Phytopathology®
PERSPECTIVES

New Technologies Provide Innovative Opportunities to Enhance Understanding of Major Virus Diseases Threatening Global Food Security

Jan F. Kreuze,[1,2,†] Wilmer J. Cuellar,[1,3,4] P. Lava Kumar,[1,5] Prasanna Boddupalli,[1,6] and Aman B. Omondi[1,7]

[1] One CGIAR Plant Health Initiative
[2] International Potato Center, Apartado 1558, Lima 15024, Peru
[3] One CGIAR Accelerated Breeding Initiative
[4] Alliance of Bioversity International and CIAT, Km 17 Recta Cali-Palmira, Cali 763537, Colombia
[5] International Institute of Tropical Agriculture (IITA), PMB 5320, Ibadan, Nigeria
[6] International Maize and Wheat Improvement Center (CIMMYT), ICRAF Campus, UN Avenue, Gigiri, Nairobi, Kenya
[7] Alliance of Bioversity International and CIAT, IPGRI Building, 08BP 0932–Cotonou, Republic of Benin
Accepted for publication 11 June 2023.

Abstract

Plant viruses pose a continuous and serious threat to crop production worldwide, and globalization and climate change are exacerbating the establishment and rapid spread of new viruses. Simultaneously, developments in genome sequencing technology, nucleic acid amplification methods, and epidemiological modeling are providing plant health specialists with unprecedented opportunities to confront these major threats to the food security and livelihoods of millions of resource-constrained smallholders. In this perspective, we have used recent examples of integrated application of these technologies to enhance understanding of the emergence of plant viral diseases of key food security crops in low- and middle-income countries. We highlight how international funding and collaboration have enabled high-throughput sequencing-based surveillance approaches, targeted field and lab-based diagnostic tools, and modeling approaches that can be effectively used to support surveillance and preparedness against existing and emerging plant viral threats. The importance of national and international collaboration and the future role of CGIAR in further supporting these efforts, including building capabilities to make optimal use of these technologies in low- and middle-income countries, are discussed.

Keywords: banana bunchy top, cassava mosaic, maize lethal necrosis, potato, sweetpotato, virome

Increasing global trade and movement of people and goods, intensification of farming, and perturbance of natural ecosystems, as well as climate change, are exacerbating the incidence and impacts of plant pathogens, including viruses (Jones 2020, 2021). At the same time, novel technological developments, including high-throughput sequencing (Villamor et al. 2019), isothermal nucleic acid amplification methods (Bhat et al. 2022), remote sensing tools (Wang et al. 2022), geographical information systems, information and communication technology, and artificial intelligence (Mrisho et al. 2020; Ramcharan et al. 2019; Selvaraj et al. 2019, 2020), offer a powerful set of tools for detection, diagnostics, monitoring, and prediction of such threats. Although such tools can be used proactively to scan the existence and evolution of plant viral threats, most often, they are used reactively as an emergency occurs, particularly in food-insecure low- and middle-income countries that have limited resources to invest in proactive measures. Examples of successful reactive deployment of such tools in managing plant viral outbreaks in developing countries during the last 10 years include the maize lethal necrosis in East Africa (Boddupalli 2021; Boddupalli et al. 2020), banana bunchy top virus (BBTV) in West and East Africa (Alabi et al. 2022; Shimwela et al. 2022), and the cassava mosaic disease in Southeast Asia (Chittarath et al. 2021; Siriwan et al. 2020) (Fig. 1).

Proactive approaches have also been implemented, providing information that helped suppress or avoid major outbreaks of plant viruses. These can be categorized into (i) those that target a specific known disease that is considered a threat and (ii) those that take a generic approach to identify and prevent occurrence of any potential new threat. Examples of specific proactive surveillance activities include those to monitor germplasm to prevent transboundary spread of seedborne pests and pathogens (Kumar et al. 2019), whereas generic approaches to map entire viromes have been implemented at

†Corresponding author: J. F. Kreuze; j.kreuze@cgiar.org

Funding: Support was provided by the Bill and Melinda Gates Foundation (grants OPP1019987, OPP1130216, and OPP1199467) and CGIAR Trust Fund Contributors (https://www.cgiar.org/funders/).

The author(s) declare no conflict of interest.

different geographic scales, crops, ecosystems, and their interfaces (Maclot et al. 2020 and references therein), including major food security crops, such as wheat (Redila et al. 2021; Singh et al. 2020), maize (Lappe et al. 2022), cassava (Scussel et al. 2019), sweetpotato (Bachwenkizi et al. 2022; Nakasu et al. 2022), and potato (Okonya et al. 2021). These actions have only been possible through collaboration between several international and national partners from public, academic, and private sector representatives to coordinate country and regional actions, and international agricultural research centers have often played an important role in facilitating these networks. In the following sections, we will describe some of the mentioned cases, which present specific examples and are by no means exclusive, highlighting the successes and learnings, and then synthesize them into a set of recommendations for better management of plant viral diseases in the future.

Maize Lethal Necrosis in Africa

Maize was domesticated in Central America/Mexico and is the world's most important staple food crop, fourth most important in low-income food-deficit countries of the world, and third most important in the least developed countries (FAOSTAT 2021). Maize lethal necrosis (MLN) emerged and was first reported from Kansas as corn lethal necrosis in the late 1970s and associated with co-infections of maize chlorotic mottle virus (MCMV) and maize dwarf mosaic virus or wheat streak mosaic virus. Since then, reports have emerged from several Latin American countries and then Asia (Redinbaugh and Stewart 2018). The first outbreak of MLN in Africa (Fig. 1B) occurred in Kenya in 2011, followed by its rapid spread to several countries in East Africa within a span of 3 to 4 years (Mahuku et al. 2015). This caused huge concern to stakeholders, including maize-dependent smallholder farmers, researchers, national plant protection authorities, the commercial seed sector, and governments across the African continent, where maize is a crucial staple crop. Effectively countering the incidence, spread, and adverse impacts of MLN in Africa required strong, coordinated, and synergistic efforts from multiple institutions, as the challenge is complex and multifaceted. Since 2012, a team including CIMMYT, the Kenya Agricultural and Livestock Research Organization, national plant protection organizations and commercial seed companies across sub-Saharan Africa, the International Institute of Tropical Agriculture, the International Centre of Insect Physiology and Ecology, several advanced research institutions in the United States of America and Europe, and nongovernment organizations, such as the Alliance for Green Revolution in Africa and African Agricultural Technology Foundation, have intensively implemented a multidisciplinary strategy for curbing the spread and impact of MLN in Africa (Boddupalli 2021; Boddupalli et al. 2020).

The first step, identifying the causal agent(s) of MLN in Africa, was achieved in parallel through high-throughput sequencing (Adams et al. 2013) and serological (Wangai et al. 2012) approaches, resulting in the recognition of MCMV and sugarcane mosaic virus (SCMV) as the causal agents. Whereas SCMV is endemic in Africa in grasses, it causes little or no damage by itself, whereas sequence analysis revealed that MCMV was possibly introduced in infected maize seed from China (Braidwood et al. 2018). It has since been recognized that other potyviruses besides SCMV, such as johnsongrass mosaic virus, can cause MLN in combination with MCMV in Africa (Stewart et al. 2017). MLN management in Africa included (i) breeding and deployment of resistant cultivars, (ii) establishing and implementing an MLN monitoring and surveillance system in East and Southern Africa, (iii) production and exchange of MLN virus-tested commercial seed, and (iv) operating an MLN phytosanitary community of practice, especially to share learning across borders on key aspects, such as standardized MLN diagnostics procedure(s), providing training on MLN diagnostics, expediting adoption of appropriate phytosanitary and diagnostic procedures (e.g., use of MCMV lateral flow assay test strips and enzyme-linked immunosorbent assay [ELISA] for virus detection, maize-free crop period for at least 2 to 3 months in a year, and systematic sampling and analysis of commercial seed production plots for possible presence of MLN-causing viruses), and identifying/validating and deploying novel and low-cost MLN diagnostic protocols (Boddupalli 2021; Boddupalli et al. 2020).

