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Banana streak virus is very diverse in Uganda

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Abstract

Banana streak virus (BSV) is a badnavirus that causes a viral leaf streak disease of banana and plantain (*Musa* spp.). Identified in essentially all *Musa* growing areas of the world, it has a deleterious effect on the productivity of infected plants as well as being a major constraint to *Musa* breeding programmes and germplasm dissemination. Banana is a staple food in Uganda which is, per capita, one of the worlds largest banana producers and consumers. BSV was isolated from infected plants sampled across the Ugandan *Musa* growing area and the isolates were analysed using molecular and serological techniques. These analyses showed that BSV is very highly variable in Uganda. They suggest that the variability is, in part, due to a series of introductions of banana into Uganda, each with a different complement of infecting viruses.

Keywords: Banana streak virus; Banana; Uganda; Diversity; Yield decline

1. Introduction

Banana streak virus (BSV) family Caulimoviridae, genus *Badnavirus* has a circular, non-covalently closed double-stranded DNA genome of 7.4 kbp (AJ002234, Harper and Hull, 1998) encapsidated in bacilliform particles. The virus is highly variable both serologically and genomically. Lockhart and Olszewski (1993) recognized three distinct serotypes and four different isolates based on PCR amplification with degenerate primers followed by a DNA hybridisation analysis. Geering et al. (2000) identified four distinct BSV isolates from Australia that differed by 20–30% in sequence from each other. The very different techniques, of serology and PCR each assay different functional parts of the virus. That both techniques indicate variation is significant, as these are the methods of choice in virus diagnostics.

BSV occurs worldwide and is distributed throughout Africa, including Uganda (Tushmereirwe et al., 1996). Characteristic symptoms of BSV infection in banana plants are continuous or dis-continuous chlorotic or necrotic streaks on the leaves. Additional symptoms can sometimes include necrosis of the pseudostem and stunting, and infection occasionally leads to plant death. A variety of factors including virus isolate, host genotype, level of crop management and environmental conditions influence symptom expression which is variable and discontinuous (Lockhart, 1986; Gauhl and Pasberg-Gauhl, 1995; Dahal et al., 1998; Lockhart and Jones, 2000). Estimates of yield loss due to BSV infection range from 7 to 90% (Lassoudière, 1974; Dahal et al., 2000; Daniells et al., 2001). The differences in yield loss reported may reflect the differences in banana genotypes grown and in cultural conditions, but all studies identified a yield loss attributed directly to virus infection.

Badnaviruses are typically transmitted by mealybug species of the family Pseudococcidae. In the greenhouse, BSV is transmitted by the citrus mealybug (*Planococcus citri*) (Jones and Lockhart, 1993) while the pink sugarcane mealybug (*Saccharicoccus sacchari*) transmits the closely related badnavirus Sugarcane bacilliform virus (SCBV) to banana (Lockhart and Autrey, 1988). Kubiriba et al. (2001) identified *S. sacchari* and the pineapple mealybug (*Dysmicoccus brevipes*) in Uganda and a badnavirus was detected in both species. Moreover, the abundance of *D. brevipes* was correlated with BSV incidence (Kubiriba et al., 2001). Other mealybug species occur on banana and may also transmit BSV. As for some other badnaviruses, there may also be non-mealybug vectors, e.g. Rubus yellow net virus (RYNV) is transmitted by raspberry aphids (Stace-Smith and Jones, 1987). However, most virus dissemination is likely to be through vegetative propagation of BSV-infected *Musa*.

Uganda, with a population of 23 million, is the world's highest per capita consumer of bananas, which constitute a subsistence staple for around one third of the population. The principal type grown in Uganda, constituting 85% of

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production, is the AAA genome East African Highland banana group (EAH-AAA) (Karamura et al., 1996). The bananas currently cultivated are derived from a few introductions from which variation by somatic mutation followed by farmer selection has generated the wide diversity of clone types now grown. These have been grouped subjectively into five sets (Karamura, 1998). Other *Musa* genotypes, including beer bananas (AB and ABB) and desert-type banana (AB and AA) are also grown. All bananas produced in Uganda are seedless and all propagation is vegetative.

