Monitoring the distribution of banana bunchy top virus in South Africa: a country-wide survey

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Abstract
Banana bunchy top disease is the most devastating viral disease of bananas worldwide and is caused by banana bunchy top virus (BBTV). The disease is spread by the banana aphid Pentalonia nigronervosa Coquerel (Hemiptera: Aphididae) and through infected propagation material. In 2016, the virus was detected for the first time in an isolated area in the South Coast region of KwaZulu-Natal Province (KZN), South Africa. The aim of this study was to conduct surveys across all banana-producing regions in South Africa, viz. KwaZulu-Natal, Mpumalanga, and Limpopo provinces. Over 1700 plant and aphid samples were collected from commercial farms and rural households in the three provinces, and more-intense sampling was done in the affected KZN region. A BBTV-specific PCR targeting DNA-R (encoding the master replication initiation protein, M-Rep) was used to detect virus-infected samples, and amplicons of the expected size were sequenced. Comparative phylogenetic analysis showed that the South African BBTV isolates clustered within the Pacific Indian Oceans genomic group, which includes isolates from India and other regions in Africa, with a bootstrap value of 94%. To date, the virus has been identified only in the South Coast region of KwaZulu-Natal Province. Intense management strategies, including scouting, removal of infected plants, and control of aphids, have been implemented in areas where positive samples were identified to minimize the spread of the virus.

Introduction
Banana (genus Musa, family Musaceae, order Zingiberales) is one of the most important economic crops in developing countries in tropical and subtropical areas [9] and is cultivated in about 120 countries [23]. Available estimates indicate that the average global banana production rose from 69 million tonnes in 2000-2002 to 116 million tonnes in 2017-2019, at an approximate value of 31 billion USD. These values are an estimate, as the bulk of banana production is conducted informally, thus making it difficult to obtain accurate figures [8]. An important subgroup is ‘Cavendish’, which may have originated in South China [12]. The ‘Cavendish’ subgroup yields the most common fruit and forms the backbone of the domestic industries in Australia, India, China, and South Africa [22].

Banana bunchy top virus (BBTV), a multi-component, circular, single-stranded DNA virus with 18–20 nm diameter virions, is the type member of the genus Babuvirus in the family Nanoviridae [2]. The viral genome comprises six encapsidated components (DNA-R, DNA-S, DNA-M, DNA-N, DNA-C, and DNA-U3), each approximately 1100 nucleotides in length [31], and sometimes additional alphsatellite molecules of a similar size [30]. Phylogenetic analysis, largely based on the DNA-R, -N, and -S segments, has shown BBTV isolates worldwide to be of ‘South Pacific’ or ‘Asian’ origin [16], and it has been proposed to classify them as members of the Pacific Indian Oceans (PIO) group or the Southeast Asian (SEA) group [34].
Banana bunchy top disease (BBTD), caused by BBTV, is spread in a circulative manner, predominantly by *Pentalonia nigronervosa* Coquerel (Hemiptera: Aphididae), commonly known as the banana aphid [17]. The first symptom of the disease is the appearance of dark green streaks on the minor leaf veins when the leaf is viewed from the underside with transmitted light, or on the midrib [17]. As the disease progresses, infected leaves become progressively stunted and malformed and have an upright bearing, eventually resulting in a ‘bunchy’ display. Yield losses of up to 100% can be experienced when plants are infected with BBTV and fail to produce bunches [25].

BBTV was reported for the first time in the Fiji Islands in 1889 [17], and it has since been identified in 44 countries in Africa, Australia, Asia, and the South Pacific Islands [4]. In Africa, BBTD was first reported in 1901 in Egypt. It has since been reported in 17 African countries, including Cameroon, Zambia, Mozambique, Malawi, and Nigeria [1, 10, 18]. The presence of BBTV in South Africa was confirmed in 2016 in a banana production area located in the South Coast region of KwaZulu-Natal Province [14]. The original source of infection in this region is currently unknown. Prior to the identification and confirmation of BBTV in South Africa in 2016; the last survey in 1996 provided no evidence for the presence of this virus in the country [20]. BBTV is a quarantine virus included in the South African Phytosanitary Services list of pathogens that must be absent in imported Musaceae propagation material under the Agricultural Pests Act, 1983 (Act no. 36 of 1983).