MCMV has primarily driven the emergence of MLN in East Africa, South America, and some countries in Asia. MCMV transmission through seed could be a major channel for the spread of the disease. Identification of infected seed lots is therefore critical

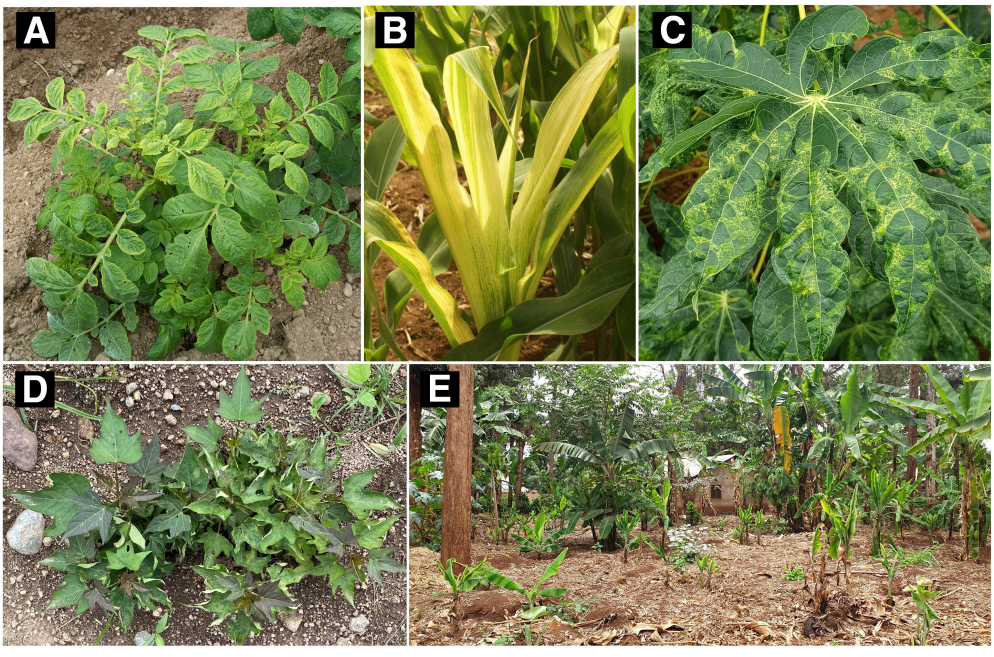

FIGURE 1
Symptoms of virus diseases affecting major food security crops: **A,** virosis of potato caused by co-infection of potato leaf roll virus, potato virus X, potato virus S, and potato virus V; **B,** maize plant affected by maize lethal necrosis caused by co-infection of maize chlorotic mottle virus and sugarcane mosaic virus; **C,** cassava leaf with symptoms of cassava mosaic disease caused by Sri Lankan cassava mosaic virus; **D,** a sweetpotato plant affected by "sweetpotato virus disease" caused by co-infection of sweetpotato chlorotic stunt virus, sweetpotato feathery mottle virus, and sweetpotato leaf curl virus; and **E,** a banana plot with plants heavily affected by banana bunchy top disease (stunted and dwarfed plants), caused by banana bunchy top virus.

for preventing the spread of MCMV through seed. Bernardo et al. (2021) evaluated different protocols, including ELISA, reverse-transcription polymerase chain reaction (RT-PCR), and quantitative RT-PCR for detection of MCMV in maize seed lots from Kansas, Mexico, and Kenya. The study demonstrated that although both ELISA and RT-PCR were effective in detecting MCMV in seed lots, ELISA provided a reliable and inexpensive diagnostic assay for routine implementation in seed testing facilities.

Biswal et al. (2022) analyzed the impacts of MLN in Africa and found that resource-poor farmers and low-income consumers are the most vulnerable populations. They also highlighted the possible molecular mechanism in transmission of MLN viruses, the role of vectors, and host plant resistance, identifying a range of potential opportunities for genetic and phytosanitary interventions (including cultural practices) to control MLN. Recent studies also indicated that microRNAs could have a role in host plant response to MLN-causing viruses (Liu et al. 2022).

The fact that no maize-growing country in Southern or West Africa has reported further outbreak of MLN is a testimony to the successful initiative to collectively manage MLN in East Africa. Nevertheless, there is no room for complacency. MLN is still prevalent in East Africa and has not been eradicated. The threat of the disease spreading to other regions in sub-Saharan Africa still looms. It is, therefore, imperative to sustain MLN disease management, which is being done through the CGIAR Plant Health Initiative, including continued surveillance of countries in Southern and West Africa with potential risk of MLN invasion; training and capacity building of national plant protection organizations and seed companies on MLN diagnostics and management practices for MLN-free commercial seed production and exchange; and scaling and deployment of MLN-resistant cultivars together with sensitization of farming communities on cultural management.

Cassava Mosaic Disease in Southeast Asia

Cassava originates from the Amazon region of South America and is currently the sixth most important staple food crop globally and the second most important in the low-income food-deficit and least developed countries of the world (FAOSTAT 2021). Cassava mosaic disease (CMD) in Asia can be caused by single or mixed infections of Indian cassava mosaic virus and Sri Lankan cassava mosaic virus (SLCMV; Fig. 1C), and neither has been reported from Africa so far. It was first characterized from symptomatic plants collected in Colombo, Sri Lanka, in 1998. In Africa, CMD is present in all cassava-growing countries, where it is caused by a different set of begomovirus species, new variants of which have driven successive outbreaks of the disease over the last century (Legg et al. 2014). Begomoviruses are circular DNA viruses transmitted by whiteflies of the *Bemisia tabaci* species complex and/or by distribution of contaminated vegetative propagation material (cassava nodal cuttings, or "stakes"); experimentally, SLCMV is more virulent and can be more easily mechanically transmitted to *N. benthamiana* than Indian cassava mosaic virus (Saunders et al. 2002). Over the past 20 years, the cultivated area of cassava in Southeast Asia has significantly increased, and cassava is now considered the second most important crop after rice in this region (Malik et al. 2020). Although Southeast Asian cassava has been virtually free of phytosanitary constraints for most of its history, recent region-wide monitoring activities unveiled a complex of invasive pests and pathogens increasingly affecting cassava in this region (Graziosi et al. 2016; Siriwan et al. 2020). Reports of CMD in Southeast Asia increased from a single plantation reported in Cambodia in 2015 (Wang et al. 2016) to several reports from Thailand, Laos, Vietnam, and South China in less than 6 years and identifying only SLCMV in these countries (Chittarath et al. 2021; Siriwan et al. 2020; Wang et al. 2019). Regional monitoring of whiteflies showed that *B. tabaci* Asia II 1, a known vector of SLCMV (Chi et al. 2020), and Asia II 6 are present in Southeast Asia but in low abundance (Leiva et al. 2022), suggesting that the observed geographical spread of the virus was related to human movement of contaminated cassava stakes, likely facilitated by the efficient yet "informal" network of cassava stakes traders in the region (Delaquis et al. 2018).

