KOR. JOUR. MICROBIOL. Vol. 9, 179~188(1971)

<綜說> <Review>

Fungi에 의한 식물성 Virus의 전파

이 미 순
(원자력청 방사선농학연구소)

Dissemination of Plant Viruses by Fungi

LEE, Mie-Soon
(Radiation Research Institute in Agriculture, Office of Atomic Energy)

ABSTRACT

There is a good evidence that tobacco necrosis virus, lettuce big vein virus, and tobacco stunt virus are transmitted by *Olpidium brassicae*, although absolute proof in aseptic condition is lacking. Some evidence suggests that *Polymyxa graminis* may be involved in transmission of wheat mosaic virus. One report claims that *Synchytrium endobioticum* can transmit potato virus X. The cultivated mushroom, *Agaricus bisporus*, is known to act as a host of a virus and is apparently involved in the spread of the virus.

Some plant viruses are spread exclusively below the ground with no known aerial vector, and "a virus with an underground natural method of spread which does not depend simply on contact between tissues of infected and healthy plants" has been called a soil-borne virus(1960). Soil-borne viruses have revealed markedly efficient means of perpetuation and dissemination, and their transmission in soil appears to be a function of specific biological agents (1963). In fact, soil-inhabiting organisms have been confirmed as biological vectors of several plant viruses (1965).

Hewitt et al.(1958) showed that fanleaf virus of grapevine was transmitted by an ectoparasitic nematode, *Xiphinema index* Thorne & Allen. This important discovery evoked intensive research on the transmission of soil-borne plant viruses(Cadman, 1963, Smith, 1965). Recently, certain root-infecting fungi have been implicated as vectors of some plant viruses.

This paper will attempt to categorize the available information of fungus-assisted spread of plant viruses according to the identity of the fungus vectors and the relationship with the viruses which they transmit.

OLPIDIUM-TRANSMITTED VIRUSES. *Olpidium*, a chytrid, is a fungal genus in which zoospores are the active stage. Although it is generally recongnized that fungi concerned with the spread of soil-borne viruses belong to *Olpidium brassicae*(Wor.) Dang., the unqualified name *Olpidium* is often used because of the incomplete taxonomy of this genus(1964).

The life cycle of *Olpidium* is simple. Uniciliate zoospores are liberated into the surrounding medium through exit tubes in zoosporangia occurring in cells near the root surface. The motile zoospores subsequently infect other root cells, producing new zoosporangia. Zoospores often fuse in pairs to produce thick-walled resting sporangia. In due course, the resting sporangia which are

resistant to drying, germinate to produce zoosporangia, from which zoospores are liberated(1964).

Tobacco necrosis virus(*TNV*). Since Bawden and Kassanis(1947) failed to transmit TNV with the soil-inhabiting fungi *Rhizoctonia solani* and *Thielaviopsis basicola*, its method of transmission remained unknown for a long time.

The first circumstantial evidence of the association of *Olpidium* with the spread of this virus was obtained by Teakle (1960). He discovered that many lettuce seedlings became infected when watered with a combined suspension of virus and *Olpidium* zoospores, whereas only few did when watered with suspension of either virus alone or *Olpidium* zoospores alone. Therefore he suggested that this fungus might act as a virus vector or predispose roots to virus infection.

