Chapter

Challenges of Cassava Mosaic Begomoviruses, Cassava Brown Streak Ipomoviruses and Satellites to Cassava Production

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Abstract

Cassava is an important food security and industrial crop. Its production is constrained by viral diseases such as cassava mosaic disease (CMD) and cassava brown streak disease (CBSD), caused by cassava mosaic begomoviruses (CMBs) and ipomoviruses, respectively. In recent years, CMBs have been associated with satellite DNAs. Food security status of cassava coupled with high demand for cassava as feed and industrial uses has been the driving force for scientists and the research community in Africa and beyond. In this review, cassava production, uses of cassava, production constraints, begomoviruses, satellite DNAs, *Bemisia tabaci,* cassava mosaic disease (CMD), *Cassava brown streak virus (*CBSV), current and future efforts in cassava production and research are discussed. This was done in an effort to create a knowledge pool that can promote cassava food security status and mitigate disease and yield loss.

Keywords: cassava, production, constraints, cassava mosaic disease, cassava brown streak disease

1. Introduction

Roots and tubers are important food crops, marketed globally with an income generation and food security role recognized by consumers and the research community [1]. Cassava (*Manihot esculenta* Crantz) is grown in the tropics (sub-Saharan Africa, Asia and Latin America). The crop has diverse uses and applications in food, green energy and feed and an important source of income for local farmers at the subsistence level [2, 3]. In sub-Saharan Africa, cassava production has been a major contributing sector with a steady increase in annual production since the last two decades [4]. In Ghana, farmers are self-sufficient in cassava production with high per capita consumption [4, 5]. In Latin America, cassava produced is utilized as food and feed mostly, with few used for industrial purposes [3, 6].

Amidst the role of cassava in food security, there is the existence of a large yield gap in the sector due to diseases, inadequate research funding, unbalanced crop

nutrition, poor agronomy and soil fertility management and low level of adoption by local farmers in using tolerant cultivars [7, 8]. Cassava mosaic disease (CMD) is the most prevalent biotic limitation in sub-Saharan Africa (SSA) with newer reports of its incidence in Asia [7, 8]. Lower yield values are recorded which can also be attributed to recombinant *begomovirus* strains and the emergence of satellites that modulate and increase disease severity in SSA [8]. Occurrence of cassava brown streak in SSA further threatens cassava production. The current trends on cassava as a food security crop, cassava viruses and their effects on cassava production in the last few decades and the way forward have been discussed.

2. Cassava production

Cassava (*M. esculenta;* family *Euphorbiaceae*) is a food source for large number of people in developing countries. It is cultivated mostly in the tropics [9]. According to [10, 11], global cassava production has doubled from 124 to 277 million tons in 36 years (1980–2016) due to the ever-increasing demand for cassava for food, feed and industrial products such as biofuel and starch. Africa contributes 57% of the world's cassava production, with Nigeria contributing 21% of global production and thus considered the top global producer, followed by Asia with a production 32% and Americas about 11% [3].

In Asia, production area was estimated around 4.0 million ha [6, 12] with output of 76.6 million tons [6]. In Latin America and the Caribbean, where cassava originated, the area cultivated to cassava was 2.6 million ha with and output of 34.3 million tons [6]. In Cote d'ivoire, 6.7 t/ha productivity has been recorded, which is lower than the 9.8 t/ha average yield in Africa [13]. The ten leading cassava producing countries are presented in **Table 1**.

2.1 Cassava as a food security, feed and industrial crop

Cassava is a food security crop with characteristic high calorie yield per hectare, disease tolerance, flexible time to harvest as compared to other crops [3]. The crop is cultivated in over 40 countries worldwide and over 70% of SSA's production recorded in Nigeria, Congo DRC and Ghana [10]. The crop is grown in less fertile marginal soil conditions thus providing income for farmers in marginalized areas, and food for households [14]. The crop provides 250 kcal/ha/day of energy compared to maize, which provides 200 kcal/ha/day [7]. Cassava tuberous roots, a staple food for many across Africa provides rich carbohydrate energy source and an essential food security crop [14]. In sub-Saharan Africa, cassava is processed into producys such as attiéké (cassava couscous), gari (toasted granules), placali (paste), and futu (pounded cassava mixed with pounded plantain), and several other forms [13].

As a food crop, cassava is the most beneficial stable crop consumed by over 800 million people [3, 15]. Cassava provides over 700 million people an energy calorie of 500 cal/day of energy with a 100 cal/day consumption of the roots in tropical areas [3]. The tuber is also processed into animal feed [13]. In Asia, cassava is cultivated for human consumption with yield averaged at 34 t/h, and serves as a secondary staple crop and delicacy in households and hotels whilst 10% of production is processed into fermented flour products [3]. The crop is also consumed as dried cassava chips and biofortified commercial livestock feed for animals [6].