Over recent decades there has been a marked decline in yields in traditional banana growing areas. Surveys showed that BSV is widespread in Uganda and it is therefore a threat to banana production (Tushmereirwe et al., 1996; Kubiriba et al., 2001). However, the surveys were not designed to determine which types of BSV occur. This study was undertaken to provide baseline information for future research on the epidemiology of BSV in Uganda.

2. Materials and methods

2.1. Sample collection

Sampling was carried out in farmers' fields in banana growing regions across the country (Fig. 1). At each farm, a plot was surveyed qualitatively and, at some sites, quantitatively by scoring all the plants, for the presence of BSV symptoms. From each plot one to two typically BSV-symptomatic leaf samples (20–200 g) were collected and the cultivar/clone noted. Leaf samples were also taken from plants not displaying classical BSV symptoms and mostly having faint mosaic symptoms. For convenience, the leaf sheath was removed and the leaves were wiped clean to remove obvious biotic contamination. The samples were packed in plastic bags and transported to The John Innes Centre, Norwich, UK, for further analysis.

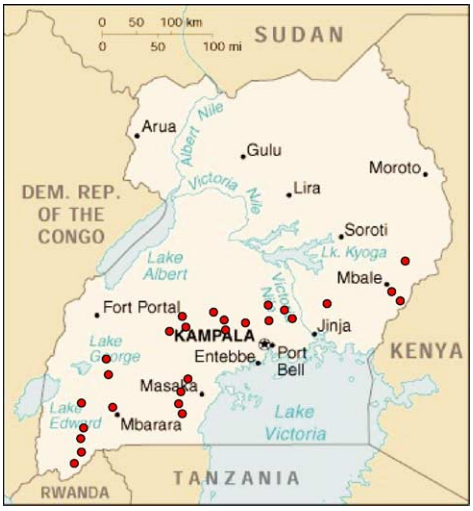

Fig. 1. Map of Uganda showing sites of field sampling. BSV-infected *Musa* collection sites are marked by red circles and cover the major banana growing regions of Uganda.

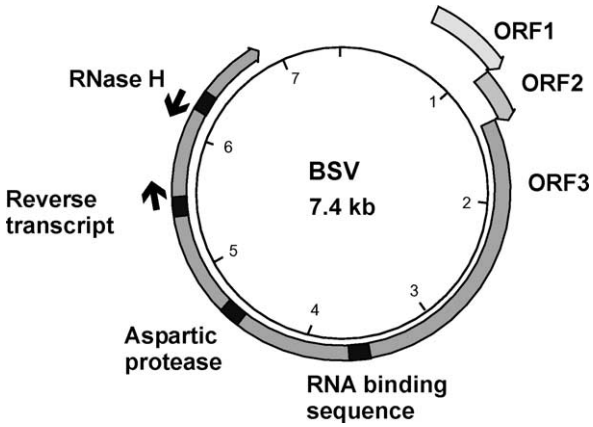

Fig. 2. Map of the BSV genome. The approximate positions of the degenerate primers used for amplification of conserved reverse transcriptase sequences from infected plants are shown as black arrows. Conserved sequence motifs of badnaviruses are indicated as black segments. The positions of the three ORFs of BSV are given by filled arrows.

2.2. Virus purification

Virus was partially purified, DNA isolated and leaf sap samples prepared and concentrated as described in Harper et al. (2002).

2.3. Electron microscopy, serology and PCR

All samples were analysed for BSV by serological methods using a composite polyclonal anti-BSV anti-Sugar cane bacilliform virus (SCBV) antiserum, supplied by Dr. B. Lockhart (Ndowora and Lockhart, 2000). Double-antibody sandwich (DAS) ELISA followed the procedure of Ndowora and Lockhart (2000). lmmunosorbent electron microscopy (ISEM) was by the procedure of Ahlawat et al. (1996). PCR was carried out on DNA isolated from partially purified virus preparations and immune-capture-PCR (IC-PCR) was used on partially purified virus preparations and leaf sap samples. Degenerate primers, based on conserved replicase sequence motifs of badnavirus genomes and designed by Drs. B. Lockhart and N. Olszewski were used to amplify badnavirus sequences. The position of the primers is shown in Fig. 2. These are, primer 1A (forward, relative position in BSV-Ol AJ002234, nt 5537) 5′CTNTAYGARTGGYTGTNATGCCNTTYGG, primer 4′ (reverse, relative position in BSV-Ol AJ002234, nt 6134) 5′TCCAYTTRCANAYNSCNCCCCANCC. IC-PCR and PCR conditions and procedures were as described in Harper et al. (2002).

