

REVIEW

Cassava (*Manihot esculenta*) dual use for food and bioenergy: A review

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Funding information

Royal Society and African Academy of Sciences, Grant/Award Number: FLR\R1\201370

Abstract

Cassava (*Manihot esculenta*, Crantz) is a starch-rich, woody tuberous, root crop important for food, with little being done to investigate its potential as a bioenergy crop despite its enormous potential. The major bottleneck in the crop being able to serve this dual role is the competition of its storage roots for both purposes. The major cassava production regions primarily use the tuberous roots for food, and this has resulted in its neglect as a bioenergy crop. The use of non-food cassava parts as a feedstock in cellulosic biofuel production is a promising strategy that can overcome this challenge. However, in non-tuber parts, most of the sugars are highly sequestered in lignin complexes making them inaccessible to bacterial bioconversion. Additionally, cassava production in these major growing areas is not optimal owing to several production constraints. The challenges affecting cassava production as a food and bioenergy crop are interconnected and therefore need to be addressed together. Cassava improvement against biotic and abiotic stresses can enhance productivity and cater for the high demand of the roots for food and bioenergy production. Furthermore, increased production will enhance the usability of non-food parts for bioenergy as the bigger goal. This review addresses efforts in cassava improvement against stresses that reduce its productivity as well as strategies that enhance biomass production, both important for food and bioenergy. Additionally, prospective strategies that could ease bioconversion of cassava for enhanced bioenergy production are explored.

KEYWORDS

bioenergy, biomass and improvement, cassava, food, roots

1 | INTRODUCTION

Cassava is an important food crop with an average consumption of 50 kg/capita/year in Africa (FAO, 2018). The global cassava production stands at slightly over 11

tonnes per hectare. Over 63% of the 303 million tonnes produced globally in 2019 was from Africa (FAO, 2019). Despite being the leading region in cassava production, only 3000 tonnes of the produce are dedicated to non-food uses. The challenges associated with global fossil fuels

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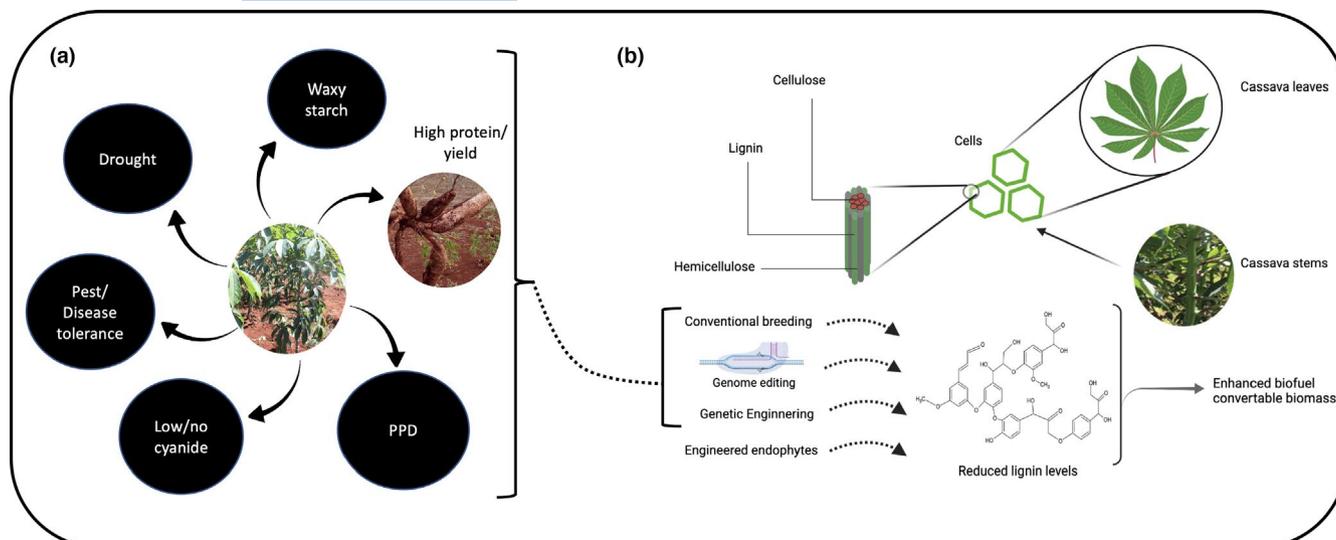


FIGURE 1 Schematic representation of challenges that affect the use of cassava for food and bioenergy and approaches towards minimizing these constraints. (a) Target traits in improving cassava for food and bioenergy, (b) approaches that can be used to reduce lignin levels in cassava biomass, PPD – Post-harvest physiological deterioration

have necessitated the development of alternative energy technologies. One such is the use of plant biomass as feedstock in the production of clean energy. Cassava is a potentially scalable high biomass producing crop. Compared to other potential bioenergy crops, cassava is adaptable to low fertile lands and less favourable climatic conditions like drought (Jolayemi & Opabode, 2018). First-generation biofuels are mainly produced from fermentation of sugars derived from food crops (Hirani et al., 2018). The second-generation biofuels are derived from non-food crops (Awogbemi et al., 2021) or lignocellulosic feedstocks and agricultural residues (Morato et al., 2019). Cassava's tuberous root is the main part used for both bioethanol and food, resulting in direct competition. However, plant parts like stem are only used as planting materials with leaves minimally used as food and the remains from the two are disposed off after harvest. The stems and leaves also have bioenergy potential. The cassava stem contains about 11.62% hemicellulose and 21.43% cellulose as fermentable sugars in the form of lignocellulose (Sovorawet & Kongkiattikajorn, 2012). This means cassava can serve as feedstock to produce both first- and second-generation biofuels. The bioethanol production potential of cassava was found to be like other major bioenergy crops such as corn (Pradyawong et al., 2018). The growing demand for bioethanol has resulted in a 2% increase in global production from 111 billion litres in 2018 to 114 billion litres in 2019 (REN21, 2019). This demand has turned cassava into a cash crop, with countries like Thailand, Cambodia, Colombia, Vietnam, China and India dedicating production to bioethanol (Marx, 2019). In regions where cassava is mainly cultivated for food, there is a strong cultivar preference by farmers and non-preferred varieties could

be dedicated to industrial purposes. This, coupled with access to arable land could enable the expansion of cassava-based bioethanol production.

Despite this possibility, the non-food use of cassava root tubers in the producing belt is minimal due to their dedication to food. The utilization of cassava residues with high levels of fermentable but inaccessible sugars is a promising strategy for second-generation bioenergy production (Wei et al., 2015). This approach ensures that tubers are dedicated for food, and the stems (remaining after planting) together with the leaves (normally left to rot in the field) are used for bioethanol. Additionally, the development of genotypes with reduced lignin recalcitrance as reviewed by Christensen and Rasmussen (2019) for exclusive bioenergy use will have less food security concerns.

Notwithstanding cassava's importance in food and bioenergy, its cultivation is faced with a myriad of challenges. These include the emergence and re-emergence of pests and diseases, which are a direct threat to the existing cultivars, most of which lack resistance (Ogwok et al., 2016). Among the major cassava diseases are cassava mosaic disease (CMD) caused by mosaic virus (CMV) variants (Houngue, Pita, et al., 2019), cassava brown streak disease caused by cassava brown streak virus (CBSV)/Uganda cassava mosaic virus (UCBSV) (Alicai et al., 2007; Tomlinson et al., 2018) and cassava bacterial wilt resulting from *Xanthomonas axonopodis* pv. *manihotis* (Fanou et al., 2018). Cassava diseases can be devastating, leading to complete loss of productivity. In addition to diseases, cassava is attacked by equally devastating pests, including mites, whiteflies and thrips (Lebot, 2020). Change in climate in the regions where cassava is grown is additional stress that negatively impacts production (Pipitpukdee

et al., 2020). Cultivars with unfavourable physiological adaptations to the changing climate will produce less. Additionally, climate change results in the spread of pests and diseases to areas where they previously did not exist. The increased pest and disease burden leads to less productivity. Improving cassava's resilience to the different challenges is the most sustainable and sure way of enhancing productivity. Cassava improvement is particularly critical if cassava is to serve the dual role as a food and bioenergy crop (Figure 1).