	Country	Production volumes							
		2013	2014	2015	2016	2017	2018	2019	2020
1	Global	275.98 M	282.63 M	282.10 M	281.77 M	275.15 M	285.01 M	293.15 M	296.22 M
2	Nigeria	47.41 M	56.33 M	57.64 M	59.57 M	55.07 M	55.87 M	59.41 M	60.00 M
3	Democratic Republic Congo	33.92 M	34.87 M	34.93 M	35.50 M	37.70 M	38.87 M	40.05 M	41.01 M
4	Thailand	30.23 M	30.02 M	32.36 M	31.16 M	30.50 M	29.37 M	31.08 M	29.00 M
5	Ghana	15.99 M	17.80 M	17.21 M	17.80 M	19.01 M	20.85 M	19.37 M	21.81 M
6	Indonesia	23.94 M	23.44 M	21.80 M	20.26 M	19.05 M	16.12 M	16.35 M	18.30 M
7	Brazil	21.48 M	23.25 M	23.06 M	21.04 M	18.50 M	17.88 M	17.59 M	18.21 M
8	Vietnam	9.76 M	10.21 M	10.74 M	10.91 M	10.27 M	9.85 M	10.17 M	10.49 M
9	Angola	16.41 M	7.64 M	7.73 M	7.92 M	8.33 M	8.73 M	9.00 M	8.78 M
10	Cambodia	7.55 M	7.50 M	7.50 M	7.50 M	7.50 M	7.50 M	7.50 M	7.66 M

(Credit https://www.tridge.com/intelligences/mandioca/production); M, million metric tons.

Table 1.
Cassava production trends of the top 10 producers of cassava from 2013 to 2020.

Over the past 10 years, increasing demand for cassava processed starch has been attributed to the high attractiveness of its allergy-free, and freeze-thaw stability properties to diverse food and non-food industries [16]. Cassava starch has 0.06–0.75% protein, 0.11–1.9% fiber, 0.03–0.29% ash, 0.0029–0.0095% phosphorous, 0.01–1.2% lipid contents, respectively [17]. Furthermore, a new trend of growing demands towards starch-based ingredients has been reported; an interesting focal point of starch processing [16]. Despite Nigeria's role as the top producer of cassava globally, Thailand tops the chart for the leading producer of cassava starch [16].

Low gelatinization and retrogradation, viscosity and higher water-binding capacity properties of cassava starch makes it preferable in food, pharmaceutical and chemical products [18]. Nevertheless, the high digestion rate of cassava starch resulting in the increased risk of cardiovascular disease has been the major drawback [16]. Cassava starch has diverse applications in the food industry with products such as noodles, tapioca pearls, sweeteners (e.g. dextrin, glucose, monosodium glutamate and high-fructose syrup), pastry products, yoghurts and microbial fermented feedstock [17]. Inclusion of products in rations increased cattle liveweight gain (LWG) and metabolizable energy content [19]. Furthermore, in the non-food industries, cassava starch is used for paper products, adhesives, pharmaceutical and textiles [16].

Cassava peels have been beneficial in the cassava utilization chain as animal feed supplement which is nevertheless not preferable [20]. Energy production is also a benefit derived from cassava peel biochemical and thermo-chemical processing [20]. Biochemical processes involve bioethanol fermentation and anaerobic digestion whereas thermochemical processes comprise pyrolysis, gasification, combustion, and liquefaction [21]. However, these processing technologies are not duly established in Africa [19, 20].

Biorefining involves the utilization of zero waste technologies to produce renewable energy [22]. Anaerobic digestion converts organic matter into biogas and biofertilizer which has led to good and controlled waste management system energy [22].

3. Production constraints

Cassava production is susceptible to several biotic constraints including pests and diseases. The most detrimental viral diseases in SSA are cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) [2, 23]. Massive crop losses and reduced crop productivity over the last two decades have been worsened by the re-emergence of CMD epidemics and the emergence and evolution of new recombinant geminiviruses, the vector population increment and whitefly 'B' biotype activities [23]. CMBs affect the yield of infected crops and reduce the growth of local unimproved varieties to its susceptibility status and can result in crop failure of up to 100% yield loss [24]. CMD and CBSD cassava sources are present in the indigenous African flora, which are influenced and made worsened by factors such as susceptible varieties cultivation, abundance of transmission efficient insect vectors, and use of infected planting materials from previous harvests [24].

