AJPP Asian Journal of Plant Pathology

OPEN ACCESS

Viruses Infecting Yam in Africa: Existing Knowledge and Future Perspectives

[1,2,4]Emmanuel Bwanampongo Kulimushi, [1]Paul Mbogo Kusolwa, [3]Espoir Basengere Bisimwa and [1]Gration Mutashoberwa Rwegasira

[1]Department of Crop Science and Horticulture, College of Agriculture, Sokoine University of Agriculture, Morogoro, P.O. Box 3000, Tanzania

[2]SACIDS Africa Centre of Excellence for Infectious Diseases, SACIDS Foundation for One Health, Sokoine University of Agriculture, Morogoro, P.O. Box 3297, Tanzania

[3]Department of Crop Science, Faculty of Agriculture, Catholic University of Bukavu, P.O. Box 285, South Kivu, Democratic Republic of Congo, Central Africa

[4]Department of Crop Science, Faculty of Agriculture, University of Goma, North Kivu, P.O. Box 204, Democratic Republic of Congo, Central Africa

ABSTRACT

Yam is one of the nutritional crops feeding a large population in West Africa in particular and currently expanding to the other parts of the continent. However, its productivity is being hampered by biotic stresses particularly viruses which are mainly propagated through infected tubers as planting materials. Viruses infecting yam have been reported worldwide in yam production areas affecting both the quality and quantity of tubers, subsequently interfering with the international germplasm exchange. There are few, not well-described yam viruses in Sub-Saharan Africa (SSA) that induce such symptoms as mosaic, chlorotic spotting, curling and mottling. Despite the strides made in describing and diagnosing yam viruses in SSA, a lot remained and is still unknown due to scarcity and limited access to knowledge, particularly the epidemiology of yam viruses. This review presented the current status of yam viruses occurring in Africa. Future directions on yam viruses and diagnostics using molecular methods are discussed.

KEYWORDS

Yam, *Dioscorea* spp., viruses, diagnostic, Africa

INTRODUCTION

The yam (*Dioscorea* spp., family Dioscoreaceae) is an herbaceous vine with underground edible tubers and major staple foods in the world, especially in some regions of the tropics and subtropics. The edible varieties of yam serve as important sources of carbohydrates for millions of people in these regions[1,2]. The yam is currently, the third most important tuber crop worldwide, while in Africa, it's a second after cassava by value and production[3,4]. Over 95% of world yam production occurs in West and Central Africa[3,4]. Due to its strength in adverse weather and wide agroecological tailoring, yam is an important crop for food security. Also, as compared to other tuber and root crops, it's offer good options for both value-addition and consumption[5].

ISSN: 1819-1541 (Print)
https://doi.org/10.3923/ajpp.2024.86.102

Received: 25 Oct. 2024
Accepted: 01 Dec. 2024
Published: 02 Dec. 2024

Besides its food and economic value, yam is also a culturally important food crop in some tropical and subtropical regions[6]. Several factors such as pests and diseases, limited access to quality planting materials and low soil fertility, are responsible for its low production[7]. Pests and diseases, such as insects, nematodes, fungi, bacteria and viruses are the major causes of global yam production decrease leading to severe economic losses[8,9].

Viruses infecting yam have been reported in yam-producing regions to affect tubers' quantity and quality subsequently interfering with the international germplasm exchange[10,11]. To date, virus species including Yam mosaic virus (YMV: *Potyvirus*), Yam mild mosaic virus (YMMV: *Potyvirus*), *Cucumber mosaic* virus (CMV: *Cucumovirus*), *Dioscorea bacilliform* AL virus (DBALV: *Badnavirus*), *Dioscorea bacilliform* SN virus (DBSNV: *Badnavirus*), *Dioscorea bacilliform* RT virus 1 (DBRTV1: *Badnavirus*), *Dioscorea bacilliform* RT virus 2 (DBRTV2: *Badnavirus*), *Dioscorea latent* virus (DLV: *Potexvirus*), *Dioscorea mottle* virus (DMoV: *Comovirus*), *Dioscorea mosaic* associated virus (DMaV: *Sadwavirus*), Yam spherical virus (YSV: *Aureusvirus*), Yam ampelovirus 1 (YaV1: *Ampelovirus*), Ethiopian yam virus (EYV: *Potyvirus*), Yam virus 1 (YV-1: *Crinivirus*), Yam virus Y (YVY: Unknown genera) and unknown species of yam badnavirus have been reported in yam producing areas in Africa[1,10,12-22]. They often induce leaf symptoms like mosaic, chlorotic spotting, curling and mottling[23]. Except for some species of *Badnavirus* and *Ampelovirus*, which can be transmitted by mealybugs in a semi-persistent manner, the rest of the viruses infecting yam are transmitted by a wide range of aphid species[11,21]. Mechanical transmission of the viruses to yam and *Nicotiana* plants has also been reported[8]. Farmers' practices like the exchange of seed materials contribute to widespread distribution and increased incidence of viral diseases in yam eld[1].

In Africa, efforts are being made to control yam viruses and increase yam production through their identification, diagnosis and control strategies[24,25]. Despite the progress on yam research in West Africa, data on the occurrence and distribution of yam viruses are scanty in other countries in SSA, particularly in Central and East Africa.

This paper presented the existing knowledge of yam viruses reported in Africa to date and the diagnostic tools developed. Finally, future perspectives on the virus infecting yam in Africa are discussed.

Diversity of viruses infecting yam in Africa: Among 16 virus species reported to infect yam in Africa (Table 1), only four viruses are most important and well characterized in some SSA countries[9,10,12,23]. These are YMV, YMMV, CMV and *Badnaviruses*. The YMV is known to be the most severe virus in reducing tubers yield, followed by YMMV[23].

Genus *Ampelovirus* (family Closteroviridae): Based on their genome organization and biological properties such as insect vectors, host plants and transmission mechanisms, the family Closteroviridae harbors viruses of the genus *Closterovirus*, *Ampelovirus*, *Crinivirus* and *Velarivirus*[26]. In the genus *Ampelovirus*, viruses have a monopartite positive-sense RNA genome and show wide variation in size and organization[26]. According to Martelli *et al.*[27] viruses of this genus are grouped into two subgroups. The YaV1 belongs to first subgroup[21].

Yam ampelovirus 1 (YaV1): The YaV1, renamed Yam asymptomatic virus 1, has been reported in yam germplasm collection from South America, Africa (Nigeria and Cote d'Ivoire), the Caribbean and South Pacific[21]. The genome sequence of YaV1 comprises 14,855 nucleotides (nt) in length and has 10 ORFs[21]. Like other *Ampelovirus*, YaV1 is transmitted by mealybugs in a semi-persistent manner[26,28]. Attempt for mechanical and seed-based transmission have not been successful[21]. Despite the presence of YaV1 in Nigeria and Cote d'Ivoire, YaV1 occurrence in others yam-producing regions in SSA is less reported and documented.

Yam virus 1 (YV-1) : Using HTS, a novel specie of the family Closteroviridae, named YV-1 was first reported on *D. rotundata* in Ethiopia[28]. The genome of YVY isolates has a monopartite positive-sense single-stranded RNA genome of 7911 nt long with three putative ORFs and 8435 nt long with eight putative ORFs, respectively for YV-1 RNA2 and YV-1 RNA1 isolates[28]. To date, no information on the epidemiology of YV-1 in other yams producing zones in Africa is available.

Genus *Aureusvirus* (family Tombusviridae): Members of the family Tombusviridae have small single-stranded, positive-sense, RNA genome. It contains the genus *Tombusvirus*, *Auresvirus*, *Carmovirus*, *Necrovirus*, *Avenavirus*, *Machlomovirus*, *Panicovirus* and *Diathovirus*. Based on genome organization, these genera are divided into three distinct groups tombusvirus-like, carmovirus-like and Diathoviruses[31]. Plant viruses in *Aureusvirus* genus have a positive stranded RNA genome with four ORFs, encoding RNA-dependent RNA polymerase (ORF1), a coat protein (ORF2), the protein involved in movement (ORF3) and a silencing suppressor proteins (ORF4)[17]. These viruses are soil-borne viruses and the mechanical transmission by sap inoculation from infected plants to health ones has been reported by Martelli *et al*.[27].

Yam spherical virus (YSV): The YSV is the first plant virus infecting yam and the fifth plant virus species of the genus *Aureusvirus*[17]. First reported from *D. rotundata* in Nigeria, the genome sequence of YSV comprises 4,464 nt and has 4 putative ORFs, anked by non-translated regions (NTR) at the 5′ and 3′ ends[17]. Mechanical transmission of YSV to other test plants is possible[17]. To date, no information on the presence of YSV in others yam producing zones in Africa is available.