Current proactive activities in management of CMD in this region include the identification of disease tolerance in local cassava genotypes (Malik et al. 2022) and regional (Thailand, Lao PDR, Cambodia, and Vietnam) virus surveillance for early detection of new incursions and for new strains of SLCMV or any new species of cassava begomovirus (Chittarath et al. 2021; Siriwan et al. 2020), such as those present in Africa (Legg et al. 2014). In addition, identification and seasonal monitoring of the insect vector *B. tabaci* in the region can help identify hotspots to target control methods (Leiva et al. 2022). These activities include the active participation of local plant health officers and the establishment of a regional network initially established by organizing advanced training courses on the use of standard field sampling protocols, image data collection, sample storage and handling (Jimenez et al. 2021), and molecular tests using specific and generic PCR primers (Leiva et al. 2022; Siriwan et al. 2020). In cases where a new infected area is reported or unusual symptoms are observed in the photographic record, rolling circle amplification using random hexamer primers is carried out to amplify complete circular genomes and confirm/discard the presence of additional begomovirus species (Leiva et al. 2020). These genome surveillance data are uploaded and communicated using Nextstrain (Hadfield et al. 2018). Incidence maps integrating symptoms and sequence data are recorded and shared with local plant health officers using open platforms (Cuellar et al. 2022) to support early interventions (Chittarath et al. 2021; Siriwan et al. 2020). On the other hand, artificial intelligence developed and validated for detection of CMD in Africa through the PlantVillage Nuru app (Mrisho et al. 2020; Ramcharan et al. 2017, 2019) can support farmers in the identification of the disease and alert local diagnostic networks, which then can validate the identity of the virus. To date, only SLCMV (two phylogenetic groups differing in the length of the *rep* open reading frame) and low abundances of *B. tabaci* have been recorded in Cambodia, Laos, Thailand, and Vietnam (Leiva et al. 2022; Siriwan et al. 2020). However, this situation will likely evolve in the near future, as cassava cultivation is intensified in some Southeast Asian regions, favoring the buildup of whitefly populations in cassava and in alternative hosts (Hemniam et al. 2022).

Future research requirements include the following:

(i) CMD in Southeast Asia emerged soon after another disease, cassava witches' broom, had just spread in the region, but co-infection is not commonly found in the field. It is necessary to investigate the differential response of cultivated cassava genotypes to both diseases (host−pathogen interactions).

(ii) Changes in whitefly (*B. tabaci*) populations and transmitted pathogens that could increase the risk of establishment of additional cassava-infecting viruses in the region should be monitored.

(iii) Awareness must be raised on the importance of having a "critical mass" of local researchers supporting and continuing to implement harmonized phytosanitary protocols for safe seed movement across borders to prevent new outbreaks.

(iv) Capacity-building activities on identification and rapid molecular diagnostics of (cassava) pests and pathogens not yet known to occur in the region should be continued.

(v) Pilot screening and large-scale production and deployment of disease-resistant/-tolerant varieties based on higher-resolution risk maps are necessary to maximize the impact of interventions.

BBTV in Africa

Bananas and plantains were domesticated in the Indonesian archipelago and are currently the tenth most important staple food crop globally and sixth most important in the low-income food-deficit and least developed countries of the world (FAOSTAT 2021). Banana bunchy top disease (BBTD; Fig. 1E) was first recorded in 1889 in Fiji, Oceania. It was first reported in sub-Saharan Africa in the 1960s in the Democratic Republic of Congo and has since spread to 16 countries in sub-Saharan Africa. It is a typical case of transboundary expansion of an introduced virus through human activities, especially perpetuation and exchange of virus-infected vegetative propagules, and ubiquitous aphid vectors (Kumar et al. 2011; Stainton et al. 2015). Reports of BBTD occurrence increased after 2000, which could be due to new spread or an increase in surveillance efforts since 2008 (Kolombia et al. 2021; Lokossou et al. 2012). After the first BBTD outbreaks in Benin in 2011 (Lokossou et al. 2012) and Nigeria in 2012 (Adegbola et al. 2013), which were the first reports of the virus occurrence in banana in West Africa, a regional alliance (www.bbtvalliance.org) was established in 2013 to organize BBTV surveillance surveys in the affected countries and monitor virus spread to initiate containment measures. Recombinase polymerase amplification-based field assays were established to help with early detection of BBTV and implement eradication of infected mats (connected groups of pseudostems originating from one rhizome). The management of BBTD has relied on approaches to detect and eradicate infected plants. Symptom-based rogueing has already been used (Omondi et al. 2020). However, this approach relies on accurate early BBTD symptom identification (Allen 1987). Tools for the effective detection of diseased plants could help in minimizing field risk of BBTD spread, especially in seed certification. Digital tools have been developed to facilitate field detection of BBTD and other banana diseases using smartphone-based applications, such as TUMAINI (Selvaraj et al. 2019). Like PlantVillage NURU, the application would enable independent disease detection and afford expert advice on disease management, reducing the reliance on expert presence (Alabi et al. 2022; Dato et al. 2021; Selvaraj et al. 2020). More recently, remote sensing approaches using medium-resolution satellite imagery and drones were used to identify banana fields to aid in targeted surveillance for BBTV control and delineate areas of possible infestation (Alabi et al. 2022; Dato et al. 2021; Selvaraj et al. 2020). These advancements helped with early detection and eradication of BBTV in Togo (Kolombia et al. 2021) and early confirmation of BBTV occurrence in Tanzania and Uganda (Ocimati et al. 2021; Shimwela et al. 2022). Vegetative propagation of bananas and maintenance of the crops as perennial plantations make every virus-infected plant a perennial source for BBTV inoculum, contributing to the further spread of the virus by human activities and vectors. Variability in BBTD expression among cultivars makes the standard Cavendish-based symptom expression inefficient, especially in multiple cultivar production systems, promoting the maintenance of diseased plants in fields. Other predisposing factors are a lack of sufficient knowledge about virus and disease identification (Abiola et al. 2020) and cultural practices linked to the propagation and exchange of planting materials among farmers (Nkengla-Asi et al. 2021). This case reflects the integration of diagnostics, surveillance tools, and epidemiology contributing to better management of BBTV in sub-Saharan Africa.

A number of gaps still remain toward the management of BBTD, especially in Africa.

(i) One gap is the variability of BBTV and vector susceptibility among banana cultivars. Although reliable immunity was not found in popularly grown cultivars in Africa, different levels of tolerance to aphids and the virus (Ngatat et al. 2022) present both an opportunity for field-level control and a risk for BBTD spread in seed systems. Lessons from Fusarium Race 1, however, suggest that mixed cultivar and multi-crop systems would be more resilient against disease spread.

(ii) An understanding of the seasonal variability in disease expression and vector behavior could help refine disease modelling efforts for a more efficient management approach.

(iii) Seed systems policies and tools integrating disease risk maps would support efforts at regional and country scales.

(iv) Collaborative mapping between states is needed. BBTD outbreak zones are, so far, mostly in border regions of most countries. Collaborative and stricter quarantine efforts are necessary.

(v) The benefit of landscape design in BBTD management remains little studied. Dato et al. (2021), for example, identified landscape complexity and crop association parameters that could be associated with BBTD prevalence. These factors may work indirectly through vector dispersal, predation, or abundance and are especially suited for tropical mixed cropping systems.

(vi) Modelling BBTD risk, including landscape, seed movement, and crop management data, at the continental and landscape scales may yield predictions of vulnerability and prevent new outbreaks within the continent, learning from existing knowledge of BBTD spread within the continent.

Sweetpotato Virome

Sweetpotato originates from Central America/Mexico and is currently the world's sixth most important staple food crop, seventh most important in low-income food-deficit countries, and fourth most important in the least developed countries of the world (FAOSTAT 2021). Viruses are among the most important constraints in sweetpotato production (Fig. 1D), particularly in Africa, where seed is often recycled, accumulating infections over generations. However, until 2012, except for in Uganda, little was known about the viruses affecting the crop throughout the continent. To get an understanding of the viruses circulating in sweetpotato on the continent, a project was launched to characterize all viruses infecting the crop using an agnostic approach based on small RNA sequencing and assembly (sRSA; Kreuze et al. 2009), collecting over 2000 leaf samples from 11 countries across sub-Saharan Africa in collaboration with national agricultural research authorities in each of these countries. The results were analyzed and published in a publicly accessible geo-referenced database associated with pictures of sampled leaves, plants, and fields with support from the Boyce Thomson Institute (http://bioinfo.bti.cornell.edu/virome). Although several novel viruses were identified, they could be categorized into several groups:

(i) Those occurring in only one or a few samples, probably reflecting chance infections or even failed infections, and are of low priority for further investigation.