Cassava brown streak disease (CBSD) and cassava mosaic disease (CMD) results in economic losses estimated at over $1.0 billion per annum, adversely threatening food security in SSA [25, 26]. Crop losses attributed to CMD is characterized and documented over the years as leaf and root damages which cause food storage deficiencies in the root region [25]. CMD characteristic symptoms in infected plants (**Figure 1**) include "green to yellow" foliar mosaic, narrowing, twisting, leaf malformation

Figure 1.
CMD-affected cassava plant.

and in most severe conditions, leaf abscission and reduction, and stunted growth, which results in few or no tuber production, causing significant yield loss [27]. CMD infection results in loss of planting materials and render stem cuttings unsuitable and unclean for propagation [27]. Furthermore, CMD-affected cassava plants exhibit varied symptom expression, of which various factors contribute to these variations. These factors include the infection time, virulence of virus species, synergism, age of the crop, genome integration of the virus, the specific strain of virus, sensitivity of plant host and other biotic factors [25, 28]. In Kenya, Sudan, Tanzania, and the Democratic Republic of Congo, CMD pandemic results in a similar poor yield in cassava cultivation [25]. CMD decrease crop yields, which is worsened by susceptible cultivar cultivation across SSA by farmers [13, 25].

The widespread and aftermath of the CMD epidemic in Uganda led to highly destructive economic losses in global cassava production, complete crop abandonment by farmers, food shortage, feed and fiber loss in rural homes, and famine-related deaths [27]. Food shortages from the catastrophic epidemic exacerbated the food supply deficit of at least 800 million people having poor nutrition which compromised economic and food security [29].

Diverse CMD economic losses estimations have been documented over the years and the difference in these reports can be attributed to the location of CMD distribution and the time and year of infection; these estimations range between 20% and 95% [30]. CMD annual losses in cassava production at an estimated amount of more than US$1 billion have been reported [25, 31].

3.1 Begomoviruses

Begomoviruses are members of the plant virus family *Geminiviridae,* characterized by twin geminate icosahedral particles (22 nm × 38 nm) with circular single stranded

DNA (ssDNA) genome [23]. These viruses are the second largest plant virus family. Begomoviruses are transmitted by the whitefly, *Bemisia tabaci* Gennadius (*Hemiptera: Aleyrodidae*), and through infected stem cuttings used routinely by most local farmers [25]. The viruses cause severe damage and negative impact on cassava production in Africa [28]. Begomoviruses have monopartite (DNA A) and/or bipartite (DNA A and DNA B) circular ssDNA molecules (2.7–3.0 kb) and are the leading biotic constraint in cassava production due to its persistent re-emergence and recombination events in Africa [30, 32].

Monopartite begomoviruses are commonly found in Africa, Indian, Mediterranean and European region, and are generally classified as the Old World begomoviruses (OW) whilst bipartite begomoviruses are frequently found in South and Central America are generally classified as the New World (NW) begomoviruses [33]. Begomoviruses have different types of genomes (**Figure 2**). The Old-World DNA A encodes six proteins (CP, Rep, Ren, V2, TrAp, and C4), of which majority are associated with betasatellites (~1350 nucleotides (nt) circular ssDNA molecules) of the family *Tolecusatellitidae* and genus *Betasatellite* [34]. These betasatellites depend on a main virus for movement, plant transmission and replication [35]. The DNA-A genome consist of 6 ORFs; 4 ORFs (AC1, AC2, AC3 and AC4) on the complementary strand and 2 ORFs on the virion strand (AV1, AV2) needed in encapsidation and replication, whilst the DNA-B genome possess two ORFs (BV1 and BC1) vital for intra- and inter- cellular movement respectively.

DNA A component encodes two overlapping virion-sense ORFs (open reading frames) involved in encapsidation (AV1) and suppressor targeting PTGS silencing (AV2), replication and transcription using overlapping complementary-sense OFRs (AC1, AC3) and host mediated gene silencing suppression (AC2, AC4) [34]. On the other hand, DNA B component encodes two nonoverlapping ORFs (BV1, BC1) on the virion and complementary strands respectively for inter- and intracellular virus trafficking [32]. DNA-A and DNA-B components are responsible for systemic infection, despite DNA-A single role in disease symptom induction [36].The leftward and rightward DNA-B and DNA-A transcriptional units are divided by a 200 nt (nucleotides) homologous intergenic region (IR) [32].

