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Response of South Dakota Adapted Sorghum Cultivars to Maize Dwarf Mosaic Virus Strains A and B

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RESPONSE OF SOUTH DAKOTA ADAPTED SORGHUM CULTIVARS TO MAIZE DWARF MOSAIC VIRUS STRAINS A AND B

BY

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This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science and is acceptable for meeting the thesis requirements for this degree. Acceptance of this paper does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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CWC

ABSTRACT

Both MDMV-A and -B were transmitted by natural infection and mechanical inoculation on South Dakota adapted sorghum hybrids and occurred at the Brookings area. Grain sorghum hybrids were found to react differently to mechanical inoculation with MDMV-A and -B, respectively. Strain A usually induced a systemic mosaic symptom, while strain B usually produced local and necrotic symptoms. However, a few cultivars infected with strain B exhibited systemic symptoms. During a comparative ultrastructural study of MDMV infection, there was an obvious difference in inclusion bodies between MDMV-A and MDMV-B. Electron microscopy revealed the presence of pinwheels, bundles, tubes, scrolls, and laminated aggregates in cells of sorghum leaf tissue systemically infected with MDMV-B, while no laminated aggregates were found in cells of sorghum leaf tissue infected with MDMV-A. Ultrastructural aspects of HOK sorghum plants in the primary acute stage of symptom development and MDMV-A interaction, exhibited obvious ultrastructural changes in host cell morphology such as cell wall abnormalities. The cell wall abnormalities involved cell wall thickenings and protrusions associated with paramural bodies, extended plasmodesmata, and extraprotoplasmic sacs.

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INTRODUCTION

Maize dwarf mosaic virus (MDMV) is considered the most important virus disease of sorghum (Sorghum bicolor L. Moench) and has a wide geographical distrubution anywhere sorghum and Johnsongrass are present. MDMV (52), a new virus disease on corn (Zea mays L.), was first noted in southern Ohio in 1962 , reported in 1963 (17), and known as an economic pathogen of corn and sorghum in the mid-1960s (19,46,54). MDMV is transmitted by mechanical inoculation and also by aphids. Many weed and crop plants have been tested to determine the host range of MDMV through broad investigations, but the reaction to this virus of many important grasses occurring in the world still remains unknown. Only 66 genera of the 122 grass genera with represntative species in the USA have been tested for reaction to MDMV (39). Numerous early workers reported annual and perennial hosts of MDMV, and concluded that Johnsongrass (Sorghum halepense L.) was the primary overwintering host of the viruses (5,9,40,42,52). Despite the fact that MDMV-B has been known to infect corn and sorghum for several years, no way for its overwintering is known.

There has been confusion as to the relationship of MDMV to sugarcane mosaic virus (SCMV). Similarities between MDMV and SCMV have been noted. Dale (9) reported a mechanically transmissible virus in Arkansas and suggested that it may be a strain of SCMV. Shepherd (42) also suggested that a California isolate was a strain of SCMV and

he named it Johnsongrass strain of SCMV, or SCMV-Jg. Bancroft et al. (5) suggested that the SCMV represented a family of mutually distinctive viruses or a series of strains with different properties. In serological and host range studies, MDMV-B showed a closer relationship to strain E and H of SCMV than did MDMV-A (15). This result was in contradiction with that of Snazelle et al. (43) in which this isolate did not react with their SCMV-H antiserum. Tosic and Ford (48) reported that there were no significant differences in physical properties among MDMV-A, MDMV-B, and SCMV strains. Their serological tests suggested MDMV-A was distinct from MDMV-B, and MDMV-B was more closely related to the SCMV strains than to MDMV-A. They believed that the reason Snazelle et al. (43) were unable to get a positive serological reaction with SCMV-H was because they may have obtained the severe strain, which has been redesignated as SCMV-I. On the basis of reaction on sorghum cultivars Atlas and TX 3197, Tosic and Ford (48) grouped MDMV and SCMV strains. Group one included MDMV-B and SCMV-E which caused identical local lesions. Group two included SCMV-H and -I which caused extensive necrosis of infected plants. Group three included MDMV-A and SCMV-Jg which caused atypical local lesions, mosaic, and rare necrosis on new leaves. Group four involved SCMV-A, -B, and -D which caused mosaic and pronounced necrosis on new leaves (48). The host range of MDMV in the Gramineae is similar to that of the SCMV (38,39), however MDMV was distinguished from strains of SCMV because it easily infects Johnsongrass and is not infectious to sugarcane cultivars (42). SCMV has not been found in or transmitted to Johnsongrass in the field in

USA and only a very low percentage of infection was obtained in inoculation tests conducted by Abbott and Tippett (1). Snazelle et al. (43) agreed that both of the sugarcane cultivars, C.P. 31-294 and C.P. 31-588, used by Abbott and Tippett (1) as symptom differentials, were susceptible to all SCMV isolates but not to MDMV-A or MDMV-B, neither of which could be recovered from the symptomless plants. Dale and Anzalone (10) failed to obtain infection of Johnsongrass with SCMV from mechanical inoculations. It is generally recognized as being highly resistant or immune to most strains of SCMV.

The reddening and stunting symptoms so common in Ohio corn were almost lacking at University Park in Pennsylvania (51). Yellowing and delay of maturity were common symptoms. MacKenzie et al. (28) found a new strain of MDMV based on host reaction and serological relationships, referred to as MDMV-B, and designated isolates of MDMV that might infect both corn and Johnsongrass as MDMV-A and isolates which only infect corn as MDMV-B. Paulsen and Sill (36) reported no cross-protection between MDMV-A and MDMV-B strains on 20 selected sorghum hybrids and lines. Their results agreed with those of Tu and Ford (49) who reported nonprotection between strain A and B in corn. The above results indicate that cross-protection as a test for relationship between MDMV strains might not be reliable, by using corn or sorghum for test plants.

Four dissimilar strains of MDMV were isolated from a series of corn lines and designated as strains MDMV-C, MDMV-D, MDMV-E, and MDMV-F based on differences in symptoms, physical properties, and

reaction of corn lines (27). They were indistinguishable from each other in particle length and morphology, infectivity to Johnsongrass, serological reaction with MDMV-A antiserum, stability in sap, and longevity in detached leaves. On the basis of symptomatology, Zummo was able to differentiate six mosaic-inducing virus isolates from California, Georgia, Kentucky, Mississippi, and Virginia. Zummo and Gordon (55) noticed pathogen variation in five isolates of MDMV-A from different locations in the USA. This information helps explain the natural occurrence of several strains of MDMV. A maize virus isolated from Texas induced symptoms on corn resembling those incited by MDMV-A (31). The host range of this mechanically transmitted isolate was similar to that of MDMV-A, exept that it infected oats (Avena sativa). The isolate, considered a new strain of MDMV, was designated MDMV-O strain. However, only MDMV strains A and B are known to be transmitted to sorghum plants naturally.

The disease symptom expression induced by the virus depends upon virus strain variability, sorghum genotype, and environmental factors. Twenty sorghum entries reacted with a systemic mosaic 5 to 8 days after inoculation with MDMV-A (36). At low temperature red leaf symptoms were also observed in some varieties (19,36). The local lesions induced by MDMV-B enlarged and elongated rapidly, becoming red and necrotic in 4 to 6 days (36). Symptoms of MDMV vary considerably, even in plants of the same hybrids in the same field. One plant may show symptoms early in the season and another not until after pollination. Typical MDMV symptoms on corn and Johnsongrass

were first described by Janson et al. (18) and Dale (9). The typical symptoms described by Sehgal (40) were as follows: 1) Initial symptoms on corn seedlings appeared 4 to 5 days after inoculation in the form of small chlorotic spots near the base of unopened leaves, which developed later into a generalized yellow-green mosaic. Occasionally, older leaves showed longitudinal streaks running parellel to the veins, or rectangular dark green areas on a chlorotic background. 2) On sorghum a brilliant yellow green mosaic persisted through the life of the plants. Two inbred lines of corn reported to be resistant at University Park in Pennsylvania, exhibited severe symptoms under field tests in Ohio (51). Other (16) workers' results compared to those of Ohio (18) were also inconsistent. Numerous explanations could be given for these inconsistent results (51). Some of these were: 1) widely extended geographic area could allow for extremes in variation of climatic factors and fluctuation and variation of vector populations; 2) genetic differences in inbreds or inbred substitutions in hybrids; 3) genetic differences in the virus isolates inoculated; 4) vector resistance of host genotypes; 5) a differences in time of inoculation; 6) a differences in time of data reading; 7) error in disease rating evaluation. Optimum conditions for study of MDMV in sorghum were 1) use of 1:10 and 1:2 dilution of inoculum (MDMV-A and MDMV-B, respectively); 2) source plants inoculated 10 days before use; 3) an incubation temperature of 25 C; 4) inoculation of the first leaf 6 days after plant emergence, of the second leaf 2 days, and of the third leaf at least 14 days after plant emergence (41). HOK sorghum reacted to mechanical inoculation with MDMV-B with local lesions and to MDMV-A with local lesions,

primary acute and chronic mosaic symptoms (W. S. Gardner, unpublished). This was similar to the symptoms induced by barley stripe mosaic virus (BSMV) in barley (32).

Maize dwarf mosaic virus belongs to the potato virus Y group of plant viruses (14,23,24), characterized by flexuous rods about 750 nm long (5,40,42,46), and induce the formation of pinwheel or cylindrical inclusions in the host (7,12,14,23,24). The formation of pinwheel, bundle, and laminated aggregate inclusions after osmic acid fixation of tissue infected with SCMV was suggested by Edwardson (11). Comparative ultrastructural studies of MDMV infection show differences in inclusion bodies between MDMV-A and MDMV-B in corn (7). However, there are some disagreements among investigators (7,14,23,24).

Major cytological changes occur in the cells of virus infected plants. The chloroplasts of virus infected plant tissues were often swollen and contain less chlorophyll than those in comparable healthy plants (14,23). Gardner (14) suggested the chlorotic pattern in the leaves induced by SCMV-Jg infection might be due to a deficiency of pigments in the chloroplasts with fewer grana. McMullen et al. (35) found aberrant plastids including swelling, deformation of membranes, cytoplasmic invaginations, peripheral vesicles, and BSMV particles attached to the limiting membrane, in systemically and mechanically infected barley leaf tissue. Cell wall abnormalities, with or without vesicles and tubles, were often associated with modification of plasmodesmata between the cell wall and plasmalemma (6,7,21,25,34,44).

Although areas of vesiculation between the cell wall and plasmalemma were often found in healthy plant tissue, they were a common formation in virus infected cells and termed boundary formations (50) or paramural bodies (29). Tu and Hiruki (50) suggested that boundary formations, accompanied by roughening of the inner cell wall, were evidence of abnormal secondary wall deposition in virus infected cells. Various investigators reported an increase in the size and number of paramural bodies associated with virus infection (20,44). Kim and Fulton (21) suggested three possible functions of paramural bodies as: 1) ectocytic transporting metabolites, 2) as endocytic assistance of transporting materials into cell, 3) and as a transitory response of the cell protoplast to unfavorable or pathological conditions. Paramural bodies and cell wall thickenings occurred not only in the cells surrounding necrotic lesions of local lesion hosts (44,50), but also in systemically infected tissues (20,21,34). Unusual membrane-bound structures termed "extended plamodesmata" (34) and "extraprotoplasmic sacs" (3,34) were often associated with the paramural bodies and cell wall thickenings. Extended plasmodesmata were compared with myelinic bodies by Kim et al. (22). The observation of primary acute symptoms in HOK sorghum inoculated with MDMV-A suggests that ultrastructural cytology might be similar to that found for BSMV in barley (34).

The objectives of this study are to determine the response of South Dakota adapted sorghum cultivars to mechanical inoculation, to identify potential reservoirs for MDMV, to compare sorghum cultivars reaction to MDMV-A and -B, and to describe the symptom development

at different stages of sorghum cultivars inoculated with MDMV. Also to observe the cytological modification of HOK sorghum cultivar inoculated with MDMV-A mechanically, and finally to compare the difference of inclusion bodies between strain A and B.

MATERIALS AND METHODS

Virus isolates and maintenance.

MDMV-A was maintained in Johnsongrass and MDMV-B was maintained in Mo 17 and N 28 corn plants. Both MDMV strains were obtained from W.S. Gardner (formerly, Department of Plant Science, SDSU). Systemically infected leaves, exhibiting conspicuous disease symptoms about 2 weeks after mechanical inoculation, served as the virus source, and were maintained under greenhouse conditions.

Assay and Inoculation.

Inoculum for symptomatology and disease severity studies of 20 sorghum cultivars was prepared by grinding infected leaves of Johnsongrass for strain A and those of N 28 corn for strain B in the water from reverse-flow osmosis (w/v), with mortar and pestle. A 1:5 dilution of plant material for strain-A and a 1:2 dilution for strain B was used for the inoculum source. Test seedlings at the fourth-leaf stage were dusted lightly with 600-mesh corundum and both surfaces of leaves were rubbed twice between thumb and forefinger, which had been soaked with the inoculum. Leaves were not rinsed after inoculation.

Greenhouse study I: symptomatology.

During these investigations the following sorghum cultivars were studied: Cargill 22, Cargill 30, Cargill 40, Dekalb-Pfizer DK-18, Dekalb-Pfizer DK-28, Disco 178, Kingswestern WS-205, PAG 2250, PAG 3339, PAG 3385, Pioneer 8680, Pioneer 8790, Pioneer 8855, Sigco Triumph 48yG, Sigco Triumph 50yG, Warner W545T, Warner WX83111, Warner WX84041, Warner WX84003, and HOK. Seeds of these cultivars were supplied by J.J. Bonnemann (Seed House, SDSU). The sorghum plants were grown in a steamsterilized mixture of soil:sand:peat (2:1:1) in 10 cm clay pots, conducted in the temperature controlled greenhouse, illuminated 12-16 hr with natural and supplemental fluorescent light per day, fertilized fortnightly, and sprayed with insecticide and miticide periodically by Kerry Parcel (Plant Science Bldg, SDSU). Tests were repeated 4 or more times with 5 replicates per each sorghum cultivar. The third and fourth leaves of four plants per pot were inoculated. One set of plants inoculated with strain A, and another set with strain B. Symptoms were observed everyday, and recorded 3-30 days after inoculations. Symptom development was based upon a system proposed by McKinney and Greeley (26) described as: local lesion, primary acute, early chronic, and late chronic and as necrosis and red leaf. Plants that remained symptomless in response to strains A and B were back inoculated to N-28 corn plants 30 days after inoculation and the N-28 corn plants were observed for 4 weeks.

Greenhouse study II: disease severity and symptomatology.

An alternative to natural infection by aphid transmission in the field was to inoculate test entries mechanically and separately with MDMV-A and MDMV-B in the greenhouse. The same procedures as those in Greenhouse study I were used to inoculate 38 grain sorghum hybrids. Entries were restricted to South Dakota adapted cultivars. Seeding time was regulated to allow entries to be inoculated on the same date. Symptom expression was recorded at 3 day intervals following and the final reading made after 21 days. Disease severity ratings for plants inoculated with MDMV-A were made on the scale 0 (no symptoms), 1 (mild mosaic symptoms), 2 (intermediate mosaic symptoms), and 3 (severe mosaic symptoms). MDMV-B disease severity ratings made on the scale 0 (no symptoms), 1 (local lesion number less than 5), 2 (local lesion number between 6 and 10 or mild necrosis), and 3 (local lesion number more than 10 or severe necrosis). The percentage of infection was calculated from number of infected plants present over total number of plants for each cultivar.

