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Ultrastructural Aspects of Mixed Infections with *Turnip mosaic virus* (TuMV-AC18 and -C5) and *Ribgrass mosaic virus* (RMV-CA1) in Oriental Cabbage

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Mixed infections of two economically important viruses, *Turnip mosaic virus* (TuMV) in the family *Potyviridae* and *Ribgrass mosaic virus* (RMV) in the genus *Tobamovirus*, were studied ultrastructurally on oriental cabbage. TuMV-AC18 (alpine isolate in Korea) induced chlorotic spots on inoculated leaves of both 'SSD63' inbred line known as susceptible to TuMV, and 'Tambok' commercial cultivar, known as resistant to the virus, in the early stages of infection. TuMV-C5 (Taiwan isolate) caused severe mosaic and malformation on the upper leaves of 'SSD63', and necrotic spots in both inoculated and upper leaves of 'Tambok'. RMV-CA1 (oriental cabbage isolate from alpine in Korea) induced vein chlorosis, leaf malformation, and midrib necrotic streak in the upper leaves of both 'SSD63' and 'Tambok'. Both oriental cabbages infected with a combination of TuMV-AC18 and RMV-CA1 showed synergistic symptoms of severe yellowing, severe mosaic, and necrotic spot or vein necrosis on their leaves. A combination of TuMV-C5 and RMV-CA1 produced synergistic symptoms only in 'SSD63'. In 'Tambok' infected with the combination of TuMV-C5 and RMV-CA1, the number of necrotic spots on the inoculated leaves was one half lesser than that on singly infected with TuMV-C5. A few necrotic spots progressed systemically. In cells infected with a combination of TuMV-AC18 and RMV-CA1 or TuMV-C5 and RMV-CA1, the particles of the two viruses made nonagon-like rings (NLR); one TuMV particle was surrounded loosely by nine RMV particles. Two unrelated viruses of TuMV and RMV were compacted in the central part of the spiral aggregates (SA) that was induced strikingly in cells by the mixed infections. The SA showed NLR in its center of the cross-sectioned side. Many particles of RMV of *Tobamovirus* were closely associated with *Potyvirus*-characteristic cylindrical inclusions. The SAs in the mixed infections were formed easily by the *Potyvirus* of TuMV-AC18 or -C5 isolates.

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Turnip mosaic virus (TuMV), *Cucumber mosaic virus* (CMV) (Lee, 1981), and *Ribgrass mosaic virus* (RMV) (Kim et al., 1993) are reported to be the major viruses of oriental cabbage, the main ingredient of the traditional Korean food 'Kimchi', in Korea. TuMV and RMV are economically important because they occurred their single and mixed infections with rates of 13.9%, 4.5%, and 31.9%, respectively (Yoon et al., 1995).

Virus diseases by mixed infection of two unrelated viruses cause severe damage, which was first reported in cowpea stunt disease in the south western states of the USA (Pio-Ribeiro et al., 1978). In Korea, virus diseases by mixed infection were known as oriental cabbage necrotic stunt disease in the mid-eastern alpine area (Kim et al., 2001) and watermelon necrosis disease in the southern parts (Cho, 1998; Kim et al., 2000).

Specific arrangements of virus particles between unrelated two viruses in plant cells might be concerned the synergism of virus diseases in connection with external symptom expression. Specific arrangements have been reported to be hexagon (Carr and Kim, 1983), octagon (Anderson et al., 1994), and nonagon (Cho, 1998; Kim et al., 2000). Hexagon in bean dwarf disease was made up one *Potyvirus* particle of *Bean yellow mosaic virus* (BYMV) surrounded by six *Comovirus* particles of *Cowpea mosaic virus*. Octagon in cowpea stunt disease consists of one *Cucumovirus* particle of *Cucumber mosaic virus* surrounded by eight *Potyvirus* particles of *Blackeye cowpea mosaic virus* (*Bean common mosaic virus*; BCMV). Finally, nonagon in watermelon necrosis disease was constructed of one *Potyvirus* particle of *Watermelon mosaic virus* (WMV) surrounded by nine *Tobamovirus* particles of *Cucumber green mottle mosaic virus* (CGMMV). In mixed infection of TuMV (Act2-4vq isolate) and RMV (Ca1dn2 isolate) in oriental cabbage by artificial inoculation, the two different

viruses were very closely related with each other (Kim et al., 2001). The two different virus particles and inclusions were fully mixed in the same cytosol of a cell, and *Tobamovirus* RMV particles were presented in the inner part of the *Potyvirus* TuMV inclusions of scrolls, pinwheels, and tubes. In this paper, cytological comparisons are studied and discussed by changing of different isolates of TuMV and RMV.