Banana is amongst the most important commercial subtropical fruit grown in South Africa and is mostly grown for home consumption. Subsistence farming of banana also contributes a staple food source for poorer communities, and income is generated through informal trade at local markets. Only a small fraction of all the bananas produced are sold on the world market [5]. Approximately 415,000 tonnes were harvested during the 2018/19 marketing season, valuing the industry at approximately 137 million USD [6]. In this study, the extent of the spread of BBTV in South African banana production areas was investigated in order to establish effective management strategies in the affected regions.

**Materials and methods**

**Surveys**

Follow-up surveys and delimiting surveys were conducted during the period of March 2017 to February 2021 to investigate the occurrence of BBTV on commercial farms and at rural households in the main banana-producing regions in KwaZulu-Natal, Mpumalanga, and Limpopo provinces of South Africa. Farms and rural households were selected based on information provided by government extension services in each province. The coordinates were recorded for each site where sampling took place, using a global positioning system (Garmin eTrex 20x) (Table 1 and Online Resource 1).

In each field of the 31 commercial farms, or at the individual households, plants were selected randomly and examined for typical BBTV symptoms. A section of emerging leaf tissue from the midrib and lamina of symptomatic and asymptomatic plants was collected and stored in a cooler box during transit from the field to the laboratory. Aphids were collected from symptomatic and asymptomatic plants using a fine-tip brush, followed by storage in a 2-ml microcentrifuge tube containing 99% ethanol. All samples were placed in labeled plastic bags and transferred to the laboratory for further analysis. Yellow bucket traps, set up on metal stands, were filled halfway with water and a drop of Sunlight® liquid soap to trap aphids on commercial farms overnight (Fig. 1). Twenty traps were placed at 10 commercial farms in the South Coast region of KZN, and the trapping was repeated four times per farm in the region. At the rest of the 21 commercial farms, located in the other production regions, trapping was done once. The traps had an opening on one side to allow for the drainage of excess water in the event of rain. This opening was covered with a very-fine-mesh cloth so that samples were not washed out (Fig. 1). The contents of the traps were sieved using muslin cloth, which was then placed in a jar containing 99% ethanol and was later examined under a microscope to check for the presence of banana aphids.

Delimiting surveys were conducted at Marburg Farm (30°45′46.6″S 30°25′00.2″E), a commercial farm 42 km from the initial outbreak site. This was done according to a surveying protocol developed by the International Institute of Tropical Agriculture (IITA). In each field, 100 plants were examined randomly for symptoms by walking across a “W” shaped path, inspecting 25 plants on each of the four transverses at an equal distance from each other. In blocks where symptomatic plants were observed, the midrib and lamina

**Table 1** Number of samples collected from various banana-growing regions in South Africa

| Location                      | Number of samples | BBTV positive |
|-------------------------------|-------------------|---------------|
|                               | Aphids | Plants | Aphids | Plants |
| South Coast (KwaZulu-Natal)   | 236    | 379    | 50     | 76     |
| North Coast (KwaZulu-Natal)   | 94     | 140    | 0      | 0      |
| Mpumalanga                    | 271    | 304    | 0      | 0      |
| Limpopo                       | 140    | 140    | 0      | 0      |

*A complete breakdown of all samples collected is available in Online Resource 1*
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of five plants and aphids from these plants were collected for virus testing, while in blocks with asymptomatic plants, the midrib and lamina from the last 25 plants were sampled [3].

Nucleic acid extraction from plant and aphid samples

Nucleic acid was extracted from aphids using a non-destructive extraction method [21]. Four to six aphids from a sample stored in 99% ethanol were dried on tissue paper and placed in a 2-ml microcentrifuge tube containing 200 µl of digestion buffer (10 mM NaCl, 10 mM Tris, and 10 mM EDTA) and proteinase K (Thermo Fisher Scientific, USA). Samples were incubated overnight in a shaking incubator at 55 °C and then centrifuged at 13,500 rpm for 10 min. Cold isopropanol was added to the aqueous phase of the supernatant in a new tube, which was then kept overnight at 10 °C for nucleic acid precipitation. Precipitated nucleic acid was collected by centrifugation at 13,500 rpm for 22 min, and the supernatant was discarded without disturbing the pellet. The pellet was washed three times with 70% (v/v) ethanol, dried for 1 h and resuspended in 100 µl of distilled water. The quality and quantity of each extraction was analyzed using a NanoDrop™ 1000 spectrophotometer (Thermo Fisher Scientific, USA).

