Maize Stripe Virus

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ABSTRACT

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Maize stripe disease, caused by the maize stripe virus (MStpV), occurs in many tropical areas of the world. The virus is persistently transmitted and transovarially passed by its only known vector, the delphacid planthopper, *Peregrinus maidis*. Infectivity was associated with a filamentous nucleoprotein (NP) 3 nm in diam. This was shown by infectivity of partially purified NP preparations, neutralization of infectivity by NP-antiserum, and correlation between the presence of NP and transmissibility by vectors. The nucleoprotein sedimented slowly (50-70S) and heterodispersely (from 4 to 6 zones) in sucrose density gradients and it banded isopycnically in CsCl at 1.280 g/ml. Purified NP contained 5.5% RNA and a single protein species of molecular weight 32,700 daltons. The nucleoprotein replicated in *P. maidis* and it was found in many planthopper organs. A noncapsid protein (NCP), serologically unrelated to the protein of the NP, was produced in large amounts (up to 2 mg/g tissue) in maize stripe-infected plants. The function of NCP is not known. MStpV is serologically related to the rice stripe virus. These viruses represent a new virus group.

The maize stripe disease was first described in detail by Storey (1936) in maize (*Zea mays* L.) in East Africa. A similar disease that may have been maize stripe had been noted 7 yr earlier in Mauritius (Shepherd, 1929). Storey described two leaf symptom types: one with narrow yellow stripes and the other with broad yellow stripes. Later, Kulkarni (1973) showed that these symptom types were associated with two distinct diseases and designated the one with narrow stripes as maize line [since shown to be maize mosaic (Bock *et al.*, 1976)] and retained the name maize stripe for the disease with wider stripes. The corn delphacid, *Peregrinus maidis* (Ashmead), transmitted both pathogens in a persistent manner. Neither was transmitted mechanically. Prior to Kulkarni's work, and to a limited extent since, confusion between maize stripe and maize mosaic has occurred. However, the diseases are readily distinguishable because the causal agent of maize mosaic is a rhabdovirus (Herold, 1972). Other diseases with symptoms similar to the East African maize stripe and whose agents were readily transmitted by *P. maidis* were reported from Australia in 1943 by Blackford (Simmonds, 1966), from Venezuela in 1974 (Trujillo *et al.*, 1974), and from the United States (Florida) in 1974 (Tsai, 1975).

Kulkarni (1973) found "empty" and complete isometric particles, 35 and 40 nm in diam, respectively, associated with partially purified preparations from maize stripe-diseased plants. He concluded that these particles were the causal agent. Trujillo *et al.* (1974) reported isometric particles, 55-60 nm in diam, associated with the hoja blanca disease, their original designation for the *P. maidis*-transmitted disease in Venezuela. However, repeated examinations of extracts or tissue thin sections from diseased plants from Florida or test plants serially inoculated with the Florida pathogen failed to reveal any isometric particles (Bradfute and Robertson, 1977). Also, no isometric particles were detected from maize stripe-diseased plants from Mauritius (Autrey, 1983) or Australia (Greber, 1981), and Lastra and Carballo (1983) have been unable to repeat the isolation of isometric particles from diseased plants in Venezuela. They now postulate that the 55-60 nm particles may have been latent *P. maidis* viruses not pathogenic to maize (R. J. Lastra, *personal communication*). The isometric particles found by Kulkarni (1973) were probably not the causal virus either because: a) partially purified or purified preparations of the isometric particles were not infective; b) Kulkarni's antiserum, widely used to diagnose maize stripe and supposedly prepared against the isometric particles, was in fact prepared against material in "light-scattering" zones from sucrose density gradients that were not shown to contain isometric particles; c) during the period that Kulkarni reported isometric particles associated with maize stripe, he also reported isometric particles associated with maize line which, as later shown by Bock *et al.* (1976), is actually caused by the rhabdovirus, MMV. Further, Bock *et al.* demonstrated that a 35 nm diam isometric particle could be isolated from randomly selected maize plants without symptoms. Apparently the 35 and 40 nm particles described by Kulkarni were contaminants in his cultures and were unrelated to MStpV.