Improvement of cassava has mainly been through conventional breeding with programmes in South America, Africa and Asia. The major breeding efforts in South America (Brazil), Eastern and Western Africa started in the 1930s and are still going on (Ceballos et al., 2020, IITA, The NextGen Cassava Project, 2021). These breeding efforts have successfully resulted in the development of disease-resistant cultivars like the CMV-resistant Namikonga among others (Kawuki et al., 2016). Despite the successes, major challenges to conventional cassava breeding in asynchronous or complete lack of flowering in potential breeding lines, long breeding cycles and poor seed set still exist. Alternative approaches in cassava improvement include genetic engineering and genome editing. Genome editing is still in its infancy in cassava but holds a lot of potential. There is substantial progress in cassava genetic engineering with the potential release of the first genetically engineered cassava with tolerance to CBSD in Kenya (National Biosafety Authority, Kenya, 2021).

This study reviews efforts geared towards improving cassava's resilience to challenges affecting its productivity. These challenges affect cassava productivity for both food and bioenergy. The article further explores potential approaches in addition to those implemented in cassava that could facilitate the use of its biomass in bioenergy. These approaches are anchored on the use of alternative feedstock like stems, leaves and peels that would otherwise be disposed after harvest of roots. These strategies would ensure farmers can venture into cassava for bioenergy without jeopardizing its status as an important food crop.

2 | IMPROVEMENT OF CASSAVA AGAINST BIOTIC STRESSES

Pests and diseases are projected to be second to drought in affecting cassava productivity (Jarvis et al., 2012). The dynamics and distribution of major cassava pests are projected to change with changes in climate. Cassava pests include, among others, whiteflies and mites, the former being the insect vector for two devastating cassava viruses (cassava brown streak virus – CBSV, and cassava mosaic

virus – CMV) (Jarvis et al., 2012). Efforts towards cassava improvement against the major pests and diseases are explored.

2.1 | Improving against pests and diseases

Whiteflies (*Bemisia tabaci*) are doubly tragic, causing direct plant damage as well as transmitting major cassava viral diseases. In a study over a 39-year period within which there were major whitefly pandemic episodes, increased cases of whitefly transmitted diseases were observed, and these correlated with improved conditions of insect proliferation (Kriticos et al., 2020). Efforts to breed cassava for insect resistance are limited since the focus has been on breeding for resistance to diseases vectored by viruses (Parry et al., 2020). However, a limited number of studies have been conducted mainly to identify sources of pest resistance in cassava populations. There are African and South American genotypes that have been reported to have some levels of resistance to whiteflies (Gwandu et al., 2019; Omongo et al., 2012). Ten cassava genotypes evaluated in Uganda showed resistance to whitefly infestation and feeding damage, suggesting that they could be used as parental materials in breeding programmes for both whitefly and viral disease resistance (Gwandu et al., 2019; Omongo et al., 2012). The South American genotype MEcu 72 and three Ugandan genotypes were observed to have resistance to whiteflies (Omongo et al., 2012). In a similar study at the International Institute of Tropical Agriculture (IITA) in Nigeria, two genotypes, 96/1089A and TMS 30572, supported the lowest number of whiteflies (Ariyo et al., 2005). These studies indicate possible resistance to whiteflies in genotypes from within the major cassava growing regions. These can be harnessed and integrated into breeding programmes for enhanced resistance. Additionally, studies to identify the mechanisms involved in the resistance could be pursued.

Unlike whiteflies, cassava green mites (*Mononychellus tanajoa*) have a limited number of diseases they vector. However, they are still extremely devastating to cassava resulting in up to 80% loss in productivity (Ezenwaka et al., 2018, 2020; Hahn, Leuschner, et al., 1980; Nukenine et al., 2002). The cassava green mites (CGM) are considered the most destructive dry season cassava pests (Ezenwaka et al., 2020). The fact that CGM affects cassava in the dry season makes it more lethal, with the projected drier future climates. Several studies have identified resistance to mites in different cassava genotypes (Ezenwaka et al., 2018, 2020; Hahn, Leuschner, et al., 1980; Nukenine et al., 2002). Over 300 of 5000 accessions in the CIAT germplasm were observed to have

some degree of resistance to CGM (Michelbacher, 1954). At IITA Tanzania, 58 of 377 clones tested under natural resistance to CGM were observed to have classes I and II resistance (Hahn, Leuschner, et al., 1980). Some of the clones with resistance identified from Zanzibar were also observed to be high yielding, had resistance to cassava mosaic disease (CMD) and acceptable consumer quality (Chalwe et al., 2015). Other than genetic improvement approaches, biocontrol approaches against CGM have successfully been used (Onzo et al., 2005). The studies on resistance to CGM, just like in whiteflies, point towards possible breeding for their tolerance or resistance. Tolerance to multiple pests has not yet been reported, and there is the possibility of resistance to multiple pests through gene pyramiding using different technologies. Pyramiding can be achieved by crossing varieties with resistance to multiple pests or use of technologies like genetic engineering and genome editing. Pyramiding of traits would not only be an efficient way to use resources but would also save breeding time.

Cassava is vegetatively propagated from stem cuttings, and farmers obtain planting material from their own farms or surplus material from their neighbours. This practice leads to the accumulation and transmission of various pathogens, particularly viruses, from the infected low-quality planting material. The three most devastating cassava diseases are CBSD, CMD and bacterial blight. CMD is caused by a group of similar bipartite single-stranded DNA Begomoviruses transmitted by whiteflies (Ariyo et al., 2005). The resistance to CMD was bred into *Manihot esculenta* beginning in 1935 well into the 1970s and is currently ongoing. Three types of CMD resistance exist in cassava: CMD1 which is by a recessive gene, CMD2 by a major dominant gene and CMD3 that has CMD2 in addition to a QTL (Hahn et al., 1980). The CMD resistance present in the tropical *Manihot* species (TMS) series has been bred into other African cultivars (Houngue, Zandjanakou-Tachin, et al., 2019; Nzuki et al., 2017; Okogbenin et al., 2007; Rabbi et al., 2014; Wolfe et al., 2016). Resistant cultivars have also been identified in farmer-preferred cultivars exemplified by efforts in Benin and Nigeria. Recently, there have been observations of the breakdown in CMD2 resistance breakdown when genotypes go through tissue culture (Beyene et al., 2016). Furthermore, two sequences enhancing CMV symptoms (SEGs) found within the cassava genome have been observed to breakdown CMD2 resistance (Ndunguru et al., 2016). The CMD2 resistance is the dominant resistance, and the observations of breakdown are worrying, although additional efforts to identify other forms of resistance are going on.

CBSD is considered the most devastating cassava disease in Africa (Pariyo et al., 2015). Unlike CMD, whose resistance breeding is well established, CBSD tolerance

is not as elaborately implemented mainly due low levels of resistance, lack of appropriate CBSD characterization in resistant genotypes as well as genotypes–environment interactions (Kayondo et al., 2018). The sources of CBSD resistance are the species *M. glaziovii* and *M. melanobasis* through breeding efforts that began in Tanzania in the late 50s and early 60s (Ogburia et al., 2000; Rao 2018). These early breeding efforts were entirely based on the polygenic inheritance nature of CBSD resistance (Shirima et al., 2020). Efforts to characterize and map the resistance in farmer-preferred cultivars in Tanzania and from other regions have resulted in the identification of loci in a number of these cultivars (Shirima et al., 2020). Due to complexity in the inheritance of CBSD resistance, efforts to characterize and map resistance will continue in tandem with breeding efforts.

