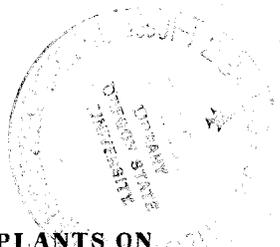


S105  
E55  
no. 127  
cop. 2



**EFFECTS OF INSECT AND VIRUS HOST PLANTS ON  
TRANSMISSION OF VIRUSES BY INSECTS**

K. G. Swenson



Reprinted from  
ANNALS OF THE NEW YORK ACADEMY OF SCIENCES  
Volume 105, Article 13, Pages 730-740  
November 18, 1963

# EFFECTS OF INSECT AND VIRUS HOST PLANTS ON TRANSMISSION OF VIRUSES BY INSECTS\*

K. G. Swenson

*Oregon State University, Corvallis, Ore.*

Plant virus transmission by insects can be divided into four components: transmissibility of the virus, transmitting ability of the vector, availability of virus in the diseased source plant, and susceptibility of healthy plants used as indicators of transmission. This review is concerned primarily with the last two of these components and the numerous factors which influence them. Consideration is also given to recent evidence that virus transmission by aphids is influenced by the host plants on which the aphids are produced for use in transmission tests.

Experimentation on insect transmission of numerous viruses has been greatly facilitated by the selection of better plants as virus sources and indicators of transmission. For example, pathogenicity of peach yellow leaf roll virus to the leafhopper vector, *Colladonus montanus* (Van D.),<sup>26</sup> would probably not have been discovered if peach had not been replaced with celery as an experimental host plant. Leafhoppers infected one of 168 plants when peach was used as virus source and indicator plants, compared to 232 of 546 plants infected when celery was used.<sup>25</sup> The effects of plants on transmission through their use as virus sources, indicator plants, or insect hosts is, however, considerably more complicated than simply finding a better source or indicator plant, or a plant on which insects will better develop or survive. This will become evident in the following pages.

## *Virus Source Plant*

Recovery of virus from plants by insects has sometimes been used to measure relative virus concentration and some attempts have been made to correlate such results with virus concentration measured by other means. Availability of potato virus Y to aphids was related to concentration determined by serological methods.<sup>2,4,10</sup> Simons<sup>47</sup> followed the concentration cycle of potato virus Y and cucumber mosaic virus in pepper and found a close correlation between numbers of plants infected by aphid transmission and results of rubbing plants with sap diluted 1:500. Although pepper

\*Approved for publication as miscellaneous paper number 127, Oregon Agricultural Experiment Station. The writer's work on this subject was supported in part by a Public Health Service research grant, E-2202, from the National Institutes on Health.

was a much better source of cucumber mosaic virus for aphids than was cucumber, no difference was found when the two plants were used as virus sources for mechanical inoculation.<sup>46</sup> Transmission of bean yellow mosaic virus from broad bean by aphids was related to severity of symptoms. This, in turn, was related to virus concentration as measured by local lesions on *Chenopodium amaranticolor* Coste and Reyn and to the number of bean plants infected by mechanical inoculation with diluted sap.<sup>58</sup>

Much work has been done on the effects of nutrition and environment on virus concentration in plants, although assay of virus concentration has usually been by mechanical inoculation to local-lesion hosts. This work is, nonetheless, directly related to the present discussion because virus acquisition by insects would, in general, be expected to be related to concentration in the source plants.