Field studies

Experiments were conducted to determine the field response of South Dakota adapted sorghum cultivars to natural transmission of MDMV by aphids. The sorghum seeds were planted on 2-3 dates each year in 1984 and 1985 in the field at Brookings, SD. MDMV-induced symptoms were observed and recorded from the first appearance and development of symptoms. Plants showing systemic symptoms were

indexed on indicators such as HOK sorghum, N 28 corn, and Johnsongrass in the greenhouse to determine if MDMV was present in the field sorghum samples. The plot sizes in both years were 6.71 meters in length, 1.02 meters between rows with 61 centimeters divider spacers, and 30.48 centimeters space between hills with 3 to 4 seeds planted per hill with the hand planter.

The 1984 planting was delayed until July 15 due to excessive soil moisture. The seeds of 20 sorghum cultivars were planted in three randomized replications on July 15 and 16, 1984. Plants were inspected weekly for symptom development.

The 1985 study was conducted to determine the response of 51 sorghum cultivars and the presence of MDMV in late planting. Plantings were on June 28, 29, and 30, 1985. The 1985 growing season was characterized by frequent rains and cool temperatures. These weather conditions contributed to a reduced population of aphids. The 51 sorghum cultivars were grown in four randomized replicate single-row plots. The plots were maintained free of weed competition throughout the growing season.

Electron microscopy

Plants for electron microscopy were inoculated at the fourth-leaf stage of growth. The third and emerging fourth leaves of HOK sorghum plants were mechanically inoculated with MDMV-A from Johnsongrass and grown in the greenhouse. HOK sorghum leaf tissues exhibiting primary acute symptoms described by McKinney and Greely

(26) and Pioneer 8680 sorghum leaf tissues inoculated with MDMV-B showing chronic phases of mosaic symptoms 3 weeks after inoculation were prepared for ultrastructural study.

Both HOK and Pioneer 8680 tissues were cut under a drop of 2.5 % glutaraldehyde in 0.1 M potassium phosphate buffer (PH 7.2) placed on the top cover of plastic petri dish filled with crushed ice, into portions at 1 by 6 mm and fixed in the same buffer solution for about 60 minutes in snap cap vials kept in ice bath. Vacuum was used to remove air from tissues while in the glutaraldehyde fixative. The glutaraldehyde was removed using a pasteur pipet, and vials were drained on a paper towel. Post fixation, without intermediate rinsing, used 1 ml cold 1 % osmium tetroxide in 0.1 M potassium phosphate buffer (PH 7.2) for about 60 minutes. The tissues were dehydrated in a cold acetone series starting at 25 % for 15 minutes, repeated twice, to repeated twice 50 % acetone followed by two changes of acidified 100 % DMP (Dimethoxy propane) solutions. After dehydration, the tissues were soaked for 2-4 hours at room temperature in an aluminum weighing dish in a mixture of Spurr low-viscosity plastic (77) and Bo-Jax Mixture (59) (23:77 v/v) with DMP-30 (Tridimethylamino methyl phenol) used as the accelerator. The tissues were transferred to a fresh plastic mixture in "micron" molds and polymerized at 60 C for 24 hours.

Thin sections were cut with glass knives on a Porter Blum MT-2 ultramicrotome, placed on uncoated 200-mesh copper grids, stained with uranyl acetate for 2 hours followed by lead citrate staining for 1 minute at room temperature, and viewed with a Hitachi HU-12A at 75 KV

and 100 KV.

RESULTS AND DISCUSSION

Greenhouse study I: Symptomatology.

In this study 20 grain sorghums were tested for reaction to MDMV-A and MDMV-B. The data (Table 1) as a result of mechanical inoculation show that eighteen sorghum cultivars gave a different response to strain A and B of MDMV, and two cultivars had a similar response to both strains of virus. These two strains are certainly different in the symptomatology. Symptoms on susceptible plants were usually expressed within 10 days of inoculation of both strains. There was some variability in the percentage of infection among sorghum cultivars. The data (Table 2) show that 337 of the 400 (84.25 %) sorghum seedlings inoculated with MDMV-A developed systemic mosaic symptoms while 164 of the 400 (41.00 %) sorghum seedlings inoculated with MDMV-B developed local and systemic symptoms.

The symptoms induced by MDMV-A were as follows. Tiny and atypical local lesions (L) were commonly found on inoculated leaves of PAG 2250 and HOK 3-5 days after inoculation. They were also observed but rarely found in Dekalb-pfizer DK-18, DK-28, Kings Western WS-205, and Pioneer 8680. The local lesions induced by MDMV-A, differed from those caused by MDMV-B in size and shape. Similar results were described by Tosic and Ford (47,48). They suggested that the tiny and elliptical local lesions were not always recognized easily.

Table 1 : Reactions of 20 sorghum cultivars to MDMV-A and MDMV-B

Sorghum cv.	Symptoms induced by indicated strain *	
	Strain A	Strain B
Cargill 22	PAc, PAn, EC, LC **	rLty
Cargill 30	PAc, EC, LC, rLN	Lty, N
Cargill 40	PAc, PAn, EC, LC	rLty
Dekalb-Pfizer DK-18	Lr, PAc, PAn, EC, LC, N, R	Lty
Dekalb-Pfizer DK-28	Lr, PAc, PAn, EC, LC, N	Lty
Disco 178	PAc, EC, LC, rLN	.
Kings Western WS-205	Lr, PAc, EC, LC	.
PAG 2250	La, PAc, PAn, EC, LC, N	Lty, LN
PAG 3339	PAc, EC, LC	.
PAG 3385	PAc, EC, LC	Lty
Pioneer 8680	Lr, PAc, EC, LC	EC, LC, LN, R
Pioneer 8790	PAc, EC, LC, rLN	EC, LC, LN, R
Pioneer 8855	PAc, EC, LC	.
Sigco Triumph 48yG	PAc, EC, LC	Lty
Sigco Triumph 50yG	PAc, EC, LC	.
Warner W545T	PAc, EC, LC	rLty, LN
Warner WX83111	PAc, EC, LC	rLty
Warner WX84041	PAc, EC, LC	rLty
Warner WX84003	PAc, EC, LC, rLN	Lty
HOK	La, PAc, PAn, EC, LC, R	Lty, N

* Used strains are explained in Materials and Methods.
** Abbreviations are : L = Local symptoms on inoculated leaves, N = Necrosis, LN=Local necrosis, r= Rare, a= Atypical--usually tiny, ty= Typical necrotic, PA= Primary acute systemic, c= chlorotic, n= Necrotic, EC= Early chronic systemic, LC= late chronic systemic and R= Redleaf.

Primary acute symptoms (PA) consisted of short chlorotic spots on the fifth leaves of inoculated plants of all 20 sorghum cultivars and usually appeared at the base of the youngest developing leaf in the terminal whorl 5-7 days after inoculation (Fig. 2). The infected tissues in the PA phase sometimes became necrotic. Sorghum cultivars with this symptom were Cargill 22, Cargill 40, Dekalb-Pfizer DK-18, DK-28, PAG 2250, and HOK. In the early chronic (EC) stage the chlorotic spots became numerous and elongated as the leaves increased in size, and resulted in the formation of chlorotic stripes on the fifth and sixth leaves of all 20 sorghum cultivars 7-13 days after inoculation (Fig. 3). In the late chronic (LC) stage uninoculated leaves of infected 20 sorghum cultivars usually showed a chlorotic appearance with mottling islands as rectangular dark green areas in a lighter green background 2 weeks after inoculation. Occasionally, MDMV-A induced a necrosis on inoculated leaves accompanied by a mild mottle on several sorghum cultivars. Severe necrosis was observed in Dekalb-Pfizer DK-18 and PAG 2250. All 20 sorghum entries usually showed PAc, EC, and LC in common. Symptom variations were observed even in the same cultivar and suggested that the virus might survive in susceptible, possibly symptomless plants. The 20 sorghum entries inoculated with MDMV-A were highly susceptible from 65 to 100 % of infection (Table 2). Three sorghum cultivars, PAG 2250, PAG 3385, and Pioneer 8855, were 100 % susceptible to MDMV-A. The reaction of sorghum cvs. HOK, Dekalb-Pfizer DK-18, DK-28, and PAG 2250 to MDMV strains has not been reported. These cultivars on the basis of MDMV-A reaction obviously differentiate strains, and show more diverse reactions to MDMV-A than

Table 2 : Susceptibility of 20 sorghum entries to MDMV-A and MDMV-B

Sorghum Cv.	MDMV-A No.infect/ No.inoc.	% inf.	Back assay	MDMV-B No.infect/ No.inoc.	% inf.	Back assay
Cargill 22	15/20	75	8/10	2/20	10	0/10
Cargill 30	16/20	80	.	15/20	75	3/10
Cargill 40	17/20	85	.	6/20	30	1/10
Dekalb-Pfizer DK-18	18/20	90	.	19/20	95	.
Dekalb-Pfizer DK-28	18/20	90	.	18/20	90	.
Disco 178	18/20	90	.	0/20	0	0/10
Kings Western WS-205	14/20	70	6/10	0/20	0	0/10
PAG 2250	20/20	100	.	18/20	90	4/10
PAG 3339	15/20	75	7/10	0/20	0	0/10
PAG 3385	20/20	100	.	19/20	95	5/10
Pioneer 8680	18/20	90	.	11/20	55	9/10
Pioneer 8790	18/20	90	.	9/20	45	7/10
Pioneer 8855	20/20	100	.	0/20	0	0/10
Sigco Triumph 48yG	15/20	75	.	3/20	15	2/10
Sigco Triumph 50yG	13/20	65	6/10	0/20	0	0/10
Warner W545T	19/20	95	.	3/20	15	1/10
Warner WX83111	16/20	80	.	10/20	50	4/10
Warner WX84041	17/20	85	.	1/20	5	0/10
Warner WX84003	15/20	75	.	12/20	60	3/10
HOK	15/20	75	.	18/20	90	.
Total No. infected/ Total No. inoculated	337/400			164/400		
Average infection (%)		84.25			41.00	

the other cultivars.

There has been some disagreement in the literature on the reaction to MDMV-B of the various sorghum cultivars. Paulsen and Sill (36) reported MDMV-B induced only local lesions on their sorghum entries. Some researchers reported mosaic symptoms on the sorghum cultivar Atlas (47). Alexander and Toler (2) reported on the effect of MDMV-B infection on sorghum cultivars, where some cultivars developed "red leaf" and necrotic symptoms, while the other cultivars developed only mosaic symptoms. Some minor differences existed between those results and some of my Greenhouse study I data (Table 1) on the basis of symptom expression of sorghum cultivars. MDMV-B usually induced local lesions and necrosis, but sometimes developed systemic symptoms depending upon cultivars. The local lesions elongated, enlarged, and became necrotic in 5 to 6 days (Fig. 4). The sorghum cultivars with this symptom are contained in Table 1. Sorghum cvs. Cargill 30, Dekalb-Pfizer DK-18, DK-28, PAG 3385, and HOK produced a large number of local lesions and were highly susceptible to MDMV-B. Within 2 weeks after inoculation, added necrosis developed in Cargill 30, PAG 2250, Warner W545T, and HOK. There was a wide variation among cultivars in response to MDMV-B from 0 to 95 % of infection (Table 2). Sorghum cvs. Pioneer 8680 and 8790 showed obviously systemic mosaic symptoms with local necrosis 10-21 days after inoculation. The initial symptoms appeared as chlorotic stripes and developed as mosaic symptoms. There were no typical differences between mosaic symptoms induced by MDMV-A and those induced by MDMV-B. Sorghum cvs.

Cargill 30 and HOK have not been reported as local lesion hosts of MDMV-B, however they show clearly many necrotic local lesions and may be useful in the identification and classification of MDMV isolates from different geographical areas, and in establishing the identity of the virus as a strain of MDMV. The following cultivars were not susceptible to MDMV-B: Disco 178; Kings Western WS-205; PAG 3339; Pioneer 8855, and Sigco Triumph 50yG. These cultivars were observed as no response when inoculated with MDMV-B, and no virus was recovered by back inoculation from symptomless plants to N-28 corn.

Sorghum cvs. Dekalb-Pfizer DK-18 and DK-28 were highly susceptible and showed more than 90 % of infection to both strains (Table 2). Both PAG and Pioneer lines were highly susceptible while Sigco Triumph lines were less susceptible to MDMV-A than average infection percentage of 20 sorghum cultivars inoculated with MDMV-A. The Sigco Triumph lines were also less susceptible to MDMV-B. Red leaf symptoms (2,19,36) were observed in both Dekalb-Pfizer Dk-18 and HOK inoculated with MDMV-A, and in Pioneer 8680 and 8790 inoculated with MDMV-B. Symptom variation may be attributed to use of different genotype, virus cultures, and/or environmental conditions under which the test was conducted. These reactions in the greenhouse may be changed in the field due to stress with environmental influences.

Greenhouse study II: Disease severity and symptomatology

Thirty-eight additional sorghum entries were evaluated for susceptibility to two strains of MDMV using mechanical inoculation methods in the greenhouse. The data and statistical analyses are presented in Table 3 (MDMV-A) and Table 5 (MDMV-B). The average final percent infection of MDMV-A was 59.74 % while that of MDMV-B was 65.26 %. According to chi-square analyses, significant differences in the percentage of plants displaying symptoms were observed among 38 hybrids at 9 days after inoculation with MDMV-A, and at 9 days, 12 days, 15 days, 18 days, and 21 days after inoculation with MDMV-B. Significant differences were also observed at 3 and 6 days after inoculation for both strains; however, due to large number of hybrids with no infected plants at these two time periods, the chi-square test is not valid.

In addition to total number of infected plants, the use of individual rating values may reflect the resistance or susceptibility of the entries to MDMV-A. Out of a total of 760 sorghum plants inoculated with MDMV-A, 730 showed no symptoms at the first 3 day-period. This was the largest number of symptomless plants. Two hundred and six sorghum plants rated 1 at 9 day-period. This indicated that sorghum plants inoculated with MDMV-A usually showed mild mosaic symptom expression within 9 days after inoculation. Among infected sorghum plants at 15 day-period, the largest number of sorghum plants rated 2. This indicated that 313 sorghum plants showed intermediate mosaic symptoms usually developed from the mild mosaic symptoms. In the final

rating, 214 sorghum plants rated 3. This indicated that the severe mosaic symptoms occasionally developed from mild mosaic symptoms, but more often from intermediate mosaic symptoms. After 21 days, about 60 % of the total sorghum plants inoculated with MDMV-A rated 2 or 3 (Table 4).

The hybrids with the highest ratings in susceptibilty were Keltgen KG57T, Dekalb DK-39Y, Funk G-421, and Cenex 310 (Appendix A). They exhibited comparatively higher ratings than those of other hybrids and are considered to be highly susceptible hybrids. This result was consistent with the percentage of infection at the final day period. Sorghum hybrids Dekalb Dk-39Y and Western WS-203 were significantly highly susceptible to strain A among hybrids at the 9 day-period. Sorghum hybrids NK 2030, Hoegemeyer GT 620, Seed Tec. 8501, Cenex 228, and Dekalb X-550 were less susceptible to strain A than average percentage of infection at the 9 day-period and were less than 50 % of infection at each day period. This result was consistent with the disease rating values and suggested they might be considered more resistant than any other hybrid. Most hybrids showed initial symptoms between 6 and 9 days after inoculation and developed no further increase in infection between 15 and 21 days after inoculation. Disregarding significant differences in the level of infection, there appeared to be seven day periods in which infection increased. For example, in the 3 day-period, the initial rating day of MDMV-A showed a low average percentage (3.95 %) of plants infected, but a high increase in average percentage (59.74 %) of plants was observed (Table

3). Similarly in seven period ratings were comparable at 3 day-period with an increase in rating values at the 15 day-period (Table 4). Usually most hybrids showed typical mosaic symptoms, however Seed Tec. 8502, Warner W-523T, Pay Master 1022, and Pay Master 930 often developed red leaf symptoms. This symptom on certain hybrids may be influenced by low night temperatures (2,19,36).

