) at room temperature for at least 30 min and then reacted with anti-PepMoV Ig or -CMV Ig diluted in TBS at room temperature for at least 3 h or overnight at 4 C. The membranes were rinsed in TBS and incubated in TBS-powdered milk containing goat anti-rabbit Ig conjugated to alkaline phosphatase (Sigma) for at least 2 h at room temperature. After rinsing in TBS, colorimetric reactions for the presence of alkaline phosphatase were performed according to Leary et al (12).

## RESULTS

**Response of Avelar and R Naky to inoculation with PepMoV.** PepMoV-infected Avelar plants developed diffuse chlorotic lesions on inoculated leaves approximately 10 dpi, with no symptoms observed on uninoculated leaves during the 21 days of this experiment. In R Naky plants, inoculated leaves developed chlorotic lesions by 5–7 dpi, which often coalesced making the entire leaf appear chlorotic by 7–10 dpi. Systemic vein-clearing, mottling, and blistering developed on the uninoculated leaves of PepMoV-infected R Naky plants; these plants were stunted relative to uninoculated controls.

PepMoV antigen accumulation in inoculated and the second pair of uninoculated leaves of Avelar and R Naky plants was examined using ELISA at 21 dpi (by 21 dpi, the fifth-sixth pair of true leaves had just begun to expand). PepMoV antigen was detected in the inoculated leaves of all 10 Avelar plants (the mean ELISA absorbance value [405 nm] $\pm$ standard deviation was 0.232 $\pm$ 0.054) but was not detected in the second pair of uninoculated leaves from any of the 10 plants (0.057 $\pm$ 0.009). In contrast, PepMoV antigen was detected in the inoculated leaves (0.476 $\pm$ 0.060) and the second pair of uninoculated leaves (0.832 $\pm$ 0.251) of all five R Naky plants.

We extended these analyses to examine PepMoV accumulation at selected positions in Avelar and R Naky plants through time by immuno-tissue blot analysis. In R Naky, PepMoV antigen was weakly detected in the inoculated central zone by 4 dpi, and by 10 dpi, viral antigen was detected throughout the plant (Fig. 1). The number of days postinoculation that it took PepMoV to systemically infect R Naky plants, determined by immuno-tissue blot analysis, varied from one experiment to another but always occurred between 5 and 10 dpi. The strong reaction observed in inoculated and uninoculated leaf tissues of R Naky by 10 dpi indicated that PepMoV antigen accumulated to fairly high levels in these tissues and corroborates the ELISA results. PepMoV antigen accumulation was more sporadic in R Naky stem sections, especially above the inoculated leaves (e.g., internodes two and three).

In Avelar, PepMoV was weakly detected in the inoculated central zone by 4 dpi, and by 10 dpi, was present to a limited extent in the basal portion of the inoculated leaf and the stem below the inoculated leaves. PepMoV antigen accumulation in Avelar was more apparent in the central and basal portions of the inoculated leaf and the stem below the inoculated leaves by 15 dpi (data not shown). By 25 dpi, the sixth pair of true leaves had just begun to expand; PepMoV antigen was detected throughout the inoculated central and basal portions of the inoculated leaves as well as in the first two internodes of the stem (the second internode being above the inoculated leaves). Based on the intensity of antibody reaction on these blots, the systemic spread and amount of accumulation of PepMoV antigen in Avelar was clearly less than in R Naky. PepMoV antigen was detected in the first and sometimes in the second pair of uninoculated Avelar leaves 2–3 mo postinoculation, and a mild mottle often developed on these leaves, presumably in response to the gradual increase in accumulation of PepMoV in those leaves (data not shown).

We tested whether various concentrations of purified PepMoV used as inoculum would overcome the resistance expressed by Avelar. Inoculum was applied to the first pair of true leaves, and the second pair of uninoculated leaves of Avelar and R Naky plants were tested for the presence of PepMoV antigen at 4 wk

postinoculation by ELISA. PepMoV antigen was not detected in the second or third pairs of uninoculated leaves from Avelar even when inoculum consisted of PepMoV at 2.5 mg/ml, whereas R Naky plants became systemically infected with inoculum concentrations as low as 2.5 $\mu$g/ml. The inoculated leaves of these plants often abscised by 3 wk postinoculation and, therefore, were not tested for the presence of PepMoV (data not shown).