*Inherent variation.* The number of insects that acquire virus has been frequently shown to vary with the species or variety selected as a source plant. Among nonpersistent aphid-borne viruses, chard was a better source of cucumber mosaic virus for aphids than was pepper,<sup>45</sup> and pepper markedly better than cucumber.<sup>46</sup> Broad bean was the best of four species tested as sources of bean yellow mosaic virus,<sup>1</sup> and yellow lupine better than two other lupine species.<sup>15</sup> Potato varieties differed as sources of potato virus Y,<sup>4</sup> and tobacco was better than potato.<sup>2</sup> Parsley was a poor source of poison hemlock ringspot virus for aphids as compared to celery and poison hemlock.<sup>20</sup> On the other hand, no consequential difference was noted between tobacco and *Hyoscyamus* as sources of henbane mosaic virus for aphids<sup>65</sup> or between *Brassica juncea* Coss. and *B. chinensis* L. as sources of *Brassica nigra* virus.<sup>63</sup> Diploid *Physalis floridana* Rydb. and potato were better sources of the persistent aphid-borne potato leaf roll virus than was autotetraploid *P. floridana*.<sup>16</sup> Potato varieties varied significantly as sources of leaf roll virus but were, in general, better than *P. floridana* and *Datura stramonium* L.<sup>35</sup> Transmission of peach yellow leaf roll virus by the leafhopper, *Colladonus montanus*, was much more efficient from celery than from peach.<sup>25</sup>

Individual plants within a species may vary greatly as virus sources, although some of this variation may be due to segregation of virus variants or amount of inoculum established in the plant, as well as to genetic variation among plants. Individual plant variation occurred in the aphid transmission of beet yellows virus from sugar beet,<sup>8</sup> *Brassica nigra* virus from *B. juncea*,<sup>59</sup> and bean yellow mosaic virus from broad bean, more transmission of bean

yellow mosaic virus occurred from broad bean plants with severe symptoms than from plants with mild symptoms,<sup>57</sup> but such a relationship did not occur for beet yellows virus transmission from sugar beet or *Brassica nigra* virus from *B. juncea*. Inoculation with a single strain of bean yellow mosaic virus resulted in great variation in symptom expression among red clover clones.<sup>17</sup> Inherent source plant variation in beet yellows transmission was avoided by using single sugar beet clones within experiments. Broad bean is generally regarded as self-pollinated and, therefore, varieties from good seed sources might be expected to be highly uniform genetically, but recent work indicates a high degree of outcrossing.<sup>42</sup>

That leaves of the same plant differ as virus sources for insects has been shown repeatedly <sup>2,30,53,55,59,62,65</sup> Furthermore, some viruses have a definite infection cycle in plants, reaching a maximum concentration for the plant as a whole and then decreasing. This is true of alfalfa mosaic virus,<sup>41</sup> cucumber mosaic virus,<sup>47</sup> potato virus Y,<sup>47</sup> and potato leaf roll virus.<sup>16,27</sup> On the other hand, availability of bean yellow mosaic virus from comparable leaves of individual broad bean plants was remarkably constant over a period of several weeks.<sup>55</sup> *Brassica nigra* virus appears to behave similarly in *B. juncea*.<sup>59</sup> Different areas of a single leaf may also vary as sources of virus.<sup>10</sup>

*Environment and nutrition.* Effect of temperature on virus multiplication in plants has been reviewed by Kassanis.<sup>38</sup> Two patterns of host-virus relationship occur. In one type an optimum temperature exists for maintenance of maximum virus concentration over a period of time, the other type involves viruses which go through a definite concentration cycle in their host plants. Rate of progression of the cycle and maximum concentration vary with different temperatures and may also vary for the same virus in different plants.<sup>40</sup> Temperatures optimal for multiplication are quite different among plant viruses.

Decreased light intensity favored the multiplication of four viruses in tobacco,<sup>6</sup> whereas increased light intensity and day length favored the multiplication of cucumber mosaic virus in spinach, although light effect was not completely separated from that of temperature.<sup>13</sup> No fixed optimal light intensity and day length were indicated for tobacco mosaic virus multiplication in tobacco, the effect of light depending on the stage of the infection.<sup>3</sup>

Increased nitrogen was accompanied by increased infectivity of expressed sap for cucumber mosaic virus in spinach,<sup>14</sup> tobacco mosaic virus in tobacco,<sup>51,52,66</sup> tobacco ringspot virus in cucumber,

