Chapter 1
Genomic Designing for Biotic Stress Resistant Cassava

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Abstract Cassava is essential food security, mostly in Africa, South America, and other major regions of the world where cassava is cultivated. It is very high in caloric value and resilient to climate change, drought, and low fertility. Biotic stress limits cassava cultivation and utilization with an impact that could range from 20 to 90% loss in yield and food quality. Diseases including viral, fungal, bacterial, and nematodes as well as diverse kinds of pests such as cassava whitefly and cassava green mites (CGM) are considered important biotic factors that impact cassava production. Diverse measures and techniques have been implored in cassava towards genomic designing for biotic stress resistance. These techniques range from traditional breeding to genomic selections and other new breeding technologies such as genetic engineering and genome editing. This chapter outlines the most significant biotic stresses in cassava, their prevalence, and impact on yield as well as different technologies being utilized towards the development of biotic stress-resistant cassava.

Keywords Cassava · Biotic stresses · Genomic selection · Genetic engineering · Genome editing

1.1 Biotic Stress in Cassava

Cassava, *Manihot esculenta* Crantz, (Family Euphorbiaceae) is an essential staple crop cultivated across the tropics and subtropics primarily for its starchy roots, which for over a billion serves as a source of calories and for industrial purposes (Lyons et al.

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2021; Rabbi et al. 2014a). Cassava leaves also have considerable nutritional qualities and serve as food for humans and animals alike (El-Sharkawy 2004; Wasonga et al. 2020). Cassava is an ideal food security crop with the ability to produce optimal yields and can be stored in the ground for long periods allowing harvest flexibility while adapting to the effects of drought and marginal soils (Ceballos et al. 2020). Despite its many strengths, cassava production is hindered by a myriad of abiotic and biotic stresses. Across cassava growing regions, diverse pathogens (including viruses, phytoplasma, bacteria, or fungi) have been implicated in several cassava diseases, and approximately 200 pests (insects and mites) are known to feed off the crop inadvertently causing severe damages and enabling the spread of diseases (Herren and Neuenschwander 1991; Lozano and Booth 1974). Over the years, pests and disease management strategies have seen some successes in mitigating the spread of cassava pests in regions where they are alien, however, mitigation or elimination efforts for diseases caused by viruses or pests native to a region had been challenging (Herren and Neuenschwander 1991; Legg et al. 2015). Current efforts to combat cassava diseases include the development of early phenotyping and detection tools (Okereke et al. 2017; Ramcharan et al. 2017; Sambasivam and Opiyo 2021), cleaning infected planting materials (Maruthi et al. 2019), and genetic improvement for disease resistance through conventional and molecular breeding techniques (Ezenwaka et al. 2018; Rabbi et al. 2014b; Tembo et al. 2017; Wolfe et al. 2015), genetic engineering (Vanderschuren et al. 2012), and genome editing (Gomez et al. 2019; Mehta et al. 2019). This book chapter will focus on the most economically important biotic factors that impede cassava production and we will be reviewing the current biotechnological strategies to develop disease-resistant cassava varieties. In so doing, we identify challenges from these approaches, highlight avenues for further research and conclude with an outlook for pest and disease management in cassava.

1.1.1 Prevalent Cassava Biotic Factors

1.1.1.1 Cassava Diseases

Like most root and tuber crops, cassava is propagated vegetatively to ensure crop uniformity from one planting season to the next. This, unfortunately, contributes to the proliferation and spread of diseases throughout cassava-producing regions. With increasing globalization and urbanization in cassava growing regions, as well as the variability and pervasiveness of climate change, native and emerging cassava disease outbreaks are on the rise in Africa, the Asia–Pacific, and Latin America. Both foreign or alien and native pests and disease pathogens that negatively impact cassava production are not so easy to mitigate (Legg et al. 2015). In sub-Saharan Africa (SSA), viral diseases including cassava mosaic disease (CMD) and cassava brown streak diseases (CBSD) cause devastating losses, affecting the food and income of, especially limited-resource farmers. Many economically important diseases significantly

contribute to yield losses of the host crop, attacking the roots, stems, or leaves. The pathogen, *Xanthomonas axonopodis* pv. *manihotis* which causes cassava bacterial blight (CBB) disease ranks as the 6th most relevant bacterial pathogen in the world (Mansfield et al. 2012). For some of these diseases, their transmission to a cassava host plant is carried out by destructive pests, which feed off the crop, including its succulent green leaves and stems.

1.1.1.2 Cassava Pests

By damaging the leaves, cassava pests affect the photosynthetic capacity of the crop. Several pests damage cassava while feeding, but only a few are considered to be economically important (Table 1.1). There is a significant variation among pests that attack cassava by continent, and foreign pests that are inadvertently introduced in a region where they are not common, cause devastating losses. For example, arthropods such as the cassava mealybug (*Phenacoccusmanihoti* Mat.-Ferr.) and CGM (*Mononychellus tanajoa* Bondar), introduced into Africa and South-East Asia in the 1970s and early 2000s, respectively, potentially cause up to 50% yield losses in local cassava crops (Graziosi et al. 2016). Also, prevailing seasons impact the activities of pests. Arthropod pest complexes for instance, mostly occur in the dry season and not so much in humid regions of heavier rains (Lebot 2008).

Table 1.1 Some economically important biotic stresses across cassava growing regions

Type of pathogen	Disease	Regions		
		Africa	Asia–Pacific	Latin-America
Virus	Cassava mosaic disease	x	x	
	Cassava brown streak disease	x		
	Cassava frogskin disease		x	x
Bacteria	Cassava bacterial blight	x	x	x
Fungi	Cassava brown leaf spot	x	x	x
	Cassava white leaf spot	x	x	x
	Cassava root rot disease	x	x	x
	Cassava anthracnose disease	x	x	x
Pests	Cassava mealybug disease	x	x	x
	Cassava green mite disease	x	x	x

Source Lebot (2008)

1.1.2 Regional Incidence of Cassava Pests and Diseases

There are molecular and archaeological pieces of evidence that support the origin and domestication of cassava from Latin America (Ceballos et al. 2012). In the sixteenth century, cassava was introduced to the Gulf of Guinea by Portuguese slave traders and adopted as a staple in several African countries. Similarly, it is believed that cassava was introduced in southern Asia within the late eighteenth and early nineteenth centuries from Mexico (Liu et al. 2011). Compared to Latin America, Asia and Africa have relatively lower incidences of cassava pests and diseases with studies attributing these low incidences to cassava being an exotic plant in these regions and the presence of cyanogenic glucosides as a deterrent to native pests or disease pathogens (Herren and Neuenschwander 1991). In SSA, the viral diseases, CMD and CBSD are the most economically important, hindering cassava production. Cassava mosaic disease was initially detected in 1894 in Tanzania and has currently become prevalent across multiple cassava-growing regions in Africa. The disease is also a major limiting biotic factor of cassava production in south Asia. Cassava brown streak disease, on the other hand, is most prevalent in East Africa and the Great Lakes region while the bacterial pathogen that causes CBB occurs in all cassava growing regions across the globe. Cassava bacterial blight was previously reported in Brazil in 1920 and has been implicated, in over 40 countries, for devastating losses with a significant economic impact on production and utilization. Apart from the wider continental disparity in incidence, within a country and local agroecological variations in cassava biotic stress prevalence exist (Chikoti et al. 2019; Eni et al. 2021).

1.1.3 Economic Impact of Biotic Stress on Cassava Production and Utilization

Unlike in SSA, where cassava is still primarily a food security crop, the use of Asian grown cassava is incredibly diverse, providing raw materials for biofuels, industrial starch, animal feed, and other cassava-derived products. Over the years CBB has been implicated in several severe epidemics across Africa and south-east Asia (Graziosi et al. 2016). Usually exacerbated by environmental conditions, CBB may cause up to 100% loss of yield or planting materials in regions with very low cassava diversity. Similarly, CBSD and the fungal cassava root rot disease are the major cause of post-harvest losses, rendering cassava roots unusable (Kawuki et al. 2016; Kayondo et al. 2018). This has had huge implications for regions, especially, smallholder farmers that rely strongly on cassava roots for food, income, and industrial raw material. Diseases including brown leaf spot (BLS) and white leaf spot (WLS), as well as pests, have deleterious effects on the quality of cassava leaves which is the most nutritional component of the crop (Wasonga et al. 2020). Broadly, cassava diseases potentially threaten these affordable healthy alternatives, especially in small rural

communities where access to healthcare facilities is limited. Therefore, diseases and pests pose significant threats to the agricultural food sectors of several economies, and embracing control measures, including the development and adoption of cassava varieties resistant to these biotic stresses is imperative to save the livelihood of over 800 million people around the world.

1.2 Biotic Factors Affecting Cassava Production

1.2.1 Diseases

1.2.1.1 Viral Diseases

Cassava Mosaic Disease

Prevalence and Distribution of Cassava Mosaic Disease

The mosaic disease in cassava was first observed more than a century ago in Tanzania and was later in other SSA countries in the twentieth century (Fargette et al. 1990; Fauquet 1990; Thresh and Cooter 2005). The disease is common in all the cassava-growing regions across Africa but has not been verified in Asia, or America (Thresh et al. 1994). It is the most fully documented disease of cassava in Africa in the twentieth century and has been given more attention than any other disease, even before the recent increase in cassava research (Legg and Thresh, 2003). In some African countries, CMD is considered a major disease of cassava whereas, in some other areas, it is regarded as less damaging than CBB and CBSD (Akinbo et al. 2007). The prevalence of CMD exceeds 50% in the leading cassava-producing countries in Africa—Nigeria, the Republic of Congo (DCR), and Ghana (Thresh et al. 1994). Cassava varieties differ largely in their response to CMD with various degrees of symptoms on the crop tissues. Some are from severe stunting, with little or no yield of foliage leaves, stem cuttings, or tuberous roots, whereas other varieties are relatively unaffected and sustain little or no damage (Eni et al. 2021; Fargette et al. 1990; Hillocks et al. 2000).

Causative Agent and Pathogenesis of Cassava Mosaic Disease

Cassava mosaic gemini virus belonging to the genus *Begomovirus* is the actual causative agent of CMDs (Ndunguru et al. 2005). The viral etiology of CMD was first stipulated in 1936 when the disease was suspected to be a viral disease and graft transmissible from cassava to cassava was observed (Swanson and Harrison 1994). In 1975, virus particles were detected following isolation and observation by electron microscopy of geminivirus particles and the successful mechanical transmission of sap from infected cassava to the experimental herbaceous host, *Nicotiana benthamiana,* and back to a susceptible Brazilian cassava cultivar (Bock 1983).