Kulkarni's antiserum reacted with sap from plants infected with the Florida pathogen and the hoja blanca virus from Venezuela (Gingery *et al.*, 1979b), indicating that some common factor other than isometric particles existed among these diseases. We suspected that the common factor was probably an unusual nucleoprotein (NP) consistently associated with maize stripe-diseased, but not healthy, maize from Florida (Gingery *et al.*, 1979a, 1981) (Fig. 1). Extracts from such plants as well as purified NP reacted with Kulkarni's antiserum. Although it cannot be proven, the light-scattering zones used by Kulkarni for antiserum production probably contained, among other things, a nucleoprotein similar, if not identical, to that found in diseased Florida maize. In fact, recent evidence suggests that Kulkarni's antiserum reacts with at least three known maize viruses and two unidentified isometric particles in immune-specific electron microscopy (Jones, 1983).

Other countries in which virus isolates serologically related to the East African MStpV have been identified include Peru (Nault *et al.*, 1979), Nigeria and Sao Tome, an island off the western coast of Africa (H. W. Rossel, *personal communication*), Australia (Greber, 1981), Mauritius (Autrey, 1983), Guadeloupe (Migliori and Lastra, 1980), and Botswana (P. Jones, *personal communication*). A disease with similar symptoms whose causal agent is transmitted by *P. maidis* has been described from the Philippines (Exconde, 1977), but it has not been serologically tested. Losses caused by maize stripe have generally been minor, although serious outbreaks have occurred in Florida (Niblett *et al.*, 1981), Sao Tome (Rossel, 1982), and Venezuela (Lastra and Carballo, 1983).

The rice stripe virus from Japan also appears to be composed of a 3 nm nucleoprotein strand (Koganezawa *et al.*, 1975) and has recently been shown to be serologically related to the maize stripe NP (Gingery *et al.*, 1983; E. Shikata, *personal communication*).

PROPERTIES OF THE MAIZE STRIPE NUCLEOPROTEIN

The 3 nm nucleoprotein purified by the method of Gingery *et al.* 1981) exhibited slow (50-70S), heterodisperse (from 4 to 6 zones) sedimentation on sucrose density gradients. The buoyant density of all the zones from sucrose gradients was 1.280 g/ml in CsCl. The extinction coefficient of purified NP was 2.3 cm^2/mg at 260 nm, and the A280/A260 ratio was 0.72. The NP contained 5.5% RNA and a single protein subunit of molecular weight 32,700 daltons. From Venezuelan