<sup>22</sup> turnip virus 1 in *Nicotinna* species,<sup>40</sup> and tomato spotted wilt virus in tomato.<sup>43</sup> Results of supplying nitrogen in excess of that favorable for growth are conflicting,<sup>14,40,51</sup> and the effect may depend upon the particular virus-host combination involved. The number of aphids acquiring potato leaf roll virus from potato was decreased by increasing nitrogen available to the source plants.<sup>27</sup> Concentration of cucumber mosaic virus in spinach,<sup>14</sup> of turnip virus 1 in *Nicotiana* species,<sup>40</sup> of tobacco mosaic virus in tobacco mosaic virus in tobacco,<sup>66</sup> and of tobacco ringspot virus in cucumber and potato virus X in *Nicotiana* species<sup>22</sup> were increased by additional phosphorus. The effect of potassium on virus concentration was related to plant growth.<sup>14,40,66</sup>

Among minor elements, tobacco mosaic virus concentration was higher in manganese-deficient tobacco plants than in normal plants.<sup>67</sup> Tobacco mosaic virus concentration in plants with sub-optimal levels of zinc or sulfur was lower than in plants receiving adequate amounts.<sup>23,34</sup>

#### Susceptibility to Inoculation

*Inherent variation.* For many viruses, plant species or varieties vary in their susceptibility to inoculation by insects. Among aphid-borne viruses, tobacco was slightly more susceptible than *Hyoscyamus* to henbane mosaic virus,<sup>65</sup> pepper more susceptible than chard to cucumber mosaic virus,<sup>45</sup> and *Physalis floridana* more susceptible than *P. angulata* L. to potato leaf roll virus.<sup>30</sup> Potato varieties differed in susceptibility to potato virus Y,<sup>4</sup> as did bean varieties to bean yellow mosaic virus<sup>1</sup> and crucifer varieties and species to *Brassica nigra* virus.<sup>59</sup> Celery was more susceptible than peach to inoculation with peach yellow leaf roll virus by *Colladonus montanus*.<sup>25</sup> *Euscelis plebejus* transmitted strawberry green-petal virus to several species but not to strawberry.<sup>18</sup>

Aphid-test plant interactions occurred in the transmission of *Brassica nigra* virus.<sup>63</sup> *B. juncea* was highly susceptible to inoculation by *Myzus persicae* (Sulz.), whereas *B. chinensis* was quite resistant. A similar difference was not found in susceptibility to inoculation by *Rhopalosiphum pseudobrassicae* (Davis). An environment-bean variety interaction was indicated for aphid inoculation with bean yellow mosaic virus.<sup>1</sup> Two varieties differed greatly in susceptibility at one time of the year but were almost identically susceptible at another time. A leafhopper test plant interaction was found in the transmission of aster yellows virus.<sup>44</sup> Celery was readily inoculated by *Euscelis maculipennis* (*Euscelidius variegatus* (Kbm.)) but this leafhopper did not transmit the virus to aster. The

short-winged race of the leafhopper, *Macrostelus divisus* (*M. fascifrons* Stal), transmitted the virus readily to both aster and celery, whereas the long-winged race transmitted inefficiently to celery.

Susceptibility of pineapple plants to inoculation with cucumber mosaic virus by aphids decreased with increasing age,<sup>12</sup> as did susceptibility of maize plants to inoculation with maize streak virus by leafhoppers.<sup>53</sup> Susceptibility of *Brassica juncea* to inoculation with *Brassica nigra* virus did not change with plant age.<sup>60</sup>

Environment and nutrition. Little information is available concerning the effects of environment and nutrition on susceptibility of plants to virus inoculation by insects, although such effects on the susceptibility of local-lesion hosts to mechanical inoculation have received considerable attention. The two inoculation methods cannot be assumed to give the same susceptibility ranking among groups of differently treated plants because adequate comparisons have not been made. There is, in fact, evidence that such ranking would not be the same.<sup>48,50</sup> Optimal conditions for susceptibility to inoculation should not be confused with optimal conditions for subsequent virus multiplication and symptom expression which are not necessarily dependent on the same processes as susceptibility to inoculation.<sup>5</sup>

