Soybean Dwarf Virus: Experimental Host Range, Soybean Germ Plasm Reactions, and Assessment of Potential Threat to U.S. Soybean Production

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ABSTRACT

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Current and recent public cultivars, miscellaneous commercial cultivars, ancestral lines of *Glycine max*, and a broad range of leguminous and nonleguminous species were evaluated for susceptibility to strains of soybean dwarf virus (SDV). Most susceptible hosts were found within the Fabaceae with a few susceptible species in the Chenopodiaceae and Polemoniaceae. There was greater similarity in symptoms and host range between the yellowing strain of SDV (SDV-Y) and the subterranean clover red leaf strain of SDV from New Zealand (SDV-NZ) than between SDV-Y and SDV-D (dwarfing strain). Soybean dwarf virus does not appear to pose an economic threat to U.S. soybean production, but it or virus strains closely related to it may be the cause of widespread disease in forage legumes.

Additional keywords: *Acyrthosiphon pisum*, *Aulacorthum solani*, threat potential

Soybean dwarf virus (SDV) is the causal agent of a severe disease of soybeans (*Glycine max* (L.) Merr.) in Japan (23,24). The subterranean clover red leaf virus (SCRLV), now considered a strain of SDV (1,14), causes a yellowing disease of sugar beets (*Beta vulgaris* L. subsp. *vulgaris*) (15), a leaf-roll disease of broad bean (*Vicia faba* L.), a top-yellowing disease of pea (*Pisum sativum* L. subsp. *sativum*) (2,9), a dwarfing disease of french bean (*Phaseolus vulgaris* L.), and a leaf-reddening disease of subterranean clover (*Trifolium subterraneum* L.) in Tasmania and New Zealand (2,17,29).

Japanese SDV isolates have been grouped into two strains, dwarfing (SDV-D) and yellowing (SDV-Y), on the basis of host range and symptomatology in soybeans (22). Both strains are limited to hosts in the Fabaceae (21,23) and are transmitted specifically by *Aulacorthum solani* (Kaltenbach). The Australasian (Australia and New Zealand) strains of SDV (SCRLV), transmitted by *A. solani*, are similar to SDV-Y (2), although there are some differences in reported host range and number of aphid vectors (21,29).

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Before the introduction of *Acyrthosiphon pisum* into Tasmania in 1980, all field isolations of SCRLV were transmitted only by *A. solani*. By 1986, *A. pisum* had become a major component of the aphid fauna and most SCRLV isolates were *A. pisum* specific (12). In 1983, a SDV-like pathogen was isolated from legumes in California that reacted serologically with SDV (SCRLV) antisera from Australia and was specifically transmitted by *A. pisum* (13). Subsequently, several additional *A. pisum* specific isolations of SDV-like pathogens have been made from *Trifolium* spp. in Florida, Maryland, Mississippi, South Carolina, and Virginia that react with SDV-D antisera in double antibody sandwich-ELISA and produce typical marginal leaf reddening in *T. subterraneum* (18; *unpublished personal data*).

Severity of SDV in soybeans in Japan prompted an intensive search for resistant *G. max* germ plasm and, although no immunity was found in more than 2,300 soybean lines and cultivars exposed to natural disease pressure in the field, sources of tolerance and resistance were identified (especially in early maturing lines) (25,26).

The ARS Foreign Disease-Weed Science Research Unit initiated research on SDV in 1981 in special quarantine containment facilities at Fort Detrick, Frederick, MD (19) as part of the laboratory mission to determine the potential threat SDV would pose to U.S. soybean production should SDV become established in the continental United States. Several aspects of that research have been reported elsewhere (3,4,6,7); we report here on the experimental host range of SDV, the vulnerability of the principal commercial soybean germ plasm, and a summary of our assessment of the potential of SDV to adversely affect commercial soybean production in the United States.