Three CMGs including *African cassava mosaic virus* (ACMV), *East African cassava mosaic virus* (EACMV), and *Indian cassava mosaic virus* (ICMV) have been characterized serologically (Hong et al. 1993; Ndunguru et al. 2005). These three CMGs consist of three different types of iteron sequences, identified and classified into three groups namely ACMV type with isolates of ACMV, EACMZV, and Sri Lanka cassava mosaic virus (SLCMV), EACMV type encompassing all the other EACMV-like viruses and South African mosaic virus (SACMV) and the ICMV type with ICMV isolates alone (Kittelmann and Jeske 2008). Gemini viruses make up a large and diverse group of plant viruses and are characterized by geminate shaped particles of 30 × 20 nm that replicate their circular single-stranded DNA genome (genome size, 2.7–2.8 kb) in the nuclei of infected cells through double-stranded DNA intermediates by rolling circle replication or a recombination-dependent replication mechanism (Jeske et al. 2001). The geminate particles which encapsulate the ACMV genomic components are believed to release their genomic DNA via breaks that occur at the top and shoulders of the virus particles (Kittelmann and Jeske 2008). The *Begomovirus* genome components *DNA-A* and *DNA-B* share a common region of about 200 nucleotides having a high nucleotide sequence identity above 80% (Harrison and Robinson 1999). The common region possesses several regulatory elements as well as two *TATA* motifs and multiple copies of *cis*-elements known as iterons, which are the binding sites for the replication-associated protein (Hanley-Bowdoin et al. 1999).

Mode of Cassava Mosaic Disease Transmission

Cassava mosaic disease is commonly propagated through infected planting material—stem cuttings (Delaquis et al. 2018). Also, the whiteflies species complex plays a natural role in the transmission of CMD in a non-propagative and circulative approach (Islam et al. 2018). The species status of *B. tabaci* (whitefly) has been determined by the phylogenetic relationship of nucleotide sequences of the mitochondrial cytochrome C-oxidase subunit I gene (*cox1*) (de Barro et al. 2011). While whiteflies play a role as disease vectors in short-distance dissemination that is within 20 m (Maruthi et al. 2017), the dissemination of infected cassava planting materials plays a significant role in the long-distance spread of CMD (Delaquis et al. 2018). The use of insecticides that target whitefly density helps to limit short-distance dissemination (Horowitz and Ishaaya 2014). Also, integrated pest management could be adopted to control the population and reduce the build-up of resistance to insecticides by whiteflies.

Symptoms of Cassava Mosaic Disease

Mosaics caused by CMD could be green mosaics or yellow mosaics. Generally, CMD symptoms differ by type, extent, and severity. Plants that are affected by green mosaics have leaves with different sectors of dark and light green tissue and the green mosaics symptoms are clear only when the plants are observed closely. Green mosaics are not usually associated with a distinct decrease in leaf area, leaf number,

plant size, or yield of tuberous roots. On the other hand, plants affected by yellow mosaics are much clearer, as they have leaves with different areas of normal green and yellow tissue (Thresh and Cooter 2005). The chlorotic areas may expand less than other parts of the leaf lamina, which can lead to the folding of the leaflets and rupturing of the tissues, and some CMG strains produce more severe symptoms and greater damage to the growth and yield of cassava than others (Legg et al. 2006). However, there is no evidence for regular disparities between the symptoms caused by the different CMGs so far. Studies have shown that complex infections with more than one different CMGs cause more severe symptoms than a single virus infection (Fondong et al. 2000; Pita et al. 2001). Also, the impact of the environment on CMD symptoms has been documented. Usually, leaves produced during cool weather tend to show more symptoms than those produced during hot seasons (Gibson 1994). Multiple infections with other disease complex or nutrient deficiency, especially, zinc deficiency, make CMD diagnosis difficult since similar damages are observed on the plant tissue (Howeler 2017).

Cassava Brown Streak Disease

Prevalence and Distribution of Cassava Brown Streak Disease

Different strains of CBSD have been identified to be most prevalent in different parts of East Africa. The *cassava brown streak virus* (CBSV) is mainly found in the coastal lowlands of Mozambique and Tanzania, while the *Uganda cassava brown streak virus* (UCBSV) mainly occurs in the highland regions of Uganda and Tanzania (Mbanzibwa et al. 2009). Yield losses associated with CBSD could range from 70 to 100% in the most susceptible cultivars (Hillocks et al. 1999, 2001; Kawuki et al. 2016). Cassava brown streak disease impacts the number, weight, and quality of cassava roots through pitting, constrictions, and root necrosis (Legg and Hillocks 2003). There are several undocumented economic impacts of CBSD and the indirect or unquantifiable consequences on yield related to the deleterious effects on starch quality of non-necrotic portions of affected roots, as well as the additional labor cost incurred in separating necrotic from non-necrotic portions of affected roots have been highlighted (Kawuki et al. 2016).

Causative Agent of Cassava Brown Streak Disease

The etiology of CBSD was uncertain over the past decades since it was thought to be initiated by a virus when the disease was successfully transmitted by grafting (Legg et al. 2015; Tumwegamire et al. 2018). However, the first actual evidence of the causal agent of CBSD was confirmed by mechanical transmission of the virus in a range of herbaceous hosts plants (Kawuki et al. 2016; Legg et al. 2015). These viral particles were subsequently detected by electron microscopy in leaf samples showing symptoms of CBSD (Hillocks et al. 2000). Recent characterization based on a comparison of coat protein and full-length sequences has shown that CBSD is

caused by isolates of at least two phylogenetically distinct species of single-stranded RNA (ssRNA) filamentous virus particles belonging to the *Potyviridae* family and genus *Ipomo* virus (Mbanzibwa et al. 2009; Winter et al. 2010). The first species of *Ipomo* viruses to be discovered was monopartite with a linear, positive-sense, ssRNA genome consisting of about 9000 nucleotides and predicted to produce a polyprotein of 2902 amino acids (Mbanzibwa et al. 2009).

Mode of Transmission of Cassava Brown Streak Disease

In the early 1930s, cassava brown streak viruses were believed to be transmitted by whitefly, *Bemisia tabaci* (Genn.), and was reported in the coastal zone of Tanzania, in East Africa (Storey 1936). Later in the years, the viral etiology was confirmed with a classical demonstration of Koch's postulates (Maruthi et al. 2005; Winter et al. 2010). Unlike CMGs, which are persistently transmitted by *B. tabaci*, CBSVs are transmitted less persistently and are not preserved for more than 24 hours (Dombrovsky et al. 2014). For the later years of the 20th century, the distribution of CBSD was largely restricted to lowland coastal regions of Kenya, Tanzania, and Mozambique, and the surroundings of Lake Malawi in Tanzania and Malawi. The disease is mostly disseminated through cuttings taken inadvertently from infected parent materials (Hillocks et al. 1999; Kawuki et al. 2016; Maruthi et al. 2005).

Symptoms of Cassava Brown Streak Disease

All parts of the cassava plant including leaves, stem, and roots may show CBSD symptoms although, there are differences in the degree of the symptoms based on the factors such as environmental conditions, the growth stage of the crop, relative humidity, the time of infection, and the genetics of the cultivar (Hillocks et al. 1999). There are two types of foliar symptoms from CBSD, type 1 and type 2. Type 1 initially appears as chlorosis along the margins and later tertiary veins, while type 2, is characterized by chlorosis spread in areas between the main veins and later covering much of the leaf lamina (Legg et al. 2014). The root symptoms are considered very lethal and usually develop following foliar symptoms (Hillocks and Jennings 2003). In the most susceptible cultivars, root necrosis may appear within six months of planting cassava cuttings derived from infected plants (Okul Valentor et al. 2018). As the cassava grows into maturity, root symptoms become increasingly destructive and an undocumented secondary impact is the early harvesting of the roots to further spoilage (Hillocks et al. 2001) (Fig. 1.1).

1.2.1.2 Bacterial Diseases

Bacterial and viral diseases constitute the major diseases of economic importance in cassava production and utilization while most others are regarded as minor or of local importance (Hillocks and Wydra 2002). Some of the prevalent bacterial diseases in cassava include CBB caused by *Xanthomonas axonopodix* pv. *manihotis* (Xam),

Fig. 1.1 Healthy (**a**) versus CMD (**b**) and CSBD (**c**) infested cassava tissues (Ano et al. 2021)

prevalent in Africa, South America, and Asia, angular leaf spot (bacterial necrosis) caused by *Xanthomonas campestris* pv *cassava*, reported in East Africa and South Africa, and soft rot of stems and roots caused by *Erwinia carotovora* spps. *carotvora.* Most recently, a new bacterial disease caused by *Enterobacter cloacae* was identified in South America (Santana et al. 2012).

Cassava Bacterial Blight

Prevalence Cassava Bacterial Blight

Cassava bacterial blight is regarded as the major bacterial disease and limits the productivity of cassava in different major cultivation regions including South America, Asia, and Africa, where yield losses could be as high as 80–90% during high epiphytotic periods (Fanou et al. 2018). Disease epidemic and impact on yield vary from year to year which makes its incidence unpredictable and a major risk to subsistent cassava cultivation by smallholder farmers. Cassava bacterial blight is believed to originate from South America due to the high diversity of the pathogen in the region, however, with the dissemination and cultivation of cassava to many

other regions, CBB is currently widespread and prevalent in various regions of the world (López and Bernal 2012).

Symptoms of Cassava Bacterial Blight

The initial symptoms of CBB appear at the start of rains following the end of dry seasons and reach their climax at the height of the rainy season (Hillocks and Wydra 2002). The documented symptoms of CBB include wilting, leaf spotting, die-back, discoloration of vascular tissues in mature stems, and roots of susceptible cultivars with the production of gum exudates on young shoots (Fanou et al. 2018). The CBB cycle is characterized by an epiphytic and parasitic phase. The pathogen survives on seemingly healthy stems during the dry season at the epiphytic phase while at the onset of the raining season it transcends into the parasitic phase when the pathogen multiplies and gains access into the plants through epidermal wounds or natural openings on the leaf (Zárate-Chaves et al. 2021). Initial symptoms appear after about one week as visible translucent water-soaked spots on the abaxial surface of the leaves which eventually become angular dark green spots. These spots later enlarge with adjoining spots joining together to form large brown patches. Lesions formed on the leaves produce creamy white oozes that eventually turn yellow. As the disease progresses, the blight symptom characterized by a superficially burnt appearance usually appears on the affected leaves and leaf tips (Fanou et al. 2018; Hillocks and Wydra 2002; Lozano 1974).

The disease progresses systemically from the leaves into the petiole and woody stem then throughout the entire plant. Multiplication of the pathogen in the vascular system obstructs the movement of water and nutrients thereby inducing leaf wilting which leads to defoliation of the shoot tip. Also, the young growing shoot tip dies producing a characteristic candlestick symptom or tip-dieback. This also affects the newly growing shoots at the lower stem part which also begins to wilt and experience tip dieback. A characteristic brownish discoloration of the vascular systems is easily observed in stems. Primary CBB symptoms in fields newly planted with infected materials are the wilting of the young germinating sprouts with subsequent dieback (Fanou et al. 2018; Lozano 1974).