PCR detection of BBTV

Banana bunchy top virus was detected by polymerase chain reaction (PCR) using the primer pair BBT-1 (5'-CTC GTC ATG TGC AAG GTT ATG TCG -3') and BBT-2 (5'-GAA GTT CTC CAG CTA TTC ATC GCC -3'), designed to amplify a 349-bp product corresponding to a portion of the BBTV M-Rep gene [29]. PCR was performed in a 25-µl reaction containing 1x reaction buffer, 0.5 µM each primer, 5 U of MyTaq DNA Polymerase (Bioline, USA), and 1 µl of sample nucleic acid. The temperature profile was as follows: initial denaturation at 95 °C for 1 min, 40 amplification cycles of denaturation at 95 °C for 15 s, annealing at 60 °C for 10 s, and extension at 72 °C for 10 s, and a final extension for 5 min at 72 °C. All PCR reactions were carried out using a Proflex PCR cycler (Applied Biosystems, USA). For electrophoretic analysis, 10 µl of the PCR product was run on a 1.5% (w/v) agarose gel in Tris-acetate EDTA (TAE) buffer containing ethidium bromide. The amplified DNA bands were visualized using a UV transilluminator (Quantum CX 5, Vilber Lourmat, France).

Sequencing and phylogenetic analysis

Amplicons from 14 representative PCR-positive samples from the KZN South Coast region were sequenced at Inqaba Biotechnical Industries (Pretoria, South Africa). The nucleotide sequences were aligned using MAFFT and BioEdit [11, 15] software. For genetic analysis, nucleotide sequences from DNA-R components were aligned with closely related BBTV M-Rep gene sequences downloaded from the National Center for Biotechnology Information (NCBI).
database, including two South African isolates (GenBank accession numbers KY770984 and KY770985) from a previous study [21]. A phylogenetic tree was constructed using MEGA 11 [28], and abaca bunchy top virus (ABTV, genus Babuvirus, GenBank accession no. EF546813) was used as an outgroup. The best-fit model was determined using MEGA X. The evolutionary history was inferred using the maximum-likelihood method based on the Tamura 3-parameter model with a gamma distribution [27]. The bootstrap consensus tree was inferred from 1000 replicates. Branches with bootstrap values less than 70% were collapsed.

Results

Surveys

Surveys were initially carried out in the KZN South Coast region where the BBTV outbreak was confirmed, including the region within a 30-km radius of the initial outbreak site. This region consists of rural households that cultivate banana for home consumption and subsistence farming. Commercial farms 50 km south of the initial outbreak site were also surveyed. The surveys were then extended to the North Coast of KwaZulu-Natal as well as the Mpumalanga and Limpopo provinces of South Africa, covering over 5000 ha in total (Table 1 and Online Resource 1). A total of 1704 plant and aphid samples were collected in the three provinces (Fig. 2). BBTV symptom expression was only observed in samples collected from the KZN South Coast region (Fig. 3). Surveys were conducted in rural communities from the four local municipalities (Ray Nkonyeni, Umdoni, Umzumbe, and uMuziwabantu) within the Ugu District. The number of banana plants per rural household ranged from three plants per household to more than 100 plants, and the level of infection per household ranged from just a few diseased plants to complete infection of all plants. The exact range of infection per household was not determined because the aim was to map infection sites. Therefore, the visual scoring of symptoms was done per site to determine the radius of BBTV spread from the initial outbreak site. Plant and aphid samples were collected from plants at each site, even if no symptoms were observed. During the 2018 survey, BBTV was detected in banana plants at five households from a total of 15 visited sites (Online Resource 1), and a second trip that year to a different location resulted in eight households with positive plants out of 10 sites visited. A further survey of seven sites in 2018 resulted in all seven sites with having at