Genus *Badnavirus* (family Caulimoviridae): The plant viruses of the family Caulimoviridae have a non-covalently closed circular dsDNA genomes of 7.1-9.8 kbp with a bacilliform or isometric particles non-enveloped[32]. This family contains genera *Caulimovirus*, *Soymovirus*, *Cavemovirus*, *Petuvirus*, *Solendovirus*, *Rosadnavirus*, *Badnavirus* and *Tungrovirus*. However, the last two have a bacilliform virion whilst others have an isometric virion[32]. The *Badnaviruses* are a circular double stranded DNA genome of around 7.3-9.2 kbp with at least 3 ORFs[19,33]. In some regions of Africa, yams are infected by several species of *Badnavirus*[19,34] and induce severe chlorosis and distortion on leaves. The virus can be transmitted in a semi-persistent manner by mealybugs between yams species, but mechanical transmission can also be possible[13,15,19,33].

The presence of endogenous pararetrovirus in the genome of Africa yam *D. cayenensis*-rotundata complex, called endogenous *D. bacilliform* viruses (eDBVs) and the high level of sequence variation among *Badnavirus* complicates the development of specific reliable molecular detection tests for yam-infecting badnaviruses[18,35].

***Dioscorea bacilliform* AL virus (DBALV) Syn.**
***Dioscorea alata* bacilliform virus (DaBV):** The DaBV occurs on *Dioscorea* spp., in Africa[13] and was first reported on *D. alata* in Nigeria[36]. The complete genome of the DaBV isolates from Nigeria was reported by Bhat *et al*.[36] and comprises 7413 and 7415 bp for two isolates. Its sequence has three ORFs. However, the comparison of DaBV sequence with others *Badnavirus* shows the highest levels of similarity to the Cacao Swollen Shoot Virus which occurs in the same regions where the DaBV isolates from Nigeria were described by Briddon *et al*.[37]. Data on geographical distribution and epidemiology of DaBV in others yam producing countries in Africa, particularly in Central and Eastern Africa, where badnaviruses were reported in other tropical crops[36,38,39], remains scarce.

***Dioscorea bacilliform* SN virus (DsBV) Syn.**
***Dioscorea sansibarensis* bacilliform virus (DsBV):** The DsBV was first reported by Seal and Muller[15] on a wild plant named *D. sansibarensis* from Benin. However, in other yam-producing areas in Africa, no information on the occurrence of DsBV is available. The genome size of DsBV is ~7.3 kbp, encoding for three open reading frames[40]. However, the molecular analysis of a full-length sequence shows that DsBV shared the most identity of around 61.9% to DaBV[15].

***Dioscorea bacilliform* RT virus 1 (DBRTV1) and *Dioscorea bacilliform* RT virus *2* (DBRTV2):** The two *Badnavirus* species (DBRTV1 and DBRTV2) were first detected on *D. rotundata* from Nigeria[19]. They have a single molecule of circular double-stranded DNA genome of 7438-7708 bp in length[19,41]. The genome sequence of DBRTV1 and DBRTV2 has three to four ORFs[19,41]. However, the ORF 4 partially overlapped the 3′ end of ORF3 and encodes a 138 amino acid putative protein[41]. Despite the existence of DBRTV1 and DBRTV2 in West Africa, no available information on their presence in other African countries is up to date.

Genus *Cucumovirus* (family Bromoviridae): Plant viruses of the family Bromoviridae are among the most important viruses which attack a wide host's range including herbaceous plants, shrubs and trees. The members of the Bromoviridae family have a tri-segmented, positive-sense, single-stranded RNA genomes of 8 kb with a spherical or bacilliform virion non-enveloped[42,43]. However, Bujarski *et al.*[43] report that viruses of this family Bromoviridae have three genomic RNAs from the end 5′. The RNA1 and RNA2 code for viral replicase proteins, respectively while the RNAs 3 encode the movement (MP) and coat proteins (CP).

Plant viruses of the family Bromoviridae include genera; *Alfamovirus*, *Ilarvirus*, *Bromovirus*, *Cucumovirus*, *Oleavirus* and *Idaeovirus*[44-46]. Members of the genus *Cucumovirus* have a wide host range where more than 1200 plant species are infected and some of them are responsible of major disease epidemics in crop plants[47]. Also, viruses in the *Cucumovirus* genus have tri-segmented, positive-sense, single-stranded RNA genomes of 8 kb with a spherical virion particle of a diameter 26-35 nm[47]. Transmission occurs mechanically or in insect vectors in a non-persistent manner[47]. Among virus species of *Cucumovirus* genera, CMV is the most economic and has already been reported on yam in Africa[29].

***Cucumber mosaic* virus (CMV):** The CMV was first described as the causal agent of plant diseases reported on cucumber by Roossinck[48] and has a wide range of host plants[48-50]. On yam, it has been reported on *D. alata* and *D. rotundata* in West Africa[16,29,51,52] and well characterized by Eni *et al.*[53]. To date, no information on the presence, distribution and incidence of CMV in others yam producing zones in central and Eastern Africa are available.

The CMV has a tripartite plus-sense RNAs virus non-enveloped[54]. A part of genomic RNAs, a subgenomic RNA and named RNA 4 is enveloped in virion of all strains of CMV with the genomic RNA3. In strains of subgroup II, an additional subgenomic RNA called RNA 4A is also enveloped[55]. Rizos *et al.*[50] showed that more than one hundred isolates of CMV have been well characterized and are available in GenBank. In this fact, the existence of these isolates confirms the greatest degree of variation of CMV[50]. Based on serological relationships and nucleic acid hybridization, CMV isolates are split into two subgroups (I and II)[56]. However, CMV strains infecting yam belong to subgroup one[53].

More than 80 species of Aphids are responsible for CMV transmission from infected plants to healthy ones in a non-persistent manner; among them, *Aphis gossypii* and *Myzus persicae* are the most efficient[57]. Apart from the transmission by vectors, CMV can also be spread mechanically or through infected seeds[58,59].

Unresolved genera of the family Secoviridae: Members of the Secoviridae family have positive-sense single-stranded RNA genomes (mono or bi-partite) of 9-13.7 kb in size with an icosahedral virion particle non-enveloped of 25-30 nm of diameter[60].

In Africa, DMaV and DMoV have been reported in yam production areas[14,22,61]. The DMaV was first detected in Nigeria by HTS. Currently, it is likely to be distributed across West Africa on *Dioscorea* sp.[22,61], but remains less documented. The plant-to-plant transmission has been described by Bakayoko *et al.*[22]. Apart from DMaV, Nyaboga *et al.*[14] reported the existence of another member of the family Secoviridae infecting *D. alata* in West Africa named DMoV and susceptible to being spread throughout West Africa.

Genus *Potexvirus* (family Alphaflexiviridae): Viruses of the Alphaflexiviridae family have a single-stranded, positive-sense RNA genome of 5.4 -9 kb with flexuous filamentous virions ranging in size from 470-800 nm in length and 12-13 nm in diameter[62]. The family Alphaflexiviridae contains plant viruses of genera *Potexvirus*, *Mandarivirus*, *Lolavirus*, *Allexivirus*, *Botrexvirus*, *Platypuvirus* and *Sclerodarnavirus*[63,64].

Among genera belonging to Alphaflexiviridae family, species of the genus *Potexvirus* have been detected in yam growing regions in Africa[9] but remain less documented. Although, the geographical distribution of their host plants makes the members of potexvirus genus, the broadest host range plant virus, despite some members can infect a limited number of host plants[65].

***Dioscorea latent* virus (DLV):** The DLV was first reported on an asymptomatic plant of *Dioscorea* spp., in West Africa[9]. To date, no information on the occurrence, distribution and incidence of DLV in other yam-producing zones in Africa is available. The DLV has a single-stranded RNA genome of 7.5 kb with a flexuous filamentous virion of 445 nm in length[66,67] and it is mechanically transmitted to *Dioscorea* spp. and some herbaceous hosts.

Unknown genus of family Betaflexiviridae: The family of Betaflexiviridae contains two subfamilies (Trivirinae and Quinvirinae) including 15 genera[68,69]. It has a monopartite positive-sense single-stranded RNA genome of 6.5-9 kb with non-enveloped flexuous filamentous virions ranging in size from 600-1000 nm in length and 12-13 nm in diameter[63,68].

Viruses belonging to this family infect mostly woody plants while only some herbaceous plants can be infected[70]. The transmission plant to plant by insect vectors like aphids, mealybugs, mites and scale insects and mechanical transmission is also possible[68,69]. The representative species belonging to the Betaflexiviridae family that occurs in yam-production area in Africa is Yam virus Y.