Etiology of Cassava Bacterial Blight

Cassava bacterial blight is caused by a gram-negative rod Xam which is related to the bacteria from the genre Xanthomonads that cause disease in a host of other plants including rice (He et al. 2010), soya bean (Chatnaparat et al. 2016), citrus (Ference et al. 2018), pepper and tomatoes (Potnis et al. 2011). Though related, each bacterium is proven to be host-specific and Xam is known to be associated only with cassava and other closely related plant species (López and Bernal 2012). *Xanthomonas axonopodis* pv. *manihotis*, produces disease in cassava by delivering type III effector proteins into the plant cell to suppress or modulate host innate immunity and promote pathogenesis. Studies have shown that most Xam strains studied contain from one to five transcription activator-like (TAL) effectors (Castiblanco

et al. 2013; Cohn et al. 2014), which has been associated with virulence for other xanthomonads (Cernadas et al. 2014; Cohn et al. 2014). The TAL effectors when delivered into the host cell are translocated to the plant nucleus where they bind to specific DNA sequences to activate the expression of host genes that facilitates the proliferation and colonization of the host by the bacteria (Cohn et al. 2014; Mak et al. 2012).

There is evidence of classical genetic approaches from mutagenesis and complementation to determine the pathogenicity determinant of the causative agent of CBB. As applicable in other Xanthomonas, different clusters of genes important for pathogenicity in Xanthomonas species have been traced using these methods and other studies and the important pathogenicity factors identified include genes in the Type III secretion system that secretes and translocate effector proteins into the plant cells, cell wall degrading enzymes, exopolysaccharides, and toxins (López and Bernal 2012).

Comparative evaluation of Xam and other Xanthomonas shows a high degree of conservation in gene content and order with no prominent differences found in important pathogenicity factors in the genus. This then infers that the rate of infection lies in differences in specific gene sequences and/or regulatory regions (López and Bernal 2012). Studies of factors that contribute to Xanthomonas disease in their corresponding host plants show that Xanthomonas has developed a range of well-regulated and coordinated traits necessary to adhere to plant tissue, acquire nutrients, suppress plant defense responses, and eventually lead to disease (An et al. 2019).

Response of cassava cultivars to CBB varies and ranges from very susceptible to moderately resistant (López and Bernal 2012). These responses could be expressed as variations in the rate of colonization of the bacterium. Genetic diversity studies of Xam carried out in different regions of the world including African and South America show an increase in Xam diversity over the past three decades which makes the adoption of resistant cassava varieties intricate. Therefore, the continuous evaluation of the bacterial population in fields cultivated with cassava is highly recommended (López and Bernal 2012).

Epidemiology and Control Measures of Cassava Bacterial Blight

Cassava bacteria blight is the most important bacteria affecting cassava production in all the cassava-growing regions globally. Disease occurrence and impact on yield vary from year to year. The first symptom of CBB is usually at the onset of the first rain after the dry season and reaches its maximum when the rains are at their peak (Hillocks and Wydra 2002). Pathogen dispersal within a field is aided by high wind conditions which enable the transfer of Xam from plant to plant in water droplets while dispersal between fields occurs mainly with the exchange of infected propagative material (Lozano 1974). Symptom development on infected plants is favored by rainfall, high temperature, high relative humidity, the incidence of insect vectors, and wounds on the leaves, in addition to high differences between day and night temperatures. The disease is usually managed by employing an integrated control strategy which includes the use of resistant cultivars and improved cultural

methods such as the use of clean planting materials, planting outside of peak epidemic periods, weeding, excluding bush fallow around cassava field, and use of quarantine measures that prevents the introduction of the disease into low disease pressure areas (Banito 2003; Fanou 1999). An excellent method for breaking the life cycle of the pathogen that might persist in the environment in the epiphytic phase is to employ crop rotation between successive cultivation of cassava as well as removing infected leaves by burning and burying infected debris (Banito 2003). Although the use of resistant cultivars has proven to be the most effective control measure for CBB, there is a tendency for reduced durability of resistance as the diversity of the pathogen population increases (Restrepo et al. 2000). It is therefore pertinent to ensure that implementing varietal resistance is coupled with assessing the diversity of pathogen populations in the field and deploying cultivars resistant to the local pathogen populations.

Impact of Cassava Bacterial Blight on Yield

Up to 80–90% yield losses could be attributed to CBB during high epiphytotic periods affecting both fresh root yield and planting materials (Santana et al. 2012). The devastating symptoms of CBB contributing to cassava loss include wilting and leaf defoliation which can be high under favorable climatic conditions. Various climatic, inoculum pressure and cultivar responses affect the rate of susceptibility to the disease. Also, CBB can contribute to a low accumulation of starch in cassava roots (Fanou et al. 2018).

Angular Leaf Spot (Bacterial Necrosis) of Cassava

Angular leaf spot is caused by *Xanthomonas campestris* pv. cassava reported only from East Africa and Southern Africa. The disease is characterized by the secretion of bright yellow exudates from infected leaf tissue during periods of high humidity. Oftentimes, severe necrosis leads to the defoliation of plants. The disease is localized in the cortex of the stems and spreads to the vascular tissues. Predisposing factors to the disease include cultivation on very poor soils and plant injuries resulting from severe rainstorms (Hillocks and Wydra 2002).

Soft Rot of Cassava Stems and Roots

Cassava soft rot of stems and roots is caused by *Erwinia carotovora* sp. *carotovora.* The disease is characterized by internal rotting of stems and branches, dark lesions, external cankers, root necrosis, wilting of young shoots, and tip dieback. Control of diseases could be achieved by the use of uninfected, healthy cuttings of varieties resistant to fruit fly and the use of insecticides (Hillocks and Wydra 2002).

1.2.1.3 Fungi Diseases of Cassava

Fungi threaten cassava production in different parts of the world, destroying the stems or killing the roots of the plant (Bellotti et al. 2012a). The degree of damage, however, is mostly affected by different cassava clones, strains of the pathogen, and the environment (Hillocks and Wydra 2002). Most of the soil-borne fungi spread within the root system and will attack healthy cassava if their specially adapted hyphae come in contact with the young roots, leaf petioles, or stems (Hillocks and Wydra 2002). Some of them can attack older cassava plants by penetrating through old wounds and lesions in stems and through cracks and lesions in the leaves. Some fungal pathogens attack all forms of cassava, causing anthracnose, leaf spots, leaf blight, stem rot, root rot, and sometimes complete crop loss (Hillocks and Wydra 2002). Fungal attack on susceptible varieties causes premature aging of plants, yellowing, or even death of leaves, petioles, or stems. Under favorable conditions, some fungal populations can build up very rapidly resulting in expanse infections on cassava.

The control measures of cassava fungal diseases include the use of well-established scientific methods and good cultural practices (Legg et al. 2006). Cassava varieties with improved fungal resistance can be used for disease control as they reduce the rate of spore penetration on the leaves, allow extended cassava growth under field conditions, and generally help cassava plants resist infection within the field even under high fungal populations (Ahmad et al. 2021; Hussain 2015). Fungi diseases are still major agricultural problems in cassava production and require a biotechnological approach for sustainable management (Aerni 2006). A scientific approach based on the understanding of pathogen biology, epidemiology, and ecology of plant disease has been promoted and should apply to fungi disease control in cassava (Rimbaud et al. 2015). The fungal diseases that attack cassava with their biology, epidemiology, and ecology are discussed below.

Cassava Anthracnose Disease

Cassava anthracnose disease (CAD) caused by *Colletotrichum gloeosporoides* f.sp. *manihotis*, Henn. (Penz) Sacc. is a common and widespread disease that attacks cassava in nearly all cassava growing areas (Akinbo et al. 2007; Owolade et al. 2005). It is one of the major economic diseases of cassava in the tropics. The fungal pathogens can attack cassava stems, leaves, and root tubers, causing disease symptoms ranging from brown to necrotic spots on the leaves, stem and root lesions, and girdling of the plant (Theberge 1985). Cassava anthracnose is regarded as a serious and important disease of cassava with a record of epidemic levels in high rainfall regions.

Symptoms of Cassava Anthracnose Disease

Cassava anthracnose disease (CAD) is characterized by the presence of sunken leaf spots on the leaf lamina measuring 1–10 mm in diameter and up to 30 mm in diameter

in advanced cases. When the disease is fully developed, the center of the spot is white and studded with pinkish fruit bodies of the fungus (Fokunang et al. 1997, 1999b). Infection on the petiole is initiated by hyphae growing from the infected lamina through conducting tissues. In highly susceptible cassava varieties, the leaves blight, wilt, and sometimes defoliation may occur. The pathogen weakens the sprouting of planted cassava cutting where the infection sets in early, causes young stems to wilt and induces cankers on mature stems (IITA 1990). Fresh leaves produced at the beginning of the rainy season are usually the most susceptible and the disease tends to disappear when the dry season begins. At a relative humidity below 70%, the fungus will stop invading plant tissues (IITA 1990). The symptoms of CAD include the development of cankers on stems, branches, and fruits, leaf spots and tip dieback, green portions with shallow oval depressions that are usually pale brown, but with a point of normal green tissue in the center (Fokunang et al. 1999a). In the mature portions of the stems, anthracnose lesions are round, swollen, and in bands, forming deep cankers on the epidermis and cortex, and sometimes deforming the stem as it destroys the eye buds on cassava stems thereby reducing the sprouting potential of cassava stems.

Etiology Cassava Anthracnose Disease

The organism causing this disease has been variously called *Glomerellamanihotis, Colletotrichum manihotis*, *Gloeosporiummanihotis*, and *Glomerellacingulate* (Weir et al. 2012). These are likely traceable to one species, generally characterized by a relatively short straight cylindrical to broadly ellipsoidal conidia, with obtuse ends and truncated attachment points. Under natural conditions, *C. gloeosporioides* f.sp. *manihotis*, penetrates the host through mechanical wounds or sucking insect vectors (*Pseudotheraptusdevastans*, Dist Het. Coriedae) punctures (Weir et al. 2012). The CAD pathogen penetration after insect puncture of young cassava stems, the cracks extend through the cork layer or the epidermis up to the underside of the sclerenchyma, then immediately the lesion extends tangentially under lignified fibers (Owolade et al. 2005; Theberge 1985). The host reacts to the invasion through the generative zone, the layer of cork more precariously formed at the level of the initial necrotic lesion than in the primary healthy stem (Sinkovics 2011). New races of the pathogen can arise by mutation in somatic cells, recombination of nuclear genes during sexual reproduction, by reassortment or exchange of genetic material in somatic cells, and by mutation of extrachromosomal or cytoplasmic genes (Esser 2016). *Colletotrichum loeosporioides* f.sp. *manihotis*, is a specialized fungus on the cassava host, and sporulation and germtube development of the physiologic races of the fungus is highly correlated with pathogenicity and virulence on the cassava host plant (Fokunang et al. 2001).