MATERIALS AND METHODS

The yellowing (SDV-Y) and dwarfing (SDV-D) strains of SDV were obtained from T. Tamada, Hokkaido, Japan, and the SCRLV strain of SDV (SDV-NZ) was obtained from J. W. Ashby, Christchurch, New Zealand. Populations of *A. solani* were obtained from T. Tamada (Japan), J. W. Ashby (New Zealand), J. Duffus (USA), and G. Boiteau (Canada). Routine maintenance of the aphid colonies and virus isolates has been described (3,4). The aphid populations were compared as vectors of SDV strains (3), and the Japanese population was selected for all host range studies because of their feeding preference on soybean and their greater efficiency of transmission (3,4). Back inoculations from test plants to healthy soybean seedlings of the cultivar Wayne were done with 10–20 Japanese *A. solani* per seedling.

For DAS-ELISA, paired wells of round-bottom Immulon I microtiter plates (Dynatech, Chantilly, VA) were incubated with 2 μg/ml anti-SDV-D immunoglobulin in 50 mM sodium carbonate coating buffer, pH 9.6 for 2 hr at 30 C. A 100-μl sample of tissue extract in 50 mM phosphate buffer was added and incubated at 4 C overnight. Alkaline phosphatase (Sigma Chemical Company, St. Louis, MO) conjugated immunoglobulins diluted 1:400 in PBS were added, and the plates were incubated overnight at 4 C. Finally 1 mg/ml p-nitrophenyl phosphate in 10% diethanolamine buffer, pH 9.8, was added and the absorbance read at 405 nm with a Bio-Tek Model EL-307 EIA Reader (Winooski, VT) (6).

Seed from 27 selected ancestral soybean cultivars that provide the bulk of the germ plasm base for commercial soybean cultivars and 40 recent and current "northern" public cultivars in maturity groups 000-IV were obtained from Richard Bernard, USDA, ARS,

Plant Physiology and Genetics Research Unit, Urbana, Il. Twenty-four recent and current "southern" cultivars in maturity groups V-VIII were obtained from E. E. Hartwig, USDA, ARS, Soybean Production Research Unit, Stoneville, MS. Seed of 19 selected exotic and domestic soybean lines, leguminous species and cultivars, and nonleguminous species were obtained from USDA Regional Plant Introduction Stations, State Agricultural Experiment Stations, commercial companies, and colleagues. Test species were selected from reported host lists of at least one SDV strain, species related to known SDV hosts, and common virus host range indicators subject to availability. Authenticity of species and cultivar name was determined by seed supplier.

Disease reactions in the 64 public cultivars were rated as mild (little dwarfing, deformation, or discoloration), moderate (dwarfing evident with leaf curling and yellowing), and severe (strong dwarfing and leaf curling [SDV-D], upward cupping of leaf margins, undulated leaf margins, and vivid interveinal yellowing [SDV-Y]).

RESULTS

All soybean lines tested were susceptible to one or more of the three SDV strains. Susceptibility to inoculation differed from relative symptom severity. In certain cultivars, high percentages of the plants were infected but exhibited mild symptoms (Maple Crest, Maple Ridge, McCall), whereas other soybean cultivars had fewer than 50% of the plants infected, but the infected plants had severe symptoms (Bragg). The average percentage infection in the public cultivars was 91%, SDV-D; 87%, SDV-Y; and 78%, SDV-NZ.

The 27 ancestral soybean lines were inoculated with SDV-D and SDV-Y but not SDV-NZ. Most lines were rated as very susceptible to both SDV strains except for Laredo (SDV-Y), Biloxi, Clemson (CNS), Dunfield, and Manitoba Brown (SDV-D), which produced only mild disease reactions.

All 40 public cultivars from maturity groups 000-IV (Northern) were rated as very susceptible to all three SDV strains. Among the 24 cultivars from maturity groups V–IX (Southern), several were rated as intermediate or mild to SDV-NZ and SDV-D; SDV-Y was severe in nearly all cultivars. All 19 cultivars from miscellaneous sources were highly susceptible.

The SDV host range was restricted to the Fabaceae (Leguminosae) except for a few species in the Chenopodiaceae and Polemoniaceae (Table 1). Not all species or cultivars were inoculated with all three SDV strains. Entries were considered susceptible to infection if symptoms were exhibited or if back assay to Wayne soybean or ELISA were positive. In some cases an entry was susceptible to one virus strain but not to others.