The same thirty-eight sorghum hybrids were evaluated for their reaction to strain B of MDMV based on local lesion and necrosis symptoms (Table 5). Although there were differences in percentage of infection, most inoculated sorghum entries developed local lesions upon inoculation with MDMV-B; 65.26 % of the total plants of the 38 sorghum entries produced local lesions. The average percentage indicated some differences in susceptibility in sorghum entries. Symptoms on susceptible plants were usually expressed within 4 to 15 days after inoculation. In percentage of infection there were highly significant differences after 9 day-period among sorghum hybrids inoculated with MDMV-B. There was a great variation in the degree of susceptibility of plants. In the level of disease rating values, there appeared to be seven day periods in which the severity increased. The initial rating of MDMV-B at the first 3 day-period showed no symptoms, however there was a high increase in rating values at the final rating. Three hundred and twenty-four sorghum plants rated 1 at the 12 day-period, indicating that they usually showed initial local symptom expression within 12 days and produced 5 or fewer local lesions. At the 18 day-period, the largest number of infected sorghum plants rated 2 among

Table 3 : Percentage of mechanically inoculated sorghum plants showing symptoms of MDMV-A infection at different intervals following inoculation.

Variety	Day 3*	6	9	12	15	18	21
Keltgen KG57T	0	0	55	80	85	85	85
Dekalb DK-39Y	0	10	70	75	75	75	75
Funks G-421	0	25	55	70	65	75	75
Cenex 310	0	35	55	70	75	75	75
Western WS-203	35	55	70	70	70	70	70
Sigco 46YG	20	55	65	70	70	70	70
Warner W-501T	10	20	60	70	70	70	70
Seed Tec. 8502	0	25	55	65	70	70	70
Cenex 226	0	15	50	70	70	70	70
Funks HW5883	0	20	50	70	70	70	70
Warner W-551A	15	55	65	65	65	65	65
Warner W-523T	20	45	60	65	65	65	65
McCurdy M450	0	15	55	65	65	65	65
Funks G-251	0	40	50	65	65	65	65
Hoegemeyer 606	0	35	50	65	65	65	65
Dekalb DK-38	0	5	40	65	65	65	65
Pay Master 1022	0	45	60	60	60	60	60
Seed Tec. 8503	10	50	55	60	60	60	60
McCurdy M410	0	0	40	60	60	60	60
Asgrow Corral	0	10	35	50	60	60	60
Keltgen KG63T	0	10	35	60	60	60	60
McCurdy M687	15	25	35	60	60	60	60
NK 2244	10	10	30	50	60	60	60
Western WS-212	0	35	55	55	55	55	55
Warner W-560T	5	25	50	55	55	55	55
Dekalb X-538	5	15	45	55	55	55	55
Asgrow Mesa	0	10	40	50	55	55	55
Pay Master 930	0	15	35	50	55	55	55
Cenex 230	0	15	30	55	55	55	55
Cenex 224	0	0	45	50	50	50	50
NK 1210	0	20	45	50	50	50	50
McCurdy M51YG	0	5	35	50	50	50	50
Asgrow Dorado E	0	15	30	45	50	50	50
NK 2030	0	10	30	35	45	45	45
Hoegemeyer GT620	0	10	25	35	45	45	45
Seed Tec. 8501	0	0	30	40	40	40	40
Cenex 228	0	0	25	40	40	40	40
Dekalb X-550	0	0	15	30	30	30	30
Mean % infection	3.95	20.53	45.39	57.63	59.74	59.74	59.74

*	Chi-square	df	prob
3.	119.101	37	0.0001#
6.	131.055	37	0.0001#
9.	55.423	37	0.0263

12.	42.484	37	0.2466
15.	39.476	37	0.3598
18.	39.476	37	0.3598
21.	39.476	37	0.3598

Chi-square analyses may be invalid due to large number of hybrids with no infected plants.

Table 4 : Distribution of rating values of sorghum plants inoculated with MDMV-A at different time intervals.

	Day / No. infected plants						
Rating	3	6	9	12	15	18	21
0	730	604	415	322	306	306	306
1	30	135	206	121	23	1	0
2	0	21	136	277	313	270	240
3	0	0	3	40	118	183	214

time intervals. This indicated that 188 out of the total sorghum plants produced between 6 and 10 local lesions and/or mild necrosis, which were increased from rating value 0 very occasionally, but most often from rating value 1. The largest number of plants in infected sorghum plants rated 3 in severity was at the final ratings, indicating that 54 out of the total sorghum plants produced more than 10 local lesions and/or severe necrosis which increased the rating values from rating value 1 very occasionally, but most often from rating value 2 (Table 6). A summary of the results of disease ratings of MDMV-B is given in Appendix B.

Sorghum hybrids Seed Tec. 8502, NK 1210, and McCurdy M687 were the least susceptible to MDMV-B. Their infection percentage at each day period was less than average percentage of infection at each day period and less than 25 %, which suggested they might be considered resistant to MDMV-B. This result was consistent with the disease rating values. Sorghum hybrids Pay Master 1022, Cenex 230, and Funks G-251 were significantly the most susceptible among hybrids at the 9, 12, 15, 18, and 21-day-periods. Their infection percentage at each day period was more than average percentage of infection at each day period and more than 90 %. The highest rated hybrid in susceptibility to strain B was Pay Master 1022. This result was consistent with the percentage of infection (Appendix B). Often the sorghum hybrid Cenex 930 initially showed indistinct chlorotic spots and flecks 6-9 days after inoculation, however this symptom disappeared or did not develope further.

Table 5 : Percentage of mechanically inoculated sorghum plants showing symptoms of MDMV-B infection at different intervals following inoculation.

Variety	Day 3*	6	9	12	15	18	21
Pay Master 1022	0	35	95	95	95	95	95
Cenex 230	0	35	45	90	90	90	90
Warner W-560T	0	5	50	85	90	90	90
Funks G-251	0	15	45	80	90	90	90
Western WS-203	0	5	25	85	90	90	90
Seed Tec. 8503	0	40	60	85	85	85	85
Seed Tec. 8501	0	35	60	80	85	85	85
Cenex 310	0	20	30	80	85	85	85
Hoegemeyer GT620	0	25	55	65	85	85	85
Warner W-551A	0	15	35	80	80	80	80
Keltgen KG63T	0	10	50	75	80	80	80
Dekalb DK-38	0	20	40	45	80	80	80
Cenex 224	0	0	5	50	80	80	80
Western WS-212	0	25	40	75	75	75	75
McCurdy M410	0	10	25	75	75	75	75
Pay Master 930	0	0	15	70	75	75	75
Asgrow Dorado E	0	15	30	70	70	75	75
Sigco 46YG	0	15	50	70	70	70	70
Warner W-501T	0	0	30	65	70	70	70
Funks G-421	0	0	10	65	70	70	70
Asgrow Mesa	0	0	5	65	70	70	70
Dekalb X-550	0	5	30	50	60	60	60
Asgrow Corral	0	5	5	40	60	60	60
Funks HW5883	0	0	0	20	60	60	60
Dekalb X-538	0	0	20	45	55	55	55
Dekalb DK-39Y	0	0	10	45	55	55	55
Keltgen KG57T	0	0	25	50	55	55	55
NK 2244	0	15	30	45	55	55	55
Cenex 228	0	5	35	50	50	55	55
Hoegemeyer 606	0	0	0	20	50	55	55
Cenex 226	0	15	40	50	50	50	50
McCurdy M450	0	10	45	50	50	50	50
McCurdy M51YG	0	0	0	45	50	50	50
Warner W-523T	0	5	25	30	40	40	40
NK 2030	0	0	0	15	40	40	40
Seed Tec. 8502	0	5	20	25	25	25	25
NK 1210	0	0	0	10	15	15	15
McCurdy M687	0	0	5	5	5	5	5
Mean infection %	0	10.13	27.76	55.79	64.87	65.26	65.26

*	Chi square	df	prob
3.	.	.	.
6.	113.373	37	0.0001#
9.	171.375	37	0.0001

12.	166.442	37	0.0001
15.	148.090	37	0.0001
18.	147.306	37	0.0001
21.	147.306	37	0.0001

Chi-square analyses may be invalid due to large number of hybrids with no infected plants.

Table 6 : Distribution of rating values of sorghum plants inoculated with MDMV-B at different time intervals.

	Day / No.infected plants						
Rating	3	6	9	12	15	18	21
0	760	683	549	336	267	264	264
1	0	77	174	324	289	268	266
2	0	0	36	90	176	188	176
3	0	0	1	10	28	40	54

The percentage of infection was usually related to severity of infection in individual plants as expressed by the extent and intensity of symptoms. The time-period tended to become progressively more extended with increase in the degree of susceptibility (Table 4, Table 6). This study determined that South Dakota adapted sorghum hybrids showed varying degrees of susceptibility to MDMV-A and -B, however there will be a possibility that this reaction may be changed because of environmental factors.

Field studies

In 1984 initial observations for occurrence of MDMV at Brookings began on August 15 and continued through the end of August. Plants were judged as infected or healthy based on the presence or absence of typical mosaic symptoms. The symptoms of the disease were a mild mosaic or chlorotic stripes with spots beginning at the base of youngest leaves followed by the development of mottling appearance (Fig. 1). The following cultivars of the sorghum entries were found to be systemically susceptible to the virus under natural conditions: Cargill 22; PAG 3385; Pioneer 8680; Pioneer 8855; and Warner WX84041. Approximately 2 months after planting infected plants were indexed on indicator plants such as N 28 corn, HOK sorghum, and Johnsongrass to identify this virus definitely. Differences in the index range symptoms indicated the presence of two strains of MDMV in the Brookings area. Sorghum cvs. Cargill 22, PAG 3385, Pioneer 8855, and Warner WX84041 revealed that they carried MDMV-A. Pioneer 8680 exposed to natural infection revealed the presence of MDMV-B, the

strain which did not infect Johnsongrass. This result was consistent with Pioneer 8680 mechanically inoculated with strain B in Greenhouse study I result (Table 1). On the basis of these observation, a late trial planting of sorghum cultivars in 1984 revealed the presence of both MDMV-A and MDMV-B at Brookings. A natural MDMV field transmission experiment with 51 sorghum cultivars in 1985 produced no visibly infected plants. Both MDMV-A and MDMV-B and wheat streak mosaic virus were recovered from N-28 corn border plants.

Electron microscopy

Comparative ultrastructural studies of sorghum cv. HOK and Pioneer 8680 leaf cells separately infected with MDMV-A and -B respectively revealed the formation of numerous cylindrical inclusions characteristic of infection by viruses of the potyvirus group (8,11) in both cross and longitudinal section. The terms "cylindrical inclusions", "bundles", "pinwheels", "scrolls", and "laminated aggregates", as defined by Edwardson (12), were used for describing various types of viral inclusions found in cells infected with MDMV. Various profiles of inclusions induced by MDMV-A and MDMV-B separately were randomly distributed in cells of thin sectioned infected sorghum leaf tissue. Pinwheel inclusions which had curved arms centered on a core resulting from cross-sectioning of cylindrical inclusions, were frequently found in some area of the cytoplasm of cells infected separately with MDMV-A (Figs. 5, 6) and MDMV-B (Figs. 7, 8). Bundles, consisting of plates or rods of different thickness and length and resulting from longitudinal sections of cylindrical inclusions, were found either abutted to the

plasmalemma (Fig. 7) or free in the cytoplasm (Figs. 6, 8). Frequently, the ends of bundles appeared to be continuous with elements of endoplasmic reticulum (Figs. 6, 7). Scrolls appeared to consist of one or more coiled pinwheel extensions derived from a cross section of a tube (Figs. 6, 7). Tubes appeared to be pinwheel arm-like structures in longitudinal section (Fig. 6-B). Laminated aggregates (LA), as a large flat plate composed of several parallel and thin plates resulting from cross sectioning of cylindrical inclusions, were found only in Pioneer 8680 sorghum tissues infected with MDMV-B, and often had mutual connections with several pinwheels (Figs. 7, 8). Loose aggregates of flexuous rod particles in the cytoplasm of Pioneer 8680 infected with MDMV-B are believed to represent actual virus particles (Fig. 7).

The MDMV-A and MDMV-B are distinguishable by their inclusion bodies in the cytoplasm. Electron microscopy revealed the presence of pinwheels, bundles, scrolls, and laminated aggregates in cells of Pioneer 8680 soghum leaf tissue infected with MDMV-B while no laminated aggregates were found in cells of HOK sorghum leaf tissue infected with MDMV-A. The appearance of structures associated with pinwheels exhibited virus-specific variations which are independent of the host species (13) suggest that the type of sorghum cultivars may not be related with the formation of different inclusion bodies. Edwardson (12) classified the potyviruses into the following subdivision: viruses which induce scrolls or tubes in cross section belong to Subdivision I; viruses which induce laminated aggregates belong to

Subdivision II; viruses which induce both laminated aggregates and scrolls belong to Subdivision III. Edwardson (12) assigned MDMV-A to Subdivision I while assigning MDMV-B to Subdivision III. Electron microscope studies of two strains of MDMV indicated specific differences in inclusion bodies, particularly with respect to LAs induced by MDMV-B. The presence of LAs in a sorghum cultivar infected with MDMV may designate it as MDMV-B and assign it to Subdivision III while the absence of LAs may designate it as MDMV-A and assign it to Subdivision I accoding to classification system of Edwardson (12). Ultrastructural studies of tissue infected with MDMV have reported no laminated aggregates and a few virus rods (14,23). Krass and Ford (23) in a comparative study could not distinguish ultrastuctural differences in tissue infected separately with MDMV-A and MDMV-B. Gardner (14) suggested that no observation of LAs might be due to fixation and staining characteristics, or to virus strain variability. Later Langenberg and Schroeder (24) found MDMV-B virions and virus-induced LAs. They explained the differences between their results and those of two previous investigations (14,24) might be due to fixation problems or morphological changes during fixation. They also suggested that pinwheels represent a stable structure while LAs represent unstable inclusions during fixation. However, several investigators showed that these inclusion bodies are reliable structures of potyvirus-infected cells which are stable under varying conditions of fixation (8,12,30). McMullen and Gardner (33) also suggested imperceptible change of the morphology in pinwheels and associated inclusions induced by wheat streak mosaic virus in using various fixations. Bradfute and

Robertson (7) found cylindrical inclusions of the pinwheels and tubes induced by MDMV-A, however flexuous rod virus particles, cylindrical inclusions, and LAs were found in maize tissues infected with MDMV-B. They suggested virus particles of strain A may not be evident in cells with abundant virus-induced inclusions. My results agree with those of Bradfute and Robertson (7).