Reduced light intensity generally increases susceptibility to mechanical inoculation.<sup>6,7</sup> Reduced light intensity did not, however, change susceptibility of *B. juncea* to inoculation with *Brassica nigra* virus by aphids,<sup>59</sup> of *Nicotiana rustica* to henbane mosaic virus,<sup>9</sup> and of broad bean to inoculation with bean yellow mosaic virus by aphids.<sup>24</sup> Numbers of lettuce plants infected with lettuce mosaic virus were increased by 24 or 48 hour periods of darkness before inoculation by aphids.<sup>61</sup> Contradictory results were obtained on the relation of light to susceptibility of bean plants to inoculation with bean yellow mosaic virus by aphids.<sup>56</sup>

Susceptibility of plants to mechanical inoculation increases as the temperature becomes higher.<sup>28</sup> The susceptibility of cucumber to tobacco mosaic virus has been reported as an exception to this,<sup>33</sup> but may have been due to the unusually high temperature at which the plants were grown.<sup>49</sup> Susceptibility of bean plants to bean yellow mosaic virus inoculation by aphids was, however, lower at 27° C, than at 18° C.<sup>57</sup> This relationship, different from that prevailing with mechanical inoculation, could not be explained by the temperature at which the plants were grown, about 23° C. Further work showed decreasing susceptibility of pea plants to aphid inoculation with bean yellow mosaic virus as temperature increased, so that about seven times more plants were infected at 15° C, than at 30° C.<sup>68</sup>

The relation of plant nutrition to susceptibility to virus inoculation by aphids is virtually unknown. The number of potato plants inoculated with potato virus Y by aphids was increased by additional phosphorus and slightly decreased by additional nitrogen.<sup>5</sup> Susceptibility of bean plants to inoculation with bean yellow mosaic virus by aphids was increased by raising the general nutritional level (N, K, P) of the plants.<sup>56</sup>

#### *Aphid Host Plant*

*Myzus persicae* reared on peach transmitted lettuce mosaic virus to fewer plants than did *M. persicae* reared on mustard, sugar beet, or radish.<sup>61</sup> The aphids reared on peach were from different stock than those reared on other plants and, therefore, may have had an inherently different ability to transmit the virus. *M. persicae* reared on chard transmitted southern cucumber mosaic virus to more plants than did *M. persicae* reared on pepper.<sup>45</sup> The difference was small, however, and well within the variation possible among samples from aphids with equal transmission efficiency.

MacKinnon<sup>36</sup> showed that more plants were inoculated with turnip latent mosaic virus by *M. persicae* reared on detached leaves of *Physalis floridana* infected with potato leaf roll virus than by aphids reared on either detached leaves of *Datura stramonium* infected with potato leaf-roll virus or on detached leaves of healthy rape plants. Also, more plants were infected with turnip latent mosaic virus when aphids were reared on detached leaves of healthy rape plants than when reared on detached leaves of healthy *D. stramonium*. Similar effects did not occur in the transmission of potato leaf-roll virus.<sup>36</sup> Most forms of the aphid, *Rhopalosiphum fitchii* (Sand.), from primary hosts did not transmit barley yellow dwarf virus although transmission tests with forms from secondary gramineous hosts have repeatedly showed this species to be a common vector of the virus.<sup>38</sup> Lack of transmission by aphid forms from the primary host may be due to the feeding behavior on the virus hosts which are unsuitable host plants for these forms.

*M. persicae* from thriving colonies on young leaves of *Brassica pekinensis* Rupr. transmitted the stylet-borne bean yellow mosaic virus to more plants than did a comparable group of aphids from mature leaves.<sup>57</sup> Likewise, aphids from thriving colonies on young leaves transmitted the virus to more plants than did aphids from older colonies on heavily infested, deteriorating plants. Not all comparisons between crowded colonies gave these results, but transmission by aphids from crowded colonies never exceeded that by aphids from uncrowded colonies. Age and condition of plants at

the time of aphid infestation appeared to influence the results obtained.<sup>56</sup> Orlob<sup>57</sup> reported that the forms of *Aphis nasturtii* Kltb. occurring on the primary host did not transmit potato virus Y, whereas transmission did occur by forms of the aphid occurring on secondary host plants. Effects of the aphid host plants was suggested as a possible explanation for these differences. Swenson<sup>55</sup> suggested that some of the difference in virus transmission by aphid forms or stages reported by various workers may have been due to condition of the aphid colony plants.

