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Optimizing Cassava for Bioenergy: Genetic Foundations and Biochemical Mechanisms of Biomass Conversion

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Abstract This systematic review aims to consolidate current knowledge on the genetic and biochemical strategies that can enhance cassava (*Manihot esculenta* Crantz) as a bioenergy source. Cassava is a staple food crop with significant potential in bioenergy development due to its high carbohydrate content and adaptability to tropical climates. Recent advancements in genetic engineering have enabled the improvement of cassava traits, such as pest and disease resistance, starch quality, and biofortification, thus overcoming the limitations of traditional breeding methods (Liu et al., 2011; Jiang et al., 2019). Additionally, the application of cassava harvest residues in various biochemical and thermochemical conversion processes has been explored, highlighting the versatility of cassava biomass in the bioenergy industry (El-Sharkawy, 2003). Genetic approaches to modify the polysaccharide properties and composition of cassava biomass have shown promise in increasing the proportion of fermentable sugars and reducing the recalcitrance of the plant cell wall, thereby enhancing bioenergy crop efficiency (Ihemere et al., 2006). Furthermore, the genetic modification of cassava to increase starch production by altering the expression of key enzymes involved in carbohydrate metabolism has demonstrated a substantial increase in root biomass, which is crucial for bioenergy applications (Okudoh et al., 2014). The review concludes that through targeted genetic and biochemical interventions, cassava can be optimized for bioenergy production, offering a sustainable alternative to fossil fuels and contributing to energy security. The findings underscore the importance of continued research and development in this field to fully realize the bioenergy potential of cassava.

Keywords Cassava; Bioenergy; Genetic engineering; Biomass conversion; Polysaccharide modification; Starch production; Biochemical conversion; Thermochemical conversion

1 Introduction

Cassava (*Manihot esculenta* Crantz) has emerged as a crop of great significance in the realm of bioenergy due to its high biomass yield and substantial starch content. Recognized as a major food source in the tropics and subtropics of Africa and Latin America, cassava also serves as a raw material for starches and bioethanol production, particularly in tropical Asia (Liu et al., 2011). Its ability to thrive in stressful environments, including poor soils and drought conditions, positions cassava as a reliable source of bioenergy (El-Sharkawy, 2003).

The global interest in cassava as a sustainable bioenergy source is driven by its remarkable yield potential and efficiency in converting biomass to energy. Cassava's starch, which constitutes up to 35% of its fresh weight and about 80.6% on a dry weight basis, is a key resource for bioenergy production, with the crop outperforming many others in terms of carbohydrate yield per hectare (Okudoh et al., 2014). This has led to its consideration as a strategic crop to meet biofuel targets in various countries (Okudoh et al., 2014).

This systematic review, titled "Optimizing Cassava for Bioenergy: Genetic Foundations and Biochemical Mechanisms of Biomass Conversion" aims to explore the genetic and biochemical underpinnings that can be harnessed to enhance cassava's bioenergy potential. Specifically, the review will focus on the genetic transformation of cassava to overcome traditional breeding limitations and achieve improved traits such as pest and disease resistance, biofortification, and starch quality (Liu et al., 2011). Additionally, it will delve into the physiological traits that contribute to cassava's high productivity, such as its photosynthetic efficiency and drought tolerance mechanisms (El-Sharkawy, 2003).

Furthermore, the review will examine the advancements in metabolic engineering to increase starch production in cassava roots, which is pivotal for bioenergy applications (Ihemere et al., 2006). The potential of cassava biomass for biogas production and the technologies applicable for its optimization will also be critically assessed (Okudoh et al., 2014). By integrating insights from life cycle assessments and biogeochemical models, the review will evaluate the energy saving and carbon emission mitigation potential of cassava-based bioenergy (Jiang et al., 2019).

The objectives of this review are to synthesize current knowledge on the genetic and biochemical optimization of cassava for bioenergy, identify bottlenecks in root yield and starch production, and propose strategies for crop improvement through metabolic engineering (Sonnewald et al., 2020; Obata et al., 2020). By doing so, the review expects to provide a comprehensive understanding of the opportunities and challenges in transforming cassava into an optimized bioenergy crop, thereby contributing to global efforts in sustainable energy production.