CBB, a cassava bacterial disease widespread in all production belts, is caused by *Xanthomonas axonopodis* pv. *manihotis*. The CBB is manifested as damage to the root and leaf, with the level of severity being cultivar dependent (Fanou et al., 2018). Like other cassava diseases, overcoming CBB can be sustainably achieved through cultivar improvement. The CBB resistance is equally polygenic and was first obtained by crossing cultivated cassava with its wild relative *M. glaziovii* (Hahn, 1978). Evaluation of crosses made in the 1970s continued in IITA where the sources of resistance were found to be recessive and additive. Following conventional breeding efforts, CBB resistance was observed to be stable (Hahn, 1978). Further characterization of CBB resistance in Colombia has unearthed 29 resistance genes associated with a QTL that account for up to 22% of the resistance (Soto Sedano et al., 2017). Several other studies have also identified the levels of QTL contribution to CBB resistance (Jorge et al., 2001; López et al., 2007). The polygenic nature of inheritance to CBB means that the environment plays a big role and must be considered during screening. Efforts to identify the actual cassava genomic regions contributing to resistance will ensure a complete understanding of the nature of resistance.

3 | CASSAVA IMPROVEMENT AGAINST ABIOTIC STRESSES

Compared to other major cultivated crops, cassava is relatively tolerant to major abiotic stresses, including drought and low nutrient soils (Alves, 2002; El-Sharkawy, 2004, 2012a; Splittstoesser & Tunya, 1992). Drought is, however, predicted to affect future cassava productivity the most owing to the dramatic changes in climate. Cassava overcomes drought through escape or avoidance, tolerance and recovery (Oliveira et al., 2015).

3.1 | Enhancing drought resilience

Cassava tolerance to drought is a polygenic trait; therefore, variations in its levels vary with genotype. Cassava cultivation under prolonged drought (>6 months) conditions adapts by rapid stomatal closure (El-Sharkawy, 2004), shedding of existing leaves and production of small and fewer leaves (Alves, 2002; Splittstoesser & Tunya, 1992). These coping mechanisms result in reduced photosynthesis and starch accumulation in the roots. Drought tolerance in cassava therefore comes at the cost of yield (El-Sharkawy et al., 2012b; Okogbenin et al., 2013). The continued climate changes are anticipated to result in the spread of drought and drought-like conditions across cassava production belt (Jarvis et al., 2012). Therefore, it is imperative that enhancing drought resilience in cassava is pursued more so for cultivars that have comparatively lower levels of tolerance.

The main requirement towards enhancing drought tolerance is, first, the identification of genotypes with known tolerance within germplasm collections. These efforts have been ongoing for years in various national agricultural research organizations and the two major international research centres working on cassava: The Centro Internacional de Agricultura Tropical (CIAT) in Columbia and IITA in Nigeria. In Brazil, dry conditions in the North have favoured screening of wide germplasm under drought conditions where extensive variation was observed (El-Sharkawy, 1993; Oliveira et al., 2015). Similar screening has been achieved in Africa and Asia (Jolayemi & Opabode, 2018; Orek et al., 2020; Shan et al., 2018), with all the studies grouping cultivars as drought susceptible or tolerant. Methods for phenotyping drought have extensively been reviewed, and the target parameters include, among others: the number and height of primary stems, leaf stomatal conductance, retention and abscisic acid (ABA) content (Okogbenin et al., 2013). The genotypes with enhanced drought tolerance levels are ultimately integrated into breeding programmes.

In addition to improved drought phenotyping approaches, genetic approaches have also been integrated into cassava breeding. These markers include simple ones like isoenzymes (Sumarani et al., 2004), expressed sequence tags (ESTs), simple sequence repeats (SSRs) (Wang et al., 2017), random amplified polymorphic DNA (RAPD) and random fragment length polymorphism (RFLP) (Soto et al., 2015). More complex approaches utilizing whole-genome single-nucleotide polymorphisms (SNPs) like genotyping by sequencing and genome-wide association mapping (dos Santos Silva et al., 2021) have also been harnessed. The major traits targeted in breeding for drought tolerance include enhanced leaf retention (stay green)

(Adetoro et al., 2021), root and shoot storage yields, dry matter and starch content (Oliveira et al., 2015).

4 | ENHANCING OTHER IMPORTANT TRAITS IN CASSAVA

4.1 | Improving cassava for food starch

Starchy cassava roots are prepared as food in different ways including boiling, pounding of flours and in drinks like bubble tea. The culinary qualities of different foods depend on the physicochemical characteristics of starch (Nuwamanya et al., 2008). Starch is primarily composed of a combination of amylopectin and amylose, which are glucose polymers. Amylopectin, the branched longer molecule, also constitutes the largest part in comparison to amylose, which is linear. The structural and physicochemical differences in amylopectin molecules are a consequence of the level of branching (Chisenga et al., 2019). The physicochemical characteristic of starch is genotype dependent, with the levels of amylose being the main factor affecting culinary qualities. Some of the qualities involved include pasting and gelatinization, both of which affect flour quality (Chisenga, 2021). Genotypes are categorized into four classes based on the levels of amylose: waxy, semi-waxy, normal-regular and high, with maximum amounts of 2, 15, 35 and >35% of amylose per total starch respectively (Chisenga, 2021). Most cultivated genotypes fall within the normal-regular group, but genotypes completely lacking amylose, aka waxy category, have been naturally reported (do Carmo et al., 2020; Toae et al., 2019). Mutants of the *granule-bound starch synthase (GBSS)* gene that is involved in amylose biosynthesis equally results in amylose-free cassava starch (Bull et al., 2018). One major application of waxy starch in the food industry is in food storage. Comparison of different waxy starches from cereals and tuber observed no syneresis in cassava waxy starch after 5 weeks of freezing (Sanchez et al., 2010). This observation makes cassava waxy starch the best food stabilizer among the waxy starches evaluated. Efforts to reduce amylose, a consequence of which is waxy starch, are underway using both conventional (Anggraini et al., 2009) and biotechnology approaches (Bull et al., 2018).

Another major characteristic gaining prominence is resistant starch (RS). The RS results from variation in the complexity of amylopectin branching, which consequently influences enzymatic breakdown in the human gut (Sanchez et al., 2010). The RS mimics dietary fibre by being indigestible in the small intestine, a consequence of which is lowering of large intestine pH, increase in faecal bulk, improvement in glucose tolerance and reduction in risks of colon cancer (Charles et al., 2005). The complexity

in amylopectin branching is genotype dependent (Ogbo & Okafor, 2015), and this trait could be enhanced through breeding and biotechnology.

The prospects of cassava being a raw material in beer brewing further diversifies its starch use. The beer brewing company DIAGEO is using cassava in brewing as an approach of mitigating climate change-associated risks to traditional brewing grains (Bedol, 2017). Other companies that have ventured into beer brewing using cassava include SABMiller through its subsidiary Cervejas de Mocambique (CDM) in Mozambique (France-Pressé, 2017).

4.2 | Cassava improvement against post-harvest physiological deterioration (PPD)

Post-harvest physiological deterioration (PPD) in cassava roots reduces shelf life and makes distribution laborious. The PPD is defined as an abiotic stress response caused by the oxidation of phenolic compounds (Reilly et al., 2003). Starch, the major component in the roots, deteriorates from PPD and further microbial attacks make it unsuitable to animal or human consumption (Okigbo et al., 2009; Reilly et al., 2003).

The various physical methods employed to tackle PPD have been both ineffective and expensive, especially with bulk harvest (Sanchez et al., 2013). Several studies to address PPD reported that reactive oxygen species (ROS) play a significant role (Michelbacher, 1954; Reilly et al., 2003). These major forms of ROS are free radicals including superoxide anion (O_2^-), hydroxyl radical (HO^\bullet) and non-radicals like hydrogen peroxide (H_2O_2) (Ray et al., 2012). The oxidative stress related to the onset of PPD can be delayed by either circumventing the ROS production or scavenging the ROS produced. It was found that the expression of cyanide-insensitive alternative oxidase (AOX) from *Arabidopsis* in cassava roots significantly reduced the ROS and thereby delayed the process of PPD (Sayre et al., 2011). Another strategy adopted was to propagate cassava roots in higher β -carotene levels, which exhibited longer shelf life (Sánchez et al., 2006). Furthermore, bio-fortification of cassava with pro-vitamin A was observed to result in reduced post-harvest physiological deterioration (Beyene et al., 2018). The reduced levels of PPD in presence of carotenoids is associated with their high ROS scavenging abilities. Breeding efforts to increase the levels of pro-vitamin A can therefore result in reduced PPD, although this is at the cost of dry matter (Beyene et al., 2018). Apart from proteins associated with oxidative stress, certain other proteins involved in phenylpropanoid biosynthesis, glutathione cycle, fatty acid oxidation and folate transformation were also found to have significant roles in delaying PPD in cassava (Djabou et al., 2017).