Materials and Methods

Viruses used in this study. Two isolates of TuMV-AC18 (Korean isolate) from oriental cabbage (Kim et al., 1994) and TuMV-C5 (Taiwan isolate) (Green and Deng, 1985) were used in mixed infection with RMV-CA1 isolate from oriental cabbage in Korea (Kim et al., 1993). TuMV-C5 was obtained from Asian Vegetable Research & Development Center (AVRDC) and used in this study.

Virus inoculum source. Leaves of leaf mustard, *Brassica juncea,* showing systemic symptom by mechanical inoculation of each virus isolate were used as virus source.

Cultivar or line used. Oriental cabbages of 'Tambok', a commercial cultivar known as resistant to TuMV, and 'SSD63', an inbred line with elite-horticultural characteristics and known as susceptible to TuMV, were used.

Mixed infection. The same volume of leaf mustard leaves infected with each virus in 4 vol. of 0.01M Na-phosphate buffer, pH 7.0, were macerated simultaneously with mortar and pestle. Combinations of mixed inoculums were TuMV-C5 + RMV-CA1 and TuMV-AC18 + RMV-CA1. The mixed virions were inoculated with wooden towel after scattering carborundum 600 mesh at 3 or 4 leaf stage of oriental cabbage.

Electron microscopy. Leaves of oriental cabbage infected systemically were collected at 16 or 28 days after mechanical inoculation. Leaf fragments were immersed for fixation into 2.5% glutaraldehyde in Millonig's phosphate buffer and then osmicated in 2.0% solution diluted in distilled water. The treated samples were dehydrated with 50-100% alcohol in six steps. The alcohol was transited by propylene oxide and then changed gradually with low viscosity Spurr resin. The samples in pure resin were shaken overnight at room temperature. The samples placed in embedding molds were hardened at 60°C overnight. Sections of 70-80 nm thickness were stained with uranyl acetate and lead citrate for 10 and 5 minutes, respectively.

Results

Symptom expression of single infections. The C5 strain of TuMV produced mosaic, severe mosaic, and malformation symptoms on the upper leaves of 'SSD63' (Table 1, Fig. 1C). In 'Tambok' cultivar, necrotic spots were produced on the inoculated leaves at 5 days and on the upper leaves at 8 days after mechanical inoculation. The inoculated leaves became yellow and fell off at 2 weeks after inoculation. On the upper leaves, the necrotic spots were continuously observed on the newly developed leaves (Fig. 1H). However, the number of necrotic spots was fewer than that of the inoculated leaves. The average number of necrotic spots for the mixed inoculum of TuMV-C5 and sodium phosphate buffer was about two-folds higher than that of the mixed inoculum of TuMV-C5 and RMV-CA1 (Table 2).

In oriental cabbage, TuMV-AC18 isolate occurred chlorotic spots on the inoculated leaves and severe mosaic, malformation, and yellowing symptoms on the upper leaves in 'SSD63' inbred line. However, symptoms were milder than those in oriental cabbage infected with C5 strain of TuMV (Table 1, Fig. 1A). In 'Tambok' cultivar, chlorotic spots with faint margin were produced on the inoculated and the upper leaves at 5 days and 8 days, respectively, after mechanical inoculation. It also continuously produced chlorotic spots on the newly developed leaves (Table 1, Fig. 1F). RMV-CA1 produced vein chlorosis on the upper leaves of 'SSD63' (Fig. 1B) and leaf dwarf and midrib necrotic streaks on the upper leaves of 'Tambok' (Fig. 1G). However, no symptoms were produced on the inoculated leaves.