**The effect of coinfection with CMV on PepMoV distribution.** The accumulation and movement of PepMoV were examined in Avelar and R Naky plants coinfected with CMV-V27 by ELISA and immuno-tissue blot analysis. ELISA was used to monitor the accumulation of viral antigen in the second pair of uninoculated leaves at 21 dpi. In Avelar plants inoculated with PepMoV alone, PepMoV antigen was not detected in the second pair of uninoculated leaves at 21 dpi but was detected in comparable leaves of R Naky (Table 1). CMV-V27 antigen was detected in all plants tested, regardless of whether the inoculum consisted of CMV-V27 alone or a mixture of CMV-V27 and PepMoV. When plants were inoculated with PepMoV and CMV-V27, PepMoV antigen was detected in the second pair of uninoculated leaves from nine of 12 Avelar plants (Table 1). The number of Avelar plants systemically infected with PepMoV when coinfected

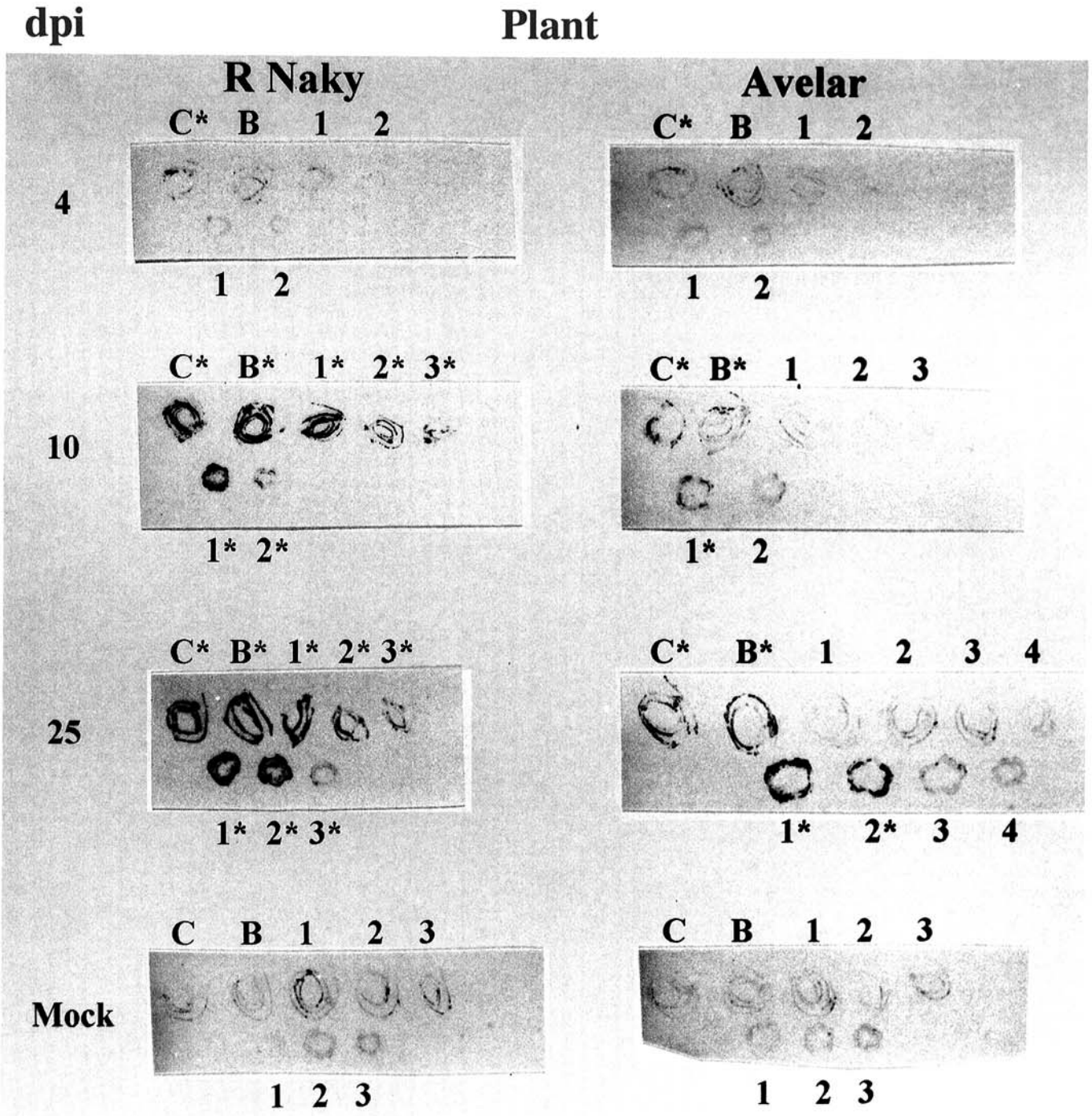


**Fig. 1.** Immuno-tissue blot analysis of pepper mottle virus (PepMoV)-infected and mock-inoculated *Capsicum annuum* NuMex R Naky (R Naky) and Avelar tissues through time. Tissues were blotted onto nitrocellulose membranes and reacted with anti-PepMoV immunoglobulin, which was detected using an alkaline phosphatase detection system (12). The upper row of tissue blots for each of the plant genotypes at each time period represents leaf tissue, and the lower row represents sections through the stem. Leaf tissue blots are presented as C for the inoculated central zone, B for the basal portion of the inoculated leaf, and 1–4 for the first through the fourth pairs of uninoculated leaves, with the first pair being the next younger pair of leaves above the inoculated leaves. Stem section blots are presented as internodes 1–4, with internode 1 being the first internode (below the inoculated leaves), and internodes 2–4 in consecutive order, with 2 being just above the inoculated leaves. An asterisk beside a letter or number indicates a positive reaction for the presence of PepMoV antigen. dpi = days postinoculation.

