

The Variations among Isolates of Sugarcane Mosaic Virus in Thailand as Determined by Virus-Host Interaction

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ABSTRACT

Six isolates of sugarcane mosaic virus (SCMV) were collected from infected sugarcane and their variations were studied using symptom expression in sugarcane, corn and sorghum cultivars. Virus titer of each isolate in sorghum plant was also compared. Mechanical inoculation was applied for virus infection and ELISA was used for virus titer assay. The incubation period for symptom expression of SCMV in sugarcane, corn and sorghum was 4-15 days depending on host cultivars. Virus infection rates varied from 15-92% in sorghum, 17-90% in corn, and 0-88% in sugarcane. On sugarcane, symptoms mostly appeared to be chlorotic or necrotic streak, chlorotic mild mottle or mild mosaic. The UT-3 and Q-67 sugarcane were the most susceptible cultivars to SCMV isolates as evaluated by infection rate. On sorghum, three types of expressed symptom were observed as lethal necrosis, chlorotic spot, and severe mosaic associated with streak or stripe pattern. On corn, symptoms were generally whitish mosaic or streak, mottle, except for leaf chlorosis on DK888 or CP888 commercial hybrid corn. Isolates UD7 from Udon Thani and SP9 from Supan Buri were the most aggressive isolates based on the infection rate. Isolates NP5 from Nakhon Pathom and UT6 from U-Thong were likely to be the same while NS1 from Nakhon Sawan and KB2 from Kanchanaburi were different from the others. Virus titer in individual sorghum species varied upon SCMV isolates. High titer of virus was detected in UT-1 sorghum at 10-15 days post inoculation for all isolates tested. Necrosis and severe chlorosis were observed with high virus titer for isolates NS1, UD7 and NP5. The obtained results demonstrated the variations among SCMV isolates in Thailand and this information could be used in breeding program for SCMV resistance.

Key words: sugarcane mosaic virus, sugarcane, corn, sorghum, ELISA, symptom, virus titer

Running head: Variations of Sugarcane Mosaic Virus in Thailand

INTRODUCTION

Sugarcane mosaic virus (SCMV) is one of the economically important viruses causing severe effect on sugarcane production world wide. The virus can also infect other economic crops such as

corn (maize) and sorghum (Teakle *et al.*, 1989). Natural infections of SCMV have been reported on a number of cultivated crops and wild grass species which may serve as virus infection sources. Historically, SCMV contains numerous strains that were distinguished based on symptom

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expression on differential hosts as well as serological properties (Pirones, 1982; Shukla *et al.*, 1989). Various sets of host plants were studied to be used for strain differentiation.

In Thailand the first mosaic symptom on sugarcane was observed in Nakhon Sawan province in 1973 and had been previously characterized to be SCMV strain A, F, and H according to the reactions on a set of sorghum assay hosts (Nateewatana, 1985; Teakle *et al.*, 1989; Koike and Gillaspie, 1989). During 1990s numerous strains of SCMV had been re-classified based on coat protein gene sequence analysis in combination with immunoassay using polyclonal and monoclonal antibodies against the N-terminus of the virion proteins (Shukla *et al.*, 1994). Using these approaches, four distinct potyviruses designated as sugarcane mosaic virus (SCMV), Johnson grass mosaic virus (JGMV), maize dwarf mosaic virus (MDMV), and sorghum mosaic virus (SrMV) were accepted as SCMV subgroups (Shukla *et al.*, 1992; Teakle *et al.*, 1989). In 2004 two isolates of SCMV from Supan Buri and Udon Thani province in Thailand have been characterized to be closely related to SCMV-MBD strain based on their coat protein sequence information (Gemetchu *et al.*, unpublished data). However, the biological properties and host range of the studied isolates are not yet elucidated.

Serological detection method such as ELISA can distinguish SCMV from other mixed infecting viruses such as MDMV-A, JGMV and SrMV (Tosic *et al.*, 1990). Many researchers have worked and developed different sets of sorghum and corn for the differentiation of SCMV but supply for those sets of plant for routine test is restricted. Moreover, SCMV strains are found to be very diverse and there are more than 19 strains and 100 isolates reported so far based on viral genome characterization. Most of the report on coat protein gene analysis revealed SCMV from the same geographic region to be closely related to each other rather than the SCMV from different

regions (Handley *et al.*, 1998; Chen *et al.*, 2002; Jiang and Zhou, 2002; Alegria *et al.*, 2003). However, only coat protein gene does not directly correlate or involve with biological reaction of SCMV on individual host species. Plant responses to virus as well as virus multiplication may be affected by some genes and proteins such as HC-Pro upon potyvirus infection (Strenger and French, 2004).