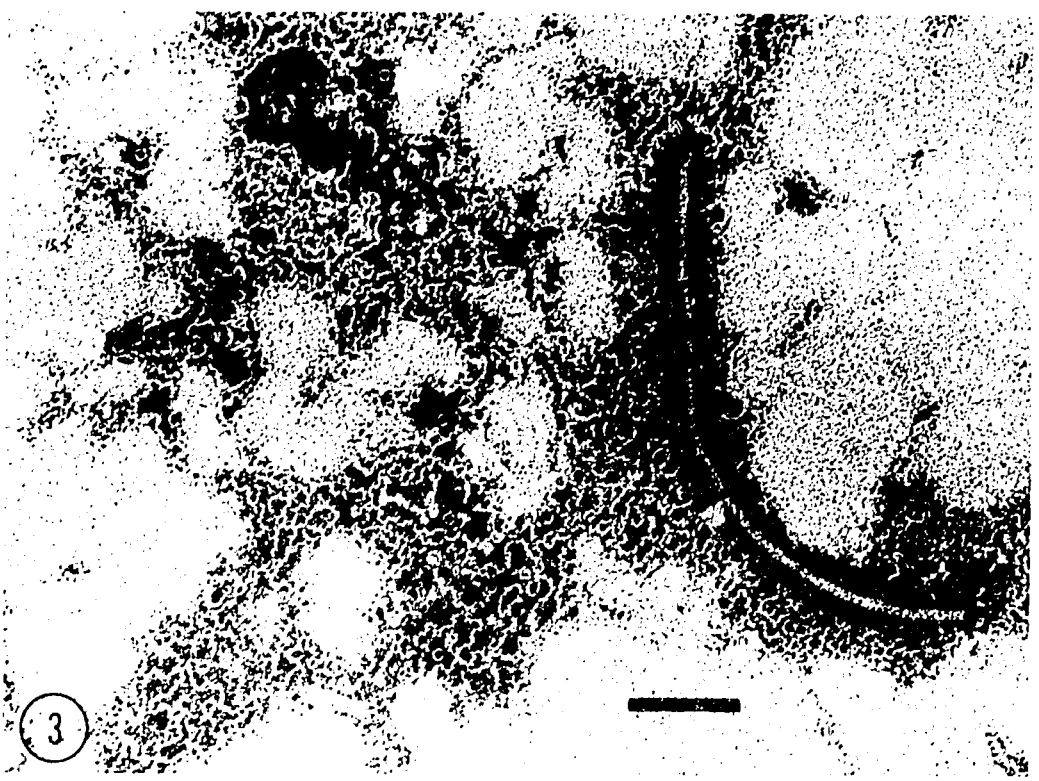

Fig. 1. Electron micrograph of negatively stained maize stripe nucleoprotein from sucrose density gradient zone showing fine strands, approximately 3 nm wide. For comparison, note PVY-type flexuous rod (maize dwarf mosaic virus, strain B) and phytoferritin molecules (light rings with dense centers approximately 11 nm in diam). The MDMV-B particle was introduced as a size and resolution standard; phytoferritin was frequently found in preparations at this level of purity. Magnification bar 100 nm long. From Gingery *et al.*(1981). (Photo reproduced with permission of Academic Press, Inc.)

maize stripe-infected plants, Lastra and Carballo (1983) isolated a similar ribonucleoprotein that contained a single protein species of about 33,000 daltons. Greber (1981) also reported a 33,000 dalton protein associated with the Australian isolate.

The descriptions of several other particles associated with plant diseases resemble that of the maize stripe NP. For example, the rice hoja blanca virus (RHBV) was described by Shikata and Galvez (1969) as a fine, flexuous, threadlike particle. However, it was considerably thicker (8-10 nm in diam) and much less flexuous than maize stripe NP. RHBV appears morphologically similar to beet yellows virus, a member of the closterovirus group. Other structures that resemble the NP are the gene-5 product-DNA complex found in cells infected with filamentous bacterial viruses such as fd and M13 (Alberts and Frey, 1972) and the fibrillar form of aggregated winter wheat mosaic virus protein (Atabekov *et al.*, 1968). Whether these chemically different entities have any structural similarities to the NP is not known.

The NP resembles partially degraded nucleocapsids isolated from large, enveloped, single-stranded RNA viruses, such as those in the arenavirus, bunyavirus, myxovirus, paramyxovirus, rhabdovirus, and retrovirus groups. For example, electron micrographs of nucleocapsid isolated from vesicular stomatitis virus, a rhabdovirus, revealed structures quite similar to the NP from maize stripe-infected plants (Simpson and Hauser, 1966). Of the animal enveloped virus groups, only rhabdoviruses are known to occur in plants (Francki *et al.*, 1981; Jackson *et al.*, 1981). One other possibly enveloped plant virus is the tomato spotted wilt virus, but its characterisics are not well known (Francki and Hatta, 1981).

INFECTIVITY OF MAIZE STRIPE NUCLEOPROTEIN

Although NP was consistently found in MStpV-infected plants, direct evidence relating it to infectivity has been difficult to obtain because of marked instability during purification. Results of experiments designed to purify the infective agent are presented in Table 1. Pelleting by centrifugation apparently was detrimental because infectivity was much higher if the extract was pelleted through a 40% sucrose cushion and higher still if not pelleted at all but rather recovered from the top of a 60% sucrose-in-D_2O cushion. Material from the sucrose-D_2O cushion was then isopycnically banded in either CsCl, Cs_2SO_4, or sucrose-D_2O. Significant infectivity was obtained only from the sucrose-D_2O gradient. Examination of the infective fraction from these gradients again revealed the fine-stranded material.

Experimental results using other methods also showed a correlation between infectivity and the NP. The most compelling evidence came from neutralization of infectivity studies in which the infectivity of extracts was blocked by treatment with antiserum prepared against purified NP. In five separate experiments, a total of 40/149 (27%) *P. maidis* injected with clarified extracts transmitted MStpV. Transmission after treatment of the extract with preimmune serum was 33/132 (25%), whereas treatment with NP-antiserum completely neutralized infectivity (0/147) (Gingery *et al.*, 1981). A relationship between infectivity and NP was shown also by experiments correlating transmissibility by and the presence of NP in *P. maidis* (see next section).

VECTOR TRANSMISSION OF MStpV

MStpV was transmitted in a persistent, intermittent pattern by *P. maidis* with a mean latent period of 15.6

TABLE 1. Infectivity during maize stripe virus purification.