Yam virus Y (YVY): The YVY was first described on *D. rotundata* from Nigeria and Ghana by HTS[20]. The complete genome of YVY isolates (YVY-Dan and YVY-Mak isolates) has been sequenced and has a monopartite positive-sense single-stranded RNA genome of 7557 and 7584 nt in length, respectively for YVY-Dan and YVY-Mak isolates, with five ORFs encoding large replication protein (ORF1), the three proteins involved in viral movement (ORF2 orF3 and ORF4) and a putative coat protein (ORF5)[20,71].

Genus *Potyvirus* (family Potyviridae): Viruses in the Potyviridae family constitute the most important group of plant viruses which cause yield losses and affect the quality of many crops worldwide[72]. The family of Potyviridae has a positive-sense, single-stranded RNA genome of 8-11 kb in size with a exuous laments particles ranging in size from 11-20 nm in diameter and 680-900 nm in length for some viruses in Potyviridae family and others have a virion with two modal lengths of 200-300 and 500-600 nm[73,74].

Based on host range, genomic features and phylogeny, Yang *et al.*[75] showed that plant viruses in Potyviridae include *Bevemovirus*, *Brambyvirus*, *Bymovirus*, *Celavirus*, *Ipomovirus*, *Macluravirus*, *Poacevirus*, *Potyvirus*, *Roymovirus*, *Rymovirus* and *Tritimovirus*. The *Potyvirus* genus is the most economically important and contains 167 to 183 out of 228 species belonging to the Potyviridae family[75].

Viruses in Potyviridae are usually transmitted by insect vectors (Aphids, whiteflies and mites) in a non-persistent manner. An exception of Bymoviruses which have a bipartite genome are transmitted by the fungus *Polymyxa graminis* and mechanically by inoculation of sap[73,75].

Species of *Potyvirus* genus are widely distributed in the world, especially in tropical and sub-tropical regions and have a greater diversity of vectors than other members of Potyviridae[73,76].

Yam mosaic virus (YMV): The YMV was first reported on *D. cayenensis* in Côte d'Ivoire[12] and it occurs in many yam production areas worldwide on several species of *Dioscorea*[77,78]. To date, the complete genome of two isolates (Côte d'Ivoire and YMV-NG) have been sequenced and are respectively a single-stranded RNA genome of 9608 and 9594 nt in length[79,80]. According to Bousalem *et al.*[77] and Mendoza *et al.*[81], YMV has a monopartite positive-sense single-stranded RNA genome of 9-12 kbp exhibiting high genetic diversity and consisting of more than one serotype. Njukeng *et al.*[23] have shown that the prevalence of YMV depends on host plants, varieties and regions. However, the information on YMV prevalence in other yam producing zones, particularly in Eastern and Central Africa remains scanty. This information is relevant to understand epidemiology of YMV and develop control strategies for effective management.

The use of YMV infected tuber seeds, mechanical and insect vector transmissions are the most important mechanisms of transmission through which YMV is known to be spread[8,77]. The efficiency of transmission of YMV by insect vectors has little been explored[12] and has never been compared between yam species and other YMV strains. Although, the transmission test made by Thouvenel and Fauquet[12] using YMV isolates from Cote d'Ivoire, suggested that YMV was being transmitted by a wide range of aphid species (*A. gossypii*, *A. craccivora*, *M. persicae*, *Rhopalosiphum maidis* and *Toxoptera citricida*) in a non-persistent manner.

Yam mild mosaic virus (YMMV): The YMMV was first reported on *D. alata* in West Africa[10] and described to be the most important virus on yam which reduces tuber yield and quality after YMV[23]. Based on serological and molecular characterization of isolates from Martinique, Colombia and Brazil, Mumford and Seal[24] confirmed YMMV as a distinct *Potyvirus*.

To date, the virus occurs in other yam growing areas worldwide, particularly on the most widely cultivated *D. alata* than other yam species[1,16,23,24,40,82-85].

The YMMV has flexuous filamentous virions with around 750 nm in length[10]. The complete genome sequences of YMMV isolates available in the NCBI nucleotide database range from 9521 to 9538 nt in length, without the poly (A) tail. The coat protein (CP) gene of YMMV is 798 nt in length and encodes for a protein of 266 aa and 30 kDa[2,86]. The YMMV is transmitted by aphid vectors from the natural host to herbaceous hosts, particularly cowpea. However, as with other Potyviruses, the DAG motif belonging to this protein plays an important role in aphid transmission[87]. Also, it is mechanically transmitted by inoculation sap within some *Dioscorea* and *Vigna* sp.[10]. No information on the epidemiology of YMMV in other yam-producing countries in Central Africa is available, except in Cameroon where YMMV was first detected in single or mixed infection with YMV[1].

Ethiopian yam virus (EYV): The EYV was first reported on *D. rotundata* from Ethiopia by high-throughput sequencing (HTS)[28]. Using HTS, the genome of EYV has been sequenced and has a monopartite positive-sense single-stranded RNA genome of 9557 nt in length with the ORF encoding a protein of 3087 aa with around 347.5 kDa of molecular mass[28]. To date, no information on the occurrence and epidemiology of EYV in other yams-producing zones in Africa is available.

Distribution of yam viruses reported in Africa: Studies on the geographical distribution of yam viruses reported the presence of sixteen yam virus species in Africa (Table 1). The occurrence of YMV in several countries revealed that it's the most important virus in the yam field across Africa[23]. However, some yam virus-like symptoms have been reported in yam field in Eastern and Central Africa[84,88,89], although the current status of yam viruses in these areas remains unknown.

Disease symptoms and yield losses in yam field: The yam viruses reported in Africa can induce yam leaves common symptoms like mosaic, chlorosis, mottling and leaf deformation[20,23,24,61]. However, typical symptoms of yam viruses on leaves have been reported and are variable depending on the yam species or cultivars, nature of virus species/strains and agroecological zones[17,90].

Table 1: List of viruses infecting yam in Africa

Family	Genus	Species	Transmission	Diagnostic tools	First report	References
Alphaflexiviridae	*Potexvirus*	*Dioscorea latent* virus (DLV)	Aphids and mechanical	ELISA and RT-PCR	Cote d'Ivoire	Bakayoko *et al.*[22]
Betaflexiviridae	Unknown	Yam virus Y (YVY)	Unknown	RT-PCR	Nigeria, Ghana	Silva *et al.*[20]
Bromoviridae	*Cucumovirus*	*Cucumber mosaic* virus (CMV)	Aphids	ELISA and IC-RT-PCR	West Africa	Diouf *et al.*[29]
Caulimoviridae	*Badnavirus*	*Dioscorea bacilliform* AL virus (DBALV)	Mealybugs	DAS-ELISA and IC-PCR	Nigeria	Phillips *et al.*[13]
		Dioscorea bacilliform SN virus (DBSNV)	Mealybugs	PAS-ELISA and IC-PCR	Benin	Seal and Muller[15]
		Dioscorea bacilliform RT virus 1	Mealybugs	IC-PCR	Nigeria	Bömer *et al.*[19]
		Dioscorea bacilliform RT virus 2	Mealybugs	IC-PCR	Nigeria	Bömer *et al.*[19]
		Uncharacterized species of yam badnavirus	Unknown	IC-PCR	Benin, Nigeria	Eni *et al.*[30], Umber *et al.*[18] and Bömer *et al.*[19]
Closteroviridae	*Ampelovirus*	Yam ampelovirus 1 (YaV1)	Mealybugs	RT-PCR	Nigeria	Marais *et al.*[21]
	Crinivirus	Yam virus 1 (YV-1)	Whiteflies	RT-PCR and HTS	Ethiopia	Gogile *et al.*[28]
Potyviridae	*Potyvirus*	Yam mosaic virus (YMV)	Aphids	ELISA and RT-PCR	Cote d'Ivoire	Thouvenel and Fauquet[12]
		Yam mild mosaic virus (YMMV)	Aphids	ELISA and RT-PCR	Nigeria	Odu *et al.*[10]
		Ethiopian yam virus (EYV)	Unknown	ACP-ELISA and RT-PCR	Ethiopia	Gogile *et al.*[28]
Tombusviridae	*Aureusvirus*	Yam spherical virus (YSV)	Mechanical	ELISA and RT-PCR	Nigeria	Menzel *et al.*[17]
Secoviridae	Unknown genera	*Dioscorea mosaic* associative virus (DMaV)	Beetle	HTS	Nigeria	Silva *et al.*[20]
		Dioscorea mottle virus (DMoV)	Beetle	ELISA	West Africa	Nyaboga *et al.*[14]