Two possible explanations are proposed to interpret the differences between my results and those of three previous investigations (14,23,24): 1) Variation of strain may induce the variation of inclusions rather than various types of fixation differences; 2) Another possibility of missing inclusion components may be how long sampling tissues have been infected. The former explanation is more reliable than the latter one. Time in sampling tissues of HOK sorghum infected with MDMV-A are different from those of previous investigators. In previous investigations samples were prepared two and five weeks (23), and 8 days (14) after inoculation while my samples were prepared 5-6 days after inoculation. However, no typical differences of inclusion bodies induced by MDMV-A exist between previous investigations and my results. Andrews and Shalla (4) reported that LAs were formed late in the infective process. However, the number of LAs in my samples prepared 25 days after inoculation with MDMV-B was not different from that of 10-14 days after inoculation (24). Previous investigations have not reported the occurrence of LAs in soghum cultivars infected with MDMV-B or the absence of LA's in sorghum infected with MDMV-A.

In these cytological studies the most distinctive structural modifications at the cell wall-plasmalemma interface of MDMV-A infected HOK sorghum leaves were noted 5-6 days after inoculation. Examination of leaves with primary acute symptoms revealed cell wall abnormalities, notably thickenings (Fig. 16) and protrusions (Fig. 17) of the cell wall into the cytoplasm. Also observed were plasmodesmata, extraprotoplasmic sacs, paramural bodies, and membranous vesicles. The abnormalities included formation of multivesicular structures associated with the plasmalemma which were classified under the general term paramural bodies (29) regardless of origin. However, the origin and function of the paramural bodies is still unknown. In the primary acute stage of symptom response there were many paramural bodies containing variously extensive accumulation of vesicles and/or tubules between the plasmalemma and cell wall (Figs. 12-B, 15-A, 16-B). Sunken areas of the cytoplasm by the paramural body appeared to be a membrane-bound body separated from the ground cytoplasm. The plasmalemma bodering wall abnormalities was irregularly curved (Fig. 15-A). In some areas it appeared to be discontinuous or disrupted (Figs. 10, 11, 13). Ruptured membranes of the plasmalemma released the vesicles free into the area between the cell wall and plasmalemma. Many flattened and membranous tubules or vesicles, which appeared to be derived from the contents of paramural bodies, were scattered between the cell wall and plasmalemma (Figs. 13, 17-A). These irregular profiles of membranous vesicles lead me to conclude that such formations are not artifacts or contamination as a result of an analysis of similar structures described in published results (21,34). Presumably these cell

abnormalities due to plasmolysis represent the primary acute symptoms in infected tissue just before necrosis develops. Because the paramural bodies and cell wall outgrowths were present together at the same site, they appeared as the paramural bodies extended, and were closely associated with groups of vesicles or tubules of paramural bodies. I propose that paramural bodies may participate in the production of new cell wall material as wall thickenings. It was hypothesized that they might represent an enhanced activity of the plasmalemma, in relation to synthesis of extra cell wall material (6). McMullen et al. (34) agreed with this possible explanation. Paramural bodies and cell wall thickenings were suggested as a physical barrier to cell-to-cell movement of virus not only in the cells surrounding necrotic local lesions of local hosts (44,50), but also in the systemically infected tissues (20,21,34). However, the cell wall abnormalities in systemic infection might be a response to virus infection but were ineffective in blocking the systemic movement of virus particles (21). It is obvious from the present evidence that MDMV may stimulate the host cell to produce additional cell wall material in the formation of abnormalities in MDMV-A infected sorghum leaf tissue.

Extended plasmodesmata were membrane bound, terminated in bulbous protrusions, and contained no virus particles (Fig. 10). The protrusions were usually found between the plasmalemma and cell wall (Figs. 11, 15) while a few extended into cytoplasm (Fig. 13). Similar results have been reported in which these protrusions extended far into the cytoplasm (21). Finger-like wall projections (6) occurred both in

localized and in systemic infections. They were unusual structures associated with plasmodesmata and have been termed as "extended plasmodesmata" (34). Their number and size varied considerably according to the inducing virus (29). These elongated protrusions were not empty but contained plasmodesma-like channels (6) which often contained rows of virus particles (20). According to Bassi et al. (6) they may be channels of communication between adjacent cells. A similar concept was supported by Kim and Fulton (21). The Fig. 16-B demonstrates cell wall thickenings containing extended plasmodesmata associated with paramural bodies. Some cell wall outgrowths occured around the extended plasmodesmata. Kim and Fulton (21) suggested that formation of finger like projections of the plasmalemma may pass through the plasmodesmata and be transfered to the paramural bodies. This hypothesis strongly supports the view that cell wall outgrowths consist of new-wall material with a similarity in nature to tubules or bulbous terminals of extended plasmodesmata and they are continuous with the paramural bodies. Elongated plasmodesmata containing desmotubules (37) were often found (Fig. 11). Extended plasmodesmata (34) were similar to myelinic bodies (22) which were associated with tubules containing virus particles. My report of extended plasmodesmata with accompanying cell wall abnormalities and paramural bodies in HOK sorghum leaf tissue systemically infected with MDMV-A supports the hypothesis that these unusual structures are modified plasmodesmata.

Another kind of inclusion, extraprotoplasmic sac, containig aggregates of entangled virus particles associated with plasmodesmata,

was observed in cells from longitudinal sections of infected tissue (Fig. 9). The sac was located between the plasmalemma and cell wall, bound around membrane, and appeared to be associated with extended plasmodesmata at the same location along the cell wall. This sac was shown to be a closed structure completely excluded from the protoplast. Structures similar to extraprotoplasmic sacs were found with the contents of sacs empty (Figs. 13, 14). Such virus bundles were also observed in wheat streak mosaic virus infection (26). Extraprotoplasmic sac as a general term was reported previously (3,34). However, there were differences between contents of sacs described by Allison and Shalla (3) and those of McMullen et al (34). The former contained virus particles and it was suggested that they prevented intracellular movement of virus due to deposits of callose. The latter occured in the primary acute phase (32) of systemically infected tissue and did not contain virus particles, but small spherical granules. McMullen et al. (34) hypothesized that these structures were a protective response by the plant to restrict the movement of virus. The important function of these structures may involve cell-to-cell movement of viruses.

McMullen et al. (34) suggested that previous investigators could not find these cell wall abnormalities probably because they did not examine the primary acute stage of virus infection. Kim et al. (21) suggested the possibility of disappearance of cell wall abnormalities at a late stage of infection because of degeneration of cell wall protrusions. However, the relationship between these structures associated with cell wall abnormalities and plant virus infection are still unknown.

To my knowledge, no electron micrograph has been published confirming such an interpretation in sorghum or with a flexuous rod plant virus.

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KEY TO ABBREVIATIONS USED IN FIGURES

B	Bundle inclusions
Ch	Chloroplast limiting membranes
Cp	Plastid
Cr	Chromatin
De	Desmotubule
Ep	Extended plasmodesmata
ER	Endoplasmic Reticulum
Es	Extraprotoplasmic sac
G	Grana lamellae
IS	Intracellular space
LA	Laminated aggregates
M	Mitochondrion
Mb	Microbody
Ml	Middle lamella
MV	Membranous vesicles
N	Nucleus
Ne	Nuclear envelope
Nu	Nucleolus
P	Paramural body
Pd	Plasmodesma
Pl	Plasmalemma
PW	Pinwheel
R	Ribosome
RER	Rough Endoplasmic Reticulum
S	Scrolls
T	Tubes
V	Virus particles
Va	Vacuole
W	Cell wall
WP	Wall protrusion

Figure 1 : Occurrence of mosaic symptoms on the sorghum cultivar PAG 3385 infected with MDMV-A in the field at Brookings, SD in 1984.

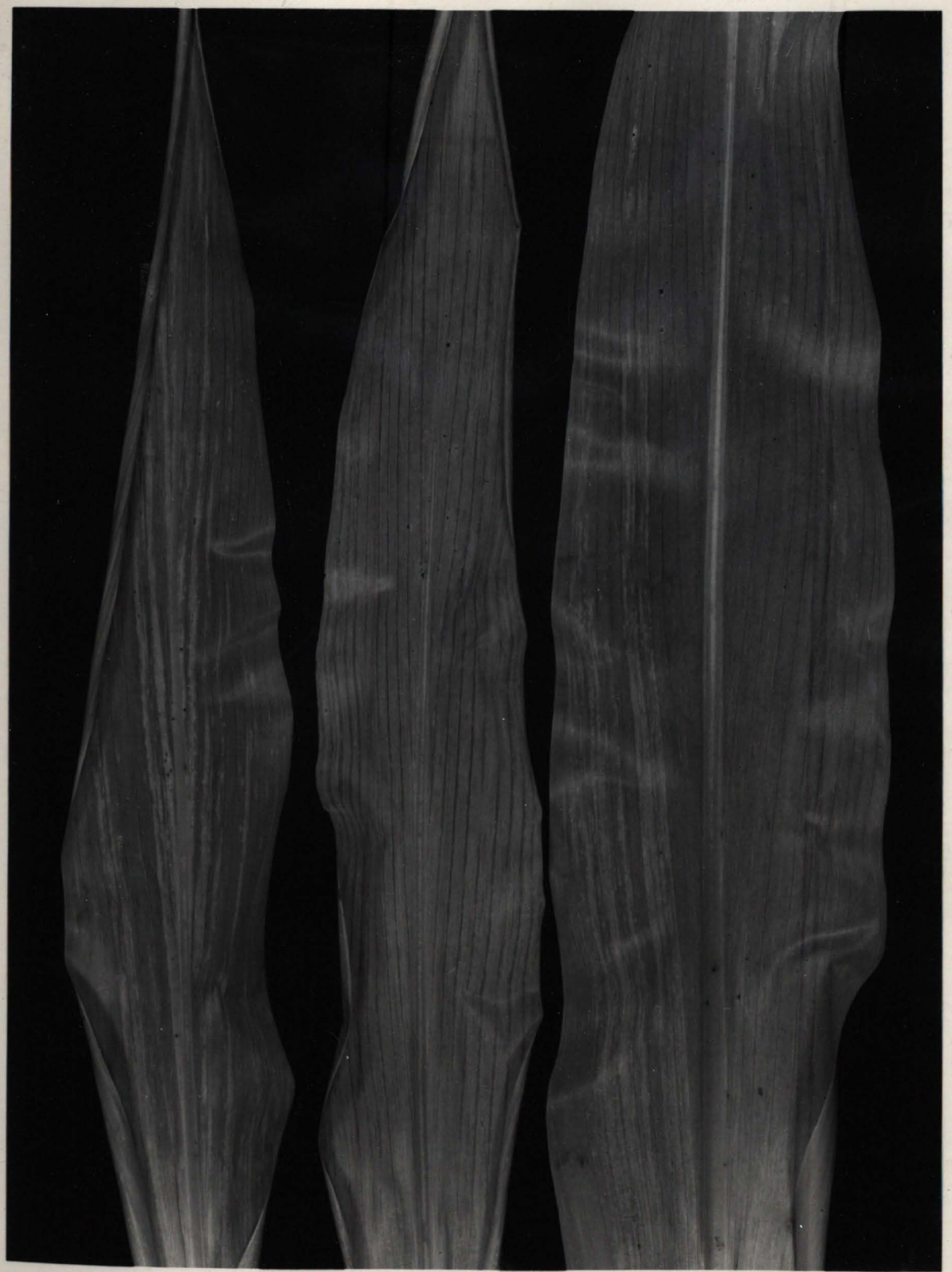


Figure 2 : Primary acute symptoms on the sorghum cultivar HOK inoculated with MDMV-A mechanically in the greenhouse. Chlorotic spots appeared at the base of the terminal whorl 5-7 days after inoculation.

Figure 3 : Symptoms on the sorghum cultivar HOK mechanically inoculated with MDMV-A. From the left leaf there are atypical and tiny local lesions, the central leaf shows mild mottle mosaic, and on the right a red leaf with chlorosis.

Figure 4 : Typical necrotic local lesions were produced on the sorghum cultivar HOK inoculated with MDMV-B mechanically. Healthy leaf (right), Infected leaf (left).

Figure 5 : Ultrastructure of chloroplasts and nucleus of HOK sorghum leaf cells infected with MDMV-A. The cell on the upper left contains pinwheels (arrow head), bundles (arrow) and a normal chloroplast with chloroplast limiting membranes. Normal C4 chloroplasts containing starch granules are present in the cells on the upper right. A normal nucleus containing chromatin is located in the cell on the lower left.


Ch4
S
G
Ch3
CM
W
Pl
Cr
Va
IS
N
1 µm

Figure 6 : Cylindrical inclusions in a sorghum leaf cell infected with MDMV-A.

A) Pinwheels, bundles, and scrolls are distributed randomly throughout the cytoplasm.

B) Portion of a sorghum leaf cell exhibiting a conglomeration of MDMV-A induced inclusions: PW, cross sectioned cylindrical inclusion; B, cylindrical inclusions in longitudinal section; S, cross sectional view of tubes; T, longitudinal section of pinwheel arms.

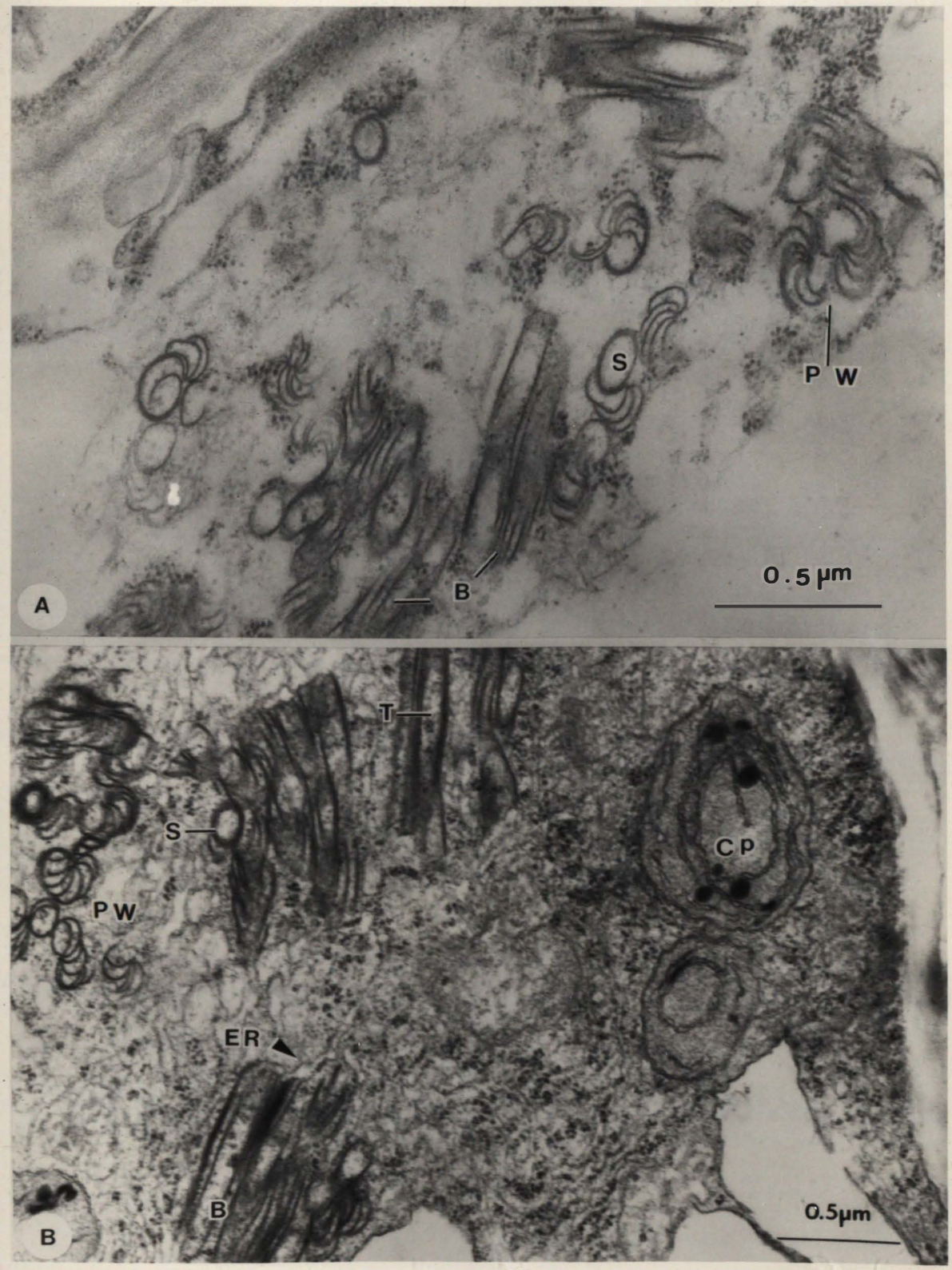

S
P W
B
0.5 µm
A
T
S
C P
P W
ER
B
0.5µm
B

Figure 7 : Areas between a chloroplast and a nucleus of a Pioneer 8680 sorghum leaf cell infected with MDMV-B are rich in various profiles of cytoplasmic virus inclusions: pinwheels, scrolls, laminated aggregates, and bundles. Note ends of bundles abutted against the plasmalemma and possibly contiguous with endoplasmic reticulum. Flexuous rod virus particles are evident in cells with abundant virus-induced inclusions.