2 Genetic Foundations for Biomass Production in Cassava

The genetic foundation for biomass production in cassava is being strengthened through the identification of key genetic traits, molecular genetic advancements, and strategic breeding approaches. These efforts are paving the way for optimizing cassava as a sustainable and efficient source of bioenergy.

2.1 Genetic traits

Cassava (*Manihot esculenta* Crantz) is known for its high rates of CO_2 fixation and sucrose synthesis, which are foundational for its potential as a bioenergy crop. However, the actual field yields often fall short of their potential. Research has identified that genetic traits such as enhanced tuberous root ADP-glucose pyrophosphorylase (AGPase) activity can lead to substantial increases in starch production and biomass yield. Transgenic cassava plants expressing a modified bacterial *glgC* gene, which encodes for AGPase, have demonstrated up to a 2.6-fold increase in total tuberous root biomass under controlled conditions (Ihemere et al., 2006). Additionally, traits like improved leaf retention have been associated with increased total fresh biomass and root dry matter yield, suggesting that leaf longevity is a valuable trait for enhancing cassava productivity (Lenis et al., 2006).

2.2 Molecular genetics

Genetic modifications have been employed to optimize cassava for bioenergy production. For instance, the expression of a more active bacterial form of AGPase in cassava roots has been shown to increase starch production, which is a key component for bioenergy applications (Ihemere et al., 2006). Moreover, genetic engineering approaches have been used to overcome the limitations of traditional breeding in cassava, such as high heterozygosity and trait separation, allowing for the rapid improvement of target traits like pest and disease resistance, biofortification, and starch quality (Liu et al., 2011). The engineering of bioenergy crops has also focused on improving the polysaccharide properties and composition of biomass to reduce recalcitrance to enzymatic deconstruction (Table 1, adopted from Brandon and Scheller, 2020), which is crucial for efficient bioenergy conversion (Brandon and Scheller, 2020).

2.3 Breeding strategies

Traditional breeding techniques, coupled with modern genetic tools, have been utilized to enhance bioenergy traits in cassava. Selection for traits such as leaf retention, which is highly heritable and positively correlated with root yield, has been suggested as an effective breeding strategy (Lenis et al., 2006). Additionally, the development of short-duration cassava genotypes allows for the effective utilization of resources and diversification of income for smallholder farmers, which is beneficial for bioenergy crop production systems (Suja et al., 2010). Genetic transformation technologies have matured over the years, enabling the transition from model cultivars to farmer-preferred varieties, thus facilitating the breeding of cassava with improved traits for bioenergy (Liu et al., 2011).

Table 1 Summary of dominant approaches to modify biomass polysaccharide composition (adopted from Brandon and Scheller, 2020)

Engineered species	Transgene expressed	Effects on biomass composition and conversion	References
A. thaliana	AtCesA2, AtCesA5, AtCesA6	(+)29-37% Cel	Hu et al., 2018
	GhCOBL9A	(+)59% Cel	Niu et al., 2018
	AtGalS1::AtUGE2::AtURGT1	(+) 80% Gal	Gondolf et al., 2014; Aznar et al., 2018
	pSAG12:OsCSLF6	(+) non-Cellulosic Glc	Vega-Sánchez et al., 2015
	AtIRX10G283D, AtIRX10E293Q	（-） 39-55% Xyl	Brandon et al., 2019
	AtSBD123	(+)76% FW;(+)50% HC;(+)30% Pec;(+) 100% non-crystalline Cel; (+)28% IVD	Grisolia et al., 2017
Populus spp.	pEST:PcPL1	(+) 90-100% SE, post-induction	Tomassetti et al., 2015
	pSAG12:AnPGA2	(+) 50-100% SE, post-senescence	Tomassetti et al., 2015
	AtPMEI-2	(+) 50% SE: (+) 68% DW	Lionetti et al., 2010
	GhSuSy	(+) 2-6% Cel; (+) Crl	Coleman et al., 2009
	PdDUF266A	(+）17-34% DW：（+）37% Cel;（+）13% Cel DP; (+) 38% SE	Yang et al., 2017a
Tobacco	AnAXE1	(+) 26% SE	Pawar et al., 2016; 2017
	PdDUF231A	(+) 8-21% Cel (-) 6-8% lignin	Yang et al., 2017b
	AaXEG2	(+) DW; (+) 81% SE	Kaida et al., 2009; Park et al., 2004
	PtPL1	(+) SE	Biswal et al., 2014
	PsnSuSy1/2	(+) 18% Cel; (-) 28% ligrin	Wei et al., 2015; Li et al., 2019
	AcCel5	(+) 10-15% SE	Brunecky et al., 2011
	TrCel5	(-) FW; (-) Cel	Klose et al., 2015
	ClEXPA1/2	(+) FW; (+) 30-50% Cel	Wang et al., 2011
	AnPGA2	(+) 100% SE: (-) 50-84% FW	Lionetti et al., 2010
P.virgatum	PvCesA4,PvCesA6	(-DW: (-) 6-33% Cel: (+) 2-12% Xyl	Mazarei et al. 2018
	OSAT10	(+) 40% Cel	Li et al., 2018
O.sativa	OsSuSy3	(+) 15-26% Cel: (+) 11-13% HC	Fan et al., 2017, 2019
	OsGH9B1,OsGH9B3	(+) 63% SE	Huang et al., 2019
	OsARAF1,OsARAF3	(-) 19-25% Ara; (-) 28-34% Cel	Sumiyoshi et al.. 2013
	OsAT10	(+)8-19% Cel; （+） 40% SE	Bartley et al., 2013
Saccharum spp.	CsCESA	(+) 31% Cel;(+) 28-69% SE; (+) 25% Suc;(+) 56% non-Cel Glc; (+) 22% Gal; (+) 53% GalA	Ndimande, 2018
F.arundinacea	AnFAE	(+) 10-14% IVD	de Buanafina et al., 2008; 2010; Morris et al., 2017