Purification step[a]	Transmission by injected *Peregrinus maidis*		
Initial extract	394/1057	(37)[b]	14-67%[c]
Clarified extract ($CHCl_3$)	29/92	(5)	18-53%
Concentrated preparation:			
Resuspended pellet after high-speed centrifugation	1/154	(5)	0-4%
Resuspended pellet after high-speed centrifugation through 40% sucrose cushion	12/84	(3)	11-9%
Zone isolated from top of 60% sucrose-D_2O cushion after high-speed centrifugation	13/63	(2)	7-31%
Isopycnically banded preparation[d] in:			
Sucrose-D_2O	9/62	(2)	7-19%
CsCl	0/50	(1)	0%
Cs_2SO_4	1/44	(1)	2%

[a] Purification was performed as described in Gingery *et al.* (1981).
[b] Rate of transmission. In each experiment about 40 *P. maidis* were injected. The fraction is the number of insects that transmitted MStpV to test plants over the number of injected insects that were placed on test plants. The number in parentheses is the number of experiments.
[c] The range of transmission among individual experiments.
[d] Material from the top of 60% sucrose D_2O cushions was used.

days (Gingery *et al.*, 1979b; Nault *et al.*, 1983; L. R. Nault and D. T. Gordon, *personal communication*). In one series of experiments, 59% of the offspring of nine viruliferous females also transovarially transmitted the virus (Gingery *et al.*, 1981). MStpV did not shorten the life span of viruliferous individuals, but in some experiments it reduced fecundity by as much as 50% (L. R. Nault, *personal communication*).

By enzyme-linked immunosorbent assay (ELISA), NP was found in viruliferous *P. maidis* in the muscle, brain, midgut, hindgut, Malpighian tubules, salivary glands, ovaries, eggs, spermatheca, and male sperm sac, but only once in ten trials from the testes (Nault *et al.*, 1983; L. R. Nault and D. T. Gordon, *personal communication*). In experiments in which individual organs were assayed for NP at various times after acquisition, NP was detected first in the midgut and later in the ovaries and salivary glands; in all three organs the amount of NP increased with time. The presence of high concentrations of NP in the salivary glands was highly correlated with the ability of the insect to be a vector of MStpV, further associating the NP with infectivity.

Persistent transmission, transovarial passage, and impaired fecundity strongly suggested that the infective virus replicated in *P. maidis*, whereas the increase of NP with time demonstrated replication in *P. maidis* (D. T. Gordon and L. R. Nault, *personal communication*). Thus, an additional link was established between the infective agent and NP.

THE RELATIONSHIP BETWEEN MAIZE STRIPE AND RICE STRIPE VIRUSES

The rice stripe virus (RSV) from Japan is similar to MStpV in many ways. RSV, like MStpV, was first reported to have an isometric particle (Kitani and Kiso, 1969), but more recently has been described as a 3 nm diam filament that can assume several configurations. One of these was thought to be a supercoiled, circular configuration designated as a branched filamentous particle (Koganezawa *et al.*, 1975; Koganezawa, 1977). Other configurations included an open circular form and linear fragments. The branched filamentous particles were about 400 nm long and the contour length of the open circular form and the longest linear form was about 800 nm. The branched filamentous particles were infective as determined by injection into its delphacid vector, *Laodelphax striatellus* (Fallen) (Koganezawa *et al.*, 1975). Koganezawa (1977) reported that the different zones in centrifuged sucrose density gradients contained different configurations of the 3 nm filament. Micrographs of the filaments in a linear configuration looked remarkably similar to those observed for maize stripe NP. Branched filamentous structures have not been observed for the maize stripe NP even after using the RSV purification procedure, nor have differences in filament configuration been seen from the various sucrose density gradient zones. Recently, E. Shikata (*personal communication*) has purified branched filamentous particles from RSV-infected rice (*Oryza sativa* L.) and maize by the procedure used for maize stripe NP purification. The apparent ease of isolation of branched filamentous structures for RSV and the inability of doing so for MStpV suggests that MStpV branched filamentous forms are less stable than those of RSV, or that they do not occur.

Toriyama (1982) recently described an 8 nm wide rod-shaped particle of uncertain length that occurred in extremely low amounts in RSV-infected plants and was thought to be yet another configuration of the 3 nm filament. In his report, the rod-shaped configuration, not the branched filamentous configuration, was infective. Structures in maize stripe NP preparations which may be similar to the rod-shaped form have been observed occasionally (Gingery, *unpublished*).