#### *Transmission Variation*

Simons showed that the amount of aphid transmission of cucumber mosaic virus depended on the particular combination of virus and aphid host plants selected.<sup>45</sup> A high degree of inter-replicate and inter-experiment variation may result even with constant aphid-virus-plant combinations. Watson used aphids to inoculate tobacco plants with henbane mosaic virus over a two year period and noted a seasonal trend in the number of infected plants.<sup>65</sup> More plants were infected in winter than in summer. This was attributed to increased plant susceptibility at lower light intensities and shorter days. Results of these transmission experiments were combined in weekly totals which were highly variable. Lack of correlation between weekly totals and meteorological conditions was attributed to variation in aphid colonies, among other things

In transmission of strawberry mottle virus by *Pentatrachopus jacobii* (H. R. L.), infection in groups of five plants varied from 0 to 5, and 0 to 14 in groups of 15 plants.<sup>19</sup> Hamlyn commented on the great variation in cauliflower mosaic virus transmission by *M. persicae*<sup>21</sup> and Sylvester pointed out a variation of from 2 to 29 per cent transmission in replicates of 100 plants in the transmission of beet yellows virus by *M. persicae*.<sup>62</sup> Experiments using three aphids per test plant yielded a lower proportion of plants inoculated with bean yellow mosaic virus by aphids than did experiments using two aphids per plant.<sup>24</sup> Similar results were obtained in beet yellows transmission by *M. persicae*.<sup>62</sup>

A highly significant inter-replicate variation occurred frequently in aphid transmission experiments with bean yellow mosaic virus,<sup>54</sup> indicating a difference in transmission potential among replicates on these occasions. Further work showed that condition of aphid colonies could introduce a high degree of variation unless care was taken to maintain uniformity in the aphid colonies with respect to environment, age of colony plant, and degree of infestation.<sup>55</sup> Differences resulting from colony condition were not due

to different aphid forms (alatiform vs. apterous) and no evidence was obtained of indirect effects on virus transmission through changes in aphid feeding behavior. Such differences are known to exist, however, depending on humidity<sup>11,65</sup> or temperature.<sup>64</sup>

### *Discussion*

The foregoing review indicates that the selection of plants as virus sources, indicators of transmission, and aphid hosts, and the way in which these plants are maintained, determine not only the amount of transmission, but also repeatability of results and a large amount of experimental variation. Transmission experiments can be regarded as samples estimating a transmission parameter or potential. That the parameter estimated for a particular insect-virus-plant combination frequently changes, even within experiments, is demonstrated by the high incidence of significant inter-experiment and inter-replicate differences. When such differences occur, introduced variables or treatments are compared under different conditions from one replicate or experiment to another. This is not a matter of concern if all treatments are influenced proportionately by the changed conditions, that is, if interactions are absent, a condition more often assumed than proved. Opportunities for environmental variation are considerable in virus transmission experiments. Most experimental material is maintained in greenhouses characterized by marked environmental changes during the course of the seasons and, frequently, by wide fluctuations during relatively short periods of time.<sup>32</sup>

Extrapolation of data on plant susceptibility from experiments based on mechanical inoculation of local-lesion hosts to field situations cannot be justified. Since information on factors affecting susceptibility to insect inoculation is so scant, we are virtually without information on the relation of variations in plant susceptibility to virus incidence in the field. Kennedy<sup>29</sup> stated that aphids appear so ideally fitted, behaviorally, for spreading virus in the field that one might expect far more virus spread than actually occurs. Perhaps, however, the answer is that virus transmission systems are inefficient at the level of individual insects and only infrequently do optimum combinations of aphid host-plant condition, availability of virus in the source plants, and plant susceptibility occur together.