Cassava mosaic begomoviruses occur both in sub-Sahara Africa and parts of Asia (**Figure 3**). Different *Cassava mosaic begomovirus* species have been classified; *African*

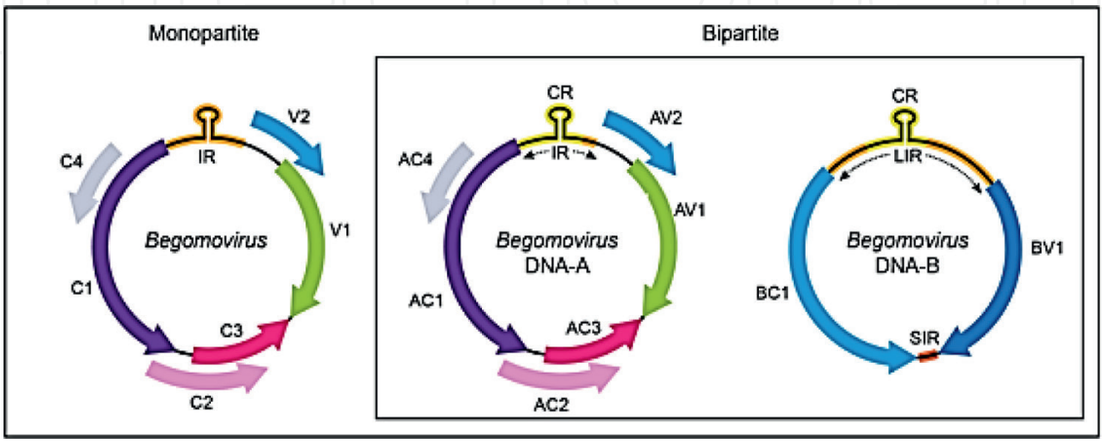

Figure 2.
Genome organization of begomoviruses. The open reading frames (ORFs) are on the complementary and virus strands (credit: ICTV).

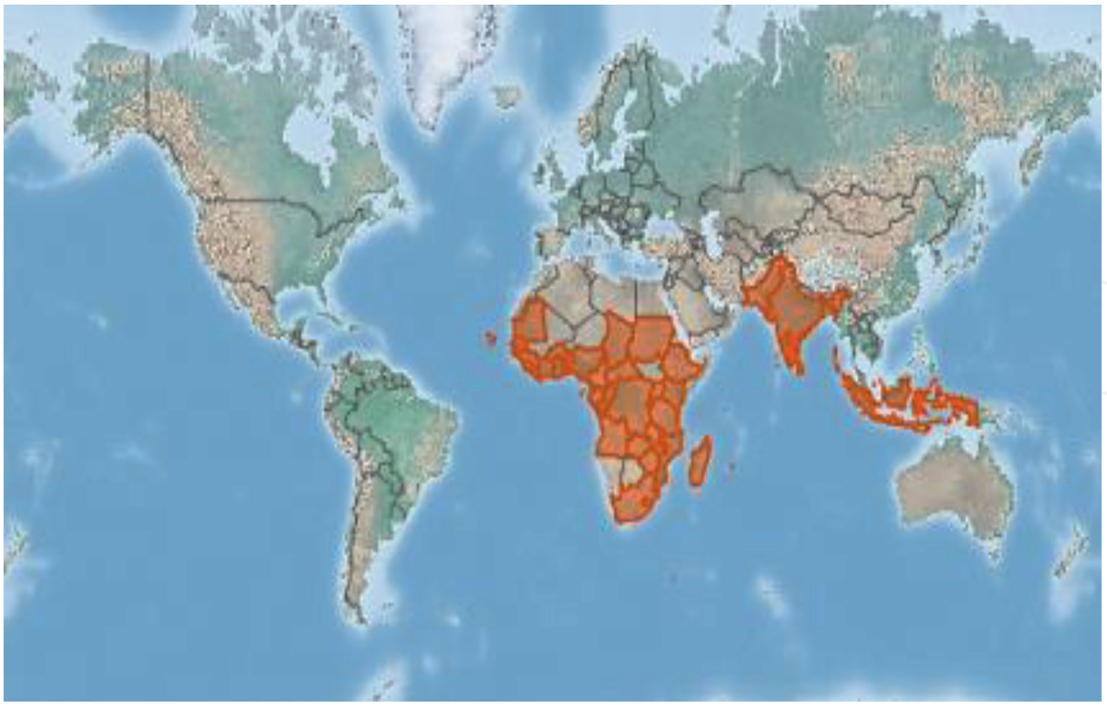

Figure 3.
Distribution of cassava mosaic begomoviruses in the world (credit: CABI).

cassava mosaic virus (ACMV), *East African cassava mosaic Cameroon virus* (EACMCV), *East African cassava mosaic virus* (EACMV), *East African cassava mosaic Zanzibar virus* (EACMZV), *East African cassava mosaic Kenya virus* (EACMKV), *South African cassava mosaic virus* (SACMV), *East African cassava mosaic Malawi virus* (EACMMV), *Indian cassava mosaic virus* (ICMV) and *Sri Lanka cassava mosaic virus* (SLCMV) [37] and *Cassava mosaic Madagascar virus* (CMMGV) [38].