ELISA: Enzyme Linked Immunosorbent Assay, RT-PCR: Reverse Transcriptase Polymerase Chain Reaction, DAS: Double antibody sandwich, IC: Immuno capture, PAS: Protein a-sandwich, HTS: High throughout sequencing and ACP: Antigen-coating plate

https://doi.org/10.3923/ajpp.2024.86.102

Some yam viruses such as DaBV, DsBV, DLV and YSV-infected plants can reveal symptoms like mild chlorosis and leaf distortion which can differ from yam species, while others plants remain symptomless despite YSV and yam badnaviruses infection[17,36]. In addition, other studies[9,24,28] reported that some species of Dioscoreaceae (*D. alata*, *D. cayenensis-D. rotundata* complex and *D. trifida*) infected by YMMV, EYV and YV-1 shown symptoms like mild mosaic and mild mottle, while others yam species (*D. rotundata* for example) remain symptomless despite viral infection. Otherwise, YVY induces symptoms like mosaic and chlorotic on leaves of infected plants especially in mixed infection with YMV whilst singly-infected plants remain asymptomatic[20]. On *D. alata*, YMMV induces similar symptoms to those induced by YMV, in addition to mild chlorosis and severe stunting[1,16,23,24,40,82,83,85]. Moreover, YMV induces leaves symptoms like mosaic, chlorotic spotting and curling[23]. The similar symptoms induced by YMV can be observed in yam infected with DsBV, DMoV and DMaV[14,15,61]. Eni *et al*.[53] showed that the strain of CMV-infecting yam induces systemic chlorosis, necrotic lesions and leaf distortion on *Nicotiana glutinosa* and systemic mosaic on *Cucumis sativus*. To date, no apparent symptoms are visible on African yam infected by YaV1[21].

These characteristics of yam infected by viruses with no apparent symptoms show that some species or cultivars are resistant to viral infection but can make it difficult to develop the control strategies. As a consequence, yam tubers' quantity and quality are affected and so the international movement of germplasm is restricted[10]. Thus, the evaluation of species/cultivars of yam for tolerance to yam viruses is relevant to develop control strategies based on preventing or reducing spread of yam viruses.

Yield losses estimated due to plant virus diseases are not easy due to different parameters that must be considered to produce effective results[91]. The impact of yam virus diseases on yield in Africa remains less documented, except for some yam viruses such as YMV, YMMV and CMV[52,92-95]. Amusa *et al*.[95] reported that yield loss due to yam mosaic virus in the field of around 50% and more could be unregistered. However, studies in Cote d'Ivoire and Nigeria have shown that the significant yield losses of 30-50% could be caused by YMV and CMV[52].

Mainly focused on viruses in single infection, the results of these experiments are not only sufficient but for a good assessment, other parameters such as yield losses due to yam viruses in mixed infection, decreased tuber size and different agroecological zones, should have been considered. In addition, some biotic factors such as viral loads and symptom severity may influence yield losses in the field. So, for a good assessment, it will be important to consider these factors[96].

Diagnostic tools: Currently, available methods for diagnosis of yam viruses are biological assays, immunoassays and nucleic acid-based techniques. Various epidemiological factors such as the nature of isolates or strains of pathogens, appearance of symptoms origin of inoculum, mixed infections, environmental conditions and choice of the indicator plant, can affect the results of diagnosis using biological assays and therefore their reliability[97]. For example, many yam viruses like YSV, CMV, DLV, YVY, YMMV and some *Badnavirus* species, which remain symptomless on herbaceous hosts or clearly appear in mixed-infection and non-transmissible mechanically by inoculation of sap, diagnostic using biological assays shall be less sensitive and not reliable[9,17,19,20,24].

Recent progress in immunology, biochemistry and molecular biology makes serological and molecular analysis the most common methods known to detect and identify pathogens and thus, could provide a reliable alternative to biological assays. Due to their high sensitivity and reliability, ELISA and PCR are largely useful in yam viruses' diagnosis and hence used for certification of planting materials[24]. Many serological and PCR-based techniques have been developed for diagnosis of yam viruses[2,16,19,24,25,35,98-106].

The triple antibody sandwich enzyme-linked immunosorbent assay (TAS-ELISA), protein A-sandwich enzyme-linked immunosorbent assay (PAS-ELISA) and immunocapture reverse transcription polymerase chain reaction (IC-RT-PCR) are largely used for yam potyviruses detection[24,25,77,100]. These methods offer

some advantages such as reliability, sensitivity, specificity and results available in a short time[105]. However, some of them such as PCR require high-quality DNA/RNA which takes time and can hardly be done in the field.

Silva *et al.*[105] reported a rapid test for yam potyviruses (YMV and YMMV) called Direct Reverse Transcription-Recombinase Polymerase Ampli cation (Direct RT-RPA). Through this method, the virus is directly detected from plant leaf extract prepared with inexpensive reagents which provide high-quality of nucleic acids and take a short time (~30 min) to get results. In addition, Nkere *et al.*[104] developed a method for the detection of YMV called Closed-Tube Reverse Transcription Loop-Mediated Isothermal Amplification (CT-RT-LAMP). They asserted that this method had the same specificity and was 100 times more sensitive compared to the RT-PCR standard.

Since the discovery of CMV serotypes, the ELISA test using polyclonal or monoclonal antibodies has become very useful for routine detection of CMV[107]. To date, the polyclonal antibodies against CMV isolates infecting yam are available and already used by Eni *et al.*[108]. In case of low concentration of virus in the CMV infecting plants and mixed infections, this method tends to provide false results[107]. However, to resolve this problem, PCR-based methods variants (RT-PCR, IC-RT-PCR) have been developed to detect and identify CMV in the plants[98,99,109,110]. A multiplex RT-PCR which can detect, identify and subgroup CMV isolates including their satellite RNA has already been developed by Chen *et al.*[110] and provides good results.

Among the diagnosis methods used for virus species, including *Badnavirus*, ELISA is very useful for routine detection and identification[111]. However, the high level of natural variation of *Badnavirus* infecting yams, the existence of endogenous pararetrovirus in the genome of yam plants and the unavailability of antibodies in adequate numbers, constitute the main limiting factors for the development of serological and molecular diagnostic tools for *Badnavirus* infecting yam plants[35,106,112]. To solve these problems, several diagnostic methods were evaluated. For example, Eni *et al.*[35] developed a multiplex PCR-DGGE for screening of badnavirus sequences from African yam germplasm. In addition, Bömer *et al.*[19] evaluated a sequence-independent multiply-primed rolling circle ampli cation (RCA) method to determine which episomal viruses have integrated *Badnavirus* sequences in some yam genomes. This approach shows the existence of eleven full-length yam badnavirus sequences, giving a total of four species groups that can occur in single or mixed infections in Western Africa.

For the detection of unknown viruses or strains of known viral species or novel pathogens, Next-Generation Sequencing (NGS) based detection has been described in diagnosing yam viruses[28,113]. For example, Silva *et al.*[20] reported the presence of a new yam viral species named YVY in leaf samples of *D. rotundata* from Nigeria and Ghana using NGS technique. In addition, Gogile *et al.*[28] reports two new species named EYV and YV-1 in symptomatic and asymptomatic yam plants from Ethiopia. These discoveries show that, in the areas where data on yam viruses are scanty like in SSA regions, NGS technique will be very helpful for the discovery of new viral species on yam.

Using PCR-dependent denaturing gradient gel electrophoresis (PCR-DGGE) methods, Turaki *et al.*[103] showed that this method was capable of detecting the virus in the complex mixtures of potentially episomal and endogenous *Badnavirus* sequences. Moreover, numerous RCA protocols including random-primed RCA (RP-RCA), primer-spiked random-primed RCA (primer-spiked RP-RCA), directed RCA (D-RCA) and specific-primed RCA (SP-RCA) have been evaluated and optimized for use on yam, taro, banana and sugar cane infected with DBALV[106]. They, therefore, suggest that using optimized RCA protocols together with NGS was reliable enough to characterize and detect other species of yam *Badnavirus*.

Future perspectives: Increasing yam productivity in SSA through improved knowledge of the occurrence and detection of types of yam viruses' diseases for effective management is one of the factors important for poverty elimination. Several scientific publications have shown very strong findings in yam viruses' research in West Africa and demonstrate that yam viruses are one of the major causes of global yam production decrease leading to severe economic losses and limiting the exchange of planting materials between yam-producing zones[1,10-13,16-24,29,30,34,35,40,51,61,77,90,96,104,114].