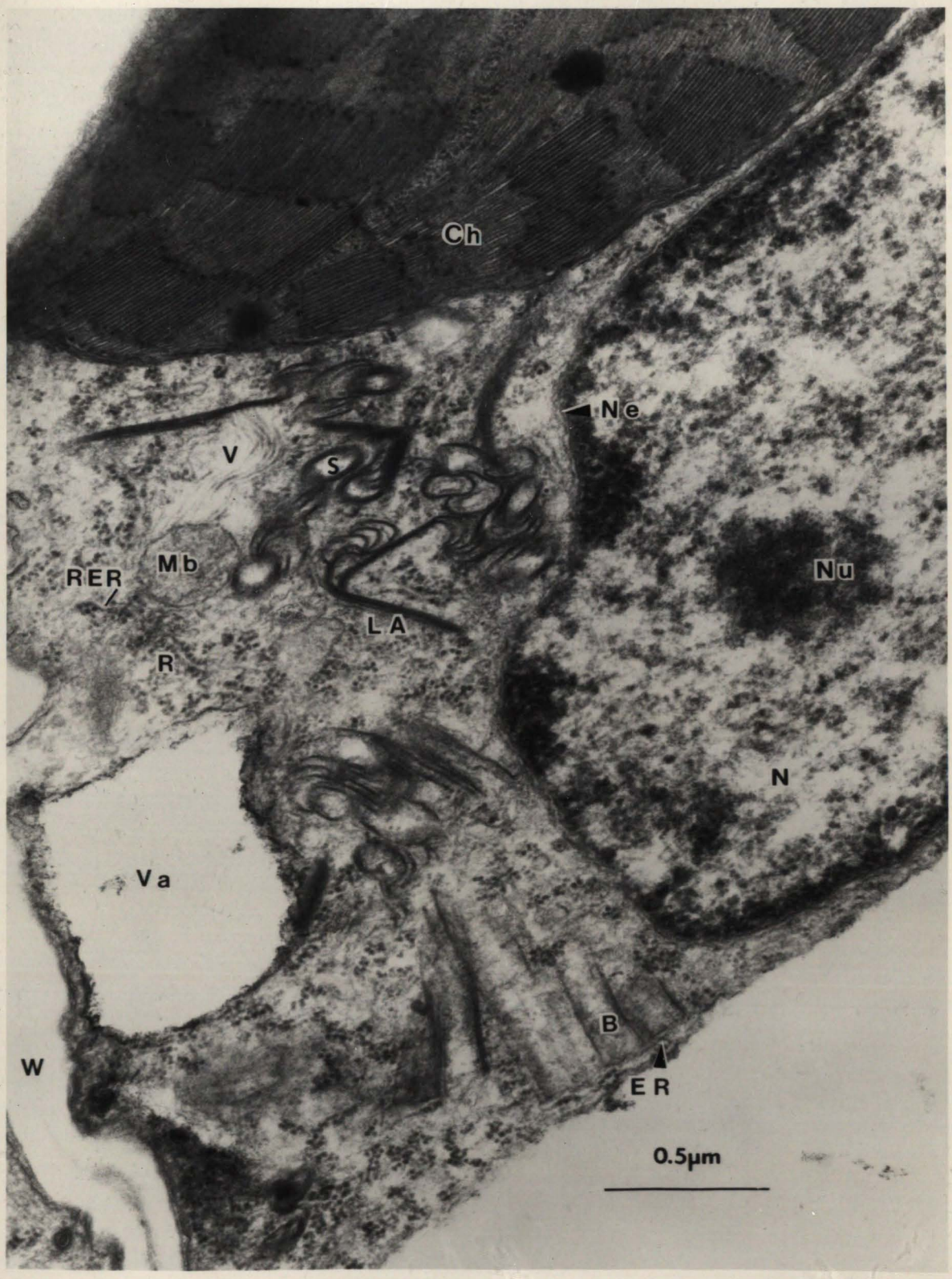

Ch
Ne
V
S
Mb
RER
LA
Nu
R
N
Va
B
W
ER
0.5µm

Figure 8 : Laminated aggregates in Pioneer 8680 sorghum tissue induced by MDMV-B show association with pinwheels (arrowheads).

A) Cylindrical inclusions in longitudinal section. Fine structure of laminated aggregates, consists of closely associated parallel plates.

B) Electron micrograph of MDMV-B infected Pioneer 8680 sorghum leaf cell showing cylindrical inclusions with some laminated aggregates in different planes of sectioning.

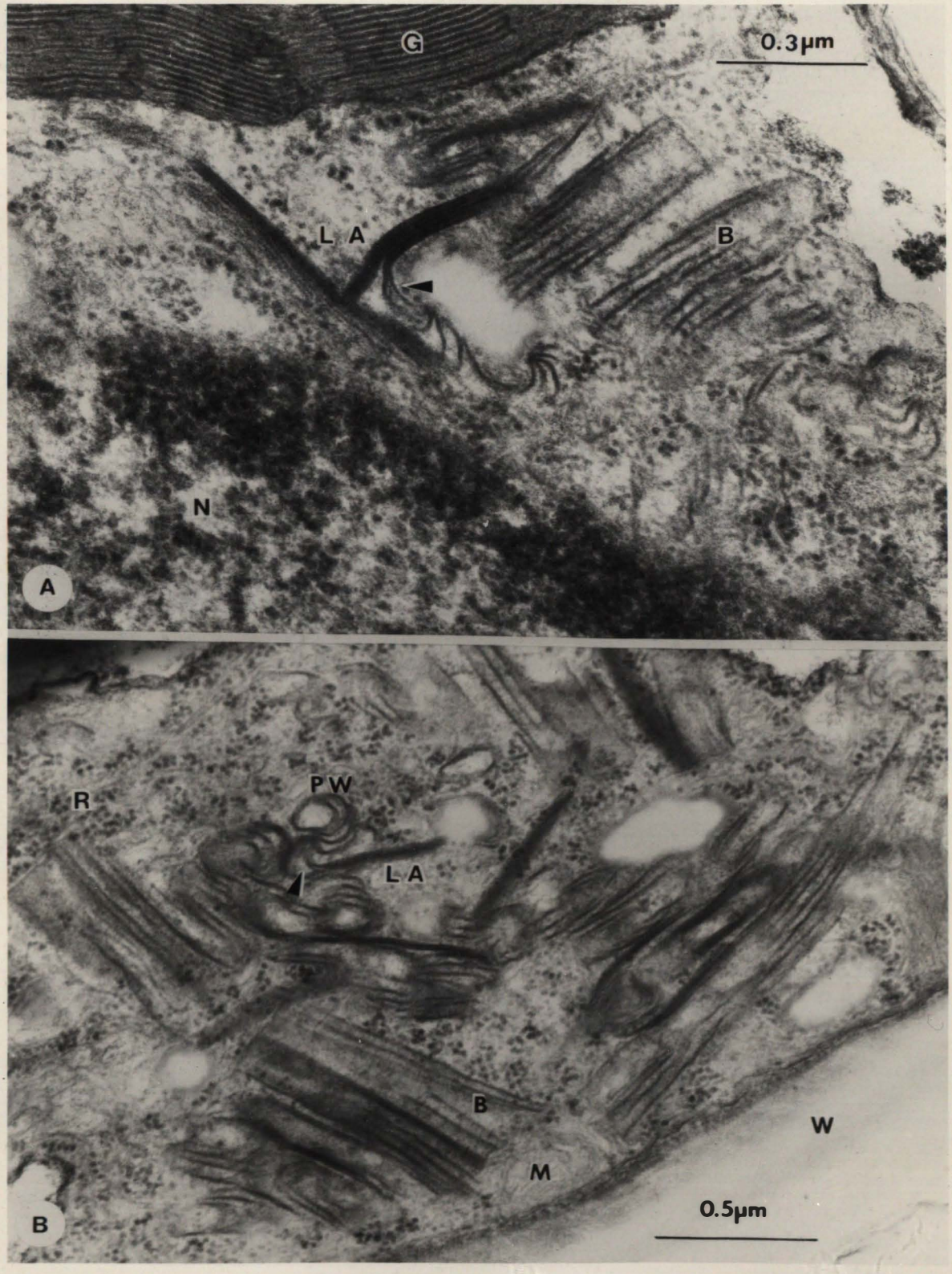

G
0.3μm
L A
B
N
A
PW
R
L A
B
W
M
0.5μm
B

Figure 9 : Longitudinal section through extraprotoplasmic sacs and association with extended plasmodesmata in HOK sorghum leaf infected with MDMV-A. Note the rod-shaped MDMV particles within the the extraprotoplasmic sac and limiting membrane of the sac is not continuous with the plasmalemma.

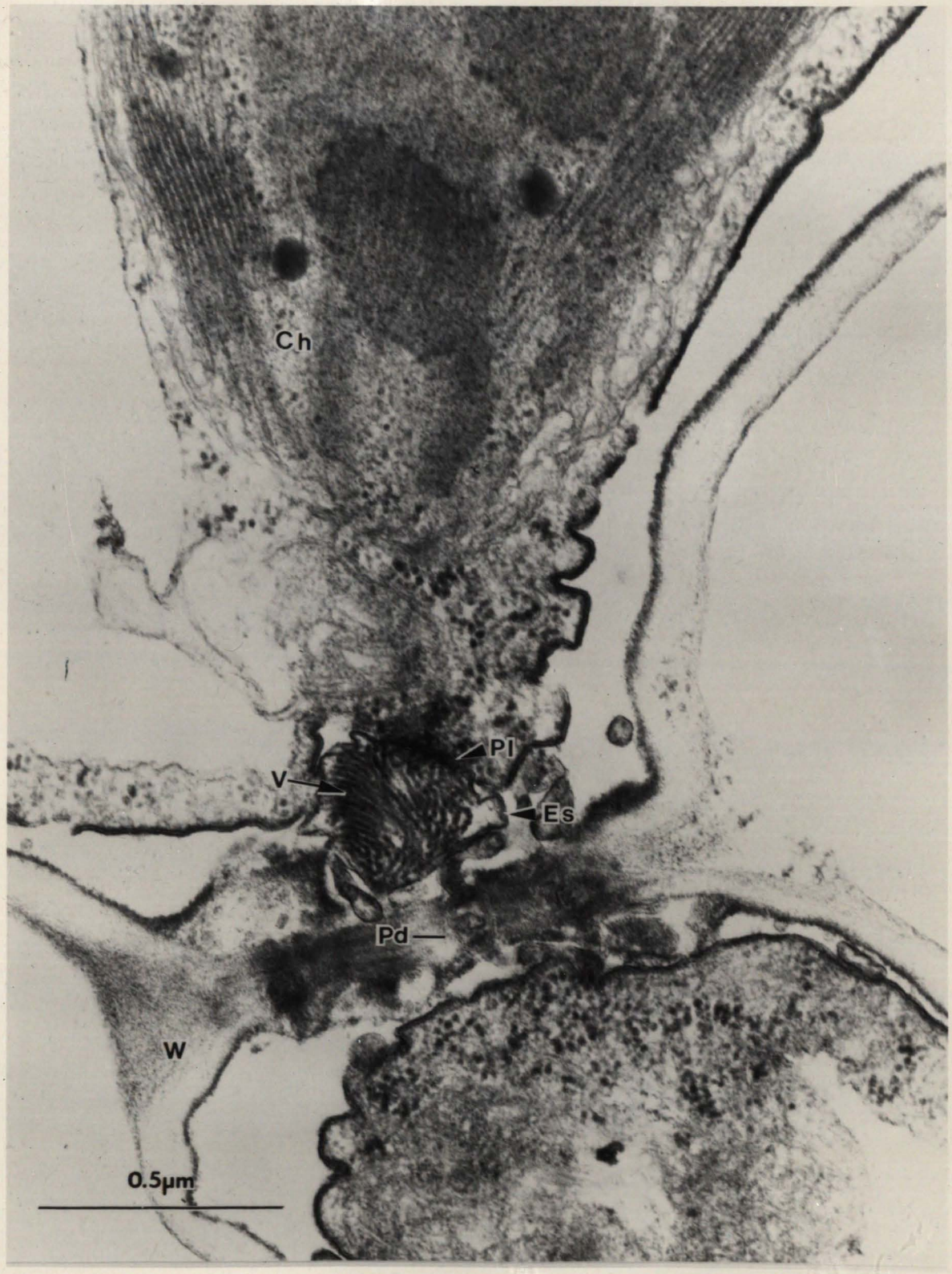

Ch
Pl
V
Es
Pd
W
0.5μm

Figure 10 : Ultrastructure of primary acute tissue in HOK sorghum leaf infected with MDMV-A. Note bulbous-shaped extended plasmodesmata and cell-wall outgrowths (unlabeled arrow). The areas between stars show dissolution of the plasmalemma.