Symptom expression of mixed infections. 'SSD63' produced malformation, severe yellowing, severe mosaic, and necrotic spots on the upper leaves (Table 1). Generally, the symptoms in 'SSD63' infected with a combination of

Table 1. Symptoms of oriental cabbage inoculated mechanically with TuMV, RMV-CA1, and their mixed inoculum

Virus	Symptoms[a] produced on oriental cabbage	
	'SSD63'	'Tambok'
TuMV-AC18+RMV-CA1	–/SY, MAL, SM,, NS	CS/ SY, SM, VN, D
TuMV-C5+RMV-CA1	–/SY, MAL SM, NS	NS/ VCH, MAL, NS, MRNS
TuMV-AC18	–/SM, MAL, Y	CS/ CS
TuMV-C5	–/SM, MAL	NS/ NS
RMV-CA1	–/VCH, MAL, MRNS	–/VCH, MAL, MRNS

[a] SY; severe yellowing, MAL; malformation, SM; severe mosaic, VN; vein necrosis, D; dwarf, NS; necrotic spots, CS; chlorotic spots, VCH; vein chlorosis, MRNS; midrib necrotic streak, Y; yellowing, and –; no symptom. Inoculated leaf/upper leaf symptoms were investigated at 5-14 days after mechanical inoculation.

Fig. 1. Mosaic and severe mosaic symptoms were produced on oriental cabbage 'SSD63' inbred line by TuMV-AC18 (**A**) and TuMV-C5 (**C**), respectively. The symptoms of vein chlorosis, malformation, and midrib necrotic streaks were produced by the infection with RMV-CA1 (**B**). Synergistic symptoms of severe mosaic, stunt, and yellowing occurred on the upper leaves by the combinations of TuMV-AC18+RMV-CA1 (**D**), and TuMV-C5+RMV-CA1 (**E**) at 14 days after mechanical inoculation. In 'Tambok' cultivar, TuMV-AC18 (Korean isolate) produced chlorotic spots on the inoculated and upper leaves (**F**). However, TuMV-C5 (Taiwan isolate) produced necrotic spots on the inoculated and upper leaves (**H**). RMV caused vein chlorosis and midrib necrotic streak on the upper leaves of 'Tambok' cultivar (**G**). The mixed virions of TuMV-AC18+RMV-CA1 caused synergistic symptoms of severe mosaic, necrosis, and yellowing on leaves (**I**), but TuMV-C5 + RMV-CA1 caused vein chlorosis, necrotic spots, midrib necrotic streaks, and malformation on the upper leaves (**J**).

Table 2. Number of necrotic spots in oriental cabbage 'Tambok' inoculated with TuMV-C5, RMV-CA1 and their mixed inoculum

Combination	Necrotic spots on	
	Inoculated leaf	Upper leaf
TuMV-C5	25.5[a]	NS[b]
TuMV-C5 + P.B[c] (1:1)	39.2	NS
TuMV-C5 + P.B (1:2)	22.8	NS
TuMV-C5 + RMV-CA1(1:1)	18.0	–(+)[d]
TuMV-C5 + RMV-CA1(1:2)	13.8	–(+)
RMV-CA1	0.0	–[e]

[a] Necrotic spots were averaged on 20 leaves in 10 plants (2 leaves/plant, 1 mm^2, 2/3 replications/leaf).
[b] Necrotic spots developed continuously on the upper leaves.
[c] 0.01M sodium phosphate buffer, pH 7.0.
[d] A few necrotic spots developed in two plants out of ten plants.
[e] Negative reaction.

TuMV-C5+RMV-CA1 (Fig. 1E) were more severe than those infected with a combination of TuMV-AC18+RMV-CA1 (Fig. 1D).

In 'Tambok' cultivar infected with a combination of TuMV-AC18+RMV-CA1, large and severe chlorotic spots were produced on the inoculated leaves at 5 days after inoculation (Table 1, Fig. 1I). On the upper leaves at 8 days after inoculation, large chlorotic spots were observed followed by severe yellowing, but the leaves did not show small necrotic spots. The symptoms of severe mosaic, dwarf, vein necrosis, and severe yellowing induced by the synergism from the mixed infection of TuMV-AC18 and RMV were not seen in the single infection.

In 'Tambok' cultivar infected with a combination of TuMV-C5+RMV-CA1, the necrotic spots were produced first on the inoculated and the upper leaves at 5 days and 7 days after mechanical inoculation, respectively (Table 1, Fig. 1J). On the upper leaves, symptoms of necrotic spots, vein chlorosis, malformation, and midrib necrotic streak were observed. However, the number of necrotic spots was much less than that in single infection of TuMV-C5.