with CMV-V27 varied between experiments but was always greater than 50% (data not shown). Symptom development in Avelar plants infected with PepMoV and CMV-V27 consisted of chlorosis of uninoculated leaves and stunting of plants similar to but more severe than symptoms observed when plants were infected with CMV-V27 alone. R Naky plants infected with PepMoV and CMV-V27 typically expressed symptoms similar to those observed in R Naky plants infected with PepMoV alone.

Immuno-tissue blot analysis was used to detect viral antigen in the inoculated leaves, the first and second pairs of uninoculated leaves, and the first two internodes of the stem (the first being below the inoculated leaves and the second being the first internode above the inoculated leaves) at 21 dpi (Fig. 2). In Avelar plants inoculated with PepMoV alone, PepMoV antigen was detected in the inoculated leaf and in internodes one and two (Fig. 2), whereas PepMoV antigen was detected in all tested tissues from R Naky plants (data not shown). When plants were inoculated with CMV-V27 alone, CMV-V27 antigen was detected from all tested tissues from Avelar (Fig. 2) and R Naky (data not shown) plants at 21 dpi. In Avelar plants coinfected with PepMoV and CMV-V27, PepMoV antigen accumulation was no longer restricted to the inoculated leaves but also was detected in both pairs of uninoculated leaves (Fig. 2). CMV-V27 antigen accumulation in Avelar and R Naky plants coinfected with PepMoV was similar to what was observed when inoculum consisted of CMV-V27 alone (Fig. 2). Based on the intensity of antibody reaction, PepMoV antigen accumulation in Avelar plants coinfected with CMV-V27 (those in which complementation was observed) was much greater than in Avelar plants infected with PepMoV alone, especially in stem sections. Neither PepMoV antigen nor CMV-V27 antigen was detected in tissue blots of mock-inoculated controls or in tissue blots of plants inoculated with one virus and then reacted with Ig to the other virus (Fig. 2).