Later he claimed that *Olpidium* zoospores transmit TNV in a vectorlike manner and gave the following various reasons in support of this conclusion(1962). It was shown that virus enters roots at about the same time as the fungus, i.e., 2-3 hours after inoculation. When mung bean roots were inoculated with *Olpidium* zoospores and TNV, and exposed in water at 50C for 10 seconds to destroy the *Olpidium* without inactivating virus, TNV infection did not occur when the heat treatment was applied up to 2 hours after inoculation, which is known as approximately minimum time for actual penetration of *Olpidium*; however, rapid multiplication of TNV in roots took place when treatment was made 3 or more hours after inoculation. It appeared that infection did not merely predispose roots to subsequent TNV infection, since mung bean roots treated with hot water 1, 2, 3, or 4 hours after exposure to TNV-free *Olpidium* zoospores did not become infected when roots were placed in TNV suspension. According to him, the agent responsible for transmission of TNV was similar to *Olpidium* zoospores in that it attached to roots within a very short time, and like the cysts of *Olpidium*, was not removed by washing. Some root infection developed when roots were immersed in a suspension containing virus and zoospores for only 1 minute and subsequently washed in running tap water. He also demonstrated that the amount of TNV infection was closely correlated with the number of zoospores. All the above results have been confirmed by Kassanis and MacFarlane (1964), and they seem to be good evidence that *Olpidium* zoospores are involved in the transmission of TNV.

As additional evidence, Teakle(1962) cited the fact that TNV and zoospores entered the same portion of the root; the procedure doesn't seem valid, since root growth during incubation was not considered and no TNV only control was included(1966). However, Fry and Campbell(1966) later furnished evidence that the site of heaviest TNV infection coincided with the site of greatest infection by *Olpidium*. Teakle (1962) also indicated that various mild treatments causing zoospores to lose motility permanently, such as aging for 30 minutes, heating to 35 C for 10 minutes and addition of dilute copper sulphate, destroyed the ability of *Olpidium*-TNV suspensions to transmit TNV, although they did not inactivate the virus in inoculum. Grogan and Campbell (1966) argues that these results imply that infectivity, motility, and virus-transmitting ability of zoospores are synonymous, but no data

are presented concerning the effect of the treatments on infectivity and development of *Olpidium*. They are doubtful whether the treatments affected TNV transmission by affecting zoospore encystment, penetration, and infection, or possibly by affecting the attachment of virus to the zoospore plasma membrane prior to infection. In that Teakle(1962) has not investigated the aspect of *Olpidium* infection, the reliability of this result seems uncertain.

Fry and Campbell (1966), through a filtration experiment, provided additional data supporting the concept that *Olpidium* zoospores transmit TNV. Removal of *Olpidium* zoospores from suspensions of zoospores plus TNV gave TNV-containing filtrates that did not transmit TNV to lettuce roots.

Some workers (Kassanis, 1964, Campbell, 1966) found that transmission is prevented by high-titered, homologous antiserum specific for the TNV isolate, and thus concluded that TNV is not internal in the *Olpidium* zoospore protoplasm (Kassanis, 1964, Campbell,1966). On the other hand, Teakle and Gold (1963) reported that TNV transmission was not prevented by antiserum and suggested that *Olpidium* zoospore acquired and harbored TNV in such manner that cannot inactivate the virus and that TNV was not merely a surface carriage. Since no information is available that virus culture of Teakle and Gold (1963) contained only one strain of TNV, it is possible that their antiserum may have been prepared against one strain of virus and used in transmission experiments against another, or they may have used low-titer antiserum, as indicated by Kassanis and MacFarlane(1964).

Kassanis and MacFarlane (1964) further suggested that virus is on the zoospore surface and that the attachment is loose, since centrifugation of TNV-zoospores mixtures disrupted the association. In contrast to this report, Campbell and Fry(1966) showed that TNV was intimately associated with *Olpidium* zoospores, since TNV transmission was not prevented when zoospores were washed by consecutive centrifugations that removed T NV demonstrable by mechanical assay. This differential reaction might be simply the result of experimental conditions, such as the use of different solution to prepare TNV zoospore suspension(1966), or to zoospore damage of centrifugation reported in the experiment of Kassanis and MacFarlane (1966).