In this report the variations of SCMV isolates in terms of plant response to virus and virus aggressiveness were determined using symptom expression and infection rate of virus on three host species, sugarcane, sorghum and corn. Virus titers in sorghum propagation host were also examined to compare the ability of virus multiplication within the plant. This study offered an alternative method to distinguish SCMV isolates when restricted differentiate host cultivars were not available. Results on virus-plant interaction obtained in the study could be applied to sugarcane breeding program for SCMV resistance.

MATERIALS AND METHODS

Virus isolates and antiserum

Infected sugarcane leaves were collected from several planting sites in 5 provinces of Thailand during April 2002 and May 2003. Leaves were diagnosed for SCMV infection and positive samples were stored at -20°C before further propagation of the virus. Six isolates of SCMV were selected and designated as NS1:Nakhon Sawan, KB2:Kanchanaburi, NP5:Nakhon Pathom, UT6:U-thong district in Supan Buri province, UD7:Udon Thani, and SP9:Supan Buri. Isolate NP5:Nakhon Pathom was kindly provided by Dr.Kanungnit Reanwarakorn, Department of Plant Pathology, Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom province. Antiserum used, provided by S. Klinkong, Department of Plant Pathology, Kasetsart University, Kamphaeng Saen Campus, was raised in rabbit against SCMV

isolate from Kamphaeng Saen district in the year 2002.

Each isolate of SCMV was individually propagated by separate inoculation of sap from infected sugarcane leaves onto seedlings of grain sorghum, *Sorghum bicolor* cv.UT-1. Virus infection was confirmed by ELISA at 15 days post inoculation before infected leaves were harvested and stored at -20°C. All experiments were conducted using SCMV infected sorghum leaf tissues as virus source.

Host plants and inoculation

Sorghum. Seven sorghum cultivars used in this study were UT-1, UT-423B, UT-3225B, Supanburi1, UT-1409B, A2667-2, and SPLB-94022 received from the National Research Center for Corn and Sorghum(NRCCS), Thailand. Seeds were grown in steam sterilized soil in small pots under greenhouse condition. About 50 seedlings (2-3 leaf stage) per SCMV isolate were inoculated mechanically(Koike and Gillaspie, 1989) with sap of infected sorghum leaves.

Corn. Seven corn cultivars were used. Three sweet corn cultivars from local market in Kamphaen Saen were Ago, sticky corn#1 and sticky corn#2. Three corn hybrids from seed companies were DK888, CP888 and sticky hybrid sweet corn. Suwan 5 hybrid corn was from the National Corn and Sorghum Research Center, Thailand. Ten seeds of each cultivar were sown in a pot containing sterilized soil. Five pots of 2-3 leaf stage seedlings were used per isolate.

Sugarcane. Two types of sugarcane plant were used. The cutting stocks of five cultivar supplied by the experimental station of sugarcane in Supan Buri, Thailand were used. They were Q-67, UT-1, UT-3, QT97-496(wilt) and KU205(wilt). Cutting stocks of each cultivar were singly planted until 2-3 new leaves developed. Number of inoculated plants varied between 9-12 stocks. Another type of sugarcane plant used was seedling developed from hybrid seed derived from five

crosses in sugarcane breeding field supplied by R. Lersrutaiyotin, Department of Agronomy, Kasetsart University, Kamphaeng Saen Campus. Six seedlings of 7-9 leaf-stage per cultivar per isolate were used for virus inoculation.

Inoculation. Preparation of virus inoculum was performed by pulverization of 10 g frozen sorghum leaf tissues in liquid nitrogen and grinding with 5 ml of 0.1M phosphate buffer, pH 7.0. Cool sap were mixed with 600 mesh carborundum powder before rubbing onto seedling leaves of sorghum and corn followed by washing with tap water. For sugarcane inoculation, the method described by Koike and Gillaspie (1989) was applied. A hypodermic syringe with inoculum sap was pricked into the center of tightly whorled shoot. Leaves were briefly washed with tap water and plants were kept for symptom observation in the greenhouse temperature about 29-32°C for 30 days. Symptoms on inoculated plants and virus titer were evaluated at four interval periods of 10, 15, 25 and 30 days post inoculation(dpi). Infection percentages were recorded at 30 days post inoculation.