Targeted agronomic practices like pruning have also been observed to result in reduced levels of cyanide in cassava roots (van Oirschot et al., 2000; Narayanan et al., 2019). In the report by van Oirschot et al (2000), the effects of pruning time (0–39 days to harvesting) on the levels of PPD in six cultivars with inherent variability to PPD tolerance was assessed under field conditions in CIAT. The observations made were that pruning at 300 cm above ground reduced PPD levels to a minimum of 25% of the original irrespective of the cultivar's nature of tolerance. Owing to hydrolysis of starch, pruning resulted in increased sugar levels up to a maximum of 25 days post-pruning when new canopy developed. In another study, a combination of pruning and post-harvest tuber waxing resulted in up to 43% reduction in PPD in five Ugandan cultivars (Narayanan et al., 2019). Combined, these results provide diverse strategies that can be used to reduce PPD in cassava.

4.3 | Reducing cyanide levels

Cassava contains substantial amounts of cyanide, which is present in the form of cyanogenic glycosides linamarin and lotaustralin (Cooke, 1978), cyanohydrins and free cyanide. These potentially toxic compounds release hydrogen cyanide (HCN) on hydrolysis (Bolarinwa et al., 2016). Pounding or tissue maceration could be done to reduce the cyanide content of the cassava foods (Montagnac et al., 2009). However, consumption of poorly processed cassava or chronic exposure of low levels of cyanide can lead to respiratory, cardiovascular thyroid defects and neurological disorders (Dhas et al., 2011). The levels of cyanide in cassava have not only been shown to vary with the processing method but with the cultivar and growth conditions as well (El-Sharkawy, 1993; El-Sharkawy & Cadavid, 2002; Njankouo Ndam et al., 2019). It has been noted that the 'bitter' and 'sweet' groupings of cassava correspond to the levels of HCN, the former having HCN levels of >100 mg/kg wet tuber weight and the later <100 mg/kg (McKey et al., 2010). Due to inherent variability in the HCN content in different cultivars, conventional breeding efforts are being used to develop low HCN cultivars (Vieira et al., 2018). Variation in cyanide levels in different cultivars has been observed to vary under variable agronomic conditions including water stress (El-Sharkawy, 1993), varying potassium amounts (El-Sharkawy & Cadavid, 2002), nitrogen–phosphorous–potassium (NPK) fertilizer and grass biomass mulch (Cadavid et al., 1998). These variations are all appropriate avenues that can be used to reduce the levels of cyanide in cassava.

In addition to conventional breeding, genetic engineering and genome editing approaches have also been employed to reduce the levels of HCN in cassava (Gomez

et al., 2021; Siritunga & Sayre, 2004). To reduce cyanide levels, transgenic cassava plants were generated where expression of the genes CYP79D1/D2 was inhibited by antisense expression or CRISPR/cas9-mediated gene knock-out (Gomez et al., 2021; Siritunga & Sayre, 2004). These genes are involved in the biosynthesis of cyanogenic glycosides. Another strategy adopted to reduce the cyanide content was to overexpress HNL (hydroxynitrile lyase) in roots which resulted in rapid volatilization of cyanide (Siritunga & Sayre, 2007).

4.4 | Improving cassava quality for animal feed

Traditional animal feed sources face unsustainable competition from humans and industries. This, therefore, requires diversification of these feed sources to reduce competition and ensure sustainability. The alternative sources include but are not limited to the use of non-traditional feed plants and plant materials, which are normally considered 'waste'. Cassava roots and residues like leaves, peels and additional remains from cassava processing industries have been used as animal feed (Anaeto & Adighibe, 2011). The cassava-derived feeds still contain fibre and carbohydrates and can replace the more expensive maize-based animal feeds. These feeds have served as an energy source for lactating cows (Zheng et al., 2020) and have also been fed to poultry (Morgan & Choct, 2016) and pigs (Balogun & Bawa, 1997). However, cassava as animal feed requires processing to reduce cyanide levels and improve nutritive properties (Stupak et al., 2006). Improving the dietary protein content in cassava leaves and roots can simultaneously convert cyanides to thiocyanates, a detoxification reaction that is sulphur dependent. The sulphur needed for this detoxification reaction can be obtained from the sulphur-containing amino acids methionine and cysteine (Tor-Agbidye et al., 1999). Therefore, the development of cultivars with high protein content is a sustainable way of ensuring nutritive and cyanide-free cassava for animal feed. The high protein cassava variety ICB300 was developed by interspecific hybridization of *M. esculenta* (cassava) and *M. oligantha* (Nassar & Sousa, 2007). Chemical and physical processing methods (Nambisan, 2011) and genetically modified cassava varieties (Gomez et al., 2021; Siritunga & Sayre, 2004) have also shown reduced cyanide levels in cassava. The cassava peel mash can be mixed with animal feed to improve its nutrient value and was shown to effectively replace maize feed (Chang'a et al., 2020). The efforts on large-scale conversion of cassava peels into animal feed was initiated by the International Livestock Research Institute (ILRI) and IITA under the CGIAR Research Program on Roots,

Tubers and Bananas (RTB) in Nigeria (Amole et al., 2019). The successful outcome of the project produced about 5 million tonnes of high-quality cassava peel mash from about 15 million tonnes cassava peel waste.

5 | COMPLEMENTING CASSAVA BREEDING WITH MODERN BIOTECHNOLOGIES

Conventional breeding efforts have consistently been successful but are rather time involving and limited by photoperiod-dependent flowering (Pineda et al., 2020). These limitations mean that desirable genotypes cannot be bred with less desirable but hardy genotypes if flowering is not synchronous.

Genetic engineering in cassava is mainly *Agrobacterium* mediated and requires the use of easily transformable explants. The most common explant used is friable embryogenic callus (FEC) (Bull et al., 2009; Chauhan et al., 2015; Zainuddin et al., 2012). A majority of transformation experiments in cassava so far have mainly focussed on enhancing tolerance to diseases like CMD (Vanderschuren et al., 2012; Zhang et al., 2005) and CBSV (Beyene et al., 2017), with others focusing on post-harvest deterioration. The most successful effort in improving cassava against diseases is the recent approval for release of cassava Event 4046 resistant to CBSV in Kenya (NBA, 2021). Other efforts have tried to adopt FEC and transformation protocols to local and farmer-preferred cultivars (Elegba et al., 2021; Nyaboga et al., 2015; Zainuddin et al., 2012).

Genetic engineering of cassava has also spread to target other traits including: post-harvest physiological deterioration (Xu et al., 2013), drought (Yan et al., 2021), induction of early flowering (Adeyemo et al., 2017; Bull et al., 2017; Odipio et al., 2020), insect resistance (Duan et al., 2013), nutritional improvement including vitamin, starch (Wang et al., 2018), proteins (Zhang et al., 2003) and minerals – mainly iron and provitamin-A (Beyene et al., 2018); (Ihemere et al., 2012; Narayanan et al., 2019). Other efforts towards reduction or complete rid of antinutritional cyanide from roots are by targeting genes involved in cyanogenic glycoside synthesis (Siritunga & Sayre, 2004). Most of the efforts to improve cassava through genetic engineering are at the experimental stage (Narayanan et al., 2011; Siritunga & Sayre, 2003) owing to the inherent difficulties in cassava tissue culture transformation and regeneration.