2.4. Cross-hybridisation

Individual plasmid clone inserts were ^{32}P radiolabelled using the Gibco-BRL random primers DNA-labelling

system. Purified individual sample PCR reactions (2 λ*l*) were spotted onto nylon membranes (Hybond X, Amersham). Processing, hybridisation and washing, were carried out using the membrane manufacturers protocols. Hybridisation was at 65 °C overnight, and washing at 65 °C with 1 × SSC/0.1% SDS, followed by 0.1 × SSC/0.1% SDS.

2.5. Cloning, sequencing and phylogenetic analysis

PCR reactions were purified using the Promega Wizard DNA clean-up system and PCR products were cloned using the Invitrogen TOPO TA cloning system. Plasmids were isolated using the Qiagen QIAprep Spin Miniprep kit and ABI BigDye was used for sequencing. Sequences were compared to each other following removal of all vector and PCR primer sequences. Sequence alignments and construction of bootstrapped, neighbor-joining trees were carried out using Clustal X (Thompson et al., 1997).

The following badnavirus sequence accessions were used for comparison to Ugandan BSV sequences: BSV-Ol, AJ002234 (Harper and Hull, 1998); BSV-GF, AF215814; BSV-Cav, AF215815 and BSV-Mys, AF214005 (Geering et al., 2000); Citrus mosaic virus (CMBV) AF347695 (Huang and Hartung, 2001); Cacao swollen shoot virus (CSSV) L14546 (Hagen et al., 1993); Commelina yellow mottle virus (CoYMV) X52938 (Medberry et al., 1990); Dioscorea alata bacilliform virus (DaBV) X94576, X94581 (Briddon et al., 1999); Gooseberry vein banding associated virus (GVBAV) AF298883 (Jones et al., 2001); Rice tungro bacilliform virus (RTBV) D10774 (Hay et al., 1991); Spiraea yellow leaf spot virus (SYLSV) AF299074; Sugarcane bacilliform virus (SCBV) M89923 (Bouhida et al., 1993) and isolate Ireng Maleng (SCBV-IM) AJ27709.

3. Results

Fifty-one field samples were collected at 30 farms at locations across Uganda (Fig. 1). At 28 of the farms, BSV symptoms were readily observable in at least one plant. A survey at six of the 30 farms found symptoms in 10–72% of the plants. Symptoms varied from mild to severe chlorotic and/or necrotic streaking. The streaks themselves varied from fine, long and narrow to short and broad and plants sometimes had different symptoms on different leaves. It was usual that not all leaves on an infected plant had symptoms. The banana plants sampled were from a range of *Musa* genotypes but mostly belonged to genotype EAH-AAA. The local names of each cultivar were taken, and compared and allocated to one of the five clone sets described by Karamura (1998). The samples contained representatives of all five clone sets, and of the other genotypes found in Uganda (AB, AAB and AAA). One BSV-symptomatic plant of *Ensete* sp., another genus of the family Musaceae, was sampled. No relationship between symptom type and banana clone/cultivar was detected. The proportion of BSV symptomatic plants appeared higher in those plots which had lower standards of cultivation as judged by the level of weed control.

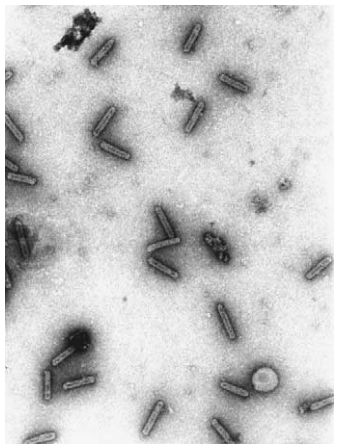

Fig. 3. Electron micrograph of BSV. Bacilliform particles isolated from BSV-infected Ugandan banana leaf, trapped on anti-BSV antiserum coated grids. The particle sizes are ca. 120 nm × 30 nm.

