MISSISSIPPI SOYBEAN PROMOTION BOARD PROJECT NO. 66-2014 (YEAR 2) 2014 FINAL REPORT

Title: Soybean vein necrosis virus in Mississippi

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BACKGROUND AND OBJECTIVES

A new, widespread disease with virus-like symptoms was observed initially in soybean fields in Tennessee and Arkansas in 2008 followed by characterization of a novel, thrips-transmitted virus named *Soybean vein necrosis virus* (SVNV).

The virus was consecutively identified in Kansas, Missouri, Illinois, Kentucky and Mississippi and recently reported also from New York, Maryland, Delaware, Virginia in 2011, and finally in 2012, from soybean fields in Pennsylvania, Indiana, Wisconsin, Michigan and Ontario.

Despite the fact that SVNV has already been reported from a number of US states, the overall knowledge of this virus is still very limited. Therefore, this study (sponsored by MSPB) is designed to complement an on-going USB project and to further current knowledge about this emerging and potentially important pathogen of soybean in Mississippi for the benefit of soybean growers in the state/nation. The planned project duration is three years.

This project has multiple goals:

- To observe and annotate symptoms observed on infected plants and estimate incidence of SVNV in soybean fields in MS
- To identify alternative hosts that may harbor the virus
- To study genetic diversity of SVNV population in MS

REPORT OF PROGRESS/ACTIVITY

Preamble

Due to overall budget cuts in 2015, the final (third) year of this project was not funded which caused difficulties in generating more complete data, as we originally planned. However, after a considerable effort, we successfully executed the majority of activities in order to provide meaningful results for soybean farmers in Mississippi and for the scientific community in USA and abroad.

Objectives 1 and 2.

During funded period of this project (2013 and 2014) we dedicated a total of 25 days to scouting of soybean fields across Mississippi in order to observe and notify of virus symptoms and to collect samples for further lab testing and analyses. In order to reduce overall costs and to increase efficiency, several trips were often performed jointly with other MSU personnel involved in soybean research sponsored by MSPB (i.e. Drs. Billy Moore and Tom Allen, and Mr. Jeff Standish).

We have scouted soybean fields in 37 counties in Mississippi (see map) and collected a total of 456 samples. Symptoms observed on virus-infected samples varied and consisted of vein discoloration and necrosis, mosaic/mottling-like, general stunting, leaf deformation, crinkling, rugosity, etc. Preliminary laboratory analyses consisted of 4 virus-specific tests for: *Soybean vein necrosis virus* (SVNV), *Bean pod mottle virus*, (BPMV), *Soybean mosaic virus* (SMV), and *Tobacco ring spot virus* (TRSV). We also

routinely applied and one general (potyvirus genus-specific) ELISA test. These tests showed the presence of all target viruses in MS in various rates. The most prevalent viruses by far were *Soybean vein necrosis virus* followed by *Bean pod mottle virus*.

Soybean vein necrosis virus was found in 16 Counties in 2013 (see map in Fig. 1). Curiously, we failed to find any SVNV-infected samples in several southern counties surveyed that year. Nevertheless, in 2014 we extended "geographic coverage" of SVNV isolates by collecting samples from the southeast corner of Mississippi.



Figure 1. Map of Mississippi showing counties surveyed during 2013 season (indicated by both types of stars). Dark stars (*****) indicate counties where SVNV was found.

Severity of SVNV symptoms varied from very mild (initial stage of infection or due to resistant soybean genotype?) to multiple extensive necrotic areas covering the majority of the leaf blade in advanced stages of infections in susceptible varieties (Fig. 2 A-C)



Figure 2. SVNV symptoms observed on affected soybean plants during the survey in Miss. Symptoms were always associated with major veins and differed in intensity from very mild (panel A) to severe symptoms covering considerable surface of the leaf blade (panel C), eventually turning necrotic as the diseases progresses (not shown).

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Timing of SVNV symptom appearance in the field varied among different project years. In 2013 the virus infections in Miss. could be observed only from mid-July onwards. Considering that 2013 was characterized by an unusually rainy springtime, we assume that postponed timing of soybean planting in many areas of MS resulted in later appearance of SVNV symptoms than reported in literature. However, in 2014, first SVNV symptoms could be observed from mid-June. SVNV symptoms were much more frequent later in the season (and on late soybeans). SVNV was studied in more detail and results are presented further in this report (see results of Objectives 3 and 4).