Indirect ELISA

The virus detection method used in this study was direct antigen coating-indirect ELISA (DAC-ELISA) modified from indirect ACP-ELISA(Jordan and Hammond,1991). Each microwell of ELISA plate was coated with plant sap extracted with sample buffer (phosphate buffer saline, PBST, containing 0.5% Tween 20, 0.2% polyvinyl pyrrolidone) and diluted to 1: 20 with coating buffer (0.05M carbonate buffer, pH 9.6, containing 0.2% Na.DIECA). After incubation for an hour at 37°C the coated well was washed three times with PBST. Anti-SCMV polyclonal antiserum was diluted to 1: 1000 dilution in conjugate buffer (PBST containing 0.2% ovalbumin) and cross absorbed with 1:100 dilution of healthy plant sap. After incubation with SCMV-antiserum for one hour, the well was washed as

above. An AP-enzyme conjugate goat anti-rabbit IgG of 1:30,000 dilution was added into well, incubated for one hour, followed by PBST washing. The p-nitrophenyl phosphate-substrate dissolved in diethanolamine buffer (1mg/ml) was added and left for 30-40 min. The reaction was stopped by adding 3M NaOH solution. Volumes of reagent in each step was 200 µl/well except for the 50 µl/well of NaOH stop solution. ELISA valued was measured from optical density (OD) at 405 nm wavelength by an ELISA reader (Labsystem-Uniscan362). Sap extracted from healthy sorghum leaves was used as negative control and coating buffer was used as a blank control.

RESULTS

Symptom expression and virus infection rate

Different SCMV isolates produced various symptoms on host plants tested (Table 1-3). In this study, regardless of symptom type or severity the incubation period for symptom expression varied from 4-15 days on sorghum, corn and sugarcane cutting stocks. It took more than 25-30 days for symptom development on sugarcane hybrid seedlings. The infection percentage of host cultivars recorded at 30 dpi varied from cultivars to cultivars ranging from 30-92% in sorghum, 34-

90% in corn, and 0-90% in sugarcane. Among three species of host plants tested, sorghum showed more diverse symptoms than those of the others. Three distinct symptom types observed on sorghum cultivars were given as lethal type or necrosis (NS), chlorotic spot (ChSpt), and streak (Sk) or stripe (Sp) mosaic pattern (Figure 1). On cultivar A2267-2 five isolates induced streak or stripe mosaic consistently with 70% or more infection rate. Four cultivars of corn plants reacted similarly to most isolates tested by expressing streak type of mosaic or mottle (Mo), while three cultivars, hybrid sweet sticky corn DK888 and CP888 showed leaf chlorosis or chlorotic spot (Figure 2). On sugarcane cuttings, the susceptible cultivars Q-67 and UT-3 showed severe streak or stripe mosaic (Figure 3) and the infection rate varied depending on SCMV isolates (Table 3). In this study, symptoms on five crosses of sugarcane hybrid were faint or mild mosaic (Mi) and detection for the present of virus by ELISA gave very low positive signal. Development of symptom was comparatively delayed to about 40 days or more for all isolates tested. Inoculated plants without symptom were randomly back-inoculated onto standard susceptible TL01B6109-28 hybrid corn (CIMMYT) for confirmation.

Table 1 Symptom expression on seven sorghum cultivars and virus infection rates.

Cultivar	Symptom on sorghum and infection rate of SCMV isolate					
	NS1	KB2	NP5	UT6	UD7	SP9
UT-1	Sk/58 ^{1/}	Mo/56	Mo/74	Mo/52	ChSk/70	ChSp/p86
UT-423B	Sk/74	Sk/74	Mo/62	Mo/70	ChSk/66	ChSp/86
UT-3225B	Ns/56	Mo/62	Sk/60	Sk/76	Ns/82	Ns/82
Supanburi1	Ns/62	Mo/82	Sk/50	Sk/78	ChSk/76	ChSk/76
UT-1409B	Sk/66	Mo/50	Sp/86	Sp/58	ChSk/62	ChSk/88
A2667-2	Sk/76	Mo/48	Sp/68	Sp/82	Sk/84	ChSk/90
SPLB-94022	Sk/68	Mo/62	Sp/38	Sp/88	ChSk/88	ChSk/82

^{1/} Letters are abbreviations of symptom type and numbers are virus infection percentages.

Sk=streak, Ns=necrosis, Mo=mosaic, Sp=stripe, ChSk=chlorotic streak, ChSp=chlorotic stripe

Table 2 Symptom expression on seven corn cultivars and virus infection rates.

Cultivar	Symptoms on corn and infection rates of SCMV isolate					
	NS1	KB2	NP5	UT6	UD7	SP9
Ago	Mo/58 ^{1/}	Mo/48	Mo/66	Sk/58	Sk/58	Sk/68
Sticky#1	Sk/50	Sk/56	Sk/42	Sk/54	Sk/74	Sk/74
Sticky#2	Sk/42	Sk/46	Sk/74	Sk/68	Sk/68	Sk/78
DK888	ChSk/86	ChSk/72	ChSk/54	ChSk/92	ChSpt/92	ChSpt/70
Hybrid sticky	Sk/38	Sk/64	Sk/72	Sk/86	Sk/80	Sk/78
Suwan 5	Ns/30	Mo/56	Sp/70	Mo/80	Mo/88	ChSk/66
CP888	ChSk/48	ChSk/66	ChSk/54	ChSk/60	ChSk/68	ChSk/76

^{1/} Letters are abbreviations of symptom type and numbers are infection percentages.