Development of necrotic spots in 'Tambok' cultivar. TuMV-C5 strain produced necrotic spots in oriental cabbage cultivar 'Tambok'. To count the necrotic spots on the inoculated leaves, the leaf-sap of leaf mustard infected with TuMV-C5 was diluted by one-half and one-third with 0.01M sodium phosphate buffer, pH 7.0, or sap from leaf mustard infected with RMV. The original sap was made by maceration with mortar and pestle in 4 vol. of 0.01M sodium phosphate buffer, pH 7.0.

The number of necrotic spots on 'Tambok' inoculated singly with TuMV-C5 was about two-folds more than that in mixed infection of TuMV-C5 and RMV on the inoculated leaves (Table 2). RMV did not produce necrotic spots on the inoculated and upper leaves of 'Tambok'. On the oriental cabbage infected with a combination of TuMV-C5+RMV-CA1, a few necrotic spots in two plants out of 10 plants were produced. However, TuMV-C5 continuously produced large number of necrotic spots on the upper newly-developed leaves.

Ultrastructure of single infection. The cells infected with TuMV-C5 or AC18 had the same typical potyvirus inclusions as pinwheels, scrolls, laminated aggregates, and tubes. The inclusions were observed in cells of mesophyll, epidermal, xylem, and phloem parenchyma cells. The potyvirus particles arranged lineally along with tonoplast and located closely with the inclusions of potyvirus. The observation of potyvirus inclusions was relatively easier in cells infected with TuMV-AC18 than that with TuMV-C5 (Fig. 2A).

RMV-CA1 made stacked-band structure having about 300 nm in bandwidth, and the bands were compiled several layers in the cytosol. Virus particles of RMV located in-group in the cytosol, and were somewhat elastic and spiral aggregates (Fig. 2B). The RMV particles were scattered in vacuoles and vessels, and sometimes stacked in sieve tubes. The RMV could invade all type cells and organs of sieve tubes and vessels (Oshima and Harrison, 1975).

Ultrastructure of mixed infection. Specific arrangements could be observed in cells of oriental cabbage showing synergism such as 'SSD63' with mixed infection of TuMV-C5 + RMV and TuMV-AC18 + RMV and 'Tambok' with mixed infection of TuMV-AC18 + RMV (Table 3).

The strictly vertical cross-sections of the arrangements gave the morphology of nonagon-like ring (NLR) with 1:9 arrangement: one TuMV particle in the center and nine loose RMV particles in the outer portion. In both virus particles of NLR, the width of TuMV particles has a range of about 16.7-18.0 nm while the width of RMV particles has a range of about 8.0-10.0 nm, which were very different compared with widths by dip preparations of the two viruses at 10-11 nm and 18 nm, respectively.

The specific arrangements were observed in the cytoplasm (Fig. 2D), the cluster of RMV particles (Figs. 2E, G, and H), and the scrolls of potyvirus inclusions (Figs. 2C and F). However, NLRs could not be seen in vacuoles, and vascular cells of vessels and sieve tubes containing RMV particles. SAs, a unique ultrastructure of RMV (Oshima and Harrison, 1975), were made easily by the mixed virions of RMV and TuMV in spite of the SA could be seen hardly in single infection of RMV (Fig. 2A). The NLRs were found in the center of the SA cluster sectioned crossly (Figs. 2E, G, and H). The specific arrangement of NLR was commonly flattened by the mechanical force of neighboring materials such as potyvirus inclusions (Figs. 2C, D, and F). The ultrastructures of NLR, SA, tobamovirus stacked-band structure, and potyvirus inclusions were mixedly present at the same cytosol in a