## DISCUSSION

The accumulation and movement of PepMoV in the resistant genotype Avelar was compared with a susceptible control, R Naky, with the intent of characterizing the resistant response of Avelar. The initial series of experiments with ELISA demonstrated that by 21 dpi (the fifth-sixth pair of true leaves had just begun to expand) PepMoV antigen accumulated to detectable levels in inoculated leaves but not in the second pair of uninoculated leaves of Avelar plants. In contrast, PepMoV antigen was detected in inoculated and comparable uninoculated leaves of R Naky plants by 21 dpi. Furthermore, the amount of PepMoV antigen was significantly less in inoculated leaves of Avelar than in those of R Naky. These data are consistent with the original description of the PepMoV-Avelar interaction, which indicated, based mainly on symptom development, that PepMoV remained localized to the inoculated leaves and the first or second pair of uninoculated leaves of Avelar plants (30).

The nature of the resistance observed in Avelar, based on the experiments described above, appeared to result from reduced accumulation and restricted systemic movement of PepMoV. ELISA data for PepMoV accumulation and movement within the inoculated leaf (data not shown) and the immuno-tissue blot data at additional locations indicated that less PepMoV accumulated at any given point within Avelar and movement throughout Avelar plants was restricted relative to R Naky. PepMoV antigen was first detected, albeit in weak reactions, in both genotypes in the inoculated central zone by 4 dpi; however, by 10 dpi the amount of PepMoV antigen accumulation and the extent of systemic spread varied greatly between Avelar and R Naky plants. In R Naky, systemic infection developed quickly, and generally, PepMoV antigen accumulated to high levels and was distributed throughout all leaves tested and all tissues within those leaves. In contrast, in Avelar plants less PepMoV antigen accumulated, and its systemic spread occurred slowly during the course of each experiment. Moreover, PepMoV antigen was not detected in leaves other than inoculated leaves or above the second internode by 25 dpi. Stem tissues, on the other hand, were somewhat similar between the two genotypes (i.e., there usually was more PepMoV antigen in stem sections below the inoculated leaves with sporadic distribution of PepMoV antigen in stem sections above the inoculated leaves). The irregular distribution of PepMoV antigen in stem sections above the inoculated leaves apparently did not affect PepMoV movement into uninoculated leaves as illustrated in R Naky plants.

Resistance to viral movement can occur in various ways, including restricted cell-to-cell movement (7,18), localization to the inoculated leaf (5,13,20), and limited systemic spread (5,8,11,19, 20,25). The resistance expressed by Avelar against PepMoV appears to limit the extent of PepMoV systemic movement but, in fact, could actually affect replication (accumulation), which is manifest as reduced movement. For example, if a critical amount of virus and/or viral gene product(s) were required for efficient movement, then reduced levels of replication would result in a delay in accumulation and turn movement. It was difficult to determine from these experiments whether the reduced amount of antibody reaction for the presence of PepMoV in Avelar tissues was due to less PepMoV antigen per cell (and thus less color reaction) and/or fewer cells containing viral antigen.

Long-distance movement of PepMoV within *Capsicum* may depend on host physiology to some extent, as has been observed in other plant-virus interactions (14,15). The resistance expressed by Avelar against PepMoV, whether actually directed at viral replication or movement, may retard PepMoV infection to the extent that long-distance movement is no longer affected by the source-sink flow of photoassimilates; thus, movement into all younger tissues would not occur (14,15). This type of physiological effect probably does not have a major influence on the restricted systemic spread of PepMoV in Avelar (i.e., PepMoV is detected in stem sections within 10 dpi, and the growth rate of *Capsicum* is relatively slow).