Sk=streak, Ns=necrosis, Mo=mosaic, Sp=stripe, ChSk=chlorotic streak, ChSpt=chlorotic spot

Table 3 Symptoms on six cultivars of sugarcane and virus infection rates.

Cultivar	Symptoms on sugarcane and infection rates of SCMV isolate					
	NS1	KB2	NP5	UT6	UD7	SP9
Q-67	ChSk/40 ^{1/}	ChSk/70	ChSk/60	ChSk/30	ChSk/70	ChSk/90
UT-1	MoSk/33	MoSk/22	MoSk/56	MoSk/44	MoSk/56	MoSk/56
UT-3	Mi/56	Mi/67	ChSp/78	ChSp/89	ChSpt/34	Mi/67
QT97-496(wilt)	Mi/33	ChSp/25	ChSp/25	Mi/50	Sk/67	Mi/56
KU205(wilt)	Mi/0	Mi/0	Mi/0	Mi/0	ChSpt/8.3	Mi/8.3

^{1/} Letters are abbreviations of symptom type and numbers are infection percentages.

Sk=streak, Mi=mild mosaic, Mo=mosaic, Sp=stripe, ChSk=chlorotic streak, ChSp=chlorotic stripe, ChSpt=chlorotic spot

Table 4 ELISA values (OD₄₀₅) of virus titer in inoculated sugarcane leaves at 30 days post inoculation (dpi). Mean (\bar{x}) ELISA value of healthy plant sap equalling 0.0192.

Cultivar	ELISA values of virus titer in inoculated sugarcane leaves at 30 dpi from SCMV isolates					
	NS1	KB2	NP5	UT6	UD7	SP9
98-038 x UT-3	0.25	0.158	0.126	0.101	0.072	0.075
94-12-13 x 98-2-005/1	0.052	0.055	0.043	0.126	0.141	0.17
98-2-038-98-2-005/1 x UT-3	0.031	0.04	0.058	0.097	0.132	0.247
94-12-13 x UT-3	0.096	0.133	0.064	0.044	0.044	0.056
99-14-63 x 98-2-005/1	0.198	0.177	0.095	0.024	0.031	0.149
MT1 17/11/43 x UT-3	0.074	0.12	0.283	0.311	0.056	0.067

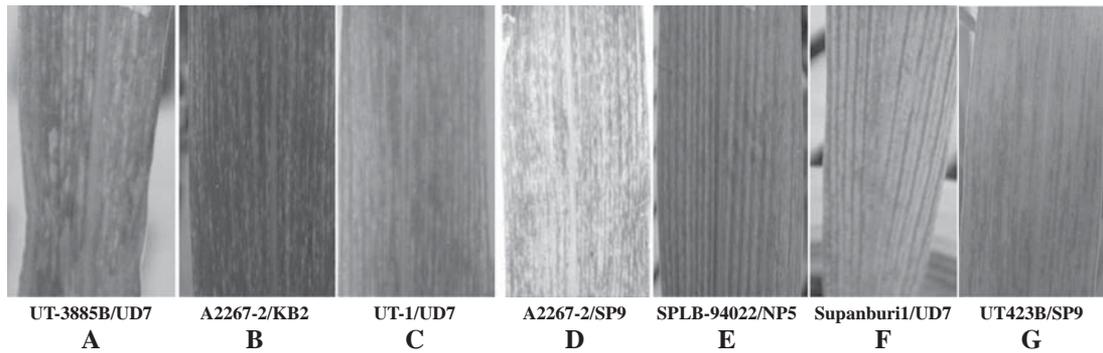


Figure 1 Various symptom types on sorghum cultivars induced by sugarcane mosaic virus isolates from Thailand.