Epidemiology of Cassava Anthracnose Disease

Cassava anthracnose disease is one of the important cassava diseases and prevalent in most cassava growing regions of Africa, South America, and Asia (Fokunang et al.

2000, 2002). The pathogen survives environmental conditions in its perfect state and *Gloeosporiumcingulata* appears to increase during the dry season. The prevalence, occurrence, and dissemination of CAD pathogens are huge and occur across many ecozones in Africa with incidences ranging from 68 to 100% (Fanou et al. 2018; Fokunang et al. 1999a). Cassava anthracnose disease survival and transmission occur through breeder seeds and post-harvest debris in the field (Fokunang et al. 1997). Also, water splash, air current, insect, or other forms of contact can disperse the disease. The rainfall regime plays an important role in the development and dispersal of CAD pathogens. The rain splash dislodges spores from the acervuli and spreads them along the young cassava stems.

Impact of Cassava Anthracnose Disease on Cassava Yield

Precise yield loss due to CAD has not been quantified specifically due to the occurrence of multiple disease complexes in the field, however, losses could be devasting in certain areas (Makambila 1994). There are also many unreported cases of infection in farmers' fields and experimental plots severely invaded by CAD in rainfall cassava growing zones. Cassava anthracnose disease severity could lead to a significant loss in planting materials and low biomass production. Severely infected cassava stem in some cases results in a 40–60% loss in germination rate. Total crop failure has been reported in cases where infected stem cuttings have been used for planting (Fokunang et al. 2001, 2002).

Control Strategies of Cassava Anthracnose Disease

Cultural Control
The cultural control measures implemented to reduce or eradicate the spread of CAD range from crop rotation, fallow, and manipulation of planting times (Latah 2016).

Chemical Control Measures
The use of chemicals offers control that may not be sustainable due to bioaccumulation and pathogen mutation.

Resistant Varieties
The use of resistant varieties remains a sustainable and most efficient means of controlling CAD.

Quarantine/Sanitation Measures
Major means of dissemination of cassava diseases and pests have been from the exchange of disease-infested cassava stem cuttings for propagation. The origin of CAD has not been reported but its ubiquitous nature in the cassava growing regions is an indication of exchange through the distribution of infected materials. A recent report shows that anthracnose is seed-borne and can be transmitted by infected cassava seeds (Fokunang et al. 1997). Several sanitation measures, in addition to those

legally established by quarantine regulations, could reduce the risk of disseminating the disease (Lozano and Booth 1974).

White Leaf Spot (*Phaeoramularia manihotis*)

White leaf spots caused by *phaeoramularia manihotis* are small in spot size diameter and with a difference in whiteness to the white color spot induced by *Cercospora henningsii.* They vary from circular to angular spots with a diameter between 1 and 7 mm. They are normally clear white, but in some cases, yellowish tending towards brown.

Symptoms of White Leaf Spot

White leaf spot lesions are sunken on both sides of the leaf lamina when compared to half of the thickness of a normal healthy leaf blade. The white spots on the lower leaf surface can be distinguished, although they are sometimes diffusely colored which makes them appear as brown-violet irregular lines that are usually surrounded by brown to yellowish halos. The centers of the spots have light grayish characteristics during the pathogen's fruiting.

Etiology Cassava White Leaf Spot

During the process of infection, the pathogen (*P. manihotis)* forms thin stomata in lesions on leaves. The stromata produce conidiophores in loose fascicles that emerge through the stomata (Fokunang et al. 1997). The fungus penetrates the host through stomatal cavities and then invades the host's tissues through the intercellular spaces. When leaf spots reach 5–7 mm in diameter, a stroma is formed which produces conidiophores. The secondary cycles of the disease are repeated throughout the rainy season as conidia are dispersed by wind or rain splash.

Epidemiology of Cassava White Leaf Spot

The white leaf spot fungus survives the dry season in old, infected tissues and resumes activity at the beginning of the rainy season following the host's new growth.

Impact of White Leaf Spot on Cassava Yield

Yield loss due to WLS is not quite damaging in cassava production but can seriously affect cassava leaves, which can negatively impact the food and income of the population that uses cassava leaves as vegetables.

Management and Control of Cassava White Leaf Spot

The best control for this disease is by using resistant varieties. Significant differences in varietal resistance have been reported. To reduce the severity of infection, recommended cultural practices include reducing excess humidity during planting.

Cassava Brown Leaf Spot

The brown leaf spot is caused by *Passalora henningsii* (previous names include: *Cercosporidium henningsii, Cercospora henningsii,* and *Mycospaerella henningsii*, named after the sexual state). The disease has a broad geographical distribution and can be found in Asia, North America, Africa, and Latin America. The disease naturally attacks *M. esculenta*, *M. glaziovii,* and *M. piauhynsis* (Legg and Alvarez 2017). In the tropics, *C. henningsii* is an important pathogen, causing severe defoliation (Legg and Alvarez 2017; Teri et al. 1981).

Symptoms and Life Cycle of Cassava Brown Leaf Spot

The BLS disease usually occurs between 5 and 6 months after planting on the older and lower leaves of the plant. Leaf spots caused by BLS are circular and up to 15 mm in diameter, becoming angular and limited by veins. The spots are brown on upper surfaces with dark borders, sometimes surrounded by indistinct yellow margins. On the underside, the spots are gray with less distinct borders. Minor veins crossing the spots appear as black necrotic lines. The centers of the spots dry crack and may fall out. As the spots enlarge, the leaves will turn yellow and fall off.

Warm and humid weather increases the severity of cassava BLS. Spores of the fungus produced on the lower surface are spread by wind and water splash. Long-distance spread occurs when spores are carried on planting materials. In general, older leaves are more susceptible to the disease than young leaves. The fungus can continue to live on old fallen leaves until favorable conditions return (Legg and Alvarez 2017).

Impact of Cassava Brown Leaf Spot on Yield

Cassava yield losses up to 30% in Africa, 23% in South America, and 17% in India have been reported due to BLS infection. It generally affects older leaves and is usually late in the growth of the plants.

Management and Control of Cassava Brown Leaf Spot

Cultural Method of Controlling Cassava Brown Leaf Spot
The disease is of minor importance, and good cultural practices such as wide spacing, crop rotations, and early planting should reduce any potential impact. Spacing

between plants helps to lower relative humidity which increases the spread of the disease (Ayesu-Offei and Antwi-Boasiako 1996).

The Use of Resistant Varieties in Controlling Cassava Brown Leaf Spot
There are no known varieties that are resistant to the BLS disease in the Pacific islands, although in other regions there are reports of potential resistant clones although constant evaluation and selection for resistance are recommended (Ayesu-Offei and Antwi-Boasiako 1996; Teri et al. 1981).

Chemical Control of Brown Leaf Spot
If warranted, use copper fungicides or mancozeb for chemical control.

Super-Elongation Disease

The causal agent of cassava super-elongation disease is the fungus *Sphaceloma manihoticola.* The pathogen produces distortion or curling in young leaves, and cankers on the underside of leaves, petioles, and stems. These cankers are lens-shaped and show different sizes. The affected leaves show white irregular spots. The over-amplified elongation of the stem internodes is a characteristic symptom of this disease. The affected stem is thin, weak and the diseased plants are much taller and spindly than the healthy ones. The disease causes progressive dieback of the plant and partial or total necrosis of the leaf blades, resulting in severe defoliation.

Symptoms Cassava Super-Elongation Disease

Super-elongation disease symptoms are more common in the wet season than at other times and that is when the infection spreads rapidly because the spores are distributed easily by wind and rain. High humidity is required for spore germination. Infected plants are taller than surrounding healthy ones. Young shoots, leaves, and petioles become distorted, and bear eye-shaped cankers appear along the midribs and veins. White, irregular spots may occur on the leaf lamina. There may also be dieback and defoliation.

Management of Cassava Super-Elongation Disease

Planting material should be selected from disease-free plants and treating cuttings with captafol solution can control the spread of the disease. The use of cassava cultivars that are resistant to the disease is the most sustainable management measure. In areas where the pathogen is endemic, planting should be carried out during periods with the least precipitation (Table 1.2).

Table 1.2 Major cassava fungal diseases and mean severity in Nigeria

Cassava fungal disease	Responsible pathogen	Distribution	Mean severity
Cassava foliar fungal diseases			
Super-elongation	*Sphaceloma manihoticola*	41.82% in rainforest areas	1.51
Cassava anthracnose disease (CAD)	*Colletotrichum gloeosporioedes*	98.80% of the fields surveyed	2.84
Cassava brown leaf spot (CBLS)	*Cercosporidium henningsii*	93.98% of the fields surveyed	2.4
Cassava white leaf spot	*Phaeomularia manihotis*	84.22% of the fields in Southeast Nigeria	1.62
Cassava root rot fungal diseases			
Phytophthora	*Phytophthora* spp		
Fusarium spp.	*Fusarium solani* *Fusarium oxysporum*	9.1–11.7% in rain forest zones	1.25
Rhizoctonia solani	*Rhizoctonia solani*	1.9% in rain forest zones	1.7
Botryodiplodia theobromae	*Botryodiplodia theobromae*	66.7% in all fields surveyed	2.22

Source Nwokacha and Nwadili (2011), Onyeka et al. (2004)

Cassava Root and Stem Rot

The next most important group of diseases in both Africa and South America are the root rots. The major pathogens of economic significance for root diseases include *Sclerotium rolfsii, Botryodiplodia theobromae, Fomes lignosus, Rosellinia necatrix, Rhizoctonia solani, Phytophthora* spp., and *Fusarium* spp. (Hillocks and Wydra 2002). Cassava root rots are caused by a complex of soilborne pathogens which induce damages that eventually reduce the yield (Ibrahim and Shehu 2014). Cassava yield losses of up to 80% due to rot diseases have been reported (Cock 1987; Theberge 1985). In some areas, total crop losses have been attributed to rot diseases. Among the organisms commonly reported are *Phytophthora drechsleri*, *Rosellinia necatrix*, *Armillaria mellea*, *Rigidoporus lignosus*, *Botryodiplodia theobromae, Sclerotium rolfsii*, and *Colletotrichum gloeosporioides* f.sp. manihotis (Fokunang et al. 2002). The prevalence of cassava of root and stem rot diseases could be higher in the forest than in the wet savanna zones, especially in Africa.

Cassava Soft Root Rot Disease

Several *Phytophthora* species have been associated with soft rots of cassava roots and these often occur with a few other soil-borne fungi, particularly *Pythium* spp. and *Fusarium* spp. *Phytophthora drechsleri* Tucker has been reported from Latin America and *Phytophthora erythropseptica* Pethy from Africa. Soft rot, in general,

is a worldwide problem and cool wet conditions and root damage predispose the tuberous roots to infection. In areas close to drainage ditches or poorly drained soils, losses can be up to 80% (Hillocks and Wydra 2002; Theberge 1985).