Advances in genome editing have further opened opportunities for improvement in cassava. Researchers have quickly taken up the new genome editing technologies and co-opted them into cassava research. Among the few studies using genome editing in cassava include protocol optimizations where the PDS gene was silenced and

resulted in the leaf discoloration (Odipto et al., 2017). The CMD has also been targeted (Mehta et al., 2019) despite this effort resulting in a lack of resistance to CMD. The other major cassava disease CBSD has also been targeted in a recent study where two cassava cap-binding proteins were edited, and the resultant mutant showed enhanced disease tolerance (Gomez et al., 2019). It is anticipated that efforts to improve cassava through genome editing will go on into the future. However, since genome editing is still highly dependent on tissue culture, immediate challenges are anticipated due to cassava tissue culture being highly genotype dependent. Table 1 shows a summary of methods to improve target traits in cassava.

6 | CASSAVA AS A BIOENERGY CROP

Plant biomass can be used to obtain fermentable sugars that can be easily metabolized by various microorganisms to produce high energy compounds such as ethanol and butanol, which are substitutes for petroleum-based fuels (Pandey et al., 2019). Cassava biomass has been estimated to produce high theoretical ethanol yields of about 4.95% compared to corn 2.38% per unit area per time (Krajang et al., 2021). A direct comparison of yields from different crops placed cassava at 6000 L/Ha bioethanol, the highest level of the six crops compared. This value was higher than sugarcane and sweet sorghum (Jansson et al., 2009). Cassava can, therefore, be used as an inexpensive and promising feedstock for biofuel production (Sriroth et al., 2010). Several methods for the downstream processing of the cassava raw material to produce biofuels employing microbial fermentation have been adopted. We summarize some of these processes for (i) starch hydrolysis from cassava tuber roots and conversion into bioalcohols, which is the most established and relied upon first-generation bioenergy source; (ii) conversion of less starchy, lignocellulosic cassava agricultural residues (after root tuber harvest) into bioalcohols; (iii) genetically modified plants for enhanced starch and lignocellulose hydrolysis; (iv) utilization of endophytes for plant biomass hydrolysis and (v) genome editing approaches for improved cassava bioconversion. We also review (vi) the effects that growing of food crops (including cassava) for bioenergy has on food security. Lastly (vii), we compare and evaluate cassava's bioenergy potential with other major bioenergy crops.

6.1 | Cassava root tubers for bioenergy

Cassava root tubers predominantly contain starch. Starch requires pretreatment steps prior to undergoing

fermentation. Traditionally, starch is gelatinized and liquefied to reduce viscosity, followed by enzymatic conversion into fermentable sugars at optimal pH and temperature (Naguleswaran et al., 2013; Shariffa et al., 2009). The enzymatic conversion of starch into fermentable sugars involves synergistic hydrolysis using alpha amylase and glucoamylase (Naguleswaran et al., 2012). The enzyme alpha amylase converts starch into oligosaccharides, maltose and dextrans. The enzyme glucoamylase converts dextrin and oligosaccharides released from amylase activity into glucose (Purkan et al., 1888). In simultaneous saccharification and fermentation (SSF) using cassava flour, the fermentative microbes in combination with the amyolytic enzymes are added to a single fermentation system (Chu-Ky et al., 2016; Nguyen et al., 2014). The glucose monomers are then converted into ethanol using *Saccharomyces cerevisiae* strains (Ajibola et al., 2012; Pervez et al., 2014). The addition of cellulases to the SSF improved ethanol yields by converting the 4–5% (w/w) of cellulose present in the cassava tubers (Wang et al., 2020). The addition of novel glucoamylase enzymes with higher substrate absorption and efficient enzyme activity shows potential use for scaled-up industrial fermentations of cassava starch (Krajang et al., 2021; Xu et al., 2016). In most cases, the ethanol titre is affected by the microbial tolerance to ethanol as a stress response (Gibson et al., 2007). The fermentation of cassava starch by subjecting the amyolytic hydrolysates produced from *Aspergillus* fermentation to ethanol production using protoplast fusion recombinants of yeast strains showed superior tolerance to a higher ethanol concentration of up to 25% v/v (Adeleye et al., 2020). On the other hand, use of butanol as a biofuel has remarkable advantages over ethanol in terms of higher energy, low volatility and can be mixed or completely replace current fuel systems (Green, 2011). Cassava flour, gelatinized starch and starch hydrolysate have been fermented to produce butanol (Lin et al., 2019; T. Li et al., 2015; Thang et al., 2010). The fermentation of cassava starch hydrolysate produced the highest butanol concentration of 25.7 g/L (Lépiz-Aguilar et al., 2013). A very high gravity fermentation method using cassava root could be an energy-saving process, thereby improving the enzymatic hydrolysis process (Kawa-Rygielska & Pietrzak, 2014; Puligundla et al., 2011; Sakdaronnarong et al., 2018).

6.2 | Cassava residues as raw materials in bioenergy production

After root tuber harvest, the non-food parts of cassava, including stem, leaves and by-products, such as cassava peel, bagasse or pulp generated from starch separation normally go to waste. These contain higher amounts of

TABLE 1 Studies on various approaches used in improvement of cassava genotypes

Cassava Genotype	Target trait improvement	Approach	Major outcome	Reference(s)
Cultivar TMS 71173	Starch accumulation in roots	Overexpression of modified bacterial <i>glgC</i> gene encoding ADP-glucose pyrophosphorylase	2.6-fold increase in root tuber biomass	Ihemere et al. (2012)
Cultivar TMS60444 (MNig11)	Low protein in cassava roots	Expression of synthetic storage protein ASP1	Cassava root tuber enriched with essential amino acids (80%)	Zhang et al. (2003)
Cultivar 60444	South African cassava mosaic virus (SACMV) disease	RNAi lines targeting viral replication-associated protein (rep) and viral silencing suppressor protein	Enhanced symptom recovery	Walsh et al. (2019)
Thai non-GM bred cassava cultivars (Bwx 09–562–19, HBwx 09–754–16, HBwx 09–612–18, HBwx 09–1041–6, HBwx 09–826–2, HBwx 09–317–6, HBwx 09–19–2, HBwx 09–635–4 and HBwx 09–989–9)	Amylose content	Conventional Breeding	Reduced levels of amylose content/waxy starch. Better starch characteristics in terms of stability, viscosity and paste clarity compared to commercial starches suitable for	Toae et al. (2019)
Cultivar 60444	Low amylose content for enhanced culinary properties	Downregulation of granule-bound starch synthase I (GBSSI) gene using RNAi CRISPR-Cas9-targeted mutagenesis of GBSSI	Reduction in amylose by 5% Reduction in amylose by 13%	Zhao et al. (2011) Bull et al. (2018)
Cultivar TMS60444	Drought stress	Expression of isopentenyl transferase	Delayed leaf senescence and drought tolerance	Zhang et al. (2010)
Cultivar TME 419	Post-harvest control of fungal root rot	Application of <i>Piper guineense</i> , <i>Ocimum gratissimum</i> , <i>Casia alata</i> and <i>Tagetes erecta</i> plant extracts	Reduced fungal toxicity (as a protectant) when used before pathogen inoculation.	Amadioha et al. (2019)
Genotypes MNIG11, MPER183, MCOL22, MCOL1505, AM206-5 and HMC-1	Post-harvest physiological deterioration (PPD)	Pruning	Pruning before harvest reduced PPD	Luna et al. (2021)
Cultivar 60444	Post-harvest physiological deterioration (PPD)	RNAi lines with downregulated feruloyl CoA 6'-hydroxylase gene	Reduced scopoletin biosynthesis involved in causing PPD symptoms during storage	Liu et al. (2017)
Cultivar 60444 and TME 419	Cyanide content	CRISPR-Cas9-targeted mutagenesis of CYP79D1 and CYP79D2	Elimination of toxic cyanogen glycosides	Gomez et al. (2021)

