Persistence: A Vector Relationship Not Applicable to Fungal Vectors

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As the study of fungal vectors of plant viruses developed, two types of virus-vector relationships were established (3,6,13,18,19). These relationships, which have been reviewed in detail (4), were defined by whether the virus was acquired in vivo or in vitro and by whether the virus survived externally or internally to the resting spores in the absence of a living host plant. Because these characteristics were correlated, only two groups were defined: one in which the viruses were acquired in vitro and survived externally to the resting spore and one in which viruses were acquired in vivo and survived internally. Hence, the groups can be designated either by the method of acquisition or by the site of virus survival. Both groups have been confirmed (1,9,15). The only qualification to this terminology is recognition that in vitro acquisition is not restricted to a laboratory environment but also occurs in a natural setting when a virus is adsorbed by zoospores in soil water (4).

Teakle (17) reviewed fungal transmission of viruses and acknowledged the two groups but termed them persistent and nonpersistent—terminology used more recently by Adams in an otherwise excellent review (2). I argue that it is inappropriate to redefine persistence, which is a well-established characteristic of the invertebrate vector-virus transmission process, or to apply the term to the mechanism or inferred route of fungal transmission.

The terms persistent and nonpersistent were coined for two types of virus-insect vector relationships (21). Watson (20) noted that the "much abused" terms still were regarded as definitive and that three criteria described them: the latent period, the persistence of infectivity of the vectors, and the passage of a virus through the molt. She defined persistence as "the time for which a vector *can go on infecting healthy plants* after it leaves the infected ones" or more briefly as "persistence in *feeding* vectors" (emphasis added). Sylvester (16) added a third group, the semipersistent viruses, and applied the concept of half-life for acquisition and for retention of a virus by feeding vectors. He proposed that the half-life was minutes for nonpersistent viruses, hours for semipersistent viruses, and days for persistent viruses.

Kennedy et al (10) recognized that persistence, latent period, and retention through a molt were characteristics of the transmission process, and the mechanism or inferred route of virus transmission was a better basis for classifying virus-insect vector relationships. This philosophy is applicable regardless of the type of vector. Terminology for the groups has evolved from stylet-borne or circulative (10) to noncirculative or circulative (8) and to foregut-borne, circulative, or propagative (11,12).

Teakle (17) offered these definitions: "persistent viruses are borne internally in zoospores and survive, often for many years, in dormant resting sporangia", whereas the "nonpersistent viruses are borne on the surface of zoospores and do not persist in the resting sporangia." A dormant resting spore is not feeding on the host plant in any sense of the word and certainly not in the same sense as invertebrate vectors. How is one to determine that a virus is nonpersistent in a fungus when the minimum feeding time one can test is one vegetative generation (about 3 days for *Olpidium brassicae*)? This time exceeds the generation time for the virus, and new virions and zoospores will be produced at the first feeding period that can be tested. It is not surprising that a so-called "nonpersistent" virus may be maintained for months by zoospore transfer (7). Furthermore, viruses acquired in vitro probably are taken into the zoospore protoplasm during encystment and carried within the infecting zoospore protoplast (15,18) and so are thought to be in the same site at this stage as the viruses acquired in vivo. Thus, the definition that "nonpersistent viruses are borne on the surface of the zoospore" can be misleading.

Other terms used for the mechanism or route of transmission by invertebrate vectors (stylet-borne, noncirculative, foregut-borne, or circulative) remain inapplicable to fungi that have no stylet, circulative system, or foregut. Furthermore, two corollaries of nonpersistent transmission are that a preacquisition, starvation period increases efficiency of transmission, and molting prevents transmission. No effect of starvation has been suggested for zoospore acquisition, and fungi do not molt.

The use of unique terminology for fungal transmission is justified. This terminology should emphasize not only unique virus-vector relationships but also account for unique epidemiological features that are a consequence. In vitro acquisition is the only instance in which the vector of a plant virus naturally comes in contact with and acquires a virus outside the cells of living virus source plants. Likewise, these viruses survive between crops in plant debris or free in the soil, independent of vector or living plants. Survival is highly dependent on the physical environment (e.g., the dryness of the soil) (14). In contrast, viruses acquired in vivo are thought to survive only in the resting spores. Because none of these viruses are seed-borne, the main virus reservoir is the viruliferous resting spore of the vector, which can survive for many years in infested soil and which may lead to nearly permanent infestation of fields (5). The time span for virus survival in the vector far exceeds that for any dormant or diapausing insect vector, although propagative viruses theoretically could be maintained for many years in vectors reared on virus-immune hosts.