Both MStpV and RSV: a) are composed of 3 nm nucleoprotein filaments; b) are propagative in and transovarially transmitted by delphacid planthoppers; c) exhibit slow, heterodisperse sedimentation in sucrose density gradients; d) have single-stranded RNA genomes; e) have a single protein species [molecular weight (MW) of 32-33,000 daltons] associated with the 3 nm filament; and f) elicit large quantities of a non-capsid protein (MW of 16-17,000 daltons) in infected leaves (see discussion below). These similarities suggest that RSV and MStpV may be members of a new group of viruses. This conclusion is supported by recent work showing a close serological relationship between MStpV and RSV. In agar-gel double-diffusion tests (Gingery *et al.*, 1983), MStpV and RSV antisera reacted with both viruses, with no detectable spurring of precipitation zones. In neutralization of infectivity tests, MStpV and RSV antisera both eliminated MStpV infectivity (Gingery *et al.*, 1983). E. Shikata (*personal communication*) observed by electron microscopy MStpV antibody decoration of RSV branched filamentous structures.

European wheat striate mosaic virus (EWSMV) is another delphacid-transmitted, transovarially passed, viruslike disease of uncertain etiology (Serjeant, 1967). No typical viruslike particles were identified in infective fractions from centrifuged sucrose density gradients, suggesting that EWSMV may be similar to MStpV and RSV.

NONCAPSID PROTEIN

A remarkable feature of the maize stripe disease is the production of very large amounts (up to 2 mg/g fresh tissue) of a 16,300 dalton protein in MStpV-infected leaves (Gingery *et al.*, 1981). By phase-contrast microscopy, the protein was frequently seen in expressed sap as 10-50 μm needle-shaped crystals. The crystals dissolved above pH 6.0, recrystallized at pH 5.4 or below, and isopycnically banded in CsCl gradients at 1.28 g/ml. This protein is referred to as the noncapsid protein (NCP) because it was serologically unrelated to the 32,700 dalton protein associated with the NP. A serologically similar protein was detected in MStpV-infected *Rottboellia exaltata* L. (Gingery, *unpublished*). RSV-infected rice plants also contained large amounts of an NCP that produced needle-shaped crystals (Kiso and Yamamoto, 1973). Neither the function of these NCP's nor their effect on host plants is known. The presence of

the NCP in MStpV-infected plants was the basis for an assay for maize stripe developed by Falk and Tsai (1983).

SPECULATIONS ABOUT MStpV

It has not yet been irrefutably established that the NP is the infective agent of the maize stripe disease despite the fact that infectivity has been demonstrated for highly purified NP. It is clear, however, that the NP is serologically related to the infective MStpV. Therefore, it can be concluded either that the NP is one of two or more components that make up the infective virus, or that the NP is the only component of the infective virus whose infective configuration is uncertain. Even in the case of RSV, which apparently is more stable than MStpV, structures associated with infectivity are not necessarily the infective form *in situ*, especially considering that a discrepancy exists as to whether the infective RSV is a branched, filamentous (Koganezawa *et al.*, 1975) or a rod-shaped particle (Toriyama, 1982). Both could conceivably be infective and still be degradation products of the native virus. The above reservations, of course, apply to all described viruses. The main difference between MStpV or RSV and most other viruses is that the other viruses have structures that better fit classical ideas about virus morphology and that are observed in both purified preparations and *in situ*. Structures associated with maize and rice stripe are quite unusual and have not been identified in infected tissue. Such studies are needed.

It can be hypothesized that MStpV and RSV are aberrant forms of viruses that at one time had a more classical morphology. The 3 nm filament might reflect a changed attraction between coat protein and genome such that the original morphology has been altered, or the filament may be a component of the ancestral virus whose other structural components have been lost (*e.g.*, nucleocapsid of an enveloped virus). Thus, studies comparing MStpV, RSV, and other enveloped viruses need to be done, even if the other viruses seem unlikely to be related.

The origin and function of the NCP is a mystery at this time. If it is a product of the virus, it is difficult to imagine why the energy used to synthesize the massive amounts of NCP found has been expended for a protein which no longer serves a vital function. Of course, the NCP may play an important but unrecognized role in the maize stripe disease cycle. One hypothesis suggests that NCP was at one time a virion structural protein that is now no longer functional. During this alteration, the regulation of its synthesis may have been affected also and it now accumulates unrestrictedly. If this is true, one would expect NCP to increase in *P. maidis* also. However, Falk and Tsai (1983) were unable to detect NCP in viruliferous *P. maidis*.

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