(ii) New viruses that were found commonly but only locally, represented by a group of new ampelovirids in Angola and a new potyvirus found in Malawi, Mozambique, Zimbabwe, and Angola. The new potyvirus is closely related to known sweetpotato-infecting potyviruses and is therefore expected to have similar properties, which have been well investigated in its relatives, and should therefore be considered just as relevant. The new ampelovirus, however, is unrelated to known viruses, and its effect on sweetpotato remains unclear. Because of its frequency in Angola, it appears established in sweetpotato and therefore should be considered a priority for further study and monitoring in Angola and neighboring countries.

(iii) Known viruses occurring at a much larger frequency than previously known, exemplified by a group of begomoviruses

referred to as sweepoviruses. These were found to be the third most common viruses infecting sweetpotato after sweetpotato feathery mottle virus and sweetpotato chlorotic stunt virus, which combined cause the most devastating and common yield impacts, known as sweetpotato virus disease. Sweepoviruses have previously been reported to be largely symptomless (Cuellar et al. 2015; Ling et al. 2010, 2011; Trenado et al. 2011; Wasswa et al. 2011) but could nevertheless cause significant yield losses (Ling et al. 2010) depending on the genotype. This prompted further research into the impact these viruses might have on African sweetpotato cultivars. Subsequent experiments revealed that also in Africa, these viruses could cause a significant yield loss of up to 40% without showing obvious symptoms, and this was independent from resistance/tolerance to sweetpotato feathery mottle virus and sweetpotato chlorotic stunt virus (Wanjala et al. 2020). By applying ecological niche modeling with the data from the African virome database, areas could be predicted where this virus would likely be prevalent and for which virus resistance should be a priority breeding target. To support this, using the sequences generated in the virome study, we were able to develop and validate generic primers able to detect all variants of this highly variable group of viruses (Wanjala et al. 2021).

(iv) The two most prevalent viruses identified were novel DNA viruses that had previously been discovered by sRSA in apparently healthy plants: a badnavirus, named sweetpotato pakakuy virus (SPPV), and a mastrevirus, sweetpotato symptomless mastrevirus 1 (SPSMV-1) (Kreuze et al. 2009). These have since been detected from all continents. Particularly, SPPV was found to be nearly ubiquitous and highly variable, meriting further investigation into its interaction with other viruses, even if there was no previous evidence of observable damage. Results showed that the detection did not represent integrated sequences and occurred at extremely low concentrations in the plants, well below one copy per plant cell, but that it nevertheless could be transmitted to an indicator host at low frequency, but again only accumulating to very low concentrations and without showing discernable symptoms (Kreuze et al. 2020a). No significant interactions with other viruses could be discerned, and therefore, it is considered likely not to have any impact on sweetpotato production. Its extremely common occurrence may be due to efficient seed transmission in sweetpotato rather than vectors, which have yet to be described (Kreuze et al. 2020a). SPSMV-1 has also been reported to be seed transmitted (Qiao et al. 2020), although at a much lower rate than reported for SPPV. Several studies also confirm its symptomless nature (Fiallo-Olivé et al. 2022), although studies into interactions and possible yield effects are still lacking. Contrary to SPPV and other geminiviruses, in this virus, very little sequence variability is identified across the world (Cao et al. 2017; Fiallo-Olivé et al. 2022). Although the situation with SPSMV-1 seems analogous to that of SPPV, experiments are currently underway to determine possible yield impacts of SPSMV-1 alone and in combination with other common sweetpotato viruses.

Thus, through the sweetpotato virome analysis, we were able to identify and alert to new possible risks in particular geographies of the continent (new ampeloviruses in Angola), identify likely relevant new viruses that merit testing in healthy vegetative seed production systems (new potyvirus belonging to a well-characterized group with known relevance), and identify an unexpected high frequency of known symptomless viruses (begomoviruses), leading to follow-up research and new resistance breeding priorities.

Future research requirements include the following:

(i) Conducting biological characterization, including possible yield impacts, modes of transmission, and alternative hosts of novel viruses identified, starting with the most common (e.g., SPSMV-1 and the new ampelovirus from Angola).

(ii) Evaluating antiviral treatments to enable germplasm cleanup, particularly for SPPV and SPSMV-1, which seem to be resistant to current virus cleaning procedures. On the other hand, experiments to understand the unusual persistence of these viruses despite low concentrations are likely to reveal exciting new insights into virus−host interactions.

(iii) Developing quantitative diagnostic methods for breeders to enable high-throughput screening for virus resistance for symptomless viruses that have been shown to have a significant impact on yield (e.g., begomoviruses).

Potato Virome

Potato originates from the Andean region of South America and is currently the fourth most important staple food crop globally and the fifth most important in the low-income food-deficit countries and least developed countries of the world (FAOSTAT 2021). Like all clonally propagated crops, potato is heavily affected by viruses (Fig. 1A), the most important of which have likely spread with the crop from its center of origin. Despite this, by 2015, from the several hundred potato virus genomes deposited in the gene bank, not one was from the crops' center of origin in Peru. However, several previous studies based on classical virology suggested that many more species of viruses affected potato in Peru than in the rest of the world (Kreuze et al. 2020b). Therefore, in a similar approach as described for the sweetpotato virome above, over 1,000 samples were collected from throughout Peru and sequenced. Again, the results could be categorized into different groups, which were, however, different from those of sweetpotato in Africa.

(i) Known viruses that infect potato frequently across the globe and representing the most frequent infections (>14% of samples each), including potato viruses X, Y, V, A, and S (Fuentes et al. 2019, 2021a, b, 2022; Santillan et al. 2018). The exception in this group was potato virus B (De Souza et al. 2017), which was found to infect 20% of samples and that has not been reported from elsewhere in the world. Little is known about the biology, symptomatology, and possible yield effects of this virus; however, due to its frequency, further research on it should be a priority.

(ii) Eleven viruses occurring in 1 to 7% of samples, about half of which were previously characterized viruses (Silvestre et al. 2020) and half were new. This group included potato leaf roll virus, which is an important virus elsewhere in (sub-)tropical countries of the world, and potato mop top virus, which has become an important pathogen in cool and humid temperate regions of the world. Included in this group were also Andean potato mottle virus, potato yellowing virus, Andean potato latent virus, and Andean potato mild mottle virus. New viruses included those belonging to the genera *Nepovirus*, *Badnavirus*, *Fabavirus*, *Ophiovirus*, and *Potyvirus*. A new torradovirus, potato brown rugose stunting virus, found in this group was associated with a historic disease outbreak in Southern Peru (Alvarez-Quinto et al. 2023; Kreuze et al. 2020b), indicating that such viruses can be a source of serious disease outbreak when conditions become favorable and deserve close monitoring, particularly in the context of a changing climate.

(iii) Eleven viruses occurring in less than 1% samples, which were mostly new. These included arracacha virus B, potato virus T, and potato black ringspot virus, as well as new viruses belonging to the genera *Enamovirus*, *Betaflexivirus*, *Potexvirus*, *Carlavirus*, *Tobravirus*, *Polerovirus*, *Tepovirus*, and *Tymovirus*.