A. Necrosis, B.C. Chlorotic spot, D. Chlorotic streak, E. Chlorotic stripe, F. G. Severe mosaic.

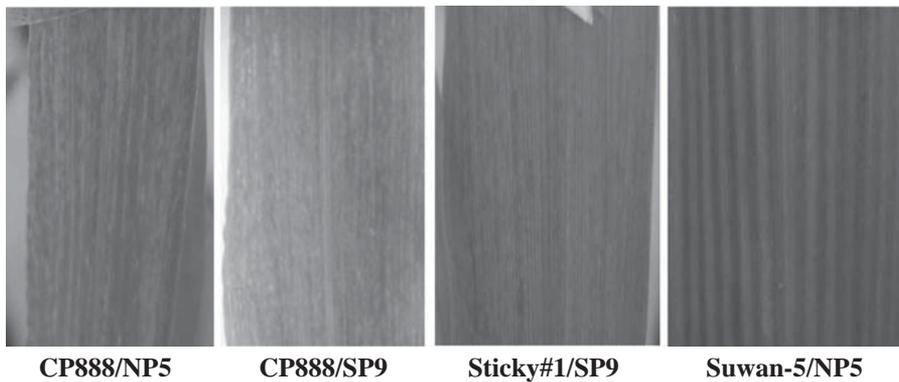


Figure 2 Chlorotic spot, streak and stripe symptom types induced on different cultivars of corn by sugarcane mosaic virus isolates from Thailand.

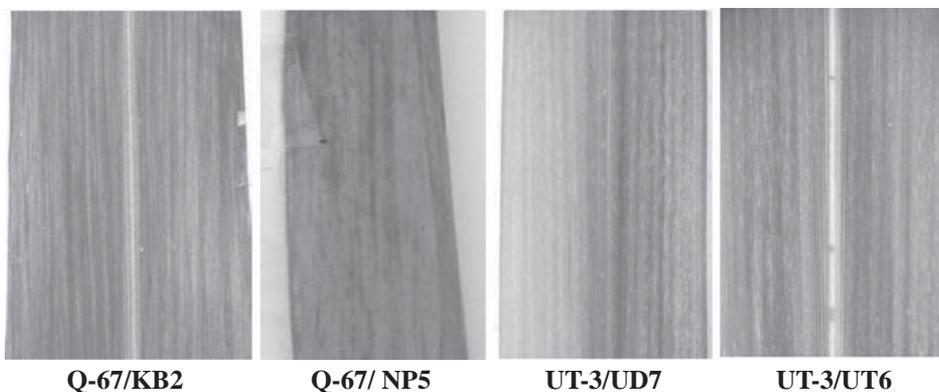


Figure 3 Severe mosaic symptoms associated with streak or stripe pattern on different sugarcane cultivars by different isolates of sugarcane mosaic virus in Thailand.

To indicate aggressiveness of SCMV isolates, virus infection rate on each host species were plotted against virus isolates. On sorghum plant the most aggressive SCMV isolate found was SP9(Supanburi), followed by UD7(Udon Thani) and UT6(U-Thong), descendantly. Necrosis symptom was found on UT3225B sorghum by isolate UD7 with high virus titer at 15 dpi. On corn plant isolates SP9 and UD7 again were more aggressive than the others (Figure 4A). Most SCMV isolates used were aggressive to the DK888 hybrid commercial corn (Figure 4B). On sugarcane, isolates SP9 and UT6 showed their aggressiveness on UT3 and Q67 cultivars (Figure 4C).

Virus titer

Sorghum plants were investigated for virus titer and host resistance. At each interval of assay, leaves were collected, weighed and cut into pieces before keeping at -20°C until all samples were subjected for ELISA one at a time. The result from the first experiment indicated that six sorghum cultivars reacted differently to different SCMV isolates. Virus titer indicated level of plant resistance to SCMV infection which may result on suppression of virus multiplication or virus spread in individual host. We used ELISA value as an index to evaluate resistance level of tested host by plotting ELISA values of all isolate and assigned the index constant as indicated in Figure 5. Responses of sorghum cultivars to SCMV isolates were evaluated as resistance (R), moderate (M) or susceptible (S) by using ELISA value of virus titer in plants ($R=OD<0.4$, $M=OD\ 0.4-0.8$, and $S=OD>0.8$) as summarized in Table 5.

To examine SCMV multiplication pattern in host plant, UT-1 sorghum was used as propagation host. Virus titer of all SCMV isolates at 10, 15, 25 and 30 dpi as determined by DAC-ELISA exhibited similar pattern of SCMV multiplication curve (Figure 6) which resembled that of some potyviruses (Tosic *et al.*, 1990). The highest peak of the titer was around 15 days and

decreased thereafter. Some necrosis plants showed higher titer of virus when compared to the milder symptom of the same cultivar.

DISCUSSION

SCMV has been presently classified as one of the four SCMV subgroups designated SCMV, MDMV-A, SrMV and JGMV based on serological properties and genome sequences (Teakle *et al.*, 1989). In Thailand the identification of SCMV has been conducted based on serological properties, and strain differentiation was by host symptoms which preliminary assigned Thai SCMV as strain A, F, and H (Natewatana, 1985; Koike and Gillaspie, 1989). Recently there has been research results on coat protein gene sequence analysis which reveal that SCMV isolates from sugarcane in Supan Buri and Udon Thani, Thailand are more closely related to SCMV-MDB than other strains mentioned above (Gemechu *et al.*, unpublished data).