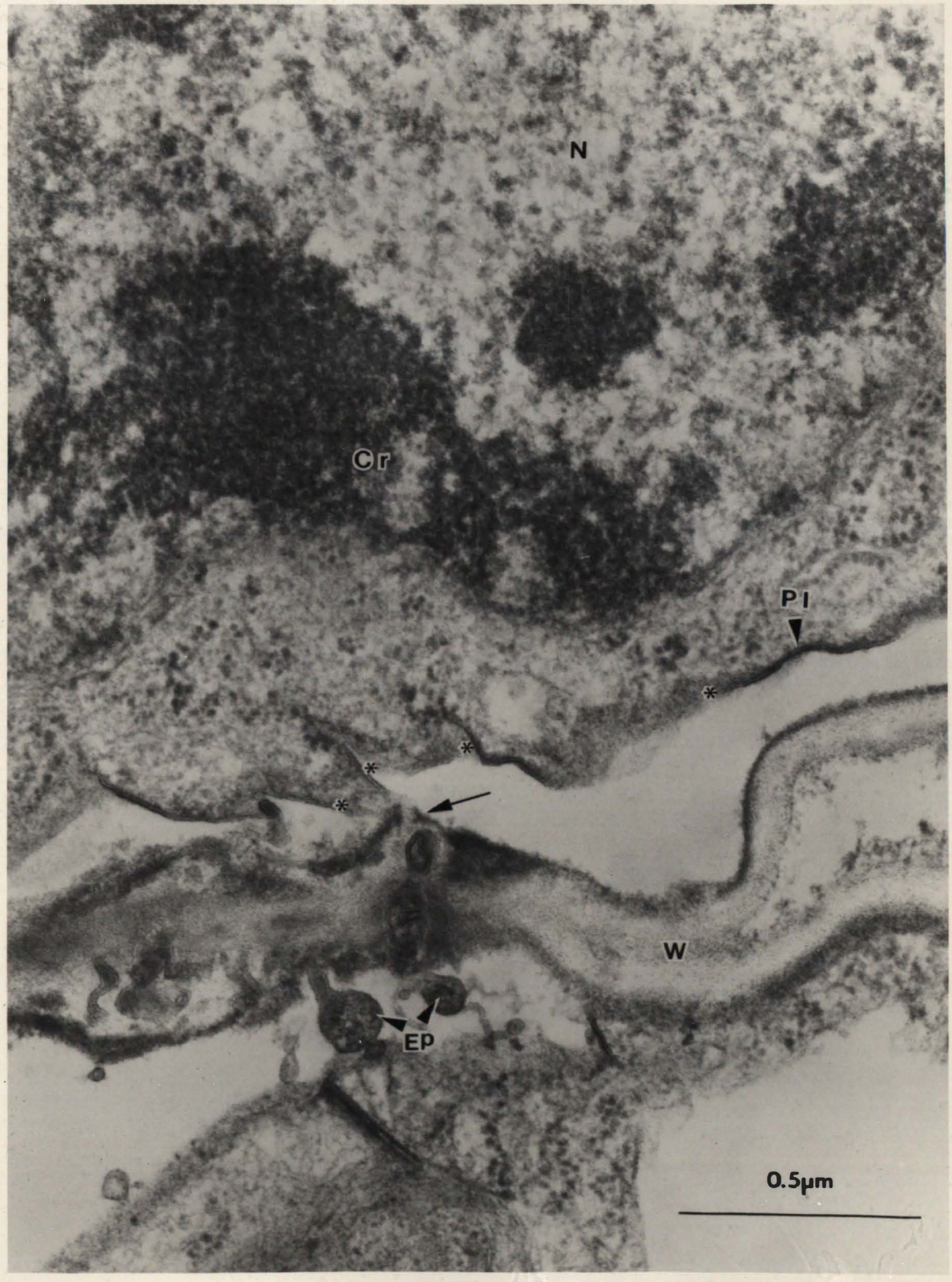

N
Cr
Pl
W
Ep
0.5µm

Figure 11 : Electron micrograph showing cell-wall outgrowths (unlabeled arrowheads) associated with plasmodesmata. Note extended plasmodesmata (unlabeled arrow) terminated in bulbous protrusions and the ruptured plasmalemma (stars).

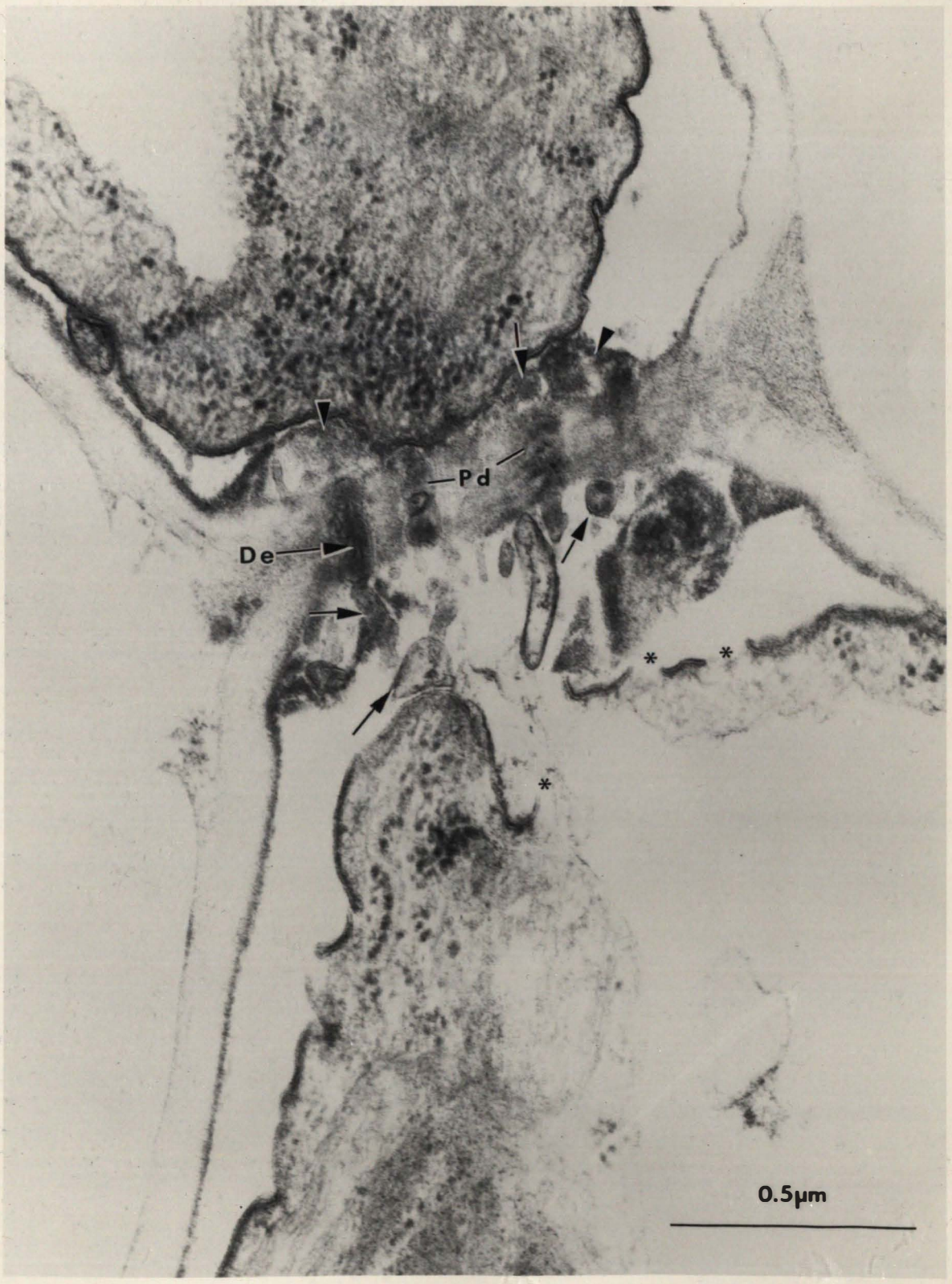

Pd
De
*
*
*
0.5µm

Figure 12 : Paramural bodies containing flattened tubules and vesicles associate with plasmodesmata in the primary acute stage of HOK sorghum leaf tissue infected with MDMV-A.

A) Paramural bodies and membranous vesicles (unlabeled arrwheads) are present between the plasmalemma and the cell wall.

B) Paramural bodies are associated with extended plasmodesmata (unlabeled arrowheads).

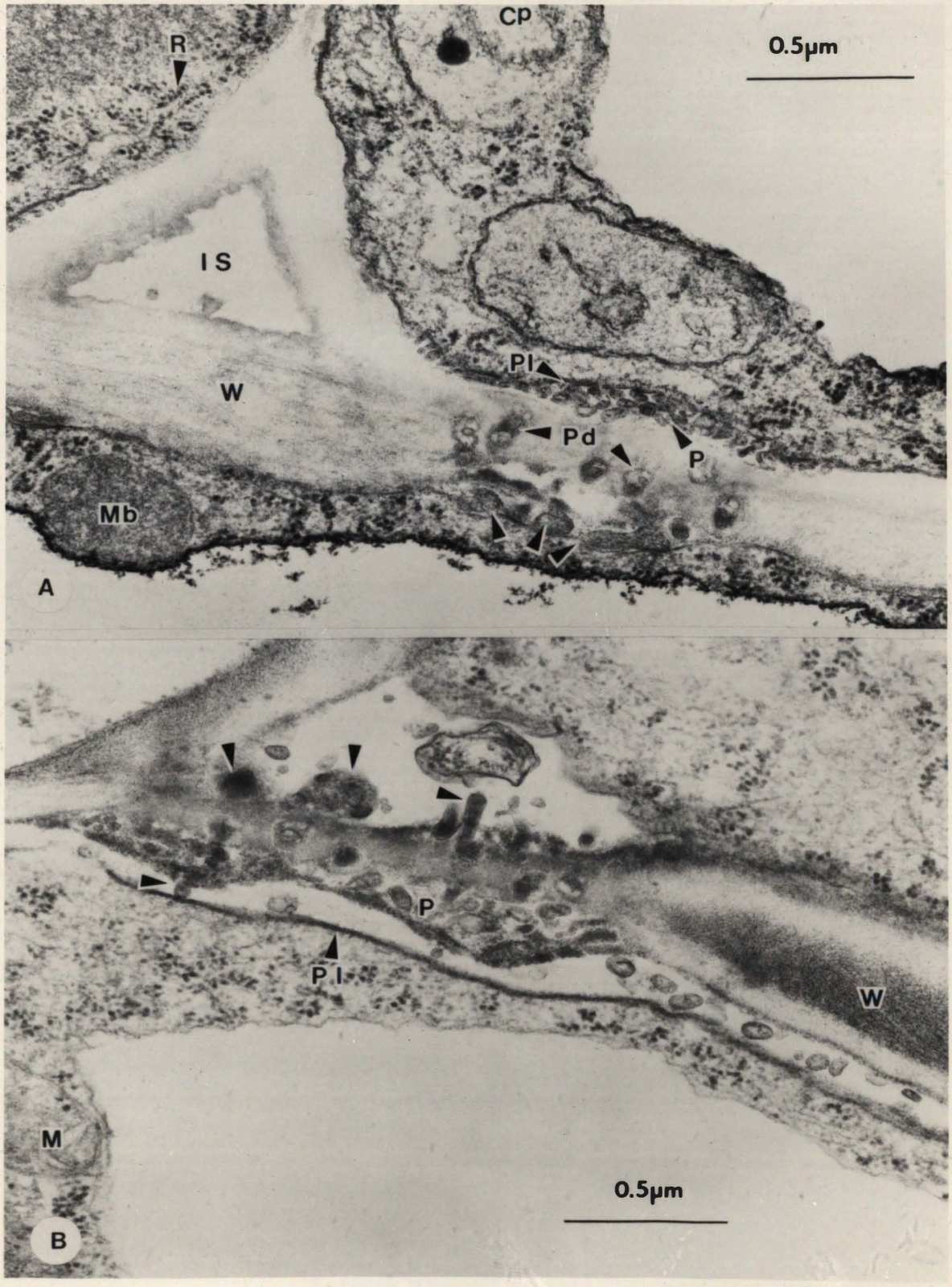

Cp
R
0.5μm
IS
Pl
W
Pd
P
Mb
A
P
Pl
W
M
0.5μm
B

Figure 13 : Ultrastructure of HOK sorghum leaf cell infected with MDMV-A shows ruptured plasmalemma and membranous vesicles. Note the projection of cell wall material into cytoplasm (unlabeled arrowhead). Note the empty extraprotoplasmic sac (star) and extended plasmodesmata into cytoplasm.

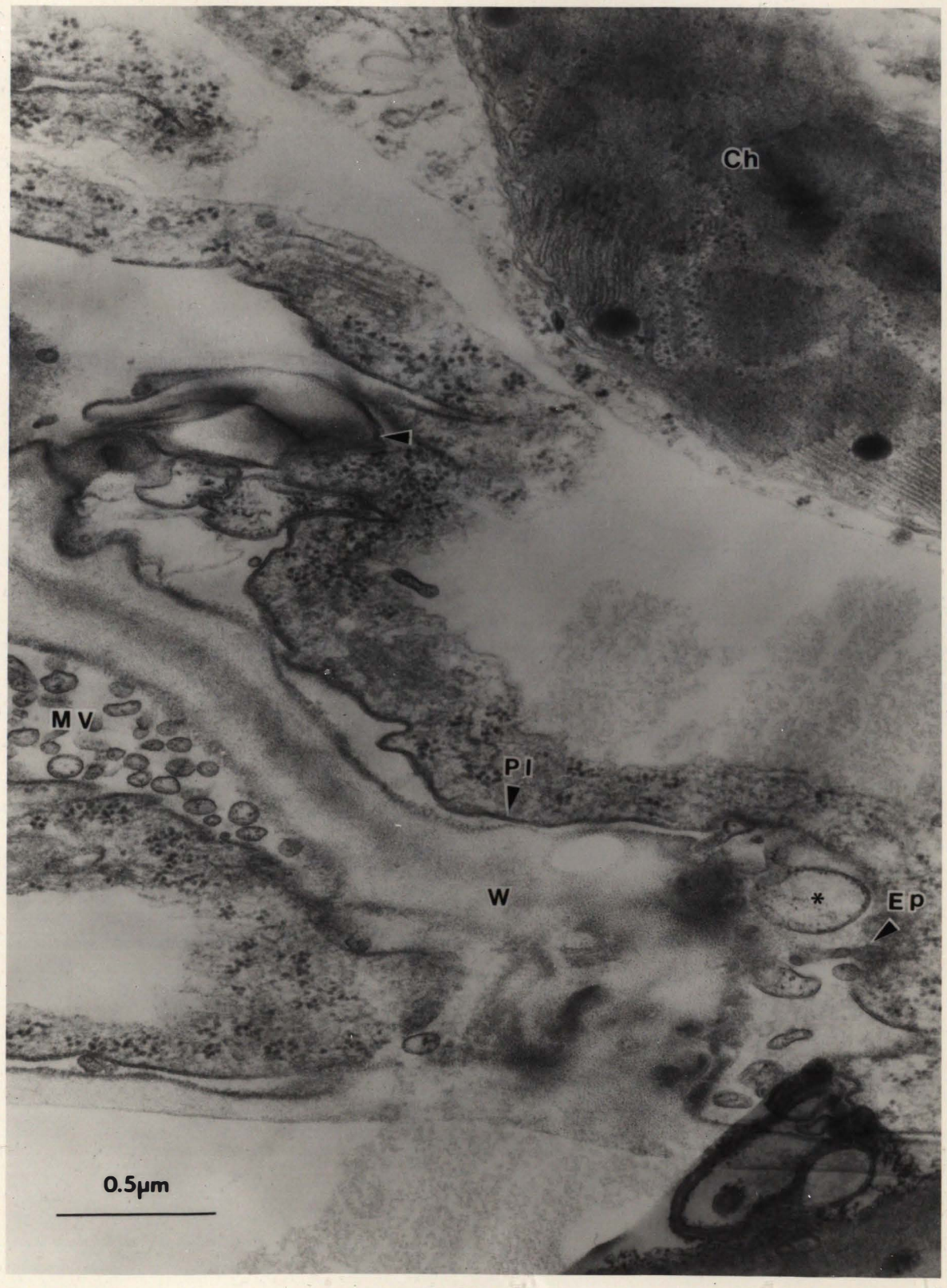

Ch
MV
Pl
W
*
Ep
0.5µm

Figure 14 : Ultrastructure of unusual cell wall abnormalities involving paramural bodies, extended plasmodesmata, and extraprotoplasmic sacs. Unlabeled arrow locates an intermediate shape between the extraprotoplasmic sac with contents and the empty extraprotoplasmic sac (stars), located between the plasmalemma and the cell wall.