Sugar beets were susceptible to all virus strains, although symptoms were not diagnostic. Peanuts (*Arachis hypogaea* L. cv. Florunner) could only be infected with SDV-Y in a symptomless manner, despite repeated inoculations. Sunn hemp (*Crotalaria juncea* L.) gave strong yellowing symptoms with SDV-Y but no symptoms with SDV-D. Several *Lupinus* spp. were hosts of SDV-Y and SDV-NZ but were immune to infection with SDV-D. Topcrop bean was susceptible to all strains but Black Turtle Soup was only susceptible to SDV-Y. California Blackeye cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata*) was symptomless in repeated inoculations with all strains, but plants inoculated with SDV-D produced positive back assays to Wayne soybean and ELISA.

Several *Trifolium* spp. were susceptible to SDV (Table 1), and several *Trifolium* spp. were immune. *Trifolium campestre, T. pratense, T. tembense, T. tomentosum, T. variegatum, T. wormskioldii*, and certain *T. subterranean* cultivars were susceptible to SDV-D but not SDV-Y. *T. repens* was susceptible but symptomless to SDV-Y and SDV-NZ and immune to SDV-D. No infection occurred with any SDV strain in an additional 60 species, in 38 genera, representing 13 different plant families.

DISCUSSION

Host range studies in Japan indicated differences in susceptibility to SDV-D and SDV-Y within the Fabaceae, the host range was limited to the Fabaceae, and the sole aphid vector was *A. solani* (21). The SCRLV strain of SDV from New Zealand and Australia (17, 29) had originally been considered a different virus because it infected hosts outside the Fabaceae and had additional aphid species as vectors. Our results indicate that the host range for all strains extends beyond the Fabaceae, at least 2 different aphid species are vectors of strains of SDV, and the host range and symptomatology of SDV-Y and SDV-NZ infections are more similar than that of SDV-Y and SDV-D.

T. pratense (red clover) was susceptible to SDV-D in Japan (22) but not to SDV-Y. Ashby, et al (2) and Kellock (17) reported it a symptomless host of SDV-NZ (SCRLV) in New Zealand (2); Johnstone and Duffus found it immune to SDV-TAS-C (SCRLV) in Tasmania (10); and we found it susceptible to SDV-D and immune to SDV-Y and SDV-NZ. *T. repens* (white clover) is asymptomatically infected by SDV and most strains can be recovered from inoculated plants (2,17,22); SDV-D could not be recovered from *T. repens* in Japan (22) and we never recovered it from inoculated plants. SDV-NZ and SDV-TAS-C have been purified from *P. sativum* cv. Puget (1,11,27). All our early attempts to infect Puget pea with any SDV strain were negative. Our routine virus harvests from Wayne soybean were 17–20 days postinoculation, and in that time frame no symptoms were visible in Puget. When the plants were allowed to grow 30–35 days postinoculation, yellowing and dwarfing symptoms were common for SDV-Y and SDV-NZ, dwarfing only for SDV-D. However, infection levels in Puget pea were less than 50% of that found in Wayne soybean when inoculated in the same manner. *Erodium* spp. have been cited as susceptible species to strains of SDV (2). In repeated inoculations we were not able to infect *E. circutarium* or *E. texanum* with SDV-D, SDV-Y, or SDV-NZ.

We did not find any diagnostic host which could be used to separate all strains. We could separate SDV-D from SDV-Y and SDV-NZ by using *T. pratense, Lupinus albus*, and *Phaseolus vulgaris* but could not separate SDV-Y from SDV-NZ.

The original objective of the research was to provide data necessary for determination of the potential threat SDV poses to U.S. soybean production. Host range studies were initiated with only SDV-D and SDV-Y, but, with the placement of SCRLV strains in synonymy to SDV (14) and the isolation of SDV-like pathogens in the U.S. (13,18), the research scope had to be modified to include them. We have exained the biology and ecology of known SDV vectors (3,5), explored an experimental SDV host range (Table 1), searched for sources of resistant soybean germ plasm, purified and characterized SDV strains (7), and developed diagnostic tools for identification and quantification of the virus (6,8).