Symptoms of Cassava Soft Root Rot Disease
In soft root rot disease, young roots initially show water-soaked patches that eventually turn brown and death of the feeder roots. As the rot progresses, the starch-bearing tissues disintegrate and the affected roots develop a pungent odor. Root dysfunction causes dieback of the terminal shoots and leads to sudden wilting in advanced stages of root decay.

Impact of Cassava Soft Root Rot Disease on Yield
Soft rot infection can cause greater than 80% total root yield loss and loss of planting material (Cock 1987). This happens mainly in susceptible cultivars.

Management of Cassava Soft Root Rot Disease
The use of cultural practices such as good drainage, selection of loose-textured soils, crop rotation, early harvest, and avoiding soils prone to flooding are important in controlling soft root rot in cassava. Treatments with fungicides may help establish the crop, preventing root rots from attacking during the crop's first months. Fungicides based on plant extracts, oils, and cytokinins help control soil fungi while offering a nonpolluting organic alternative. The use of resistant varieties is also important in controlling the disease.

Cassava Dry Root Rot

Cassava dry root rot is usually caused by *Rosellinia necatrix* (Hartig) Berl. or *Armillariella mellea* (Vahl.) Pat. (*Armillaria mellea* (Vahl) Fr.), or by both fungi together (Msikita et al. 2007; Onyeka et al. 2021). These pathogens have been recorded on cassava in different parts of the world, especially in places where the crop is growing in moist soils high in organic matter. The pathogens have a wide host range among woody perennials. The dry root rot fungi normally attack cassava planted after forest clearance and can destroy the roots of affected plants. It can be managed by planting annual crops after forest clearance before planting cassava (Makambila 1994).

Symptoms of Cassava Dry Root Rot
Both fungi produce rhizomorphs which appear as thickened mycelial strands on the outside of the roots. They are white at first and later begin to turn black. Infected roots are discolored and exude a watery liquid when squeezed. Rhizomorphs penetrate the infected tissues. The above-ground symptoms include plant wilting though the plants do not shed their leaves but eventually desiccating to assume a scorched appearance (Theberge 1985).

Impact of Cassava Dry Root Rot on Yield
Cassava yield reduction due to dry rot infection is relatively reduced as it rarely occurs except in newly opened forests and pathogen endemic areas.

Management/Control of Cassava Dry Root Rot

Although the disease has not been reported in young plants, the recommendation control measure is to avoid selecting planting materials from infected crops. Also, establishing cassava fields in newly opened forests should be avoided or proceeded with caution. The use of resistant varieties as planting materials is a good alternative. Crop rotation with grasses should be carried out whenever the incidence of plant death or root rot reaches 3% in the field. Infected cassava residues and/or litter from perennial trees (e.g., trunks and decaying branches) should be eliminated as they can serve as alternate hosts. Loose-textured soils with improved soil drainage should be used for planting cassava.

1.2.2 Pests

1.2.2.1 Cassava Green Mite

Life Cycle of Cassava Green Mite

Cassava green mite is a very serious dry season pest in Africa. Reproduction in CGM is arrhenotokous (Roy et al. 2003); it is a form of parthenogenesis in which unfertilized eggs develop into males. There are four active stages: a six-legged larva, two nymphal stages (proto- and deutonymph), and the adult stage. The growth rate and development of CGM depend on temperature, rainfall, humidity, host plant, and sex (Yaninek and Hanna 2003). In a study in Nigeria, at a temperature of 27 °C, relative humidity of 70% and a photoperiod of 12 h light and 12 h darkness, the development of the egg, larva, protonymph, and deutonymph on leaves of cassava (TMS 30,572) have been recorded at 5.4, 3.0, 1.1 and 2.8 days, respectively (Yaninek et al. 1989a). At the same temperature of 27 °C, the adult female mite lives for 11.6 days including a day for preoviposition and 9.8 days of oviposition, and lays an average of 62.8 eggs over 9.8 days with a maximum reproduction rate of 43.2 progeny. Egg to adult developmental periods has been estimated to be 21.3, 15.5, 12.3, 7.7, and 6.9 days at 20 °C, 24 °C, 27 °C, 31 °C, and 34 °C, respectively. The average life span of these females is 24.4 days. There are two population peaks per year of CGM especially in the tropics. The first peak occurs at the end of the wet season around November to December while the second peak happens at the start of the rainy season between March and April. Cassava green mite is considered a dry-season pest and thrives in the lowlands where high temperatures prevail. Low temperatures and constant rainfall increase the mortality rate of the mites and population density.

Distribution and Prevalence of Cassava Green Mite

Mites have been reported to feed on cassava in the Americas, Africa, and Asia (Bellotti et al. 2012a; Bellotti 2009). The most important are *Mononychellus tanajoa*,

M. caribbeanae, *M. mcgregori*, *Tetranychus cinnabarinus, T. urticae*, *T. truncates*, *T. kanzawai, T. neocalidonicus, Oligonychus biharensis* and *O. peruvianus*. Cassava is the major host for the *Mononychellus* species, while the *Tetranychus* species tend to have a wide host range. The *M. tanajoa* is native to the Neotropics and is the most important mite species, limiting cassava production, causing huge yield losses in both the Americas and Africa.

The first record of a mite attack on cassava was in 1971 in Uganda, East Africa. The mite was identified as *Mononychellus tanajoa* (Bondar), an exotic species of Neotropical origin (Lyon 1973; Yaninek and Herren 1988). This mite was introduced into Uganda on cassava cuttings imported from Colombia, South America and by 1974, the mite had spread to all countries bordering Uganda (Lyon 1973; Yaninek and Herren 1988). It continued to spread from Tanzania into Zambia, Malawi, and Mozambique (Bellotti et al. 1987; Yaninek and Herren 1988). By 1977, it had infested most of the cassava in East Africa (Yaninek et al. 1993). Spreading west from Uganda, *M. tanajoa* made a sudden leap across much of central Africa to Congo and was first found in West Africa in Nigeria in 1979 where it moved rapidly across the broadly similar vegetation from Nigeria to Benin, Togo, Ghana, Ivory Coast at an average speed of spread of 600 km/year (Yaninek et al. 1989b). By 1985, the speed of spread has decreased to 250 km/year as the mite moved through the rain forest in the Ivory Coast, Liberia, Sierra Leone, and Guinea Conakry (Yaninek et al. 1989b). The mite continues to spread throughout the African cassava belt and is threatening a crop that is often the last major food source available for harvest during drought conditions (Herren and Neuenschwander 1991). Cassava green mite could be spread by infected planting material however, the most important method by which CGM is dispersed is by the wind. In the morning, adult mites lower themselves from the leaves on silken threads so that even low wind currents can carry them over long distances. This may account for the rapid spread of the mite (300 km/ year) (Mutisya et al. 2016). The *M. tanajoa* can easily survive on leaves and stems removed from the field. Cassava leaves gathered and sold locally as a vegetable usually remain infested with mites for up to five days before the leaves become shriveled.

Mode of Infestation, Symptoms, and Economic Impact Cassava Green Mite

Cassava green mite is greenish-yellow in color and can hardly be seen with naked eyes. It is a dry-season pest that has piercing and sucking feeding habits (Jiwuba et al. 2020). It feeds by inserting their chelicerae (stylets) into the abaxial surface of cassava leaves and extracting the fluid content of palisade and spongy mesophyll cells (Yaninek and Hanna 2003). This causes chlorosis which increases from a few whitish to yellowish appearance to complete loss of green pigment (Bellotti et al. 2012b). The damage first appears on the surface of developing and newly formed leaves. Symptoms vary from a few chlorotic spots to complete chlorosis, stunted and deformed leaves that it is often mistaken for CMD symptoms.

Heavy infestations of CGM can cause defoliation starting from the apical tip of the plant and lateral buds down to the shoots, resulting in severe candlesticks and

possible dieback. Cassava green mite diminishes the plant's photosynthetic capacity and growth rate, by reducing the leaf area of the plant (Tomkiewicz et al. 1993). Damage by the mite affects the quantity and quality of planting material, increases weed infestation and root rot disease in cassava (Yaninek et al. 1989a).

Cassava green mite incidence is high in the dry season and leads to a 20–80% tuber yield loss, depending on the severity of the attack. Cassava yield and economic losses due to CGM severity threaten rural household incomes and global food security. The results of the multivariate regression analysis studied by Jiwuba et al. (2020) revealed the negative significance of CGM severity on FRY which caused a loss of 20% average yield. From that study, negative correlations between CGM and yield traits (biomass, fresh root yield, and root dry matter content) were also observed. Increasing populations of CGM during the dry season can significantly reduce the dry matter content on the leaves, stems, and roots up to 10–30% during the dry season and 25–45% during the wet season in the roots (Yaninek 1994). Environmental stress such as drought can contribute to a significant reduction of up to 73% root yield loss and a 67% reduction in stem yield in susceptible cultivars (Byrne et al. 1983). Also, a 10% drop in the photosynthetic rate of cassava leading to a 20% decline in dry matter production has been reported (Cock 1982). Schulthess et al. (1987), found that the dry matter lost during the dry season depended on the amount of stress caused by drought, other pests, or pathogens. From that study, the presence of CGM on drought-stressed plants significantly increased dry matter losses in cassava. Losses in unimproved varieties were generally much higher. A strong negative correlation was observed between plant height and CGM severity (Egesi et al. 2007). Ezenwaka et al. (2018), results showed that leaf pubescence, leaf retention, stay green, shoot tip size, and shoot tip compactness are significantly and negatively correlated with CGMs.

Cassava plants recover from drought stress during the subsequent rainy season, but not from mite damage (Yaninek and Hanna 2003). New plant growth is triggered by rainfall and mites are washed off the leaves during rainy seasons. Mites can survive on leaves, stems, and cuttings removed from the field for a period of up to 60 days (Yaninek and Hanna 2003).

Measures of Controlling Cassava Green Mite

Chemical Control of Cassava Green Mite

Cassava is a long-cycle crop and is mostly grown by small-scale farmers with few resources. Chemical control, although technically possible, is not economically feasible for low-income farmers (Bellotti et al. 2012b). Even low doses of pesticides have adverse effects on natural enemies and reduce the yield by up to 33%. Chemical treatments usually cause secondary pest outbreaks and pose a threat of pest resurgence due to rapidly induced pesticide resistance in the long term (Maclntyre and Graham 1976; Nyiira 1982).

Cultural/Agronomic Practices for Cassava Green Mite Control

Early cassava research concentrated on modifying cultural/agronomic practices to reduce losses due to mites. Most of the recommendations are still useful, but their impact is limited owing to technical, social, and economic factors (Bellotti et al. 1999; Byrne et al. 1983; Nyiira 1982) Cassava plants that are 2–9 months are the most vulnerable to CGM infestation (Bellotti et al. 2012). Adjusting the planting times, the way the cuttings were planted, intercropping, de-topping, and removal of infested leaves have been the principal forms of protecting cassava plants from CGM attack. Ezulike et al. (1993), reported that the cuttings planted in a slanting position had mites on the leaves soon after sprouting, but those planted horizontally did not. Cassava intercropped with pigeon pea suffered less damage from CGM and gave higher yield than those grown on a pure stand (Ezulike and Egwuatu 1990). Also, de-topping of the infested shoot tip has been recommended (Lyon 2009), but that aggravates the problem since the resulting lateral shoot growth produces even more new leaves.

