Identification, Disease Incidence, and Distribution of Viruses Infecting Peppers in California

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ABSTRACT

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In a 2-yr survey during 1984 and 1985, a total of 1,195 pepper (*Capsicum annuum*) samples were collected from Ventura, Tulare, and Imperial counties in California. An indirect enzyme-linked immunosorbent assay (ELISA) technique was used to test all samples for the presence of one or more of the following viruses: potato virus Y (PVY), tobacco etch virus (TEV), pepper mottle virus (PeMV), cucumber mosaic virus (CMV), potato virus X (PVX), alfalfa mosaic virus (AMV), and tobacco mosaic virus (TMV). Eight hundred and sixty samples were collected at random, and the rest of the samples were collected in a nonrandom manner based on selection of plants expressing symptoms. The percent virus incidence in the 486 random samples collected during the 1984 season was as follows for Ventura County: CMV, 39.1; TEV, 36.1; PVY, 31.5; PeMV, 28.2; AMV, 11.5; PVX, 9.7; and TMV, 7.6%. For Tulare County, the incidence was as follows: TEV, 98.8; PVY, 85.2; PeMV, 70.4; CMV, 67.9; AMV, 64.2; PVX, 60.5; and TMV, 22.2%. Incidence in Imperial County was as follows: TEV, 88; PVY, 82.7; PeMV, 76; TMV, 60; AMV, 54.7; PVX, 50.7; and CMV, 49.3%. The percent virus incidence in the 374 random samples collected during the 1985 season were as follows for Ventura County: TEV, 58.4; PVY, 51.7; PeMV, 40.4; CMV, 39.2; AMV, 39.2; TMV, 29.4; and PVX, 18.8%. For Tulare County, incidence was as follows: CMV, 97.5; TEV, 90; AMV, 50; PVX, 37.5; PeMV, 17.5; PVY, 10; and TMV, 0%. Incidence was as follows for Imperial County: PeMV, 87.3; PVY, 86.1; TEV, 82.3; AMV, 7.6; TMV, 2.5; CMV, 0; and PVX, 0%. In the 335 nonrandom, symptomatic samples gathered in 1985, the seven viruses were found in the following frequencies: TEV, 84; CMV, 67; PVY, 60; PeMV, 58; AMV, 51; PVX, 38; and TMV, 19%. Ten percent of the samples with viruslike symptoms were negative for the seven viruses for which tests were carried out. Mixed virus infections were dominant over single infections in the field and accounted for 64% of infected samples during the 1984 season and 90% during the 1985 season. The importance of PeMV in California has not been emphasized before this survey.

Virus diseases cause serious losses in the pepper industry and can become the most limiting factor affecting pepper production (10). Several viruses have been reported from peppers both nationally and internationally (5,6,13,16, 19,20,22). At least 10 different viruses have been isolated from peppers in California (7,10,16).

Virus detection in this survey has been achieved mainly by the use of indirect enzyme-linked immunosorbent assay (ELISA). However, in some instances, ELISA was coupled with host reaction and/or electron microscopy. ELISA, first introduced to the field of plant pathology by Clark and Adams in 1977 (4), has been adapted for detection of several plant viruses and has been used recently for numerous virus surveys, including surveys of pepper (3). It has also been used to determine virus titer in peppers and has been recommended as a tool for field surveys of viruses that infect peppers (11).

The present study was initiated to survey for the following seven viruses: potato virus Y (PVY), tobacco etch virus (TEV), cucumber mosaic virus (CMV), alfalfa mosaic virus (AMV), potato virus X (PVX), tobacco mosaic virus (TMV), and pepper mottle virus (PeMV). With the exception of PeMV, all of the viruses were previously reported in pepper in California. Because the previous surveys were limited both in terms of number of samples studied and the area surveyed, it was thought that reinvestigation of these viruses would better reveal their significance and relative importance under diverse pepper-growing conditions. Therefore, large numbers of samples were collected and tested in this survey from three different counties (Ventura, Imperial, and Tulare), which represented the coastal, the desert, and the central regions of California, respectively.

PeMV was included in the survey because it has been reported to cause serious pepper disease problems in other states (12,21,23) and because it was claimed to be introduced into Arizona from California (13). Preliminary results of this study have been reported (1,2).

