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COCOYAM GENOMICS: PRESENT STATUS AND FUTURE PERSPECTIVES

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Abstract
Cocoyams (*Colocasia esculenta* and *Xanthosoma sagittifolium*) are functional food crops grown in many agro-ecological zones around the world. The crop is mostly cultivated by subsistence farmers and serves as food and source of income for millions of people. Based on importance, it ranks third among the root and tuber crops grown in sub-Sahara Africa. Despite its cultural importance, world production and yield continue to dwindle. In addition to the several physiological and biological constraints contributing to production decline, cocoyam research is underfunded to the point of neglect. There is very little understanding of the complexities of cocoyam genetics and its genome which has severely hampered conventional efforts at improving the crop. Compared to crops like yam and cassava, cocoyam genomic research is limited. Despite this, over the years, molecular technologies have been applied in cocoyam research to develop molecular markers, genetic linkage maps, conduct functional genomic analysis and develop molecular diagnostic tools. Cocoyam transformation and tissue culture protocols have been developed for certain cocoyam varieties. These tools have provided a better understanding of the crops origins, genetic diversity within available germplasm and the pathogens that affect it, rapid detection of major diseases, conservation and genetic improvement of complex traits including disease resistance and improved yields. With reducing costs in next-generation sequencing, further efforts need to be directed towards funding genomic research that allows for novel gene discovery, molecular pathway analysis, genetic engineering and molecular breeding in non-model organisms like cocoyam.

Keywords: Cocoyam genomics, genetic diversity, transformation, molecular technologies, genetic engineering, and molecular breeding

Introduction

Two of the most important edible aroid species are *Colocasia esculenta* (L.) Schott (taro) and *Xanthosoma sagittifolium* (L.) Schott (tannia). In certain regions of West and Central Africa, these species are broadly referred to as Cocoyam (Onyeka, 2014). They belong to the monocotyledonous family *Araceae* and the sub-family *Colocasioideae*. For centuries, these cocoyam species have served as sources of subsistence and income for millions of small scale farmers across Africa, Asia, the Americas and Oceania. Its parts, including leaves, petioles, corms and cormels, are excellent sources of carbohydrates and have been utilized for both human and animal nutrition (Quero-Garcia et al., 2010). Like banana leaves, leaves of cocoyam are often used as wraps for foods and in parts of Asia, the crop is grown as ornamentals (Mikami and Tsutsui, 2019). According to current FAO estimates, global cocoyam production is over 11.1 million metric tonnes on nearly 1.7 million hectares of harvested land area, with Africa accounting for just over 70% and 86.3% respectively (FAO, 2018) (Table 1). Per hectare basis, Asia gave the highest average yield, while Africa had the least in 2018. Among root and tuber crops cultivated in sub-Sahara Africa, the crop is ranked sixth in importance with Nigeria, Cameroon, and Ghana being the highest producing African nations (FAO, 2018). Cocoyam is considered an emerging health food because it is enriched with vitamins, potassium, phosphorus, calcium, magnesium, dietary fibre, etc.(Ramdeen et al., 2019).

Despite its importance, world cocoyam production has remained stagnant, and in some African countries, production decline has been reported (Boakye et al., 2018). This has been attributed to several limiting factors including narrow genetic base, low input utilization, scarcity of planting materials, diseases and physiological attributes that hinder genetic improvement. Overcoming many of these challenges would require a lot more attention from researchers, funding bodies and policymakers as the crop is currently under-researched and underfunded, resulting in the crop becoming underutilized. These ultimately hinder the crops export potentials and its potential as a reliable

alternative during food scarcity and economic downturns (Obidiegwu, 2015). Although the use of biotechnology in cocoyam research is still considered to be at its infancy, some molecular tools have been developed and utilized in improving genetic gains, enhancing disease detection, conducting genetic diversity studies and rapidly producing disease-free planting materials. This paper reviewed the status of genomic research in cocoyam and highlight the role emerging technologies can play in addressing many of the challenges hindering cocoyam production.