Thus, the potato virome analysis doubled the number of virus species known to infect potato in Peru. Whereas all the new viruses were relatively infrequent (infecting <6% of samples), historical data indicate that some of them have potential to cause significant disease outbreaks. Whereas molecular diagnostic assays have been rapidly developed based on sequences, biological characterization is expensive and should be prioritized based on frequency of infections and association with symptomatology or known biological properties of the virus group. It is unknown whether any of the new viruses also occur in countries neighboring Peru, such as Ecuador, Bolivia, and Chile, but considering frequent informal exchange of potatoes over the borders, it can be regarded as quite likely. International movement of potatoes over longer distances, where no direct land borders exist, will likely be more limited, and formal movement is strongly regulated and restricted to in-vitro plants but can also include botanical seed. Still, several of the newly identified viruses have been detected in intercepted potatoes transported by private travelers in Europe and the United States (Alvarez-Quinto et al. 2023), highlighting the risk that inadvertent introductions can happen and will increase as the volume of travel from the Andes to other parts of the world increases. Until studies have been performed to identify exact yield impacts, host ranges, and mode of spread of the new viruses, it is difficult to estimate the degree of risk they pose to the rest of the world and particularly food-insecure low- and middle-income countries. The ability to rapidly develop nucleic acid amplification-based detection methods based on the identified sequences should at least enable detection during formal international transfer and in healthy seed systems.

Future research priorities include the following:

(i) Developing and validating diagnostic assays for each of the new viruses to enable detection and control.

(ii) Biological characterization, including identification of yield impacts, modes of transmission, and alternative hosts of the newly identified viruses, starting with the most frequent ones.

(iii) Determining the extent of occurrence of these viruses in neighboring countries in South America.

Conclusions

The presented virus disease cases illustrate a range of successful partnerships that have resulted in the control or prevention of outbreaks or generated new knowledge and better preparedness to address existing or emerging threats that had not previously been noticed. Importantly, most of these efforts were mobilized through international collaborations and funding by international donors, highlighting the importance of partnerships and international assistance in understanding plant virus disease threats to secure plant health and ensure sustainable food production in low- and middle-income countries of the world. Further coordination and harmonization of efforts, approaches, and strategies to confront current and emerging viral threats are needed to improve both proactive and reactive responses. In that respect, the recent effort to harmonize the CGIAR research strategy across centers through a dedicated Plant Health Initiative (PHI) should play an enabling role in fostering regional and global strategies and collaborations. The magnitude of plant health challenges in the food-insecure regions of the world are too enormous for any single initiative to tackle. Most international consortia, such as the PHI and others, have prioritized limited resources to contain transboundary spread of viruses and for managing emerging plant viral threats in targeted geographies based on the risk and damage. Additional investments, especially from the country governments, are necessary to generate complementary actions to increase the impact of individual efforts. Encouraging and promoting the creation of regional and global surveillance and diagnostic networks, employing harmonized or compatible protocols, sharing services and expertise, and enabling learnings from successful models implemented in different continents is a major goal of the PHI. In this respect, among the specific examples described in this perspective, some obvious areas for improved efficiencies can be identified: Different organizations and projects have developed and used different tools for similar purposes (e.g., image recognition of diseases), whereas different protocols and database structures are used to collect and analyze data, even for similar diseases and crops. At the same time, plant health information is dispersed over the internet and not always easy to find unless users know exactly what they are looking for. Although not everything can be completely standardized and needs to be adjusted to specific contexts and needs, at least, information should follow the FAIR principles (Findable, Accessible, Interoperable, and Reusable).

On the other hand, results of applying high-throughput sequencing tools should also raise awareness of the needed research investment in confirming the yield impact of novel viruses, evaluating the effectiveness of costly cleaning protocols, and updating regional quarantine lists, all of which will ultimately favor the movement and utility of germplasm collections in breeding programs and large-scale healthy seed multiplication to control the impact of pests and diseases. Thus, the PHI has the opportunity, in coordination with other CGIAR initiatives, such as the Accelerated Breeding Initiative and Seed Equal, to develop into a platform where global plant health research involving viruses can be coordinated as a one-stop shop with inventory of plant health research for food-insecure regions of the world, where an increasing number of local plant health officers can easily find information and each other for collaboration and learning.

The COVID-19 pandemic helped many countries strengthen diagnostics and surveillance capacity, including establishing systems that integrated information and communication technologies with diagnostics for testing and traceability, such as using high-throughput sequencing-based methods. It was a successful case of a threat catalyzing an opportunity to improve capacity, thanks to decent funding support and government interest in uplifting capacity to counter the pandemic of the century. However, a similar level of change has not taken place in the case of plant virus disease outbreaks, pandemics, and major epidemics due to limited funding and not giving due importance to plant health protection, despite the severe impact on food and income security. Investments are necessary in low- and middle-income countries to enhance not only the understanding of virus epidemic drivers and the effectiveness of control measures but also the capacity for early detection and rapid response to avoid the recurrence of devastating virus disease outbreaks. The examples cited in this article showcase the width and flexibility of modern technologies for tailoring and adoption to fit the local scenarios. It is high time for country governments to invest in strengthening plant health capacity to tackle virus diseases.

Acknowledgments

The example cases presented in this perspective were supported by the following funders: Australian Centre for International Agricultural Research, Banco Interamerican de Desarollo, Bill and Melinda Gates Foundation, National Science Foundation of the U.S.A., USAID, U.K. Department for International Development, Alliance for Green Revolution in Africa, African Agricultural Technology Foundation, and the CGIAR Research Programs on Roots, Tubers and Bananas and MAIZE, as well as, since 2022, through One CGIAR initiatives on Plant Health, Genebanks, and Accelerated Breeding supported by the donors of the CGIAR Trust Fund (http://www.cgiar.org/about-us/our-funders/).

Literature Cited

Abiola, A., Zandjanakou-Tachin, M., Aoudji, K. N. A., Avocevou-Ayisso, C., and Kumar, P. L. 2020. Adoption of roguing to contain banana bunchy top disease in south-east Bénin: Role of farmers' knowledge and perception. Int. J. Fruit Sci. 20:720-736.

Adams, I. P., Miano, D. W., Kinyua, Z. M., Wangai, A., Kimani, E., Phiri, N., Reeder, R., Harju, V., Glover, R., Hany, U., Souza-Richards, R., Nath,

P. D., Nixon, T., Fox, A., Barnes, A., Smith, J., Skelton, A., Thwaites, R., Mumford, R., and Boonham, N. 2013. Use of next-generation sequencing for the identification and characterization of Maize chlorotic mottle virus and Sugarcane mosaic virus causing maize lethal necrosis in Kenya. Plant Pathol. 62:741-749.

Adegbola, R. O., Ayodeji, O., Awosusi, O. O., Atiri, G. I., and Kumar, P. L. 2013. First report of banana bunchy top virus in banana and plantain (*Musa* spp.) in Nigeria. Plant Dis. 97:290-290.

Alabi, T. R., Adewopo, J., Duke, O. P., and Kumar, P. L. 2022. Banana mapping in heterogenous smallholder farming systems using high-resolution remote sensing imagery and machine learning models with implications for banana bunchy top disease surveillance. Remote Sens. 14:5206.

Allen, R. N. 1987. Further studies on epidemiological factors influencing control of banana bunchy top disease and evaluation of control measures by computer simulation. Aust. J. Agric. Res. 38:373-382.

Alvarez-Quinto, R., Amao, M., Muller, G., Fuentes, S., Grinstead, S., Fuentes-Bueno, I., Roenhorst, A., Westenberg, M., Botermans, M., Kreuze, J., and Molov, D. 2023. Evidence that an unnamed isometric virus associated with potato rugose disease in Peru is a new species of genus *Torradovirus*. Phytopathology 113:1716-1728.