Note: Stong, constitutive promoters were used unless otherwise indicated; Cel: Cellulose; Ara: Arabinose; Glc: Glucose; Gal: Galacturonic acid; Suc: Sucrose; Xyl: Xylose; HC: Hemicellulose; Pec: Pectin; FW: Fresh weight; DW: FDry weight; DP: Degree of polymerization; Crl: Cellulose crystallinity index; SE: Saccharification effciency; IVD: In vitro digestibility

3 Biochemical Mechanisms of Biomass Conversion

3.1 Starch conversion processes

The enzymatic breakdown of cassava starch into sugars suitable for fermentation involves a series of biochemical reactions. Cassava pulp, a by-product of starch extraction, contains a high level of starchy-lignocellulosic biomass. An adapted one-step enzymatic hydrolysis process has been developed to convert this biomass into reducing sugars, which are then suitable for fermentation. This process has shown to reduce the treatment time to 2 hours and yield a reducing sugar level comparable to the conventional two-stage acid and enzymatic hydrolysis (Li, 2024). Novel enzymes such as Spezyme® Xtra and Stargen™ 001 have been optimized for the liquefaction and saccharification of cassava starch, with Spezyme optimally active at 90 °C and pH 5.5, and Stargen effective at room temperature. These advancements in the enzymatic conversion of cassava starch to sugars are crucial for efficient bioethanol production.

3.2 Fermentation efficiency

The conversion of cassava biomass to bioethanol involves fermenting the hydrolyzed sugars using various microorganisms. Saccharomyces cerevisiae and Clostridium butyricum have been used to ferment the reducing sugars obtained from cassava pulp, yielding ethanol concentrations of up to 12.9 g/L when cassava starch wastewater is used (Virunanon et al., 2013). Another study demonstrated the use of a genetically engineered Thermoanaerobacterium aotearoense in a fibrous-bed bioreactor, achieving an ethanol yield of 0.364 g/g from glucose (Cai et al., 2012). Additionally, the fermentation of hydrolyzed cassava stem using Saccharomyces cerevisiae resulted in an ethanol concentration of 7.55 g/L (Han et al., 2011). These studies highlight the potential of various biochemical pathways in converting cassava biomass to bioethanol and other biofuels.

3.3 Genetic engineering

Genetic engineering has been employed to increase the fermentable sugar yields from cassava. A genetically engineered strain of Thermoanaerobacterium aotearoense, for instance, has been used to ferment cassava pulp hydrolysate in a fibrous-bed bioreactor, resulting in high ethanol yields and productivity (Cai et al., 2012). Additionally, the use of a multi-enzyme activity from Aspergillus niger and simultaneous fermentation with Candida tropicalis has been shown to produce ethanol from cassava pulp efficiently, suggesting that genetic and enzymatic enhancements can significantly improve bioenergy production (Rattanachomsri et al., 2009). Furthermore, the use of a co-culture of Aspergillus sp. and Saccharomyces cerevisiae has been explored for the direct bioconversion of raw starch from wild cassava to bioethanol at low temperatures, achieving high yields and efficiencies (Moshi et al., 2016). These advancements in genetic engineering and enzyme technology are pivotal for optimizing cassava as a bioenergy crop.