Campbell and Fry did not coin a name for the two types of fungal vector-virus relationships (6) because too few examples had been studied, and the mechanisms of transmission were not elaborated. This remains the case (2). Perhaps the International Working Group on Plant Viruses with Fungal Vectors should decide if it is time to select terms and which terms to use.

LITERATURE CITED

1. Abe, H., and Tamada, T. 1986. Association of beet necrotic yellow vein virus with isolates of *Polymyxa betae* Keskin. Ann. Phytopathol. Soc. Jpn. 52:235-247.
2. Adams, M. J. 1991. Transmission of plant viruses by fungi. Ann. Appl. Biol. 118:479-492.
3. Campbell, R. N. 1962. Relationship between the lettuce big-vein virus and its vector, *Olpidium brassicae*. Nature (London) 195:675-677.
4. Campbell, R. N. 1979. Fungal vectors of plant viruses. Pages 8-24 in: Fungal Viruses. XIIth Int. Congr. Microbiol., Mycol. Sect., Munich, 1978. H. P. Molitoris, M. Hollings, and H. A. Wood, eds. Springer-Verlag, Berlin.
5. Campbell, R. N. 1985. Longevity of *Olpidium brassicae* in air-dry soil and the persistence of the lettuce big-vein agent. Can. J. Bot. 63:2288-2289.
6. Campbell, R. N., and Fry, P. R. 1966. The nature of the associations between *Olpidium brassicae* and lettuce big-vein and tobacco necrosis viruses. Virology 29:222-233.
7. Campbell, R. N., Lecoq, H., Wipf-Scheibel, C., and Sim, S. T. 1991.

Transmission of cucumber leaf spot virus by *Olpidium radicale*. J. Gen. Virol. 72:3115-3119.
8. Harris, K. F. 1983. Sternorrhynchous vectors of plant viruses: Virus-vector interactions and transmission mechanisms. Adv. Virus Res. 28:113-140.
9. Jianping, C., Swaby, A. G., Adams, M. J., and Yili, R. 1991. Barley mild mosaic virus inside its fungal vector, *Polymyxa graminis*. Ann. Appl. Biol. 118:615-621.
10. Kennedy, J. S., Day, M. F., and Eastop, V. F. 1962. A conspectus of aphids as vectors of plant viruses. Commonw. Agric. Bur., Farnham Royal, England. 114 pp.
11. Matthews, R. E. F. 1991. Plant Virology. 3rd ed. Academic Press, Inc., New York. 835 pp.
12. Nault, L. R., and Ammar, E. D. 1989. Leafhopper and planthopper transmission of plant viruses. Annu. Rev. Entomol. 34:503-529.
13. Rao, A. S., and Brakke, M. K. 1969. Relation of soil-borne wheat mosaic virus and its fungal vector, *Polymyxa graminis*. Phytopathology 59:581-587.
14. Smith, P. R., Campbell, R. N., and Fry, P. R. 1969. Root discharge and soil survival of viruses. Phytopathology 59:1678-1687.
15. Stobbs, L. W., Cross, G. W., and Manocha, M. S. 1982. Specificity and methods of transmission of cucumber necrosis virus by *Olpidium radicale* zoospores. Can. J. Plant Pathol. 4:134-142.
16. Sylvester, E. S. 1956. Beet mosaic and beet yellows virus transmission by the green peach aphid. J. Am. Soc. Sugar Beet Technol. 9:56-61.
17. Teakle, D. S. 1983. Zoosporic fungi and viruses. Double trouble. Pages 233-248 in: Zoosporic Plant Pathogens. A Modern Perspective. S. T. Buczacki, ed. Academic Press, Inc., London.
18. Temmink, J. H. M. 1971. An ultrastructural study of *Olpidium brassicae* and its transmission of tobacco necrosis virus. Ph.D. thesis. Landbouwhogeschool, Wageningen, Netherlands. 135 pp.
19. Temmink, J. H. M., Campbell, R. N., and Smith, P. R. 1970. Specificity and site of in vitro acquisition of tobacco necrosis virus by zoospores of *Olpidium brassicae*. J. Gen. Virol. 9:201-213.
20. Watson, M. A. 1960. The ways in which plant viruses are transmitted by vectors. Rep. 7th Commonw. Entomol. Conf. 1960:157-161.
21. Watson, M. A. and Roberts, F. M. 1939. A comparative study of the transmission of *Hyoscyamus* virus 3, potato virus Y and cucumber mosaic virus 1 by the vectors *Myzus persicae* (Sulz), *M. circumflexus* (Buckton), and *Macrosiphum gei* (Koch). Proc. Roy. Soc. London B. 127:543-575.