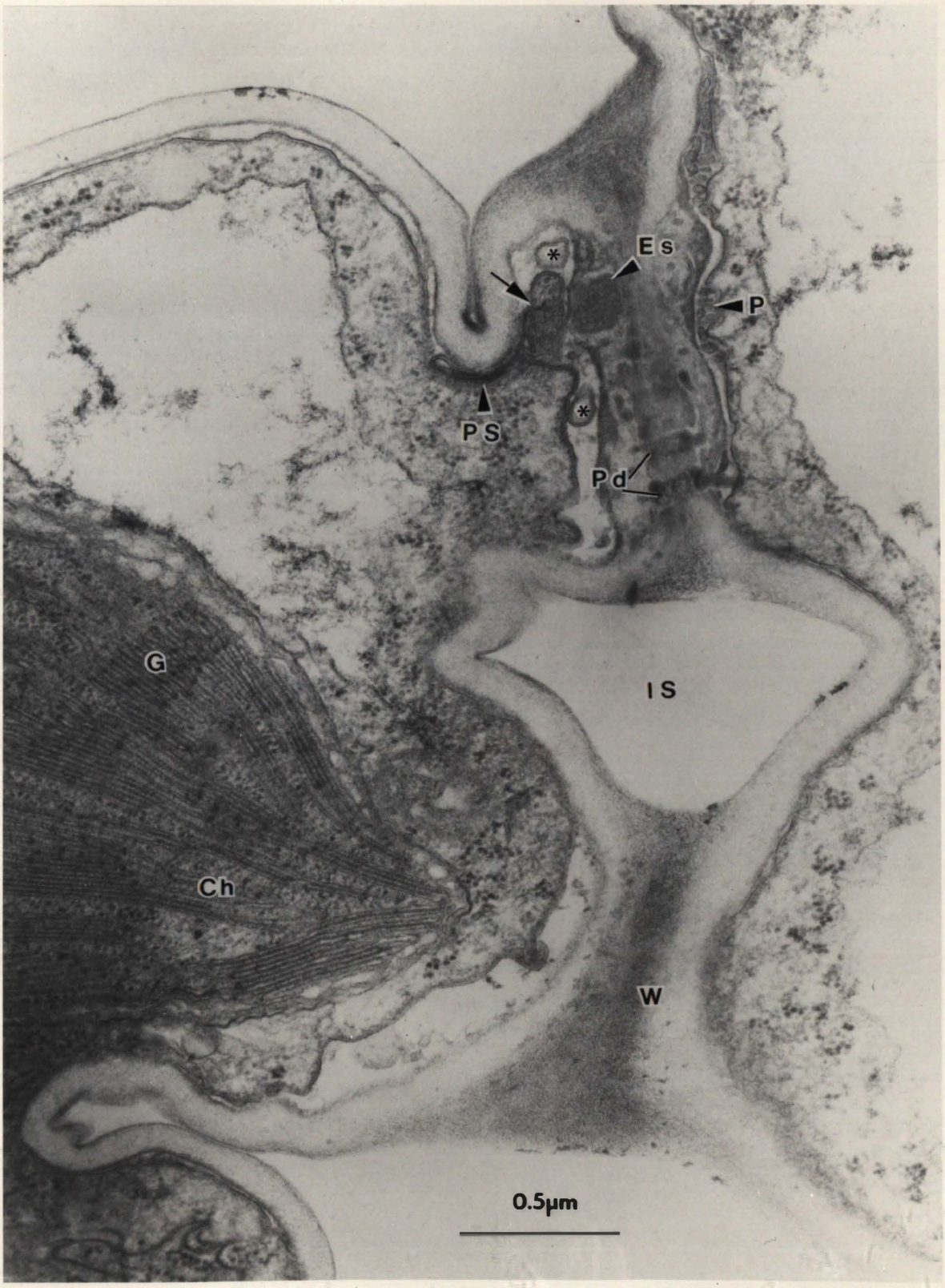

Es
P
PS
Pd
G
IS
Ch
W
0.5μm

Figure 15 : Sunken areas of plasmalemma by the paramural bodies associated with extended plasmodesmata.

A) Note the numerous extended plasmodesmata (unlabeled arrowheads) related with formation of paramural bodies.

B) cell wall outgrowths associated with extended plasmodesmata which are located in the area between the plasmalemma and cell wall.

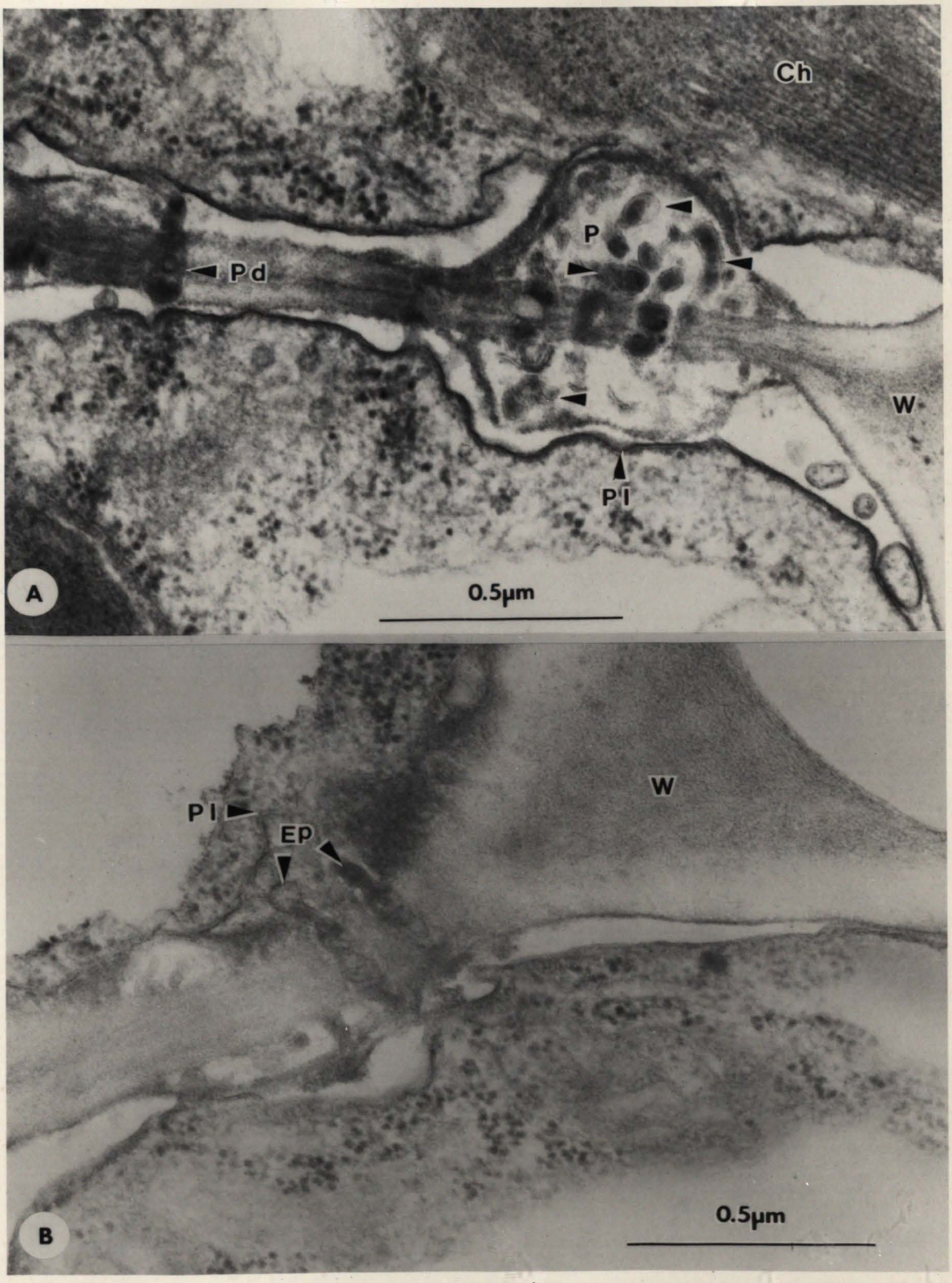

Ch
P
Pd
W
Pl
A
0.5µm
W
Pl
Ep
B
0.5µm

Figure 16 : Cross section of a modified plasmodesmata field showing cell wall abnormalities in HOK sorghum leaf tissues infected with MDMV-A.

A) Cell wall thickenings associated with various sized extended plasmodesmata.

B) Cell wall abnormalities accompanying paramural bodies at both sides of the cell wall. The vesicles and tubules of paramural bodies are associated with extended plasmodesmata.

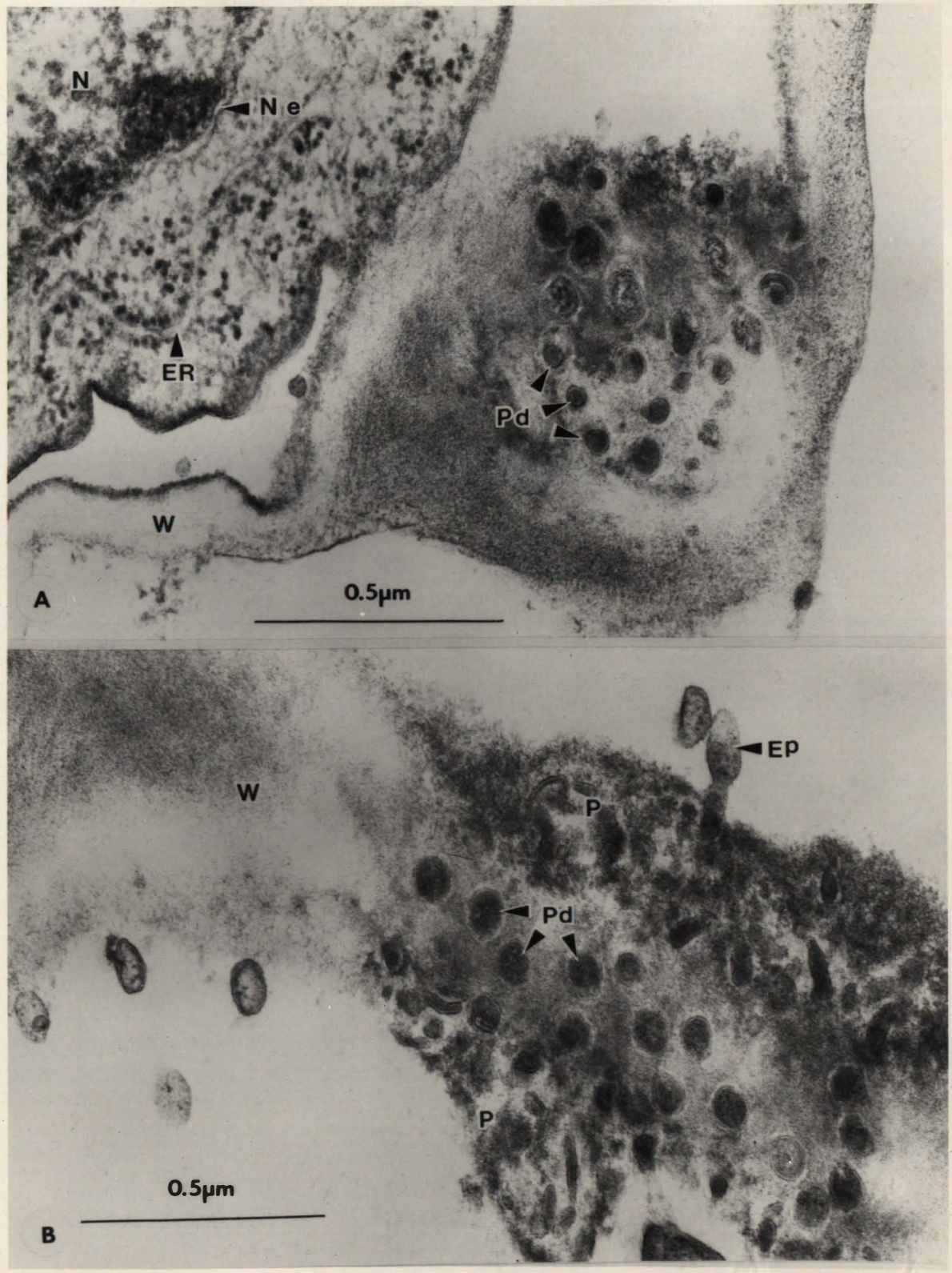
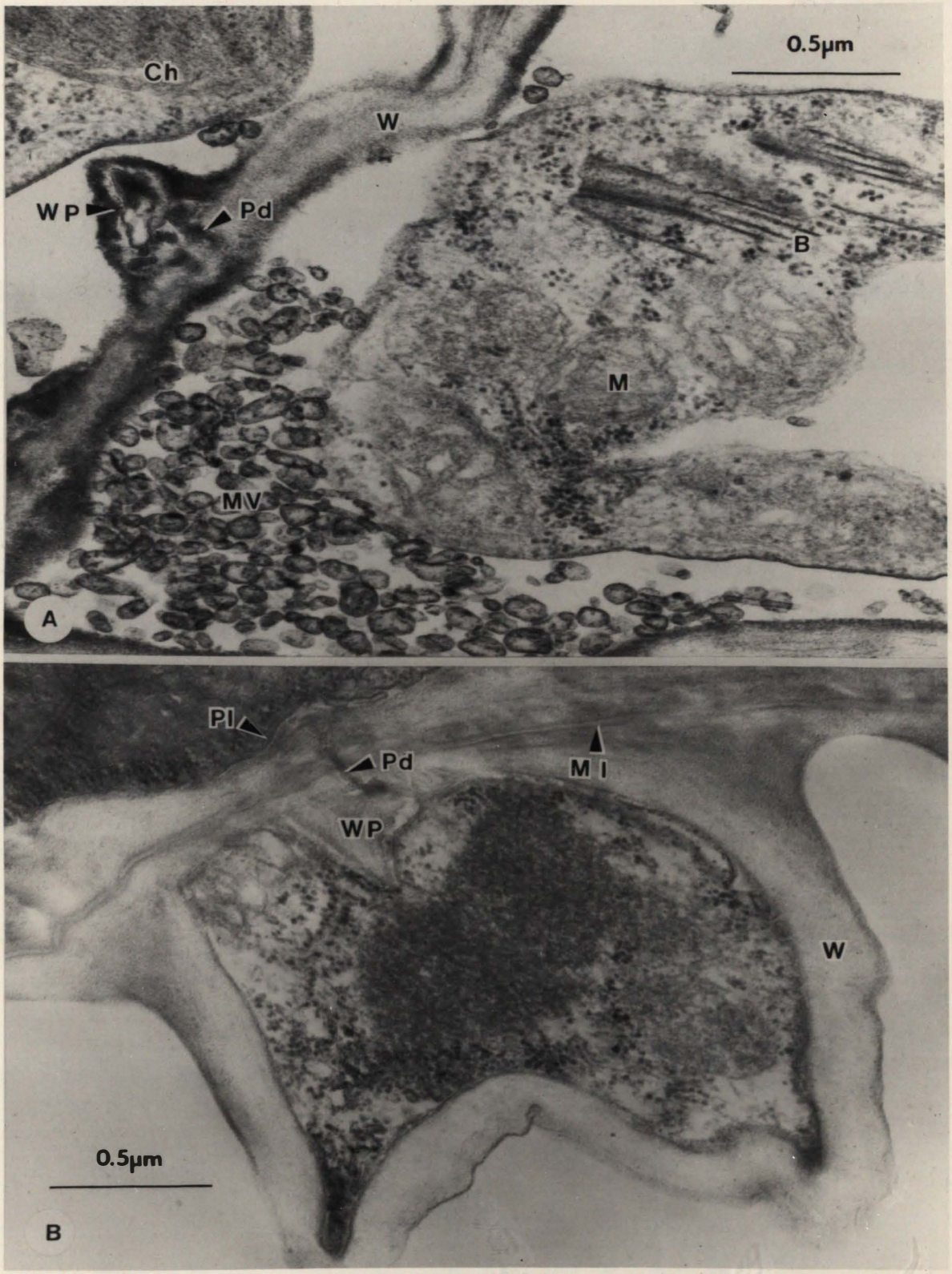

N
Ne
ER
Pd
W
A
0.5µm
W
Ep
P
Pd
P
0.5µm
B

Figure 17 : Cell wall protrusions induced by MDMV-A in HOK sorghum leaves are associated with plasmodesmata.