Forty seven samples were subjected to the BSV partial purification protocol and analysed for the presence of BSV by ISEM and also by ELISA. By ISEM, the characteristic virion particles (Fig. 3) of ca. 120 nm × 30 nm were detected in all but one of the samples, with some having very high particle counts. ELISA results indicated the presence of BSV antigen in 22 of the samples but for many of the other samples the optical density results were difficult to interpret as the absorbance value was close to that of the negative control values. In general, a high virion particle count in ISEM also gave an unambiguous positive ELISA result but, with two samples, moderate virion counts did not give positive ELISA values whereas, with four samples low virion counts gave positive ELISA values.

Degenerate primers were used in PCR to amplify a product which, based on the BSV-Ol genome, was expected to be of ca. 597 bp. This size product was found with all but one sample, although virions were seen in this sample by ISEM. Cross-hybridisation was used to determine the relationships between different virus samples. Cloned PCR products from samples 3, 9 and BSV-Ol were radiolabelled and hybridised to dot blots containing aliquots of PCR products of individual purified virion samples. Washing at 65 °C was carried out sequentially to two different stringencies to reveal levels of homology between target and probe. The results indicate considerable cross-hybridisation between the PCR products, even under high stringency conditions (Table 1). That there are differences between samples indicates that this is not due to hybridisation to a common sequence.

The PCR product from each sample was cloned and 6–12 colonies from each transformation picked for analysis. Plasmids were digested with restriction enzyme *Eco*R1 to release the entire insert. This digest indicated variation in the

Table 1
Cross hybridisation of BSV sequences between different samples

Plasmid probe sequence	Samples hybridising at intermediate stringency	Samples hybridising at high stringency
3.1	1, 2, 3, 4, 5, 16, 17, 42	3, 16, 42
9.1	3, 6, 7, 8, 9, 11, 13, 14, 15, 16, 17, 30, 33, 34, 36, 37	7, 8, 9
BSV-Ol		1, 2, 3, 34, 36

Three different cloned BSV PCR products, 3.1, 9.1 and BSV-ol, were radiolabelled and hybridised to a dot blot containing aliquots of PCR products from the amplification of partially purified virus samples. Hybridisation at 65 °C was followed by washing at 65 °C in 1 × SSC (intermediate stringency) followed by exposure of the blot to X-ray film. The blot was then washed at 65 °C to 0.1 × SSC (high stringency).

individual clones from a transformation. Fig. 4 shows that there were at least two restriction fragment length polymorphisms (RFLP) in six clones from a single sample. Restriction endonucleases having four base recognition sequences were also used on PCR-amplified plasmid insert templates (Fig. 5). This was more informative as shown by *Mse*1 which revealed that plasmid 5–6 differs from 5–1, –2, –3 and –5 (Fig. 5), whereas using *Eco*R1 they appeared identical, as in Fig. 4. Even four base recognition sequences are not informative in all cases, for example in Fig. 5 when samples digested with *Hin*F1 (tracks 1–6) did not reveal the number of RFLPs found when using *Mse*1 (tracks 7–12).

The variation of BSV within the samples was also analysed by sequencing. Sequences of around the expected length, were obtained from each of the Ugandan samples and the predicted amino acid sequence translation contained characteristic motifs of reverse transcriptase (RT). These sequences and those of other known badnaviruses were aligned to each other and a phylogenetic tree calculated. For clarity, only representative sequences from a particular clade are included in the phylogenetic tree (Fig. 6). This shows that the diversity of the BSV RT sequence in