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MATERIALS AND METHODS

Purification of potyviruses (PVY, TEV, and PeMV). *Nicotiana tabacum* L. 'Glurk' was used to propagate each of the three potyviruses. Infected leaf tissue was harvested 2–3 wk after inoculation, and the viruses were purified according to a modification of a method described by Kositratana (8). Leaf tissues infected with the three viruses were homogenized for 1.5–2.0 min in a precooled Waring blender in a mixture of 0.1 M sodium citrate buffer, pH 7.2, containing 0.01 NaEDTA and a 1:1 mixture of chloroform and carbon tetrachloride. For each 1 g of tissue, 1 ml of buffer and 1 ml of the organic solvent mixture was used. In addition, 0.05 g of sodium sulfite was added to the buffer for each gram of tissue.

The filtrate of the homogenate, after passage through eight layers of cheesecloth, was given a low-speed centrifugation at 13,200 *g* for 10 min. Triton X-100 was added at a concentration of 1% to the supernatant of the PVY and TEV preparations. Supernatants were stirred for 30 min at 4 C. Triton X-100 was not added to the supernatant of the PeMV preparation because it adversely affected the virus. The virus suspensions were stirred for 30 min after the addition of 4% polyethylene glycol 8000 (PEG) and 0.25 M NaCl. The mixture was maintained at 4 C for at least 5 hr and then centrifuged at 13,200 *g* for 15 min. The resulting pellet was resuspended in 0.03 M KPO_4 buffer, pH 7.2, in a ratio of 5.5 ml per 25 g of original tissue weight.

The virus-enriched suspension was then centrifuged (177,500 *g* for 2.5 hr at 10 C in a Beckman SW41 rotor) through a Cs_2SO_4 step gradient prepared with 15% sucrose (w/w) in 0.03 M KPO_4 buffer, pH 7.2. The steps contained 0, 15, 22.5, and 30% (w/w) Cs_2SO_4 dissolved in the 15% sucrose-buffer solution. Virus zones were identified by electron microscopic examination of negatively stained preparations from the light-scattering bands that were visible in each tube. The contents of each selected zone were collected by tube puncture.

The virus in each case was then centrifuged through a linear gradient of Cs_2SO_4 (initial concentration of 2.8 g of Cs_2SO_4 per 10 ml of 0.03 M KPO_4 buffer, pH 7.2) at 177,500 *g* at 10 C in a Beckman

SW41 rotor for 20 hr. Virus zones were again identified by electron microscopic methods. Virus-containing fractions of each virus were pooled and dialyzed overnight against several changes of 0.03 M KPO_4 buffer, pH 7.2.

When young infected leaves were the source of the virus, this method worked equally well even if the Cs_2SO_4 step gradient step was not used. However, the step gradient enabled us to obtain a more pure virus preparation when the virus was purified from relatively old infected leaves. Virus purity was determined by electron microscopy and UV spectroscopy. Samples with an A_{260}/A_{280} ratio of 1.2 were considered to be pure (9).

Antisera production. *Rabbit antisera.* Antisera were prepared for the three potyviruses (PVY, TEV, and PeMV) by immunization of female New Zealand white rabbits. Purified virus at a concentration of 1 mg/ml was emulsified with Freund's incomplete adjuvant and injected intramuscularly at three weekly intervals.

Antisera to TMV and AMV was prepared by the same method with highly purified preparations of virus from our laboratory. Antisera to CMV and PVX were purchased from the American Type Culture Collection (ATCC). γ-Globulin was prepared from antisera by the method described by Clark and Adams (4), and goat-antirabbit antiserum was purchased from Boehringer and Mannheim Biochemicals Co.

Rat antiserum. Rats were used to prepare antisera to PVY, TEV, and PeMV. Purified virus at a concentration of 1 mg/ml emulsified in Freund's incomplete adjuvant was injected intramuscularly three times at weekly intervals. Blood was collected in small tubes and processed for antiserum. γ-Globulin was purified from rat antisera by the same method used for the rabbit antiserum.

Cross-absorbed antisera. To cross-absorb for antibodies to host antigens, rat IgG was added at a rate of 2 μg/ml to a 10-ml volume of healthy tissue extract. The extract was prepared in coating buffer using 1 g of healthy tissue per 10 ml. The IgG healthy extract mixture was diluted to a concentration of 1 μg/ml of rat IgG and used to coat microtiter plates in tests for PVY, TEV, and PeMV.