Distribution map of BPMV was generally similar to that presented for SVNV and was present across the state. Incidence of BPMV symptoms in affected fields varied from occasional symptomatic plants to almost 50-60% incidence in affected fields with serious damages (as observed for example in Washington and Bolivar Counties). Those fields were poorly managed and were heavily infested by BPMV vector – bean leaf beetle (*Cerotoma trifurcata*).

Soybean mosaic virus was found in several different locations (Leaky, Amite, Yazoo, and Washington Counties) over the 2-year survey and was probably introduced by contaminated seeds. *Tobacco ring spot virus* was the least frequent virus among the tested ones as it was found in only 5 samples originating from 2 different localities (Pontotoc and Monroe Counties).

Curiously, about 5% of symptomatic samples did not react with any of 4 viruses we tested for. Due to budget restrictions it was impossible to ascertain each single symptomatic sample that resulted negative in tests against SVNV, BPMV, SMV and TRSV. However, in order to understand what are additional viruses in Miss., we selected few samples for further characterization by biological, molecular and electron microscope characterization (see Chapter: Additional viruses).

As SVNV is transmissible by thrips, insect population was monitored in two different locations (Oktibbeha and Stone Counties) by applying and changing 4 yellow sticks/field on a weekly basis in 2013. In 2014 this activity was compromised by unfortunate circumstances and was not considered for this report. The peak of thrips population in studied fields corresponded to early late May/June (500-650 thrips counted) followed by relatively "flat phase"; i.e. capture of 150-200 thrips per week in all locations. With help of Mr. R.C. Stephenson (MSU County Extension Agent), we attempted to preliminarily identify thrips to the species level: ~ 60% of captured thrips were identified as soybean thrips, ~30% as flower thrips, and ~10% as tobacco thrips.

Objective 3.

A part of this study focused on understanding the ecology and epidemiology of SVNV by searching for possible alternative hosts that may serve as reservoirs for the virus. Therefore, we also collected and tested 145 samples of native flora (i.e. weeds), either from within fields or from the edges of several productions fields from different parts from the state.

The collected samples embraced redroot pigweed, pokeweed, horsenettle, dogfennel, horse weed, goat weed, wild radish, curly dock, Sesbania, Johnsongrass, *Chenopodium* spp, various clover species, coffee weed, morning glory and few not identified weeds. The only species that resulted naturally infected by SVNV was morning glory and was found in two different fields: in addition to the original infection from Monroe Co, an additional SVNV-infected sample of morning glory collected from Washington Co. However, morning glory samples from other 6 locations resulted negative for SVNV.

Nevertheless, in the framework of the activities aimed at identification of alternative hosts for SVNV in Mississippi, we have particularly targeted wild onion and kudzu.

Wild onion was targeted because it is (i) widespread in Miss., (ii) it is an early emerging plant, and (iii) it is a good host for thrips (possible vectors for SVNV). In addition, we surveyed wild and cultivated onions because they are susceptible to *Iris yellow spot virus* (IYSV), a virus taxonomically related to

SVNV (belong to the same genus as SVNV). However, none of 78 onion samples collected for this project throughout the state resulted infected by SVNV (Our thanks to Dr. D. Nagel – MSU for help in collecting onion samples statewide).

After discovering that few symptomatic samples collected in the first project year resulted infected by TRSV (see a separate section for more detailed results) and inconclusive initial results regarding Soybean vein necrosis virus (few samples resulted positive in one test but failed in independent confirmatory tests), our investigation focused on this particular invasive plant that covers millions of acres in Miss. and southeastern USA as a potential host for SVNV. To that aim we collected 85 kudzu samples collected from 15 counties and tested by serological test (DAS-ELISA) for the infections by this virus. Curiously, three samples (collected in Carroll and Marshall Counties) reacted clearly positive in ELISA with specific SVNV antibodies. In order to verify/confirm ELISA results, virus-specific RT-PCR tests were performed on nucleic acid extracts from all ELISA-positive samples along with three SVNV-free kudzu plants and controls, represented by SVNV-infected and healthy soybeans. A specific DNA band of 236 bp was only amplified from the three ELISA-positive kudzu samples and positive controls. The PCR products were directly sequenced in both directions and confirmed to be SVNVspecific as they shared 96-99% nt identity with corresponding region of the SNSV reference isolate (GenBank Acc No GU722319). Therefore, in this study we identified kudzu as potential reservoir for SVNV infections. Additionally, in the framework of collaborative study, under greenhouse conditions colleagues from University of Arkansas successfully inoculated kudzu seedlings with SVNV using first instar larvae of soybean thrips (Neohydatothrips variabilis Beach). Results of study on kudzu as a new host for SVNV are reported in a manuscript submitted to a peer-reviewed journal on June 18, 2016 (Zhou, Aboughanem-Sabanadzovic, Sabanadzovic and Tzanetakis).