Cassava mosaic begomoviruses are persistently transmitted and can occur in both single and co-infections [39]. ACMV, EACMCV and EACMV are widely prevalent and distributed in sub-Saharan Africa and a recombinant EACMV-UG strain has been reported with shared genomic properties with both ACMV (16% similarity of DNA-A genome) and EACMV (84% similarity of DNA-A genome) [9, 27]. EACMV-UG reports have been documented in SSA [27, 40]. The rapid spread of EACMV-UG can be attributed to inefficient sub-regional quarantine programmes in many countries and the indiscriminate dissemination of CMD-affected stem cuttings across sub-Saharan Africa [27]. Nevertheless, other recombinant CMBs are localized in distribution, confirming EACMV-UG better viral adaptation in sub-Saharan Africa [27].

3.2 *B. tabaci*

Whiteflies, *B. tabaci* (Hemiptera: *Aleyrodidae*) (**Figure 4**), are responsible for transmission of CMBs. CMB acquisition time is accelerated when non-viruliferous whiteflies are starved before acquisition feeding on CMD-affected cassava plants, following 6–8-hour latent period prior to transmission of virus and virus retention for about 9 days [41]. Inoculation access period of 10–30 minutes is required by viruliferous whiteflies for virus inoculation into healthy cassava plants [28]. Considerable amount of resources, and breeding efforts on *B. tabaci* and its role in CMD spread is vital for successful management of the disease.

Figure 4.
Whitefly (Bemisia tabaci) infestation on leaf tissues (credit: CABI).

3.3 Satellite DNA

DNA satellites are monopartite virus-associated subviral agents, circular ssDNAs with a conserved nonanucleotide sequence "TAATATTAC" that depend on the host cell co-infection with a helper virus for multiplication [42]. Satellites do not replicate within host cell without the helper virus and do not play any role in helper virus' life cycle [28].

DNA satellites presence in *Cassava mosaic begomovirus* infection magnifies, CMD symptom severity through constitution and host cells activities, increases viral accumulation, further worsening symptoms expression and increase CMD-induced losses which differs significantly from disease symptoms of the helper virus only [30]. Molecular characterization led to the detection of two novel small DNA molecules (satII and satIII), and confirmed these molecules as satellite DNAs due to their dependency on geminiviruses for movement and replication [43]. SatDNAs have a vital characteristic feature of breaking down resistance in resistant cultivars such as the West African cassava landrace TME3. SatDNAs have GC-rich region with direct repeats of short pentanucleotides CCGCC, trinucleotides CGC, and hexanucleotides CCGCCG, and have no origin of replication [44]. Bipartite begomoviruses associated satellites are found in replication and movement within the plant [28]. SatDNA-II has one putative TATA Binding Protein (TBP) motifs [43] and SatDNAIII have three putative TATA Binding Protein (TBP) motifs (GATATAAATA, TACATATATAT and TCTGTATATA) [28]. SatDNAs genomes have putative consensus transcription poly (A) signal AATAAA, with a positioned motif TTGTA upstream, making SatDNAs biologically functional [28, 30, 43].

DNA satellites have raised concerns pertaining to its impact on cassava production and vital role in exacerbating CMD severity caused by CMBs and substantial reduction in yield across Africa [28]. DNA satellites reduce yield as a result of virus infection, limits the distribution, exchange and multiplication of stem propagules, affecting conventional cassava breeding programmes [44]. SatDNA-II induced severe CMD symptoms expressed through mosaic, yellowing and distorted leaf symptoms and has been reported to be mostly associated with EACMV-UG whereas SatDNA-III

induces unique CMD symptoms expressed through prominent yellowing and severe narrowing of leaves and mostly associated with EACMV-TZ [44].

The effectiveness of interaction between begomoviruses and satellites have common features such as the presence of stem loop for DNA replication, common genetic architecture, differentiated phloem-associated cells replication, length of individual genes at specific locus and localization [28]. In Tanzania, [28] stressed widespread occurrence of satellites (SatDNA-II and SatDNA-III) concurs with main CMB distribution and an evident of sequence integration of satellite into host cassava genome and satellites isolates mixed existence in the infected plant genome. From the study, the diversity in biological functions of SatDNA-II and SatDNA-III were confirmed [44]. In Ghana, [8] reported occurrence of SatDNAII and III for the first time, and its potential threat to the nation's food security and that of the sub-region cannot be overemphasized.

3.4 Cassava mosaic disease (CMD)

CMD is widespread and has been reported in major cassava growing regions of SSA. Severe CMD transmission is influenced by the flight and feeding activities of superabundant *B. tabaci* populations at 20 to 30 km/year [45].