In contrast to the PepMoV-Avelar results, in Avelar plants coinfected with PepMoV and CMV-V27, PepMoV antigen accumulated to higher levels with no apparent delay or restriction in systemic spread (Table 1; Fig. 2). Immuno-tissue blot analysis of coinfected Avelar plants showed extensive accumulation of PepMoV antigen in all inoculated and uninoculated tissues examined, especially stem sections. This complementation was

TABLE 1. Accumulation of pepper mottle virus (PepMoV) antigen and cucumber mosaic virus (CMV) antigen in the second pair of uninoculated leaves of *Capsicum annuum* Avelar and NuMex R Naky in singly and doubly infected plants

| Virus[a] / Genotype | ELISA value with immunoglobulins from antiserum[b] | |
|---|---|---|
| | PepMoV | CMV |
| PepMoV | | |
| Avelar | 0.109 ± 0.028 (0/10) | 0.170 ± 0.032 (0/10) |
| NuMex R Naky | 1.791 ± 0.209* (3/3) | 0.174 ± 0.018 (0/3) |
| CMV-V27 | | |
| Avelar | 0.127 ± 0.042 (0/10) | 0.810 ± 0.332* (10/10) |
| NuMex R Naky | 0.097 ± 0.036 (0/3) | 0.482 ± 0.095* (3/3) |
| PepMoV + CMV-V27 | | |
| Avelar | 0.473 ± 0.253* (9/12) | 0.747 ± 0.474* (12/12) |
| NuMex R Naky | 1.496 ± 0.297* (3/3) | 0.535 ± 0.149* (3/3) |

[a] Inoculum consisted of three PepMoV-infected NuMex R Naky pepper or CMV-infected Caserta squash leaves ground in 3 ml of 50 mM potassium phosphate buffer, pH 7.0. Mixed inoculum consisted of two PepMoV-infected NuMex R Naky leaves and two CMV-infected squash leaves ground together in 5 ml of buffer. Samples were collected at 21 days postinoculation and consisted of the second pair of uninoculated leaves.

[b] Values represent the mean absorbance (405 nm) ± SD, determined by direct double-antibody sandwich enzyme-linked immunosorbent assay (ELISA). Numbers in parentheses indicate the number of plants infected per number of plants inoculated based on ELISA. An asterisk indicates that the mean absorbance value is positive for the presence of PepMoV antigen or CMV-V27 antigen, defined as any value above the average absorbance value for mock-inoculated controls plus 3 SD.

not specific to CMV-V27; two other isolates of CMV also complemented systemic spread of PepMoV in Avelar, including a relatively severe isolate, CMV-Fny, and a mild isolate, CMV-CA (data not shown). The molecular basis for the PepMoV-CMV complementation in Avelar is unclear; although like the PepMoV-Avelar interaction, the dramatic change in PepMoV accumulation and spread in coinfected plants may be a consequence of altered PepMoV replication and/or movement. Infection with CMV may enhance PepMoV replication thereby allowing accumulation to the critical level of virion or viral gene product(s) for efficient movement. Alternatively, CMV may actually complement PepMoV movement with little effect on PepMoV replication. In the latter case, the apparent increase in PepMoV accumulation in CMV-coinfected Avelar plants may result from an increase in the number of cells infected and not the amount of PepMoV per cell. Complementation of PepMoV in Avelar was reported previously in plants coinfected with an isolate of tobacco mosaic virus (TMV) (21). The ubiquitous distribution of CMV in pepper crops, the fact