### *References*

1. ADLERZ, W. C. 1959. Factors affecting transmission of bean yellow mosaic virus. *J. Econ. Ent.* 52: 260-2.

2. BAGNALL, R. H., & R. H. E. BRADLEY. 1958. Resistance to virus Y in the potato. *Phytopathology* 48: 121-5.
3. BANCROFT, J. B. & G. S. POUND. 1956. Cumulative concentrations of tobacco mosaic virus in tobacco and tomato at different temperatures. *Virology*, 2: 29-43.
4. BAWDEN, F. C. & B. KASSANIS. 1946. Varietal differences in susceptibility to potato virus Y. *Ann. Appl. Biol.* 33: 46-50.
5. BAWDEN, F. C. & B. KASSANIS. 1950. Some effects of host nutrition on the susceptibility of plants to infection by certain viruses. *Ann. Appl. Biol.* 37: 46-57.
6. BAWDEN, F. C. & F. M. ROBERTS. 1947. The influence of light intensity on the susceptibility of plants to certain viruses. *Ann. Appl. Biol.* 34: 286-96.
7. BAWDEN, F. C. & F. M. ROBERTS. 1948. Photosynthesis and predisposition of plants to infection with certain viruses. *Ann. Appl. Biol.* 35: 418-28.
8. BJORLING, K. & F. OSSIANNILSSON. 1958. Investigations on individual variations in the virus-transmitting ability of different aphid species. *Socker*. 14: 1-13.
9. BRADLEY, R. H. E. 1952. Studies on the aphid transmission of a strain of henbane mosaic virus. *Ann. Appl. Biol.* 39: 78-97.
10. BRADLEY, R. H. E. 1962. Different areas of tobacco leaves as sources of potato virus Y for aphids. *Virology*. 16: 366-370...
11. BRCAK, J. 1959. Transmission of beet mosaic virus by the green peach aphid starved before infection feeding under different conditions of air humidity. *Biol. Plants*. 1: 330-2
12. CARTER, W. 1937. Aphid transmittal of *Commelina nudiflora* L. mosaic to pineapple. *Ann. Ent. Soc. Amer.* 30: 155-162
13. CHEO, P. C. & G. S. POUND. 1952. Relation of air temperature, soil temperature, photoperiod, and light intensity to the concentration of cucumber virus 1 in spinach. *Phytopathology*. 42: 306-10
14. CHEO, P. C., G. S. POUND & L. G. WEATHERS. 1952. The relation of host nutrition to the concentration of cucumber virus 1 in spinach. *Phytopathology* 42: 377-81.
15. CORBETT, M. K. 1958. A virus disease of lupines caused by bean yellow mosaic virus. *Phytopathology*. 48: 86-91.
16. DAY, M. F. 1955. The mechanism of the transmission of potato leaf roll virus by aphids. *Aust. J. Biol. Sci.* 8: 498-513.
17. DIACHUN, S., & L. HENSON. 1956. Symptom reaction of individual red clover plants to yellow bean mosaic virus. *Phytopathology*. 46: 150-2.
18. FRAZIER, N. W. & A. F. POSNETTE. 1957. Transmission and host-range studies of strawberry green-petal virus. *Ann. Appl. Biol.* 45: 580-8.
19. FRAZIER, N. W. & E. S. SYLVESTER. 1960. Half-lives of transmissibility of two aphid borne viruses. *Virology*. 12: 233-44.
20. FREITAG, J. H. & H. H. P. SEVERIN. 1945. Poison-hemlock-ringspot virus and its transmission by aphids to celery. *Hilgardia* 16: 389-410.
21. HAMLYN, B. M. G. 1955. Aphid transmission of cauliflower mosaic on turnips. *Plant Path.* 4: 13-16.
22. HELMS, K & G. S. POUND. 1955. Host nutrition in relation to concentration of potato virus X and tobacco ringspot virus. *Phytopathology*. 45: 567-73
23. HELMS, K. & G. S. POUND. 1955. Zinc nutrition of *Nicotiana tabacum* L. in relation to multiplication of tobacco mosaic virus. *Virology*. 1: 408-23.