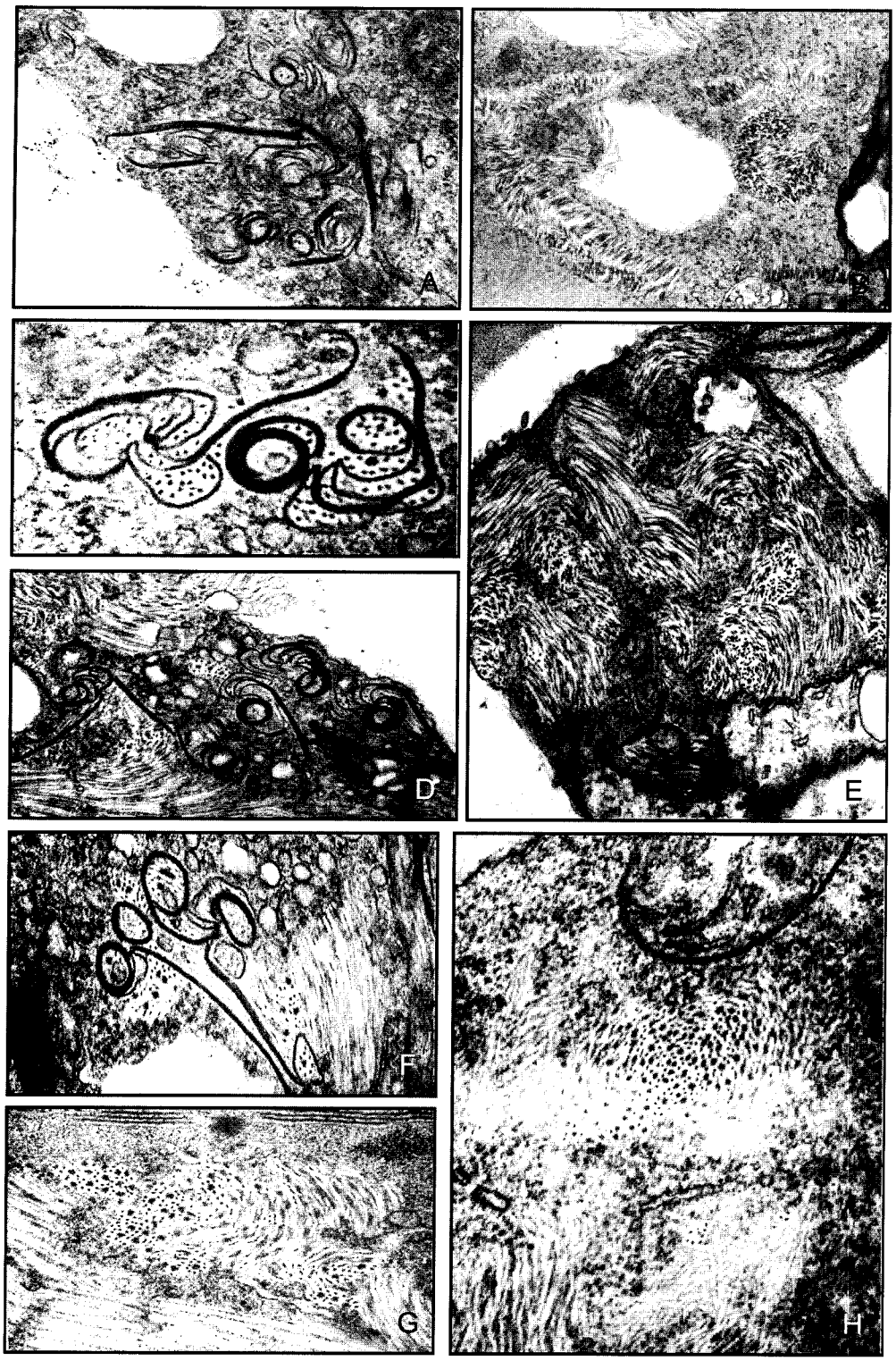

Fig. 2. The typical ultrastructures of potyvirus inclusions were present in the cytosol by the single infection of TuMV-C5 or TuMV-AC18 (**A**). The RMV particles were present elastically as somewhat spiral aggregates in single infection. Typical stacked-band structures of RMV were in the cytosol (**B**). In 'Tambok' infected with TuMV-AC18+RMV (**C**, **D**, **E**) and in 'SSD 63' infected with TuMV-AC18+RMV (**F**, **G**) or TuMV-C5+RMV (**H**), NLRs could be seen in the cytosol (**D**, **H**), in the SAs group (**E**, **G**), and in potyvirus inclusion bodies flattened by mechanical forces (**C**, **F**).

Table 3. Ultrastructures induced in the mixed infections of the different virus combinations in oriental cabbages

Ultrastructure	'Tambok'		'SSD63'	
	TuMV-AC18+RMV-CA1	TuMV-C5+RMV-CA1	TuMV-AC18+RMV-CA1	TuMV-C5+RMV-CA1
Nonagon-like ring	++	–	+++	+
Spiral aggregate	++	–	+++	++
Mixing of the two virions	++	+	+++	++
Potyvirus inclusions	++	+	+++	++
Tobamovirus particles	++	+++	+++	++
Synergism[a]	+++	–	++	++

[a] Degrees of synergistic external symptoms.

cell (Figs. 2D, E, and F).