Bachwenkizi, H. S., Temu, G. E., Mbanzibwa, D. R., Lupembe, M. D., Ngailo, S., Tairo, F. D., and Massawe, D. P. 2022. Recombination and Darwinian selection as drivers of genetic diversity and evolution of sweet potato leaf curl viruses in Tanzania. Physiol. Mol. Plant Pathol. 120:101853.

Bernardo, P., Frey, T. S., Barriball, K., Paul, P. A., Willie, K., Mezzalama, M., Kimani, E., Mugambi, C., Wangai, A., and Prasanna, B. M. 2021. Detection of diverse maize chlorotic mottle virus isolates in maize seed. Plant Dis. 105:1596-1601.

Bhat, A. I., Aman, R., and Mahfouz, M. 2022. Onsite detection of plant viruses using isothermal amplification assays. Plant Biotechnol. J. 20: 1859-1873.

Biswal, A. K., Alakonya, A. E., Mottaleb, K. A., Hearne, S. J., Sonder, K., Molnar, T. L., Jones, A. M., Pixley, K. V., and Prasanna, B. M. 2022. Maize Lethal Necrosis disease: Review of molecular and genetic resistance mechanisms, socio-economic impacts, and mitigation strategies in sub-Saharan Africa. BMC Plant Biol. 22:1-21.

Boddupalli, P. 2021. Maize Lethal Necrosis (MLN): A Technical Manual for Disease Management. CIMMYT, CDMX.

Boddupalli, P., Suresh, L. M., Mwatuni, F., Beyene, Y., Makumbi, D., Gowda, M., Olsen, M., Hodson, D., Worku, M., Mezzalama, M., Molnar, T., Dhugga, K. S., Wangai, W., Gichuru, L., Angwenyi, S., Alemayehu, Y., Hansen, J. G., and Lassen, P. 2020. Maize lethal necrosis (MLN): Efforts toward containing the spread and impact of a devastating transboundary disease in sub-Saharan Africa. Virus Res. 282:197943.

Braidwood, L., Quito-Avila, D. F., Cabanas, D., Bressan, A., Wangai, A., and Baulcombe, D. C. 2018. Maize chlorotic mottle virus exhibits low divergence between differentiated regional sub-populations. Sci. Rep. 8:1-9.

Cao, M., Lan, P., Li, F., Abad, J., Zhou, C., and Li, R. 2017. Genome characterization of sweet potato symptomless virus 1: A mastrevirus with an unusual nonanucleotide sequence. Arch. Virol. 162:2881-2884.

Chi, Y., Pan, L.-L., Bouvaine, S., Fan, Y.-Y., Liu, Y.-Q., Liu, S.-S., Seal, S., and Wang, X.-W. 2020. Differential transmission of Sri Lankan cassava mosaic virus by three cryptic species of the whitefly *Bemisia tabaci* complex. Virology 540:141-149.

Chittarath, K., Jimenez Polo, J., Vongphachanh, P., Leiva, A. M., Sengsay, S., Lopez-Alvarez, D., Bounvilayvong, T., Lourido, D., Vorlachith, V., and Cuellar, W. J. 2021. First report of Sri Lankan cassava mosaic virus and cassava mosaic disease in Laos. Plant Dis. 105:1861.

Cuellar, W., Mwanzia, L., Lourido, D., Martinez, A. F., Rodriguez, R., and Garcia, C. 2022. PestDisPlace: Monitoring the distribution of pests and diseases. Version 3.0 in: International Center for Tropical Agriculture (CIAT).

Cuellar, W. J., Galvez, M., Fuentes, S., Tugume, J., and Kreuze, J. F. 2015. Synergistic interactions of begomoviruses with Sweet potato chlorotic stunt virus (genus *Crinivirus*) in sweet potato (*Ipomoea batatas* L.). Mol. Plant Pathol. 16:459-471.

Dato, K. M. G., Dégbègni, M. R., Atchadé, M. N., Zandjanakou Tachin, M., Hounkonnou, M. N., and Aman Omondi, B. 2021. Spatial parameters associated with the risk of banana bunchy top disease in smallholder systems. PLoS One 16:e0260976.

Delaquis, E., Andersen, K. F., Minato, N., Cu, T. T. L., Karssenberg, M. E., Sok, S., Wyckhuys, K. A., Newby, J. C., Burra, D. D., and Srean, P. 2018. Raising the stakes: Cassava seed networks at multiple scales in Cambodia and Vietnam. Front. Sustain. Food Sys. 2:73.

De Souza, J., Müller, G., Perez, W., Cuellar, W., and Kreuze, J. 2017. Complete sequence and variability of a new subgroup B nepovirus infecting potato in central Peru. Arch. Virol. 162:885-889.

FAOSTAT. 2021. Statistical Database. Food and Agriculture Organization of the United Nations (FAO), Rome.

Fiallo-Olivé, E., García-Merenciano, A. C., and Navas-Castillo, J. 2022. Sweet potato symptomless virus 1: First detection in Europe and generation of an infectious clone. Microorganisms 10:1736.

Fuentes, S., Gibbs, A. J., Adams, I. P., Hajizadeh, M., Kreuze, J., Fox, A., Blouin, A. G., and Jones, R. A. C. 2022. Phylogenetics and evolution of potato virus V: Another potyvirus that originated in the Andes. Plant Dis. 106: 691-700.

Fuentes, S., Gibbs, A. J., Adams, I. P., Wilson, C., Botermans, M., Fox, A., Kreuze, J., Boonham, N., Kehoe, M. A., and Jones, R. A. C. 2021a. Potato virus A isolates from three continents: Their biological properties, phylogenetics, and prehistory. Phytopathology 111:217-226.

Fuentes, S., Gibbs, A. J., Hajizadeh, M., Perez, A., Adams, I. P., Fribourg, C. E., Kreuze, J., Fox, A., Boonham, N., and Jones, R. A. C. 2021b. The phylogeography of potato virus X shows the fingerprints of its human vector. Viruses 13:644.

Fuentes, S., Jones, R. A. C., Matsuoka, H., Ohshima, K., Kreuze, J., and Gibbs, A. J. 2019. Potato virus Y; the Andean connection. Virus Evol. 5:vez037.

Graziosi, I., Minato, N., Alvarez, E., Ngo, D. T., Hoat, T. X., Aye, T. M., Pardo, J. M., Wongtiem, P., and Wyckhuys, K. A. 2016. Emerging pests and diseases of South-east Asian cassava: A comprehensive evaluation of geographic priorities, management options and research needs. Pest Manage. Sci. 72:1071-1089.

Hadfield, J., Megill, C., Bell, S. M., Huddleston, J., Potter, B., Callender, C., Sagulenko, P., Bedford, T., and Neher, R. A. 2018. Nextstrain: Real-time tracking of pathogen evolution. Bioinformatics 34:4121-4123.

Hemniam, N., Roekwan, S., Vannatim, N., Malichan, S., Saokham, K., Chaowongdee, S., and Siriwan, W. 2022. Natural infection of Cnidoscolus and Jatropha by Sri Lankan cassava mosaic virus in Thailand. J. Gen. Plant Pathol. 88:386-391.

Jimenez, J., Leiva, A. M., Olaya, C., Acosta-Trujillo, D., and Cuellar, W. J. 2021. An optimized nucleic acid isolation protocol for virus diagnostics in cassava (*Manihot esculenta* Crantz.). MethodsX 8:101496.

Jones, R. A. C. 2020. Disease pandemics and major epidemics arising from new encounters between indigenous viruses and introduced crops. Viruses 12:1388.

Jones, R. A. C. 2021. Global plant virus disease pandemics and epidemics. Plants 10:233.

Kolombia, Y. A., Oviasuyi, T., Dzola, A. K., Ale Gonh-Goh, A., Atsu, T., Oresanya, A., Ogunsanya, P., Alabi, T., and Kumar, P. L. 2021. First report of banana bunchy top virus in banana (*Musa* spp.) and its eradication in Togo. Plant Dis. 105:3312.