Table 1: Cocoyam distribution across cocoyam producing regions

Region	Area Harvested (Ha)	Production (tonnes)	Average Yield (Hg/Ha)
Africa	1,468,192	7,874,571	53,634
Americas	43,155	500,181	204,419
Asia	137,647	2,310,513	167,858
Oceania	49,258	412,000	83,641

Source: FAO (2018) estimates of Average yield, Area harvested and Production in Hg/Ha, hectare and tones respectively

Origin and Domestication

For many centuries, taro has been cultivated in Asia but its history cannot be traced to one centre of origin. Two independent centres of domestication for taro has been linked to Asia and the Pacific, with the reduction in toxicity of the crop's tissues the main focus of domestication (Matthews and Nguyen, 2018). Earlier research had suggested Asia as the origin based on the presence of related species that were found exclusively in north-east India and south-east Asia (Lebot, 2009). Morphological diagnostics of some starch granules found on pre-historic Papua New Guinea starch processing tools were determined to be *C. esculenta* residues, revealing that taro cultivation was active as early as over 10,000 before present (BP) (Fullagar et al., 2006). With the aid of biochemical and molecular tools such as isozyme variation (Lebot and Aradhya, 1991) and amplified fragment length polymorphism markers (Kreike et al., 2004), the evidence of these independent centres of domestication has been further strengthened. Unlike taro, *X. sagittifolium* origin and domestication is from the Amazon basin in South America, and is considered to be the only aroid native to that region (Castro, 2006). Historical texts recorded that taro had reached north-east Africa from Asia via the Nile over 2000 BP, while it was well-established that there had been taro cultivation in West Africa in the 1300s well before the arrival of Portuguese colonialists (Power et al., 2019). By the 17th century, tannia was recorded in West Africa and its dispersal in that region has been attributed to the activities of missionaries and other travelers (Quero-Garcia et al., 2010; Castro, 2006).

Characterization and Genetic Diversity

Taro and tannia are highly polymorphic, and taro's wide genetic diversity is believed to be as a result of both human and natural selection pressures and insular isolation of wild populations for long periods (Lebot, 2009). Fertile diploids and sterile triploids have been reported in cocoyam (Chair et al., 2016) with isozyme analysis further revealing that triploids have an autopolyploid origin (Isshiki et al., 1999). Studies have shown that taro has a basic chromosome number of 14, while tannia has 13 (Doungous, 2011; Jiménez, 2018). Using molecular markers, several genetic diversity and population structure studies have been conducted to characterize taro cultivars in India (Das et al., 2015), South-Africa (Mwamba et al., 2016), and Kenya (Palapala and Akwee, 2016). Tannia cultivars have been similarly researched upon in Ghana (Offei et al., 2004), Nigeria (Osawaru and Ogwu, 2015) and Cuba (Jiménez et al., 2018). Molecular markers are unaffected by environmental factors and are mostly reproducible, making them effective tools for determining relationships at the species and sub-species levels (Brown and Asemota, 2009). Morphologically, taro can be distinguished from tannia by the position of the leaf meeting the petiole '(Manner, 2011). While tannia leaves are sagittate, taro leaves are peltate and without the leaves, these closely related species are not very easy to distinguish. Doungous *et al.* (2015), reported the first tannia derived –retrotransposon markers which were used to characterize both species by ploidy formation and variety. With molecular markers coupled with morphological characteristics, Sepúlveda-Nieto *et al.,* (2017) and Mwenye *et al.,* (2016) also reported distinctive variations between both species. Molecular markers have also proved useful in correlating genotypes with their geographical origins. Chair *et al.,* (2015), using 11 micro satellites, confirmed that taro cultivars from Asia and the Pacific have a wider genetic diversity than cultivars from the Americas and Africa. This is because taro is predominantly reproduced vegetatively in the Americas and Africa. The study also confirmed that most African cultivars were from Asia, especially India and Japan.