We also started a greenhouse-based study on possible hosts of SVNV as we ordered seeds of 25 legumes common in Miss. from the USDA National Seed Storage Laboratory. Unfortunately, the majority of this study was planned for the third project year for which we did not get funded; therefore, we only tested 6 species (four different *Trifolium* spp, *Desmodium cuspidatum* and *Crotolaria ochroleauca*) for SVNV susceptibility by mechanical inoculation. None of the plants belonging to these 6 botanical species resulted to be susceptible to SVNV infections in mechanical transmission tests in the greenhouse.

In addition to 6 legumes common in Miss., for the experimental host range study we used several additional plants belonging to different botanical families. For this experiment young symptomatic leaves from the field collected soybean sample referred to as SVNV-Ok01, were crushed in the presence of phosphate buffer 0.1M pH7.2. The slurry was rubbed over cellite-dusted leaves of a range of herbaceous plants: *Nicotiana tabacum* cv. Turkish (tobacco), *N. benthamiana, Capsicum annuum* cv. 'Sweet banana' (pepper), *Solanum lycopersicum* cvs. 'Celebrity' and 'Big Boy' (tomato) [fam. Solanaceae], *Chenopodium quinoa* [fam. Chenopodiaceae], *Phaseolus vulgaris* cv. 'Black Valentine' (bean) [fam. Fabaceae], *Cucumis sativus* cvs 'Straight Eight' and 'Long Green' [fam. Cucurbitaceae]. Each species/cultivars were represented by at least 5 replicates. Inoculated plants were kept in a greenhouse under natural light and were checked daily for the symptom appearance for a total period of 6 weeks. Presence/absence of latent infections were ascertained by ELISA.

Two out of nine tested plants were susceptible to SVNV-Ok01. *Nicotiana bethamiana* developed local lesions on inoculated leaves 6-7 DPI (Fig. 3, panel A) and developed systemic infection resulting in necrosis of the apical portion of the affected plant (Fig. 3, panel B). Infected plants collapsed approximately a month post-inoculation and died (Fig. 3, panel C). Tobacco plants (*N. tabaccum*) reacted to SVNV inoculation by producing chlorotic local lesions on inoculated leaves 5-7 DPI (arrows in Fig , panels D and E).



Figure 3. Symptoms observed on *Nicotiana benthamiana* (A-C) and *N. tabaccum* plants mechanically inoculated with the isolate SVNV-Ok1.

In order to further the study of SVNV we performed electron microscope-based investigation on changes in the susceptible hosts at the cellular level caused by SVNV infections. The study on cytopathologial effects of SVNV infections on the host was executed on artificially inoculated *Nicotiana benthamiana* and field collected soybean plant SVNV-Ok1. In general, modifications due to SVNV infections did not vary between the two hosts and consisted of the presence of densely stained amorphous masses found in the cytoplasm and interpreted as viroplasm and plenty of virus particles in various stages of maturation (see Fig 4). Viroplasm, likely composed of ribonucleoprotein, are assumed to be involved in early phases of virion formation. Mature virus particles appeared nearly spherical in shape, 80 nm in diameter, and were grouped in membrane-bound compartments that contained no other structured components. We thank Ms Amanda Lawrence for skillful help in electron microscopy.



Figure 4. Ultrathin sections of *Nicotiana benthamiana* leaves infected with Miss. isolate of SVNV (SVNV-Ok1) showing inclusions, possible viroplasm and virus particles in different stages of maturation (panels A, B, C). Mature, cisternae-bound virus particles are easily found throughout the specimens and enlarged in panel C. Similar membrane-bound virions were observed in SVNV-infected soybeans (panel D).