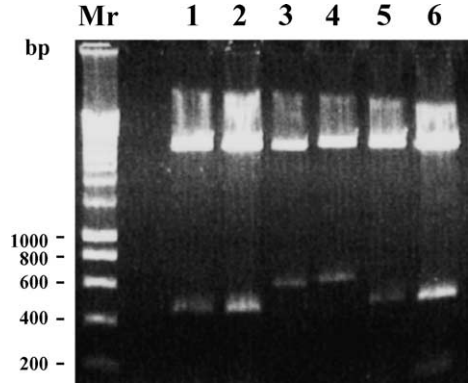

Fig. 4. Restriction digest analysis of plasmids from PCR product transformation. Gel electrophoresis of *Eco*R1 digestion products of six independent clones from sample 5 PCR reaction using primers 1A and 4′. Tracks 1–6 are plasmids 5–1, –2, –3 and –5 and –6, respectively. Track Mr is molecular size markers of bp sizes shown.

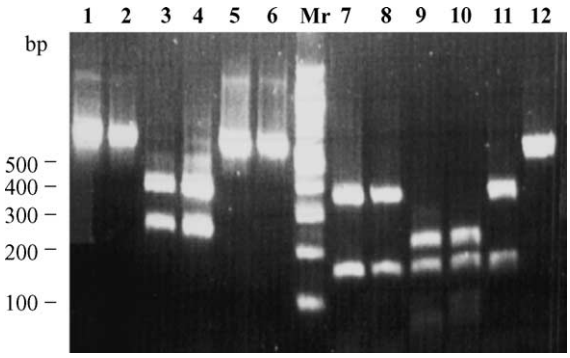

Fig. 5. Restriction digest analysis of PCR product plasmid clone insert. Four base recognition sequence restriction endonucleases *Hin*F1 and *Mse*1 were used to reveal RFLPs within plasmid clone inserts. Six independent clone inserts of sample 5–1 to –6 (as in Fig. 4) digested with *Hin*F1, tracks 1–6, or *Mse*1, tracks 7–12. Track Mr is 100 bp molecular size markers.

Uganda is very high and by implication that the diversity of BSV is high. The ∼10% of the virus genome amplified by the primers (Fig. 2) covers the most conserved region of badnaviruses, whereas the rest of the genome has very much less homology to other badnaviruses. If differences greater than 20% across the RT indicate different species, then there are 12 new species of BSV infecting Ugandan banana, represented by circles in Fig. 6. Also, more than one species was sometimes found in a single sample.

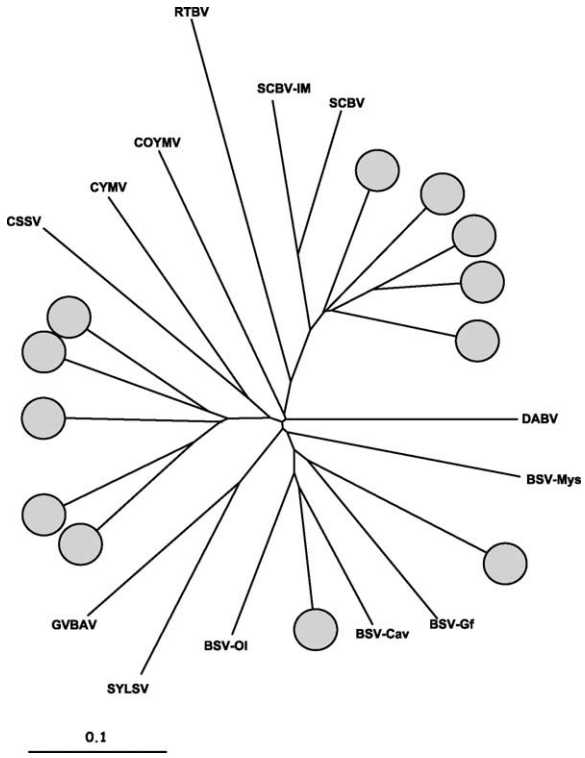

Fig. 6. Phylogeny of BSV sequences. A neighbour-joining tree comparing BSV sequences in Uganda and other badnavirus sequences. Each clade of Ugandan BSV sequence is represented by a single sequence, shown as a grey circle. The similarity of a sequence to any other is <80%.