It is still uncertain how TNV is introduced into the root cells by *Olpidium*, as all above workers gave different hypotheses. Teakle and Gold(1963) stated that the most plausible possibility for mode of entry is that TNV is acquired by the *Olpidium* protoplast by which it is carried into the root. Kassanis and MacFarlane(1964) suggested that the simplest explanation of transmission is that virus enters the host by the same route as the fungus does. According to them, transmission appears to be most certain when virus is already attached to the area of the root cell wall through which the zoospore will penetrate, and then virus particles would almost inevitably be pushed into the host cell by the advancing front of zoospore. Campbell and Fry (1966) proposed that TNV is acquired by zoospores after the separate entities are independently released from roots, rather than being carried internally by these zoospores. This acquisition, they propose, is probably achieved by adsorption of TNV to the zoosporic plasma membrane, from which it is released after

the fungal protoplasm infects the host.

Although it is possible that TNV is adsorbed to the flagellum and enters the zoospore protoplasm when the flagellum is withdrawn during zoospore encystment (1966), there is no evidence to support this idea.

It appears evident that TNV is not internally borne in resting spores, since TNV transmission was not obtained from roots air dried for 8 days and was prevented by acid treatment of resting spores from freshly harvested roots.

In regard to the method of survival of TNV in the soil, Grogan and Campbell (1966) states that it seems likely that TNV survives as free virus, as virus adsorbed on soil colloids, or as virus released by infected plant residues. This concept is based on the belief that TNV does not survive within the vector, and zoospores acquire TNV after they are released from zoosporangia. If so, the virus probably is acquired by zoospores after release into the rhizosphere in a manner similar to that when zoospores and TNV are mixed *in vitro*.

The difference in the ability of different *Olpidium* strains to transmit TNV has been demonstrated (Teakle, 1962, 1964, Kassanis, 1965).

Lettuce big-vein virus (BVV). Although early workers (Jagger, 1934, Dooclittle, 1945) knew that the big-vein disease of lettuce is soil-borne and suspected that virus might be involved in this disease, the nature of this disease was not been elucidated until recently. Allen (1948) discovered that symptoms of BV did not develop if precautions were taken to prevent soil contamination with the inoculum, and Grogan (1958) from a review of the literature up to 1958, concluded that there was no proof that this disease is caused by a virus. Grogan et al. (1958) and Fry (1958) found that *Olpidium brassicae* was constantly associated with the roots of big-vein plants, and these workers suggested that *Olpidium* might be the direct cause of BV. Grogan et al. (1958) favored the theory, without excluding a virus ,that the symptoms of BV are caused by some substance produced by *Olpidium* that induces symptoms after being translocated to the leaves.

Campbell et al. (1961) provided the evidence that a graft-transmissible infectious agent, other than *Olpidium*, causes big-vein of lettuce and hypothesized that *Olpidium* might be a vector of a virus causing big-vein. That the causal agent of the leaf symptoms of BV could be transmitted directly from a diseased scion to healthy stock without entry through the roots has been confirmed by Tomlinson et al. (1962). Campbell and Grogan (1963) demonstrated that this disease is caused by BVV which was graft transmitted to 6 consecutive *Olpidium brassicae*-free generations of lettuce plants and provided evidence that *Olpidium* functions as a vector of BVV. Now it is generally accepted that the graft-transmissible BVV is the causal agent of this disease (1966).

Campbell (1965) reported that sow thistle (*Sonchus oleraceus L.*) is one of the plants functioning as a natural reservoir host of both BVV and *Olpidium*. The occurrence of TNV in roots of BVV-infected plants was reported by various workers (Fry, 1952, 1958, Yarwood, 1954); however, failure to cause BV symptoms by inoculation with TNV argues against the direct involvement of TNV in BV disease.