Kreuze, J. F., Perez, A., Gargurevich, M. G., and Cuellar, W. J. 2020a. Badnaviruses of sweet potato: Symptomless coinhabitants on a global scale. Front. Plant Sci. 11:313.

Kreuze, J. F., Pérez, A., Untiveros, M., Quispe, D., Fuentes, S., Barker, I., and Simon, R. 2009. Complete viral genome sequence and discovery of novel viruses by deep sequencing of small RNAs: A generic method for diagnosis, discovery and sequencing of viruses. Virology 388:1-7.

Kreuze, J. F., Souza-Dias, J., Jeevalatha, A., Figueira, A., Valkonen, J. P. T., and Jones, R. A. C. 2020b. Viral diseases in potato. Pages 389-430 in: The Potato Crop. H. Campos and O. Ortiz, eds. Springer, Cham, Switzerland.

Kumar, P. L., Hanna, R., Alabi, O., Soko, M., Oben, T., Vangu, G., and Naidu, R. 2011. Banana bunchy top virus in sub-Saharan Africa: Investigations on virus distribution and diversity. Virus Res. 159:171-182.

Kumar, P. L., Legg, J. P., Ayodele, M., Mahuku, G., Ortega-Beltran, A., and Bandyopadhyay, R. 2019. Disease surveillance, diagnostics and germplasm health in crop protection. Pages 41-74 in: Critical Issues in Plant Health: 50 Years of Research in African Agriculture. P. Neuenschwander and M. Tamo, eds. Burleigh Dodds Science Publishing, Philadelphia.

Lappe, R. R., Elmore, M. G., Lozier, Z. R., Jander, G., Miller, W. A., and Whitham, S. A. 2022. Metagenomic identification of novel viruses of maize and teosinte in North America. BMC Genomics 23:767.

Legg, J., Somado, E. A., Barker, I., Beach, L., Ceballos, H., Cuellar, W., Elkhoury, W., Gerling, D., Helsen, J., Hershey, C., Jarvis, A., Kulakow, P., Kumar, L., Lorenzen, J., Lynam, J., McMahon, M., Maruthi, G., Miano, D., Mtunda, K., Natwuruhunga, P., Okogbenin, E., Pezo, P., Terry, E., Thiele, G., Mike, T., Wadsworth, J., Walsh, S., Winter, S., Tohme, J., and Fauquet, C. 2014. A global alliance declaring war on cassava viruses in Africa. Food Security 6:231-248.

Leiva, A. M., Chittarath, K., Lopez-Alvarez, D., Vongphachanh, P., Gomez, M. I., Sengsay, S., Wang, X.-W., Rodriguez, R., Newby, J., and Cuellar, W. J. 2022. Mitochondrial genetic diversity of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) associated with cassava in Lao PDR. Insects 13:861.

Leiva, A. M., Siriwan, W., Lopez-Alvarez, D., Barrantes, I., Hemniam, N., Saokham, K., and Cuellar, W. J. 2020. Nanopore-based complete genome sequence of a Sri Lankan cassava mosaic virus (Geminivirus) strain from Thailand. Microbiol. Resour. Announc. 9.

Ling, K. S., Harrison, H. F., Simmons, A. M., Zhang, S. C., and Jackson, D. M. 2011. Experimental host range and natural reservoir of sweet potato leaf curl virus in the United States. Crop Prot. 30:1055-1062.

Ling, K.-S., Jackson, D. M., Harrison, H., Simmons, A. M., and Pesic-VanEsbroeck, Z. 2010. Field evaluation of yield effects on the U.S.A. heirloom sweetpotato cultivars infected by Sweet potato leaf curl virus. Crop Prot. 29:757-765.

Liu, X., Liu, S., Chen, X., Prasanna, B. M., Ni, Z., Li, X., He, Y., Fan, Z., and Zhou, T. 2022. Maize miR167-ARF3/30-polyamine oxidase 1 module-regulated H2O2 production confers resistance to maize chlorotic mottle virus. Plant Physiol. 189:1065-1082.

Lokossou, B., Gnanvossou, D., Ayodeji, O., Akplogan, F., Safiore, A., Migan, D., Pefoura, A., Hanna, R., and Kumar, P. L. 2012. Occurrence of Banana bunchy top virus in banana and plantain (*Musa* sp.) in Benin. New Dis. Rep. 25:13.

Maclot, F., Candresse, T., Filloux, D., Malmstrom, C. M., Roumagnac, P., Van der Vlugt, R., and Massart, S. 2020. Illuminating an ecological blackbox: Using high throughput sequencing to characterize the plant virome across scales. Front. Microbiol. 11:578064.

Mahuku, G., Lockhart, B. E., Wanjala, B., Jones, M. W., Kimunye, J. N., Stewart, L. R., Cassone, B. J., Sevgan, S., Nyasani, J. O., and Kusia, E. 2015. Maize lethal necrosis (MLN), an emerging threat to maize-based food security in sub-Saharan Africa. Phytopathology 105:956-965.

Malik, A. I., Kongsil, P., Nguyễn, V. A., Ou, W., Srean, P., López-Lavalle, L. A. B., Utsumi, Y., Lu, C., Kittipadakul, P., and Nguyễn, H. H. 2020. Cassava breeding and agronomy in Asia: 50 years of history and future directions. Breeding Sci. 70:145-166.

Malik, A. I., Sophearith, S., Delaquis, E., Cuellar, W. J., Jimenez, J., and Newby, J. C. 2022. Susceptibility of cassava varieties to disease caused by Sri Lankan cassava mosaic virus and impacts on yield by use of asymptomatic and virus-free planting material. Agronomy 12:1658.

Mrisho, L. M., Mbilinyi, N. A., Ndalahwa, M., Ramcharan, A. M., Kehs, A. K., McCloskey, P. C., Murithi, H., Hughes, D. P., and Legg, J. P. 2020. Accuracy of a smartphone-based object detection model, PlantVillage Nuru, in identifying the foliar symptoms of the viral diseases of cassava–CMD and CBSD. Front. Plant Sci. 11:1964.

Nakasu, E. Y., Silva, G., Montes, S. M., and Mello, A. F. 2022. Virome analysis of sweetpotato in three Brazilian regions using high-throughput sequencing. Trop. Plant Pathol. 47:800-806.

Ngatat, S., Hanna, R., Lienou, J., Ghogomu, R. T., Nguidang, S. P. K., Enoh, A. C., Ndemba, B., Korie, S., Fotso Kuate, A., and Nanga Nanga, S. 2022. Musa germplasm A and B genomic composition differentially affects their susceptibility to banana bunchy top virus and its aphid vector, *Pentalonia nigronervosa*. Plants 11:1206.

Nkengla-Asi, L., Eforuoku, F., Olaosebikan, O., Adejoju Ladigbolu, T., Amah, D., Hanna, R., and Kumar, P. L. 2021. Gender roles in sourcing and sharing of banana planting material in communities with and without banana bunchy top disease in Nigeria. Sustainability 13:3310.

Ocimati, W., Tazuba, A. F., Tushemereirwe, W. K., Tugume, J., Omondi, B. A., Acema, D., Were, E., Onyilo, F., Ssekamate, A., and Namanya, P. 2021. First report of banana bunchy top disease caused by banana bunchy top virus in Uganda. New Dis. Rep. 44:e12052.

Okonya, J. S., Gamarra, H., Nduwayezu, A., Bararyenya, A., Kroschel, J., and Kreuze, J. 2021. Serological survey and metagenomic discovery of potato viruses in Rwanda and Burundi reveals absence of PVY in Burundi and first report of TRV in potatoes in sub-Saharan Africa. Virus Res. 302:198487.