Despite this progress on yam viruses' research in West Africa, data are scanty in other countries of SSA, particularly in Central and Eastern parts of Africa continent, probably due to the inattentiveness of research centers in some countries where yam is considered an orphan crop[1,7,89]. Although, based on yam virus-like symptoms, the data on the presence of yam virus diseases have been reported in these areas[84,88,89]. Thus, suggesting their possible existence. So, additional studies in other yam-producing zones in Africa are needed for the development of diagnostic methods and disease control strategies to prevent or control yam virus diseases and increase yam productivity.

Serological and molecular methods are most common for the diagnosis of yam viruses. The reliability of each diagnostic method depends on the nature of the virus, plant species, plant tissue samples and the objective of assay[115,116]. However, the secondary metabolites like glutinous polysaccharides and polyphenols, presents in high concentration in yam plants can limit getting of good quality DNA for PCR analysis[25]. In parallel with secondary metabolites, virus infecting plant induce a high concentration of these compounds[117]. So, the identification of the plant part with high viral titer would contribute to the quick detection of pathogens using molecular methods.

In addition, the efficiency of these methods for the detection of yam viruses has little been explored[52,100,115] and never compared yam plant tissues from different species and at specific growing periods for YMV detection. This will represent an ideal step for future perspectives and will not only add to the efficiency, reliability and quick detection but also a cost-effective option.

CONCLUSION

This review paper presented the existing knowledge on yam viruses across Africa, their biological characteristics and geographical distribution. The reported symptoms of diseases and yield losses associated with viral infections and the existing diagnostic tools have been elucidated. Based on the available data, the most important viruses infecting yam in SSA have been documented. This includes YMV, YMMV, CMV and some species of *Dioscorea* infecting *Badnavirus*. Other new yam viruses such as YaV1, YSV, EYV, YV-1, DMaV, DMoV, DLV and YVY have likewise been reported on yam in West Africa. Further studies are needed in order to prevent or control yam virus diseases in all yam-producing zones in Africa. Also, several methods and techniques have been developed to diagnose and detect yam viruses with high sensitivity, specificity and reliability. However, enhancing the reliability of molecular detection will pass through the use of plant parts which high viral titer. We, therefore, suggest that the selection of the most suitable plant part will contribute to the reproducibility of yam viruses' detection by PCR. This review will serve as a reference for advances in research on yam viruses worldwide particularly in yam-producing countries in Africa.

SIGNIFICANCE STATEMENT

The yam viruses are one of the constraints of yam production decrease leading to severe economic losses. Increasing yam productivity through improved knowledge of occurrence and detection of yam viruses' diseases for effective management is an important factor for poverty elimination in Africa. This paper provides the existing information on yam viruses in Africa and diagnostic tools developed up to date. In conclusion, further studies on knowledge of occurrence of yam viruses in yam fields are needed to prevent or control yam virus diseases in Africa. Also, enhancing the reliability of molecular detection through the use of plant parts with high viral titer will facilitate quick detection and action against viral diseases for effective management.

ACKNOWLEDGMENTS

We acknowledge the Partnership for Skills in Applied Sciences, Engineering and Technology (PASET) through the Regional Scholarship and Innovation Fund (RSIF) awarded to Emmanuel Kulimushi to carry out doctoral studies at SACIDS Africa Centre of Excellence for Infectious Diseases, SACIDS Foundation for One Health, Sokoine University of Agriculture, Morogoro, Tanzania. The authors thank the direction of the Smart services sarl and Dr Isaac BALUME for spelling and grammar check.

REFERENCES

1. Azeteh, I.N., R. Hanna, A.P. Njukeng, A.O. Oresanya, P.N. Sakwe and P.L. Kumar, 2019. Distribution and diversity of viruses infecting yams (*Dioscorea* spp.) in Cameroon. VirusDisease, 30: 526-537.
2. Nkere, C.K., E. Otoo, G.I. Atiri, J. Onyeka and G. Silva *et al*., 2020. Assessment of *Yam mild mosaic virus* coat protein gene sequence diversity reveals the prevalence of cosmopolitan and African group of isolates in Ghana and Nigeria. Curr. Plant Biol., Vol. 23. 10.1016/j.cpb.2020.100156.
3. Sunitha, S., J.S. Kumar, J. Sreekumar, M. Nedunchezhiyan and K. Mamatha *et al*., 2022. Influences of intercropping on productivity and profitability of greater yam (*Dioscorea alata* L.). J. Crop Weed, 18: 85-93.
4. Cornet, D., J. Sierra, R. Tournebize, K. Dossa and B. Gabrielle, 2023. Expected yield and economic improvements of a yam seed system in West Africa using agro-physiological modelling. Plants People Planet, 10.1002/ppp3.10446.
5. Adjei, E.A., W. Esuma, T. Alicai, R. Bhattacharjee and I.O. Dramadri *et al*., 2022. Phenotypic diversity within Ugandan yam (*Dioscorea* species) germplasm collection. Int. J. Agron., Vol. 2022. 10.1155/2022/5826012.
6. Maroya, N., M. Balogun, B. Aighewi, D.B. Mignouna, P.L. Kumar and R. Asiedu, 2022. Transforming Yam Seed Systems in West Africa. In: Root, Tuber and Banana Food System Innovations: Value Creation for Inclusive Outcomes, Thiele, G., M. Friedmann, H. Campos, V. Polar and J.W. Bentley (Eds.), Springer, Cham, Switzerland, ISBN: 978-3-030-92022-7, pp: 421-451.
7. Mabou, L.C.N., M.L. Sameza, S.N. Tchameni, P. Eke and R.M.K. Toghueo *et al*., 2020. Molecular identification of fungal pathogens associated with post-harvest yam tubers rot in Mbam et Kim Division (Cameroon) with emphasis on *Penicillium monomenatosum* (Frisvad, Filt. & Wicklow) as a first report. Am. J. Microbiol. Res., 8: 73-78.
8. Odu, B.O., J. d'A. Hughes, R. Asiedu, N.Q. Ng, S.A. Shoyinka and O.A. Oladiran, 2004. Responses of white yam (*Dioscorea rotundata*) cultivars to inoculation with three viruses. Plant Pathol., 53: 141-147.
9. Tariq, H., C. Xiao, L. Wang, H. Ge, G. Wang, D. Shen and D. Dou, 2024. Current status of yam diseases and advances of their control strategies. Agronomy, Vol. 14. 10.3390/agronomy14071575.
10. Odu, B.O., J. d'A. Hughes, S.A. Shoyinka and L.N. Dongo, 1999. Isolation, characterisation and identification of a potyvirus from *Dioscorea alata* L. (water yam) in Nigeria. Ann. Appl. Biol., 134: 65-71.
11. Ita, E.E., E.A. Uyoh, I. Nakamura and V.O. Ntui, 2020. Efficient elimination of *Yam mosaic virus* (YMV) from white yam (*Dioscorea rotundata* Poir.) by cryotherapy of axillary buds. S. Afr. J. Bot., 130: 123-129.
12. Thouvenel, J.C. and C. Fauquet, 1979. Yam mosaic, a new potyvirus infecting *Dioscorea cayenensis* in the Ivory Coast. Ann. Appl. Biol., 93: 279-283.
13. Phillips, S., R.W. Briddon, A.A. Brunt and R. Hull, 1999. The partial characterization of a badnavirus infecting the greater asiatic or water yam (*Dioscorea alata*). J. Phytopathol., 147: 265-269.
14. Nyaboga, E., J.N. Tripathi, R. Manoharan and L. Tripathi, 2014. *Agrobacterium*-mediated genetic transformation of yam (*Dioscorea rotundata*): An important tool for functional study of genes and crop improvement. Front. Plant Sci., Vol. 5. 10.3389/fpls.2014.00463.
15. Seal, S. and E. Muller, 2007. Molecular analysis of a full-length sequence of a new yam badnavirus from *Dioscorea sansibarensis*. Arch. Virol., 152: 819-825.