The particles of RMV were abundantly present in the cytosol of all cell types. In vascular tissues, RMV particles were packed densely in the parenchyma cells of sieve elements and vessels. The potyvirus inclusions such as pinwheels, scrolls, laminated aggregates, and tubes were observed in the cytosol. The potyvirus inclusions were also embedded randomly in the cluster of RMV particles. In 'Tambok' cultivar, the potyvirus inclusions and the arrangements of two viruses were located locally in cells based on observation of the serial section of the same specimen block.

Discussion

Symptoms of severe yellowing and stunting, and necrosis of the whole plant by mixed infection of TuMV isolates of C5 or AC18 and RMV-CA1 were not observed in single infection, which suggest that these might be considered as synergistic symptoms. In 'Tambok' cultivar, the number of necrotic spots produced on the inoculated and upper leaves was about two-folds lower in the mixed infection of RMV-CA1 and TuMV-C5 than that in the single infection of TuMV-C5. The serial sections of Tambok cultivar showed no clear difference in ultrastructures between single and mixed infection in conjunction with the reduction of necrotic spots by mixed infection without virus localization. Necrotic spot generally was thought as one of the resistant symptoms. 'SSD63' cultivar, known as susceptible to TuMV-C5, expressed systemic symptoms but not necrotic spots. 'Tambok' cultivar, known as resistant to TuMV, showed highly reduced necrotic spots in mixed infection with RMV, which means that it might become susceptible because the resistant level of 'Tambok' to TuMV-C5 might be lowered by mixed infection with RMV-CA1.

The enhancement of symptom severity by the mixed infections have been reported on oriental cabbage necrotic stunt disease (Kim et al., 2001) and watermelon necrosis disease (Cho, 1998; Kim et al., 2000) in Korea, and cowpea stunt disease (Anderson et al., 1994) and bean dwarf disease (Carr and Kim, 1983) in the USA. Those diseases were caused by the mixed infection of unrelated plant viruses that might have induced a synergistic interaction in symptom expression. Several factors involved in synergism have been studied in terms of ultrastructural characteristics, viral synthesis, localization, and movement of viral agents due to mixed infections. The viral infection in systemic symptom expression is achieved by penetration in cells, multiplication and translocation to the adjacent cells, and finally moving through vascular organs of sieve tubes and xylem vessels (Seron and Haemni, 1996). The RMV could infect all type cells of epidermal, mesophyll, and vascular cells and was present normally in xylem vessels. The potyviruses might be moved easily through xylem vessels and sieve tubes in mixedly infected plant, which would give an important role in the expression of synergistic symptoms. However, a few results were known as to the titer enhancement and the positive effects about the partner virus localized in cells and tissues.

Specific arrangements between unrelated viruses in mixed infection have been known as hexagon, octagon, and nonagon. All these specific arrangements had *Potyvirus* of BYMV, BCMV, and WMV as a partner. The octagon and nonagon had the potyvirus in the center, while the hexagon had the potyvirus in the outer portion. When compared with the morphology of virus particles, the hexagon and octagon were made by filamentous rod- and sphere-shaped particles. Nonagon and NLR had a filamentous rod-shaped potyvirus particle located in the center and nine rigid rod-shaped tobamovirus particles in the outer portion. However, the relationship between the specific arrangements and external synergistic symptoms was little understood.

The NLR in this study might be made wherever potyvirus is present. Therefore, the potyvirus of TuMV might have a major role in the making of NLR. The NLRs were not so perfect as the nonagons in watermelon necrosis disease. The mechanism of combining the two unrelated viruses was not known, while the tension by interactions between coat proteins of both viruses might be present. The tension between TuMV and RMV might be relatively lower than

those in WMV and CGMMV in watermelon necrosis disease.

The inclusions of potyvirus were involved in the coat protein synthesis and viral RNA replication for virion assembly in *Tobacco vein mottling virus* (Ammar et al., 1994). The proteins of potyviral inclusions had different properties among three strains of TuMV (McDonald and Hiebert, 1975). It is a general fact that the potyviruses and isolates of potyvirus have different pathogenicity on natural and indicator host plants. From the specific arrangements of unrelated viruses in mixed infections, the two different viruses may have a role as helper for the partner virus replication followed by synergism.