Host-Plant Resistance in Cassava Green Mite Management

Cassava clones with pubescent leaves, large compact shoot apices, and enhanced leaf retention and stay green ability suppress the initial buildup of the CGM population and offer higher levels of resistance to CGM than cultivars that lack these characteristics (Jiwuba et al. 2020). Ultimately, leaf pubescence has been shown to favor the colonization of the predatory mite (*T. aripo*) and enhance the ability of the predator to find the prey (CGM) due to the production of herbivore-induced plant volatiles (Onzo et al. 2012).

Biological Control of Cassava Green Mite

The biological control method involves the use of CGM natural enemies to control the population of CGM. Natural enemies of CGM are found in the families of Chrysopidae, Cecidomyiidae, Syrphidae, Anthocoridae, Lygaeidae, Staphylinidae, Coccinellidae, and Phytoseiidae (Byrne et al. 1983; Murphy 1984; Yaseen and Bennett 1977). However, Phytoseiidae is the most common predator of mite in the Neotropical region (Bellotti et al. 2012; Byrne et al. 1983; Yaseen and Bennett 1977). The first introduction of a natural enemy of CGM into Africa was by scientists from the Commonwealth Institute of Biological Control. Later in 1980, IITA began the Africa-wide Biological Control Project (ABCP) to control exotic cassava pests using enemies introduced from the Neotropical region. More than ten species of phytoseiids were shipped from Colombia and Brazil to Africa. The Colombian species were *Galendromus annectens* (De Leon), *Euseius concordis* (Chant) and *Amblyseius limonicus* Garman and McGregor, *Euseius ho*, *Typhlodromalus tenuiscutus, Neoseiulus californicus*, and *Galendromus annectens* while the Brazilian were *Neoseiulus idaeus*, *Typhlodromalus aripo* and *Typhlodromalus manihoti*. None of the Colombian species survived in Africa but the three Brazilian species did. In 1993, *T. aripo* was reported

to be the most successful species released in Africa. A post-release survey showed that the natural enemies are associated temporally and spatially with CGM (Yaninek et al. 1993). The disappearance of *T. aripo* increased the severity of CGM on cassava plants. Cassava green mite is still a serious arthropod pest causing considerable damage to cassava in Nigeria, the largest producer of cassava, so there is a need to look for a genetic source of resistance to CGM.

Genetic Control of Cassava Green Mite

There has been limited work on the genetic control of CGM to uncover genomic regions associated with natural resistance to *M. tanajoa.* Some of the successes recorded include the identification of two SSR markers, NS 1099 and NS 346 which showed high association with CGM resistance (Choperena et al. 2012). Also, two quantitative trait loci (QTL) namely, qCGMc5Ar and qCGMc10Ar were identified on chromosomes 5 and 10 using a biparental population (Nzuki et al. 2017). Also, the genetic mechanisms underlying the resistance to CGM and its phenotypically associated traits (leaf pubescence, leaf retention, stay green, shoot tip size, and compactness) have been studied in diversity panels using genome-wide association mapping (Ezenwaka et al. 2018). The study identified the most significant SNP marker S8_5962253 on chromosome 8. Seventeen candidate genes including, Manes.08G058500, Manes.08G048200, Manes.08G048800, Manes.08G034200, Manes.08G046400, Manes.08G041900, Manes.08G026500, Manes.08G053900, Manes.08G060500, Manes.08G058000, Manes.08G045400, Manes.08G035100, Manes.08G043900, Manes.08G024700, Manes.08G046700, Manes.08G044000, and Manes.08G026900 were found to have a strong association with the genes conferring resistance to insects/pests in plants. Recently, using 109 F_1 progeny derived from a cross between CGM resistant parent, TMEB778, and a very susceptible parent, TMEB419, nine novel candidate genes on chromosome 12 were reported to be linked to CGM resistance (Ezenwaka et al. 2020).

Conventional phenotype-based recurrent selection to breed CGM-resistant varieties is lengthy and resource-intensive due to several biological aspects associated with cassava including low seed set, slow multiplication rate of planting materials, and 12-month growing cycle (Ceballos et al. 2012). Moreover, phenotypic selection for CGM resistance requires dry environmental conditions that favor *M. tanajoa* infestation for the identification of resistant varieties. When and where such conditions occur irregularly or non-uniformly, screening for the trait can be difficult. These challenges can be overcome using genomic-assisted and marker-assisted breeding tools that can facilitate indirect selection (Wolfe et al. 2016) (Fig. 1.2).

1.2.2.2 Cassava Mealybug

This is a distinct dry season pest in Africa that builds up during drought and high temperatures. It is indigenous to South America but was accidentally introduced into Africa in the early 1970s through vegetative planting material. First reported in the

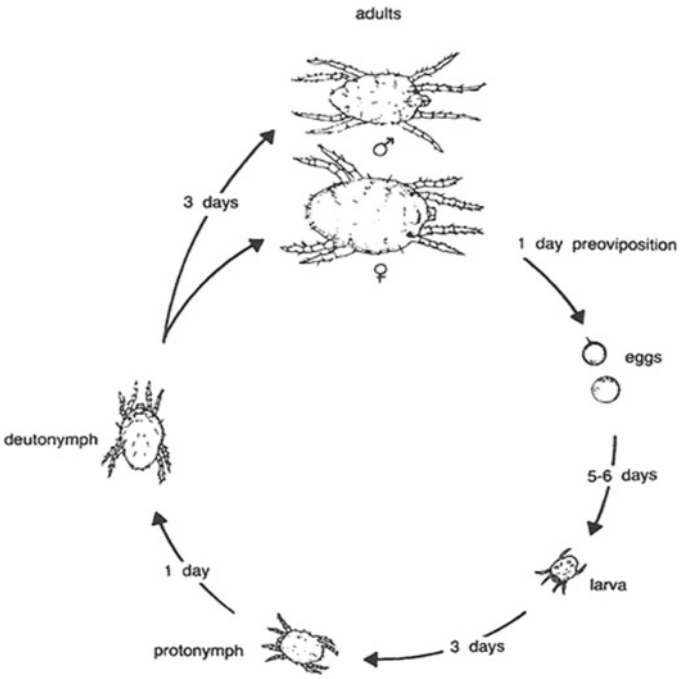

Fig. 1.2 Life cycle of CGM at a temperature of 27 °C with a relative humidity of 70%. Eggs to adult—12.5 days, adult life span—24 days, and fecundity—60 days. *Source* Yaninek et al. (1989a)

Congo Republic in 1973, it has spread to almost all cassava-growing areas in Africa from West through to East Africa and down to the eastern edge of South Africa (Herren and Neuenschwander 1991). The mealybug sucks sap from the phloem. Initially, it attacks the terminal ends of cassava shoots and later spreads to the petiole and expanded leaves. Shoot stunting and shortening of the internodes are believed to be caused by a toxigenic substance present in the insect's saliva. In cases of severe infestation, green shoots die but die-back may not occur. Tuber loss resulting from mealybug infestation has been estimated to range from 70 to 80%.

1.2.2.3 Cassava Whitefly

Worldwide, one of the biggest problems in the production of cassava is the presence of whiteflies (Hemiptera: Aleyrodidae), these whiteflies are complex species that cause direct damage by feeding on the phloem and indirectly by transmitting more than 100 different virus species (Navas-Castillo et al. 2011). A total of 1556 species of whitefly has been described (Forero 2008), but only 15 have been identified to be associated with cassava cultivation (Vásquez-Ordóñez et al. 2015). The genera, Bemisia and Trialeurodes, are only vectors of disease-causing viruses (Navas-Castillo et al. 2011).

In East Africa, the whitefly, *Bemisia tabaci* is among the most challenging to control because it is recognized as a pest species complex which means that multiple biologically distinct species exist within the species complex but cannot be readily differentiated due to the lack of distinct morphological attributes (Boykin and de Barro 2014). The *B. tabaci* cryptic species complex is agriculturally important because members within this complex are important vectors for the transmission of several plant viruses including begomoviruses, which are the most devastating group of viruses in the tropics (Maruthi et al. 2007). In Uganda, several *B. tabaci* putative species have been observed on cassava, including sub-Saharan Africa 1 (SSA1), SSA2, and the Indian Ocean (Boykin et al. 2018). In this group of species, SSA1 transmits viruses that cause the two most devastating cassava diseases namely, CMD and CBSD. These two diseases greatly reduce yields and compromise the quality of cassava tubers (Pennisi 2010). Many CMD-infected cassava varieties produce few or no tubers depending on the severity of the disease and the age of the plant at the time of infection. Phloem-feeding by *B. tabaci*, indirect damage caused by sooty mold, and transmission of plant viruses can cumulatively reduce yields by up to 80% (Kalyebi et al. 2018).

According to records, there has been an increase in the frequency of outbreaks of indigenous SSA members of the *B. tabaci* complex in the cassava growing regions of East Africa over the last 20 years, without much understanding of the ecological factors driving population peaks in *B. tabaci* (Legg et al. 2014; MacFadyen et al. 2018). However, there is no general agreement on managing African cassava *B. tabaci*. Instead, the breeding of new cassava varieties that are resistant or tolerant to CMD and CBSD continues to be the main approach for the management of cassava yield losses. In Uganda, about five improved cultivars are currently in use, including the numerous landraces that vary in yield and general tolerance to pests and diseases (Tumwegamire et al. 2018). Although the improved cassava varieties are generally preferred by farmers because of higher yields, early maturity, and greater resistance to diseases, most smallholder farmers engage in a mixture of varieties either as a mixed planting in one field or planted adjacently to other fields (Akoroda et al. 1987).

During colonization, certain factors may influence *B. tabaci* population growth or lead to adult preferences when colonizing a new plant. Although *B. tabaci* adults are known for long-distance migration, most times, not all movements to new plants are in response to reduced availability of feeding and oviposition sites (Isaacs and Byrne 1998; Mansveld et al. 1982). The *B. tabaci* may have a preference to host plants on which to oviposit via small-scale movements between plants within a field (Costa et al. 1991). Knowing the preferences of *B. tabaci* to oviposit on different cassava varieties and plants of different ages may lead to new management strategies that disrupt the colonization process. These strategies which could reduce *B. tabaci* population growth and ultimately the transmission of diseases may include changing planting time, alternating the variety planted, and increasing planting space (Fig. 1.3).