Objective 4.

Study of SVNV population structure was carried out in order to provide an insight into virus evolution and to allow better understanding epidemiological nature of the virus (i.e. presence of distinct genetic variants with potentially different biological/pathological properties).

Computer-based analyses of SVNV genome sequences resulted in identification/design of three sets of primers for each of the two target genomic regions: RNAs 2 and 3 (six primer sets in total). After a preliminary test performed on limited number of SVNV isolates, we identified the two best-performing primer sets (one for each genomic RNA) that were applied later in this study on a larger number of isolates collected in Miss. A total of 25 SVNV isolates collected in 2013 and 2014 from 16 different counties (Coahoma, Bolivar, Sunflower, Washington, Lafayette, Montgomery, Pontotoc, Oktibbeha, Leake, Prentiss, Lowndess, Webster, Wayne, Jones, Marion, Union) were included in this study.

We successfully amplified and cloned a 1,424 and 1,294 nt long portions of genomic RNA2 and RNA3, respectively (see Fig. 5). We cloned amplicons for all isolates in pGEM-TEasy vector and selected 3-5 clones per isolate for custom sequencing. Sequence data were assembled/analyzed by the ApE program in order to generate consensus for each isolate.

Results of pairwise comparisons between isolates collected from distinct geographical locations and in different seasons (2013 and 2014) showed that the SVNV population in Mississippi has limited variability. The maximum nucleotide sequence variation in one of the studied genome portion (RNA2) is 1.54% (between isolates collected in Leake and Jones Counties), while RNA3 region showed up to 3% nt differences in the studied genome portion among the most distant isolates. Few SVNV isolates collected from the same field in the same year (i.e. isolates collected in Lafayette and Prentiss Counties) resulted 100% between each other.



Figure 5. Schematic representation of SVNV genome. Genomic regions studied in this project are indicated by red arrows.

In phylogenetic analyses, independent of the method used for inferring relationships (i.e. Neighbor joining or Maximum Likelihood), the SVNV isolates grouped in two clades with no specific reference to geography. However, the topology of the tree constructed for RNA2 differed from that of RNA3 (see Fig. 6). The incongruent phylogenetic relationships suggest different evolutionary history shaped possibly by frequent recombination events in SVNV population and possibly reassortments of genetic materials among isolated in the vector (thrips) or in host plants. This study will be continued to include analyses of RNA1 of the same isolates. The results will be submitted for publication in a peer-reviewed journal along with cytopathological observations.



Figure 6. Phylogenetic tree based on 1424 and 1294 nt long fragments of RNAs 2 and 3 respectively of SVNV isolates from Miss. and reference isolate from Tenn. The tree was constructed in MEGA7 software applying Neighbor-joining method.

Multiple alignments of our data with the reference isolate of SVNV showed their perfect colinearity (no deletions or insertions) concerning RNA3. However, studied genomic portion of RNA2 in all 25 studied Miss. isolates contained a three nucleotide deletion compared to the Tennessee isolate (Fig 7). Whether this differences will have any biological meaning is yet to be understood.



Figure 7. Nucleotide and amino acid alignments of a portion of RNA2 of SVNV isolates from MS compared to reference isolate Milan from Tenn. As shown in red letters, all isolates from Miss. have a deletion of one codon (coding for proline) compared to isolate from Tenn. Deletion points are indicated by arrows. Variable region between Miss. isolates and reference is represented by blue box.

ADDITIONAL DATA GENERATED IN THIS PROJECT

Discovery of kudzu as a host for *Tobacco ringspot virus*

While looking for alternative hosts for SVNV, we collected few kudzu patches showing vein feathering/discolorations and leaf deformations symptoms (Fig 8, A, B) that resulted negative for SVNV. Therefore, they were submitted to lab tests for other 3 major viruses affecting soybeans (*Bean pod mottle virus -* BPMV, *Soybean mosaic virus -* SMV and *Tobacco ring spot virus -* TRSV) in order to investigate possible role of this invasive plant as alternative host for other-than-SVNV major soybean viruses. Both symptomatic samples resulted positive for TRSV. Indeed, virus could be purified (Fig. 9A) and induced typical bud blight symptoms when inoculated on soybean seedlings (Fig. 9B).