24. HOOF, H. A. VAN. 1958 Onderzoekingen over de biologische overdracht van een non-persistent virus. Meded. Inst. PlZietk. Onderz. No. 161.
25. JENSEN, D. D. 1957. Differential transmission of peach yellow leaf roll virus to peach and celery by the leafhopper, *Colladonus montanus*. Phytopathology. 47: 575-78.
26. JENSEN, D. D. 1959. A plant virus lethal to its insect vector. Virology. 8: 164-75.
27. KASSANIS, B. 1952. Some factors affecting the transmission of leaf-roll virus by aphids. Ann. Appl. Biol. 39: 157-67.
28. KASSANIS, B. 1957. Effects of changing temperature on plant virus diseases. Adv. Virus Res. 4: 221-41.
29. KENNEDY, J. S. 1960. The behavioural fitness of aphids as field vectors of viruses. Rep. 7th Commonwealth Ent. Conf. Pp. 165-8.
30. KIRKPATRICK, H. C., & A. F. ROSS. 1952. Aphid-transmission of potato leafroll virus to solanaceous species. Phytopathology. 42: 540-6.
31. KUNKEL, L. O. 1943. New hosts as a key to progress in plant virus disease research, Pp. 63-82. In Virus Diseases, Messenger Lectures, Cornell University Press, Ithaca, N. Y.
32. LAWRENCE, W. J. C. 1957. The glasshouse as an environment for plant experiments. In Control of the Plant Environment, J. P. Hudson, Ed. Pp. 129-37. Academic Press. New York, N. Y.
33. LINDNER, R. C., H. C. KIRKPATRICK & T. E. WEEKS. 1959. Some factors affecting the susceptibility of cucumber cotyledons to infection by tobacco mosaic virus. Phytopathology. 49: 78-88.
34. LING, K. C., & G. S. POUND. 1962. Sulfer nutrition of *Nicotiana tabacum* in relation to multiplication of tobacco mosaic virus. Phytopathology 52: 155-158.
35. MACCARTHY, H. R. 1954. Aphid transmission of potato leafroll virus. Phytopathology. 44: 167-74.
36. MACKINNON, J. P. 1961. Transmission of two viruses by aphids reared on different hosts. Virology. 13: 372-73.
37. ORLOB, G. B. 1962. Further studies on the transmission of plant viruses by different forms of aphids. Virology. 16: 301-4.
38. ORLOB, G. B. & D. C. ARNY. 1960. Transmission of barley yellow dwarf virus by different forms of the apple grain aphid, *Rhopalosiphum fitchii* (Sand.) Virology. 10: 273-4.
39. POUND, G. S. & J. B. BANCROFT. 1956. Cumulative concentrations of tobacco mosaic virus in tobacco at different photoperiods and light intensities. Virology. 2: 44-56.
40. POUND, G. S. & L. G. WEATHERS. 1953. The relation of host nutrition to multiplication of turnip virus 1 in *Nicotiana glutinosa* and *N. multivalvis*. Phytopathology. 43: 669-74.
41. ROSS, A. F. 1941. Purification and properties of alfalfa mosaic-virus protein. Phytopathology. 31: 394-410.
42. SCRIVAN, W. A. B. A. COOPER & H. ALLEN. 1961. Pollination of field beans. Outlook on Agr. 3: 69-75.
43. SELMAN, I. W. & S. A. GRANT. 1957. Some effects of nitrogen supply on the infection of tomato plants with tomato spotted wilt virus. Ann. Appl. Biol. 45: 448-55.
44. SEVERIN, H. H. P. 1947. Newly discovered leafhopper vectors of California aster-yellows virus. Hilgardia. 17: 511-23.
45. SIMONS, J. N. 1955. Some plant-vector-virus relationships of southern cucumber mosaic virus. Phytopathology. 45: 217-9.