lignocellulose that can be efficiently converted into biofuels (Lu et al., 2012; Zhang et al., 2016). The cassava stem comprises 15% of starch, cellulose (30–50%) and hemicellulose (20–30%) (Han et al., 2011; Sovorawet & Kongkiattikajorn, 2012). Hence, cassava stems and peels require additional pretreatment steps including dilute acid and thermal treatment followed by enzymatic saccharification for efficient release of sugars due to the complex lignin layers surrounding cellulose fibres (Aruwajoye et al., 2020; Pooja & Padmaja, 2015; Pothiraj et al., 2006). The subsequent pretreatment of acid- or alkali-treated cassava stems with cellulase and amylase enzymes improved the ethanol and butanol titres (Sudha et al., 2017); (Martín et al., 2017; Saekhow et al., 2020; Tanaka et al., 2019). The raw cassava pulp was enzymatically pretreated using an enzyme mixture containing amylases, pectinase, glycosyl hydrolases and xylanase that degrade cell wall polysaccharides, releasing a high concentration of 736.4 mg/g of cassava pulp for ethanol production using SSF at a 96.7% theoretical yield (Poonsrisawat et al., 2017). Other methods where fermentative yeast cells are engineered to express heterologous proteins and enzymes have been successfully employed over many years to improve bioethanol production and other biocatalytic applications (Chen, 2017; Ueda, 2019). Previously this method was also used for ethanol production from cassava pulp using engineered yeast *S. cerevisiae* directly displaying and co-displaying starch and cellulose degrading enzymes (Apiwatanapiwat et al., 2011; Kosugi et al., 2009). Recently, biogas derived from pretreated cassava peel fermentation produced methane yield of 62.3% (Aisien & Aisien, 2020). Cassava waste pulp was used as a substrate to produce biogas with significant amount of biohydrogen ($18.69 \pm 1.71\%$) concentration (Jaro et al., 2021). A paper by Okudoh et al. (2014) extensively reviewed the promising technologies to optimize and improve biogas production using cassava as the raw material. Additionally, cassava rhizome and stalk are pyrolysed to produce bio-oil, which is majorly used to substitute heat energy in the process of biofuels production (Osorio & Chejne, 2019). Table 2 summarizes studies on bioconversion of cassava for bioethanol, biobutanol and mixed alcohol production.

6.2.1 | Limitations of cassava raw material processing

The cassava roots are more critical as a food source where it serves as a staple to hundreds of millions of people. The use of cassava agricultural residues in bioenergy production is limited due to several factors. The plant cell walls in the cassava stem have up to 25% lignin, a complex compound that is not readily degradable by microbes

and therefore renders fermentable sugars inaccessible. Conventionally, chemical and enzymatic methods (as discussed in previous sections) have been used to break the complex lignin and hemicellulose cross-linkages surrounding cellulose. However, these pretreatment methods substantially add to process costs which make bioenergy production from plants unsustainable. Previously research has put the cost of enzymatic and chemical conversions at \$0.09/L and \$0.29/L respectively (Humbird et al., 2011). The techno-economic analysis has put the cost of bioethanol production to as high as US \$1.47/gal mainly due to ensuing enzyme costs (Klein-Marcuschamer et al., 2012). The high enzyme costs will undoubtedly limit the development of the cellulosic biofuel industry. The dilute acid pretreatment results in low glucan yields, hence reducing the quantities of the product (Martín et al., 2007). Another limitation is the presence of microbial inhibitory by-products such as furfural generated during pretreatment steps that needs to be reduced to increase biofuel productivity (Yu et al., 2018).

6.3 | Genetic engineering of Cassava for improved bioenergy raw materials

Genetically modified plants with the ability to self-process starch can eliminate the limitations with raw material processing (Santa-Maria et al., 2011; Xu et al., 2008). Transgenic cassava expressing bacterial thermostable multi-enzymes for starch accumulation and self-hydrolysis showed up to 10-fold higher starch degrading activity (Ligaba-Osena et al., 2018). Another important aspect is the granular structure of starch, which differs in morphology among plant species and these differences may greatly affect the bioconversion efficiency to produce biofuels (Naguleswaran et al., 2012). Starch granule morphological characteristics have remained stable in cassava over generations and not affected by changes in the environment, making this plant a more reliable source of biomass (Gu et al., 2013; de Oliveira et al., 2018). The natural addition of phosphate group to the starch polymer at C3 and C6 carbon of the glycosyl residues provides changes to the physicochemical properties of starch granules (Mahlow et al., 2014). The presence of these bound phosphate groups alters the structure of starch granules, making them more susceptible to amylolytic enzymes, which is important for enhancing the release of monosugars. Transgenic plants with overexpressing *Glucose water dikinase (GWD)* gene showed two-fold increase in bound phosphates (Wang et al., 2018). The majority of C6 sugars, such as cellulose, are bulked inside the plant cell wall and protected by a lignin layer that is a significant barrier for the accessibility of cellulose for microbial conversion

TABLE 2 Summary of studies on use of cassava as raw material for bioenergy

Product	Cassava raw material	Pretreatment	Fermentation method	Maximum sugar concentration	Maximum total solvent concentration	Reference(s)
Ethanol	Cassava starch	Raw starch hydrolysing enzyme – StargenTM002	Consolidated bioprocessing	176.41 g/L	81.86 g/L	Krajang et al. (2021)
Ethanol	Cassava peel	Acid hydrolysis at 100 C for 60 min and sulfonated carbon catalyst	Batch fermentation	13.5 g/L	3.75 g/L	Mardina et al. (2021)
Ethanol	Delignified cassava waste	Acid hydrolysis	Batch fermentation	6.8%(v/v)	6.8% (w/v)	Heriyanti et al. (2020)
Ethanol	Cassava pulp and peel Cassava cultivar (IBA980505, IBA950289 and IBA010040)	Acid hydrolysis	Sequential saccharification and fermentation	96–110 g/L	98.9 g/L	Efevbokhan et al. (2019)
Ethanol	30% cassava starch	Alpha-amylase and glucoamylase	Batch fermentation and membrane-based ethanol separation	273.1 g/L	43.5 g/L	Wangpor et al. (2017)
Butanol	Cassava Stem	Alkaline thermal treatment followed by cellulase – amylase – amyloglucosidase treatment	Batch fermentation	47.09 g/L	12.15 g/L	Saekhow et al. (2020)
Butanol	Cassava waste residue	Acid and alkaline hydrolysis	Batch fermentation	60 g/L	8.01 g/L	Johrnavindar et al. (2021)
n-butanol	Concentrated cassava bagasse hydrolysate	-	Fed batch fermentation and gas stripping	584.4 g/L	108.5 g/L	Lin et al. (2019)
Acetone-butanol-ethanol	Cassava flour as substrate and cassava peel residue as immobilization media	Alpha-amylase and b-glucoamylase	Three-stage continuous fermentation	-	16.8 g/L	Lin et al. (2019)
Acetone-butanol-Ethanol	Cassava chip flour	Amylase and glucoamylase	Batch fermentation	-	42.56 g/L	Qi et al. (2018)
Acetone-butanol-Ethanol	Cassava rhizome hydrolysate	Alkaline thermal enzymatic treatment	Removal of inhibitory compounds in hydrolysate and batch fermentation	60 g/L	10.57 g/L	Lépiz-Aguilar et al. (2013)
Isopropanol and n-butanol	Cassava bagasse hydrolysate	Dilute sulphuric acid and thermal	Immobilized fermentation	51.18 g/L	Isopropanol – 7.63 g/L, Butanol – 13.26 g/L	Zhang et al. (2016)