Although pure cultures have not been obtained, various kinds of indirect evidence

that *Olpidium* functions as a vector of BVV have been presented. As mentioned before, the constant association of *Olpidium* and BV has been reported by previous workers(Fry, 1958, Grogan, 1958). Campbell and Grogan (1963) reported that *Olpidium* zoospores could readily pass through 4- to 5.5-μ pore size sintered glass filters and that plants inoculated with filtered zoospore suspensions from BV-infected plants consistently developed this disease if they became infected with *Olpidium*. In an earlier experiment (1958), however, no infection developed in roots inoculated with zoospore suspensions that had been passed through a 14-μ filter. This discrepancy might be due to the use of different growing medium, since prolonged washing was necessary to remove soil in the previous work whereas the sand culture in latter experiment allowed rapid and complete removal of sand before the zoospores were released so that few zoospores are lost(1952). Since the average diameter of *Olpidium* zoospores is 4-5μ, the result of Grogan and Campbell(1952) provided good evidence concerning the size of transmitting agent.

Heat-killed *Olpidium* zoospores do not transmit BVV (Grogan, 1958, Campbell, 1963, 1964). Infection by *Olpidium* zoospore suspension is also prevented by dilution (1964) or chemical treatments (1958).

Probably the most convincing evidence of a fungus vector relationship is that BVV is no longer soil transmitted when *Olpidium*-free plants are infected with BVV by graft inoculation(Campbell, 1962, 1963, Tomlinson, 1962, 1964); however, soil transmissibility is restored by introducing virus-free *Olpidium*, (1964, 1962, 1964).

Tomlinson and Garett(1962) reported that *Olpidium* acquired BVV from grafted plants or rooted cuttings of BV plants and transmitted BVV to healthy plants. BVV doesn't appear to multiply within fungus vector, since BVV could be eliminated from *Olpidium* isolates by culture for several weeks in sugar beet (1962) and in *Plantago* roots (1964). According to Campbell and Grogan (1964), *Olpidium* isolates free of BVV were obtained by heat treatments of zoospores and of resting sporangia; however, the reason for loss of virus is uncertain because of the lack of *in vitro* inactivation studies of BVV.

Stored air-dry soil remains infective for at least 8 years(1946). This fact might reflect that BVV survives within the resting spores of *Olpidium* (1962, 1966). Since BV V is internal in resting spores, it is likely that this virus is carried internally by zoospores as well.

The presence of physiological strains of *Olpidium* isolates carrying BVV has been demonstrated by Campbell (1962).

Tobacco Stunt Virus (TSV). Tobacco stunt disease is soil borne and occurs in seedbed of tobacco; it has been only known in Japan(1956).

Hidaka (1954) first reported that tobacco stunt disease is caused by a sap inoculable virus but later(1956) claimed that the disease is inoculable artificially by grafting only; the previously reported mechanical transmissibility, he suggested, might have been due to the mixing of this virus with some other virus. Hiruki(1964) later reported that mechanical transmission is possible with the aid of chelating agents, such as 1-phenyl thiosemicarbazide; no infectivity was detected in the extract with distilled water. It is uncertain, however, whether the increased infectivity is due to chelating ability or the

influence of enzyme inhibition, reducing capacity, or control of *p*H(1966).

The relationship of TSV with *Olpidium* appears very similar to that of BVV. *Olpidium brassicae* was associated with tobacco stunt disease(1960, 1962), and Hidaka(1960) suggested that this fungus might be a vector of this virus.

Later Hiruki (1965) reported that stunt occurred when zoospores or resting sporangia of *Olpidium brassicae* were transferred from stunted tobacco plants to healthy ones but not when TSV alone was added to roots of tobacco seedlings. He showed that soil transmissibility of TSV is closely correlated with root infection by *Olpidium*, through experiments with heat, freezing, and chemical treatments.

According to Hidaka et al.(1956), TSV persisted without showing a loss of infectivity for at least 4 years in the soil, and there was no difference in infectivity of infested soil when treated with O_2 or CO_2 for 20 and 40 days, respectively. Hiruki (1965) claimed that tobacco plants became infected in TSV-infested soil stored for 9 to 12 years after air drying. This suggestes that TSV is internally borne like BVV, although the relationship of TSV with the resting spore has not been investigated.