Enzyme-linked immunosorbent assay (ELISA). The indirect ELISA method described by Clark and Adams (4) was adapted. A 200-μl aliquot of the cross-absorbed rat IgG preparation was added to coat each well of the microtiter plates in the tests for the potyviruses. Microtiter plates used to test for the presence of CMV, AMV, PVX, and TMV were coated directly with extracts from the field samples. Each step of ELISA was followed by a 4-hr incubation at 37 C or a 12-hr incubation at 4 C. This was followed by three washes with washing buffer. Five milliliters of sample buffer, pH 7.4, was added to 1-g tissue samples that had been ground in liquid nitrogen, and 200 μl of this extract was added to each well.

Subsequently, 200 μl of cross-absorbed rabbit IgG (1 μg/ml) in PBS-Tween-OVP buffer was added to each well. A 200-μl aliquot of goat antirabbit IgG conjugated to alkaline phosphatase enzyme and diluted 1:3,000 in PBS-Tween-PVP-ovalbumin buffer was added to each well. The enzyme substrate (p-nitrophenol phosphate) was dissolved in substrate buffer, pH 9.8, at a concentration of 0.6 mg/ml. A volume of 200 μl of the substrate solution was then added to each well. The reaction was stopped after 20 min by the addition of 50 μl of 3 N NaOH, and optical densities at A_{405nm} were read with the Biotek EIA reader.

Specificity and sensitivity of ELISA. One-gram samples of pepper plants singly infected with each of the seven viruses included in the study were collected and ground in liquid nitrogen in a mortar and pestle. Each virus was then tested with homologous antiserum and with the antisera of the other six viruses with the ELISA technique. One-gram samples from uninoculated pepper plants were also prepared and tested against the various antisera as uninoculated controls.

A 1-g sample of leaf tissue of a pepper infected with PeMV was prepared in the same way. Extract dilutions of 1:5, 1:10, 1:100, and 1:1,000 were made and tested with PeMV antiserum to determine the sensitivity of the ELISA method used. Each of the samples used in testing the specificity and sensitivity of the ELISA was replicated five times.

Pepper sample collection. Random and nonrandom pepper samples were collected from pepper fields in Ventura, Tulare, and Imperial counties in California. The collection of nonrandom samples was based primarily on symptom expression of the plants. All samples were kept in ice chests for transportation to the laboratory. One-gram samples were weighed from leaves collected from individual plants, ground in liquid nitrogen in precooled mortars and pestles, and stored in plastic vials at −20 C until used in tests.

RESULTS

Specificity and sensitivity of ELISA. Antisera to CMV, AMV, PVX, and TMV used in this study did not react with sap from uninoculated plants (e.g., pepper and tobacco) nor with sap from plants inoculated with the heterologous viruses, including PVY, TEV, and PeMV. Antisera to the three potyviruses did not react with uninoculated plant extracts nor with extracts of plants infected with CMV, AMV, PVX, or TMV, but the study did demonstrate the serological relatedness of the three potyviruses. ELISA gave an average value of 0.06 at A_{405nm} for heterologous reactions involving antisera for TMV, AMV, CMV, and PVX with one another and with the potyviruses as well as those with healthy extract. Homologous antigen-antibody reactions gave an average ELISA value of 1.0 or greater A_{405nm} for each of the seven viruses.

PeMV gave the following average ELISA values: 0.231 with PVY antiserum, 0.148 with TEV antiserum, and 1.322 with its homologous antiserum. PVY gave the following average ELISA values: 0.248 with PeMV antiserum, 0.219 with TEV antiserum, and 1.152 with its homologous antiserum. The average ELISA values for TEV were as follows: 0.194 with PeMV antiserum, 0.141 with PVY antiserum, and 1.302 with its homologous antiserum. These serological relationships were taken into consideration when the results from ELISA plates for the three potyviruses were analyzed.

Results were considered positive when ELISA values of double or more than that of the control were obtained. Examination of negatively stained electron microscope preparations of samples with ELISA values as low as double the control values verified whether virus particles were present. Samples could be considered positive when particles were present.