Curiously, out of 127 kudzu samples collected from 28 counties in 2013, a total of 11 samples collected from 8 different counties of Mississippi resulted TRSV-infected (see map of TRSV distribution in Miss. in Fig 10).



Figure 8. Discolorations along the main veins (A) and vein necrosis resulting in malformation of leaf shape observed on TRSV-infected patches of kudzu in 2013 in Mississippi.



Figure 9. **A.** Electron micrograph showing partially purified virions (virus particles) of TRSV. **B.** Typical tip necrosis symptoms induced by isolate of TRSV from kudzu inoculated on soybean.

Eleven kudzu samples collected in 8 different counties were positive for TRSV. To confirm these results, one step RT-PCR test was performed on total nucleic extracts from all ELISA-positive and 4 negative kudzu samples using TRSV-specific primers. A PCR product of 766 bp was present in all TRSV samples and positive controls, whereas no visible bands were present in negative samples. PCR products generated from samples, collected in Kemper, Tippah and Jefferson Davis Counties, were cloned and custom sequenced. Pair-wise comparisons indicated conserved nucleotide (95 to 98%) and amino acid (98 to 99%) contents among sequenced products. Kudzu isolates from Miss. shared 91 to 96% and 98 to 99% conserved nucleotides and amino acids, with TRSV sequences currently available in the NCBI/GenBank database. This is the first report of TRSV infection of kudzu in Mississippi. Possible implications to the soybean industry are yet to be determined, however these data (along with discovery of natural infections of SVNV in kudzu) strongly suggest that kudzu, due to its widespread distribution in the region, may represent a major reservoir of TRSV in the southeastern United States.

This is the first record of infections of kudzu by TRSV in Miss. and demonstrates that kudzu may play a role as a reservoir for this virus reported to induce bud blight symptoms in affected soybeans.



Figure 10. Map reporting counties where kudzu patches infected with TRSV were found during the survey (indicated with red dots).

The results of this study were published in Plant Disease (Aboughanem-Sabanadzovic et al., 2014).

Additional viruses discovered and partially characterized in this study

As previously mentioned, about 5% of symptomatic samples did not react with any of 4 viruses we tested for. In order to understand what are additional viruses in Miss., due to greenhouse space limitations and budget cuts, we selected few samples for further studies.

Two symptomatic soybean samples collected in Oktibbeha and Tishomingo Counties were inoculated onto young seedlings of 2 soybean varieties in a greenhouse. As presented in Figure 11, sap from two soybean samples (collected from Oktibbeha and Tishomingo Counties) induced symptoms on variety AG4730 confirming that originally observed symptoms were indeed virus-induced. However, when compared to each other, symptoms observed on AG4730 plants were different (see Fig. 11), indicating that different viruses infect samples collected from production fields in these two counties.



Figure 11. Symptoms on variety AG4730 induced by viruses collected in Oktibbeha Co. (left) and Tishomingo Co. (right). Differences in symptoms indicate possible infections by two distinct viruses.

Molecular cloning and sequencing results showed that the virus from Oktibbeha Co. resulted to be an isolate of *Peanut mosaic virus* (PeMoV) as it shared 98% of amino acid sequence identity, in the portion used for comparison, with isolate Habin reported from South Korea (GenBank Acc No KF977830). The same virus was found infecting soybeans in Montgomery and George Counties as well.

Analyses of the genome of a virus isolated from Tishomingo Co. (Belmont) suggested that the virus is an isolate of *Bean yellow mosaic virus* (BYMV) as it resulted closest to isolate LPexFB of that virus reported from faba bean in Australia (GenBank Acc No HG970868) and from lisianthus from Taiwan (GenBank No AM884180) sharing 85% and 79% nt identity. In 2014 BYMV was identified in samples from Ft. Adams and Oktibbeha Co.

After dsRNA isolation and electrophoretic analysis, soybean plant displaying severe leaf crinkling symptoms collected in Weir (Chocktaw Co. – see Fig 12 panel A) contained patterns resembling cucumovirus infections (Figure 12, panel B lane 2). In RT-PCR tests performed using degenerate primers for the taxon cucumovirus, amplified DNA band of expected size from previously mentioned sample and another sample affected by similar symptoms (Fig. 12C Lanes 1 and 2) as well as from a positive control (Fig 12, panel C lane 4). Cloning and sequencing of RT-PCR product showed that virus from crinkly soybean plants is an isolate of *Peanut stunt virus*. Soybean isolate from Miss. shared 96% identical nucleotides with strain ER reported from Georgia.