4 Case Studies

4.1 Successful modifications

Genetic and biochemical modifications have played a pivotal role in enhancing cassava's potential as a bioenergy crop. One of the landmark studies in this area demonstrated that genetic transformation could overcome the challenges of high heterozygosity and trait separation in traditional breeding, leading to rapid improvement in target traits such as pest and disease resistance, biofortification, and starch quality (Liu et al., 2011). Another significant advancement was the discovery of a single nucleotide polymorphism in the phytoene synthase gene, which led to a substantial increase in provitamin A accumulation in cassava roots. This modification not only has implications for bioenergy but also for combating vitamin A deficiency (Welsch et al., 2010). Furthermore, the development of transgenic technologies has enabled the production of cassava with enhanced resistance to diseases and pests, improved nutritional content, and modified starch metabolism, which are essential for bioenergy applications (Taylor et al., 2004).

4.2 Pilot projects

Pilot projects have been instrumental in testing the scalability and practicality of cassava-based bioenergy production. The optimization of Agrobacterium-mediated transformation systems for the large-scale production of transgenic cassava plants is a notable example. This system has been successfully applied to elite cassava cultivars, resulting in the integration of genetic constructs for disease resistance and nutritional enhancement into a significant number of plants, which is a critical step towards commercial bioenergy production (Chauhan et al., 2015).

4.3 Key research papers

Key research papers have laid the foundation for cassava as a bioenergy research subject. The progress in cassava molecular breeding, particularly for bioenergy development, has been substantial. Studies have focused on enhancing stress resistance and starch content through genetic engineering, which is crucial for bioenergy crops (Pen, 2014). Additionally, the potential of cassava as a bioenergy crop has been further explored through insights into photosynthesis and associated physiology, aiming to improve yield potential (Souza et al., 2017). These studies, along with others that have engineered disease resistance (Figure 1) (Bart and Taylor, 2017) and addressed the challenges of clonal propagation (Wolfe et al., 2015), have been instrumental in advancing cassava as a viable bioenergy source.

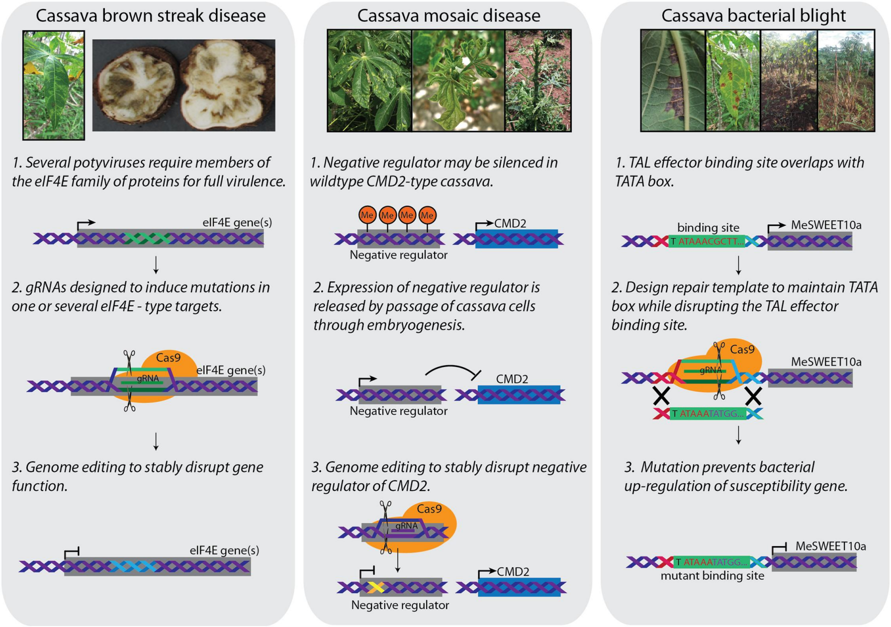

Figure 1 Genome-editing strategies to create resistance against three major pathogens of cassava (Adopted from Bart and Taylor, 2017)