With the information gained from these studies and that published elsewhere, the following general conclusions can be derived on the potential threat of SDV to soybean production in the United States.

1. Soybean dwarf virus exists as a group of closely related strains.

- Strains transmitted by *A. solani* are exotic to the United States and cause diseases of soybeans, peas, french beans, broad beans, and sugar beets (1,2,9,14, 15,17,23,24,29).
- All *A. solani* biotypes tested to date transmit all *A. solani*-specific strains (3,4).
- All SDV-like isolates endemic to the United States are *A. pisum*-specific (13,18).

2. The SDV strains are indistinguishable by conventional diagnostic methods (2,8).

- The SDV-Y strain from Japan is indistinguishable by symptomatology, host range, and serology from the SDV (SCRLV) strains (Table 1) (1,2,6).
- The SDV-D strain is serologically

Table 1. Leguminous and nonleguminous hosts of strains of soybean dwarf virus (artificial inoculation)

Test species/common name	SDV-D			SDV-Y			SDV-NZ		
	Reaction data[a]	Back assay[b]	ELISA[c]	Reaction data	Back assay	ELISA	Reaction data	Back assay	ELISA
Family Chenopodiaceae									
Beta vulgaris L. subsp. vulgaris (sugar beet)	11/22	+	+	11/22	+	+	6/21	+	−
Spinacea oleracea L. cv. Bloomingdale spinach	3/10	−	+	0/17	+	+	1/19	+	+
Family Fabaceae (Leguminosae)									
Alysicarpus vaginalis (L.) DC. (alyce clover)	2/6	+	()	2/4	+	()	N.T.		
Arachis hypogaea L. cv. Florunner	0/10	−	()	0/12	+	()	0/13	−	()
Astragalus sinicus L. (milk vetch)	0/4	+	+	0/4	+	−	0/4	+	+
Crotalaria brachystachys Benth. (Am 61) syn. *C. micans* Link	1/1	+	()	2/2	+	()	N.T.		
C. brevidens var. *intermedia* (Kotschy) Polhill (P.I. 244587)	0/2	+	()	1/1	+	()	N.T.		
C. brownei Bert. in DC. (P.I. 228264)	0/8	−	()	3/9	+	()	N.T.		
C. juncea L. sunn hemp)	0/18	+	()	20/23	+	()	N.T.		
C. saltiana Andr.	1/4	+	()	0/5	+	()	N.T.		
C. spectabilis Roth. (showy crotalaria)	3/11	+	+	12/12	+	+	9/10		+
C. stipularia Desv.	7/7	+	()	2/4	+	()	N.T.		
C. zanzibarica Benth.	16/16	+	()	15/15	+	()	N.T.		
Glycine max (L.) Merr. (110 cvs.)	1392/1698	+	+	1304/1550	+	+	1041/1320	+	+
Indigofera hirsuta L. (hairy indigo)	1/1	+	−	0/1	+	+	1/1	+	+
Lens culinaris Medik. cv. Chilean	30/50	+	+	40/50	+	+	35/50	+	+
cv. Laird	20/25	+	+	20/30	+	+	20/30	+	+
Lespedeza cuneata (Dum. Cours.) G Don (sericea lespedeza)	4/4	+	()	1/5	+	()	N.T.		
L. stipulacea Maxim. (Korean lespedeza)	1/4	+	()	0/3	−	()	N.T.		
L. striata (Thunb. ex Murr.) Hook & Arn. (common lespedeza)	0/5	+	()	0/3	+	()	N.T.		
Lupinus albus (white lupine)	0/46	−	−	17/48	+	+	8/10	+	+
L. bicolor Lindl. (pigmy-leaved lupine)	0/8	−	()	5/10	+	()	N.T.		