Major Cocoyam Diseases

The narrow genetic diversity of cocoyam in some regions makes this already neglected crop vulnerable to the effects of pathogens. Cocoyam root rot disease (CRRD) caused by *Pythium myriotylum,* and Taro leaf blight (TLB), caused by *Phytophthora colocasiae*, are two of the most devastating diseases that result to significant post-harvest losses of cocoyam in sub-Saharan Africa (Onyeka, 2014). Pathogens of both

diseases are oomycete with TLB symptoms ranging from water-soaked lesions on the leaves to the destruction of the entire leaves within 3-5 days. Cocoyam root rot disease symptoms include leaf loss and stunting when the root system is attacked by the oomycete. Molecular analysis of *P.colocasiae* and *P. myriotylum* isolates have been revealed to have high levels of variation and some polymorphism (Nath et al., 2014a; Le et al., 2017). The severity of the symptoms mostly depends on optimum conditions for the pathogens to thrive. Several viral pathogens have also had significant detrimental effects on cocoyam yield (Yusop et al., 2019). The most common virus, *dasheen mosaic potyvirus* (DsMV), has a worldwide distribution and its symptoms include leaf chlorosis and stunting of the plant. *Colocasia bobone disease virus* has been described as the most dangerous virus, responsible for the taro diseases Alomae and Bobone. These diseases are predominantly found in the Pacific region (Lebot, 2009). Both viruses are occasionally spread by aphids but mostly through infected planting materials. Over the years, several molecular diagnostic tools have been developed from genome sequences of these viruses (Nath et al., 2014b; Yusop et al., 2019). These tools provide a more rapid and accurate detection that better informs the implementation and development of mitigating strategies against their proliferation (Anukworji et al., 2012).

Genetic Improvement in Cocoyam

In addition to pests and diseases, there are several other factors limiting cocoyam production and its genetic improvement. Through conventional breeding, many cocoyam breeding schemes have targeted such objectives as enhancing genetic gains such as; improved flowering, increased yields, resistance to pests and diseases, petiole colours, corm shapes, reduced corm acridity and improved food qualities –(Sreekumari et al., 2004; Singh et al., 2006; Fonoti et al., 2008; Obidiegwu et al., 2016). Unfortunately, these breeding strategies are not specific and have been reported to confer undesirable traits to progenies (Quero-Garcia et al., 2010). In crops like rice and maize, introduction of molecular breeding and genetic transformation strategies into these breeding schemes has significantly improved genetic gains (Cobb et al., 2019). Compared to conventional breeding, both unconventional strategies are more useful in handling complex traits heavily influenced by environmental factors and are more specific with reduced chances of conferring undesirable traits to progenies. Developing genomic resources such as molecular markers and genetic linkage maps are imperative for plant breeders to better understand crop genetics. For taro, the first linkage map was constructed mainly with 169 dominant markers (161 AFLPs and 8 SSRs). The linkage groups of the map were of short length and some contained gaps and few markers. The maps low chromosome coverage did not allow its use in marker assisted breeding, and the AFLP markers could not be used across different taro populations. Despite these shortcomings, Quero-García *et al*., (2006) used the map to identify several putative quantitative trait loci (QTLs) for corm yield, corm dimensions and corm flesh colour–. Most recently, two genetic linkage maps of taro were constructed using single nucleotide polymorphism and simple sequence repeats (Soulard et al., 2017). This is the first reported use of SNPs generated in the Archaea family from genotyping by sequencing, a cost-effective high throughput genotyping method. Deep sequencing of taro transcriptome has led to the identification of candidate genes for starch synthesis –(Liu et al., 2015), development of expression sequence tag (EST-SSR) micro satellites (You et al., 2015) and a *de novo* assembly of RNA sequencing micro satellites (Wang et al., 2017). Over the years, two genetic transformation technologies, *Agrobacterium*-mediated (He et al., 2008) and particle bombardment transformation –(He, 2010) have been employed in developing transgenic taro with varying levels of resistance to pathogenic oomycetes. Studies have shown that *the Agrobacterium*-mediated transformation has a higher efficiency rate than the particle bombardment method (He et al., 2015). Currently, there has only been one reported attempt at genetic transformation in tannia, where a reporter gene was expressed after particle bombardment of embryonic calluses (Castro, 2006). He *et al.,* (2015) reported an efficient transformation system that includes a regeneration method using shoot tip explants that could eliminate DsMV from infected taro plantlets. The efficiency of transformation systems is variety dependent, so protocols must be optimized and expanded to farmer preferred varieties.