Symptom expression of SCMV infection on several hosts were previously reported to be affected by several environmental factors, for example, low and high temperature may cause severe and mild mosaic on sorghum plants, respectively (Tosic *et al.*, 1990). Under rather hot climatic condition of our screen house in this study, (35-39°C) the typical symptoms induced by SCMV-MDB, e.g. mosaic, necrosis, red leaf, streak or stripe (Tosic *et al.*, 1990) were usually observed on sorghum cultivars tested. The incubation period of SCMV in sorghum and corn was short whereas the infection percentage was rather high. This indicated that the rapid multiplication and spread of the virus within susceptible host plant might support their infectivities and movement. Putra *et al.* (2003) reported that SCMV moved more slowly in the moderately resistant than in the susceptible cultivars, and from the point of inoculation to younger leaves, roots and tillers and eventually to leaves growing next to the inoculated leaves.

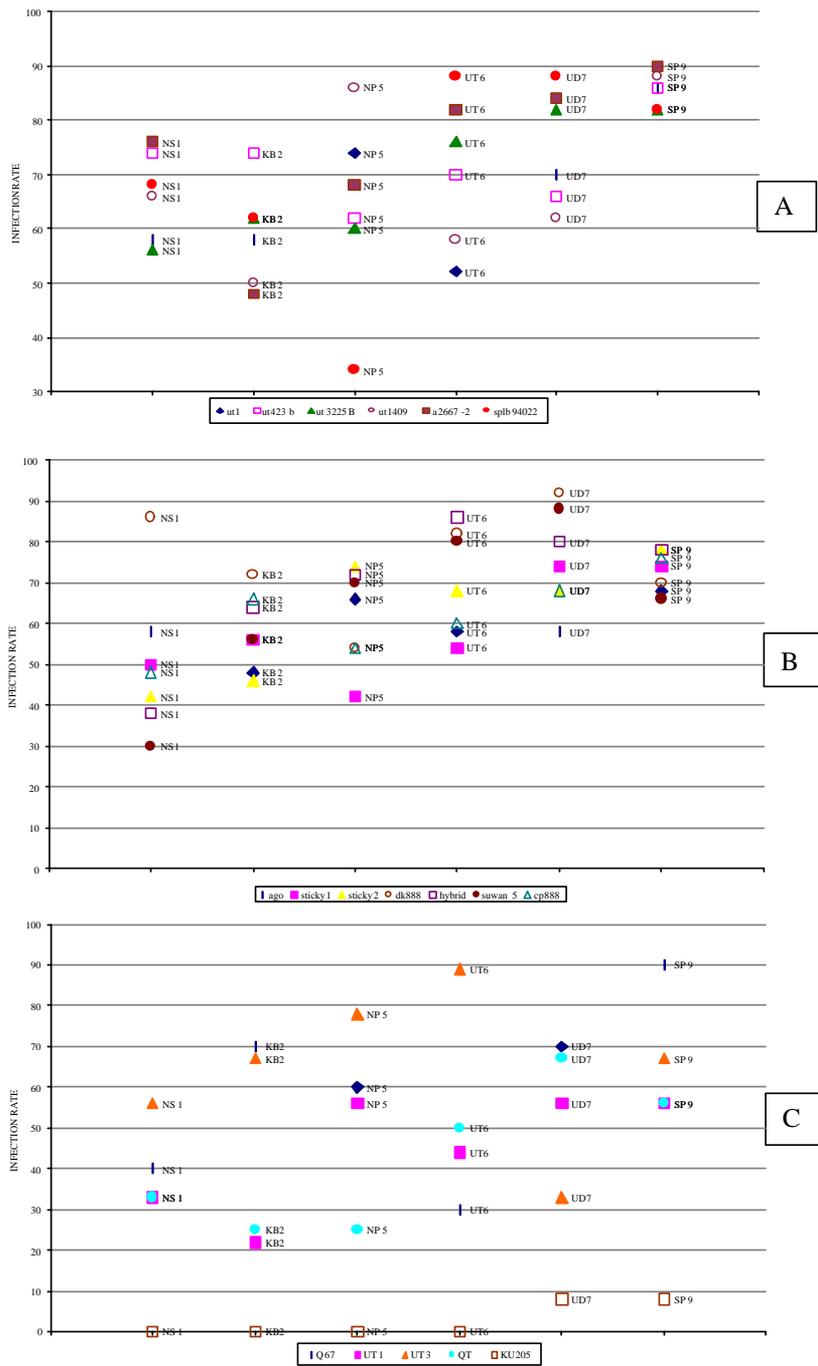


Figure 4 Plotting of SCMV infection rate (%) on sorghum (A), corn (B) and sugarcane (C) plants to evaluate the aggressiveness of six SCMV isolates: NS1, KB2, NP5, UT6, UD7 and SP9. Indices for the aggressiveness designated in this study as follows:- Aggressive=80-100% infection, Moderate=40-70% infection, Weak=<40% infection.