Cassava mosaic disease has three distinguishing disease situations (epidemic, endemic and benign) as assessed in relation to pests and diseases; with rapid spread and transmission in epidemic situations causing severe and prevalent impact as reported in Uganda in 1990s [24, 28]. *East African cassava mosaic virus*–Uganda (EACMV-UG), a co-infected recombinant virus formed through a synergistic interaction of EACMV and ACMV caused the CMD epidemic in Uganda in the late 1980s and early 1990s [45]. Endemic areas were characterized with high incidence of CMD but relatively low symptoms expression whereas the benign situation is characterized with below 20% (low) CMD incidence [28, 43].

Three decades of the severe CMD pandemic in Uganda has passed and the devastating widespread of CMD continuous advancements to Democratic Republic of Congo in southern Africa and West African countries such as Nigeria and Ghana [8, 13, 45]. The CMD pandemic continues to pose a threat to cassava production in sub-Saharan Africa [45].

There have been reports from various countries in sub-Saharan Africa confirming CMD occurrence across the continent [36]. These reports established and revealed that CMD severity is influenced by CMBs mixed infection and synergistic effects with associated DNA satellites [44]. A nationwide survey by [29] confirmed a new recombinant strain of EACMV and six CMG species with novel begomoviruses; revealing increased CMD geographical distribution and diversity in Kenya. Also, CMD is endemic in the northern and coastal regions of Ivory Coast [13].

Reports have confirmed the distribution of the CMD viruses in a dynamic fashion; EACMV and ACMV is restricted to "non-overlapping geographical areas" in southern Africa, whereas EACMV only occurred in the Mozambique, Malawi, Zimbabwe and Madagascar [46]. Recent reports by [2, 36] re-confirmed EACMVs in Togo, Western Kenya, Nigeria, North-Eastern Zambia, Ivory Coast, Western Tanzania, Cameroon, Democratic Republic of Congo and Guinea.

Molecular detection (using Enzyme linked immunosorbent assay and Polymerase chain reaction) and CMB distribution maps revealed the presence of ACMV in all regions across SSA; from the northern regions of South to the savannah zones of Sahel [27, 36]. In Madagascar, a strong cohesive evolutionary interaction in CMB species, coupled with EACMV-like lineages in the archipelagos of Seychelles and Comoros

which was transmitted to these islands three decades ago fits through recombinant of CMBs and abundant whitefly population [23].

3.5 Cassava brown streak virus (CBSV)

CBSVs belong to genus, *Ipomovirus* and family *Potyviridae*. *Ipomoviruses* possess single-stranded genomes, positive sense in nature and have large polyproteins and ten mature proteins [47]. Molecular characterization of coat protein sequences confirmed and established two genetically distinct species: *Ugandan Cassava brown streak virus* (UCBSV; 87–90% amino acid identity) and *Cassava brown streak virus* (CBSV; 76–78% nucleotide). CBSV and UCBSV are African indigenous ipomoviruses and occur in Africa only; whitefly vectors are the transmitting vectors [48].

CBSVs share unusual features when analyzed at the genomic level and do not possess the multi-functional helper-component proteinase protein (HCPro) (**Figure 5**), which is present in other *Potyviridae* viruses except for *Squash vein yellowing virus* (SqVYV) and *Cucumber vein yellowing virus* (CVYV) [47, 49]. The absence of HCPro is replaced by P1 serine proteinase's silencing suppressor activity [49]. The P1 proteins of UCBSV and CBSV contain LXKA motifs and zinc finger [50]. Occurrence of CBSV in infected cassava in East Africa has been reported. Recent whole genome sequencing and phylogenetic analysis proved the existence of three new species in the clade of UCBSV and the non-limitation of the viral species to agro-ecological zones [51].

The crop cultivars respond diversely to CBSD through range of symptoms in sensitive cultivars and foliar symptoms coupled with mild root necrosis in tolerant cultivars at different infection time [50, 52]. NASE 3 cultivar remained susceptible to