Cocoyam Conservation and Rapid Seed Multiplication

Tissue and cell culture techniques are plant-regeneration technologies that allow several possibilities including plant conservation, production and rapid multiplication of pathogen-free seeds, and as earlier mentioned, genetic transformation. Several tissue culture protocols have been developed for varieties of both taro and tannia species (Obidiegwu, 2015). Studies have shown, in terms of yield and speed of cormel growth, that planting materials conserved through meristem cocoyam cultures do better than field conserved planting materials. Cryopreservation –(Sant et al., 2006) and bioreactor (Niemenak et al., 2013) technologies have been employed to sustain the genetic stability of taro and tannia respectively.

Emerging Biotechnology Trends to Exploit for Cocoyam Research

With populations set to increase significantly by 2050, greenhouse emissions rapidly increasing, emerging pests and diseases; food supplies are constantly being threatened. An increase in production of improved cocoyam varieties will provide significant increases in income, and access to an affordable and healthier root crop alternative, enabling millions in the developing world and especially sub-Saharan Africa address these daunting realities. Studies have shown that plant genomic research provides opportunities that exploit complexities in crops, allowing enhancement of desirable traits. With recent advancements in, and

reducing costs of next-generation sequencing (such as whole-genome sequencing and genotyping by sequencing), it is important that more research and funding into cocoyam genomics be pursued to address some of the factors inhibiting cocoyam production. Compared to major root and tuber crops like cassava and yam, cocoyam has a dearth of genomic resources developed, especially the tannia specie. Developing high-quality genome sequences of cocoyam will greatly enhance our understanding of major biological pathways that can be exploited through genetic engineering and molecular breeding. Cocoyam's narrow genetic diversity and scarcity of planting materials/seeds are some factors that inhibit breeding in the crop. A major focus of many cocoyam breeding programs is to widen the genetic diversity of the crop through an international germplasm exchange. The use of high-quality molecular markers and tissue culture technologies when implemented in such programs will allow the accurate characterization, evaluation, preservation and rapid multiplication of elite cultivars that are free of pathogens. Cocoyams' biological traits such asallogamy and protogyny contributes greatly to its high heterozygosity, making introgression of traits time-consuming. For some years, the application of gibberellic acid has been used, with mixed results, to induce flowering in cocoyam (Amadi et al., 2014), while conventional breeding methods have had some success in developing TLB resistant and high yielding varieties. Genome editing technologies, like the clustered regularly interspaced short palindromic repeats –Cas9 (CRISPR - associated protein 9) system has been used to induce flowering and modify amylose in another highly heterozygous root crop, cassava (Bull et al., 2018). Modern breeding technologies like genomic selection make use of information from large sets of molecular markers to develop genomic-estimated breeding values; allowing accelerated genetic improvement by reducing generational interval and increasing selection intensity (Rabbi et al., 2020). Early detection of endemic and emerging diseases is imperative to prevent the spread to susceptible farmer preferred varieties. Implementing cost-effective molecular tools that rapidly and accurately detect viral pathogens should be pursued in cocoyam research, especially third-generation sequencing (Dumschott et al., 2020) to especially detect emerging diseases that are becoming prevalent during these times of global climate change.

Conclusion

Cocoyam holds a lot of promise as a potential food security crop, and its declining production over the years is troubling for millions of cocoyam farmers across the world. Biotechnology and genomics research holds the key to understanding cocoyam biology and unlocking genetic potentials that are difficult to unravel.

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