46. SIMONS, J. N. 1957. Three strains of cucumber mosaic virus affecting bell pepper in the Everglades area of south Florida. *Phytopathology* 47: 145-50.
47. SIMONS, J. N. 1958. Titters of three nonpersistent aphid-borne viruses affecting peopper in south Florida. *Phytopathology*. 48: 265.8.
48. SIMONS, J. N. 1960. Effects of foliar sprays of cytovirin on susceptibility to and transmissibility of potato virus Y in pepper. *Phytopathology*. 50: 109-11.
49. SINHA, R. C. 1960. Some effects of temperature and of virus inhibitors on infection of French-bean leaves by red clover mottle virus. *Ann. Appl. Biol.* 48: 749-55.
50. SOHI, S. S. 1962. Factors affecting the susceptibility of bean plants to inoculation with bean yellow mosaic virus. M. S. Thesis, Oregon State University, Corvallis, Ore.
51. SPENCER, E. L. 1939. The effect of host nutrition on concentration of tobacco-mosaic virus. *Plant Physiol.* 14: 769-82.
52. SPENCER, E. L. 1941. Inhibition of increase and activity of tobacco mosaic virus under nitrogen-deficient conditions. *Plant Physiol.* 16: 227-39.
53. STOREY, H. H. 1928. Transmission studies of maize streak disease. *Ann. Appl. Biol.* 15: 1-25.
54. SWENSON, K. G. 1960. Aphid-virus relationships in the transmission of bean yellow mosaic virus by *Myzus persicae*. *Ann. Ent. Soc. Amer.* 53: 521-4.
55. SWENSON, K. G. 1962. Bean yellow mosaic virus transmission by *Myzus persicae*. *Aust. J. Biol. Sci.* 15: 468-82.
56. SWENSON, K. G. Unpublished data.
57. SWENSON, K. G. & S. S. SOHI. 1961. Factors determining the rate of bean yellow mosaic virus transmission. by the aphid *Myzus persicae*. (Abstract). *Phytopathology*. 51: 67.
58. SWENSON, K. G. & S. S. SOHI. Unpublished data.
59. SYLVESTER, E. S. 1953. *Brassica nigra* virus transmission. *Phytopathology*. 43: 209-14.
60. SYLVESTER, E. S. 1953. Host range and properties of *Brassica nigra* virus. *Phytopathology*. 43: 541-6.
61. SYLVESTER, E. S. 1955. Lettuce mosaic virus transmission by the green peach aphid. *Phytopathology*. 45: 357-70.
62. SYLVESTER, E. S. 1956. Beet yellows virus transmission by the green peach aphid. *J. Econ. Ent.* 49: 789-800.
63. SYLVESTER, E. S. & J. N. SIMONS. 1951. Relation of plant species inoculated to efficiency of aphids in the transmission of *Brassica nigra* virus. *Phytopathology*. 41: 908-10.
64. VOLK, J. 1961. Vorläufige Mitteilung über Versuche zur Übertragung eines nichtpersistenten Virus durch Blattläuse bei verschiedenen Temperaturen. *Proc. 4th Conf. Potato Virus Diseases*. 121-4.
65. WATSON, M. A. 1936. Factors affecting the amount of infection obtained by aphid transmission of the virus Hy. III. *Phil. Trans. Royal Soc. London*. 226: 457-89.
66. WEATHERS. L. G. & G. S. POUND. 1954. Host nutrition in relation to multiplication of tobacco mosaic virus in tobacco. *Phytopathology*. 44: 74-80.
67. WELKIE, G. W. & G. S. POUND. 1958. Manganese nutrition of *Nicotiana tabacum* L. in relation to multiplication of tobacco mosaic virus. *Virology*. 5: 92-109.
68. WELTON, R. E. & K. G. SWENSON. Unpublished data.