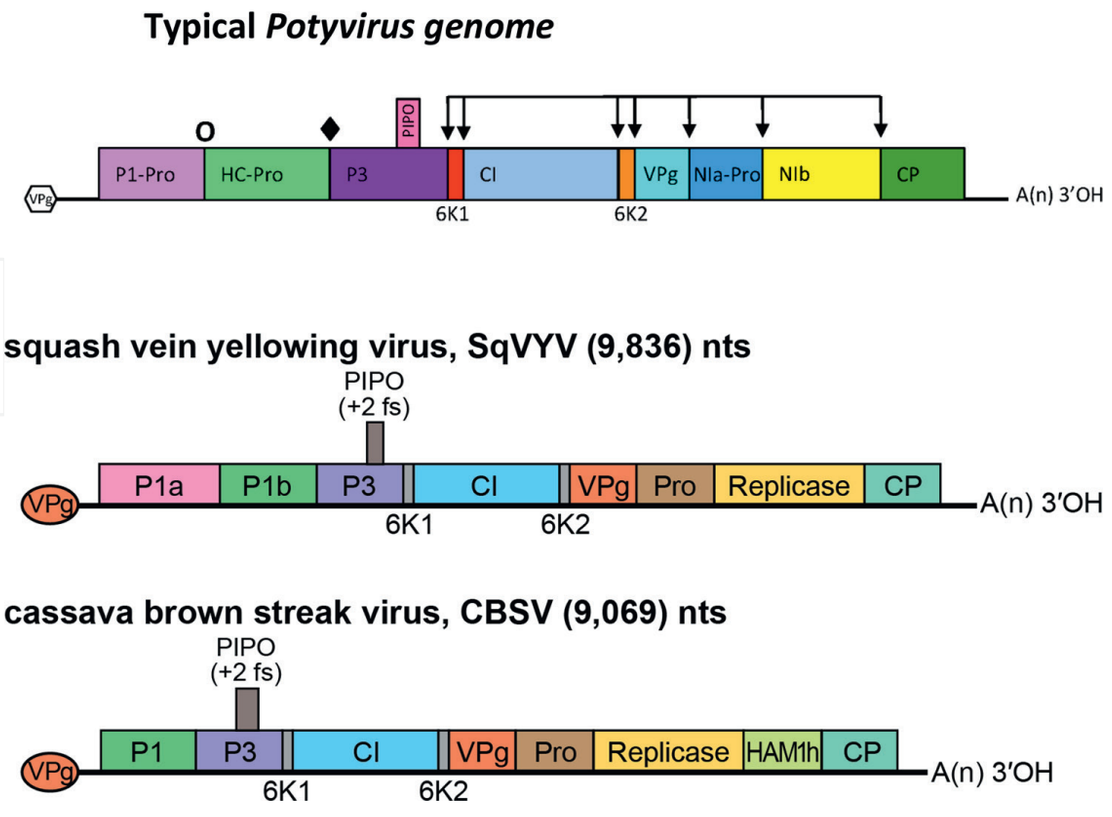

Figure 5.
Genomic organization of Squash vein yellowing virus (SqVYV) and Cassava brown streak virus in comparison with a typical Potyvirus genome (Credit: ICTV).

CBSV but exhibits high levels of resistance to UCBSV infection [53]. However, [54] reported that tolerant cultivars withstood lower viral titres as compared to susceptible cultivars. No correlation between symptom severity and viral load has been established; NASE 14 cultivar expresses severe root necrosis even with low viral accumulation whereas NASE1 cultivar expresses no foliar or root necrosis symptoms despite having a high viral accumulation [52].

3.6 Cassava brown streak disease (CSBD)

CBSD was detected initially in infected cassava crops in Tanzania in 1936; and in inland Uganda and Malawi in 1950 [50]. Aftermath of CSBD ignorance and undue lack of attention over several decades resulted in its re-emergence as an epidemic in the 1990s that devastated cassava production and a shocking threat to food security [55].The sudden occurrence was reported initially in the East African region, and spread to other countries in the region [55]. By 2010, CBSD had translated into a regional pandemic in Central and East Africa; with a strong spread signal to other sub-Saharan countries, posing serious menace to tuber yield [56, 57].

The disease results in infected crops expressing symptomatic brown-black, necrotic root rot and constriction, brown stem streaking and adversely diminishes tuber root yields [55]. For CBSD varying foliar symptoms, chlorotic mottles, blotching, leaf vein chlorosis are eminent but very subtle for morphological detection and even asymptomatic in certain reports [55]. As such, asymptomatic infected cuttings are distributed and transplanted by local farmers, increasing the disease spread [56]. The whitefly *B. tabaci* semi-persistently transmits CBSV and UCBSV [58]. CBSD symptoms vary and is influenced by the biotic conditions present, viral strain present, cassava cultivar, severity, crop part affected, age of the cassava crop during infection time, and onset of symptom expression [50]. Foliage and root symptoms expressed by the two causal agents differ; UCBSV elicits circular leaf vein chlorotic blotches, whilst CBSV elicits feathery chlorosis of the vein, blotches, developed chlorotic and severe root necrosis [50]. CBSD-affected cassava roots showing necrosis symptom are presented in **Figure 6**.

No recombination event exists currently but co-infection synergy has been reported which may lead to severe symptoms expression [55]. The CBSD pandemic disease are a threat to food security in sub-Saharan African and are further exacerbated by the distribution of CMD-resistant cassava that are asymptomatic for CBSD, CBSD-infected cassava propagule transportation without the necessary inter-regional phytosanitary measures and frequency and abundance in polyphagous whitefly vectors [48, 59].