The sensitivity of the ELISA method was determined by testing different dilutions of extracts from plants infected with PeMV. The tests were positive for all dilutions made. The highest dilution made (1:1,000) gave an average value of 0.590 at A_{405nm}. All of the results obtained from the tests of specificity and sensitivity of ELISA were averages of five replications.

Pepper sample collections. All 486 samples collected from pepper fields in Ventura, Imperial, and Tulare counties during 1984 were collected at random. Of the samples collected from the same counties in 1985, the random samples totaled 374 and the nonrandom (symptomatic) samples totaled 335. The results of the ELISA tests on the total of 1,195 pepper samples collected during the two-season survey are presented according to year and type of sample (random or nonrandom).

1984 season. All seven viruses were detected in the three counties surveyed. The number of positive tests for each virus in the total 486 random samples are listed in Table 1 according to county. The fact that a total of positive results for all viruses is greater than the total number of samples is a reflection of the great number of mixed infections. (Mixed infections will be discussed further.)

The disease incidences expressed as percentages of the total samples for each

virus in a decreasing order of frequency are as follows for Ventura County: CMV, 39.1; TEV, 36.1; PVY, 31.5; PeMV, 28.2; AMV, 11.5; PVX, 9.7; and TMV, 7.6%. Values for Tulare County are as follows: TEV, 98.8; PVY, 85.2; PeMV, 70.4; CMV, 67.9; AMV, 64.2; PVX, 60.5; and TMV, 22.2%. For Imperial County, disease incidence was as follows: TEV, 88; PVY, 82.7; PeMV, 76; TMV, 60; AMV, 54.7; PVX, 50.7; and CMV, 49.3%.

1985 season. Both random (374) and nonrandom (symptomatic) (335) samples were collected during the 1985 season. The results of tests on the two different types of samples were kept segregated and are reported separately.

Random samples. All seven viruses were detected and numbers of positive tests for the seven viruses for the three counties are listed in Table 2. The disease incidence expressed as the percentage of total samples for each virus in a descending order of frequency is as follows for Ventura County: TEV, 58.4; PVY, 51.8; PeMV, 40.4; CMV, 39.2; AMV, 39.2; TMV, 29.4; and PVX, 18.8%. All seven viruses were detected and the disease incidence was greater than the previous season for all viruses except for PVX. Disease incidence was as follows for Tulare County: CMV, 97.5; TEV, 90; AMV, 50; PVX, 37.5; PeMV, 17.5; PVY, 10; and TMV, 0%. All viruses except TMV were detected. The disease incidence of CMV increased over the previous season, whereas the incidence of the other viruses decreased. For Imperial County, the disease incidence was as follows: PeMV, 87.3; PVY, 82.7; TEV, 82.3; AMV, 7.6; TMV, 2.5; PVX, 0; and CMV, 0%. Five of the seven viruses were detected. The disease incidence of the potyviruses remained high, but the incidence of AMV and TMV dropped rather dramatically from the previous season.

Nonrandom (symptomatic) samples. All seven viruses were detected in the 335 pepper samples exhibiting viruslike symptoms that were collected from the three counties during the 1985 season. The number of positive tests for each virus for each county are listed in Table 3. The disease incidence for each virus in decreasing order of frequency for all three counties was TEV, 84; CMV, 67; PVY, 60; PeMV, 58; AMV, 51; PVX, 38; and TMV, 19%.

Ten percent of the symptomatic (nonrandom) samples failed to react with the antisera to the seven viruses used in the study. The viruslike symptoms in this group were caused either by some virus or viruses not included in the study or by some other disease-causing agent.

Single vs. mixed virus infections. Mixed infections of two or more viruses per plant were found in random and nonrandom samples collected in the two seasons, 1984 and 1985. The presence of mixed infections can be deduced from data in Tables 1, 2, and 3 where the number of occurrences of the different viruses in the samples collected from all counties throughout the survey is appreciably greater than the total number of samples collected from the counties. Results of the two seasons indicated that mixed infections were more prevalent in the fields than single virus infections (Table 4). Of the diseased samples collected in the 1984 season, 64% were found to be multiple infections with two or more viruses. In the 1985 season, mixed virus infections were found even more frequently and constituted 90% of the diseased samples, whereas only 10% were single infections (Table 4). Thus, there was an increase in the number of mixed infections during the second year of the survey.