A) Cell wall protrusions in primary acute stage contain vesicles and tubules associated with plasmodesmata. Note the conglomeration of membranous vesicles.

B) A primary acute stage of virus-induced protrusions of the cell wall into the cytoplasm.


Ch
W
0.5µm
WP
Pd
B
M
MV
A
Pl
Pd
MI
WP
W
0.5µm
B

APPENDICES

APPENDIX A

Disease severity ratings for 38 sorghum hybrids inoculated with MDMV-A.

Hybrids	Rating	Days after inoculation						
		3	6	9	12	15	18	21
Asgrow Corral	0	20*	18	13	10	8	8	8
	1	0	2	7	5	2	1	0
	2	0	0	0	5	10	11	10
	3	0	0	0	0	0	0	2
Asgrow Dorado E	0	20	17	14	11	10	10	10
	1	0	3	3	3	2	0	0
	2	0	0	3	6	7	7	7
	3	0	0	0	0	1	3	3
Asgrow Mesa	0	20	18	12	10	9	9	9
	1	0	2	6	2	1	0	0
	2	0	0	2	8	8	7	6
	3	0	0	0	0	2	4	5
Cenex 224	0	20	20	11	10	10	10	10
	1	0	0	9	1	1	0	0
	2	0	0	0	9	5	4	3
	3	0	0	0	0	4	6	7
Cenex 226	0	20	17	10	6	6	6	6
	1	0	3	7	4	0	0	0
	2	0	0	3	8	9	9	8
	3	0	0	0	2	5	5	6
Cenex 228	0	20	20	15	12	12	12	12
	1	0	0	5	3	0	0	0
	2	0	0	0	5	7	7	7
	3	0	0	0	0	1	1	1
Cenex 230	0	20	17	14	9	9	9	9
	1	0	3	3	5	0	0	0
	2	0	0	3	6	10	10	10
	3	0	0	0	0	1	1	1
Cenex 310	0	20	13	9	6	5	5	5
	1	0	7	5	3	1	0	0
	2	0	0	6	9	8	7	7
	3	0	0		2	6	8	8
Dekalb DK-38	0	20	19	12	7	7	7	7

	1	0	1	7	6	1	0	0
	2	0	0	1	7	12	13	13
	3	0	0	0	0	0	0	0
Dekalb DK-39Y	0	20	18	6	5	5	5	5
	1	0	2	13	6	0	0	0
	2	0	0	1	9	14	9	6
	3	0	0	0	0	1	6	9
Dekalb X-538	0	19	17	11	9	9	9	9
	1	1	3	6	3	0	0	0
	2	0	0	3	7	10	8	7
	3	0	0	0	1	1	3	4
Dekalb X-550	0	20	20	17	14	14	14	14
	1	0	0	3	3	1	0	0
	2	0	0	0	3	5	6	6
	3	0	0	0	0	0	0	0
Funks G-251	0	20	12	10	7	7	7	7
	1	0	8	4	4	2	0	0
	2	0	0	6	7	7	8	7
	3	0	0	0	2	4	5	6
Funks G-421	0	20	15	9	7	5	5	5
	1	0	5	6	3	2	0	0
	2	0	0	5	8	9	9	9
	3	0	0	0	2	4	6	6
Funks HW5883	0	20	16	10	6	6	6	6
	1	0	4	8	5	0	0	0
	2	0	0	2	9	14	11	10
	3	0	0	0	0	0	3	4
Hoegemeyer GT620	0	20	18	15	13	11	11	11
	1	0	2	3	2	2	0	0
	2	0	0	2	5	6	7	7
	3	0	0	0	0	1	2	2
Hoegemeyer 606	0	20	13	10	7	7	7	7
	1	0	7	4	4	0	0	0
	2	0	0	6	8	9	5	4
	3	0	0	0	1	4	8	9
Keltgen KG57T	0	20	20	9	4	3	3	3
	1	0	0	11	6	1	0	0
	2	0	0	0	10	16	17	13
	3	0	0	0	0	0	0	4
Keltgen KG63T	0	20	18	13	8	8	8	8
	1	0	2	5	6	0	0	0
	2	0	0	2	6	12	7	6
	3	0	0	0	0	0	5	6
McCurdy M51YG	0	20	19	13	10	10	10	10
	1	0	1	6	6	1	0	0
	2	0	0	1	4	9	10	10
	3	0	0	0	0	0	0	0
McCurdy M410	0	20	20	12	8	8	8	8
	1	0	0	8	5	0	0	0
	2	0	0		7	12	12	9
	3	0	0	0	0	0	0	3

McCurdy M450	0	20	17	9	7	7	7	7
	1	0	3	8	2	0	0	0
	2	0	0	3	11	6	4	3
	3	0	0	0	0	7	9	10
McCurdy M687	0	17	15	13	8	8	8	8
	1	3	3	2	6	0	0	0
	2	0	2	5	6	10	9	8
	3	0	0	0	0	2	3	4
NK 1210	0	20	16	11	10	10	10	10
	1	0	4	6	3	0	0	0
	2	0	0	3	7	9	8	8
	3	0	0	0	0	1	2	2
NK 2030	0	20	18	14	13	11	11	11
	1	0	2	4	1	2	0	0
	2	0	0	2	6	7	6	6
	3	0	0	0	0	3	4	4
NK 2244	0	18	18	14	10	8	8	8
	1	2	2	4	4	2	0	0
	2	0	0	2	6	7	8	8
	3	0	0	0	0	3	4	4
Pay Master 930	0	19	17	13	10	9	9	9
	1	1	2	4	4	1	0	0
	2	0	1	3	5	7	6	5
	3	0	0	0	1	3	5	6
Pay Master 1022	0	20	11	8	8	8	8	8
	1	0	9	5	1	0	0	0
	2	0	0	7	11	5	2	2
	3	0	0	0	0	7	10	10
Seed Tec. 8501	0	20	20	14	12	12	12	12
	1	0	0	6	4	0	0	0
	2	0	0	0	4	8	8	8
	3	0	0	0	0	0	0	0
Seed Tec. 8502	0	20	15	9	7	6	6	6
	1	0	5	6	2	1	0	0
	2	0	0	5	9	8	7	5
	3	0	0	0	2	5	7	9
Seed Tec. 8503	0	18	10	10	8	8	8	8
	1	2	8	2	2	0	0	0
	2	0	2	8	7	6	5	4
	3	0	0	0	3	6	7	8
Sigco 46YG	0	16	9	7	6	6	6	6
	1	4	8	2	1	0	0	0
	2	0	3	11	6	5	3	2
	3	0	0	0	7	9	11	12
Warner W-501T	0	18	16	8	6	6	6	6
	1	2	3	8	3	0	0	0
	2	0	1	4	8	5	3	2
	3	0	0	0	3	9	11	12
Warner W-523T	0	16	11	8	7	7	7	7
	1	4	5	3	2	0	0	0
	2	0	4	6	6	5	3	3

	3	0	0	3	5	8	10	10
Warner W-551A	0	17	9	7	7	7	7	7
	1	3	9	4	0	0	0	0
	2	0	2	9	10	7	5	4
	3	0	0	0	3	6	8	9
Warner W-560T	0	19	15	10	9	9	9	9
	1	1	5	5	1	0	0	0
	2	0	0	5	9	8	4	3
	3	0	0	0	1	3	7	8
Western WS-203	0	13	9	6	6	6	6	6
	1	7	5	3	0	0	0	0
	2	0	6	11	10	5	2	2
	3	0	0	0	4	9	12	12
Western WS-212	0	20	13	9	9	9	9	9
	1	0	7	5	0	0	0	0
	2	0	0	6	10	6	3	2
	3	0	0	0	1	5	8	9

* 20 plants of each hybrid inoculated with MDMV-A. Values reflect the total number of plants with a given rating on a given day.

APPENDIX B

Disease severity ratings for 38 sorghum hybrids inoculated with MDMV-B.

Hybrids	Rating	Days after inoculation						
		3	6	9	12	15	18	21
Asgrow Corral	0	20*	19	19	12	8	8	8
	1	0	1	1	8	12	12	12
	2	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0
Asgrow Dorado E	0	20	17	14	6	6	5	5
	1	0	3	5	11	8	9	9
	2	0	0	1	3	6	6	6
	3	0	0	0	0	0	0	0
Asgrow Mesa	0	20	20	19	7	6	6	6
	1	0	0	1	13	11	9	9
	2	0	0	0	0	3	5	5
	3	0	0	0	0	0	0	0
Cenex 224	0	20	20	19	10	4	4	4
	1	0	0	1	10	16	15	15
	2	0	0	0	0	0	1	1
	3	0	0	0	0	0	0	0
Cenex 226	0	20	17	12	10	10	10	10
	1	0	3	8	10	8	7	7
	2	0	0	0	0	2	3	3
	3	0	0	0	0	0	0	0
Cenex 228	0	20	19	13	10	10	9	9
	1	0	1	7	10	8	9	9
	2	0	0	0	0	2	2	2
	3	0	0	0	0	0	0	0
Cenex 230	0	20	13	11	2	2	2	2
	1	0	7	5	8	7	7	7
	2	0	0	4	7	5	4	4
	3	0	0	0	3	6	7	7
Cenex 310	0	20	16	14	4	3	3	3
	1	0	4	5	13	11	9	9
	2	0	0	1	2	3	5	4
	3	0	0	0	1	3	3	4
Dekalb DK-38	0	20	16	12	11	4	4	4
	1	0	4	5	5	11	8	8
	2	0	0	3	4	5	6	5
	3	0	0	0	0	0	2	3
Dekalb DK-39Y	0	20	20	18	11	9	9	9
	1	0	0	2	9	9	9	9
	2	0	0	0	0	2	2	1

	3	0	0	0	0	0	0	1
Dekalb X-538	0	20	20	16	11	9	9	9
	1	0	0	4	9	6	6	6
	2	0	0	0	0	5	5	5
	3	0	0	0	0	0	0	0
Dekalb X-550	0	20	19	14	10	8	8	8
	1	0	1	6	10	12	12	12
	2	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0
Funks G-251	0	20	17	11	4	2	2	2
	1	0	3	7	11	8	6	5
	2	0	0	2	5	8	8	9
	3	0	0	0	0	2	4	4
Funks G-421	0	20	20	18	7	6	6	6
	1	0	0	2	13	8	8	8
	2	0	0	0	0	6	6	6
	3	0	0	0	0	0	0	0
Funks HW5883	0	20	20	20	16	8	8	8
	1	0	0	0	4	11	10	10
	2	0	0	0	0	1	2	2
	3	0	0	0	0	0	0	0
Hoegemeyer GT620	0	20	15	9	7	3	3	3
	1	0	5	8	4	4	4	4
	2	0	0	2	7	8	8	6
	3	0	0	1	2	5	5	7
Hoegemeyer 606	0	20	20	20	16	10	9	9
	1	0	0	0	4	8	9	9
	2	0	0	0	0	2	2	2
	3	0	0	0	0	0	0	0
Keltgen KG57T	0	20	20	15	10	9	9	9
	1	0	0	5	8	5	5	5
	2	0	0	0	2	6	6	6
	3	0	0	0	0	0	0	0
Keltgen KG63T	0	20	18	10	5	4	4	4
	1	0	2	10	10	5	5	5
	2	0	0	0	5	11	10	5
	3	0	0	0	0	0	1	6
McCurdy M51YG	0	20	20	20	11	10	10	10
	1	0	0	0	9	8	8	7
	2	0	0	0	0	1	0	1
	3	0	0	0	0	1	2	2
McCurdy M410	0	20	18	15	5	5	5	5
	1	0	2	4	14	10	8	8
	2	0	0	1	1	4	5	4
	3	0	0	0	0	1	2	3
McCurdy M450	0	20	19	18	11	10	10	10
	1	0	1	2	8	7	7	7
	2	0	0	0	1	3	3	3
	3	0	0	0	0	0	0	0
McCurdy M687	0	20	20	19	19	19	19	19
	1	0	0	1	1	1	1	1

	2	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0
NK 1210	0	20	20	20	18	17	17	17
	1	0	0	0	2	3	3	3
	2	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0
NK 2030	0	20	20	20	17	12	12	12
	1	0	0	0	3	8	8	8
	2	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0
NK 2244	0	20	17	14	11	9	9	9
	1	0	3	6	7	8	7	7
	2	0	0	0	2	2	2	2
	3	0	0	0	0	1	2	2
Pay Master 930	0	20	20	17	6	5	5	5
	1	0	0	3	11	9	7	7
	2	0	0	0	3	4	6	5
	3	0	0	0	0	2	2	3
Pay Master 1022	0	20	13	1	1	1	1	1
	1	0	7	10	3	1	0	0
	2	0	0	9	13	12	10	10
	3	0	0	0	3	6	9	9
Seed Tec. 8501	0	20	13	8	4	3	3	3
	1	0	7	12	14	10	10	10
	2	0	0	0	2	7	7	7
	3	0	0	0	0	0	0	0
Seed Tec. 8502	0	20	19	16	15	15	15	15
	1	0	1	4	5	1	1	1
	2	0	0	0	0	4	4	4
	3	0	0	0	0	0	0	0
Seed Tec. 8503	0	20	12	8	3	3	3	3
	1	0	8	7	8	3	3	3
	2	0	0	5	9	14	14	12
	3	0	0	0	0	0	0	2
Sigco 46YG	0	20	17	10	6	6	6	6
	1	0	3	9	13	9	9	9
	2	0	0	1	1	5	5	5
	3	0	0	0	0	0	0	0
Warner W-501T	0	20	20	14	7	6	6	6
	1	0	0	6	9	9	5	5
	2	0	0	0	4	5	9	9
	3	0	0	0	0	0	0	0
Warner W-523T	0	20	19	15	14	12	12	12
	1	0	1	5	5	5	5	5
	2	0	0	0	1	3	3	3
	3	0	0	0	0	0	0	0
Warner W-551A	0	20	17	13	4	4	4	4
	1	0	3	1	8	4	4	4
	2	0	0	6	8	12	12	12
	3	0	0	[illegible]	0	0	0	0
Warner W560T	0	20	19	10	3	2	2	2

	1	0	1	10	13	8	8	8
	2	0	0	0	4	10	10	10
	3	0	0	0	0	0	0	0
Western WS-203	0	20	19	15	7	2	2	2
	1	0	1	5	9	7	5	5
	2	0	0	0	4	11	13	13
	3	0	0	0	0	0	0	0
Western WS-212	0	20	15	12	5	5	5	5
	1	0	5	7	12	10	10	10
	2	0	0	1	2	4	4	4
	3	0	0	0	1	1	1	1

* 20 plants of each hybrid inoculated with MDMV-B. Values reflect the total number of plants with a given rating an a given day.