Table 5 Responses of sorghum cultivars to sugarcane mosaic virus (SCMV) as determined by ELISA values of virus titer in plant tissue at 15 days post inoculation. Indice for evaluating the resistance and susceptibility of plants derived from ELISA value (OD) R (resistant) = OD<0.4, M (moderate) = OD 0.4-0.8, and S (susaptable) = OD >0.8.

Sorghum cultivar	SCMV Isolate					
	NS1	KB2	NP5	UT6	UD7	SP9
UT-1	M	M	M	M	R	S
UT423B	M	M	S	S	M	S
UT3225B	R	S	M	R	S	M
UT1409B	M	R	M	M	M	R
A2267-2	M	M	S	S	S	S
SPLB92022	S	S	M	M	M	M

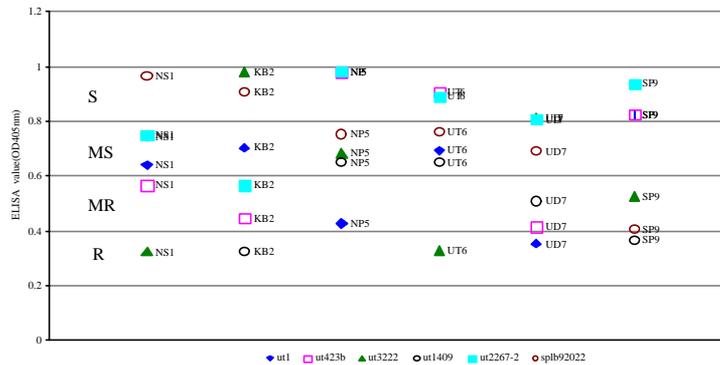


Figure 5 Disease reactions of six sorghum cultivar to six isolates of SCMV in Thailand. Leaves of inoculated sorghum plant harvested at 15 days post inoculation and assayed for virus titer by DAC-ELISA. ELISA values of virus titer calculated to make index for resistance of plant to the virus. The ELISA value(absorbance) indice used in this study were R (resistant) = <0.4, MR (moderately resistant) = 0.4-0.5, MS (moderately susaptable) = 0.5-0.8, S (susaptable) = >0.8

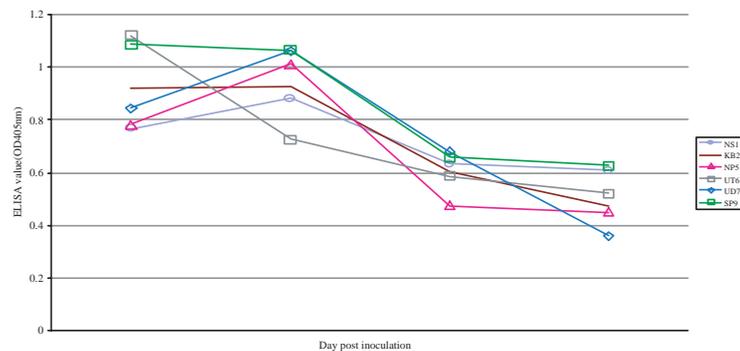


Figure 6 Virus titer and multiplication curves of six SCMV isolate in UT-1 sorghum cultivars as determined by ELISA at 10, 15, 25 and 30 days post inoculation.

For isolates SP9 and NS1, use of host symptom only could not differentiate them from each other. Determination of virus titer in a set of selected sorghum cultivars (Table 5) indicated that NS1 multiplied differently from SP9. There was similarity among isolates NP5 and UT6 based on their titer at 15 dpi in five out of six sorghum cultivars used. Both isolates infected sorghum and corn at high percentages. The differences found among them were their infection rates on sugarcane. In these trials, sugarcane was not a good host for virus differentiation due to the lack of healthy stocks for conducting the test. Regardless of results on sugarcane responses, isolates NP5 and UT6 were likely to be the same. Isolate KB2 showed aggressiveness on hybrid corn such as DK88, CP888 and sweet sticky hybrid. The reaction of virus on sugarcane suggested close relationship of isolates KB2 to NP5 and both isolates were from very near geographical area.