16. Eni, A.O., P.L. Kumar, R. Asiedu, O.J. Alabi, R.A. Naidu, J. Hughes and M.E.C. Rey, 2008. First report of *Cucumber mosaic virus* in yams (*Dioscorea* spp.) in Ghana, Togo, and Republic of Benin in West Africa. Plant Dis., 92: 833-833.
17. Menzel, W., G. Thottappilly and S. Winter, 2014. Characterization of an isometric virus isolated from yam (*Dioscorea rotundata*) in Nigeria suggests that it belongs to a new species in the genus *Aureusvirus*. Arch. Virol., 159: 603-606.
18. Umber, M., D. Filloux, E. Muller, N. Laboureau and S. Galzi *et al*., 2014. The genome of African yam (*Dioscorea cayenensis-rotundata* complex) hosts endogenous sequences from four distinct badnavirus species. Mol. Plant Pathol., 15: 790-801.
19. Bömer, M., A.A. Turaki, G. Silva, P.L. Kumar and S.E. Seal, 2016. A sequence-independent strategy for amplification and characterisation of episomal badnavirus sequences reveals three previously uncharacterised yam badnaviruses. Viruses, Vol. 8. 10.3390/v8070188.
20. Silva, G., M. Bömer, A.I. Rathnayake, S.O. Sewe and P. Visendi *et al*., 2019. Molecular characterization of a new virus species identified in yam (*Dioscorea* spp.) by high-throughput sequencing. Plants, Vol. 8. 10.3390/plants8060167.
21. Marais, A., M. Umber, D. Filloux, R.M. Gomez and C. Faure *et al*., 2020. Yam asymptomatic virus 1, a novel virus infecting yams (*Dioscorea* spp.) with significant prevalence in a germplasm collection. Arch. Virol., 165: 2653-2657.
22. Bakayoko, Y., A.M. Kouakou, A.B. Kouassi, R.M. Gomez and K.E.B. Dibi *et al*., 2021. Detection and diversity of viruses infecting African yam (*Dioscorea rotundata*) in a collection and F_1 progenies in Côte d'Ivoire shed light to plant-to-plant viral transmission. Plant Pathol., 70: 1486-1495.
23. Njukeng, A.P., I.N. Azeteh and G.A. Mbong, 2014. Survey of the incidence and distribution of two viruses infecting yam (*Dioscorea* spp) in two agro- ecological zones of Cameroon. Int. J. Curr. Microbiol. Appl. Sci., 3: 1153-1166.
24. Mumford, R.A. and S.E. Seal, 1997. Rapid single-tube immunocapture RT-PCR for the detection of two yam potyviruses. J. Virol. Methods, 69: 73-79.
25. Eni, A.O., J.D.A. Hughes, R. Asiedu and M.E.C. Rey, 2012. Re-evaluation of yam mosaic virus (YMV) detection methods. Acad. J. Plant Sci., 5: 18-22.
26. Fuchs, M., M. Bar-Joseph, T. Candresse, H.J. Maree and G.P. Martelli *et al*., 2020. ICTV virus taxonomy profile: *Closteroviridae*. J. Gen. Virol., 101: 364-365.
27. Martelli, G.P., N.A. Ghanem-Sabanadzovic, A.A. Agranovsky, M. Al Rwahnih and V.V. Dolja *et al*., 2012. Taxonomic revision of the family *Closteroviridae* with special reference to the grapevine leafroll-associated members of the genus *Ampelovirus* and the putative species unassigned to the family. J. Plant Pathol., 94: 7-19.
28. Gogile, A., D. Knierim, P. Margaria, W. Menzel and M. Abide *et al*., 2024. White yam (*Dioscorea rotundata*) plants exhibiting virus-like symptoms are co-infected with a new potyvirus and a new crinivirus in Ethiopia. Virus Genes, 60: 423-433.
29. Diouf, M.B., S. Guyader, O. Gaspard, E. Francius, P.Y. Teycheney and M. Umber, 2022. Epidemiology of yam viruses in Guadeloupe: Role of cropping practices and seed-tuber supply. Viruses, Vol. 14. 10.3390/v14112366.
30. Eni, A.O., J. d'A. Hughes, R. Asiedu and M.E.C. Rey, 2008. Sequence diversity among badnavirus isolates infecting yam (*Dioscorea* spp.) in Ghana, Togo, Benin and Nigeria. Arch. Virol., 153: 2263-2272.
31. Jiwan, S.D. and K.A. White, 2011. Subgenomic mRNA transcription in *Tombusviridae*. RNA Biol., 8: 287-294.
32. Teycheney, P.Y., A.D.W. Geering, I. Dasgupta, R. Hull and J.F. Kreuze *et al*., 2020. ICTV virus taxonomy profile: *Caulimoviridae*. J. Gen. Virol., 101: 1025-1026.
33. Kenyon, L., B.S.M. Lebas and S.E. Seal, 2008. Yams (*Dioscorea* spp.) from the South Pacific Islands contain many novel badnaviruses: Implications for international movement of yam germplasm. Arch. Virol., 153: 877-889.

34. Seal, S., A. Turaki, E. Muller, P.L. Kumar and L. Kenyon *et al*., 2014. The prevalence of badnaviruses in West African yams (*Dioscorea cayenensis-rotundata*) and evidence of endogenous pararetrovirus sequences in their genomes. Virus Res., 186: 144-154.
35. Eni, A.O., J. d'A. Hughes and M.E.C. Rey, 2010. Production of polyclonal antibody against an isolate of yam-infecting badnavirus from Nigeria. Aust. J. Basic Appl. Sci., 6: 4158-4163.
36. Bhat, A.I., T. Hohn and R. Selvarajan, 2016. Badnaviruses: The current global scenario. Viruses, Vol. 8. 10.3390/v8060177.
37. Briddon, R.W., S. Phillips, A. Brunt and R. Hull, 1999. Analysis of the sequence of *Dioscorea alata* bacilliform virus; comparison to other members of the badnavirus group. Virus Genes, 18: 277-283.
38. James, A.P., R.J. Geijskes, J.L. Dale and R.M. Harding, 2011. Molecular characterisation of six badnavirus species associated with leaf streak disease of banana in East Africa. Ann. Appl. Biol., 158: 346-353.
39. Mbanzibwa, D.R., A.K. Tugume, E. Chiunga, D. Mark and F.D. Tairo, 2014. Small RNA deep sequencing-based detection and further evidence of DNA viruses infecting sweetpotato plants in Tanzania. Ann. Appl. Biol., 165: 329-339.
40. Bousalem, M., S. Dallot, S. Fuji and K.T. Natsuaki, 2003. Origin, world-wide dispersion, bio-geographical diversification, radiation and recombination: An evolutionary history of *Yam mild mosaic virus* (YMMV). Infect. Genet. Evol., 3: 189-206.
41. Sukal, A., D. Kidanemariam, J. Dale, A. James and R. Harding, 2017. Characterization of badnaviruses infecting *Dioscorea* spp. in the Pacific reveals two putative novel species and the first report of dioscorea bacilliform RT virus 2. Virus Res., 238: 29-34.
42. Untiveros, M., Z. Perez-Egusquiza and G. Clover, 2010. PCR assays for the detection of members of the genus Ilarvirus and family Bromoviridae. J. Virol. Methods, 165: 97-104.
43. Bujarski, J., D. Gallitelli, F. García-Arenal, V. Pallás and P. Palukaitis *et al*. 2019. ICTV virus taxonomy profile: *Bromoviridae*. J. Gen. Virol., 100: 1206-1207.
44. Bujarski, J.J. and P. Kaesberg, 1986. Genetic recombination between RNA components of a multipartite plant virus. Nature, 321: 528-531.
45. Chen, Y.K., R. Goldbach and M. Prins, 2002. Inter- and intramolecular recombinations in the *Cucumber mosaic virus* genome related to adaptation to alstroemeria. J. Virol., 76: 4119-4124.
46. Gallitelli, D., M. Finetti-Sialer and G.P. Martelli, 2005. *Anulavirus*, a proposed new genus of plant viruses in the family *Bromoviridae*. Arch. Virol., 150: 407-411.
47. Bujarski, J.J., 2021. Bromoviruses (*Bromoviridae*). In: Encyclopedia of Virology, Bamford, D.H. and M. Zuckerman (Eds.), Academic Press, Cambridge, Massachusetts, ISBN: 9780128145166, pp: 260-267.
48. Roossinck, M.J., 2002. Evolutionary history of *Cucumber mosaic virus* deduced by phylogenetic analyses. J. Virol., 76: 3382-3387.
49. Kumari, R., P. Bhardwaj, L. Singh, A.A. Zaidi and V. Hallan, 2013. Biological and molecular characterization of *Cucumber mosaic virus* subgroup II isolate causing severe mosaic in cucumber. Indian J. Virol., 24: 27-34.
50. Rizos, H., L.V. Gunn, R.D. Pares and M.R. Gillings, 1992. Differentiation of cucumber mosaic virus isolates using the polymerase chain reaction. J. Gen. Virol., 73: 2099-2103.
51. Odedara, O.O., E.I. Ayo-John, M.M. Gbuyiro, F.O. Falade and S.E. Agbebi, 2012. Serological detection of yam viruses in farmers' fields in Ogun State, Nigeria. Arch. Phytopathol. Plant Prot., 45: 840-845.
52. Yeyeh, T.M.N., H.A. Diallo, S.A. Akinbade, K. Séka and P.L. Kumar, 2014. Distribution, incidence and severity of viral diseases of yam (*Dioscorea* spp.) in Côte d'Ivoire. Afr. J. Biotechnol., 13: 465-470.
53. Eni, A.O., J. d'A. Hughes, R. Asiedu and M.E.C. Rey, 2013. Incidence and diversity of mixed viruses lower in yam tubers and tuber sprouts compared with field leaf samples: Implications for virus-free planting material control strategy. Afr. J. Agric. Res., 8: 3060-3067.