L. concinnus J.G. Agardh.	1/22	+	+	5/16	+	+	0/5	+	+
L. hispanicus Boissier & Reuter	0/8	−	()	2/9	+	()	N.T.		
Medicago arabica (L. Huds. (spotted burclover)	10/10	+	()	7/8	+	()	N.T.		
M. aschersoniana Urb.	8/10	+	()	2/8	+	()	N.T.		
M. gerardii Waldst. & Kit.	2/2	+	()	N.T			N.T.		
M. littoralis Rohde ex Loisel	3/3	+	()	3/4	+	()	N.T.		
M. lupulina L. (black medic)	16/57	+	()	8/40	+	()	N.T.		
M. murex Willd.	5/5	+	()	6/7	+	()	N.T.		
M. obscura Retz.	12/17	+	()	7/20	+	()	N.T.		
M. orbicularis (L.) Bartal. (Buttonclover)	2/8	+	()	1/5	+	()	N.T.		
M. polymorpha L. (California burclover)	2/2	+	()	1/2	+	()	N.T.		
M. turbinata (L.) All.	1/4	+	()	3/9	+	()	N.T.		
Phaseolus vulgaris L. (3 cvs.)	0/20	+	+	8/14	+	+	5/14	+	+
Pisum sativum L. subsp. *sativum* (34 cvs.)	26/51[d]	+	+	47/81[d]	+	+	102/166[d]	+	+
Trifolium alexandrium L. (berseem)	10/19	+	()	6/18	+	()	N.T.		
T. argutum Banks & Sol.	14/15	+	()	2/12	+	()	N.T.		
T. arvense L. (rabbit foot clover)	6/7	+	()	1/17	+	()	N.T.		
T. campestre Schreb. (large hop clover)	4/4	+	()	0/3	−	()	N.T.		
T. dubium Sibth. (small hop clover)	3/3	+	()	1/4	+	()	N.T.		
T. hybridum L. (alsike clover)	11/19	+	()	4/24	+	()	N.T.		
T. incarnatum L. (Crimson clover)	6/9	+	()	3/11	+	()	N.T.		
T. pratense L. cv. Kenland (red clover)	13/28	+	+	0/30	−	−	0/10	−	−
T. repens L. (white [ladino] clover)	0/31	−	−	0/31	+	+	0/11	+	+
T. smyrnaeum Boiss.	7/7	+	()	4/10	+	()	N.T.		
T. subterraneum L. (subterranean clover)	201/379[e]	+	+	268/407[e]	+	+	91/94[e]	+	+
T. tembense Fles.	0/3	+	()	0/2	−	()	N.T.		
T. tomentosum L.	1/3	+	()	0/2	−	()	N.T.		
T. trichocephalum Bieb.	0/6	+	()	2/6	+	()	N.T.		
T. variegatum Nutt. (whitetip clover)	7/8	+	()	0/6	−	()	N.T.		
T. wormskioldii Lehm. (seaside clover)	2/6	+	()	0/7	−	()	N.T.		
Vicia faba L. (broadbean)	2/6	+	()	4/8	+	()	N.T.		
V. lutea L. (yellow vetch)	1/4	+	()	0/3	−	()	N.T.		
V. sativa L. subsp. *sativa* (common vetch)	15/24	+	()	3/21	+	()	N.T.		
Vigna unguiculata (L.) Walp. subsp. *unguiculata* cv. California Blackeye	0/20	+	+	0/20	−	−	0/17	−	−
Family Polemoniaceae									
Phlox drummondii (Hook) (mixed colors)	3/3	−	+	3/3	+	+	3/3	+	+

[a] Number with symptoms/total plants inoculated; N.T. = no tests run.
[b] + = Wayne assay with symptoms; − = Wayne symptomless; () = specific assay not run.
[c] + = ELISA value greater than positive threshold of $\bar{x} + 4s$; − = below positive threshold; () not tested by ELISA.
[d] 5 entries (SDV-D), 11 entries (SDV-Y), 32 entries (SDV-NZ).
[e] 48 entries (SDV-D), 54 entries (SDV-Y), 3 entries (SDV-NZ).

closely related to SDV-Y but can be separated by soybean reactions and ancillary host range (Table 1) (23).