Nowaday differentiation of SCMV at strain level is rapid and simple when molecular technique is applied (Shukla *et al.*, 1994; Alegria *et al.*, 2003). On host responses aspect, virus inducing severe symptom types such as necrosis and chlorotic streak or stripe on corn had greater damage to crops (Seifers and Kofoids, 1998) while more aggressive isolates cause high infection rate and can spread wide on several host species. The information on virus-host interaction obtained in this study could demonstrate SCMV diversities as well as virus properties within host. These informative data can be generated at particular planting area and will be useful for breeding program.

ACKNOWLEDGEMENTS

The authors thank EARO-ARTP (Ethiopian Agricultural Research and Training Program) for financial support of this work.

LITERATURE CITED

- Alegria O.M., M. Royer, M. Bousalem, M. Chatenet, M. Peterschmitt, J-C. Girard and P. Rott. 2003. Genetic diversity I the coat protein coding region of eighty-six sugarcane mosaic virus isolates from eight countries, particularly from Cameroon and Congo. **Arch. Virol.** 148: 357-372.
- Chen J., J. Chen and M.J.Adams. 2002. Characterization of potyviruses from sugarcane and maize in China. **Arch. Virol.** 147: 1237-1246.
- Handley, J.A., G.R.Smith, J.L.Dale and R.M.Harding. 1998. Sequence diversity in the coat protein coding region of twelve sugarcane mosaic virus isolates from Australia, USA and South Africa. **Arch. Virol.** 143(6): 1145-1153.
- Jiang, J.X. and X.P.Zhou. 2002. Maize dwarf mosaic disease in different regions of China is caused by *Sugarcane mosaic virus*. **Arch. Virol.** 147: 2437-2443.
- Jordan, R.L. and J.Hammond. 1991. Comparison and differentiation of potyvirus isolates and identification of strain-, virus-, subgroup-specific and potyvirus group-common epitopes using monoclonal antibodies. **J. Gen. Virol.** 72: 1531-1541.
- Koike, H. and A.G. Gillaspie Jr. 1989. Mosaic, pp. 301-322. In C.Ricaud, B.T.Egan, A.G. Gillaspie Jr. and C.G.Hughes (eds.). **Diseases of Sugarcane. Major diseases.** Elsevier Science, Amsterdam.
- Nateewatana, S. 1985. **A flexuous rod virus causing mosaic disease of sugarcane in Thailand.** M.S Thesis. Kasetsart University, Bangkok.
- Pirone, T.P. 1982. Sugarcane mosaic virus. **CMI/AAB Description of Plant Viruses** No.88.
- Putra, L.K., J.O.Helen, P.J. Anthony and J.L. Whittle. 2003. Distribution of *Sugarcane mosaic virus* in sugarcane plants.

- Australasian Plant Pathology** 32(2) 305 – 307.
- Seifers D.L. and K.D. Kofoids. 1998. Field symptom-response of sorghum hybrids infected by maize dwarf mosaic virus, sugarcane mosaic virus strain MDMV-B, and Johnson grass mosaic virus. **Kansas State University Experimental Station and Cooperative Extension Service**—Publication No. SRL 121. 3 p.
- Shukla, D.D., M. Totic, J. Jilka, R.E. Ford, R.W.Toler and M.A.C. Langham. 1989. Taxonomy of potyviruses infecting maize, sorghum and sugarcane in Australia and the United States as determined by reactivities of polyclonal antibodies directed towards virus-specific N-termini of the coat proteins. **Phytopathology** 78: 223-229.
- Shukla, D.D., M.J. Frenkel, N.M. McKern, C.W.Ward, J.Jilka, M.Totic and R.E.Ford. 1992. Present status of sugarcane mosaic subgroup of potyviruses. **Arch. Virol.** [Suppl. 5]: 363-373.
- Shukla, D.D., C.W.Ward and A.A.Brun. 1994. **The Potyviridae.** Centre for Agriculture and Biosciences International. Cambridge University Press. Cambridge. 516 p.
- Strenger,D.C. and R. French. 2004. Functional replacement of *Wheat streak mosaic virus* HC-Pro with the corresponding cistron from a diverse array of viruses in the family *Potyviridae*. **Virology** 323: 257-267.
- Teakle, D.S., D.D.Shukla and R.E.Ford. 1989. Sugarcane mosaic virus. **Descriptions of Plant Viruses**.aab 342.
- Totic,M.,R.E.Ford,D.D.Shukla and J.Jilka. 1990. Differentiation of sugarcane, maize dwarf, Johnsongrass and sorghum mosaic viruses based on reactions of oat and some sorghum cultivars. **Plant Dis.** 74: 549-552.