4. Discussion

Observations during our collecting trips confirmed previous reports that infection of banana by BSV is widespread in Uganda (Tushmereirwe et al., 1996; Kubiriba et al., 2001). ISEM confirmed that the samples with typical BSV symptoms contained bacilliform particles that could be trapped with an anti-BSV antiserum (Fig. 3). ELISA was of lesser utility for diagnosis as there were samples known to contain BSV which were not unambiguously positive with it. PCR, using the degenerate primers 1a and 4′, was very effective at amplifying BSV sequences from isolated virion DNA, partially purified virus and crude leaf sap samples. Sequence analysis of the PCR products from the samples confirmed that the bacilliform particles are those of BSV. Other virus-like symptoms were also observed in Ugandan banana plants. In one of these cases, no BSV was detected indicating that these were not atypical BSV symptoms, so presumably another virus was involved (Tushmereirwe et al., 1996).

The types of BSV symptoms seen were variable but within the range described for this virus (Lockhart and Jones, 2000). Variation was also evident in other analyses of BSV. Antisera used in this study were raised to a mixture of different BSV and SCBV isolates. Nevertheless, it appeared that additional serotypes were found in Ugandan samples, as judged by the different sensitivities of the molecular and serological techniques. Cross-hybridisation experiments with three specific BSV probe sequences to PCR products from different samples showed differential cross-hybridisation, indicating inter-sample virus sequence variation (Table 1). Different samples contained different BSV sequences as well as having some in common. RFLP analysis of cloned PCR products using six or four base restriction endonucleases showed further evidence of variation but was not sufficiently informative and so the variation in the individual plasmid clone inserts was finally evaluated by sequencing. The sequence variation was large and showed that there were a surprising number of species of BSV infecting banana in Uganda (Fig. 6). These levels of variation cause problems for detection as it is possible that the PCR method described above samples only a proportion of the available genetic variability. However, it appeared a good primary diagnostic system.

Banana has been cultivated in East Africa including Uganda for at least a millennium, with multiple introductions of different genotypes and cultivars at different times (as discussed in Purseglove, 1972). Extensive movements of banana plants, including those infected with BSV, would provide a significant dissemination route. There must have also been vector transmission as the variety of BSV sequences found indicate diverse origins, even when present within a single plant. Over prolonged periods of cultivation, even relatively slow or inefficient vectors might have significant effects. Some badnaviruses are transmitted by the relatively sedentary mealybugs of the Pseudococcidae, e.g. CSSV by 14 different species of these insects (Brunt and Kenten, 1971) and Kubiriba et al. (2001) described a number of different mealybug species in Uganda. Alternative insect vectors are known for other badnaviruses and may exist for BSV. The lace bug *Diconocoris distanti* is an inefficient vector of Piper yellow mottle virus (de Silva et al., 2002), RYNV is transmitted by raspberry aphids (*Amphorophora* spp., Stace-Smith and Jones, 1987) and GVBAV by different aphid species (Adams and Posnette, 1987). BSV is particularly unusual in that there is a potential for infection from virus sequences integrated in the host genome (Harper et al., 1999; Ndowora et al., 1999; Geering et al., 2001). However, there is no evidence that the AAA genomes that predominate in Uganda contain activatable BSV sequences. Banana is often co-cultivated with crops such as pineapple, sugarcane, and yam, each of which is known to be infected by different badnaviruses. These crops may be alternative hosts not only for insect vectors but perhaps also for the viruses themselves.

The yield decline in Ugandan banana production must partly be caused by BSV as research has previously shown substantial yield losses due to infection (Lassoudière, 1974; Dahal et al., 2000; Daniells et al., 2001). However, it is probably only one of a number of factors that are responsible for the decline. Banana is cultivated year-round and continuous cropping combined with the long duration of some of the banana plots contributes not only to the build up of viral infection but also to the accumulation of other biotic problems and to a decrease in land fertility. Practical control measures include the need to avoid propagating infected mother/source material. However, as BSV is endemic and the variability of the virus poses problems for detection, replacement with healthy material is not a simple matter. Potentially, tissue culture might be used to generate healthy material, as it can eliminate some BSV species from banana (Helliot et al., 2002).

Acknowledgements

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