Omondi, B. A., Soko, M. M., Nduwimana, I., Delano, R. T., Niyongere, C., Simbare, A., Kachigamba, D., and Staver, C. 2020. The effectiveness of consistent roguing in managing banana bunchy top disease in smallholder production in Africa. Plant Pathol. 69:1754-1766.

Qiao, Q., Zhang, Z.-C., Zhao, X.-L., Wang, Y.-J., Wang, S., Qin, Y.-H., Zhang, D.-S., Tian, Y.-T., and Zhao, F. 2020. Evidence for seed transmission of sweet potato symptomless virus 1 in sweet potato (*Ipomoea batatas*). J. Plant Pathol. 102:299-303.

Ramcharan, A., Baranowski, K., McCloskey, P., Ahmed, B., Legg, J., and Hughes, D. P. 2017. Deep learning for image-based cassava disease detection. Front. Plant Sci. 8:1852.

Ramcharan, A., McCloskey, P., Baranowski, K., Mbilinyi, N., Mrisho, L., Ndalahwa, M., Legg, J., and Hughes, D. P. 2019. A mobile-based deep learning model for cassava disease diagnosis. Front. Plant Sci. 10:272.

Redila, C., Prakash, V., and Shahideh, N. 2021. Metagenomics analysis of the wheat virome identifies novel plant and fungal-associated viral sequences. Viruses 13:10.3390/v13122457.

Redinbaugh, M. G., and Stewart, L. R. 2018. Maize lethal necrosis: An emerging, synergistic viral disease. Annu. Rev. Virol. 5:301-322.

Santillan, F. W., Fribourg, C. E., Adams, I. P., Gibbs, A. J., Boonham, N., Kehoe, M. A., Maina, S., and Jones, R. A. 2018. The biology and phylogenetics of Potato virus S isolates from the Andean region of South America. Plant Dis. 102:869-885.

Saunders, K., Salim, N., Mali, V. R., Malathi, V. G., Briddon, R., Markham, P. G., and Stanley, J. 2002. Characterisation of Sri Lankan cassava mosaic virus and Indian cassava mosaic virus: Evidence for acquisition of a DNA B component by a monopartite begomovirus. Virology 293: 63-74.

Scussel, S., Candresse, T., Marais, A., Claverie, S., Hoareau, M., Azali, H. A., Verdin, E., Tepfer, M., Filloux, D., Fernandez, E., and Roumagnac, P. 2019. High-throughput sequencing of complete genomes of ipomoviruses associated with an epidemic of cassava brown streak disease in the Comoros Archipelago. Arch. Virol. 164:2193-2196.

Selvaraj, M. G., Vergara, A., Montenegro, F., Alonso Ruiz, H., Safari, N., Raymaekers, D., Ocimati, W., Ntamwira, J., Tits, L., Omondi, A. B., and Blomme, G. 2020. Detection of banana plants and their major diseases through aerial images and machine learning methods: A case study in DR Congo and Republic of Benin. ISPRS J. Photogramm. Remote Sens. 169: 110-124.

Selvaraj, M. G., Vergara, A., Ruiz, H., Safari, N., Elayabalan, S., Ocimati, W., and Blomme, G. 2019. AI-powered banana diseases and pest detection. Plant Methods 15:92.

Shimwela, M. M., Mahuku, G., Mbanzibwa, D., Mkamilo, G., Mark, D., Mosha, H. I., Pallangyyo, B., Fihavango, M., Oresanya, A., and Ogunsanya, P. 2022. First report of banana bunchy top virus in banana and plantain (*Musa* spp.) in Tanzania. Plant Dis. 106:1312.

Silvestre, R., Fuentes, S., Risco, R., Berrocal, A., Adams, I., Fox, A., Cuellar, W. J., and Kreuze, J. 2020. Characterization of distinct strains of an aphid-transmitted ilarvirus (fam. *Bromoviridae*) infecting different hosts from South America. Virus Res. 282:197944.

Singh, K., Jarošová, J., Fousek, J., Huan, C. H. E. N., and Kundu, J. K. 2020. Virome identification in wheat in the Czech Republic using small RNA deep sequencing. J. Integr. Agric. 19:1825-1833.

Siriwan, W., Jimenez, J., Hemniam, N., Saokham, K., Lopez-Alvarez, D., Leiva, A. M., Martinez, A., Mwanzia, L., Becerra, L. A., and Cuellar, W. J. 2020. Surveillance and diagnostics of the emergent Sri Lankan cassava mosaic virus (fam. *Geminiviridae*) in Southeast Asia. Virus Res. 285:197959.

Stainton, D., Martin, D. P., Muhire, B. M., Lolohea, S., Halafihi, M. I., Lepoint, P., Blomme, G., Crew, K. S., Sharman, M., and Kraberger, S. 2015. The global distribution of Banana bunchy top virus reveals little evidence for frequent recent, human-mediated long distance dispersal events. Virus Evol. 1:vev009.

Stewart, L. R., Willie, K., Wijeratne, S., Redinbaugh, M. G., Massawe, D., Niblett, C. L., Kiggundu, A., and Asiimwe, T. 2017. Johnsongrass mosaic virus contributes to maize lethal necrosis in East Africa. Plant Dis. 101: 1455-1462.

Trenado, H. P., Orílio, A. F., Márquez-Martín, B., Moriones, E., and Navas-Castillo, J. 2011. Sweepoviruses cause disease in sweet potato and related *Ipomoea* spp.: Fulfilling Koch's postulates for a divergent group in the genus *Begomovirus*. PLoS One 6:e27329.

Villamor, D. E. V., Ho, T., Al Rwahnih, M., Martin, R. R., and Tzanetakis, I. E. 2019. High throughput sequencing for plant virus detection and discovery. Phytopathology 109:716-725.

Wang, H. L., Cui, X. Y., Wang, X. W., Liu, S. S., Zhang, Z. H., and Zhou, X. P. 2016. First report of Sri Lankan cassava mosaic virus infecting cassava in Cambodia. Plant Dis. 100:1029.

Wang, D., Yao, X. M., Huang, G. X., Shi, T., Wang, G. F., and Ye, J. 2019. First report of Sri Lankan cassava mosaic virus infected cassava in China. Plant Dis. 103:10.1094.

Wang, Y. M., Ostendorf, B., Gautam, D., Habili, N., and Pagay, V. 2022. Plant viral disease detection: From molecular diagnosis to optical sensing technology—A multidisciplinary review. Remote Sens. 14:1542.

Wangai, A. W., Redinbaugh, M. G., Kinyua, Z. M., Miano, D. W., Leley, P. K., Kasina, M., Mahuku, G., Scheets, K., and Jeffers, D. 2012. First report of maize chlorotic mottle virus and maize lethal necrosis in Kenya. Plant Dis. 96:1582-1582.

Wanjala, B. W., Ateka, E. M., Miano, D. W., Fuentes, S., Perez, A., Low, J. W., and Kreuze, J. F. 2021. Loop-mediated isothermal amplification assays for on-site detection of the main sweetpotato infecting viruses. J. Virol. Methods 298:114301.

Wanjala, B. W., Ateka, E. M., Miano, D. W., Low, J. W., and Kreuze, J. F. 2020. Storage root shield of sweetpotato as influenced by sweetpotato leaf curl virus and its interaction with sweetpotato feathery mottle virus and sweetpotato chlorotic stunt virus in Kenya. Plant Dis. 104:1477-1486.

Wasswa, P., Otto, B., Maruthi, M. N., Mukasa, S. B., Monger, W., and Gibson, R. W. 2011. First identification of a sweet potato begomovirus (sweepovirus) in Uganda: Characterization, detection and distribution. Plant Pathol. 60:1030-1039.