into fermentable sugars. Genetic modifications in plants for altering lignin composition have been a breakthrough in plant biomass engineering. The alterations in the lignin metabolic pathways could directly reduce the amount of lignin deposition in the cell wall and/or lignin structure (Liu et al., 2016). The lignin precursor monomers (monolignols) are synthesized via phenylpropanoid and monolignol biosynthetic pathways. These monolignols (*p*-coumaryl alcohol, coniferyl alcohol and sinapyl alcohol) are then transported to the cell wall, where they undergo oxidation and polymerization (lignification process). To further add to the complexity of the lignin structure, these monolignols generate phenoxy radicals (S – syringyl, G – guaiacyl and H – hydroxyphenyl) that randomly cross-link with the lignin polymer to give a three-dimensional form (Katahira et al., 2018; Patil & Argyropoulos, 2017). Experiments have shown that lowering S/G ratios of lignin improved cellulose hydrolysis and monosugar release during pretreatment steps (Davison et al., 2006). The enzymes involved in oxidation and polymerization of lignin monomers belong to one of the laccase families and these include copper oxidase/*p*-diphenol:dioxygen oxidoreductases. Seventeen members (grouped into six) of the laccase family involved in either catabolism or anabolism of lignin have been experimentally confirmed at the transcriptional level in *Arabidopsis*. The six *Arabidopsis* anabolic laccases *AtLAC2*, *AtLAC4*, *AtLAC10*, *AtLAC11*, *AtLAC16* and *AtLAC17* have been reported to have stem-specific expression. Four among the stem-specific ones (*AtLAC4*, *AtLAC11*, *AtLAC15* and *AtLAC17*) were observed to alter lignification when mutated (Berthet et al., 2011; Liang et al., 2006; C.-Y. Wang et al., 2014; Q. Zhao et al., 2013). Approaches to develop transgenic events with down-regulated monolignol biosynthetic genes 4-coumarate:coenzyme A ligase (4CL) have been reported in sorghum and switchgrass. These mutants showed an increase in glucose release efficiency (Saballos et al., 2012; Xu et al., 2011). Similar approaches in *Arabidopsis* also showed an 88% improvement in saccharification yield (Van Acker et al., 2013). Recently, overproduction of brassinosteroids, a phytohormone that controls cell wall synthesis and wood formation in transgenic poplar overexpressing *DEETIOLATED2* gene, showed increase in arabinose monosugars release and enhanced cellulose accessibility, a characteristic of desirable biomass (Du et al., 2020; Fan et al., 2020).

Several other strategies, including transgenic plants expressing cell wall degrading enzymes, have been shown to hydrolyse lignocellulosic biomass efficiently (Chatterjee et al., 2010). Transgenic tobacco expressing the endoxylanase isolated from thermophilic bacteria was expressed to hydrolyse purified birchwood xylan to monosugars (Borkhardt et al., 2010). However, the issues are

the accumulation of enzymes that can cause plant growth defects, affect the innate resistance to pests and diseases, and seed germination, all of which result in reduced yield and biomass.

6.4 | Enhancing biomass and bioconversion of cassava for energy by use of endophytes

The production of cellulosic biofuels from plant biomass holds great potential in the bioenergy industry. Therefore, an increase in the need for sustainable agricultural production has led to the development of methods that have reduced chemical inputs, including fertilizers, pesticides and plant genetic engineering (Bailey-Serres et al., 2019). Transgenic experiments for improving agronomic traits of crops have been mostly successful in plant species for which transformation has been perfected. Cassava with enormous bioenergy potential are recalcitrant to genetic transformation as the protocols optimized are cultivar dependent (Elegba et al., 2021; Liu et al., 2011; Nyaboga et al., 2013, 2015; Ojola et al., 2018; Walsh et al., 2019). Plant beneficial endophytes offer environment-friendly methods for improving plant biomass which is advantageous for bioenergy production. Most plant microbiomes contribute to tolerance in plants to abiotic and biotic stresses, which plays a very important role in enhancing plant biomass. The most frequent endophytes in cassava were identified as microbes belonging to the genus *Bacillus*, *Burkholderia*, *Enterobacter*, *Pantoea*, *Escherichia*, *Pseudomonas*, *Serratia*, *Stenotrophomonas*, *Fusarium sp.*, *Aspergillus sp.*, *Lasioidiplodia sp.*, *Nectria pseudotrichia*, *Penicillium citrinum* and *Schizophyllum commune* (Hartanti et al., 2021; Leite et al., 2018). *B. amyloliquefaciens* (GB03) inoculation of cassava stem showed improved biomass and disease resistance (Freitas et al., 2019). Previous studies showed that GB03 strain enhanced photosynthetic efficiency by increasing the chlorophyll content in *Arabidopsis* and augmenting salt tolerance in legume (Q.-Q. Han et al., 2014; X. Xie et al., 2009). The microbial volatile compounds produced by the GB03 strain were majorly found to be acetoin that significantly improved plant growth under salt-stressed conditions (Cappellari et al., 2020). The compounds produced by *Paenibacillus sp.* IIRAC-30 and *B. pumilus* MAIIM4a isolated from cassava, inhibited growth of a fungal plant pathogens (Canova et al., 2010; Melo et al., 2009). The proliferation and colonization of potential entomopathogenic fungal strains was achieved in cassava roots to control whitefly infestation (Greenfield et al., 2016). Entomopathogenic fungi have previously shown to control pests and enhanced growth in *Gossypium hirsutum* (Lopez & Sword, 2015). Li et al.,

2020, studied the distribution of bacterial and fungal communities in the cassava root rot susceptible and tolerant varieties and suggested that the interactions within the microbial population was a crucial factor that may affect level of susceptibility in these cultivars. On the other hand, endophytic bacteria have been found to secrete cell wall hydrolytic enzymes that include glycosyl hydrolases such as cellulases, hemicellulases and xylanases (Leo et al., 2016; Vegnesh et al., 2019). The endophyte *Paenibacillus polymyxa* produces multifunctional hydrolases, suggesting that these endophytes produce hydrolytic enzymes to make entry through the plant cell wall (Cho et al., 2008). Also, a few microbial communities growing on decaying plant material have been found to be potential cellulolytic and xylanolytic bacteria (Ma et al., 2016; Yang et al., 2011). An endophytic fungal strain *Phomopsis liquidambari* has shown to utilize these phenolic acids in lignocellulose as a carbon source and possibly lignolytic properties (Xie & Dai., 2015; Xie et al., 2016). Therefore, strategies using endophytic consortia for effective lignocellulose degradation in cassava can be promising.

Furthermore, plant growth-promoting endophytes can colonize most of the plant species and can be engineered for *in-planta* expression of cell wall hydrolysing enzymes. The process can be followed by a post-harvest activation of thermophilic enzymes at elevated temperatures and hydrolysis of the cell wall polysaccharides to prevent plant growth defects and plant infertility (Kim et al., 2011; Klose et al., 2012; Mir et al., 2017; Shen et al., 2012). Endophytes therefore offer environmentally friendly and cost-effective methods to increase biomass productivity and concurrently making the plant biomass easily amenable to bioenergy production.

6.5 | Potential applications of genome editing in enhanced cassava bioconversion

Genetically engineered crops using stable T-DNA integration and RNAi silencing lines have been developed for enhanced sugar hydrolysis and lignin reduction in bioenergy crops. Recently, the revolutionary TALENS and CRISPR mechanisms for targeted gene silencing and transgene-free genome editing have been applied in plants for improved bioenergy conversion (Fan et al., 2015; Odipio et al., 2017; Zhao et al., 2021). As discussed in the previous sections, cassava residues are rich in lignocellulose and can be utilized as a promising feedstock for biofuel production. The reduction in lignin content is the ultimate desirable trait for enhanced bioconversion of lignocellulosic biomass (Chen & Dixon, 2007; Hisano et al., 2011). The CRISPR Cas9 mutants of *caffeic acid O-methyltransferase 1* (*HvCOMT1*) showed reduced syringyl-like lignin units in

barley with 14% reduction in the lignin content and higher glucose release from the mutant (55.3%) compared to the WT (41.2%) (Lee et al., 2021). In sugarcane, the TALEN-mediated mutagenesis of the *COMT* gene resulted in 32% total lignin reduction with 54% reduction in the syringyl-like lignin units (Jung & Altpeter, 2016; Kannan et al., 2018). The CRISPR mutants of *COMT* in barley and sugarcane did not show any morphological defects, which is advantageous. In switchgrass, the 4-coumarate: coenzyme A ligase 1 (*4CL1*) gene involved in the monolignol pathway was expressed in abundance in stem and leaf. The CRISPR mutants of *4CL1* showed reduced lignin and enhanced sugar release (Park et al., 2017). In contrast, the gain-of-function CRISPR mutants in Arabidopsis with inserted *Lac14* gene from poplar showed higher lignin deposition (Qin et al., 2020). Targeting genes in the lignin biosynthetic pathway that directly alter lignin polymer S:G ratio and/or laccases that catalyse the oxidation of monolignols can be a straightforward approach towards lignin modification in cassava via genome editing.