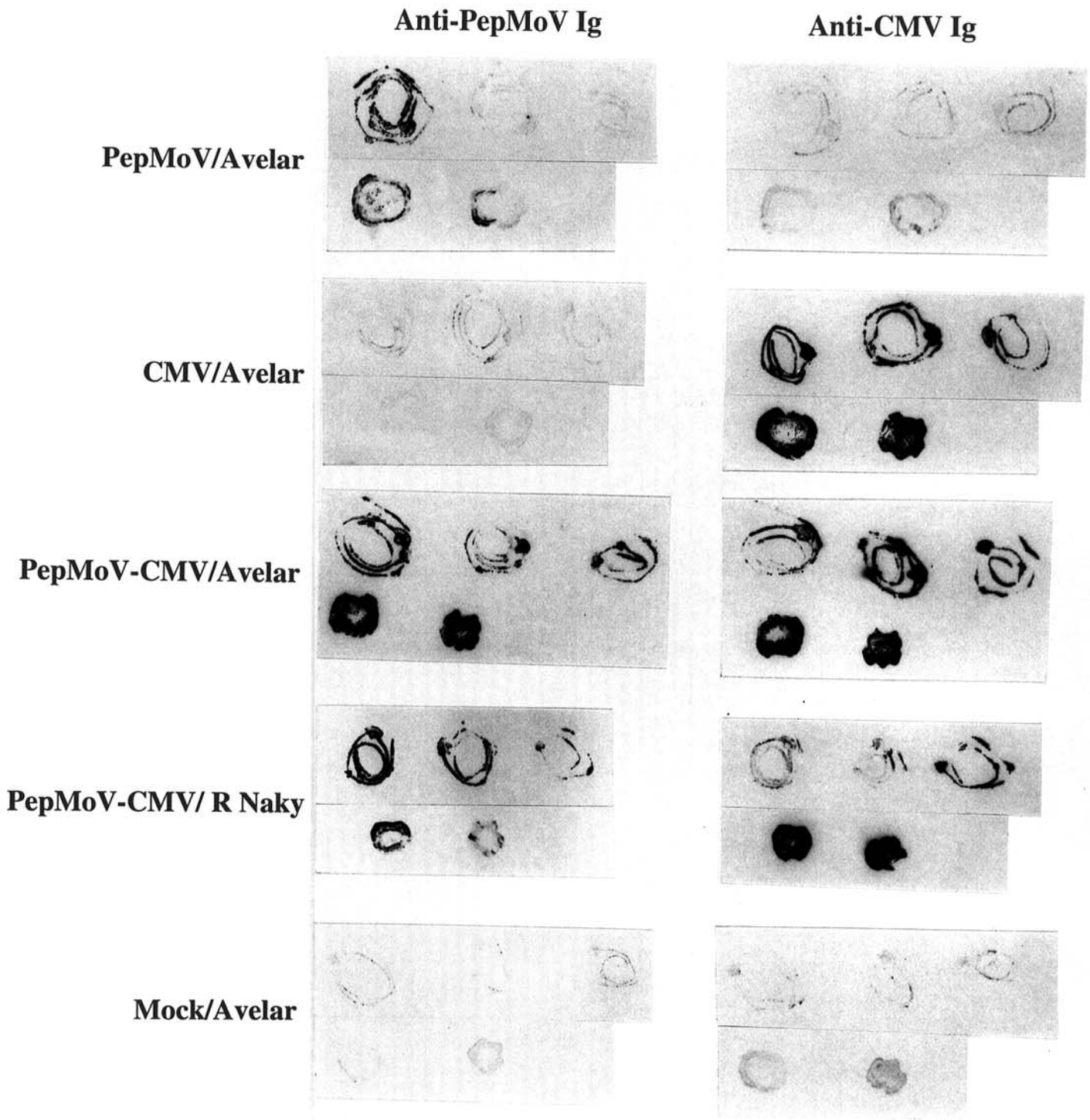


**Fig. 2.** Immuno-tissue blot analysis of pepper mottle virus (PepMoV)-, cucumber mosaic virus (CMV)-V27–, or PepMoV and CMV-V27–infected *Capsicum annuum* NuMex R Naky (R Naky) and Avelar tissues and mock-inoculated Avelar tissues at 21 days postinoculation. Each sample was blotted twice to generate duplicate blots, and each then was reacted with either anti-PepMoV immunoglobulin (Ig) or anti-CMV Ig. The antigen-Ig reactions were detected by an alkaline phosphatase detection system (12). The top row of each set of tissue blots represents leaf samples (from left to right, an inoculated leaf and one uninoculated leaf from each of the first and second pairs of leaves above the inoculated leaves), and the bottom row represents stem sections of internodes 1 and 2 (from left to right), with 1 being the internode below the inoculated leaves and 2 being the internode just above the inoculated leaves.

that CMV and PepMoV share common aphid vectors, and the prevalence of TMV-resistant varieties suggests that the PepMoV-CMV interaction may pose a greater threat to commercial production than TMV-PepMoV interactions. A more precise understanding of the cellular and molecular basis for interactions between plant viruses could allow the design of more effective control strategies for disease complexes and may reveal processes by which plant viruses cause disease.

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