Similarly, confirmed recent re-emergence of CBSD has been made in many East African countries such as Democratic Republic of Congo [60], Burundi [61] and South Sudan have been documented [50].

3.7 Economic importance of CBSD

CDSD causes detrimental damage and impact to cassava production; estimation of its impact and loss economically per annum is pegged at US$750 million across East and Central Africa [62]. CBSD is one of the devastating factors of increasing cassava yield losses in East Africa [56]. CSBD's on-going distribution worsens current food insecurity in SSA and also possible spread to West Africa [56]. The sudden attention and influx in scientific reports, reviews and community discussions on CSBD and its

Figure 6.
CBSD-affected cassava tubers (credit: CABI).

threat to food security is a topic of great concern on CSBD epidemiology [50]. CBSD expansion across Central and East Africa has heighted the sudden need for initiation and deployment of CSBD control measures [50, 56].

4. Current and future efforts in cassava production and research

Since the aftermath of CMD detection in Africa, substantial control efforts have been documented, of which phytosanitation and resistance breeding has been the most reported. Cassava breeding has resulted in the production of CMD resistant/tolerant high yielding cassava cultivars [63]. In East Africa, b-carotene (provitamin A) breeding focused objective has been implemented for the genetic improvement of cassava to produce carotenoids-rich cassava varieties which sought to promote dietary Vitamin A deficiency alleviation [64]. Cassava breeding programmes in SSA researched and exploited CMD2 locus in the deployment of highly heritable and resistant CMD genotypes [65].

Efforts to control CMD has been focused on virus-free deployment and CMD-resistant germplasm dissemination, which is restricted by long and tedious process of traditional breeding and lack of CMBs genomic characterization [27]. However, well implemented and carefully managed field research is expensive and demands more funding from stakeholders [64]. The increasing demand for food, feed and biomass-based products globally is keen in transforming SSA agriculture industry scope to a "biomass-supplying" hub [4]. The result-oriented research efforts, suitable fertilization and appropriate weed, disease and pest control, is projected to increased yields by 50–100% [66].

Amidst the efforts and research contributions over the last two decades, CMD is prevalent and cassava production has been constrained as a result of virulence of begomoviruses, co-infection synergy of CMBs, integration potential of CMBs and

associated satellites into host cell, association of CMBs with satellite DNAs through reassortment and recombination events, high fecundity and spread of *B. tabaci*, varied climatic factors, and use of infected propagules by local farmers [28]. As such we cannot ignore the activities of satellite DNAs and widespread activities of recombinant virulent strains [8]. Sub-Saharan Africa needs a phytosanitary facilities and techniques equipped with affordable detection approaches.

Limited knowledge and insights on CBSD viral variations and its complex interactions, cassava cultivars, vectors, and biotic conditions influence in disease spread [50]. CBSD prevalence, incidence, distribution and whitefly populations in farmers' fields need periodic and regular monitoring to document periodic changes in disease distribution in affected regions [50, 67]. Development of predictive models with evident-based for CSBD control decisions needs to be developed, which is dependent on farmer engagement, education on disease management and information for stakeholder awareness as implemented in Uganda [50].

Lessons need to be learnt from the ignorance and delayed attention to the CSBD outbreak to prevent and minimize the impact of future outbreaks. As such the scientific community needs to put in measures for CSBD epidemiology, outbreak into new areas prediction and spread [68].

Advances in molecular approaches including genetically modified resistant lines development, single multiplex RT-PCR reaction for CMB detection, RT-PCR optimization for CBSV and UCBSV detection, certified virus-clean planting material provision, marker-assisted breeding and sensitive diagnostics utilization have been applicable and useful in the CSBD progress status [50, 69]. Deployment of next generation high through-put sequencing (NGS) has ensured virus-free planting material (95% detection rate) through screening cassava crops for CBSVs prior to planting material dissemination [50, 70]. Despite these recent progress, CMD and CBSD biology and epidemiology areas need further attention and the accessibility of affordable diagnostic techniques in sub-Saharan Africa for local detection [50].

5. Conclusion

Cassava, a food security crop has huge potential for global food production as demand for the crop increases. In the last two decades, cassava mosaic disease and cassava brown streak disease have become major threats to food security across SSA, supply of feed and raw materials to industry. As such, further research and control efforts in achieving world food security status of cassava are necessary. Development of future research programmes is necessary to increase global cassava yield. Integration of different approaches and implementation of comprehensive cassava mosaic disease and cassava brown streak disease management in the region is required.

Conflicts of interest

The authors declare no conflict of interest.

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