The elevated concentration of virus particles in cells and tissues by the mixed infection must be an important factor in synergism. In cowpea stunt disease, the concentration of CGMMV in the center of the octagon was seven-folds higher than that in single infection. In tobacco co-infected with a potyvirus and luteovirus, the concentration of luteovirus was eight-folds higher than that in single infection. The concentration of *Tobacco mosaic virus* (TMV) on cucumber infected mixedly with TMV and *Zucchini yellow mosaic virus* (ZYMV) was four- to seven-folds higher than that in single infection. However, in the combination of CGMMV and ZYMV, the concentration of CGMMV was not higher (Otsuki and Takebe, 1976).

From the above reports of concentration enhancements of virus particles, the reaction was not constant but variable in combinations of virus isolates involved in mixed infection. Given the specific arrangements of nonagon, octagon, and hexagon, further studies are needed to determine the relationship between viruses in the center and the outer portions in relation to the synergism caused by mixed infection.

References

Ammar, E. D., Rodriguez-Cerozo, E., Shaw, J. G. and Pirone, T. P. 1994. Association of virions and coat protein of tobacco vein mottling potyvirus with cylindrical inclusions in tobacco cells. *Phytopathology* 84:520-524.

Anderson, E. J., Kline, A. S., Kim, K. S., Goeke, S. C. and Albrutton, C. W. 1994. Identification of cowpea stunt disease in south central Arkansas. *Arkansas Farm. Res.* 43:14-15.

Carr, R. J. and Kim, K. S. 1983. Ultrastructure of mixed plant virus infection: bean yellow mosaic virus with cowpea severe mosaic virus or cowpea mosaic virus. *Virology* 124:338-348.

Cho, J. D. 1998. Ultrastructural aspects of watermelon necrosis disease caused by mixed infection with *Watermelon mosaic potyvirus* and *Cucumber green mottle mosaic tobamovirus*. M.S. thesis, Seoul National University.

Green, S. K. and Deng, T. C. 1985. *Turnip mosaic virus* strains in cruciferous host in Taiwan. *Plant Dis.* 69:28-31.

Kim, J. S., Cho, J. D., Choi, H. S. and Kim, K. S. 2000. Ultrastructural aspects of the mixed infections of *Watermelon mosaic potyvius* and *Cucumber green mottle mosaic tobamovirus* isolated from watermelon. *Plant Pathol. J.* 16:211-215.

Kim, J. S., Cho, J. D., Choi, H. S. and Kim, K. S. 2001. Ultrastructural aspects of the mixed infections of *Turnip mosaic virus* and *Ribgrass mosaic virus* in oriental cabbage. *Plant Pathol. J.* 17:201-204.

Kim, J. S., Choi, G. S., Kim, J. Y., Yoon, M. K. and Kim, D. O. 1994. Biological characteristics in indicator plants and inbred line of oriental cabbage of Turnip mosaic Potyvirus isolates occurring on oriental cabbage. *Korean J. Plant Pathol.* 5:62-63(abst.).

Kim, J. S., Yoon, M. K., Lee, K. H. and Choi, H. S. 1993. Ribgrass mosaic tobamovirus occurred on oriental cabbage in Korea. *Korean J. Plant Pathol.* 9:332 (Abst.).

Lee, S. H. 1981. Studies on virus diseases occurring in various crops in Korea. *Res. Rept. RDA.* 23:62-74.

McDonald, J. G. and Hiebert, E. 1975. Characterization of the capsid and cylindrical inclusion proteins of three strains of turnip mosaic virus. *Virology* 63:295-303.

Oshima, N. and Harrison, B. D. 1975. Ribgrass mosaic virus. *CMI/AAB Descriptions of Plant Viruses* No. 152., Kew, Surrey, U.K.

Otsuki, Y. and Takebe, I. 1976. Double infection of isolated tobacco mesophyll protoplast by unrelated plant viruses. *J. Gen. Virol.* 30:309-316.

Pio-Ribeiro, G., Wyatt, S. D. and Khun, C. W. 1978. Cowpea stunt: a disease caused by a synergistic interaction of two viruses. *Phytopathology* 68:1260-1265.

Seron, K. and Haenni, A. L. 1996. Vascular movement of plant viruses. *Mol. Plant-Microbe Interact.* 9:435-442.

Yoon, M. K., Kim, J. Y., Choi, G. S. and Kim, J. S. 1995. Soil transmission, screening of resistant variety and incidence of *Ribgrass mosaic virus* occurring in Chinese cabbage in autumn growing season. *Korean J. Plant Pathol.* 11:191 (Abst.).