Several other samples with obvious virus symptoms were preserved at -80C and await additional funding for their identification.

IMPACTS AND BENEFITS TO MISSISSIPPI SOYBEAN PRODUCERS

This project contributed to further the knowledge of SVNV in Mississippi. Probably the most important impact of this study is identification of kudzu, a widespread invasive legume plant in MS and southern USA, as a potentially important reservoir for two important viruses of soybean: SVNV and TRSV. We also confirmed natural infections of morning glory by SVNV, indicating the importance of this common plant in the epidemiology of this virus. Furthermore, in the framework of this project we characterized local populations of this virus and possible forces shaping its evolution. In addition, two sets of primers developed in this study contribute to the better diagnostics for this emerging virus.

Finally, despite the fact that SVNV and BPMV are still prevailing viruses in Miss., this study identified several other viruses present in production fields as well (i.e. PeMoV. BYMV, PSV, SMV), as well as many "unknowns", showing that the "virome" (community of viruses) of soybean is much more complicated than previously known and might warrant a separate, focused study.

END PRODUCTS

<u>Peer-Reviewed publications</u>

Aboughanem-Sabanadzovic N., T.W. Allen, M. Broome, A. Lawrence, W.F. Moore and **S. Sabanadzovic**, 2014. First Report of kudzu (*Pueraria montana*) infections by *Tobacco ringspot virus* in Mississippi. Plant Disease 98: 1746

Zhou J., **N. Aboughanem-Sabanadzovic**, **S. Sabanadzovic** and I.E. Tzanetakis, 2016. First Report of kudzu (*Pueraria montana*) infections by *Soybean vein necrosis virus* in the United States. Plant Disease (submitted)

Aboughanem-Sabanadzovic N., A. Lawrence, R.C. Stephenson and **S. Sabanadzovic**, 2016. Study of population structure of *Soybean vein necrosis virus* and its cytopathological effects in susceptible hosts. Journal of Plant Pathology (in preparation)

Book Chapters

Zhou J., L. Domier, **S. Sabanadzovic** and I.E. Tzanetakis, 2015. Soybean vein necrosis. In: Hartman, G.L., Rupe, J.C., Sikora, E.J., Domier, L.L., Davis, J.A., Steffey, K.L. (Eds.): Compendium of soybean diseases and Pests, 5th Edition. American Phytopathological Society Press, St. Paul, MN, 124-125.

Web Presentations

In collaboration with Dr. Tom Allen and Dr. Angus Catchot, we posted a blog on viruses in MS soybean fields acknowledging financial support by the Mississippi Soybean Promotion Board. Post is available at:

http://www.mississippi-crops.com/2013/09/27/soybean-viruses-cause-important-diseases-too/

Conference Presentations

<u>Aboughanem-Sabanadzovic N.</u>, T.W. Allen, R.C. Stephenson, A. Lawrence, W.F. Moore and S. <u>Sabanadzovic</u>, 2014. Importance of kudzu as a reservoir for soybean viruses: Preliminary data. 2014 SSDW Annual Conference, March 5-6, 2014, Pensacola Beach, FL.

Sabanadzovic S., R. C. Stephenson & N. Aboughanem-Sabanadzovic, 2014. Soybean vein necrosis virus in Mississippi. Abstracts 2014 Joint Annual Meeting of the American and Canadian Phytopathological Societies (Minneapolis, MN) Phytopathology 104 (Suppl. 3): S3.101.

Aboughanem-Sabanadzovic N., W. Moore, T. W. Allen, A. Lawrence & **S. Sabanadzovic**, 2014. Kudzu as a reservoir for soybean viruses. *Abstracts 2014 Joint Annual Meeting of the American and Canadian Phytopathological Societies (Minneapolis, MN)* Phytopathology 104 (Suppl. 3): S3.2.

Aboughanem-Sabanadzovic N., W.F. Moore T.W. Allen, R.C. Stephenson & **S. Sabanadzovic**, 2015. Soybean vein necrosis virus and other viruses in of soybeans in Mississippi. Abstracts 2015 Annual Meeting of the American Phytopathological Society, August 1-5, 2015. Pasadena, CA. 512-P

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