![Map of surveyed locations indicated by yellow tear-drop points. Samples were collected from KwaZulu-Natal, Mpumalanga, and Limpopo provinces.](image-url)
least one BBTV-infected plant (Online Resource 1). In 2019, six sites had BBTV-positive plants, and in 2020, seven out of 11 sites at different locations had BBTV-infected plants. During the 2021 survey, nine out of 14 sites had BBTV-infected plants. The impact of BBTV infection on commercial farms was restricted to the loss of 160 ha of banana at the initial outbreak site, while infections on the second commercial farm were reported in three blocks throughout the farm. Here, the spread was contained by removal of infected plants and chemical control of the banana aphid. Symptom severity on the “Williams” cultivar, which is the most common cultivar on both rural and commercial farms, ranged from mild to severe in the field and was determined by visual inspection of plant parts. Mild symptoms included dot-dash symptoms on banana leaves and streaks on the pseudostem (Fig. 4a). Subsequently, the leaves became yellow and curled and developed a leathery feel (Fig. 4b and c). The most distinctive symptom detected in severely affected plants was the upright growth of an infected plant with severe stunting on smaller plants (Fig. 4d).

**Nucleic acid extraction and PCR detection of BBTV**

Regardless of symptom expression, all samples collected during the field surveys were screened by PCR, and positive samples yielded amplicons of ~349 bp in size, which
corresponded to a partial DNA-R sequence of the M-Rep gene. No amplification with the BBTV-specific primers was observed with asymptomatic plant samples. From 379 plants collected in the KZN South Coast region (Table 1), 76 tested positive for BBTV. A total of 236 aphids were collected (218 aphids taken from plants and 18 winged aphids from traps), and 50 of those from plants, but none from traps, tested positive for BBTV.

Rural households accounted for a larger portion of positive aphid and plant samples (104 out of 126 positive samples), while BBTV infections were confirmed at only two commercial farms in the KZN South Coast region. Upon detection of the virus at the farm (30°45′46.6″ S, 30°25′00.2″ E), delimiting surveys were conducted approximately 42 km from the initial outbreak site. At this commercial farm, two plants had previously tested positive for BBTV in a survey conducted in October 2018. Using the delimiting survey strategy, BBTV was detected on an additional four plants in two other blocks on the farm, indicating that infections had spread to more sections of the farm by January 2019.

**Sequencing and phylogenetic analysis**

Fourteen randomly selected PCR-positive amplicons were submitted to Inqaba Biotech (Pretoria, South Africa) for Sanger sequencing, and the sequences were deposited in the NCBI GenBank database under the accession numbers MT023045-58. Phylogenetic analysis showed that all of the BBTV isolates from the South Coast region in KZN grouped within the Pacific Indian Oceans (PIO) group along with isolates from India, Pakistan, Fiji, and Australia, with a bootstrap value of 94% (Fig. 5). The tree topology and branch lengths indicate that the South African isolates are closely related to the other members of the PIO group.

**Discussion**

Banana bunchy top virus poses a major threat to banana cultivation in South Africa, especially in the currently affected KZN region. In this study, plant and aphid samples were collected in the main banana-producing provinces of South Africa for detection of BBTV (Table 1 and Fig. 2). The virus was detected by PCR using BBT-1 and BBT-2 primers in positive plant and aphid samples. Multiple studies have shown the reliability of PCR as a tool for detection of BBTV [24, 26, 32]. Viruliferous aphids were detected on the majority of plants displaying clear BBTV symptoms, and 78% of the aphids collected from these plants tested positive for BBTV. *Pentalonia nigronervosa* Coquerel (Hemiptera: Aphididae), which is known to transmit BBTV [17], was found in all surveyed banana fields across the country, and the occurrence of aphids was higher where no vector control was implemented. Interrupting the virus transmission chain is not always possible, but removal of infected plant material will help to contain the spread of BBTV. Poor maintenance of the banana crop and its dense canopy might contribute to...
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the growth of the aphid vector population [33]. The dense canopy partially prevents rainfall from reaching the leaves and pseudostem, thereby favouring aphid multiplication [33].

Different scenarios can be proposed for the introduction of BBTV into South Africa. First, the virus might have been spread by aphids from Mozambique into South Africa, with which it shares a border. However, all samples collected from areas directly adjacent to the South African/Mozambican border tested negative for BBTV, arguing against this proposition. Second, the virus might have been introduced unknowingly into the KZN South Coast region in South Africa through infected planting material, resulting in its widespread dissemination. Since cultivated bananas are propagated vegetatively, the potential for human-mediated spread is high. Symptom expression can take between 25 and 85 days to develop in a BBTV-infected plant, so when an infected but asymptomatic banana propagule is introduced into a region where *P. nigronervosa* is present, there is potential for subsequent vector transmission [25]. Spread of BBTV from the first reported KZN outbreak site in a southerly direction to a farm approximately 42 km away suggests that infected aphids were carried by wind currents to this farm.