54. Kumari, A., C. Kaur, S. Kumar, P.S. Chauhan and S.K. Raj, 2021. Current Status of Three Virus Genera (*Badnavirus*, *Cucumovirus*, and *Potyvirus*) in *Canna* Species in India. In: Virus Diseases of Ornamental Plants: Characterization, Identification, Diagnosis and Management, Raj, S.K., R.K. Gaur and Z. Yin (Eds.), Springer, Singapore, ISBN: 978-981-16-3918-0, pp: 117-126.
55. Roossinck, M.J., 2001. *Cucumber mosaic virus*, a model for RNA virus evolution. Mol. Plant Pathol., 2: 59-63.
56. Piazzolla, P., J.R. Diaz-Ruiz and J.M. Kaper, 1979. Nucleic acid homologies of eighteen cucumber mosaic virus isolates determined by competition hybridization. J. Gen. Virol., 45: 361-369.
57. Palukaitis, P., M.J. Roossinck, R.G. Dietzgen and R.I.B. Francki, 1992. Cucumber MOSAIC virus. Adv. Virus Res., 41: 281-348.
58. Jacquemond, M., 2012. Cucumber Mosaic Virus. In: Advances in Virus Research, Loebenstein, G. and H. Lecoq (Eds.), Academic Press, Cambridge, Massachusetts, ISBN: 9780123943149, pp: 439-504.
59. Mochizuki, T. and S.T. Ohki, 2012. *Cucumber mosaic virus*: Viral genes as virulence determinants. Mol. Plant Pathol., 13: 217-225.
60. Thompson, J.R., I. Dasgupta, M. Fuchs, T. Iwanami and A.V. Karasev *et al*., 2017. ICTV virus taxonomy profile: *Secoviridae*. J. Gen. Virol., 98: 529-531.
61. Umber, M., D. Filloux, L. Svanella-Dumas, L. Bonheur and I. Acina-Mambole *et al*., 2022. Host range and molecular variability of the sadwavirus dioscorea mosaic associated virus. Arch. Virol., 167: 917-922.
62. Kreuze, J.F., A.M. Vaira, W. Menzel, T. Candresse and S.K. Zavriev *et al*., 2020. ICTV virus taxonomy profile: *Alphaflexiviridae*. J. Gen. Virol., 101: 699-700.
63. Adams, M.J., F.J. Antoniw, M. Bar-Joseph, A.A. Brunt and T. Candresse *et al*., 2004. The new plant virus family *Flexiviridae* and assessment of molecular criteria for species demarcation. Arch. Virol., 149: 1045-1060.
64. Grinzato, A., E. Kandiah, C. Lico, C. Betti, S. Baschieri and G. Zanotti, 2020. Atomic structure of potato virus X, the prototype of the *Alphaflexiviridae* family. Nat. Chem. Biol., 16: 564-569.
65. Lim, S.J., K. Rosario, M.E. Kernbach, A.J. Gross, B.T. Furman and M. Breitbart, 2024. Limited potexvirus diversity in Eastern Gulf of Mexico seagrass meadows. J. Gen. Virol., Vol. 105. 10.1099/jgv.0.002004.
66. Phillips, S., J. d'a. Piggott and A.A. Brunt, 1986. Further evidence that dioscorea latent virus is a potexvirus. Ann. Appl. Biol., 109: 137-145.
67. Sastry, K.S., B. Mandal, J. Hammond, S.W. Scott and R.W. Briddon, 2019. *Dioscorea* spp. (Yam). In: Encyclopedia of Plant Viruses and Viroids, Sastry, K.S., B. Mandal, J. Hammond, S.W. Scott and R.W. Briddon (Eds.), Springer, New Delhi, India, ISBN: 978-81-322-3912-3, pp: 900-912.
68. Fu, S., T. Zhang, M. He, B. Sun, X. Zhou and J. Wu, 2021. Molecular characterization of a novel wheat-infecting virus of the family *Betaflexiviridae*. Arch. Virol., 166: 2875-2879.
69. Morozov, S.Y. and A.G. Solovyev, 2003. Triple gene block: Modular design of a multifunctional machine for plant virus movement. J. Gen. Virol., 84: 1351-1366.
70. Martelli, G.P., M.J. Adams, J.F. Kreuze, and V.V. Dolja, 2007. Family *Flexiviridae*: A case study in virion and genome plasticity. Annu. Rev. Phytopathol., 45: 73-100.
71. Luo, G.F., A. Podolyan, D.B. Kidanemariam, C. Pilotti, G. Houliston and A.C. Sukal, 2022. A review of viruses infecting yam (*Dioscorea* spp.). Viruses, Vol. 14. 10.3390/v14040662.
72. Yadav, D.L., P.P. Jaisani, R.N. Pandey, R. Mawar and V.C. Chalam, 2021. Bean common mosaic virus of legumes with special emphasis on mungbean [*Vigna radiata* (L.) Wilczek]: An overview. J. Pharmacogn. Phytochem., 10: 1104-1112.
73. Xue, M., N. Arvy and S. German-Retana, 2023. The mystery remains: How do potyviruses move within and between cells? Mol. Plant Pathol., 24: 1560-1574.
74. Gibbs, A.J., M. Hajizadeh, K. Ohshima and R.A.C. Jones, 2020. The potyviruses: An evolutionary synthesis is emerging. Viruses, Vol. 12. 10.3390/v12020132.
75. Yang, X., Y. Li and A. Wang, 2021. Research advances in potyviruses: From the laboratory bench to the field. Annu. Rev. Phytopathol., 59: 1-29.

76. Nigam, D., K. LaTourrette, P.F.N. Souza and H. Garcia-Ruiz, 2019. Genome-wide variation in potyviruses. Front. Plant Sci., Vol. 10. 10.3389/fpls.2019.01439.
77. Bousalem, M., E.J.P. Douzery and D. Fargette, 2000. High genetic diversity, distant phylogenetic relationships and intraspecies recombination events among natural populations of *Yam mosaic virus*: A contribution to understanding potyvirus evolution. J. Gen. Virol., 81: 243-255.
78. Ita, E.E., E.A. Uyoh, I. Nakamura and V.O. Ntui, 2020. Transgenic tobacco lines expressing yam mosaic virus coat protein-derived dsRNA are resistant to yam mosaic virus. Am. J. Plant Sci., 11: 1487-1504.
79. Aleman, M.E., J.F. Marcos, C. Brugidou, R.N. Beachy and C. Fauquet, 1996. The complete nucleotide sequence of yam mosaic virus (Ivory Coast isolate) genomic RNA. Arch. Virol., 141: 1259-1278.
80. Bömer, M., A.I. Rathnayake, P. Visendi, G. Silva and S.E. Seal, 2018. Complete genome sequence of a new member of the genus *Badnavirus*, *Dioscorea bacilliform* RT virus 3, reveals the first evidence of recombination in yam badnaviruses. Arch. Virol., 163: 533-538.
81. Mendoza, A.R., P. Margaria, T. Nagata, S. Winter and R. Blawid, 2022. Characterization of yam mosaic viruses from Brazil reveals a new phylogenetic group and possible incursion from the African continent. Virus Genes, 58: 294-307.
82. Bousalem, M. and S. Dallot, 2000. First report and molecular characterization of *Yam mild mosaic virus* in *Dioscorea alata* on the Island of Martinique. Plant Dis., 84: 200-200.
83. Dallot, S., M. Guzmán and M. Bousalem, 2001. Occurrence of potyviruses on yam (*Dioscorea* spp.) in Colombia and first molecular characterization of *Yam mild mosaic virus*. Plant Dis., 85: 803-803.
84. Gogile, A., M. Kebede, D. Kidanemariam and A. Abraham, 2024. Identification of yam mosaic virus as the main cause of yam mosaic diseases in Ethiopia. Heliyon, Vol. 10. 10.1016/j.heliyon.2024.e26387.
85. Zou, C.W., J.R. Meng, Z.T. Yao, L. Zhang, Z.Q. Wang, B.H. Wei and B.S. Chen, 2020. Genetic diversity and genome recombination in *Yam mild mosaic virus* isolates. Phytopathol. Res., Vol. 2. 10.1186/s42483-020-00051-0.
86. de Assis Câmara Rabelo Filho, F., C. Nicolini, R. de Oliveira Resende, G.P. de Andrade, G. Pio-Ribeiro and T. Nagata, 2013. The complete genome sequence of a Brazilian isolate of yam mild mosaic virus. Arch. Virol., 158: 515-518.
87. Atreya, C.D., B. Raccah and T.P. Pirone, 1990. A point mutation in the coat protein abolishes aphid transmissibility of a potyvirus. Virology, 178: 161-165.
88. Azeteh, I.N., R. Hanna, P.N. Sakwe, A.P. Njukeng and P.L. Kumar, 2019. Yam (*Dioscorea* spp.) production trends in Cameroon: A review. Afr. J. Agric. Res., 14: 1097-1110.
89. Adejumobi, I.I., P.A. Agre, D.O. Onautshu, J.G. Adheka and M.G. Bambanota *et al*., 2022. Diversity, trait preferences, management and utilization of yams landraces (*Dioscorea* species): An orphan crop in DR Congo. Sci. Rep., Vol. 12. 10.1038/s41598-022-06265-w.
90. Ramírez, J.E.G., D.C. Mederos, V.V. Chávez, R.E.G. Vázquez and K. Ojito-Ramos *et al*., 2024. Occurrence of yam mosaic virus and yam mild mosaic virus on *Dioscorea* spp. germplasm collection in Cuba-Epidemiology of associated diseases. Plants, Vol. 13. 10.3390/plants13182597.
91. Savary, S., P.S. Teng, L. Willocquet and F.W. Nutter Jr., 2006. Quantification and modeling of crop losses: A review of purposes. Annu. Rev. Phytopathol., 44: 89-112.
92. Odu, B.O., R. Asiedu, J. d'A Hughes, S.A. Shoyinka and O.A. Oladiran, 2004. Identification of resistance to *Yam mosaic virus* (YMV), genus *Potyvirus* in white Guinea yam (*Dioscorea rotundata* Poir.). Field Crops Res., 89: 97-105.
93. Odu, B.O., R. Asiedu, S.A. Shoyinka and J. d'A. Hughes, 2006. Screening of water yam (*Dioscorea alata* L.) genotypes for reactions to viruses in Nigeria. J. Phytopathol., 154: 716-724.
94. Adeniji, M.O., S.A. Shoyinka, T. Ikotun, R. Asiedu, J. d'A. Hughes and B.O. Odu, 2012. Yield loss in Guinea yam (*Dioscorea rotundata poir*.) due to infection by *Yam mosaic virus* (YMV) genus *Potyvirus*. Ife J. Sci., 14: 237-244.
95. Amusa, N.A., A.A. Adegbite, S. Muhammed and R.A. Baiyewu, 2003. Yam diseases and its management in Nigeria. Afr. J. Biotechnol., 2: 497-502.