6.6 | Cassava's bioenergy potential compared to other crops

The bioethanol yield from cassava feedstock was comparable to sugarcane and higher in comparison with sweet potato and corn (Table 3). In considering a bioenergy crop, potential impacts on water consumption, land use and greenhouse gas (GHG) emissions were considered (Hosseinzadeh-Bandbafha et al., 2021). The water requirement for cassava ethanol production was reported to be 2300–2820 L water/L ethanol which was higher than water consumption from sugarcane molasses (1510–1990 L water/L) (Mangmeechai & Pavasant, 2013). Another study compared the surface or groundwater demand for ethanol production using cassava, sugarcane juice and molasses and reported highest consumption for molasses, i.e. around 699–1220 L of water/L ethanol; meanwhile, cassava ethanol and sugarcane juice ethanol required around 449–566 and 450–859 L of water/L ethanol respectively (Gheewala et al., 2013). The discrepancies in comparison of bioenergy crops on water requirements may show huge variations due to differences in geographical and climate conditions (Gheewala et al., 2014). Several studies have estimated the effect of bioethanol production on GHG emissions. It was reported that the production of cassava-based ethanol can reduce estimated GHG emissions by 6% (Nguyen & Gheewala, 2008). A study by Papong and Malakul (2010) showed GHG emissions were between 1402 and 2863 gCO₂e/L for cassava bioethanol. Recently, Papong et al. (2017) evaluated the environmental impacts of bioethanol production from cassava- and

Substrate	Bioethanol yield (g/L)	Reference
Cassava starch	127.9	Pradyawong et al. (2018)
Dent Corn	122.6	
Waxy Corn	126	
High Amylose Corn	22.6	
Cassava Peels	18.40	Ezebuero and Ogugbue (2015)
Sugarcane Bagasse	17.80	
Sorghum grains	40.11	Nadir et al. (2009)
Cassava tubers	34.07	
Sweet potato peels	6.5g/ cm ³	Oyeleke et al. (2011)
Cassava Peels	11.97g/cm ³	

TABLE 3 Studies comparing bioethanol potential of crops based on feedstock properties

sugarcane-based bioethanol factories in Thailand. The study showed that the GHG emission values may be comparable to sugarcane when the entire value chain was considered. The net energy return or energy ratio is defined as the ratio of energy output of the production to the input energy (Fluck, 1992). The energy ratio values from cassava in China and Thailand range between 1.3 and 1.9, and 3.1 and 9.3 from sugarcane, in Brazil, Mexico and Southern Africa (HLPE, 2013). The positive impact is more towards using sugarcane as the feedstock compared to cassava, however, the latter has its unique advantages over sugarcane. Sugarcane requires fertile land for cultivation, higher amounts of fertilizers and rainwater or irrigation water. On the other hand, cassava can be easily cultivated in less fertile lands with its ability to absorb high amounts of nutrients from marginal land soils (Byju & Suja, 2020; Howeler, 2001). A study by Shen et al. (2020) showed cassava can be grown in heavy metal-contaminated soils for the purpose of phytoremediation. This can be a sustainable method to use polluted lands and expand cassava cultivation for biomass production and conversion to biofuels. The production of second-generation biofuel (2G) or cellulosic bioethanol from cassava residues and non-food parts can be a promising strategy to ensure a sustainable food and energy system (Nuwamanya et al., 2012). The integration of 2G technology with the existing 1G facilities involving strategies such as retrofitting, co-locating or repurposing as reviewed by Susmozas et al. (2020) can greatly decrease the high production cost involved in 2G biofuels using cassava.

6.7 | Effects of growing food crops for bioenergy on food security

Cassava is currently more important as a food crop than bioenergy and it is feared that cultivation for the latter could have a negative impact on food security. Food security is defined as access to sufficient, safe and nutritious food by

people, to meet their dietary needs and preferences for an active and healthy life (FAO, 1996). Energy and food security policy analysts agree that predictions of effects of bioenergy on food security are complex to achieve due to the multidisciplinary nature of the sector (Nogueira et al., 2013; Osseweijer et al., 2015). Food security in relation to bioenergy can be assessed through four dimensions: availability, access, stability and utilization (FAO, 2010). The FAO bioenergy and food security (BEFS) framework used access and availability dimensions of bioenergy to analyse if Tanzania, Peru and Thailand could grow food crops for bioenergy (FAO, 2010). The conclusion from the analysis was that Tanzania should push for a bioenergy industry, Peru should push for policies that encourage poverty and rural development goals, whereas Thailand was to push for bioenergy and rural development promoting policies. These conclusions were informed by diagnostic, natural resources, techno-economic and environmental analyses for the different countries. This FAO BEFS approach to decision on bioenergy on a country-by-country basis has been supported by other recent studies (Osseweijer et al., 2015; Popp et al., 2014). Maltsoğlu et al. (2015) proposed a BEFS appraisal approach that calculates a country's available biomass from agriculture against current and foreseen uses. These studies conclude that the decision on viability of cultivating food crops for bioenergy should be on a country-by-country basis.

Approaches that can reduce competition between food uses and bioenergy production in food crops would be more accommodative to both uses. The current trend in bioenergy is towards second-generation biofuels which use lignocellulosic biomass from non-edible plant parts instead of first generation (starch) from edible parts that directly competes with food uses (Ahmed et al., 2021; Aron et al., 2020; Takeuchi et al., 2018). Similar suggestions in use of cassava non-edible biomass for bioenergy have been proposed as a viable option with less competition for food uses (Nuwamanya et al., 2012). A combination of country-specific bioenergy policies and a move towards

second-generation biofuels would ensure less competition for food and bioenergy in cassava.

Cassava productivity in Africa, where it is a staple food crop, is not optimal. Nigeria, the global leader in cassava production and consumption, produces a minimal 7000 kilograms per hectare (FASOSTAT, 2019). Comparatively, India and China, where cassava is minimally used for food, produce upwards of 30,000 and 16,000 kg per hectare respectively (FAOSTAT, 2019). This trend of sub-optimal productivity is observed across all the major cassava growing areas globally. Increasing cassava production in these areas is therefore critical to meeting food demand.

7 | CONCLUSIONS

The move towards more sustainable energy is urgent following the insurmountable challenges with fossil-based fuels. Plant-based biofuel promises to be more sustainable than fossil fuels. However, cassava, one of the most promising bioenergy crops, faces a dichotomy in its use as a food and energy crop. Research efforts towards enhanced cassava productivity for food and feed have been discussed in the first part of this review. These efforts include enhancing cassava resilience to biotic and abiotic stress as well as efforts that improve the quality of cassava tubers pre- and post-harvest. The review has also delved into current and potential approaches geared towards the enhanced use of cassava for bioenergy. The efforts include genetic engineering of cassava for reduced starch complexity, use of endophytes to make cassava cellulosic biomass amenable to fermentation in bioenergy production and genome editing to reduce lignin complexity in cassava stems. We also discussed the nexus between bioenergy and food security as well as a compared bioenergy potential of cassava to other crops. Combined, the review addresses the practical approaches that can promote dual use of cassava for food and bioenergy, especially in areas where it is cultivated the most.

ACKNOWLEDGEMENTS

The authors wish to thank the Royal Society and The African Academy of Sciences for funding under Grant Number FLR\R1\201370.

CONFLICT OF INTEREST

The authors declare that there is no competing financial interest.

AUTHOR CONTRIBUTIONS

AAF and SM contributed to concept development. All authors contributed to writing the manuscript.

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How to cite this article: Fathima, A. A., Sanitha, M., Tripathi, L., & Muiruri, S. (2022). Cassava (*Manihot esculenta*) dual use for food and bioenergy: A review. *Food and Energy Security*, 00, e380. <https://doi.org/10.1002/fes3.380>