Phylogenetic analysis of a partial sequence of DNA-R was carried out to determine the relationship of the South African isolates to other BBTV isolates detected worldwide (Fig. 5). The use of M-Rep and coat protein gene sequences to construct phylogenetic trees has been a common approach to study the evolutionary history of BBTV and other nanoviruses [31]. Phylogenetic analysis showed two broad clades/groups of BBTV, namely, the South East Asian and Pacific Indian Oceans groups, with high bootstrap support values of 96% and 94%, respectively. The KZN South Coast region isolates from this study clustered with members of the Pacific Indian Oceans group along with isolates from other African countries, Australia, Hawaii, Fiji, Pakistan, and India. The branch lengths indicated minimal genetic difference between the South African BBTV isolates from this study, the two South African reference isolates with GenBank accession numbers KY770984 and KY770985, and the other isolates within this group. Although the tree topology does not show the probable origin of the South Africa isolates, it does confirm its grouping within the Pacific Indian Oceans group. The monophyletic origin of the isolates within the Pacific Indian Oceans group was also confirmed by a bootstrap value of 94%. Two Malawian isolates with GenBank accession numbers JF55994 and JF55993 grouped within a separate clade, separate from the Malawian isolate with GenBank accession number JF755995.

Socio-economic factors such as a lack of funds needed to purchase chemicals for pest control and resistance to proper/adequate removal of infected plant material in the rural community contribute to the spread of the disease. Commercial farmers in the region follow management strategies such as stringent scouting and the use of chemicals as part of aphid control for orchard management and are therefore accustomed to chemical control methods, while this is not the case for rural households. In this region, the use of chemicals for aphid control is not a sustainable option due to economic constraints and environmental impact. A study showing the effectiveness of consistent rouging in managing the disease

![Phylogenetic tree showing the genetic relationships between 16 randomly selected BBTV isolates from the South Coast region of KwaZulu-Natal, South Africa, other isolates of BBTV, and an outgroup (abaca bunchy top virus [ABTV]). The 14 random samples from this study are shown in bold.](image)
concluded that it is possible for smallholder farms to recover banana productivity if such a practice is carried out diligently [19].

In the affected region, some field workers lost their jobs on the commercial farms when infected plants in various plots were uprooted. Some households that were visited had reportedly incurred loss of income generated from the sale of bananas (personal communication). This has a negative impact on food security and sustainability of banana production for the region. To reduce the impact of BBTV in the region, awareness campaigns, in conjunction with the Department of Agriculture, Land Reform and Rural Development (DALRRD) and Department of Agriculture and Rural Development (DARD), have been launched in the KZN South Coast region, and efforts are ongoing to contain the spread of the virus.

**Conclusion**

Once established, BBTV has never been completely eradicated in any country. It is, however, possible to manage the disease [13]. The spread of BBTV in the KZN South Coast region and monitoring thereof in the rest of the banana-producing regions in South Africa was discussed here. Banana plants and aphids collected from other regions of the country tested negative for BBTV. Therefore, continuous scouting to monitor any outbreaks is critical, especially in the regions neighboring Mozambique, where BBTV is present. Integrated control strategies are the key to containing the spread of BBTV in a region. Awareness needs to be raised amongst stakeholders at all levels (policymakers, extension services, commercial and small-holder farmers) by promoting regular scouting for symptoms as well as removal of infected mats to reduce inoculum pressure. Applying strict quarantine measures to avoid movement of propagation material and the use of certified tissue culture material that is free of the virus is another recommendation.

The effectiveness of consistent rouging in managing the disease is worthwhile to investigate. Omondi et al. [19] found that it is possible for smallholder farms to recover banana productivity if such a practice is carried out diligently. Such an approach can be explored in the KZN South Coast region, as it is a practical control strategy with little to no financial implementation costs. Our findings demonstrate a restricted distribution of BBTV in South Africa. Continued monitoring is required to limit its spread in the KZN South Coast region and to prevent any further spread beyond this region.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00705-022-05451-5.

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**Declarations**

**Conflict of interest** The authors declare they have no financial interests.

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