Hiruki(1965) found that a tobacco strain of *Olpidium* carrying TSV could be freed from the virus by repeated transfers of the zoospores to cowpea(*Vigna sinensis* (Torner) Savi var. Black Eye); it is impossible to compare this with data on BVV(Campbell, 1962, Tomlinson, 1964), since Hiruki(1965) didn't report the period or number of tran sfers necessary for obtaining culture free from virus. According to him, zoospores of virus-free *Olpidium* acquired TSV and transmitted it to the roots of tobacco seedlings which they infect, although the detailed information was not given.

It appears that host specificity to both *Olpidium* and the virus is involved in transmission and prevalence of TSV(1967).

POLYMYXA-TRANSMITTED VIRUSES.

Strong indication that soil-borne wheat mosaic virus is transmitted to the roots of plants by the myxomycete *Polymyxa graminis* Led. has been obtained, although the nature of virus-vector relationship is uncertain.

The possibility that subterranean vectors, including fungi, may carry wheat mosaic virus was suggested by McKinney(1930) in early days. Later McKinney et al.(1957) obtained evidence that some agent (vector) closely associated with the roots of mosaic-diseased plant growing in naturally infested soil is involved in the natural overseasoning of, and inoculation with, this virus. They showed that infection occurred when the thoroughly washed roots from diseased plants in the field were introduced to sterilized soils, whereas not when the additive was virus-laden juice, leaves, or roots from mechanically inoculated plants or leaves from diseased plants. Transmission was prevented by treating soil with fumigants (Johnson, 1945, Mckinney, 1957), but not treating with toluene(1957).

The association of *Polymyxa graminis* with the mosaic disease was first noticed by Linfold and McKinney(1954); in extensive microscopic studies, however, they didn't find evidence that this fungus functions as a virus vector or reservoir because of its inconsistent existence in diseased plants. According to Brakke et al.(1965), results suggestive of a vector relationship for WMV and this fungus were obtained by Lifnold

and McKinney in unpublished experiments.

Brakke et al.(1965) found that wheat seedlings became infected when given with water in which infected roots or debris had been previously soaked. They also found that the transmitting agent passed through a 325-mesh screen.

According to recent reports by Brakke and Estes(1967), transmission is prevented by heating the root washing and soil debris at 35C and 50C respectively; these temperature are lower than the reported thermal inactivation point of this virus(60—65C) (1953). Their results showed that debris from naturally infested field soil collected in the fall and winter was a good source of inoculum for this virus but not that collected from field in the spring and summer. It might reflect that the resting spores of the fungus must mature for a few additional months after the wheat ripens before the spores will germinate, and even then, evidently only a small percentage of the resting spores germinates at any one time.

SYNCHYTRIUM-TRANSMITTED VIRUS. Potato virus(PVX) is readily transmitted mechanically(1957). That this virus may be soil borne was previously suggested(1948), and a recent report by Nienhaus and Stille (1965) provided evidence of transmission of PVX by *Synchytrium endobioticum*. It was shown that zoospores can transmit PVX only when contact takes place in tissue infected with both virus and fungus, and not when they come into contact *in vitro*. Further work on the specific correlation between PVX and this fungus is needed.

OTHER POSSIBLE FUNGUS-TRANSMITTED VIRUSES. Although tomato bushy stunt virus(TBSV) is not generally included among soil-borne viruses(1963), experimental evidence that Petunia asteroid mosaic virus(PAMV), a strain of TBSV, is soil-borne have been reported by Lovisolo et al. (1965). The probable existence vector in the naturally infested soil was suggested by the observations that soil transmission was more active in naturally infested soil than in an experimentally infested one and that some bait plants from seed could not be root infected in the soil where artificially infected plants were growing. Because of the analogy with TNV, and because of the evidence that nematodes are not involved in the transmission of PAMV, the above workers preferred to suppose that a chytrid fungus might be involved. In their recent review, Grogan and Campbell(1966) regard fungus transmission of PAMV and related viruses a distinct possibility. At present, however, it might be premature to assume that fungus is involved, since the organism that appears to assist the spread of this virus has not been shown.