Fig. 1.3 Whitefly-infested cassava. *Source* Photo: L. A. Nwachukwu

1.3 Approaches for Developing Biotic Stress Resistant Cassava Varieties

1.3.1 Conventional Breeding Approach for Developing Biotic Stress Resistant Cassava Varieties

The use of the conventional breeding approach although it takes a longer time has been practically useful in developing outstanding cassava varieties that are resistant to major pests and diseases (Malik et al. 2020). The conventional breeding approach involves the production of full- or half-sib seeds in crossing blocks. Cassava genotypes are highly heterozygous as a result gives rise to polymorphic progenies that are genetically diverse during hybridization, which simply means that cassava at the F_1 stage is genetically distinct with a high level of segregation taking place. This invariably implies that many crosses are needed to generate seedlings with desirable interest. Cassava as an annual crop required three or more years to achieve a breeding cycle to produce enough stem cuttings for multi-location testing.

Conventional cassava breeding method shows only minor variations across many breeding programs with an emphasis on breeding objectives for pests and diseases resistance among other important agronomic and quality traits for both eastern and western Africa (Fukuda et al. 2002; Jennings and Iglesias 2002; Kawano and Cock 2005).

Breeding objectives depend on the ultimate use of the crop. In cassava, however, increased yield, drought resistance, multiple pests and disease resistance, desirable agronomic traits such as appropriate plant architecture, early bulking of storage roots, with high dry-matter content, low cyanide content, resistance to drought, and other biotic stress and consumer preference traits, e.g., easy peeling and early

vigor in plant growth (for high foliage yield for leaf vegetable) have been the main breeding objectives. Recently breeding for improved micronutrient content has been emphasized (Gregorio 2002).

The breeding values of the parents are evaluated through progeny testing in seedling nurseries. Based on evaluations, selected parental clones or half-sib progenies are hybridized for further improvement in a recurrent selection scheme. Backcrossing has also been a useful procedure for the transfer of resistance into elite populations by providing resistant lines quickly to prevent the severe infestation of relevant pests.

In cassava, resistance to pests and diseases such as super-elongation disease, or reaction to whiteflies or thrips, are considered to have high heritability. For example, the resistance to the trips *Frankliniella williamsi* depends on the pubescence on the leaves in the apical shoot which is stable and readily identifiable. Resistance to the whitefly *Aleurotrachelus socialis* is linked to antibiosis (Bellotti 2009).

Conventionally, breeding stages can be classified into the development phase (hybridization and seedling nursery stage) and evaluation phase (preliminary yield trial—PYT, advance yield trial—AYT, and uniform yield trial—UYT) (Fig. 1.4). To breed for biotic stress resistance cassava conventionally, genetically diverse populations from different backgrounds of agro-ecologies through recurrent selection and backcrossing methods are developed using multiple crossing schemes. Individuals that are resistant to biotic stress are selected as parents and segregating families are generated by multiple crosses among these resistant clones, complementing various agronomic and consumer-quality traits. These parental lines are evaluated

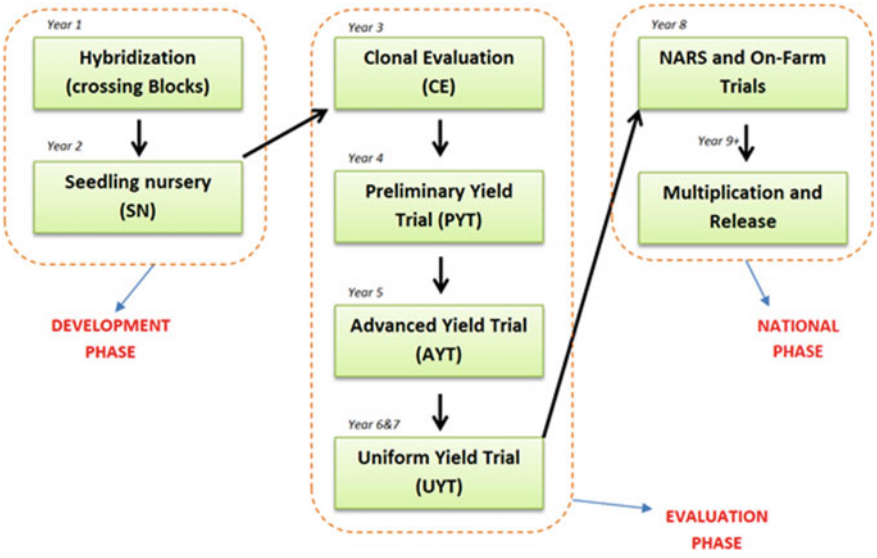

Fig. 1.4 Conventional cassava breeding pipeline

and selected using the progeny testing and breeding values of the seedlings. Resistance can be introduced into the elite population by further making crosses among the selected parental clones in both recurrent and backcrossing breeding methods to prevent infestation and infection of pest and disease respectively.

Thousands of botanical seeds produced from the crosses within one year will be grown in the F1 seedling nursery in year 2. When the seedling nursery field is matured within one year, selection will be carried out based on traits that have high heritability for vigor, architecture, quality, potential yield, pests, and diseases; After which, hundreds of selected individual plants that are pest and disease resistant in the seedling nursery are cloned for single row trials of 5–8 plants per genotype in year 3. At the subsequent stages (PYT, AYT, and UYT stages) of evaluations and selections, the number of genotypes to be evaluated reduced widely from hundreds to tens of genotypes respectively while the number of plants per clone per plot in the different stages of the evaluation process increases progressively (Ceballos et al. 2012). Multilocation evaluation of the selected genotypes is required at the AYT and UYT stages to evaluate resistance and performance across different agro-ecological zones.

High and stable cassava varieties with biotic stress resistance have the opportunity of expanding and exploiting genetic variability that would generate clones with increased value for the different industrial processes where cassava can be a strategic raw material. When cassava is used as a food security crop, additional requirements need to be addressed for a variety to be adopted (Teeken et al. 2018).

1.3.1.1 Breakthroughs of Conventional Breeding for Biotic Stress in Cassava

Conventional breeding has been useful in breeding a range of selected cassava genotypes that combine high stable yields, agronomic and consumer quality with acceptable levels of resistance to CMD, CBB, CGM, and CBSD (Ezenwaka et al. 2020; Kawuki et al. 2016; Okogbenin et al. 2012, 2007). The introduction of Latin American germplasm into the breeding programs in Africa has significantly broadened the genetic base of cassava in Africa. Genotypes with resistance to several pests and diseases have been selected and recombined by genetic crosses to form the basis of selection and breeding for different agro-ecosystem (Ceballos et al. 2016; CIAT 2009; Kawano and Cock 2005). Many breeding approaches including farmer participatory schemes have been employed to evaluate recombinant progenies and select several varieties positive for several traits and widely adapted to a range of environments (Ceballos et al. 2012a).

The presence of the major biotic constraint like CMD, which was not found in Latin America, limits the immediate use of the germplasm from that region and requires introgression of CMD resistance into the Latin American germplasm before being used for breeding. Resistance to CMD has been developed using backcrosses and wide evaluation to account for genotype-by-environment variation. The development of improved germplasm promotes the extension of cassava cultivation beyond

its traditional area in the humid and sub-humid tropics into the semi-arid zones (Kawano 2003).

1.3.1.2 Limitations of Conventional Breeding in Biotic Stress Resistant Variety Development

Most of the important traits in cassava are polygenic (Amma and Sheela 1995). Variation in polygenic traits is attributed to QTL. Quantitative traits in plants are studied using a variety of genetic models and designs including the analysis of mating designs in segregating populations to estimate effective factors using biometrical techniques. Biometrical methods can also be used to estimate useful factors for quantitative traits (Lynch and Walsh 1998). As a result of limitations found in using conventional breeding techniques, advances in molecular breeding techniques are required for breeding for the resistance of cassava varieties to major biotic stress.

1.3.2 Molecular Techniques for Biotic Stress Improvement in Cassava

Although the traditional breeding approach in cassava has been used for a long time, it still has notable drawbacks that require improvement. The traditional approach is mostly based on a single individual phenotypic selection where scanty information including family structure is available and utilized at the early stages of selection. Also, many genotypes are eliminated at this early stage of selection where trials are not replicated. For traits that are highly affected by the constantly changing environmental variables, selections without extensive multi-location and multi-year observation could be unreliable. The evaluation of many genotypes has cost implications in crop improvement. Conventional methods depend on the vast evaluation of genotypes over many years and multiple locations and require a lot of resources to sustain such efforts. Therefore, coupled with the low and somewhat variable flowering and seed-set pattern in cassava, improvement strategies based on the traditional breeding approach could be inefficient, expensive, and difficult (Ceballos et al. 2004, 2012a; Kawano et al. 1998). Therefore, the adaptation of new breeding technologies is necessary to make genetic improvement in cassava more efficient and effective.

The continuous dwindling of sequencing cost brought about by the recent innovations in genomics, molecular biology, and statistical genetics has led to the affordability and availability of molecular markers in many breeding programs, which in turn encourages the adoption of advanced marker-based breeding techniques.

Wide-distributed molecular markers have been important in dissecting the association between the markers and variation in various phenotypes of interest using distinct parents in QTL mapping or a wider diverse population in genome-wide association studies (GWAS). In marker-assisted selection (MAS), molecular markers in

or near genes that affect the phenotype of interest can be used in screening genotypes, to track if the specific gene or chromosome segment(s) known to affect the phenotype is present in a given selection of candidates, individuals, or populations. Various population designs have been adopted for QTL mapping and may include F_2, F_2-derived, backcross inbred lines (BILs), doubled haploids (DHs), recombinant inbred lines (RILs), near-isogenic lines (NILs), chromosomal segment substitution lines (CSSLs), multi-parent advanced generation intercross (MAGIC), nested association mapping (NAM), etc. (Collard and Mackill 2008; Singh and Singh 2015). Evidence of QTL mapping in cassava using mostly F_1, F_2, and backcross populations have been reported for agronomic, productivity, quality, and post-harvest traits (Akinbo et al. 2012; Fernando Cortés et al. 2002; Okogbenin et al. 2008; Okogbenin and Fregene 2003).

Specifically, many QTLs have been identified for biotic stress improvement in cassava including CMD (Akano et al. 2002; Luisa Garcia-Oliveira et al. 2020; Masumba et al. 2017; Nzuki et al. 2017; Okogbenin et al. 2007), CBB (Jorge et al. 2000; Soto Sedano et al. 2017a, b; Wydra et al. 2004), CAD (Boonchanawiwat et al. 2016), CBSD (Luisa Garcia-Oliveira et al. 2020; Masumba et al. 2017; Nzuki et al. 2017), and CGM (Ezenwaka et al. 2020; Luisa Garcia-Oliveira et al. 2020; Nzuki et al. 2017). The potentials for practical application of the dissected QTLs for selection in breeding programs have also been demonstrated, although more evidence, especially for polygenic traits are needed (Bi et al. 2010; Lokko et al. 2006; Okogbenin et al. 2007, 2012; Olasanmi et al. 2021).