DISCUSSION

Of the several viruses that infect pepper throughout the world, at least seven seem to be very important in California. With the exception of PeMV, all of the other viruses dealt with in this study were previously reported in California (7,10,16). Only random samples were collected during the 1984 season, but both random and nonrandom (symptomatic) samples were collected during 1985. The reason for collecting nonrandom (symptomatic) samples in 1985 was an attempt to identify the viruses inducing obvious viruslike symptoms observed in the field. Plants exhibiting such symptoms were often missed with random sampling.

All seven viruses were detected in the three counties surveyed. The overall average disease incidence in the three

Table 1. Occurrence of different pepper viruses as determined by ELISA in 486 random samples from three counties in California surveyed in 1984

	Virus[a]								
County	PVY	TEV	PeMV	CMV	AMV	PVX	TMV	Negative	Total
Ventura	104	119	93	129	38	32	25	128	330
Tulare	69	80	57	55	52	49	18	0	81
Imperial	62	66	57	37	41	38	45	1	75
Total	235	265	207	221	131	119	88	129	486

[a]PVY = potato virus Y, TEV = tobacco etch virus, PeMV = pepper mottle virus, CMV = cucumber mosaic virus, AMV = alfalfa mosaic virus, PVX = potato virus X, and TMV = tobacco mosaic virus.

Table 2. Occurrence of different pepper viruses as determined by ELISA in 374 random samples from three counties in California surveyed in 1985

	Virus[a]								
County	PVY	TEV	PeMV	CMV	AMV	PVX	TMV	Negative	Total
Ventura	132	149	103	100	100	48	75	59	255
Tulare	4	36	7	39	20	15	0	0	40
Imperial	68	65	69	0	6	0	2	2	79
Total	204	250	179	139	126	63	77	61	374

[a]PVY = potato virus Y, TEV = tobacco etch virus, PeMV = pepper mottle virus, CMV = cucumber mosaic virus, AMV = alfalfa mosaic virus, PVX = potato virus X, and TMV = tobacco mosaic virus.

Table 3. Occurrence of different pepper viruses as determined by ELISA in 335 nonrandom samples from three counties in California surveyed in 1985

	Virus[a]								
County	PVY	TEV	PeMV	CMV	AMV	PVX	TMV	Negative	Total
Ventura	155	212	145	181	131	102	45	21	241
Tulare	8	36	8	36	34	18	6	0	36
Imperial	38	33	42	6	6	8	2	12	58
Total	201	281	195	223	171	128	53	33	335

[a]PVY = potato virus Y, TEV = tobacco etch virus, PeMV = pepper mottle virus, CMV = cucumber mosaic virus, AMV = alfalfa mosaic virus, PVX = potato virus X, and TMV = tobacco mosaic virus.

Table 4. Single vs. mixed virus infection in pepper fields in three counties in California during the 1984 and 1985 growing seasons

	Diseased samples			Mixed
Season	Single	Mixed	Total	infections (%)
1984	128	229	357	64
1985	61	554	615	90

counties during 1984 and 1985 indicated that the order of these viruses in terms of frequency of detections was TEV, PVY, PeMV, CMV, AMV, PVX, and TMV. It should be pointed out, however, that relative importance of the viruses in each individual county does not necessarily follow the same order. For example, CMV had the greatest disease incidence in Ventura County during 1984 (Table 1) and in Tulare County during 1985 (Table 2). This confirms the conclusion of Paulus et al in their 1962 survey (15). Also, PeMV had the highest disease incidence in Imperial County during the 1985 season (Table 2).

The disease incidences of the major viruses were considerably higher in the desert and central California than in the coastal region during the 1984 season. The situation remained the same during the 1985 season, with the exception of PVY and PeMV in Tulare County. The lower disease incidence in Ventura County can probably be explained by the partial weed control activities that were practiced around the pepper fields surveyed in that county in the two seasons. Such practices were not carried out in the other two counties except to a limited extent in Tulare County during 1985. Practicing weed control may help to lower virus disease incidence in peppers but does not control the problem entirely, as disease incidence in Ventura County was still considerable.