96. Diouf, M.B., R. Festus, G. Silva, S. Guyader, M. Umber, S. Seal and P.Y. Teycheney, 2022. Viruses of yams (*Dioscorea* spp.): Current gaps in knowledge and future research directions to improve disease management. Viruses, Vol. 14. 10.3390/v14091884.
97. Legrand, P., 2015. Biological assays for plant viruses and other graft-transmissible pathogens diagnoses: A review. EPPO Bull., 45: 240-251.
98. Wylie, S., C.R. Wilson, R.A.C. Jones and M.G.K. Jones, 1993. A polymerase chain reaction assay for cucumber mosaic virus in lupin seeds. Aust. J. Agric. Res., 44: 41-51.
99. de Blas, C., M.J. Borja, M. Saiz and J. Romero, 1994. Broad spectrum detection of cucumber mosaic virus (CMV) using the polymerase chain reaction. J. Phytopathol., 141: 323-329.
100. Njukeng, A.P., G.I. Atiri and J. d'A. Hughes, 2005. Comparison of TAS-ELISA, dot and tissue blot, ISEM and immunocapture RT-PCR assays for the detection of *Yam mosaic virus* in yam tissues. Crop Prot., 24: 513-519.
101. Bousalem, M., O. Durand, N. Scarcelli, B.S.M. Lebas and L. Kenyon *et al*., 2009. Dilemmas caused by endogenous pararetroviruses regarding the taxonomy and diagnosis of yam (*Dioscorea* spp.) badnaviruses: Analyses to support safe germplasm movement. Arch. Virol., 154: 297-314.
102. Silva, G., M. Bömer, C. Nkere, P.L. Kumar and S.E. Seal, 2015. Rapid and specific detection of *Yam mosaic virus* by reverse-transcription recombinase polymerase amplification. J. Virol. Methods, 222: 138-144.
103. Turaki, A.A., M. Bömer, G. Silva, P.L. Kumar and S.E. Seal, 2017. PCR-DGGE analysis: Unravelling complex mixtures of badnavirus sequences present in yam germplasm. Viruses, Vol. 9. 10.3390/v9070181.
104. Nkere, C.K., J.O. Oyekanmi, G. Silva, M. Bömer and G.I. Atiri *et al*., 2018. Chromogenic detection of yam mosaic virus by closed-tube reverse transcription loop-mediated isothermal amplification (CT-RT-LAMP). Arch. Virol., 163: 1057-1061.
105. Silva, G., J. Oyekanmi, C.K. Nkere, M. Bömer, P.L. Kumar and S.E. Seal, 2018. Rapid detection of potyviruses from crude plant extracts. Anal. Biochem., 546: 17-22.
106. Sukal, A.C., D.B. Kidanemariam, J.L. Dale, R.M. Harding and A.P. James, 2019. Assessment and optimization of rolling circle amplification protocols for the detection and characterization of badnaviruses. Virology, 529: 73-80.
107. Kim, H.S., D.W. Kim and Y.T. Jung, 2016. Development of serological procedures for sensitive, rapid detection of Cucumber mosaic virus in *Lilium*. Hortic. Environ. Biotechnol., 57: 633-639.
108. Eni, A.O., P.L. Kumar, R. Asiedu, O.J. Alabi, R.A. Naidu, J. d'A. Hughes and M.E.C. Rey, 2013. Characterization of cucumber mosaic virus isolated from yam (*Dioscorea* spp.) in West Africa. Afr. J. Biotechnol., 12: 3472-3480.
109. Yu, C., J. Wu and X. Zhou, 2005. Detection and subgrouping of Cucumber mosaic virus isolates by TAS-ELISA and immunocapture RT-PCR. J. Virol. Methods, 123: 155-161.
110. Chen, S., H. Gu, X. Wang, J. Chen and W. Zhu, 2011. Multiplex RT-PCR detection of *Cucumber mosaic virus* subgroups and *Tobamoviruses* infecting tomato using 18S rRNA as an internal control. Acta Biochim. Biophys. Sin., 43: 465-471.
111. Kanapiya, A., U. Amanbayeva, Z. Tulegenova, A. Abash, S. Zhangazin, K. Dyussembayev and G. Mukiyanova, 2024. Recent advances and challenges in plant viral diagnostics. Front. Plant Sci., Vol. 15. 10.3389/fpls.2024.1451790.
112. Bousalem, M., E.J.P. Douzery and S.E. Seal, 2008. Taxonomy, molecular phylogeny and evolution of plant reverse transcribing viruses (family *Caulimoviridae*) inferred from full-length genome and reverse transcriptase sequences. Arch. Virol., 153: 1085-1102.
113. Bömer, M., A.I. Rathnayake, P. Visendi, S.O. Sewe and J.P.A. Sicat *et al*., 2019. Tissue culture and next-generation sequencing: A combined approach for detecting yam (*Dioscorea* spp.) viruses. Physiol. Mol. Plant Pathol., 105: 54-66.
114. Umber, M., D. Filloux, S. Gélabale, R.M. Gomez and A. Marais *et al*., 2020. Molecular viral diagnosis and sanitation of yam genetic resources: Implications for safe yam germplasm exchange. Viruses, Vol. 12. 10.3390/v12101101.

115. Njukeng, A.P., G.I. Atiri, J. Hughes and S. Winter, 2004. Development of serological procedures for rapid, sensitive and reliable detection of *yam mosaic virus* in yam tissues. Trop. Sci., 44: 136-147.
116. Rwegasira, G.M., M.E.C. Rey and H. Nawabu, 2011. Approaches to diagnosis and detection of cassava brown streak virus (*Potiviridae: Ipomovirus*) in field-grown cassava crop. Afr. J. Food Agric. Nutr. Dev., 11: 4739-4756.
117. Mishra, J., R. Srivastava, P.K. Trivedi and P.C. Verma, 2020. Effect of virus infection on the secondary metabolite production and phytohormone biosynthesis in plants. 3 Biotech, Vol. 10. 10.1007/s13205-020-02541-6.