Recently, following the increase in funding for cassava research and the availability of improved genomic and other resources, the adoption of GWAS for QTL identification has been on the increase due to the inherent limitations of QTL mapping using narrow populations. Quantitative trait loci mapping detects only a small number of QTL with major effects compared to the total genetic variation underlying most of the polygenic quantitative traits; and it leverages only on the allelic diversity present in a specific family which might not be relevant in other mapping families (Dekkers 2004; Korte and Farlow 2013). Genome-wide association studies, on the other hand, evaluate the association between each genotyped marker and a phenotype of interest that has been scored across a large number of individuals. Genome-side association studies are relevant in detecting causative/predictive factors for a given trait or to determining aspects of the genetic architecture of the trait (Korte and Farlow 2013; Spindel et al. 2015). The adoption of GWAS in the detection of the genetic basis for biotic stress resistance in cassava has been reported (Ezenwaka et al. 2018; Kayondo et al. 2018; Rabbi et al. 2014a; Somo et al. 2020; Wolfe et al. 2016, 2017).

Unlike GWAS, genomic selection (GS) combines marker data with phenotypic and pedigree data (when available) in an attempt to predict the merit or the genomic estimated breeding values (GEBVs) based on the marker genotypes of selection candidates or populations from a prior developed model on observed records (Goddard and Hayes 2007; Lin et al. 2014; Meuwissen et al. 2001). Genomic selection promises to promote rapid selection of superior clones or populations and fast-tracks breeding cycles of plants and animals. Since GS reduces breeding cycles, it saves

phenotyping and the overall cost of breeding. The option of combining genome-wide markers, phenotypic, pedigree, environmental, and omics information such as transcriptomics and metabolomics in GS creates an endless possibility of improving prediction accuracies in many settings (Pott et al. 2021; Xu et al. 2017).

Besides, the ability to leverage on correlations between traits, the possibility of multiple traits prediction and selection have been demonstrated with improved prediction accuracies over the single trait GS (Calus and Veerkamp 2011; Ikeogu et al. 2019; Jia and Jannink 2012; Okeke et al. 2017). The use of genome-wide markers ensures that all QTL in linkage equilibrium with a minimum of a single marker and hopes to capture most of the genetic variation of mostly quantitative traits. The breeding lines with high GEBVs could serve as a potential material in breeding programs. The implementation of GS in cassava breeding serves as a model for the improvement of root and tuber as well as orphan crops. It provided empirical evidence on the potential of GS in crop improvement. The practical application of GS for biotic traits improvement in cassava is well underway (Kayondo et al. 2018; Ozimati et al. 2018; Wolfe et al. 2016, 2017). It is being adopted as the modern breeding tool in many cassava breeding programs.

1.3.3 The Adoption of Genetic Engineering in Genomic Designing for Biotic Stress Resistant Cassava

Studies have shown that the introduction of genetically engineered crops has had significant impacts on disease management (Bart and Taylor 2017). Over the years, there has been a concerted effort to engineer resistance against several economically important cassava pests and diseases, due to bottlenecks encountered using conventional or molecular breeding approaches. These bottlenecks mostly stem from cassava being propagated asexually resulting in severe inbreeding depression (Ceballos et al. 2015; de Oliveira et al. 2018). Increasing investments in cassava genomics research and reducing costs of next-generation sequencing have led to the development of genomic resources that provide insight into the cassava genome, accelerating progress in cassava research and genetic improvement (Malik et al. 2020; Mbanjo et al. 2021). Engineering for genetic improvement and most especially disease resistance in cassava has mostly relied on stable *Agrobacterium-mediated* transformation of friable embryogenic calli (FEC) or pathogen-derived resistance. This transgenic technology was adapted from the mechanism by which *A. tumefacians* causes a plant tumor called "crown gall" (Howell et al. 2018). It was discovered in the '70s that a large portion of the *A. tumefaciens* tumor-inducing plasmid, called transfer DNA (T-DNA), could be transferred to plant cells causing a permanent genetic change. The T-DNA could be replaced with a gene of interest and transferred to plant cells inducing specific permanent changes. Compared to other methods of transformation like the microprojectile bombardment method, *Agrobacterium-mediated* transformation is highly efficient, with reduced risks of carrying chimeras, highly reproducible,

requiring simple equipment, and expresses stable transgenes (Bull 2015). Under contained conditions like a growth chamber or greenhouse, both methods have been used to inoculate cassava plantlets with CMD in a bid to screen for resistance among plantlets (Fofana et al. 2004; Vanderschuren et al. 2009). These methods of evaluation for resistance are usually lengthy (12–22 weeks). In 2017, (Beyene et al. 2018) reported on the use of a virus-induced gene silencing method that rapidly (2–4 weeks) screens for resistance to CMD.

In 2005, Zhang et al. (2005) demonstrated that high levels of resistance to CMD were a result of a natural defense mechanism of plants called post-transcriptional gene silencing or RNA silencing. Over the years, different laboratories have optimized interference RNA produced from this mechanism for CMD and CBSD resistant genes in the model cassava genotype TMS60444. This has produced varying levels of resistance against several *Begamoviruses* and both *Ipomoviruses* (Ntui et al. 2015; Rey and Vanderschuren 2017; Vanderschuren et al. 2012). Subsequent control field trials have been carried out to assess the efficacy of the transgenic plants in high disease locations in East and West Africa (Lin et al. 2019). In the model cassava cultivar, 60,444, there have been attempts to engineer resistance against CBB by identifying microRNAs that respond to the pathogen, over-expression, and silencing of the resistant gene *RXam1* and the over-expression of R gene *Bs2*, with varying levels of success (Quintero et al. 2013; Zárate-Chaves et al. 2021). To sustain the efficient generation of transgenic cassava transformation protocols must enable the production of stable FEC that can be sub-cultured to establish embryogenic suspensions (Zhang et al. 2017). Studies have shown that FEC induction in cassava is genotype-specific. For example, Ugandan scientists were able to produce high-quality FEC from local varieties Ebwanatereka and Aladu but not Bukalasa (Apio et al. 2015). It is therefore necessary that FEC production protocols are developed and optimized for each cassava genotype. Recent reports have identified a phenomenon where transgenic cassava carrying the CMD-type 2 resistant gene loses their disease resistance. Due to this drawback, gene editing technologies are currently being used to circumvent this sudden susceptibility.

1.3.4 Genome Editing in Genomic Designing for Biotic Stress Resistant Cassava

Pathogens in a plant-pathogen interaction have adopted different forms of circumventing a host plant immune response. One of such forms involves the pathogen secreting proteins or effectors that interact with a singular host susceptibility gene or a gene family (Bastet et al. 2017). Mutations of these susceptibility genes have been used as sources of resistance for many years (Dangl et al. 2013). Genome editing allows a rapid and more precise approach to modifying specific sequence sites conferring resistance or other genetic gains to the host organism. Because of its simple design and ease of use, clustered regularly interspaced

short palindromic repeats/Cas systems (CRISPR/Cas systems) are fast becoming the genome-editing tool of choice. It is a mechanism adapted from the defense pathway of bacteria and archaea. This technology uses *Cas* 9 (endonuclease of *Streptococcus pyogenes*) guided by a synthetic single-guide RNA to create double-stranded breaks at targeted sites of invading phages or conjugative plasmids. These breaks undergo repairs frequently through an imprecise non-homologous end-joining repair machinery that generates insertions or deletions (INDEL) altering the target gene's function. This system has been demonstrated to confer resistance to several destructive geminiviruses, *Xanthomonas,* and potyviruses in model plants like *Nicotiana benthamiana, Arabidopsis thaliana,* and tomato (Chandrasekaran et al. 2016; Nekrasov et al. 2017; Pyott et al. 2016). Gene editing technologies can accelerate this process of conferring resistance, by allowing the transfer of strategies from model plants to non-model crops like cassava. The frequently used CRISPR-Cas9 system is still in its infancy in cassava genetic improvement with varying levels of success (Bull et al. 2018; Odipio et al. 2017). The genetic editing strategy has been implemented against three major cassava diseases in SSA; CBSD, CBB, and CMD. Against CBSD, previous studies on how potyviruses evade a plant host immune system indicated that the pathogens generate viral genome-linked protein (VPg) that must interact with members of host eukaryotic translation initiation factor 4E (eIF4E). Of the five members of cassava's eIF4E, yeast two-hybrid and co-immunoprecipitation experiments showed that the viral VPg interacts mostly with novel cap-binding protein (nCBP). Editing the nCBP produced mutants in the model cassava 60,444 and on graft inoculating the plant with the pathogen revealed a delayed response with reduced symptom severity (Gomez et al. 2019). Against CBB, the effector protein *Xam-TAL20*, secreted by the pathogen, interacts with the promoter of cassava *MeSWEET10a*, altering its expression (Cohn et al. 2014). When it does not interact with this susceptibility factor, symptoms are markedly reduced (Lin et al. 2019). By exploiting the repair machinery at the cassava *MeSWEET10a* a tool was recently developed to visualize the initial steps of CBB infection, for the first time in vivo (Veley et al. 2021) Unlike the other pathogens, CMD does not have a known susceptibility factor to be altered, but the pathogen itself can be a target for genome editing (Gomez et al. 2019). Although genome editing of the CMD pathogen produced mutant forms it failed to confer resistance to the disease in cassava plantlets and subsequently produced novel viral mutants that cannot be altered by the CRISPR/Cas system. Unintended consequences like this are one of the reasons why stringent biosafety regulations are required for handling transgenic materials.

1.4 Future Perspectives in the Genomic Designing for Biotic Stress Resistant Cassava

Biotic stress affects the yield of cassava and negatively impacts the economic well-being as well as the nutrition of millions of people around the globe that depend on

the crop for their livelihood and source of food. Fortunately, besides the integrated approaches adopted in controlling biotic stress, there are genetic resources in many breeding programs that are available in combating and breeding for resistance to known and immerging pathogens of biotic stress in cassava. Although traditional plant breeding methods for improving biotic stress resistance in cassava have been successful, the method is generally laborious, inefficient, and time-consuming. The adoption of emerging technologies is therefore relevant to meet the rising demand for cassava as food, feed, and a source of industrial raw material for so many processes. Similar to integrated pests and disease management schemes, the strategic design of integrated techniques will be important in developing new products that will meet the need of farmers. The sustainability of the cheap sequencing method will continue to play important role in supporting the ongoing adoption of new breeding tools for the development of varieties that combine biotic stress resistance with high yields and good quality traits in cassava. Integrating high-throughput phenotyping or phenomics with other techniques including transcriptomics, metabolomics, bioinformatics, and genome editing will continue to revolutionize cassava breeding leading to improved selection accuracy, higher genetic gain, and reduced breeding cycle in the crop. Good data storage and management system has been pivotal and will continue to play a key role in modern cassava breeding for biotic stress improvement.

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