- SDV-D, SDV-Y, and SDV-NZ have slightly different dsRNA profiles (8).

3. Ecological and biological characteristics separate oriental and occidental biotypes of *A. solani* (5).

- Only biotypes from Japan colonize soybeans (3).
- Japanese biotypes differ morphometrically from occidental biotypes (5).
- All biotypes (populations) of *A. solani* tested in our laboratory feed on soybean but only Japanese biotypes preferred soybean as a "secondary host"; all occidental populations moved from soybean to leaf lettuce, clover, curly dock, or wild geranium if given an opportunity (3).
- Although populations of *A. solani* have been isolated from many areas in the United States, the frequency of occurrence is limited in time and location (20,28).

4. The host range of all SDV strains and SDV-like strains are largely limited to the Fabaceae including *Trifolium* spp., which may serve as virus reservoirs.

- *Trifolium* spp. are overwintering hosts for *A. solani* in Japan, New Zealand, and Australia (9,14,16), subterranean clover red leaf is a major virus disease problem in Australasia (2,17,29), and *Trifolium* spp. are a major source of SDV-like isolates in the United States (18, unpublished personal data).
- No immunity has been located in *Glycine max* germ plasm, but sources of tolerance and resistance have been identified (25,26).

Based on our current knowledge, we believe that unless Japanese biotypes of *A. solani* should become established in the United States or an endemic soybean colonizer of *A. solani* arises, SDV should not pose a serious potential threat to U.S. soybean production. However, with the increasing identification of SDV-like infections in our forage legumes, we cannot make an authoritative statement on the potential of SDV in other crops. As an outgrowth of this study, we have gained some understanding of the distribution of previously unrecognized endemic luteovirus infections in our forage legumes.