AGARICUS-TRANSMITTED VIRUS AND OTHERS. With all the above viruses described, the fungus acts as a vector of the virus without being affected by the presence of virus in it. Thus the fungus acts only as a transmitting agent between a diseased and a healthy host plant. There is, however, a virus which causes a disease of the fungus.

A degenerative disease of the cultivated mushroom, *Agaricus bisporus*(Lange) Sing., previously known as La France disease and recently called X-disease and die-back, is due to viral causal agent (Hollings, 1962, Schisler, 1967).

The infected spores carrying the virus particles apparently can be vectors between diseased and healthy mycelia because of anastomosis of their germ tubes with a he-

althy hyphal tip after germination. Infected spores also can produce an infected mycelium due to continuous growth. Since infected mycelium can mature and disseminate spores producing diseased mycelia, the rapid spread of this virus is ascribed to such spore transmission (1967).

There are some indications that other fungal viruses may be responsible for infectious abnormalities, such as the *Helminthosporium* disease and the vegetative death of *Aspergillus*, and that transmission of these viruses may occur by hyphal anastomosis of these fungi (1966); definite proof is lacking, however.

摘 要

無菌狀態하에서의 완전한 증거는 희박하지만 담배의 Necrosis Virus 및 Stunt Virus, 상치의 Bigvein Virus는 *Olpidium brassicae*에 의하여 전염된다는 유력한 증거가 있다. 어떤 자료는 *Polymyxa graminis*가 밀의 Mosaic Virus의 전염에 관여 할지도 모른다는 것을 암시해 주며, 한 報文은 *Synchytrium endobioticum*이 감자 Virus X를 전염시킬수 있다고 주장하고 있다. 재배버섯인 *Agaricus bisporus*는 Virus의 宿主역활을 한다는 것이 알려져있으며 Virus의 전염에 관여한다는 것이 명백하다.

Literature cited

1. Allen, M.W., 1948. Relation of soil fumigation, nematodes, and inoculation technique to big-vein disease of lettuce. *Phytopathology* **38**, 612-627.
2. Bawden, F.C., and B. Kassanis, 1947. *Primula obsconica*, a carrier of tobacco necrosis viruses. *Annu. Appl. Biol.* **34**, 127-135.
3. Brakke, M.K., and Alice P. Estes, 1967. Some factors affecting vector transmission of soil-borne wheat mosaic virus from washing and soil debris. *Phytopathology* **57**, 905-910.
4. Brakke, M.K., Alice P.Estes, and M.L. Schuster, 1965. Transmission of soil-borne wheat mosaic virus. *Phytopathology* **55**, 79-86.
5. Cadman, C.H., 1963. Biology of soil-borne viruses. *Annu. Rev. Phytopathol.* **1**, 143-172.
6. Campbell, R.N., 1962. Relationship between the lettuce big-vein virus and its vector, *Olpidium brassicae*. *Nature* **195**, 675-677.
7. Campbell, R.N., 1965. Weeds as reservoir hosts of the lettuce big-vein virus. *Can. J. Botany* **43**, 1141-1149.
8. Campbell, R.N., and P.R. Fry, 1966. The nature of the association between *Olpidium brassicae* and lettuce big-vein and tobacco necrosis viruses. *Virology* **29**, 222-233.
9. Campbell, R.N., and R.G. Grogan, 1963. Big-vein virus of lettuce and its transmission by *Olpidium brassicae*. *Phytopathology* **53**, 252-259.
10. Campbell, R.N., and R.G. Grogan, 1964. Acquisition and transmission of lettuce big-vein virus by *Olpidium brassicae*. *Phytopathology* **54**, 681-690.
11. Campbell, R.N., R.G. Grogan, and D.E. Purcifull, 1961. Graft transmission of big-vein of lettuce. *Virology* **15**, 82-85.
12. Campbell, R.N., R.G. Grogan, and D.E. Purcifull, 1962. Studies on the transmission of the virus causing big-vein of lettuce. *Phytopathology* **52**, 5.
13. Doolittle, S.P., and R.C. Thompson, 1945. Artificial transmission of the virus of big-vein of lettuce. *Phytopathology* **35**, 484.
14. Fry, P.R., 1952. Note on the occurrence of tobacco necrosis virus in roots of lettuce showing big-vein. *New Zealand J. Sci. Technol.* A. **34**, 224-225.
15. Fry, P.R., 1958. The relationship of *Olpidium*