Note: Left: Cassava brown streak disease (CBSD) is caused by two potyviruses; In other species, mutation of eukaryotic translation initiation factor 4E (eIF4E) family of genes promotes disease resistance; It is predicted that a similar strategy may be effective in cassava; Middle: Cassava mosaic disease (CMD) is widely controlled by the yet to be identified CMD2 resistance mechanism; For unknown reasons, passage of cassava cells through somatic embryogenesis disrupts CMD2-mediated resistance; A potential explanation involves loss of methylation (Me) that releases expression of a negative regulator of CMD2; In this case, it should be possible to use guide RNAs complexed with Cas9 to introduce genetic changes that stably disrupt expression of the negative regulator; Right: Cassava bacterial blight disease is caused by Xanthomonas axonopodis pv. Manihotis (Xam). Xam injects transcription activator like (TAL) effectors into plant cells, which activate expression of MeSWEET10a by directly binding to its promoter; The binding site overlaps with the TATA box; Using homolog recombination, it would be possible to mutate the binding site, maintain the TATA box, and disrupt TAL effector binding by Bart and Taylor (2017)

The outlined genome-editing strategies by Bart and Taylor, 2017 represent a significant breakthrough in cassava research, providing a focused approach to combating its most devastating diseases. By targeting the eukaryotic translation initiation factor (eIF4E) for CBSD, manipulating methylation patterns or gene expression for CMD, and altering binding sites for TAL effectors in CBB, these strategies employ precision breeding to enhance disease resistance. This methodological advancement not only improves cassava's resilience to pathogens but also exemplifies the potential of CRISPR/Cas9 and other genome-editing tools in crop improvement. The integration of such technologies into breeding programs promises rapid deployment of disease-resistant cassava varieties, potentially transforming agricultural practices and enhancing food security in regions heavily dependent on cassava.

In conclusion, the case studies and pilot projects discussed herein, along with the milestone research papers, have significantly contributed to the optimization of cassava for bioenergy purposes, highlighting the genetic foundations and biochemical mechanisms involved in biomass conversion.

5 Limitations and Opportunities

5.1 Technical challenges

The technical challenges in optimizing cassava for bioenergy primarily stem from the genetic complexity of the plant. Cassava (*Manihot esculenta* Crantz) is a highly heterozygous species, which complicates traditional breeding efforts and trait selection (Liu et al., 2011). Although genetic transformation has been a significant step forward, allowing for the rapid achievement of improved target traits such as pest and disease resistance, biofortification, and starch quality, the technology still faces genotype constraints and requires further refinement (Liu et al., 2011). Additionally, the biochemical and thermochemical conversion processes of cassava harvest residues into bioenergy are not fully understood, and there is a lack of information on the use of cassava residues in various conversion processes (Rodrigues et al., 2018). This indicates a need for more research to optimize these processes for bioenergy production.

5.2 Economic viability

Economic viability is a critical factor in the development of cassava-based bioenergy. The cost of bioenergy production from cassava stalks, for instance, is influenced by various factors such as transportation and enzyme costs, which can significantly affect the production costs of ethanol and electricity (García-Velásquez et al., 2020). Moreover, the determination of economically optimal plant capacities for cassava-to-ethanol conversion requires careful consideration of trade-offs between profitability and greenhouse gas emissions (Lauven et al., 2014). The economic and energy valorization of cassava waste is also dependent on the efficiency of the conversion processes, with overall energy efficiencies of gasification and ethanol fermentation reported at 68.7% and 25.1%, respectively (García-Velásquez et al., 2020).

5.3 Environmental impact

The environmental impact of cassava-based bioenergy production is a double-edged sword. On one hand, cassava-based fuel ethanol has the potential for energy saving and carbon emission mitigation, as evidenced by life cycle assessments (Jiang et al., 2019). On the other hand, the use of cassava biomass for bioenergy must be carefully managed to avoid negative impacts on food security and land use (Ozoegwu et al., 2017). The biogeochemical process model studies suggest that cassava can be grown on marginal land to avoid competition with food crops, and the potential bioenergy yield on such land in GuangXi, China, is substantial (Jiang et al., 2015). However, the debate over food versus energy remains a significant bottleneck, and a holistic approach to food and biomass energy production is recommended (Okudoh et al., 2014).