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LITERATURE CITED

1. Ashby, J. W., and Kyriakou, A. 1982. Purification and properties of subterranean clover red leaf virus. N.Z. J. Agric. Res. 25:607-612.
2. Ashby, J. W., Teh, P. B., and Close, R. C. 1979. Symptomatology of subterranean clover red leaf virus and its incidence in some legume crops, weed hosts, and certain alate aphids in Canterbury, New Zealand. N.Z. J. Agric. Res. 22:361-365.
3. Damsteegt, V. D., and Hewings, A. D. 1986. Comparative transmission of soybean dwarf virus by three geographically diverse populations of *Aulacorthum* (=*Acyrthosiphon*) *solani*. Ann. Appl. Biol. 109:453-463.
4. Damsteegt, V. D., and Hewings, A. D. 1987. Relationships between *Aulacorthum solani* and soybean dwarf virus: Effect of temperature on transmission. Phytopathology 77:515-518.
5. Damsteegt, V. D., and Voegtlin, D. J. 1990. Morphological and biological variation among populations of *Aulacorthum solani* (Homoptera:Aphididae), the vector of soybean dwarf virus. Ann. Entomol. Soc. Am. In Press.
6. Hewings, A. D., Damsteegt, V. D., Bird, A. E., and Tolin, S. A. 1990. Variations in serologically detectable antigen of soybean dwarf virus in soybean leaflets as a function of time after inoculation and plant age. Plant Dis. 74:000-000
7. Hewings, A. D., Damsteegt, V. D., and Tolin, S. A. 1986. Purification and some properties of two strains of soybean dwarf virus. Phytopathology 76:759-763.
8. Hewings, A. D., Murphy, J. F., D'Arcy, C. J., and Damsteegt, V. D. 1986. Double-stranded RNA's for identification and classification of luteoviruses. Phytopathology 76:1062.
9. Johnstone, G. R. 1978. Diseases of broad bean (*Vicia faba* L. major) and green pea (*Pisum sativum* L.) in Tasmania caused by subterranean clover red leaf virus. Aust. J. Agric. Res. 29:1003-1010.
10. Johnstone, G. R., and Duffus, J. E. 1984. Some luteovirus diseases in Tasmania caused by beet western yellows and subterranean clover red leaf viruses. Aust. J. Agric. Res. 35:821-830.
11. Johnstone, G. R., Duffus, J. E., Munro, D., and Ashby, J. W. 1982. Purification of a Tasmanian isolate of subterranean clover red leaf virus, and its serological interactions with a New Zealand isolate and other luteoviruses. Aust. J. Agric. Res. 33:697-703.
12. Johnstone, G. R., and Guy, P. L. 1986. Epidemiology of viruses persistently transmitted by aphids. Proceedings of the Workshop on Epidemiology of Plant Virus Diseases, IX/1-IX/7. International Society of Plant Pathology, Orlando, FL. Aug. 6-8, 1986.
13. Johnstone, G. R., Liu, Hsing-Yeh, and Duffus, J. E. 1984. First report of a subterranean clover red leaf-like virus in the western hemisphere. (Abstr.) Phytopathology 74:795.
14. Johnstone, G. R., and McLean, G. D. 1987. Virus diseases of subterranean clover. Ann. Appl. Biol. 110:421-440.
15. Johnstone, G. R., and Munro, D. 1980. Yellows of sugar beet caused by subterranean clover red leaf virus. Australas. Plant Pathol. 9:4-5.
16. Kanehira, O. 1978. Seasonal prevalence of foxglove aphid *Acyrthosiphon solani* (Kaltenbach) in soybean varieties—Differences in resistance to the soybean dwarf disease. Bull. Hokkaido Prefect. Agric. Exp. Stn. 40:51-60.
17. Kellock, A. W. 1971. Red-leaf virus—A newly recognized virus disease of subterranean clover (*Trifolium subterraneum* L.). Aust. J. Agric. Res. 22:615-624.
18. McLaughlin, M. R., Damsteegt, V. D., Duffus, J. E., and Hewings, A. D. 1988. Subterranean clover red leaf (soybean dwarf)-like luteovirus found in Mississippi. (Abstr.) Phytopathology 78:1584.
19. Melching, J. S., Bromfield, K. R., and Kingsolver, C. H. 1983. The plant pathogen containment facility at Frederick, Maryland. Plant Dis. 67:717-722.
20. Palmer, M. A. 1952. Aphids of the Rocky Mountain region. Vol. V. The Thomas Say Foundation. A. B. Hirschfeld Press. Denver, Colorado. 452 pp.
21. Tamada, T. 1970. Aphid transmission and host range of soybean dwarf virus. Ann. Phytopathol. Soc. Jpn. 36:266-274.
22. Tamada, T. 1973. Strains of soybean dwarf virus. Ann. Phytopathol. Soc. Jpn. 39:27-34.
23. Tamada, T. 1975. Studies on the soybean dwarf disease. Rep. Hokkaido Prefect. Agric. Exp. Stn. 25:1-144.
24. Tamada, T., and Kojima, M. 1977. Soybean dwarf virus. No. 179 in: Descriptions of Plant Viruses. Commonwealth Mycological Institute and Association of Applied Biologists, Kew, Surrey, England. 4 pp.
25. Tanimura, Y., Matsukawa, I., Chiba, I., and Banba, H. 1982. A survey of resistant varieties to soybean dwarf virus disease. Misc. Publ. Hokkaido Prefect. Agric. Exp. Stn. 13. 120 pp.
26. Tanimura, Y., and Tamada, T. 1976. Breeding for resistance to soybean dwarf disease: I. Resistance of soybean varieties to soybean dwarf disease. Bull. Hokkaido Prefect. Agric. Exp. Stn. 35:8-17.
27. Waterhouse, P. M., and Helms, K. 1984. Purification of particles of subterranean clover red leaf virus using an industrial-grade cellulase. J. Virol. Methods 8:321-329.
28. Wave, H. E., Shands, W. A., and Simpson, G. W. 1965. Biology of the foxglove aphid in the northeastern United States. U.S. Dep. Agric. ARS Tech. Bull. 1338. 40 pp.
29. Wilson, J., and Close, R. C. 1973. Subterranean clover red leaf virus and other legume viruses in Canterbury. N.Z. J. Agric. Res. 16:305-310.