brassicae(Wor.) Dang. to the big-vein disease of lettuce. *New Zealand J. Agr. Res.* **1**, 301-304.

16. Doolittle, S.P., and R.N. Campbell, 1966. The nature of the relationship between *Olpidium* zoospores and tobacco necrosis virus. *Abstr. in Phytopathology* **56**, 146-147.
17. Fry, P.R., and R.N. Campbell, 1966. Transmission of a tobacco necrosis virus by *Olpidium brassicae*. *Virology* **30**, 517-527.
18. Grogan, R.G., and R.N. Campbell, 1966. Fungi as vectors and hosts of viruses. *Annu. Rev. Phytopathol.* **4**, 29-52.
19. Grogan, R.G., F.W. Zink, W.B. Hewitt, and K.A. Kim ble, 1958. The association of *Olpidium* with the big-vein disease of lettuce. *Phytopathology* **48**, 292-296.
20. Harrison, B.D., 1960. The biology of soil-borne plant viruses. *Advan. Virus Res.* **7**, 131-161.
21. Harrison, B.D., 1964. The transmission of plant viruses in soil, p. 118 to 147. In M.K. Corbett and H.D. Sisler(ed.) Plant Virology. Univ. Florida Press, Gainsville, Fla.
22. Hewitt, W.B., D.J. Raski, and A.C. Goheen, 1958. Nematode vector of soil-borne fanleaf virus of grapevines. *Phytopathology* **48**, 586-595.
23. Hidaka, Z., 1954. Morphology of the tobacco stunt virus. Proc. Internatl. Conf. Electron Microscopy, 3rd., London, 1953. 256 (*Roy. Microscop. Soc.*, London, 1956).
24. Hidaka, Z., 1960. Quoted by Cadman, C.H., Annu. Rept. Scottish Horticul Res. Inst. for 1960-1961, p. 76.
25. Hidaka, Z., C. Hiruki, K. Nakano, T. Shimizu, and T. Uozumi, 1956. Studies on the tobacco stunt disease. Bull. *Hatano Tobacco Expt. Sta.* **40**, 1-80.
26. Hidaka, Z., and A. Tagawa, 1962. The relationship between the occurrence of tobacco stunt disease and *Olpidium brassicae*. *Annu. Phytopathol Soc. Japan* **27**, 77-78.
27. Hiruki, C., 1964. Mechanical transmission of tobacco stunt virus. *Virology* **23**, 288-290.
28. Hiruki, C., 1965. Transmission of tobacco stunt virus by *Olpidium brassicae*. *Virology* **25**, 541-549.
29. Hiruki, C., 1967. Host specificity in transmission of tobacco stunt virus by *Olpidium brassicae*. *Virology* **33**, 131-136.
30. Hollings, M., 1962. Viruses associated with a die-back disease of cultivated mushroom. *Nature* **196**, 962-965.
31. Jagger, I.C., and N. Chandler, 1934. Big-vein, a disease of lettuce. *Phytopathology* **24**, 1253-1256.
32. Johnson, F., 1945. The effect of chemical soil treatments of the development of wheat mosaic. *Ohio J. Sci.* **45**, 125-128.
33. Kassanis, B., and I. MacFarlane, 1964. Transmission of tobacco necrosis virus by zoospores of *Olpidium brassicae*. *J. Gen. Microbiol.* **36**, 79-93.
34. Kassanis, B., and I. MacFarlane, 1965. Interaction of virus strain, fungus isolate, and host species in the transmission of tobacco necrosis virus. *Virology* **26**, 603-612.
35. Linford, M.B., and H.H. McKinney, 1954. Occurrence of *Polymyxa graminis* in roots of small grains in the United States. *Plant Dis. Reptr.* **38**, 711-713.
36. Lovisolo, O., O. Bode, and J. Völk, 1965. Preliminary studies on the soil transmission of Petunia asteroid mosamic virus(Petunia strain of tomato bushy stunt virus). *Phytopathol.* **2. 53**, 323-342.
37. McKinney, H.H., 1930. A mosaic of wheat transmissible to all cereal species in the tribe Hordeae. *J. Agr. Res.* **40**, 547-556.
38. McKinney, H.H., 1953. Virus desease of cereal crops, p. 350-360. In U.S. Dept. Agr. Yearbook, 1953.
39. McKinney, H.H., W.R. Raden, and B. Koehler, 1957. Studies on chemical control and overseasoning of, and natural inoculation with, the soil-borne viruses of wheat and oats. *Plant Dis. Reptr.* **41**, 256-266.