6 Future Perspectives

6.1 Research gaps

Despite the significant role of cassava (*Manihot esculenta* Crantz) as a staple food and its potential in bioenergy production, there are several research gaps that need to be addressed to optimize its use for bioenergy efficiently. One of the primary areas needing further research is the development of rapid cassava processing equipment. Current industrial processing of cassava is limited, and there is a need for scientific improvement in processing technology to meet global development goals (Kolawole and Agbetoye, 2007). Additionally, there is a lack of understanding of the basic biological processes of this storage root crop, which is crucial for its genetic improvement (Taylor et al., 2012). This gap in knowledge hinders the development of enhanced planting materials that could be exploited by farmers and breeders. Furthermore, cassava research and development have historically been underfunded due to its perception as a "poor man's crop" and its absence from industrialized, northern agricultural systems (Taylor et al., 2012). This has led to a slower pace in uncovering the genetic foundations and biochemical mechanisms that could be targeted for biomass conversion optimization.

6.2 Emerging technologies

Emerging technologies in genetics and biochemistry hold great promise for transforming cassava bioenergy production. Advances in genetic engineering and molecular biology tools can lead to the development of cassava varieties with improved traits for bioenergy, such as increased biomass yield, enhanced starch content, and reduced cyanogenic glucosides, which are harmful compounds found in cassava (Taylor et al., 2012). The application of CRISPR/Cas9 gene-editing technology, for instance, could enable precise modifications in the cassava genome to enhance its suitability for bioenergy production. In the field of biochemistry, the use of novel enzymes and metabolic engineering could improve the efficiency of cassava biomass conversion into biofuels. Additionally, the integration of omics technologies, such as genomics, proteomics, and metabolomics, can provide a comprehensive understanding of cassava's biological processes, which is essential for the systematic improvement of the crop for bioenergy purposes (Taylor et al., 2012). These technologies, combined with computational modeling and big data analytics, could significantly accelerate the breeding and development of cassava varieties tailored for bioenergy applications.

7 Concluding Remarks

7.1 Summary of key findings

The integration of genetic and biochemical approaches has significantly advanced the optimization of cassava (*Manihot esculenta* Crantz) for bioenergy. Genetic transformation techniques have matured, enabling the enhancement of cassava's resistance to pests and diseases, biofortification, and improved starch quality (Liu et al., 2011). Transgenic technologies have been successfully employed to produce cassava with desirable agronomic traits, such as enhanced resistance to viral diseases, improved nutritional content, and modified starch metabolism (Taylor et al., 2004). Comparative genomic analyses have revealed positive selection for genes involved in photosynthesis and starch accumulation, and negative selection for genes related to cell wall biosynthesis and cyanogenic glucoside formation in cultivated varieties (Wang et al., 2014). Molecular breeding efforts are focused on increasing stress resistance and starch content to meet the demands of bioenergy development (Pen, 2014). Additionally, transcriptomic analyses under shade conditions have provided insights into the molecular mechanisms of shade response, which is crucial for intercropping practices (Ding et al., 2016).

7.2 Implications for bioenergy development

The findings from these studies have profound implications for bioenergy strategies and cassava cultivation practices. The ability to genetically engineer cassava to have higher starch content and stress resistance can lead to more efficient biofuel production. The understanding of cassava's genome and the selection pressures during domestication can guide the development of varieties tailored for bioenergy purposes. Moreover, the knowledge of shade response at the transcriptomic level can inform intercropping strategies that maximize land use without compromising cassava's productivity (Wang et al., 2014; Ding et al., 2016).

7.3 Recommendations for researchers and policymakers

Based on the review's findings, it is recommended that researchers continue to explore the genetic and biochemical pathways that contribute to increased biomass and stress tolerance in cassava. There is a need for field trials to validate the laboratory and greenhouse results and to assess the environmental and economic impacts of genetically modified cassava varieties (Taylor et al., 2004). Policymakers should consider supporting research and development initiatives that focus on sustainable bioenergy crops like cassava. Additionally, policies should be crafted to ensure the safe and responsible introduction of genetically modified cassava into agriculture, taking into account public concerns and regulatory requirements (Liu et al., 2011; Pen, 2014). It is also crucial to enhance collaboration between scientists, breeders, and farmers to ensure that the developed cassava varieties meet the needs of both bioenergy production and food security.

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Conflict of Interest Disclosure

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