TMV and AMV disease incidences dropped considerably in Imperial County during 1985 compared with the 1984 season. Reduction of the incidence of TMV can probably be attributed to the fact that growers substituted direct-seeded peppers in place of transplants. The reduction in AMV incidence is possibly attributable to the avoidance of growing peppers in close proximity to alfalfa fields. ELISA results from the serological studies on the relationship between the potyviruses confirmed the results of earlier studies (12,18) that PVY, PeMV, and TEV are distinct from each other but serologically related.

Because some of the nonrandom samples collected exhibited viruslike symptoms, some of which were unusual, it was expected that viruses other than the ones included in the study could be causing these symptoms. If this were true, the percentage of samples that tested negative would be greater in the nonrandom samples. Because this was not the case, the unusual symptoms of some of the nonrandom samples may have been caused by either different strains of the viruses included or various combinations of mixed infections of pepper. This, however, is speculation because we are not able to present evidence to prove this.

Little attention has been given to the role of multiple infections of peppers (10,17), although such infections appear to be more prevalent in the field than single infections. Mixed infections of two or more viruses in a single pepper plant have been found frequently. In fact, the data indicates that in 1984, 64% of the diseased pepper plants had multiple infections of two or more viruses, and in 1985, the proportion was even higher (90%). ELISA results showed that mixed infections of two viruses per plant were more common than other types of mixed infections. However, in a few instances, ELISA results indicated that all seven viruses used in the study were infecting single pepper plants. This almost incredible type of mixed infection should be verified by other means such as electron microscopy and differential host inoculations.

Such procedures were used to confirm results of ELISA in some instances when TMV and the potyviruses were involved in mixed infections. Expected virion morphology of the suspected viruses were found in mixed infections of TMV, TEV, and PeMV. Components of these three viruses were separated from mixed infections on *N. tabacum* 'Glurk,' *Datura stramonium* L., and *Capsicum annuum* L. 'Agronomica-8,' respectively. Thus, differential hosts may be very useful in separating and further identifying viruses involved in mixed infections.

Results of these studies should be of great interest to pepper growers. Whereas 26.5% of the random samples collected in 1984 tested negative, only 13% tested negative during 1985, indicating an increase in disease in peppers in the state.

The 2-yr survey of pepper fields in California suggested that the problem of pepper virus diseases is very serious. The following facts tend to support this statement, although certain specific factors (for example, an increase in or more active aphid populations) may be the actual reasons for the increases noted the second season: 1) the disease incidence of the major viruses causing diseases in pepper either remained high or increased from season to season with a few exceptions (e.g., PVY and PeMV in Tulare County in 1985); 2) the increase of the overall virus disease incidence from 73.5% during 1984 to 87% during 1985 as determined from the number of samples that tested negative during the two seasons (Table 1 and 2); and 3) the increase of the percentage of mixed virus infections from 64% during 1984 to 90% during 1985 (Table 4).

Although it is possible to grow more than one crop of peppers during the year in some California areas, the crops generally do not overlap in any one geographical area, and the early summer crops in the three counties were the ones surveyed in this study in 1984 and 1985.

The pepper virus disease situation in California will not improve and will probably become even more serious unless disease control measures not currently practiced are initiated. Also, other viruses not included in this study should be investigated in future studies. The unidentified viruses in our study that caused symptoms in some of the nonrandom samples accounted for 10% of the virus disease incidence because they tested negative against the viral antisera during the 1985 survey (Table 3).

Some of the nonrandom, symptomatic samples that were negative in the ELISA tests may have been infected with tomato spotted wilt virus, curly top virus, or tobacco rattle virus, which have been previously found in peppers in California (7,10,16). These viruses were not included in the survey mainly because antisera to them were not available at the time of the survey. It is, of course, also possible that other viruses not previously reported in California may have been involved (6,14).

Pepper mottle virus (PeMV) was reported for the first time in California in this survey (1). It was detected with a high disease incidence in Tulare and Imperial counties in 1984. It had the highest disease incidence in Imperial County during 1985, and its disease incidence in Ventura County increased from 28% in 1984 to 40% in 1985. Therefore, PeMV is not only present in California, but, together with the other viruses used in this survey, it consistutes a threat to the pepper industry in the state.

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