40. Nienhaus, F., and B. Stille, 1965. Transmission of potato virus X by zoospores of *Synchytrium endobioticum*. *Phytopathol.* 2. **54**, 335-337. (Abstr. in Rev. Appl. Mycol. 45, 395).

41. Pryor, D.E., 1946. Exploratory experiments with the big-vein disease of lettuce. *Phytopathology* **36**, 264-272.

42. Roberts, F.M., 1948. Experiments on the spread of potato virus X between plants in contact. *Annu. Appl. Biol.* **35**, 266-278.

43. Schisler, L.C., J.W. Sinden, and Edith M. Sigel, 1967. Etiology, symptomatology, and epidemiology of a virus disease of cultivated mushrooms. *Phytopathology* **57**, 519-526.

44. Smith, K.M., 1957. A Textbook of Plants Virus Diseases, 2nd ed. (Little, Brown, and Co., Boston, 652 pp., 1957).

45. Smith, K.M., 1965. Plant Virus-vector relationships. *Advan. Virus Res.* **11**, 61-96.

46. Teakle, D.S., 1960. Assocaitions of *Olpidium brassicae* and tobacco necrosis virus. *Nature* **188**, 431-432.

47. Teakle, D.S., 1962. Transmission of tobacco necrosis virus by a fungus *Olpidium brassicae*. *Virology* **18**, 224-231.

48. Teakle, D.S., and A.H. Gold, 1963. Further studies of *Olpidium* as a vector of tobacco necrosis virus. *Virology* **19**, 310-315.

49. Teakle, D.S., and C. Hiruki, 1964. Vector specificity in Olpidium. *Virology* **24**, 539-544.

50. Tomlinson, J.A., and R.G. Garett, 1962. Role of *Olpidium* in the transmission of big vein disease of lettuce. *Nature* **194**. 249-250.

51. Tomlinson, J.A., and R.G. Garett, 1964. Studies on the lettuce big-vein virus and its vector *Olpidium brassicae* (Wor.) Dang. *Annu. Appl. Biol.* **54**, 45-61.

52. Tomlinson, J.A., B.R. Smith, and R.G. Garett, 1962. Graft transmission of lettuce big-vein. *Nature* **193**, 599-600.

53. Yarwood, C.E., 1954. Tobacco-necrosis virus on lettuce. *Plant Dis. Reptr.* **38**, 263.